

SHORT COMMUNICATIONS

Evaluating Models of Crop Emptying in Hummingbirds

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Hummingbirds have received considerable attention in studies of feeding and energy regulation because of their small size, frequent feeding, and their use of energy-rich sugar solutions (e.g. Diamond et al. 1986, Ewald and Carpenter 1978, Hainsworth 1981). They store nectar in a crop, and this internal reservoir supplies energy between foraging bouts (Hainsworth and Wolf 1972, Karasov et al. 1986). The rate of crop emptying, therefore, should influence foraging frequency (Karasov et al. 1986, Wolf and Hainsworth 1977). Because the crop is a major interface between feeding input of energy and outflow for energy use, there has been interest in the determinants of crop-emptying rates (DeBenedictis et al. 1978, Hainsworth 1981, Hainsworth et al. 1981, Diamond et al. 1986, Karasov et al. 1986).

Karasov et al. (1986) report measurements of apparent crop volumes for seven Rufous Hummingbirds (*Selasphorus rufus*) at various times after they were fed 100 μl of 0.585 molal sucrose. Approximately 26 μl remained in the crop following prolonged times after feeding, so subtracting 26 μl from apparent volumes adjusted volumes relative to the amount fed. The authors used a negative exponential and a linear regression to characterize the pattern of crop emptying. A negative exponential regression gave higher correlation coefficients for 5 of the 7 birds (Karasov et al. 1986).

The interpretations for these regressions are inadequately tested, and there are other models that may describe crop function. Six alternative models can be compared based either on studies with other species or physical features of elastic emptying structures (Smith et al. 1984, Stubbs 1977). The models involve (1) a linear, (2) an exponential, (3) a square root, (4) a cube root, (5) a hyperbolic, or (6) an inverse cube root change in volume with time.

A linear model describes stomach emptying of glucose loads in monkeys (McHugh and Moran 1979) and laboratory rats (McCann and Stricker 1986). Negative feedback mechanisms have been suggested to produce this pattern from detection of fluid properties in the duodenum with subsequent adjustment of stomach emptying (Hunt 1983, McHugh and Moran 1979).

A negative exponential model, where the logarithm of volume decreases linearly with time, was used to describe emptying in a variety of animals where the rate of emptying decreased with time (Sibly 1981). This pattern appears when feedback mechanisms have a minimum impact on emptying (Smith

et al. 1984). An obvious appeal for this model is that it produces decreasing rates of emptying with time, but there are other models with this feature.

Hopkins (1966) suggested an alternative to a negative exponential model to describe stomach emptying in humans. A better description related the square root of volume to time. This could be explained functionally with the law of Laplace (Tension = Pressure \times Radius), where circumferential tension in the wall of the emptying structure is proportional to the radius of the compartment (Hopkins 1966). If outflow is proportional to tension and the structure approximates an elastic cylinder, radius would be proportional to the square root of volume and volume would change as a negative quadratic function of time. In this model, rates of emptying decrease over time with a functional basis in how elastic structures empty.

A fourth model, also based on the law of Laplace, relates the cube root of volume to time. This would apply to the case where the emptying structure approximates an elastic sphere.

A fifth model relates the inverse of volume to time (hyperbolic function) based on empirical description of stomach emptying, and the sixth model relates the inverse cube root of volume to time based on a combination of Laplace's law, Hooke's law, and Poiseuille's equation applied to stomachs (Stubbs 1977).

I used apparent volumes minus 26 μl (from Karasov et al. 1986) to compare these models with linear least squares regressions (Fig. 1). The cube root regression gave nearly the same calculated volumes as the square root regression. The hyperbolic regression is not

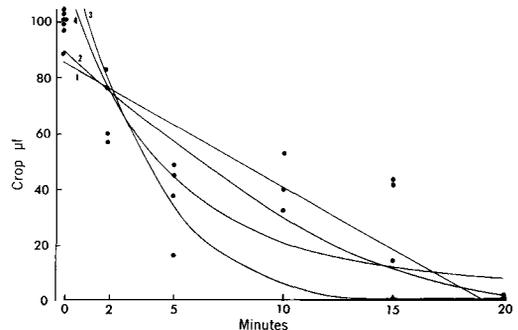


Fig. 1. Crop volume as a function of time after feeding 100 μl of 0.585 molal sucrose (data from Karasov et al. 1986). Lines are shown for (1) linear, (2) square root, (3) exponential, and (4) inverse cube root regression equations.

TABLE 1. Regression equations and statistics. Residual sum of squares (RSS) for untransformed data was calculated by solving each equation for y when $x = 0, 2, 5, 10, 15,$ and 20 min, subtracting each predicted value from observed values, squaring the difference, and adding the squares.

Equation	t	RSS
Linear $y = 85.3 - 4.4x$	7.94	7,354
Exponential $y = 148.1e^{-0.3x}$	4.17	26,300
Square root $y^{0.5} = 9.43 - 0.39x$	8.04	6,289
Cube root $y^{0.33} = 4.54 - 0.17x$	7.03	6,745
Hyperbolic $y^{-1} = -0.019 + 0.012x$	3.15	>130,000
Inverse cube root $y^{-0.33} = 0.205 + 0.016x$	4.53	7,178

shown because it predicted negative volumes at zero time and gave a poor fit to the transformed data (see below).

Two statistics were calculated to compare the regressions. The first was a "t" statistic based on slope/standard error of slope calculated from $r \cdot \sqrt{n-2} \cdot \sqrt{1-r^2}^{-1}$ (Hopkins 1966; Table 1). Because this is based on correlation coefficients after data had been transformed, it indicates how well the data fit the models once volumes had been transformed.

The second statistic was the residual sum of squares (RSS) calculated from untransformed data for each regression (Table 1, RSS). This provides a way to judge how well each regression described the measured volumes because transformation of the volumes influences correlation coefficients (Jobling 1986). I used an ANOVA of squared residuals with multiple comparison (Scheffe's test) to compare the models.

The exponential and hyperbolic regressions produced high residual variation that was statistically greater than residual variation with other regressions ($P < 0.05$, Scheffe's $F \geq 5.143$). The remaining models could not be discriminated as different based on residual variation ($P > 0.05$, Scheffe's $F \leq 0.017$). The exponential and hyperbolic regressions gave very large RSS mainly because of poor prediction of volumes for untransformed data close to zero time. The negative exponential regression predicted an initial volume of $148 \mu\text{l}$, and the hyperbolic regression predicted $-53 \mu\text{l}$. The linear regression predicted an initial volume of $85 \mu\text{l}$, the square root $89 \mu\text{l}$, the cube root $94 \mu\text{l}$, and the inverse cube root $116 \mu\text{l}$.

A negative exponential model for crop emptying does not appear to apply to these data as originally suggested by Karasov et al. (1986). Their conclusion was based on correlation coefficients for individuals considered separately.

More than one model may apply to crop emptying depending on circumstances. In humans, for example,

nonnutritious fluids are emptied from the stomach with a pattern best described by an exponential or square root model (Smith et al. 1984). This has been called the "intrinsic" emptying pattern of the stomach (Smith et al. 1984). However, this changes to a linear pattern with high-quality foods because of negative feedback mechanisms that modify the "intrinsic" pattern (Hunt 1983, McHugh and Moran 1979).

There is indirect evidence for feedback in hummingbirds because increasing food concentration reduces feeding frequency (Wolf and Hainsworth 1977). Changes in crop function are also suggested because the energy condition of hummingbirds influences their feeding frequency (Hainsworth et al. 1981). More information on crop emptying with different concentrations and bird energy states would be useful to understand how feeding and digestion influence the precision of energy regulation.

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Incubation of Dead Eggs

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Prolonged incubation has been recorded in a number of bird species (Drent 1975). We discuss two types of prolonged incubation: birds that incubate a single clutch for an extended period, and birds that lay several discrete clutches in the same nest and incubate all the clutches together. We provided an example of each type in the Negev Desert, Israel, with particular emphasis on the second type, and we attempted to provide explanations for the occurrence of this behavior.

We observed the first type of prolonged incubation in a pair of Stone Curlews (*Burhinus oedicnemus*), which incubated a clutch of two eggs containing dead embryos (determined by candling) for 75 days (1 June to 14 August 1988) at Sede Boqer (30°52'N, 34°46'E). Incubation was terminated when all the Stone Curlews in the vicinity of Sede Boqer migrated. The second type was observed in a pair of Hoopoes (*Upupa epops*), also at Sede Boqer, from June to August 1988.

On 20 June 1988, the Hoopoes had an inordinately large clutch (23 eggs) in a nest located between the ceiling and roof of an unused building. The nest was enclosed, except for a small hole (ca. 4-cm diameter) through which the adults entered. Over the study period, the Hoopoes laid 32 eggs in the nest. A normal clutch for this species is 4-10 eggs, rarely up to 12 (Cramp and Simmons 1985). In Israel, the usual clutch size is 5-6 eggs (Paz 1987). When we candled these eggs, many contained dead embryos (henceforth called *dead eggs*). We plotted egg mass against egg volume and found four clusters of egg mass. These clusters corresponded with eggshell color; the darker eggs weighed less. The eggshells presumably darken with age as the result of dirt accumulation in the nest. Because eggs lose water continuously with age, with an increased rate of water loss in dead eggs (Rahn and Ar 1974), we assumed that the eggs belonged to four different clutches. This assumption was corrob-

orated in the following manner. The five heaviest eggs (shown by candling to be live eggs) were left in the nest and all the others were removed. When these eggs died, two more clutches (totaling nine eggs) were laid in sequence, each one after the eggs of the preceding clutch had died. A plot of mass against volume for these 14 eggs revealed three clusters that corresponded with the three clutches. Mass decreased with age of clutch. Thus, a total of six clutches were laid in the same nest and none was successful. The eggs of the different clutches were arranged in no obvious pattern in the nest (determined by marking eggs). On three occasions, a broken egg was removed from the nest by the birds and placed some 30 cm away.

To examine the possibility that the retention of eggs with dead embryos in the nest acted as a heat buffer to the other eggs that contained live embryos, we measured temperatures in the nest (T_N) and in the surrounding space within the ceiling. We used copper-constantan thermocouples (calibrated against a mercury thermometer approved by the U.S. National Bureau of Standards) with an error of $\pm 0.1^\circ\text{C}$. One thermocouple connected to a Campbell model 21X datalogger was placed between the eggs (to record T_N) and a second was placed 0.5 m from the nest to record temperature between the ceiling and roof (T_C ; hereafter known as ceiling temperature). Temperatures were recorded every 5 s and averaged every 15 min. We compared the mean T_N with all the live and dead eggs ($n = 23$) in place (for two days and nights) to mean T_N of nests with all dead eggs ($n = 18$) removed (for three days and nights).

Ceiling and nest temperatures approximated sinusoidal curves over time. We divided these data into two groups (for temperatures recorded both before and after dead-egg removal). One group had increasing T_N and the other decreasing T_N . We separated the two groups at the crests and troughs of the sinusoidal