

Optimizing Migration in a Reluctant and Inefficient Flier: The Eared Grebe

J. R. Jehl Jr¹, A. E. Henry² and H. I. Ellis³

1 Introduction

Over the past several decades optimality theory (Krebs and Davies 1978) has been endorsed by many biologists (but see Gould and Lewontin 1979 and Pierce and Ollason 1987). In a comprehensive review of optimal migration, Alerstam and Hedenström (1999) discussed theoretical aspects of flight and behavior (e.g., flight speed and power, fuel deposition rates, fuel loads, departure rules) that birds might adopt to maximize their individual fitness. They also acknowledged the need for critical studies based on the natural history of individual species to test theoretical concepts.

In theoretical discussions optimal often takes on the connotation of “ideal,” even though it is a relative term meaning doing the best you can under specific circumstances. To understand what is optimal for any species requires knowledge of the evolutionary and natural history constraints it carries as baggage. Such limitations are implicit in the discussion of many species that fly and migrate strongly, such as waterfowl, hawks, and shorebirds (e.g., Butler et al. 1999; Farmer and Wiens 1999; Fuller et al. 1999). Ideas about what may be optimal for less competent fliers are rarely articulated.

The eared grebe (*Podiceps nigricollis*) serves as an extreme case of the challenges to migration faced by a species that flies inefficiently. Grebes are among the least accomplished of avian aerialists, and some modern forms (e.g., *Podilymbus gigas*, *Rollandia microptera*) have become secondarily flightless. The eared grebe, though still capable of flight, avoids flying whenever possible. For all practical purposes it flies only to migrate (Jehl 1988, 1997). Incapable of flight for months at a time, it has the longest non-flying period of any North American bird, perhaps totaling 9 to 10 months over the course of a year (Cullen et al. 1999). Yet, its existence depends on its ability to fly as much as 6000 km each year to reach high-yield, seasonal environments that are exploitable by few other species (Jehl 1994a). In comparison with that of typical migrants, its optimal migration would seem to be far less than

¹ Research Associate, Division of Birds, National Museum of Natural History, Smithsonian Institution, Washington, DC, 20560 USA, e-mail: grebe5k@cs.com.

² California Department of Fish and Game, Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, California 92037 USA.

³ Department of Biology, University of San Diego, San Diego, California 92110 USA.

ideal. By adapting its behavior to deal with severe constraints, it has not only been able to retain migration as a way of life but has become by far the most abundant grebe in the world (Jehl 2001).

2 Constraints and Costs

At all seasons, the eared grebe's diet mostly comprises small invertebrates (Cullen et al. 1999). Accordingly, its distribution and movements in the non-breeding season are controlled by the timing of prey availability of localized yet abundant resources in certain hypersaline lakes and other marine habitats. A further constraint is that grebes fly willingly only after dark. This minimizes the risk of predation by raptors, but limits the distance a bird can cover in a single flight.

The dominant constraint is the high energetic cost of flight. This results from compromises in the morphology of birds that are primarily designed for diving but which must also remain volant (Storer 1960; Croll et al. 1991; Ellis and Gabrielsen 2001). With short broad wings, large feet that extend in flight, and a chunky body whose girth is expanded by large fat stores carried at the start of migration, eared grebes have inherent high drag and a wing-loading (149 Pa; Jehl 1994b) that exceeds that of all but 1 of 27 species considered by Rayner (1985; common eider, *Somateria mollissima*, 194 Pa).

To obtain flight costs, we reanalyzed data (Jehl 1994b) on the mass lost by migrants killed in two separate downings on a single night in southern Utah, using the following information. (1) The average mass loss of grebes was 7.4 g h^{-1} . (2) The flight speed was 58.7 km h^{-1} , based on direct measurements of migrants at Great Salt Lake and on radar observations (S. A. Gauthreaux and J. R. Jehl unpubl.). (3) The flight path of the birds between departure and downing was a straight line, as further indicated on radar. (4) Weather reports indicated little to no wind at the altitudes at which grebes migrate. (5) We (H.I. Ellis and J. R. Jehl, unpubl.) measured the BMR of migrating grebes ($N = 7$; mass = $294.3 \pm 16.3 \text{ g}$) in postabsorptive condition captured in southern Wyoming and found it to be $22.5 \text{ J g}^{-1} \text{ h}^{-1}$ ($= 1.12 \pm 0.16 \text{ mL O g}^{-1} \text{ h}^{-1}$, using 20.1 J/mL O_2), which was not significantly different from that determined for post-migratory grebes captured at staging areas in early autumn. Mass-specific BMR for adult grebes in fall staging condition is independent of body size (H. I. Ellis and J. R. Jehl, unpubl.). Assuming this is true of migrants as well, for a 389-g grebe (the average mass of grebes downed at Minersville, Utah) we used a BMR value of 8.76 kJ h^{-1} or 2.43 W (3.0 % less than estimated in Jehl 1994b).

Until recently, biologists have assumed that migration is fueled entirely by fat. However, Jenni and Jenni-Eiermann (1998, 1999) argued that protein is also required, at least to renew enzymes of the citric acid cycle. In very fat birds, like departing grebes, protein contribution to energy consumption