

FACTORS INFLUENCING THE ONSET OF SPRING MIGRATION IN MALLARDS

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Abstract.—Our knowledge of factors causing intraspecific variation in timing of spring migration in waterfowl is poor, despite its potential importance for understanding reproductive patterns and the importance of the non-breeding period to reproductive success. I used radio telemetry to document initiation of spring migration by female Mallards (*Anas platyrhynchos*) wintering in Arkansas in 1989. I tested whether age, molt status, or physiological condition explained observed intraspecific variation. Migration date was independent of female age or physiological condition at time of capture in January, but not molt. Late-molting females migrated later than early-molting females. Results were consistent with the hypothesis that spring migration is influenced by the timing of earlier winter life-history events.

FACTORES QUE INFLUYEN EN EL INICIO DE LA MIGRACIÓN EN *ANAS PLATYRHYNCHOS*

Sinopsis.—Se conoce poco sobre los factores que causan variación intraespecífica en el inicio de la migración primaveral, no empee su potencial importancia para entender el patrón reproductivo y la importancia del periodo no-reproductivo en el éxito reproductivo. Durante el 1989, se utilizó radiotelegrafía para documentar el inicio de la migración primaveral por parte de hembras de *Anas platyrhynchos* que estaban pasando el invierno en Arkansas. Se examinó, si la edad, estado de la muda, o condición fisiológica podrían proveer explicación para entender la variación intraespecífica en el inicio de la migración. Se encontró que la fecha de migración es independiente de la edad o condición fisiológica del individuo al momento de su captura durante el mes de enero, pero no así la muda. Las hembras que mudaron tarde migraron más tarde que aquellas que mudaron tempranamente. Los resultados fueron consistentes con la hipótesis que la migración primaveral es influenciada por el periodo particular en que ocurren eventos particulares en la biología de las aves.

Mallards (*Anas platyrhynchos*) undergo a protracted exodus from wintering areas beginning in mid-February and lasting until early April (Bellrose 1976). However, little effort has been made to understand what proximate factors influence this variation in spring migration chronology for waterfowl. Such effort could increase our understanding of waterfowl life-history strategies (Hepp 1984, Rohwer 1992), and help explain how recently identified cross-seasonal influences on life-history events operate (Heitmeyer and Fredrickson 1981).

One idea, the Staggered Cost Hypothesis, proposes that the timing of annual events in the life cycle of birds ultimately evolved to minimize the overlap of energetically demanding activities (King 1974, Payne 1972). This hypothesis can be modified into a Staggered Event Hypothesis (SEH) which states life-history events occur in a predictable sequence whose proximate timing is dependent on physiological condition (modified from Heitmeyer 1988, Lovvorn and Barzen 1988). The storage of endog-

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enous energy is an important late winter, pre-migration event (Blem 1980, McLandress and Raveling 1981) that could be delayed by the need to allocate resources to activities such as molt (Owen 1970). If so, the SEH may help explain proximate variation in the chronology of spring migration.

Based on the observed progression and variation in timing of winter life-history events among Mallards (endogenous lipid storage > pair formation > initiation of prebasic molt > premigration fattening; Heitmeyer 1988), the SEH yields testable predictions about how age, molt status, and physiological condition affect the timing of spring migration. Specifically, birds initiating prebasic molt earlier in winter should initiate spring migration earlier; birds in better physiological condition should migrate earlier; and because older females are dominant over young females and may out compete young birds for limited resources (Heitmeyer 1988), adult females will migrate earlier than young females.

To date, studies of waterfowl during spring migration have relied on observations of unmarked birds (LeGrange and Dinsmore 1989) or samples of birds collected from migration areas (Heitmeyer 1987, Lowvorn and Barzen 1988). While this approach is valuable, it also is limited because the history of collected or observed birds (where the bird has come from, how long it has been at a particular stopover area) is unknown. An alternate approach is to follow a specific cohort of birds over time. Here I use data from radio-marked female Mallards to document their departure from a wintering area and to evaluate the SEH as an explanation for intraspecific variation in departure date.

METHODS

I trapped 50 female Mallards at two sites in east-central Arkansas during 3–24 Jan. 1989 using rocket nets and swim-in traps baited with corn or milo. Following capture, I aged females (adult vs. immature) using plumage characteristics (Krapu et al. 1979) and weighed them to the nearest 10 g. I measured flattened wing chord (mm) and divided body mass by wing chord to calculate a condition index for each bird (Johnson et al. 1985). Females were assigned to one of three molt categories (Early, Mid, Late) by visually inspecting plumage replacement in several feather tracts (Heitmeyer 1987). Early and Mid molting birds were > 50% and 1–50% completed with prebasic molt at the time of capture, respectively. Birds assigned to the Late category had not begun prebasic molt. I marked birds with a standard U.S. Fish and Wildlife Service metal leg band and a back-mounted, harness-attached radio transmitter (Dwyer 1972). Transmitters averaged $22 \pm .01$ (SE) g and no transmitter exceeded 2.5% of female body mass.

After release, I located Mallards using antennae mounted on trucks and planes at least weekly from 3 d after release to 18 March. Searches were conducted primarily in the Mississippi Alluvial Valley (MAV) of Arkansas (see Reinecke et al. 1992), but additional searches were conducted in Kentucky, Louisiana, Mississippi, Missouri, and Tennessee. Birds were

located at least weekly. Birds suspected of being dead were located on foot to confirm their status. During 17–18 March extensive systematic (parallel transect) searches were flown throughout the MAV in Arkansas to locate all remaining birds. Birds were detected moving north, out of the MAV, using antennae mounted on top of a 10-m communication tower at Duck Creek Wildlife Conservation Area in southeast Missouri (monitored mostly after 16 March).

To test predictions of the SEH, I divided birds into two groups. Individuals that could no longer be located in the MAV on 17 March were presumed to have migrated and classified as early migrants ($n = 23$). Individuals remaining in the MAV on 17 March were classified as late migrants ($n = 21$). This cutoff date was well in advance of predicted battery failure dates for any bird, thus it is unlikely that radio failure contributed significantly to results. Likewise, radio reception was unlikely to change significantly if an individual died. This in conjunction with the extensive aerial transects flown on 17–18 March make it unlikely that birds categorized as early migrants were in fact dead and simply not detected.

I used a *t*-test to test if physical condition of adults and immatures differed at capture or if migration date differed by physical condition. Variation in physical condition among molt categories was tested with one-way analysis of variance. Contingency table analyses (X^2) were used to test for dependencies among age, trapping location, molt status, and migration date. Sample sizes prohibited using log-linear analyses on categorical data, therefore, all analyses were separate 3×2 tests and no three-way interactions were considered. Statistical tests were performed using SAS (SAS Inst. Inc. 1987) and power calculations followed Cohen (1977).

RESULTS

Birds not located after an initial 3-d radio adjustment period were excluded, leaving 44 birds available for analysis. Condition indices were similar between age ($t = 0.85$, $df = 42$, $P = 0.40$) and molt status ($F_{2,42} = 2.19$, $P = 0.18$) groups at time of capture (Table 1). In addition, molt status was independent of age ($X^2 = 0.93$, $df = 2$, $P = 0.63$) and trapping location ($X^2 = 0.95$, $df = 2$, $P = 0.62$).

Marked birds began leaving Arkansas in mid-February with almost half gone by mid-March. Eight birds were detected migrating north past the monitoring tower in southeast Missouri between 17 March and 1 April. A ninth bird heard moving north on 25 February was subsequently re-located in Arkansas on 18 March. Migration date (early or late) was independent of trapping location ($X^2 = 1.59$, $df = 1$, $P = 0.21$), age ($\chi^2 = 0.35$, $df = 1$, $P = 0.56$) and condition index ($t = 1.37$, $df = 42$, $P = 0.18$) at the time of capture but not molt status (Table 2, $X^2 = 6.21$, $df = 2$, $P = 0.045$). To identify specific differences among the three molt categories and migration, I applied Fisher's exact test to all possible 2×2 combinations of the original 3×2 table. Proportions of migrants in the early and

TABLE 1. Condition indices ($\bar{x} \pm SE$), molt indices, and sample distributions for female Mallards trapped at two sites in the Mississippi Alluvial Valley of east-central Arkansas during January 1989.

	Location ^a (n)		Condition index (mass [g]/wing chord [mm])	Molt category ^b (n)		
	1	2		Early	Mid	Late
Age						
Adult	3	18	4.01 \pm 0.06	6	11	4
Immature	16	7	3.94 \pm 0.05	4	15	4
Molt status						
Early	3	7	3.96 \pm 0.08	—	—	—
Mid	12	14	3.92 \pm 0.05	—	—	—
Late	4	4	4.15 \pm 0.09	—	—	—

^a 1 = White River National Wildlife Refuge; 2 = Peckerwood Lake.

^b Early = early molting females, prebasic molt > 50% complete; Mid = females from 1-50% completed with pre-basic molt; Late = female had not yet initiated prebasic molt.

late categories differed between Mid and Late molting females ($X^2 = 5.89$, $df = 1$, $P = 0.01$), other comparisons did not differ (P 's > 0.28).

DISCUSSION

Arguably, measurements taken on birds in January may not be reliable predictors of status later in March. In particular, the physiological condition of waterfowl is known to fluctuate during winter as a result of seasonal endogenous rhythms (Loesch et al. 1992, Reinecke et al. 1982), specific physiological events like prebasic molt (Heitmeyer 1988), and short term changes in food availability (Loesch and Kaminski 1989). Such short-term variation may explain the lack of association between body condition in January and migration date, and suggests condition indices are probably not a reliable predictor of future status when considered alone. The potential for capture and handling to break pair bonds (possibly altering foraging efficiency by changing dominance status) and the

TABLE 2. Condition index ($\bar{x} \pm SE$), age, and molt status of early- and late-migrating radio-marked female Mallards trapped at two sites in the Mississippi Alluvial Valley of east-central Arkansas during January 1989.

Migration chro- nology	Condition index (mass [g]/wing chord [mm])	Age (n)		Location ^a (n)		Molt status ^b (n)		
		Adult	Imm.	1	2	Early	Mid	Late
Early	3.92 \pm 0.05	11	10	7	14	4	16	
Late	4.02 \pm 0.06	10	13	12	11	6	10	7

^a 1 = White River National Wildlife Refuge; 2 = Peckerwood Lake.

^b Early = early molting females, prebasic molt > 50% complete when captured; Mid = females between 1-50% completed with prebasic molt when captured; Late = females had not initiated prebasic molt when captured.

presence of a transmitter and harness to alter behavior and physiological condition (Rotella et al. 1993 and references therein) is acknowledged. The extent to which this may have altered the progression of winter life-history events like molt is unknown.

Molt status measured at capture was related to spring migration chronology in Mallards. Only 13% of females categorized as Late-molters in January initiated migration before 17 March compared to 62% of Mid-molting and 40% of Early-molting females. Failure to detect an age effect on migration might be viewed as inconsistent with the SEH. However, condition indices and molt status did not differ between adults and immatures at the time of capture. Therefore, the SEH predicted no age-related differences in migration timing. Admittedly, analyses were based on small sample sizes and had low statistical power (probability of Type II error > 90%). Larger sample sizes might have detected an age effect. However, the fact that molt was significantly related to migration chronology given similar sample sizes might indicate the relative importance of these two variables for explaining the variation observed.

All species do not delay prebasic molt until after pairing (e.g., Canvasbacks [*Aythya valisineria*], Lovvorn and Barzen 1988), and many species of waterfowl (including Mallards) do simultaneously undergo molt and migration (e.g., Austin and Fredrickson 1986, Heitmeyer 1988). These facts led Lovvorn and Barzen (1988) to conclude that molt represents an additional energetic cost, but not enough of a cost to prevent waterfowl from meeting the costs of additional non-breeding life-history events simultaneously. They suggested molt is controlled more by photoperiodic responses than physiological state (Lovvorn and Barzen 1988) and, therefore, has little value as a predictor of winter status or presumably as a predictor of spring migration.

Several lines of evidence indicate initiation of prebasic molt is related to physiological condition for Mallards. First, prebasic molt is initiated some time during late-November to early-March (Heitmeyer 1987). Because this wide time frame encompasses the winter solstice, it is hard to envision proximate control of prebasic molt being closely regulated by photoperiod. Second, only in one year of exceptionally good habitat conditions were any unpaired females collected that had initiated prebasic molt (Heitmeyer 1987). Third, prebasic molt takes longer to complete during years of poor habitat conditions (Heitmeyer 1987). These facts, plus results from this study, support the use of molt progression as an indicator of winter condition and are consistent with the Staggered Events Hypothesis as an explanation for differences in the initiation of spring migration for Mallards.

My reliance on only one year of data and the lack of replication in the study design prohibit me from making strong inferences and dictate that conclusions reached here be viewed cautiously. Although my data are generally consistent with the SEH, one inconsistency was apparent. Strictly speaking, the SEH predicted that Early molting birds should have migrated earlier than the Late molting birds. In fact, only the comparison

between Mid and Late molting categories was statistically different. The fact that only 40% of the Early molting females were classified as early migrants suggests that a strict sequential progression of winter life-history events culminating in spring migration is unlikely for Mallards. More likely, physiological condition is part of a suite of factors that influences the onset of migration (Baker 1978, Bellrose 1974, Ketterson and Nolan 1983). Additional data are needed to test the validity of the Staggered Event Hypothesis. For example, while the evidence that initiation of pre-basic molt is condition-dependent for Mallards is fairly strong (Heitmeyer 1987, 1988), no study has documented that prebasic molt prohibits, or more likely impedes, premigrational fattening (Owen 1970). This is the proximate mechanism proposed by the SEH for influencing migration. Finally, I was unable to study how the variation observed in this study related to behavior during migration, arrival chronology on breeding areas, breeding latitude, and potentially reproductive success. Additional research, possibly attempting to follow cohorts of birds from wintering to breeding areas would provide valuable knowledge to our understanding of the factors influencing migration strategies in waterfowl.

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