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White-throated sparrows adjust behaviour in response to manipulations of barometric pressure and temperature



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Keywords: foraging migration storm white-throated sparrow Zonotrichia albicollis Zugunruhe Correlational evidence suggests that animals may use changes in barometric pressure to predict or respond to changes in weather. Birds adjust the timing of migratory flights and migratory restlessness in response to changing weather, and they make facultative movements in response to storms during winter and breeding. Using the pressure chamber of a hypobaric climatic wind tunnel we tested the responses of white-throated sparrows, *Zonotrichia albicollis*, to experimental changes in air pressure alone, or air pressure and temperature in combination. Sparrows in wintering (short-day) condition were exposed to gradual changes in pressure/temperature at dawn that simulated large but realistic high- and low-pressure weather systems. During a drop in pressure, birds approached their food cup more quickly and moved more often. There was no effect of increasing pressure and no additional effects of temperature changes in the evening. Decreases in temperature resulted in less migratory restlessness during the first hour of night, but there was no additional effect of pressure changes. These experimental results indicate that white-throated sparrows can facultatively adjust their behaviour in direct response to changing barometric pressure and temperature.

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Storms and inclement weather can have a profound impact on an organism's survival and reproduction. Many species thus exhibit a range of mechanisms to cope with long- and short-term changes in weather. Birds respond to inclement weather in a variety of ways throughout their annual cycle. In winter, birds exhibit cold acclimatization as well as short-term adjustments in fat deposition, foraging and movement (Carey & Dawson 1999). The timing of migration is also adjusted in response to weather systems (Bagg et al. 1950; Richardson 1978), with birds often taking advantage of favourable tail winds (Shamoun-Baranes & van Gasteren 2011) and temperatures (Cochran & Wikelski 2005). In spring, storms can delay or interrupt breeding (Wingfield et al. 1983), leading birds to temporarily abandon their breeding grounds (Hahn et al. 2004). Thus, in addition to responding to long-term seasonal changes, birds show a variety of responses to rapid and unpredictable changes in weather during winter, while on migration and during breeding.

In general, storms and inclement weather form along the leading edge of moving air masses (Ahrens 2008). Cold fronts are the leading edge of a cooler, denser air mass displacing a warmer air mass. The warmer, and often moister, air is displaced upwards, potentially generating precipitation. Low-pressure systems are also associated with storms, generating high winds and precipitation. In addition, air masses of high and low pressure in the northern hemisphere are associated with clockwise and anticlockwise rotation, respectively (Bagg et al. 1950), and thus, are associated with predictable changes in weather and wind direction. Meteorologists use barometric pressure as a tool for predicting weather changes, and there is evidence that nonhuman animals respond to these changes in barometric pressure as well. Arthropod dispersal and reproduction have been correlated with changes in barometric pressure (Ankney 1984; Li & Margolies 1994), and experimental manipulation of pressure affects insect reproductive behaviour (Roitberg et al. 1993; Leskey & Prokopy 2003). In vertebrates, the behaviours of a variety of mammals are correlated with barometric pressure (Dvorak 1978; Théau & Ferron 2000), and birds show the ability to detect changes in air pressure (Kreithen & Keeton 1974; Breuner et al. 2013). Departures of migratory birds from a stopover site were correlated with preceding changes in barometric

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pressure (Sapir et al. 2011), and the intensity and directionality of migratory restlessness of birds in captivity also vary with changes in pressure (Walther & Bingman 1984; Hein et al. 2011). Thus, birds and other animals may use barometric pressure as an environmental cue to prepare for and respond to changes in weather (Carey & Dawson 1999).

Despite these numerous correlational and anecdotal observations, it remains unclear whether birds respond directly to temperature and/or barometric pressure to alter their behaviour, or whether these effects are due to other correlated variables. Because some of these studies were carried out with captive birds living in constant temperature, the birds could be responding directly to barometric pressure. Using a hypobaric wind tunnel we were able to test experimentally, for the first time, whether birds alter migratory restlessness and winter feeding behaviour in response to experimental increases and decreases in barometric pressure and temperature.

Our objective was to determine whether simulated rapid changes in air mass (systems of high and low pressure) affect the behaviour of sparrows in wintering or spring migratory condition. We predicted that rapid changes in air pressure, or air pressure and temperature, would affect birds' locomotor and feeding behaviour because such atmospheric changes may predict inclement weather (Carey & Dawson 1999). We also predicted that rapid changes in air pressure, or air pressure and temperature, would affect birds' migratory restlessness because such atmospheric changes are associated with inclement weather as well as predictable wind directions (Muller 1976; Richardson 1978). Specifically, we predicted that a simulated low-pressure system would increase movement and feeding in wintering birds, as these systems are associated with approaching winter storms. We also predicted that a simulated high-pressure system would decrease spring migratory restlessness, as approach of high-pressure systems from the west is associated with winds from the north.

METHODS

We assessed the response of white-throated sparrows, Zonotrichia albicollis, in both wintering condition and in spring migratory condition, to experimentally manipulated barometric pressure and temperature. In both conditions we measured responses to increased, decreased or stable barometric pressure while maintaining constant temperature, and to concurrent changes in both pressure and temperature. For the latter tests we paired decreased pressure with an increase in temperature to simulate a lowpressure warm front, and increased pressure with a decrease in temperature to simulate a high-pressure cold front. We used different experimental procedures to assess the effects of these manipulations when birds were in wintering condition and in migratory condition. When birds were in wintering condition, we conducted the tests in the morning and measured movement and feeding behaviours immediately following dawn to assess how the bird's foraging behaviour might be influenced by weather cues. When birds were in spring migratory condition, we conducted the tests in the evening and measured nocturnal migratory restlessness at the start of night to assess how the bird's migratory nocturnal departure might be influenced by weather cues.

Experiment 1: Wintering Condition

Animals

White-throated sparrows are medium-distance migrants and regularly experience storms on their wintering grounds (Falls & Kopachena 2010). In eastern North America this species winters from southern Ontario and the Maritimes south to the Gulf of Mexico (Falls & Kopachena 2010). This species is also exposed to storms and wide fluctuations in temperature during their migration to and from their breeding grounds in the Canadian boreal forest, and previous work with captive white-throated sparrows suggests their migratory behaviour is correlated with changes in weather (Muller 1976).

We captured 23 migrating white-throated sparrows south of London, Ontario (at approximately 42°35′N, 80°32′W) during their autumn migration in October 2009 and held them in an outdoor aviary for 3 weeks before transferring them to individual cages indoors. Birds were maintained on short days (9:15 h light:dark cycle) and provided food and water ad libitum. Short-day photoperiods such as this have previously been shown to maintain this species in a nonphotostimulated wintering condition for many months (e.g. Zajac et al. 2011). The Animal Use Subcommittee at the University of Western Ontario approved all experimental procedures (protocol 2006-011).

Apparatus

Pressure and temperature manipulations were carried out using the hypobaric climatic wind tunnel at the Advanced Facility for Avian Research, University of Western Ontario. This wind tunnel controls air pressure, temperature $(-15 \text{ to } 30 \circ \text{C})$ and humidity (10-90% relative humidity) and is used to simulate variation in environmental conditions from ground level to an altitude of 7 km. Custom computer software is used to regulate set-points and rates of change of environmental variables (Aiolos Engineering, Toronto, ON. Canada). In the present study, birds were not flying in the wind tunnel, but were held in cages in a reinforced steel room or plenum (dimensions $4.8 \times 4.2 \times 2.6$ m) surrounding the working section (flight chamber) of the wind tunnel. The plenum can be sealed with an airlock, and the atmosphere in the plenum is contiguous with that in the wind tunnel circuit. We used a baffle to increase air mixing between the wind tunnel circuit and the plenum, and monitored temperature and air pressure using data loggers mounted on the birds' cages.

Procedure

For each manipulation, eight of the birds' home cages were wheeled into the plenum prior to lights off the afternoon preceding the manipulation. Air pressure within the plenum was decreased slightly to 96.0 kPa (approximately equivalent to an increase in altitude of 200 m; Table 1) and maintained overnight. This holding pressure was low enough to allow us to further decrease or increase air pressure, but was within normal barometric pressure range for London, Ontario. To habituate birds to the plenum, each bird spent 3 nights in the plenum and was then returned to its homeroom each morning. For testing, we again housed birds in the plenum overnight, but the next morning we either maintained these conditions (no change, control condition), increased or decreased air pressure, increased air pressure while decreasing temperature, or

Table 1

Experimental pressure and temperature manipulations used for treatment groups of white-throated sparrows

Group	Treatment	Pressure (kPa)	Temperature (°C)
Control	No change	96.0	19
↑Pa	Increase pressure	$96.0 \rightarrow 97.2$	19
↓Pa	Decrease pressure	$96.0 \rightarrow 94.8$	19
↑Pa ↓°C	Increase pressure,	$96.0 \rightarrow 97.2$	19→9
	decrease temperature		
↓Pa ↑°C	Decrease pressure,	$96.0 \to 94.8$	19→27
	increase temperature		

Each pressure/temperature manipulation occurred gradually over approximately 30 min.

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