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ON THE FUNCTION OF PREY BEATING BY ROADRUNNERS

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Among the peculiar habits of the Roadrunner (*Geococcyx californianus*) is the beating of large prey against a hard substrate before eating it. Researchers familiar with the species have implied that Roadrunners kill their prey in this manner (e.g., Sutton 1922, Bent 1940, Calder 1967). We observed that two captive Roadrunners clamped their bills on the cervical vertebrae of laboratory mice (*Mus musculus*) and immobilized them, apparently either by strangulation or damage to the spinal cord. As Roadrunners swallow their prey whole, immobilization may prevent damage to the esophagus and crop during ingestion.

Rodents are among the heaviest prey of Roadrun-

ners (Bryant 1916, Herreid 1960, Zimmerman 1970, Bleich 1975). Since our birds immobilized the mice without beating them, we considered whether beating has another function. Oberholser (1974) noted, as we have, that Roadrunners beat a prey animal until it is limp. We also observed that the number of times a Roadrunner beat a mouse was variable and that not all food was beaten. We hypothesized that the main function of beating is not to "kill" prey, but to break the skeleton so that it can be swallowed more easily. Heavier mice may have sturdier skeletons. We therefore tested the prediction that the number of times a Roadrunner beat a mouse depended on the mouse's weight.

METHODS

Two sibling Roadrunners, taken as nestlings from Hagerman National Wildlife Refuge, Sherman, Texas, in June 1976, were hand-reared on grasshoppers and beef liver, and maintained on meal worms (*Tenebrio* spp.), beef heart and kidney, live laboratory mice, and supplemented with Avitrol. After reaching adult

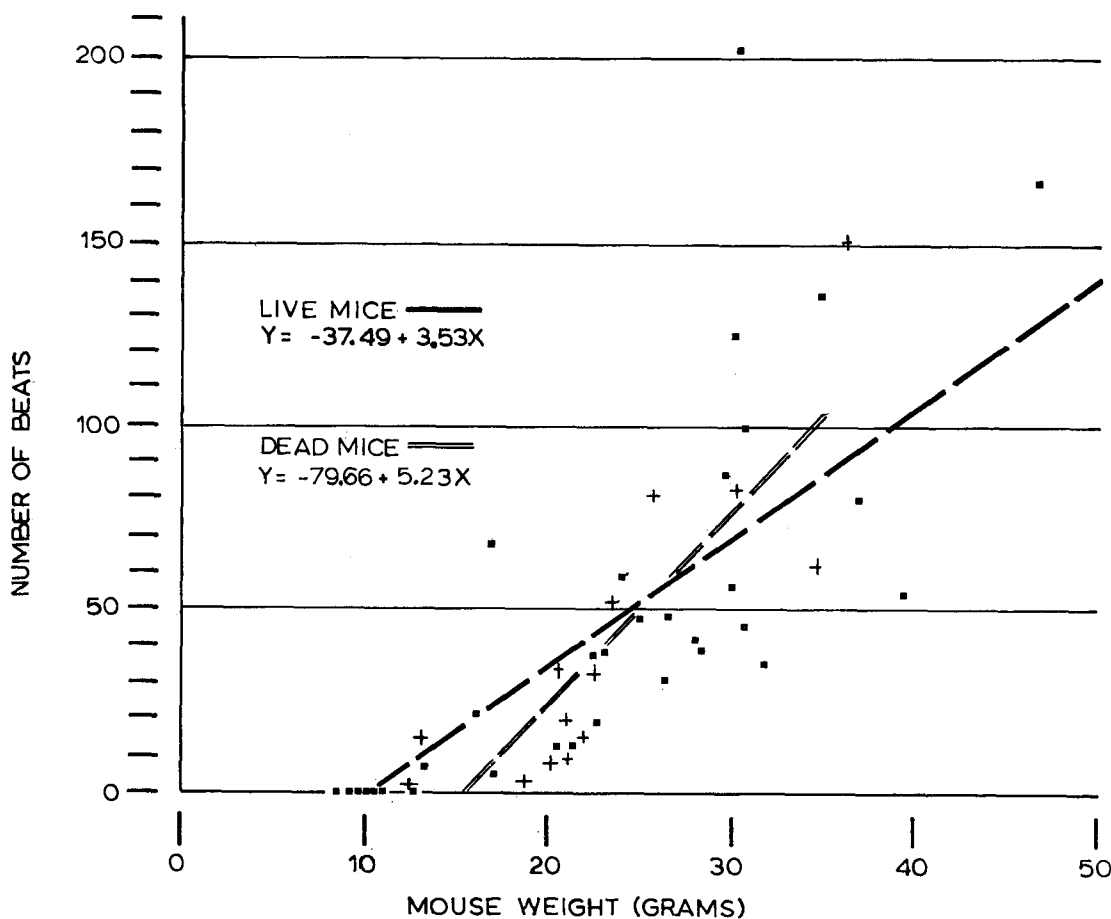


FIGURE 1. The number of times a Roadrunner beats dead and live laboratory mice is regressed on the weight of the mice. Sample sizes were 14 dead mice (+ sign) and 36 live mice (dark square). Slopes of both lines are highly significantly different from zero ($P < .001$).



FIGURE 2. X-ray of a control mouse (left, 21 g) and a mouse beaten by a Roadrunner (right, 19 g). Damage to both humeri, the cervical vertebrae, the occipital region of the skull and the ribs is evident in the mouse on the right.

weight (over 300 g), both birds were housed in an indoor room, with a concrete floor covered with mouse litter, which connected to an outdoor aviary with an earth floor. The birds were fed twice daily—between 07:00 and 10:00 and between 15:00 and 17:00.

We conducted 36 feeding experiments involving live mice on afternoons between 6 October and 17 November 1976 and 14 experiments with dead mice on afternoons between 21 July and 3 November 1977. Mice were killed by gas fumes immediately before being given to the birds. During both experimental periods, the morning feeding was controlled to ensure that the birds were hungry at experimental feeding time, a procedure which eliminated other behavior such as play from becoming confused with prey handling. Laboratory mice weighing 8–46 g were used in the first experiment, and mice weighing 13–37 g in the second. After presenting a mouse to a Roadrunner, we recorded total handling time (contact until consumption) and number of beatings. Data were taken only for the first mouse given to each bird at each feeding.

Within each experimental set (live and dead mice) the data for both birds were combined. The cause and effect relationships between mouse weight, number of beatings, and mouse movement was investigated with linear regression. All assumptions were tested according to techniques described by Neter and Wasserman (1974).

RESULTS

The number of beatings a Roadrunner gave either

live or dead mice increased with the weight of the mice ($P < .0001$, Fig. 1). The regression equations predict that the Roadrunners will not beat a live mouse weighing less than 10.6 g, or a dead mouse weighing less than 15.2 g. A statistical comparison of the two regression lines showed that the slopes and intercepts of the two lines were simultaneously equivalent ($P < .0500$, Neter and Wasserman 1974).

Beating and handling caused skeletal damage to the humeri, the cervical vertebrae, the occipital region of the skull, and the ribs (Fig. 2). A Roadrunner initially clasped its bill about the cervical vertebrae, but as beating continued, it shifted its hold on the mouse caudally along the vertebral column until the mouse was clasped in the mid-thorax region. A bird shifted its hold on the mouse between bouts of beating, if more than one. Each bird preferred a certain substrate for beating. One took the mouse outside and beat it against the ground; the other remained indoors and used a dead tree limb lying on the floor as a beating surface rather than the floor. The birds rarely dropped the mice, always held them on the dorsal surface, and always swallowed furred mice headfirst.

Other food items such as naked mouse pups, meal worms, beef heart and kidney, generally were not beaten. We once witnessed a Roadrunner beat a mouse pup after it had just eaten 6–10 pups without beating any of them. Meal worms were never beaten, but both meal worms and mouse pups were habitually run through the mandibles in a "corn on the cob" fashion, then swallowed. Larger pieces of beef heart and kidney were sometimes beaten before being swallowed.

DISCUSSION

The regression line for beating of live mice indicates that the heavier the mouse, the more it is beaten. This increase may be due to a cue of weight or movement. If Roadrunners beat mice until they cease to move, then heavier mice may require more beating.

Our comparison of regression lines for the number of times live and dead mice were beaten can be used to find out if movement is the cue. The similarity of the regression lines for live and dead mice does not support the use of movement cues, and suggests that prey weight is the most important cue determining the number of times a Roadrunner beats a particular prey mouse.

Roadrunners have a varied diet including seeds and fruits, arthropods, reptiles, birds, and small mammals (Bryant 1916, Oberholser 1974). They are capable of swallowing whole items as large as House Sparrows (*Passer domesticus*) and mice. They apparently disarticulate the skeleton by beating, in effect elongating and narrowing the carcass. Breaking of the spinal cord makes large prey more supple, and breaking of the forelimbs decreases lateral protrusion. The pelvic region of the X-rayed mouse that had been handled by a Roadrunner (Fig. 2, right) showed no damage, but this specimen was relatively small and disarticulation of the hindlimbs may not have been necessary. We think it more likely that since Roadrunners swallow mice headfirst, it may be more important to break the humeri than the pelvic region because the bird is then swallowing a roughly conical object point-first.

The extensive damage to the anterior portion of the vertebral column, forelimbs, skull, and ribs reflects a tendency for the bird to grasp the mouse at

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.

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

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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 simi-

lar 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