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ADDITIONAL EVIDENCE OF NOCTURNAL MIGRATION BY YELLOW-RUMPED WARBLERS IN WINTER¹

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Migration is a response to changing environmental conditions (Gauthreaux 1982). Migratory behavior spans a continuum from highly fixed behavior (obligate migration) to very flexible behavior (facultative migration). Whereas facultative migration occurs in response to deteriorating environmental conditions, obligate migration appears to be fundamentally a result of an endogenous, circannual program (see Gwinner 1986 for a recent review). Even obligate migrations, however, are not performed entirely without integration of environmental information. For example, migrants make daily decisions to migrate or not to migrate based upon environmental factors such as weather conditions, food and water availability at stopover sites, and competition (e.g., Rappole and Warner 1976, Richardson 1978, Mehlum 1983, Biebach 1985, Gwinner 1986, Biebach et al. 1986).

The degree to which migratory behavior is subject to environmental influence appears to be quite variable (Terrill and Ohmart 1984). There is evidence that at least some species of annual, migrant passerines facultatively extend migration after the fall migratory period if environmental conditions become unfavorable for overwinter survival at a particular locality (Perdeck 1964, Niles et al. 1969, Moreau 1972, Lack 1983; Terrill and Ohmart 1984; Terrill 1987, in press). Presumably, the ability to perform facultative migrations enables these birds to respond to relatively unpredictable winter environments by migrating in an appropriate direction if conditions necessitate it.

Patterns of migration and distribution of Yellow-rumped Warblers (*Dendroica coronata*) indicate that they switch from an obligate phase to a facultative phase over the course of fall migration (Terrill and Ohmart 1984). Winter populations shift southward if conditions become unusually severe. When placed in Emlen funnels (Emlen and Emlen 1966), Yellow-rumped Warblers showed southerly nocturnal orientation into early January (after which no birds were tested). While the orientation data support the hypothesis that winter movements like fall movements are nocturnal, the evidence is indirect.

Here we present direct evidence that winter movements by Yellow-rumped Warblers are in fact nocturnal.

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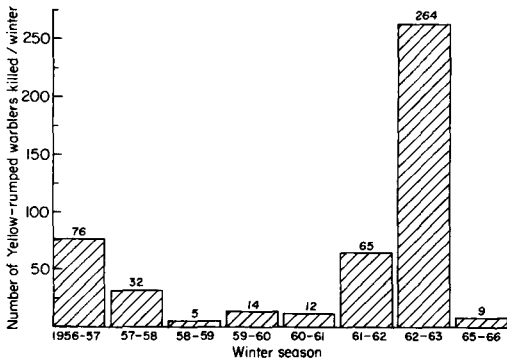


FIGURE 1. Number of Yellow-rumped Warblers killed per winter (December 15 to February 20) at WCTV tower, Leon County, Florida.

nal. Daily records of nocturnal tower kills in Florida collected by the late Herbert L. Stoddard, Sr. and associates indicate that: (1) nocturnal migration by Yellow-rumped Warblers can occur every month of the winter, and (2) the number of warblers migrating in winter varies greatly between winters.

Stoddard and associates recorded species, numbers, and locations of night migrants (only individuals killed at night are included here) killed at the 304-m WCTV tower located on the Tall Timbers Research Station, Leon County, Florida on a daily basis (Stoddard and Norris 1967). We examined records spanning a period from 15 December through 20 February, 1956-1963 and 1965-1966.

Large numbers of nocturnally migrating Yellow-rumped Warblers were killed during fall and spring each year (Crawford 1981a). Substantial mortality also occurred in winter, but not annually (Fig. 1). With respect to month, 67% of the mortality occurred in late December, 27% in January, and 6% in February. The distribution of dead birds around the base of the tower correlated with wind direction in the same manner as during fall migration (as described in Crawford 1981b).

Winter migrations by Yellow-rumped Warblers were generally associated with major cold fronts. The greatest mortality occurred between 16 December and 29 December 1962 when some 200 warblers were found at the base of the tower. This major movement corresponded to the most severe, prolonged freeze of the 50 years preceding 1962 (U.S. Department of Commerce 1956-1966).

Although most migration corresponded to the passage of major cold fronts, this pattern was not without exception. The winter of 1956-1957 was quite mild, yet tower kills did occur (Fig. 1). This mild period, however, did follow an unusually cold November which may have affected food availability later that winter.

Stoddard's daily records provide direct evidence that midwinter movements by Yellow-rumped Warblers are nocturnal. These data do not, however, preclude the possibility of diurnal movements as well. In contrast to fall migration, major winter movements are apparently not annual. The association between midwinter migration, unusually cold weather, and changes in food availability (Terrill and Ohmart 1984) support the con-

cept that nocturnal migration by Yellow-rumped Warblers is highly facultative at this time of year.

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PROTEIN COSTS OF THE PREBASIC MOLT OF FEMALE MALLARDS¹

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Key words: Mallard; *Anas platyrhynchos*; molt; protein costs; wintering ecology.

The nutritional requirements and physiological mechanisms of avian molt and the relationship of molt to other ecological requirements in birds are poorly understood. Relative to other nutritionally costly events in the annual cycle (e.g., reproduction and migration), the efficiency of feather synthesis is extremely low (King 1981, Murphy and King 1984a). Gavrilov and Dolnik (1974) suggested that this inefficiency was caused by an aminostatic regulation of food intake which allows acquisition of sufficient cysteine and cystine for construction of feather keratins. Recent investigations failed to confirm this "aminostatic hypothesis," however, and instead suggested that overall nitrogen retention (of the correct amino acid spectrum), not specific sulfur amino acid (SAA) concentrations, may be a more important constraint on feather synthesis, and that both protein and SAA requirements can be met through dietary intake without depleting tissue proteins (Murphy and King 1984a, 1984b, 1984c, 1985). Also, studies of wild Eurasian Bullfinches (*Pyrrhula pyrrhula*) (Newton 1968), the Canada Goose (*Branta canadensis*) (Raveling 1979, Mainguy and Thomas 1985), the Lesser Snow Goose (*Chen caerulescens*) (Ankney 1979), Brant (*Branta bernicla*) (Ankney 1984), and Mallard (*Anas platyrhynchos*) (Heitmeyer 1985) indicate that molting birds typically obtain protein and SAA required for feather synthesis from food.

The actual protein intake needed to synthesize feathers is not known for any bird in the wild, and only White-crowned Sparrows (*Zonotrichia leucophrys*) have been intensively studied in the laboratory in an attempt to calculate protein costs (Murphy and King 1982, 1984a, 1984b). Studying molt with captive birds has been hampered, however, because captive birds often

do not undergo a typical molt if (1) photoperiod, temperature, food quantity and quality, and social settings are artificial, (2) birds are unnaturally constrained, or (3) locations are distant from the site where molt would occur naturally (West 1968, Blackmore 1969, King 1974, Chilgren 1978).

In contrast to laboratory investigations, studying the cost of molt in the wild is hampered because variables affecting the bird and its environment are not controlled, and the intake and output of nutrients are not measured. Despite these problems bioenergetic costs can be accurately estimated from birds collected in the wild if sufficient data exist on the pattern, timing, and duration of synthesis, and composition of the synthesized product (e.g., estimates of bioenergetic costs of reproduction, Ricklefs 1974, Drobney 1980). Herein, I estimate the protein cost of the prebasic molt of adult female Mallards in late winter using birds collected in the wild.

METHODS

Adult female Mallards were collected from January through March 1981 and October through March 1981 to 1982 and 1982 to 1983 in the Mingo Basin of southeastern Missouri ($n = 175$), and during March 1981 and 1983 at the Ted Shanks Wildlife Management Area in northeastern Missouri ($n = 8$). Similar numbers of Mallards were collected each month (Heitmeyer 1987). Collected birds represented all stages (i.e., 0 to 100%) of molt completion and were representative of the population present in the Mingo Basin (Heitmeyer 1985, in press). All feathers were plucked from each bird and the percentage completion of the prebasic molt in each of 18 feather areas determined as described in Heitmeyer (1987). The mass (g, dry weight) of all feathers replaced (via the prebasic molt) on each bird when collected was calculated by multiplying the percentage of each feather area that had molted into the basic plumage by the dry mass of the completely replaced basic plumage of each area and summing all areas. The dry mass of the basic plumage was determined by plucking and drying (80°C to a constant weight) all feathers from the 18 feather areas, plus the wing, from six adult female Mallards that had completed the pre-

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