

The result was that only three of the six avian studies retained their statistical significance at the $P \leq 0.05$ level.

There is no way to assess directly the impact of observer-expectancy bias on published papers. Nor is it possible to determine whether the error found in the nine investigations of bias was representative of avian observational data. Perhaps the best one can do is to assess qualitatively the degree to which observers in the studies of bias relied on subjective assessment in documenting the behavior they expected to observe and compare this with avian studies with which one is familiar. One added problem, however, is that the observers in the studies of expectancy bias had no personal interest in the results, something that often is not the case in avian research.

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Mass or Weight: What Is Measured and What Should Be Reported?

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The terms mass and weight often are used interchangeably in the avian literature despite the fact that they are very different properties. When workers "weigh" whole animals, animal parts, or animal products they are usually interested in obtaining a measure of the amount of matter in the object. This quantity is called "mass" and is measured in grams. There are several methods of determining mass, although many are inappropriate for use in the field either because they are destructive or require sophisticated equipment, or both. The simplest and least destructive method involves the use of a balance to measure the force applied to the mass by the Earth's gravitational field. This method relies on the principle that the force required to accelerate an object is proportional to its mass. The force of gravity on a mass is termed "weight" and is measured in Newtons (N). One Newton is the force required to accelerate a mass of 1 kg at the rate of 1 m/s². Acceleration due to gravity is 9.8 m/s² and thus, a bird with a mass

of 1 kg exerts a downward force due to gravity, or weight, of 9.8 N. Although balances measure weight, they usually are rescaled so that mass in grams rather than force in Newtons can be read directly.

A potential problem with this method of determining mass is that gravitational force decreases with altitude. Over the maximum altitudinal range encountered on Earth (about 8,800 m), however, the error in the measurement of mass by this method (about 0.3%, J. Black pers. comm.) is much smaller than the precision of many balances currently in use and thus can be disregarded.

Biologists usually require measurements of mass and obtain these indirectly by the determination of weight. For consistency, and to avoid potential confusion (e.g. C. J. Pennycuik 1986, *Proc. Intern. Conf. Comp. Physiol.* in press), I suggest that the term mass be used in preference to weight, when this type of data is reported.

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Why Hummingbirds Hover: A Commentary

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A model developed by Pyke (1981) suggested small hummingbirds should hover while larger species, such as many sunbirds and honeyeaters, should perch.

The model predictions are based on the rate of net energy gain maximization from feeding. Energy costs for hovering increase with body size more rapidly than do costs for perching. Although it always costs more to hover, the net rate of energy gain can be higher for a small bird if it can forage more quickly by hovering than by perching. Perching is predicted

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for large birds because the advantage gained from spending less time feeding while hovering is off-set by the higher energy costs to hover (Pyke 1981).

Miller (1985) studied individuals of two small hummingbird species (*Archilochus colubris*, about 3.5 g; *Orthorhynchus cristatus*, about 3.0 g). The experiments were designed to test if hummingbirds would persist in hovering or would use a perching device often not available to them from the plants they visit. The birds Miller studied almost always perched to feed. The results implied that the theory based on the rate of net energy gain maximization (popularly called "optimal foraging theory") does not apply and that the lack of perches provided by plants for most hummingbirds forces the birds to hover with a cost they otherwise would avoid. I suggest this is not necessarily the case because the distance the birds travel to reach the feeders can influence whether they should perch or hover when they feed.

The theory of "central place" foraging (Orians and Pearson 1979) proposes that animals should incorporate the time and energy costs to travel from a central place, such as a non-feeding perch, to a food source and back. Sample calculations will illustrate the different predictions based on distance. The power for forward flight for a 3.0-g hummingbird is about 0.637 W, the power for hovering is about 0.75 W (Wolf and Hainsworth 1971), while the power for perching is about 0.157 W (Hainsworth and Wolf 1978). Let a hummingbird obtain 62.8 J of energy from a feeder on a visit and assume it takes 1.0 s at the feeder if it hovers but 1.10 s if it perches. If the 3.0-g hummingbird flies 20 m round-trip from perch to feeder and back at a flight speed of 2 m/s, the total time if it perches is 11.1 s, the total cost if it perches is 6.545 J, and the rate of net energy gain is $56.25/11.1 = 5.07$ J/s. If the hummingbird hovers, the total time is 11.0 s, the total cost is 7.122 J, and the rate of net energy gain is $55.68/11.0 = 5.06$ J/s. For this case perching is marginally more efficient. Even if the difference is not detected by the birds, they may adopt the least energy-demanding behavior and perch instead of hover.

Now consider the case where distance is shorter. If round-trip distance is 4 m, the total cost with perching is 1.447 J and the rate of net energy gain is $61.35/3.1 = 19.79$ J/s. The total cost with hovering is 2.024 J, and the rate of net energy gain is $60.78/3 = 20.26$ J/s. Here, hovering is the more effective be-

havior, and as distance decreases hovering becomes even more effective as a behavior to maximize the rate of net energy gain (Wolf and Hainsworth 1983).

Whenever perching takes longer for feeding than hovering, very small distances should produce hovering and very long distances should produce perching. It is not clear how far away the hummingbirds had their "central place" in Miller's study. The distance may have been considerable for the *Archilochus* because feeders were placed in the middle of a 40 × 40-m mowed field.

Miller's experiments are interesting, but they should be designed to evaluate the predicted behavior: that is, hovering where distance from a non-feeding perch to a feeder is short. The theory based on the rate of net energy gain maximization predicts what Miller observed for long distances. If the behavior can be switched back and forth as distance is varied, then the rate of net energy gain maximization model will be supported. If hummingbirds persist in perching even at very short distances and feeding rates are longer for perching, then the rate of net energy gain maximization model will be falsified.

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