we thank the Government of Norway for financial support, tissue culture materials, and laboratory space during the senior author's stay there.

Literature Cited

de Boer, L. E. M. 1976. The somatic chromosome complements of sixteen species of Falconiformes (Aves) and the karyological relationships of the order. Genetica 46: 77–113.

Bulatova, N. S. 1973. Unusually large sex chromosomes in some larks (Aves: Alaudidae). Mammal. Chromos. Newsl. 14: 150.

Hammar, B. 1970. The karyotypes of thirty-one birds. Hereditas 65: 29–58.

Kaul, D., & H. A. Ansari. 1978. Chromosome studies in three species of Piciformes (Aves). Genetica 48: 193–196.

———, & ———. 1979. Chromosomal polymorphism in a natural population of Northern Green Barbet, *Megalaima zeylanica caniceps* (Franklin) (Piciformes: Aves). Genetica 49: 1–5.

Misra, M., & M. D. L. Srivastava. 1976. The karyotypes of two species of Falconiformes. Cytologia 41: 313–317.

Ohno, S. 1967. Sex chromosomes and sex-linked genes. New York, Heidelberg, Berlin, Springer-Verlag.

———, C. Stenius, L. C. Christian, W. Becak, & M. L. Becak. 1964. Chromosomal uniformity in the avian subclass Carinatae. Chromosoma 15: 280–288.

Schmid, W. 1962. DNA replication patterns of the heterochromosomes in *Gallus domesticus*. Cytogenetics 1: 344–352.

Stefos, K., & F. Arrighi. 1971. Heterochromatic nature of the W chromosome of birds. Exp. Cell. Res. 68: 228–231.

Stock, A. D., & G. Mengden. 1975. Chromosome banding pattern conservatism in birds and nonhomology of chromosome banding patterns between birds, turtles, snakes and amphibians. Chromosoma 50: 69–77.

Sumner, A. T. 1972. A simple technique for demonstrating centromeric heterochromatin. Exp. Cell. Res. 75: 304–306.

Takagi, N., & M. Sasaki. 1974. A phylogenetic study of bird karyotypes. Chromosoma (Berlin) 46: 91–120.

———, M. Itoh, & M. Sasaki. 1972. Chromosome studies in four species of Ratitae (Aves). Chromosoma 36: 281–291.

Williams, R. M., & R. J. Benirschke. 1976. The chromosomes of four species of Falconiformes. Experientia 32: 310–311.

Received 22 October 1981, accepted 18 February 1982.

Individuality of Vocalizations in Dunlin: a Possible Acoustic Basis for Recognition of Parent by Offspring

Myron Charles Baker
Department of Zoology and Entomology, Colorado State University,
Fort Collins, Colorado 80523 USA

Calls of parents can be recognized by the young in several species of the avian order Charadriiformes (Beer 1970a,b; Evans 1970a,b). It can be predicted that parent-offspring vocal recognition may evolve in precocial species with the potential of young of different parentage becoming mixed during foraging activities.

In the eastern Canadian Arctic, I made tape recordings of breeding Dunlin (Charadriiformes, Scolopacidae, *Calidris alpina*). From these I attempted to establish the acoustic properties of a certain vocal signal that may allow young chicks to recognize their parents.

The precocial young Dunlin leave the nest cup within a few hours after hatching and begin pecking at small adult Diptera resting on vegetation. In the first two or three days, a parent broods its offspring, particularly in cold or rainy times. One or both of the parents accompanies the young, often "leading" them by walking ahead and emiting a low-intensity, "purring" vocalization. The purr vocalization is also given by a parent when gathering up its young for brooding. As the chicks wander over the prime feeding areas, two or more broods may mingle and separate.

Observations at this time indicate that adults give purr calls almost constantly and the young move toward an adult that is producing these calls. These observations raise questions about the possible acoustic basis for recognition of the correct parent. It is possible to discount the importance of visual recognition, because the uneven terrain usually prevents the tiny chicks from seeing the parent after a few meters of separation. I did not verify the occurrence of vocal recognition with individually marked birds, but I assumed that the young re-assort with the correct parent. This assumption is parsimonious and logical from an evolutionary point of view. Brooding space under an adult is limited, and the

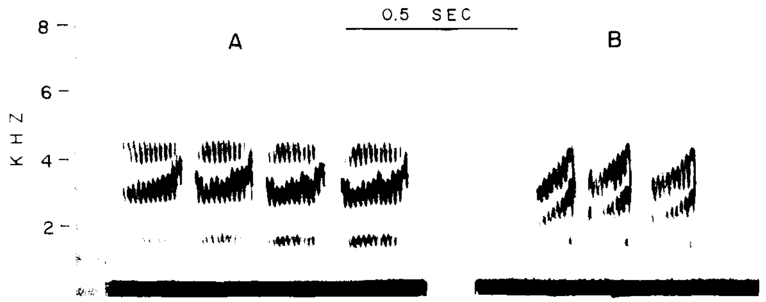

Fig. 1. Spectrograms of contact purr vocalizations of two Dunlin (A, B).

young, normally four, barely fit. Such brooding is critical to survival in the early days of life, because rain and cold are major causes of chick mortality at that time. Chicks are also led into rich foraging sites by adults at this early age. Moreover, several mammalian and avian predators prey upon young shorebirds at this time, when they are particularly vulnerable. Thus, there is strong selective pressure for considerable parent-offspring coordination and communicative interaction.

Dunlin vocalizations were recorded from a population east of Fort Churchill, Manitoba, Canada during a 2-week period in June 1976. The study area lies in the open coastal tundra of the Hudson Bay lowlands and consists of marshy habitat characterized by sedges, some grasses, and lichens. Dunlin breed as territorial, monogamous pairs in the area, but, after hatching, the young and tending parents seem virtually to ignore territorial boundaries and range widely, concentrating in places where prey are most abundant. Hatching is highly synchronous within and among broods.

I made recordings of purr vocalizations given by parents tending their broods during foraging. The vocalizations were taped on a Nagra III recorder at 3.75 inches/s using a Sennheiser 105 omnidirectional condenser microphone mounted in a parabolic reflector. In the laboratory, sound spectrograms were made with Kay Elemetric's model 6061B "Sonagraph," with the 80–8,000 Hz range and 300 Hz wideband filter settings.

Five variables for each vocalization were examined by direct measurements on the spectrograms (Fig. 1). On each individual spectrogram, the same set of measurements was made on the penultimate note. The penultimate note was chosen for the measure-

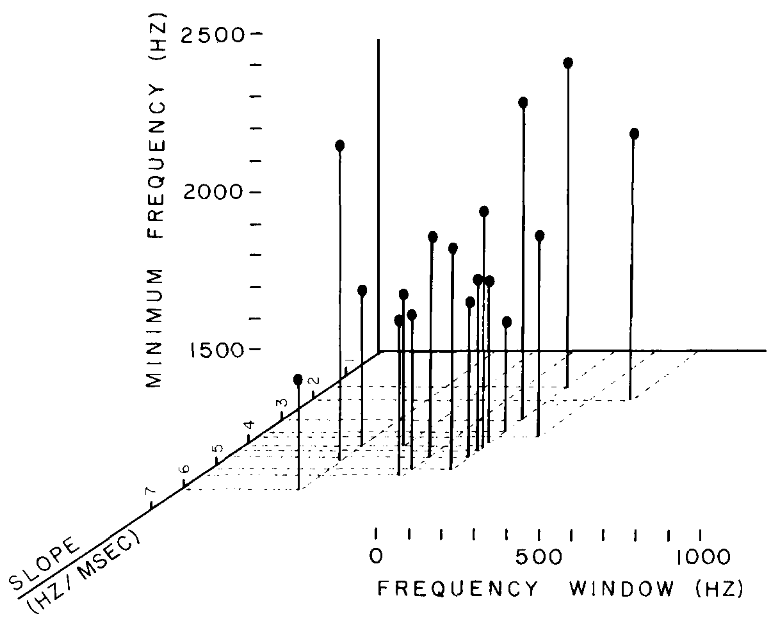

Fig. 2. A three-dimensional plot of three variables measured on each vocalization of 17 Dunlin.

ments because several of the purr calls consist of two notes and thus have only one interval. The measurements made were (1) the duration in milliseconds of the penultimate note, (2) the interval in milliseconds between the penultimate note and the ultimate note, (3) frequency window in hertz (maximum frequency minus the minimum frequency at the midpoint of the penultimate note), (4) the slope of the penultimate note (maximum frequency at the end of the note minus maximum frequency at the start of the note divided by duration), and (5) the minumum absolute frequency of the penultimate note. The measurements were made on the first harmonic, which usually contained the most energy, of the purr vocalizations of 17 individuals.

Examination of the five variables measured on the calls shown in Fig. 1 indicated that purr notes have a mean minimum frequency (±1 SD) of 2,168 Hz ± 213 (CV = 9.8%) and a mean frequency window of 669 Hz ± 176 (CV = 26.3%). Notes of contact purr calls last an average of 162 ms ± 20 (CV = 12.3%), have a mean interval to the subsequent note of 48 ms ± 8 (CV = 16.7 %), and have a slope of 4.26 Hz/ms ± 1.17 (CV = 27.5%).

The three variables (minimum frequency, frequency window, slope) that had the largest standard deviations are plotted in three dimensions in Fig. 2. The differences in variability across individuals are readily apparent from this plot.

These analyses indicate that of the variables measured the single most likely candidate for an acoustic basis of the recognition of parental-contact purr calls is the slope of the note. More individuals are unique in this character than in any other. When the joint effect of three acoustic variables is examined, the detailed morphology of purr calls (Fig. 1) suggests that several individuals are similar but that the distinctions are probably adequate as a basis of parental recognition.

In the analyses of Beer (1970a,b) of individual recognition by Laughing Gull (*Larus atricilla*) chicks, the simple "crooning" call of the parent, which elicits a strong affiliative response by the chicks, is said not to differ markedly among different adults, although parental "long calls" were individually distinctive. Evans (1970b) discovered that young Black-billed Gulls (*Larus bulleri*) responded more positively to their own parents' "mew" call than to one of a nonparent. Instrumental analysis showed that the acoustical features of the "mew" call of Black-billed Gulls were different for each individual adult. Results similar to those obtained from Black-billed Gulls were also obtained in a study of the Ring-billed Gull (*Larus delawarensis*) made by Evans (1970a).

The "mew" or "crooning" calls of these gull species are similar in acoustic parameters and are given in a similar motivational context. There appears to be variability sufficient to allow individual recognition of parent by offspring; experimental results indicated that the young distinguish between parent and nonparent calls. Learning of parental vocalizations in the context of feeding thus seems to be characteristic of the family Laridae in the Charadriiform group. Indeed, whenever one finds precocial young with the potential for mixing among different sibling groups, similar phenomena are expected. Exceptional cases exist in some bird species, such as Oldsquaw (*Clangula hyemalis*). In this species "communal" broods are said to be common (Alison 1975), although my observations of Oldsquaw suggest that such assemblages are usually found feeding in the water and that it is not clear what adult investments are being made in the offspring of others. In any case, these reports require special explanations, because it is not obvious how natural selection at the individual level would cause such behavior.

In the Scolopacidae (Charadriiformes), slightly different problems are faced by a family group in comparison to gulls. With the Dunlin behavior reported here as an example, there is a major difference between the sandpipers and gulls, because gulls feed their young by regurgitation, whereas sandpiper young are not provisioned and must begin to feed themselves immediately. Thus, the potential for mixing sibling groups is more immediate in sandpipers. Furthermore, there is no apparent food reinforcement accompanying call learning as there is in the gulls. It is possible, however, that there is subtle reinforcement from the parent leading the young to rich feeding areas. It also seems likely that the mere presence of the parent would be sufficient to reinforce call learning (Evans 1977). Studies of Bonaparte's Gull (*Larus philadelphia*), a species that is more precocial than most gulls and does not nest in colonies, and studies of other sandpipers would be helpful in illuminating the selective pressures on parental recognition by offspring.

I thank Michael Gochfeld, Steven Green, Roger M. Evans, and several anonymous reviewers for their comments.

LITERATURE CITED

ALISON, R. M. 1975. Breeding biology and behavior of the Oldsquaw (*Clangula hyemalis* L.). Ornithol. Monogr. 18.

BEER, C. G. 1970. On the responses of Laughing Gull chicks (*Larus atricilla*) to the calls of adults I. Recognition of the voices of the parents. Anim. Behav. 18: 652–660.

———. 1970b. On the responses of Laughing Gull chicks (*Larus atricilla*) to the calls of adults II. Age changes and responses to different types of call. Anim. Behav. 18: 661–677.

EVANS, R. M. 1970a. Imprinting and mobility in young Ring-billed Gulls, *Larus delawarensis*. Anim. Behav. Monogr. 3: 193–248.

———. 1970b. Parental recognition and the "mew call" in Black-billed Gulls (*Larus bulleri*). Auk 87: 503–513.

———. 1977. Auditory discrimination-learning in young Ring-billed Gulls (*Larus delawarensis*). Anim. Behav. 25: 140–146.

Received 6 August 1979, resubmitted 23 October 1981, accepted 15 March 1982.

Wetland Salinity and Salt Gland Size in the Redhead *Aythya americana*

Stephen E. Cornelius[1]
Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843 USA

Numerous investigators have shown experimentally that nasal or supraorbital salt glands exist in nonmarine waterfowl and have the ability to enlarge or atrophy in response to changes in the salt content of the drinking water (Scothorne 1959, Ellis et al. 1963, Cooch 1964, Benson and Phillips 1964, Schmidt-Nielsen and Kim 1964). Little information is available, however, about the extent to which such relationships occur in free-ranging populations (Anderson and Warner 1969).

The presence of an extrarenal, salt-elimination mechanism and its adaptability to changing salinity regimens are especially important to the Redhead (*Aythya americana*), which must adjust to marked changes in wetland salinity during its yearly activity cycle. Principal breeding grounds are the freshwater pothole region of the northern United States and adjacent Canadian provinces and the alkaline marshes of the western states. The wintering area for the majority of the Redhead population is the central and lower Texas coast (Bellrose 1976), where salinities normally range from 5 to 35 ppt chlorides. Drought and poor water circulation often result in hypersaline conditions in the coastal bays, causing salinities to reach or surpass 60 ppt. This is particularly true of Laguna Madre, which traditionally hosts the bulk of the wintering population (Weller 1964).

Anderson and Warner (1969) have suggested that the differential state of gland development in migrating Lesser Scaup (*Aythya affinis*) may have some practical application by indicating whether fresh- or saltwater wintering areas were used.

During studies of the ecology of wintering Redheads (Cornelius 1977), I removed and weighed salt glands from various waterfowl species to determine whether or not correlations exist between gland size and the severity of and/or length of exposure to saltwater environments.

Salt glands were obtained from 279 Redheads in Texas. Variation of gland weight according to wetland salinity was analyzed from 212 Redheads taken by hunters in midwinter, 1975–1976, from four bays on the central Texas coast (St. Charles, Copano, Aransas, Corpus Christi). Variation of gland weight during the entire winter season within a single bay was examined from 67 specimens either collected or confiscated as illegal kills in Laguna Madre between 1972 and 1975. Gland weights of 74 Redheads shot by hunters in October 1975 at freshwater habitats in Manitoba (Delta Marsh) and Minnesota (Thief Lake) were compared with gland weights of birds taken from the saline wetlands of Texas. In addition, salt glands were examined from 143 specimens of 11 other waterfowl species frequenting the Texas coastal zone. This series represented three seasons, 1973–1976.

Glands were either excised within 1 day after collection, or the carcass was frozen and glands removed within 3 weeks. ANOVA and Student's *t*-test of significance were conducted for mean gland weights. Unless otherwise noted, all standard error ranges and tests of significance are presented at the 99% confidence interval.

Unfortunately, an analysis of salt-gland weight variation relative to total body weight was not possible, because the majority of the specimens received from hunters were eviscerated or were only the heads. Data on bay salinities were taken from Texas Parks and Wildlife Department fish survey records.

Salt gland weights of Redheads varied greatly by collection locale (Table 1). Gross gland weights were 2.5–4.5 times greater than mean values from Manitoba and Minnesota. Highly significant variation existed in the mean salt gland weight as a function of habitat salinity of birds collected from the Texas coast in midwinter 1975–1976. The salinities of St. Charles and Copano bays were similar, and the mean gland weights of Redheads collected in the respective bays were nearly identical. A marked increase in gland size, however, was observed in the study material from Aransas and Corpus Christi bays, where salinities ranged 8–17 ppt higher.

Redhead salt glands for each wintering month were available from the Laguna Madre series (Fig. 1) and suggested an upward trend in gland weight from October through March. The mean gland weight of 41 birds collected during fall and early winter (October, November, December) was 1,440 ± 81 mg,

---

[1] Present address: R.R. 3, Box 216, Mountain View, Missouri 65548 USA.