

SHORT COMMUNICATIONS

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ABSENCE OF BREEDING READINESS IN NEOTROPICAL AND LONG-DISTANCE MIGRANT LANDBIRDS DURING SPRING STOPOVER¹

GREGORY A. JONES² AND CHRISTOPHER J. NORMENT

Department of Biological Sciences, SUNY College at Brockport, Brockport, NY 14420

Abstract. We investigated breeding readiness of selected migrant species captured at a known stopover site in western New York during the spring of 1995 and 1996. A total of 775 individuals representing 14 species were examined for outward physiological indication of male breeding readiness measured by relative size of cloacal protuberance. Only 2 of the 775 individuals exhibited a cloacal protuberance, both being captured in 1996; one Ruby-crowned Kinglet (*Regulus calendula*) and one Swainson's Thrush (*Catharus minimus*). Cloacal lavage samples were taken from 22 White-throated Sparrows (*Zonotrichia albicollis*) and 26 Swainson's Thrushes during the spring of 1996. None of the migrating individuals lavaged exhibited presence of cloacal sperm regardless of species, sex, time, or date of capture. Poor energetic condition was typical of these captured migratory landbirds. Depleted energetic stores may explain the lack of early sperm production in migrants at this stopover site.

Key words: *early sperm release, gonadal recrudescence, Neotropical migrants, reproductive timing, stopover ecology.*

Knowledge of the breeding biology and reproductive timing of many birds breeding at high latitude is limited due to restricted access to their breeding grounds (Quay 1985a, 1989). Consequently, it has been suggested that much can be learned by intensive study of temperate breeding birds passing through stopover sites as they proceed to summer nesting grounds (Blancher et al. 1993). Passerine species differ in physiological readiness for breeding (Quay 1985b, Briskie 1996). Early sperm release and enlarged cloacal protuberance in male spring migrants occur in several species of American thrushes and wood warblers (Quay 1985b, 1986), and inseminated Tennessee Warbler (*Vermivora celata*) females have been captured well south of their nesting grounds (Quay 1989). Moore and

McDonald (1993) suggest that if long-distance migratory landbirds commonly mate during migration, such behavior would have important implications for studying avian mating systems and understanding the relationships among different phases of a migrant's annual cycle. However, in small passerines such as Tennessee Warblers and Blackpoll Warblers (*Dendroica striata*), females en route to their breeding grounds lack fully enlarged uterovaginal sperm-storage tubules (Briskie 1996), structures necessary for stored spermatozoa to remain viable for long periods of time while en route (Hatch 1983, Birkhead and Møller 1992). There are few studies besides those of Quay that examine breeding readiness in temperate migrant passerines.

During a two-year study of the stopover ecology of Neotropical and long-distance migrants along the south shore of Lake Ontario, New York, we examined possible breeding readiness, occurrence of enlarged cloacal protuberance, and incidence of early sperm release in males, and incidence of insemination in females, of selected spring migrant species. Data from this study are valuable in augmenting knowledge of the breeding biology and reproductive timing of these species and in elucidating the frequency of mating en route during spring migration.

METHODS

We examined the breeding condition in males of 14 species of Neotropical and temperate landbird migrants captured with mist nets at the Braddock Bay Bird Observatory on the south shore of Lake Ontario (43°19'N, 77°43'W), approximately 24 km northwest of Rochester, New York, during spring migration of 1 May–1 June 1995 and 22 April–1 June 1996. Species selected for examination were those with a low probability of nesting at or near this study site as determined by distribution maps in Andrie and Carrol (1988). An additional criterion for selection was the probability of obtaining reasonable numbers of captures as determined by past capture data from this study site (Brooks 1994).

Presence of a cloacal protuberance is an indication of male breeding readiness in selected species (Proctor and Lynch 1993). Extent of cloacal protuberance was classified utilizing a three-point scale described by Pyle et al. (1987), with 0 representing nonbreeding, 1 representing partial breeding, and 2 representing full-breeding size. All migrant males exhibiting sexual size

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² Current address: Department of Wildlife Ecology and Conservation, University of Florida Institute of Food and Agricultural Sciences, 303 Newins-Ziegler Hall, Gainesville, FL 32611-0430, e-mail: gajo@gnv.ifas.ufl.edu

or plumage dimorphism were classified upon capture. All individuals of monomorphic species were examined as well to ensure that all possible males captured would be classified.

Cloacal lavage samples were taken during spring migration 1996 from White-throated Sparrows (*Zonotrichia albicollis*) and Swainson's Thrushes (*Catharus ustulatus*), utilizing methods of Quay (1984). These species were chosen due to their relatively large size and as representatives of a Neotropical migrant (Swainson's Thrush) and a temperate migrant (White-throated Sparrow). Additionally, previous evidence of early sperm release has been found in male Swainson's Thrushes prior to arrival at, and south of, its geographic nesting range (Quay 1986). Individuals chosen for cloacal lavage included males and females displaying sexual size dimorphism as well as several individuals that could not be sexed reliably utilizing criteria given by Pyle et al. (1987). Individuals sampled were chosen at random from those captured at various times of day during the study period. On each successive day of the study period, we lavaged several individuals so that we could compare any differences between individuals passing through this stopover site at increasingly later dates during spring migration. Disposable tapered plastic micropipet tips fitted with a small rubber squeeze bulb were utilized to extract lavage samples. Two lavage samples were prepared from each bird within 30 min of capture by the same researcher during both sampling periods. The first sample was associated with minimal stimulation of the bird. A second sample was taken immediately following a gentle bilateral anterior-to-posterior stroking of the skin anterior to the cloacal vent. The purpose of this stroking was to attempt to bring down any sperm that might be in the glomus seminale of males or in the proximal regions of the reproductive tract of females. Suspensions of cloacal samples were deposited within the center of a wax pencil ringed area on each slide, air dried, and stored in slide boxes (Quay 1984). In the laboratory, each day's slides were examined microscopically that evening for sperm and scored as either sperm present or not present within each sample.

RESULTS

A total of 775 individuals representing 14 species were examined for outward physiological indication of male breeding readiness (Table 1). No individuals examined in 1995 exhibited a cloacal protuberance. Only two individuals exhibited a cloacal protuberance in 1996; one Ruby-crowned Kinglet (*Regulus calendula*) captured on 2 May and one Swainson's Thrush captured on 21 May. In both of these individuals the extent of protuberance was barely large enough to be classified as a 1, representing partial breeding size.

Lavage samples were taken from 22 White-throated Sparrows and 26 Swainson's Thrushes. For comparison with migrant lavage samples, a cloacal lavage also was taken on 22 May from a resident male American Robin (*Turdus migratorius*) exhibiting full cloacal protuberance. None of the migrating individuals lavaged exhibited presence of cloacal sperm regardless of species, sex, time or date of capture between 8 May and

1 June 1996. The male American Robin lavaged exhibited large numbers of sperm on both sample slides.

DISCUSSION

In this study we found virtually no evidence of preparation for breeding in male migrants, regardless of species, time, or date of capture. Surprisingly, this included individuals of species known to have breeding ranges near our study site in southern Ontario as well as those breeding at much higher latitudes. As cloacal protuberance is caused by the swelling of the vasa deferentia to accommodate sperm storage (Proctor and Lynch 1993), this lack of expansion suggests that high levels of sperm production had not begun in any of these individuals.

Quay (1989) and Moore and McDonald (1993) suggested that there may be an adaptive advantage to early recrudescence of reproduction organs and reproductive activity for species nesting at high northern latitudes and subject to brief reproductive seasons. However, peak reproductive activities increase total daily energy expenditures by as much as 50% (Ricklefs 1974, Walsberg 1983). The lack of outward evidence of high levels of sperm production suggests that the energy demands of migration may limit gonadal recrudescence in these small passerines. If these species are income breeders, i.e., those species that base their reproductive strategy on resources ingested near the time of breeding, reproductive activities will be tied to available daily energy intake (Drent and Daan 1980). Therefore, reproductive activity can only begin if an individual's daily energy intake is increasingly allotted to these activities. In small female passerines the specialized sperm storage tubules (SST) are less than fully developed during spring migration (Briskie 1996). However, SST mature rapidly in migratory Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) shortly after arrival on the breeding grounds (Briskie 1994), again suggesting that reproductive readiness is limited by migratory energy demand.

Early sperm release occurs in several Neotropical and long-distance migratory landbirds during migration (Quay 1985a, 1985b, 1986, 1989). Additionally, mating behavior was suggested by the occurrence of inseminated females of two species of parulids, Blackpoll Warblers and Tennessee Warblers, well south of their nesting range (Quay 1989). Quay (1985b, 1989) found that the level of nutrition, indexed by simple body mass, appeared to be positively correlated to sperm release and insemination in these two species. The individuals examined by cloacal lavage in our study were in relatively poor energetic condition, as indicated by a predominance of low fat class scores (80.6% fell in the lowest 3 out of 6 fat classifications, $n = 1,277$). Low fat class scores suggest that energetic reserves, in the form of subcutaneous fat, were utilized during migration. If energetic stores were depleted, little energy would be available for sperm production, which may explain the lack of early sperm release in these migrants. The few birds with early stages of cloacal swelling observed during this study may have been individuals with energy reserves beyond those required for migratory activities.

Limitation of recrudescence of reproductive tissues

TABLE 1. Occurrence of cloacal protuberance found in 14 species of Neotropical and temperate landbird migrants ($n = 775$) during spring migration 1995 and 1996 at Braddock Bay Bird Observatory, near Rochester, NY.

Species	Spring 1995			Spring 1996		
	No. examined		No. exhibiting Cl. protuberance	No. examined		No. exhibiting Cl. protuberance
	Male	Unknown ^a		Male	Unknown ^a	
Yellow-bellied Flycatcher (<i>Empidonax flaviventris</i>)	0	7	0	1	22	0
Least Flycatcher (<i>Empidonax minimus</i>)	13	18	0	14	60	0
Ruby-crowned Kinglet (<i>Regulus calendula</i>)	64	0	0	37	0	1
Swainson's Thrush (<i>Catharus ustulatus</i>)	8	20	0	7	39	1
Grey-cheeked Thrush (<i>Catharus minima</i>)	0	9	0	0	5	0
Bay-breasted Warbler (<i>Dendroica castanea</i>)	2	11	0	2	6	0
Mourning Warbler (<i>Oporornis philadelphia</i>)	7	0	0	0	2	0
Blackpoll Warbler (<i>Dendroica striata</i>)	0	2	0	2	9	0
Tennessee Warbler (<i>Vermivora peregrina</i>)	1	6	0	1	2	0
Western Palm Warbler (<i>Dendroica palmarum</i>)	2	16	0	0	7	0
Wilson's Warbler (<i>Wilsonia pusilla</i>)	53	0	0	37	0	0
Lincoln's Sparrow (<i>Melospiza lincolni</i>)	0	30	0	0	10	0
White-throated Sparrow (<i>Zonotrichia albicollis</i>)	15	92	0	12	86	0
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	0	28	0	0	10	0
Totals	165	239	0	113	258	2

^a Sex unknown.

due to energetic demands during migration may not be the only explanation for inhibited breeding readiness. Proximate factors on breeding grounds such as average ambient temperature, habitat characteristics, and food availability influence reproductive timing in many passerine species (Delius 1965, Ligon 1974). Species breeding at high latitudes often encounter unpredictable environmental conditions upon initial arrival on their nesting grounds. If small long-distance migratory landbirds are income-breeders, there could be a disadvantage to arriving on breeding grounds having spent additional energetic demands on early reproductive activity, leaving no reserves for possible environmental stochasticity once there.

Poor energetic condition was typical of the long-distance migratory landbirds captured at this site during this study. Studies of stopover choice in migratory passerines have found that individuals may bypass potential stopover sites during spring migration if they possess ample energy stores (Moore and Kerlinger 1987, Kuenzi et al. 1991). This pattern also occurs in arctic shorebirds during spring migration (Gudmundsson et al. 1991). A decision to bypass the Braddock Bay stopover site also

may explain the absence of early sperm release in individuals occurring at this site. If early sperm release is indeed tied to energetic condition, we might expect individuals with high energy reserves, and therefore the greatest potential for early sperm release, to bypass this site during migration. Questions remain as to the adaptive importance of early recrudescence of reproduction organs and sexual activity during migration in long-distance migratory landbirds.

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SATELLITE TRACKING OF MAGELLANIC PENGUIN MIGRATION¹

DAVID L. STOKES AND P. DEE BOERSMA

Department of Zoology, Box 351800, University of Washington, Seattle, WA 98195,
e-mail: dstokes@u.washington.edu

LLOYD S. DAVIS

Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand

Abstract. We tracked four male Magellanic Penguins (*Spheniscus magellanicus*) from the beginning of their winter migration for periods ranging from three to six weeks. Upon leaving the colony at Punta Tombo,

Argentina where they had bred and molted, all four birds traveled northeast along the coast at speeds consistent with sighting and band-return data which suggest a round-trip winter migration in this species of up to several thousand kilometers. Three of the birds followed a similar route, moved at approximately the same rate, and were still moving northeastward at a

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