or anterior to the mid-thoracic region. Such handling probably facilitates swallowing and/or may damage the mouse's vital organs.

A similar relationship between prey weight and handling behavior was reported by Loop (1974) for the Bengal monitor (*Varanus bengalensis*). The probability that monitors shook laboratory mice increased with heavier mice, and Loop concluded that shaking caused structural damage to the prey.

According to the linear regression equation, mouse pups weighing much less than 10 g should not be beaten. Our one observation of a Roadrunner beating a mouse pup occurred when the bird had just eaten several other pups and was probably no longer hungry. Beating behavior in this circumstance suggests that Roadrunners may beat prey during play and exploration.

We believe that Roadrunners increase the efficiency of prey handling by varying the number of times they beat prey and by choosing the hardest substrate available for beating. This flexibility in behavior may have aided the recent range extension of the species, by allowing the birds to incorporate new prey into their diet.

## ACKNOWLEDGMENTS

We thank K. L. Bildstein, C. B. Brownsmith, W. D. Peters, and W. Shields for their manuscript critique. We also thank R. E. Beal for helpful suggestions and graphical aid, W. Myser for X-ray assistance, and especially T. C. Grubb, Jr., for encouragement and criticism in all aspects of this project.

## LITERATURE CITED

BENT, A. C. 1940. Life histories of North American cuckoos, goatsuckers, and their allies, Part 1. U.S. Natl. Mus. Bull. 176.

BLEICH, V. C. 1975. Roadrunner predation on ground squirrels in California. Auk 92:147–148.

BRYANT, H. C. 1916. Habits and food of the Roadrunner in California. Univ. Calif. Publ. Zool. 17:21–58.

CALDER, W. A. 1967. Breeding behavior of the Roadrunner, *Geococcyx californianus*. Auk 84: 597–598.

HERREID, C. F., II. 1960. Roadrunner as a predator of bats. Condor 62:67.

LOOP, M. S. 1974. The effect of relative prey size on the ingestion behavior of the Bengal monitor, *Varanus bengalensis* (Sauria: Varanidae). Herpetologica 30:123–127.

NETER, C., AND W. WASSERMAN. 1974. Applied linear statistical models. Richard D. Irwin, Homewood, Illinois.

OBERHOLSER, H. C. 1974. The bird life of Texas, Vol. 1. Univ. Texas Press, Austin.

SUTTON, G. M. 1922. Notes on the Roadrunner at Fort Worth, Texas. Wilson Bull. 34:3–22.

ZIMMERMAN, D. A. 1970. Roadrunner predation on passerine birds. Condor 72:475.

*Department of Zoology, The Ohio State University, Columbus, Ohio 43210. Address of second author: 173 Summit Avenue, Northfield, Ohio 44067. Present address of first author: Department of Biology, Capital University, Columbus, Ohio 43209.* Accepted for publication 30 May 1978.

---

*Condor*, 81:87–89

# THE SOURCE OF THE DIVE-NOISE OF THE ANNA'S HUMMINGBIRD

LUIS F. BAPTISTA

AND

MARGARET MATSUI

North American hummingbirds of the genus *Calypte* have two kinds of displays involving sound: (1) a so-called "static" display in which perched males sing and turn their heads slowly to flash their gorgets at rivals or intruders; and (2) an aerial or "dynamic" display in which males climb up into the air and dive at an intruding male or court a female. At the bottom of the dive, each species makes a species-specific noise (henceforth called the dive-noise). It has been suggested that dive-noises are made by the specialized outermost rectrices (Miller 1940, Rodgers 1940, Hamilton 1965, illustrations in Wagner 1966). Rodgers (1940) reported that when the modified outermost rectrices of the Anna's Hummingbird (*Calypte anna*) were attached to a strip of bamboo and then whipped through the air, a note was produced almost identical to that produced by the hummingbird at the bottom of the dive. This noise was absent when similar experiments were performed with the nonspecialized rectrices.

While studying Costa's Hummingbirds (*C. costae*), one of us (LFB) noted that they would produce the dive-noise while perched (spectrograms in Wells et al. 1978), indicating that this whistle was vocal and not mechanical in origin. Joe T. Marshall (pers. comm.) has made similar observations. This stimulated us to look closer at the displays of the congeneric Anna's Hummingbird. We present herein spectrographic evidence indicating that in Anna's Hummingbirds too, dive-noises are mostly, if not entirely, vocal in origin and represent a variant of a phrase commonly found in static songs.

## STATIC SONG

Static display and the accompanying song have been described (Wells et al. 1978). Briefly, a male sits on an exposed perch, spreads his gorget, turns his head slowly from side to side, and sings his loud and complex song. At least in southern California, those songs consist of three main types of phrases (Mirsky 1976), of which only two concern us: (1) buzzy phrases, which often introduce each song (Fig. 1C); and (2) squeaky phrases, which may be divided into three parts. The first part is a rapid trill which may range from 3.0 to 5.75 kHz (element *a* in Fig. 1A, B). The second portion is a note about 3.25 to 5.00 kHz with an overtone at 4.50 to 5.25 kHz

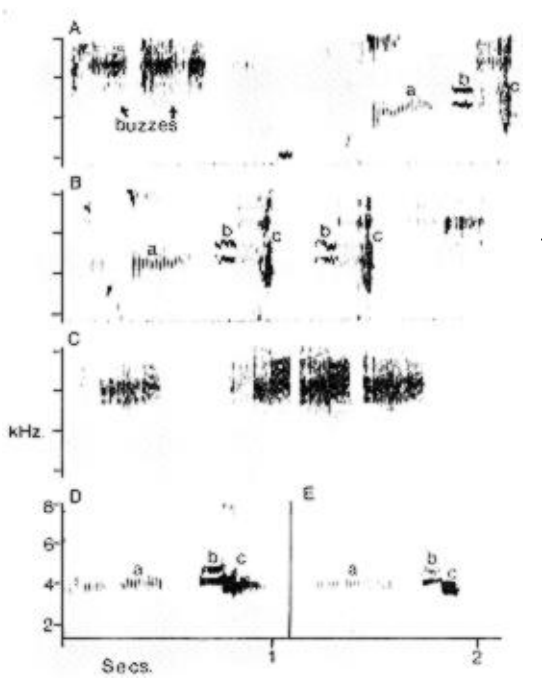

FIGURE 1. A: Portion of static song of an Anna's Hummingbird which consists of four buzzes followed by a squeak phrase. The squeak consists of *a*, *b*, and *c* components. B: Portion of static song of an Anna's Hummingbird showing two squeak phrases followed by a buzz. Element *a* is absent from the second squeak phrase. C: Aerial song of Anna's Hummingbird during a dive display, consisting of only four buzzes. D and E: Two dive-noises from the dive displays of two different Anna's Hummingbirds. The *b* elements are frequency modulated in B and E, whereas in A and D the carrier frequencies appear to be more sustained.

(element *b* in Fig. 1A, B), followed by a buzzy portion rich in overtones (element *c* in Fig. 1A, B). The squeak phrase may be repeated twice, in which case element *a* is absent from the second rendition (Fig. 1B). Some static songs, especially those following an aerial display, may contain no squeak phrases. The static display is territorial in function (Pitelka 1951, Williamson 1956).

## AERIAL SONG

The dynamic display has been described in detail elsewhere (Hamilton 1965, Wells et al. 1978). Near and at the top of the climb preceding the dive display, the Anna's Hummingbird sometimes sings while hovering. We found, however, that only the buzz phrases are used here (Fig. 1C). The hummingbird then dives, and at the bottom of his dive makes the characteristic dive-noise. Spectrograms of the dive-noise (Fig. 1D, E), indicate that it is extremely similar in structure to the squeak phrase of the static display, especially because it includes the *a*, *b*, and *c* portions.

Element *a* may sometimes be left out in the dive noise. This element is absent in the second squeak phrase of the static display (Fig. 1B). One bird recorded at San Pedro, California, sometimes omitted element *c* in the squeak phrase of its static song. The *c* portion is sometimes absent in the dive-noise (not illustrated). Thus, similar variants of the squeak phrase are sometimes to be found in the dive-noises.

TABLE 1. Duration of elements in vocalizations (ms).

| | Dynamic displays | | Static displays | |
|---|---|---|---|---|
| Element | N | ms | N | ms |
| *a* | 9 | 412.87 ± 71.99[1] | 11 | 253.23 ± 54.19 |
| *a* – *b*[2] | 9 | 134.26 ± 37.35 | 8 | 120.48 ± 21.31 |
| *b* | 9 | 117.69 ± 26.66 | 11 | 96.53 ± 22.29 |
| *c* | 9 | 65.29 ± 8.43 | 11 | 58.58 ± 6.25 |

[1] *t*-tests were conducted for all values in dive versus static display. No significant differences were found.
[2] Interval between *a* and *b* elements.

The duration of the *a*, *b*, and *c* portions overlap in both static and dynamic displays; however, these portions tend to be longer in the dive-noise (Table 1). In the Costa's Hummingbird, dive-noises are also longer than static song (Wells et al. 1978). The *c* portion in the static display of the Anna's Hummingbird is preceded, moreover, by a noisy portion separating it from element *b*. This noisy portion is absent in the dynamic display.

Pitch of elements *a* and *b* and the overtone of *b* are slightly lower in the dynamic display as compared to the static (Table 2). Pitch in element *c* of the static display is difficult to measure because of all the noise in that element. However, comparing the equivalent harmonic in element *c* of the static display with that of the dynamic, we again found a drop in pitch in all spectrograms examined. To our knowledge, the flight speed of the Anna's Hummingbird during the dive has not been determined. Pearson (1960) calculated dive-speed of the Allen's Hummingbird (*Selasphorus sasin*) to vary between 34 and 64 mph. Dive speed of the Anna's Hummingbird must be at least equivalent. At such a speed, a drop in pitch in all acoustical elements measured may be due to the Doppler effect.

Squeak phrases in the static display are also characterized by greater variability in pitch as evidenced by the larger standard deviations (Table 2). Spectrograms of squeak phrases reveal the often quavering quality of element *b* and slurred and prolonged element *c* (Fig. 1B). Elements *b* and *c* in the dive-noise are more stereotyped.

We submit that the dive-noise of the Anna's Hummingbird is mostly, if not entirely, vocal in origin. The role of the specialized rectrices, if any, in producing the dive-noise is not apparent from the sound spectrograms, and may be masked by the vocalizations. No sounds other than the *a*, *b*, and *c* elements

TABLE 2. Mean pitch[2] of elements in vocalizations (kHz).

| | Dynamic displays | | Static displays | |
|---|---|---|---|---|
| Element | N | kHz | N | kHz |
| *a* | 9 | 4.10 ± .05[1] | 8 | 4.23 ± 3.0 |
| *b* | 9 | 4.00 ± 0 | 11 | 4.34 ± .21 |
| overtone of *b* | 9 | 4.5 ± .06 | 11 | 5.08 ± .19 |

[1] *t*-tests were conducted for all values in dive versus static display. Only that for pitch of the overtone of *b* was significantly different ($P < .05$).
[2] Highest pitch + lowest pitch ÷ 2.

are evident (Fig. 1). Miller (1940) reported on the absence of the dive-noise in the displays of subadults. Pitelka (pers. comm.) noted that the dive of young males is not totally silent for there is a rush of air, which is a noise. In molting birds, he noted a rush of air which might progress to a louder click noise as the feathers mature. Whereas the developing rectrices may contribute to the louder dive-noise, it could be that ontogeny of the voice parallels development of the rectrices. "Crystallization" of the (vocal) dive-noises may be complete when the rectrices are fully mature. If so, then the function of the specialized rectrices may be to provide added maneuverability during the complex dive display.

We thank Millicent S. Ficken and Frank A. Pitelka for their valuable comments on an earlier draft of this paper.

## LITERATURE CITED

HAMILTON, W. J., III. 1965. Sun-oriented display of the Anna's Hummingbird. Wilson Bull. 77: 38–44.

MILLER, L. H. 1940. Sound produced in the nuptial dive of young Anna Hummingbirds. Condor 42:305–306.

MIRSKY, E. N. 1976. Song divergence in hummingbird and junco populations on Guadalupe Island. Condor 78:230–235.

PEARSON, O. P. 1960. Speed of the Allen Hummingbird while diving. Condor 62:403.

PITELKA, F. A. 1951. Ecologic overlap and interspecific strife in breeding populations of Anna and Allen hummingbirds. Ecology 32:641–661.

RODGERS, T. L. 1940. The dive note of the Anna Hummingbird. Condor 42:86.

WAGNER, H. O. 1966. Meine Freunde, die Kolibris. Verlag Paul Parey, Hamburg.

WELLS, S., R. A. BRADLEY AND L. F. BAPTISTA. 1978. Hybridization in *Calypte* hummingbirds. Auk 95:537–549.

WILLIAMSON, F. S. L. 1956. The molt and testis cycles of the Anna Hummingbird. Condor 58: 342–366.

*Moore Laboratory of Zoology, Occidental College, Los Angeles, California 90041.* Accepted for publication 1 September 1978.

---

*Condor*, 81:89–91

# METABOLIC RATE IN FIVE TROPICAL BIRD SPECIES

CAROL M. VLECK
AND
DAVID VLECK

Metabolic rates are often predicted from allometric equations relating metabolism to body mass. Although the relationship between metabolic rate and body mass varies among taxa of birds (Lasiewski and Dawson 1967), and with time of day (Aschoff and Pohl 1970), it has not been shown to vary predictably with climate (Scholander et al. 1950). Few metabolic data are available on birds living in the lowland tropics where ambient temperatures are usually high. A few birds from hot climates have low metabolic rates (Hudson and Kimzey 1966, Weathers 1977). It is therefore of interest to determine if metabolic rates of tropical species are lower than those predicted from allometric equations based largely on temperate species. We report standard metabolic rates of four tropical passerines, all suboscines, and one tropical nonpasserine, a dove.

## MATERIALS AND METHODS

Birds were mist-netted in August and September 1977 on several islands in Gatun Lake in central Panama, latitude 9°N. Rates of oxygen consumption were measured for at least two hours during the night after capture. We kept the birds in the dark without food for 3–8 h before testing. They were weighed to the nearest 0.5 g with a Pesola scale before and after testing. Cloacal temperatures were measured at the end of each experiment with a quick-registering Schultheis thermometer or thermocouple probe and Bailey Bat-8 digital thermometer.

We measured oxygen consumption in an open flow respirometer analogous to the mask system described by Withers (1977). Birds were placed in a plastic or glass metabolic chamber within a darkened box maintained at 30 ± 1°C and at ambient water vapor pressures which did not exceed 24 torr. Air flow through the metabolic chamber ranged from 120 to 645 cc/min. Carbon dioxide and water vapor were absorbed from air leaving the chamber by using Ascarite (sodium hydroxide asbestos) and Drierite (anhydrous calcium sulfate). Fractional concentration of oxygen was then determined with an Applied Electrochemistry S3A Oxygen Analyzer. Flow rates were measured downstream of the oxygen sensor with a Gilmont Flowmeter calibrated against a Brooks Thermal Mass Flowmeter. Oxygen consumption was calculated from equation 4a of Withers (1977). All gas volumes are reported at standard temperature (0°C) and pressure (760 torr, 1 torr = 0.133 kPa).

Birds sat in the chamber undisturbed for at least one hour before we began recording oxygen consumption. The lowest rate of oxygen consumption during the second hour of each experiment was assumed to be the standard metabolic rate at 30°C. Rate of oxygen consumption usually did not vary more than 5% throughout the last 30 min of an experiment. Oxygen consumption was converted to energy assuming a caloric equivalent of 4.8 kcal/l $O_2$ (1 kcal = 4.184 kJ) (King and Farner 1961, Lasiewski and Dawson 1967).

## RESULTS

Standard metabolic rates of the five species are shown in Table 1. Predicted metabolic rates in the resting phase of the daily activity cycle were calculated from the appropriate allometric equations of Aschoff and Pohl (1970). For nonpasserines: