



## Is flight-calling behaviour influenced by age, sex and/or body condition?

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Migratory organisms face many challenges as they travel to take advantage of changing resources, exhibiting a variety of strategies to successfully move between locations. Birds are a model taxa for understanding migratory systems, relying on a multitude of cues and showing diverse behaviours, one of which is their propensity to give calls during migratory flight. However, this behaviour is understudied and may have implications in orientation, navigation and migration monitoring. Because a variety of migratory behaviours differ among and within species as a function of age, sex and body condition, we evaluated whether flight-calling behaviour was related to any of these variables. We studied flight-calling behaviour in four species of passage migrant warblers in captivity during autumn migration at Powdermill Avian Research Center (Rector, PA, U.S.A.) and Braddock Bay Bird Observatory (Greece, NY, U.S.A.). Our results demonstrate extensive variation in flight-calling behaviour by migrant warblers. When all species were combined, young birds were more likely to call and call at a higher rate than adults. All species-specific models were consistent in suggesting a higher propensity and rate of calling by young birds, although the black-throated blue warbler, *Setophaga caerulescens*, was the only species-specific model with significant age-related differences. When all species were combined, sex did not have a significant effect on either propensity or rate of calling. The effect of sex was inconsistent across species, and only magnolia warbler, *Setophaga magnolia*, males were significantly more likely to respond to calls than females. Surprisingly, body condition did not significantly affect the propensity or rate of calling. While our results reflect the complexity of flight-calling behaviour, our finding that young migrants consistently gave more calls has broad utility, particularly in quantitative migration monitoring. These results demonstrate the need for additional study to determine the selective forces influencing flight-calling behaviour.

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In response to seasonal changes in resources, migratory organisms frequently move hundreds, if not thousands, of kilometres to exploit ephemeral, variable or specific resources critical for survival and reproduction. Migratory organisms often rely on a diverse suite of navigation, orientation and behavioural cues to arrive with spatial and temporal accuracy (e.g. Bingman & Cheng, 2005; Chapman et al., 2010; Semlitsch, 2008; Zhu, Gegeer, Casselman, Kanginakudru, & Reppert, 2009). Studying behavioural strategies of migrants is challenging because migrants cover large expanses,

traverse challenging environments and move at heights or depths typically inaccessible to standard behavioural monitoring techniques. Capturing active migratory behaviours, beyond features of geographical positioning, typically require creative design and methodology. The study of migratory songbirds embodies many of these hurdles, and understanding behaviours exhibited during flight remains a primary challenge and frontier of migration research (e.g. Bridge et al., 2011; Chapman et al., 2015; Horton, Van Doren, Stepanian, Farnsworth, & Kelly, 2016). During migratory flights, many songbirds are known to give specific vocalizations made primarily, although not limited to, flight (Farnsworth, 2005, 2007). However, flight-calling behaviour is one of the least studied behaviours in migration biology, and is a behaviour that may have foundations in navigation and orientation, in addition to

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utility in migration monitoring. Field observations of flight calls in migrating songbirds demonstrate the prevalence of this behaviour (e.g. Evans & Mellinger, 1999; Evans & Rosenberg, 2000; Farnsworth, Gauthreaux, & van Blaricom, 2004; Horton, Shriver, & Buler, 2015; Larkin, Evans, & Diehl, 2002; Van Doren, Horton, Dokter, Klinck, Elbin, & Farnsworth, 2017). Flight calls are species specific, but there may be variation in flight calls between individuals and age and sex groups (Griffiths, Keen, Lanzone, & Farnsworth, 2016; Lanzone, Deleon, Grove, & Farnsworth, 2009) and populations (Sewall, Kelsey, & Hahn, 2004).

Although flight calls were recognized by the 1890s (Libby, 1899), we know very little about different factors that may affect the propensity and rate of these vocalizations by an individual bird (Farnsworth, 2005). While the structure of flight calls of many North American warblers have been documented and compiled (Evans & O'Brien, 2002), flight calls given in free-flight are generally devoid of information about the age and sex of the caller. This problem was overcome by Lanzone et al. (2009), who developed a novel method of documenting flight calls by playing flight calls to captive birds and recording their vocal response, thus collecting flight calls by birds of known species, age and sex. In an expansion of this method, Morris, Horton, Tegeler, and Lanzone (2016) experimentally tested several aspects of flight-calling behaviour. They documented that rates of spontaneous calling were low; warblers were likely to give flight calls in response to hearing flight calls, especially conspecific flight calls; and the percentage of birds that called and the calling rate (calls/min) were variable, both among species and among individuals within a species. These results suggest that flight calls may be used to transmit information to conspecifics during migration.

While the earlier flight-calling study demonstrated that calls are likely to be used in communication, we do not know how calling may vary among individuals within a species. A variety of other migratory behaviours differ among species and may also differ within a species as a function of age, sex groups and body condition. For example, there are differences in the timing and routes of migration, stopover ecology, rates of mass gain and stopover habitat use between different species of warblers (e.g. Francis & Cooke, 1986; Moore & Kerlinger, 1987; Suomala, Morris, & Babbitt, 2012; Suomala, Morris, Babbitt, & Lee, 2010). Within a species, migratory timing, distances and behaviour may also vary with age and sex (e.g. Ketterson & Nolan, 1985; Morris & Glasgow, 2001; Woodrey & Moore, 1997). Birds in better energetic condition are more likely to exhibit nocturnal flights and orient in a direction consistent with their migratory goal (e.g. Covino & Holberton, 2011; Deutschlander & Muheim, 2009; Smith & McWilliams, 2014); thus, they may also be more likely to give and/or respond to flight calls.

Our objectives were to evaluate whether species, age, sex and body condition affect a bird's probability of flight calling and the rate of flight-calling responses. We hypothesized that (1) species would vary in the propensity and rate of calling; (2) young birds would be more likely to call and to call at a higher rate than adult birds; (3) males and females would be equally likely to call and call at the same rate; (4) birds in better body condition would be more likely to call and call at a higher rate than birds in poorer body condition.

## METHODS

We studied flight-calling behaviour in captive warblers during autumn migration (mid-August to mid-October) at Powdermill Avian Research Center (Rector, PA) from 2010 to 2012 and Braddock Bay Bird Observatory (Greece, NY) from 2010 to 2012 and 2014 to 2015. Both sites run long-term migration monitoring bird-banding stations using constant-effort mist netting. Nets were opened

30 min before sunrise and closed 6 h after sunrise, and were checked at least once every 30 min. Passage migrant birds were captured in mist nets, banded with U.S. Geological Survey aluminium bands and data were collected on age, sex, fat, unflattened wing length (to the nearest 0.5 mm) and body mass (to the nearest 0.1 g). Age and sex were determined using the keys in Pyle (1997). Age categories were 'hatch year' (young of the year, hereafter called 'young') or 'after-hatch year' (hatched at least the prior year, hereafter called 'adult'). We selected American redstart, *Setophaga ruticilla*, black-throated blue warbler, *Setophaga caerulea*, magnolia warbler, *Setophaga magnolia*, and yellow-rumped warbler, *Setophaga coronata*, as focal species. We chose these species because they give flight calls, were common at both of our field sites and can be reliably assigned to specific age–sex classes during banding.

We placed birds in a recording cone following Lanzone et al. (2009), who demonstrated that birds in captivity gave calls that were acoustically similar to those of free-flying birds. The cone was placed in a soundproof, electrically shielded recording chamber in Powdermill's Bioacoustics Lab, or in a mobile avian recording chamber at Braddock Bay. Only one bird was placed in the chamber at any time to avoid introducing additional auditory stimuli to our study. We broadcast flight calls to birds using a Pyle square dispersion horn piezo tweeter speaker connected to a Windows computer (Morris et al., 2016). We placed four microphones around the recording cone to record flight call responses (Morris et al., 2016). The power of the sound levels of the four microphones was calibrated using a tone plug and we calibrated the volume of the sound of the broadcast flight calls using a NCH tone generator (NCH Software, Greenwood Village, CO, U.S.A.).

For each bird, we had three periods of recording. The first period was an initial acclimation period (pre-stimulus) before we played any acoustic stimulus. In 2010 and 2011, the pre-stimulus period was 2 min and in 2012, 2014, and in 2015 it was reduced to 1 min, because in our initial work birds rarely called during the pre-stimulus period. An additional benefit of this reduction in recording time was shorter bird handling time. The second period was the stimulus period, during which we broadcast conspecific flight calls. The flight calls included two discrete calls from five different individual males, two adult and three young, to simulate the proportion of different ages in the migrant population. We randomized the order of the individual flight calls and the amount of time between calls (0.25–1 s) for each stimulus period using PermSound software developed for this project. All calls used as sound stimuli were recorded in the Powdermill Bioacoustics Lab. We digitally standardized the calls so the set of calls for each species had the same mean volume (ANOVA:  $F_{8,81} = 1.9$ ,  $P = 0.064$ ), while maintaining natural variation in call volume. The stimulus period was 3 min in 2010 and 2011 and was reduced to 2 min in 2012, 2014 and 2015. The reduction in recording time was based on our initial results indicating that birds either responded relatively quickly or not at all, allowing us to further reduce bird handling time. The rate of calls played (90/min) remained the same over all years. Birds remained in the cone after the stimulus ended (post-stimulus) for 2 min in 2010 and 2011 and for 1 min in 2012, 2014 and 2015. We recorded birds during all three periods (pre-stimulus, stimulus, post-stimulus) using RavenPro 1.4 (Bioacoustics Research Program, 2011). We also used RavenPro 1.4 to analyse data files to determine whether birds gave flight calls during the pre-stimulus and stimulus periods.

We visually compared recordings made in our acoustic chambers to recordings of the stimulus alone to determine whether a bird gave a vocal response (Fig. 1). Some birds gave calls during the pre-stimulus period, so we only considered the calls to be a response if the rate of calling during the stimulus was at least twice

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