

ONTOGENY OF VOCALIZATION IN THE GREATER RHEA

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ABSTRACT.—The call-notes of the Greater Rhea chick were classified according to their acoustic structure and behavioral context. Both rate of vocalization and tonal quality of call-notes were found to deteriorate as a function of maturation. Call-note production was completely eliminated by 7 weeks of age. Greater Rhea adults are silent except for such relatively infrequent vocalizations as “hissing” that sometimes accompanies agonistic behavior and a disyllabic “grunt” that only the male produces as part of a courtship display. Tracheal growth and a marked reduction in the intrusion of the internal tympanic membranes into the bronchial passages could contribute to the deterioration of vocalization. The use of vocalization as the primary channel of communication is replaced by visual display in the adults. These modalities are best suited to the ecological contingencies facing the chick and adult, respectively. *Received 17 March 1977, accepted 24 September 1977.*

A great deal of ornithological literature has focused on the vocal displays of birds (e.g. Thorpe 1961, Hinde 1969, Armstrong 1973). The attention accorded to bird vocalization is no doubt largely due to its central importance in avian social interaction. The suborder oscines of the passerine birds have been the most popular species for research in bird vocalization. There has been little interest in the vocalizations of nonoscines in general and ratite birds in particular. This is probably because the vocal repertoire of adult ratites is not very impressive. The Greater Rhea (*Rhea americana*), a large, flightless ratite native to the pampas of Argentina, is especially unimpressive. In the adult, vocal production is restricted to “hissing” during agonistic encounters and the disyllabic “grunt” of a sexually aroused male. In contrast to adults, Greater Rhea chicks are highly vocal. This is unlike most other species of birds whose vocal repertoires increase in complexity as a function of development. The ontogeny of vocalization in the Greater Rhea is a curious example of behavioral regression and may pose questions for theoretical treatments of behavioral ontogeny that treat it as a cumulative and progressive process.

METHODS

Eggs were laid by the Greater Rheas maintained at the Chicago Zoological Park, Brookfield, Illinois and incubated at the University of Chicago. A total of 33 chicks was hatched over 2 years, of which 20 survived past 2 months of age. Chicks were housed at the University of Chicago in a 0.9 × 1.2 m pen until 4 weeks of age, at which time they were transferred to a 90 m² outdoor enclosure at the Chicago Zoological Park.

Vocal behavior was recorded on a SONY tape recorder model TC-92. Over 20 h of vocalizations were recorded and are available upon request to the author. Sonagrams were made on a Kay Elemetrics, Co. audio spectrum analyzer model 6061 B. Vocal amplitude was determined by a linear scale sound level meter placed at a distance of approximately 1 m from the chick. Recordings were made daily at random times for the first 4 weeks of life. Additional recordings were also made on an intermittent basis between ages 4–8 weeks.

CALL-NOTE CATALOGUE

Several authors, from Hudson (1903) to Bruning (1973a), have used the phrase “plaintive cry” to describe a frequently heard call of the Greater Rhea chick. Bruning

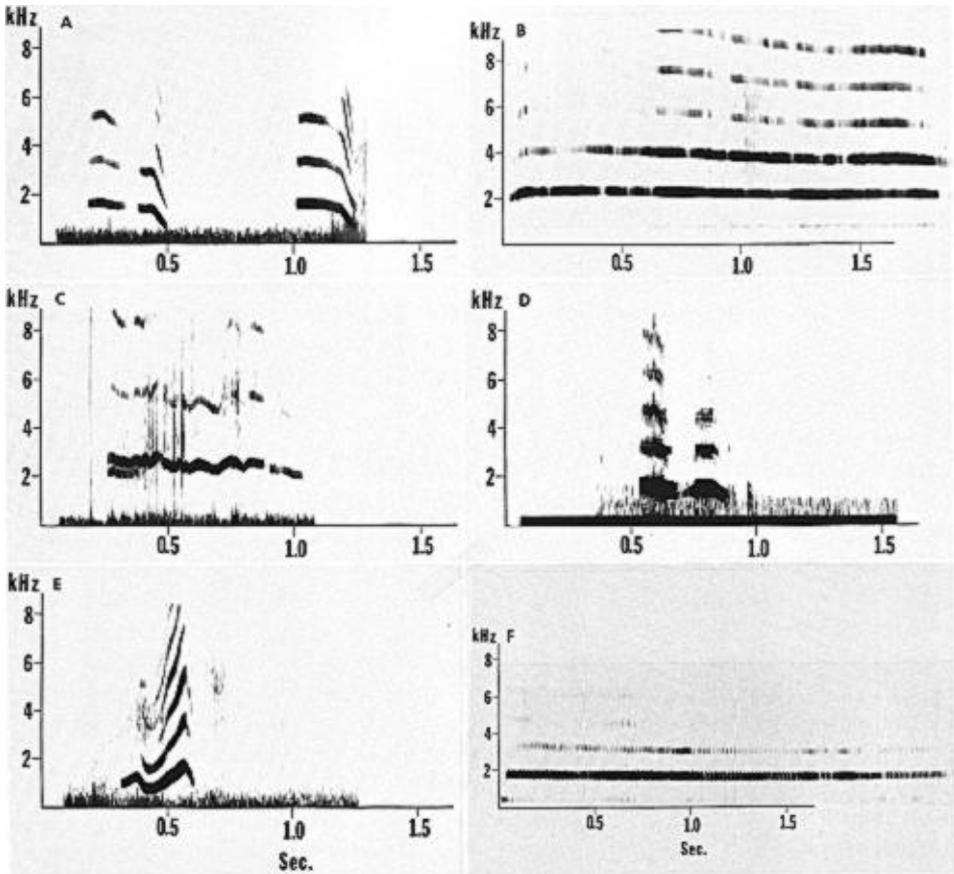


Fig. 1. Type B/65 wide-band sonograms of Greater Rhea chick call-notes: (a) contact-whistle, (b) separation-whistle, (c) alarm-trill, (d) feeding-peep, (e) contentment-chirp, (f) separation-whistle of an older chick illustrating tonal deterioration.

also makes reference to an infrequently heard alarm cry produced when the chick was in immediate danger. Beyond these observations no one has made a detailed catalogue of Greater Rhea chick call-notes.

Based on observations of captive chicks in a variety of experimental conditions, five call-notes (Fig. 1) were detected and investigated. The call-notes were supplied with terms that reflect both their function and sound: (1) contact-whistle; (2) separation-whistle; (3) alarm-trill; (4) feeding-peep; and (5) contentment-chirp.

Contact-whistle.—The contact-whistle call-note sounds much like a soft, short whistle. It is a brief, monosyllabic call-note, with a duration of 0.20–0.50 s. It is also of relatively low amplitude, rarely exceeding 75 db. The fundamental frequency is generally around 1.5–2.0 kHz. There are several harmonics, at about 2.0 kHz intervals, which reflect the brilliance of the tone. Some chicks have a sharp decrease in pitch at the end of the note, while others exhibit a sharp decrease at the beginning of the note; with others there are no sudden changes in pitch. These variations appear to be specific to individuals.

The contact-whistle call-note was initially heard after the Greater Rhea embryo

entered the air space (determined by candling), generally 2–5 days prior to hatching. The contact-whistle was emitted spontaneously by the embryo. It was also elicited on several occasions in response to the tape recorded playback of this call as well as to such mild stimulation as the slow turning of the egg. Such in-egg vocal production may act to synchronize the hatching of Greater Rhea eggs that are incubated together in a clutch. Pilot research by Bruning (1973b) indicated spectacular hatching synchrony, accelerating the time to hatching of late set eggs by as much as 7 days. In-egg vocal behavior in other species may be a potential variable in hatching synchrony (Orcutt 1974).

The contact-whistle remains very prominent in the repertoire of the Greater Rhea chick after hatching. It was frequently emitted in the presence of a human surrogate parent, especially when the chick was following or approaching. It was also frequently emitted in the presence of conspecifics with which the chick was reared. Since the call-note is heard only in these situations I suggest that it serves a social contact function.

Separation-whistle.—The separation-whistle call-note sounds much like a loud, long whistle. This call-note is the “plaintive cry” documented by Hudson (1903) and Bruning (1973a). It is a long, monosyllabic call-note, generally lasting 1.0–3.0s. The longest separation-whistle recorded was 4.48 s. The separation-whistle is a high amplitude call-note, reaching 75–100 db. The fundamental frequency is generally around 2.0 kHz. There are several harmonics, at about 2.0 kHz intervals, which reflect the brilliant tonal quality of the call-note. There are several individual-specific variations in pitch changes during separation-whistles. Some variations involve a sudden or gradual frequency decrease, which intensifies the sad or lonely quality of the call-note to the human ear. The fundamental remains level for some chicks while for others it gradually decreases, by 0.1–1.0 kHz, over 1–3 s. Some chicks show a sudden decrease in frequency at the onset of the call-note, while others show a sudden increase, but most chicks have neither. Some chicks show a sudden decrease in frequency at the tail of the call-note while others do not.

The separation-whistle is first heard within a few hours after hatching. The separation-whistle appears to be functionally related to the contact-whistle. Whereas the contact-whistle is emitted when the surrogate parent or familiar conspecifics are nearby, the separation-whistle is emitted in a condition of social isolation or when with unfamiliar conspecifics. The separation-whistle also appears to be acoustically related to the contact-whistle; its distinction is that it is longer and louder. There is no clear border between the two call-notes. If the surrogate parent is gradually displaced to some distance but the chick retains visual contact, the contact-whistle escalates in both duration and amplitude, gradually assuming the character of a separation-whistle. The inter-individual variations in pitch at the termination of the contact-whistle reflect those of the separation-whistle, again suggesting a close relationship between the two call-notes.

Alarm-trill.—The alarm-trill call-note has many acoustical features in common with the separation-whistle. It is a long, loud monosyllabic call-note. The duration is generally somewhat shorter than that of the separation-whistle, lasting 0.5–2.0 s. The amplitude measures 80–90 db. The fundamental frequency is generally around 2.0 kHz. There are several harmonics, at about 2.0 kHz intervals. The distinguishing feature of the alarm-trill is a modulation of pitch throughout the call-note.

The alarm-trill is elicited by stressing the chick with such procedures as suddenly lifting it off the ground or by administering intra-muscular injections of medicine or

vitamin supplement. The alarm-trill is not heard from all chicks as some consistently remain silent throughout these procedures.

The alarm-trill is acoustically similar and seems to be functionally related to the separation-whistle. Both probably function to attract the parent to the chick. But the modulation of pitch in the alarm-trill may serve to give it somewhat greater emphasis or urgency than the separation-whistle.

Feeding-peep.—The feeding-peep is a very quiet, short, monosyllabic call-note. From one to four feeding-peeps are generally emitted in rapid succession. The duration of a single feeding-peep is usually 0.15–0.20 s. The amplitude was not detectable above the ambient noise level of 60 db. The fundamental frequency is 1.0–1.5 kHz, slightly lower than that of the other call-notes. There are several harmonics at about 1.5 kHz intervals. No inter-individual variations were detected.

The feeding-peep is first heard shortly after the chick began to feed. Thereafter it is commonly heard during feeding. It is not heard in any other behavioral context.

Contentment-chirp.—The contentment-chirp is a short, monosyllabic call-note. Its duration was brief but more variable than that of the feeding-peep, lasting 0.10–0.35 s. Its amplitude measures 70–75 db. The contentment-chirp is characterized by sharply rising pitch. The fundamental frequency is generally low, starting at 0.5–1.0 kHz and rising 1.5–2.0 kHz. There are several harmonics, spaced at about 1.0 kHz intervals. There seemed to be individual-specific variations in the acoustical structure, such as the presence or absence of slight dips in pitch at the beginning or end of the call-note, but not enough recordings were made to permit detailed analysis.

The contentment-chirp is an infrequently heard vocalization that was recorded from one to only a few times in most of the chicks. The call-note was not reliably elicited with any condition. It was sometimes produced when the chick was reunited with the surrogate parent or a familiar conspecific after a period of isolation and was also occasionally heard when a chick found food.

VOCAL DECLINE

The most unusual aspect of vocalization in the Greater Rhea is its deterioration during ontogeny. Greater Rhea chicks have a variety of call-notes of brilliant tonal quality that are frequently emitted. But by the time they are adults they are relatively silent. Such a regression in vocal behavior deviates considerably from most species of birds in which the complexity of vocalization increases as a function of maturation.

The rate of vocalization was found to decrease steadily with age (Fig. 2). The rates of vocalization of three call-notes, the contact-whistle, the separation-whistle, and the feeding-peep, were determined during the second, fourth, and sixth weeks post-hatch. The contentment-chirp and alarm-trill were not included in the analysis since they are both relatively infrequent call-notes, not reliably elicited from all chicks. However, it appears that both of these call-notes share the general pattern of decline with increasing age. The rate of contact-whistles emitted in the presence of the surrogate parent decreased significantly as a function of age ($P < .001$, ANOCOVA). The rate of feeding-peeps emitted during feeding also decreased significantly with age ($P < .001$, ANOCOVA). Finally, the rate of separation-whistles elicited in a condition of isolation from the surrogate parent and conspecifics also decreased significantly with age ($P < .001$, ANOCOVA). The decline of vocalization rate for the separation-whistle was less severe; the regression coefficient for the separation-whistle rate was statistically different from the regression coefficients for

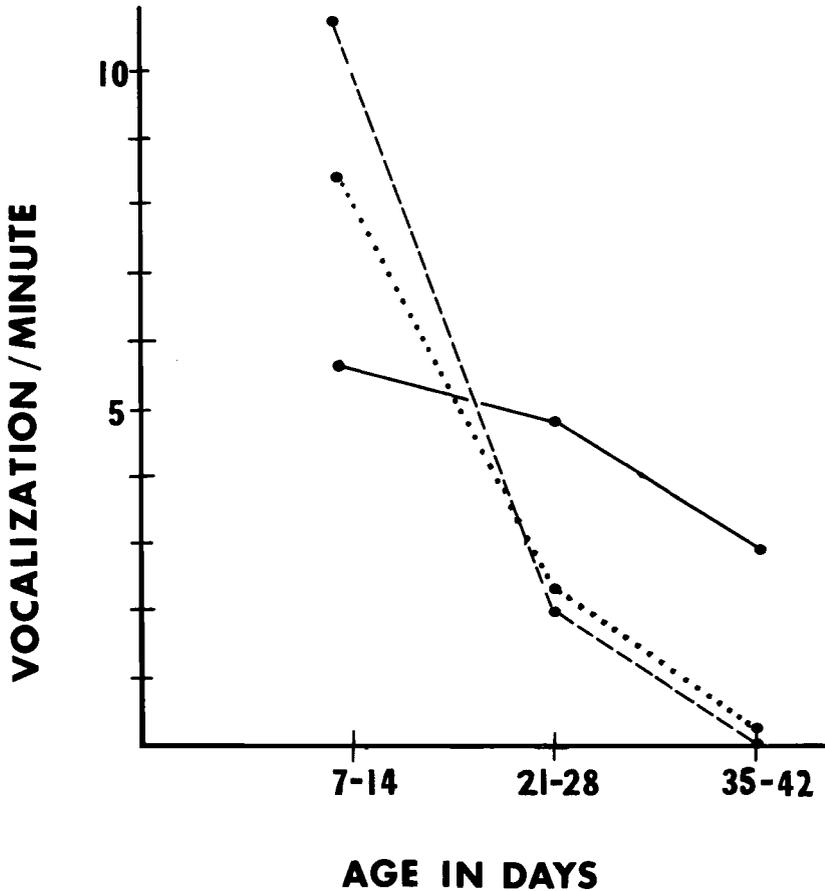


Fig. 2. The rate of vocal production as a function of age in Greater Rhea chicks. Dashed line = feeding-peep rate; dotted line = contact-whistle rate; solid line = separation-whistle rate.

the two other vocalization rates. This may reflect some extended functional significance of the separation-whistle. Only the separation-whistle call-note was still heard after 42 days of age. The oldest age at which a separation-whistle was elicited was 64 days. The call-note in this instance was very hoarse and feeble.

In addition to the decline in the rate of vocalization, there is also a deterioration in tonal quality. Changes first become evident after 17 days post-hatch. Instead of being sharp or even shrill-sounding, the call-notes sound increasingly hoarse. Call-notes showed a decrease in the number of harmonics with age (Fig. 1F). Long call-notes such as the separation-whistle or alarm-trill often had breaks in the production of a single note whereas it was smooth and continuous in younger chicks. This resulted in a choppy and guttural sound. The amplitude of the call-notes also decreased steadily past 17 days of age.

ANATOMY

Two chicks, aged 11 and 15 days, and a 1 yr old adult female Greater Rhea, all of which had died of illness, were used for a pilot investigation into the anatomical basis of vocalization. The resonant frequencies of vocal production are known to depend

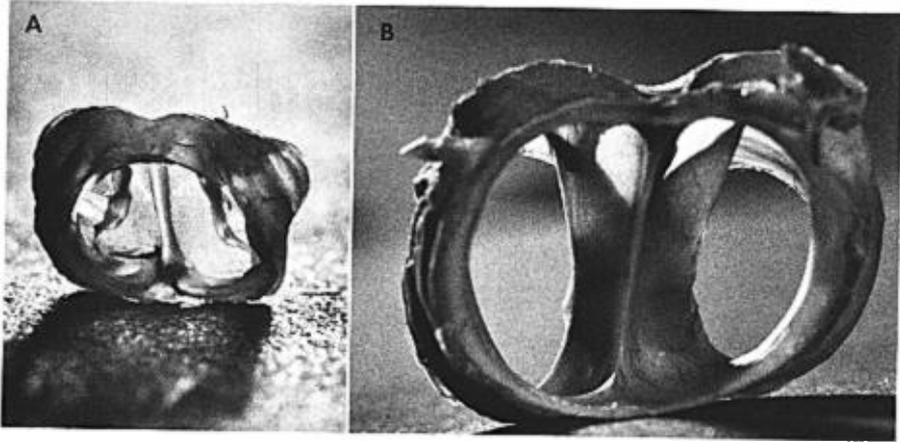


Fig. 3. Internal syrinx. Left: a cross section from an 11-day-old chick; the diameter measures approximately 0.5 cm. Right: a cross section from a 1-yr-old; the diameter measures approximately 2.0 cm. Note the reduction in the intrusion of the tympanic membranes into the bronchial passages.

on the length and diameter of the trachea. The lengths of the chicks' tracheas were 12 and 13 cm, and the diameter in both cases was approximately 0.5 cm. The length of the adult's trachea was 42 cm and its diameter varied from 2.5 cm measured just below the larynx to 2.0 cm measured just above the syrinx. Greater Rhea chicks lose their vocal ability when they reach approximately one-third of their adult height. Perhaps the growth of the trachea is a contributing factor.

A cross section incision was made through the trachea just above the syrinx, allowing for an excellent view of the internal tympanum. The tympanum is thought to be the primary source of vibration and thus the major anatomical structure in avian vocalization (Greenewalt 1968). The tympanum vibrates as air is forced past the internal membranes which are stretched into the bronchial passages at the point of entry into the trachea. In the Greater Rhea, the internal tympanic membranes intruded into the bronchial passages to a much greater extent in the chicks than in the adult (Fig. 3). The internal tympanic membranes of the adult do not seem capable of closing the air passages to the extent necessary to produce the resonance of the chick call-notes.

ECOLOGY

Levins (1968) postulated that one adaptive strategy to deal with predictable changes in ecological contingencies, such as seasonal variations, is a modification of the phenotype correspondent to the ecological parameter. Ontogeny often poses an analogous problem to an animal. The ecological contingencies that confront an animal in its infancy may be quite dissimilar from those it faces in adulthood. A consideration of this process may account for the regressive nature of vocal ontogeny in the Greater Rhea.

The vocal channel of communication seems well adapted to the ecological contingencies that confront the Greater Rhea chick. Chicks suffer greatly from predation by the Crested Caracara (*Polyborus plancus*) as well as other avian and mammalian predators. These predators rely primarily on visual cues in obtaining prey. Aided by its cryptic coloration, the Greater Rhea chick may reduce the probability of predator detection by blending in with the tall grass of its native Argentine pampas. However,

the resulting low visual profile of the chick may also increase the probability that the parent will lose visual contact with the young. Given this situation, the vocal channel seems to be the optimal method of communication for the chicks. The variety of chick call-notes seem well suited to maintain contact with the parent and to signal when the chick is lost, in danger, or feeding.

Between 6 to 10 weeks of age seems the turning point in vocal behavior and ecology. At this time chicks lose their vocal prowess, lose the cryptic coloration provided by the neossophtiles, and begin to outgrow the protective cover offered by tall grass. They are also probably too large at this age to suffer heavily from predation by the Crested Caracara. In Greater Rhea juveniles ritualized visual displays are elaborated for social communication. Descriptions of some of the adult visual displays have been provided by Raikow (1969) and Bruning (1975). The visual channel of communication seems well suited to the ecological contingencies of adults, which do not suffer from natural predators. They are also large-bodied animals, attaining a height of 1.5 m, and are not cryptically colored. They therefore stand out noticeably from the surrounding flat, grassland habitat. Visual display would seem to be the most efficient method of communication in this situation.

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LITERATURE CITED

- ARMSTRONG, E. A. 1973. A study of bird song. (Rev. ed.). New York, Dover Publications.
- BRUNING, D. F. 1973a. The Greater Rhea chick and egg delivery route. *Nat. Hist.* 82(3): 68-75.
- . 1973b. Breeding and rearing rheas in captivity. *Intern. Zoo Yearbook* 13: 163-174.
- . 1975. Social structure and reproductive behavior in the Greater Rhea. *Living Bird* 13: 251-294.
- GREENEWALT, C. H. 1968. Bird song: Acoustics and physiology. Washington, D.C., Smithsonian Institution Press.
- HINDE, R. A. 1969 (ed.) Bird vocalizations: Their relation to current problems in biology and psychology. Cambridge, England, Cambridge Univ. Press.
- HUDSON, W. H. 1903. *Naturalist in La Plata*. London, J.M. Dent & Sons.
- LEVINS, R. 1968. *Evolution in changing environments*. Princeton, N.J., Princeton Univ. Press.
- ORCUTT, A. B. 1974. Sounds produced by hatching Japanese quail (*Coturnix coturnix japonica*) as potential aids to synchronous hatching. *Behaviour* 50: 173-184.
- RAIKOW, R. 1969. Sexual and agonistic behavior of the Common Rhea. *Wilson Bull.* 81: 192-206.
- THORPE, W. H. 1961. *Bird song: The biology of vocal communication and expression in birds*. Cambridge, England, Cambridge Univ. Press.