



## Individual flight-calling behaviour in wood warblers



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Warblers regularly give flight calls during migration, but few studies have addressed flight-calling behaviour by individual birds. In this study, we investigated individual responses to flight calls. We hypothesized that birds would be more likely to give flight calls in response to conspecific flight calls than to heterospecific calls or to other sounds. We studied the flight-calling response of three species of warblers (magnolia warbler, *Setophaga magnolia*, blackpoll warbler, *Setophaga striata*, and yellow-rumped warbler, *Setophaga coronata*) to conspecific calls, calls of one of the other two species or calls of the spring peeper, *Pseudacris crucifer*, as a control. Additionally, we characterized the proportion of birds calling and the rates of calling (calls/min) for five additional warbler species. We placed each bird individually into an acoustic cone in a soundproof recording studio and recorded its vocalizations before, during and after playing sound cues in the studio. In our experiment, the three species of warblers were more likely to give flight calls in response to flight calls than to the control, and they were more likely to give flight calls to conspecific calls than heterospecific calls. The eight species of warblers that heard conspecific flight calls varied in both the likelihood of giving a response and the rate of calling, and rates of calling also varied between individuals within each species. Most birds that responded gave flight calls soon after hearing flight calls. Our results are some of the first on individual flight-calling responses and flight-calling rates.

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Monitoring active songbird migration at the species level can pose many challenges. Songbirds frequently fly at night and at high elevation, making visual identification of individual species difficult. These migrants also move between species-specific wintering and breeding grounds at large, broad-front scales, frequently exceeding the range of most monitoring tools (Diehl, Larkin, & Black, 2003; Kelly et al., 2012). For these reasons, large-scale studies in bird migration often require creative methodology (Bridge et al., 2011; Kunz et al., 2007). Meteorological radars offer a technique that provides the extensive spatial coverage needed to monitor bird migration (Kelly et al., 2012), yet preclude resolution to the species level, or even to the level of broader taxonomic

groups (Diehl & Larkin, 2005). Acoustic monitoring can provide additional information because many species of nocturnal migrants give flight calls during migration (Evans & O'Brien, 2002; Evans & Mellinger, 1999; Farnsworth, 2005). Flight calls are unique vocalizations that are generally species specific, often less than 200 ms in duration, range from 1 to 9 kHz, and are hypothesized to help maintain migratory groups and stimulate migratory restlessness (Evans & Rosenberg, 2000; Graber, 1968; Hamilton, 1962). Although these flight calls are most commonly given during migratory flights, they are also given by birds flying throughout the year, during the day, interacting with fledged young and while perched (Evans & O'Brien, 2002; Farnsworth, 2005). Because flight calls are most common during migration, acoustic records can help describe in-flight migrant species composition, which is unavailable from other standard methods such as radar, thermal imaging and moon watching. However, many aspects of flight calls and flight-calling behaviour are poorly understood (Farnsworth, 2005; Keen, Ross, Griffiths, Lanzone, & Farnsworth, 2014).

With the current library of North American flight calls exceeding 200 species, and because acoustic data are both easy and inexpensive to collect, the potential for networks of acoustic monitoring stations to provide comprehensive coverage of nocturnal migrants

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is great (Damoulas, Henry, Farnsworth, Lanzone, & Gomes, 2010). Acoustic monitoring can capture instantaneous movements of species, lending acute resolution to questions of migratory phenology and distribution. Recent advances in call detection have enhanced the efficiency of processing acoustic records (Damoulas et al., 2010; Ross & Allen, 2014), yet interpreting call detections can be difficult because calling reflects an individual bird's behaviour, not simply the presence of that bird in the air. Furthermore, few studies have investigated flight-calling behaviour at the individual level (Hamilton, 1962).

Patterns of flight calling across nights frequently align with patterns observed from weather surveillance radar detections, suggesting that the frequency with which calls are detected during the night is related to migrant density (Farnsworth, Gauthreaux, & van Blaricom, 2004; Gagnon, Bélisle, Ibarzabal, Vaillancourt, & Savard, 2010; Horton, Shriver, & Buler, 2015; Larkin, Evans, & Diehl, 2002). However, temporal patterns of flight calls within a night often do not show the same association because, during the night, flight call detections often increase while other density estimates often decrease (Farnsworth et al., 2004; Graber, 1968; Graber & Cochran, 1960; Horton, Shriver, et al., 2015; Lowery & Newman, 1955). Horton, Shriver, et al. (2015) demonstrated temporal changes in flight call detection through the night after controlling for migrant density and height above ground level, which suggests that the observed temporal changes are due to behavioural changes in calling frequency and not simply methodological bias. Other factors, including weather conditions, have also been tied to changes in calling behaviour, often involving increased calling rates under conditions of low visibility (e.g. fog, rain, ambient light; Evans, Akashi, Altman, & Manville, 2007; Evans & Mellinger, 1999; Evans & Rosenberg, 2000; Graber, 1968; Graber & Cochran, 1960; Hüppop & Hilgerloh, 2012). Yet while these studies demonstrate relationships between methods, and are suggestive of behavioural responses to ambient conditions, they do not address species-specific behaviours.

Surprisingly little is known about many basic aspects of flight-calling behaviour especially variation within individuals (Farnsworth, 2005). A lack of direct experimental studies also leaves open a number of basic questions about this form of avian communication. The work of Lanzone, Deleon, Grove, and Farnsworth (2009) using playbacks of flight calls with wild-caught birds revealed the possibility for experimental manipulations to assess basic behavioural responses. Furthermore, their work suggested that birds were likely to respond to specific flight calls, although their methods did not allow them to test this possibility. Using their method of playing calls to wild-caught birds, in this study we addressed hypotheses related to the flight-calling behaviour of individual birds. We hypothesized that (1) birds would be more likely to give flight calls when they heard flight calls than when they heard other sounds, and (2) birds would be more likely to respond with flight calls to birds of their own species than to those of another species. In addition, we present some of the first measures of migrant call rates and individual variability in calling frequency, both in the absence of sound cues and after birds had heard conspecific calls.

## METHODS

During autumn migration (mid-August to mid-October) from 2010 to 2012, we studied flight-calling behaviour in captive warblers at the Braddock Bay Bird Observatory (Greece, NY, U.S.A.) and the Powdermill Avian Research Center (Rector, PA, U.S.A.). Both of these sites host a long-term, migration-monitoring, bird-banding station using constant-effort mist netting. Nets were opened before sunrise and were checked at least once every 30 min until

6 h after sunrise. These banding stations provided data on age, sex, fat and mass of migrant birds that had been captured in mist nets and banded with U.S. Geological Survey aluminium bands.

We used the same general protocol for all birds in this study. We placed birds in a recording cone (following Lanzone et al. 2009; Fig. 1) in the Powdermill Bioacoustics Lab or in a mobile avian recording studio at Braddock Bay. Lanzone et al. (2009) demonstrated that birds in captivity gave calls that had similar acoustic structure to those from free-flying birds. Both of these locations provided an acoustically isolated, electrically shielded recording chamber. Only one bird was in the chamber at any time to avoid introducing additional auditory stimuli to our study. We played sounds to birds from the computer on speakers (Pyle square dispersion horn piezo tweeter). We recorded birds' calls directly to a computer using Behringer C-2 matched studio condenser microphones connected to a Presonus FirePod using Canare 3-Pin XLR microphone cables. The FirePod was connected to a Windows computer using a firewire connection. We used a tone plug to calibrate the power of the sound levels of the four microphones and NCH tone generator professional software (<http://www.nch.com.au>) to calibrate the volume of the sound played. After an initial acclimation period (prestimulus), we played an acoustic stimulus to the bird in the cone. Each stimulus consisted of two discrete calls from five different individuals, two adult (after hatching year) and three young (hatching year), to simulate the proportion of different ages in the migrant population (see species below). Using Perm-Sound software developed for the project, we randomized both the order of the individual calls and the amount of time between calls (0.25–1 s) for each stimulus. All calls used as sound cues in the study were recorded in the Powdermill Bioacoustics Lab, and sounds were digitally standardized to provide the same mean volume (tested by ANOVA:  $F_{8,81} = 1.9$ ,  $P = 0.064$ ), while maintaining natural variation in call volume. Birds remained in the cone for an additional silent period after the stimulus ended (poststimulus). In 2010 and 2011, the pre- and poststimulus periods were 2 min each, and in 2012, these periods were reduced to 1 min each. Likewise, the stimulus period was reduced from 3 min in 2010 and 2011 to 2 min in 2012, although the rate of calls played (90/min) remained the same over all 3 years. We recorded the birds during all three of these periods (prestimulus, stimulus and poststimulus) using RavenPro 1.4 (Bioacoustics Research Program, 2011). This software was also used to analyse data files to determine whether birds gave flight calls both before we began playing the stimuli and in response to the stimuli.

Our experiment focused on three species of warblers in the genus *Setophaga*: magnolia warbler, *Setophaga magnolia* (MAWA), blackpoll warbler, *Setophaga striata* (BLPW) and yellow-rumped warbler, *Setophaga coronata* (YRWA). These three species were chosen because they are known to give flight calls and they are common at our field sites. As a control, we used calls of a frog, the spring peeper, *Pseudacris crucifer*, which provided a natural, but nonavian, discrete vocalization. We randomly assigned each bird to hear calls of one of the three warbler species or the control. Birds were tested within 1 h of banding. To compare the rate of calling to conspecific calls across species, we also recorded additional individuals of these three species and of five other warbler species (ovenbird, OVEN, *Seiurus aurocapilla*; Tennessee warbler, TEWA, *Oreothlypis peregrina*; American redstart, AMRE, *Setophaga ruticilla*; chestnut-sided warbler, CSWA, *Setophaga pensylvanica*; black-throated blue warbler, BTBW, *Setophaga caerulescens*). Each of these birds heard conspecific calls.

We visually compared recordings of the stimulus alone to recordings made in our acoustic chambers to assess the birds' vocal responses (Fig. 2). We recorded responses during each minute of each period to provide response rates. We also recorded the

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