Animal Behaviour 86 (2013) 1285–1290

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

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

Jessica Metcalfe [a,b], Kim L. Schmidt [a,b], Wayne Bezner Kerr [b], Christopher G. Guglielmo [a,b], Scott A. MacDougall-Shackleton [b,c,*]

[a] Department of Biology, University of Western Ontario, London, ON, Canada
[b] Advanced Facility for Avian Research, University of Western Ontario, London, ON, Canada
[c] Department of Psychology, University of Western Ontario, London, ON, Canada

ARTICLE INFO

*Article history:*
Received 20 February 2013
Initial acceptance 25 April 2013
Final acceptance 17 September 2013
Available online 26 October 2013
MS. number: A13-00179R

*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 change. Sparrows in spring migratory condition (photostimulated) were exposed to pressure/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.


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

* Correspondence: S. A. MacDougall-Shackleton, Advanced Facility for Avian Research, University of Western Ontario, London, ON N6G 1G9, Canada.
*E-mail address:* smacdou2@uwo.ca (S. A. MacDougall-Shackleton).

0003-3472/$38.00 
http://dx.doi.org/10.1016/j.anbehav.2013.09.033

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 low-pressure 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 to 30 °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 × 4.2 × 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→97.2 | 19 |
| ↓Pa | Decrease pressure | 96.0→94.8 | 19 |
| ↑Pa ↓°C | Increase pressure, decrease temperature | 96.0→97.2 | 19→9 |
| ↓Pa ↑°C | Decrease pressure, increase temperature | 96.0→94.8 | 19→27 |

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

decreased air pressure while increasing temperature (Table 1). These pressure manipulations occurred gradually over 30 min, for 15 min before and after lights on. Infrared emitters were aimed at the cages, and cameras sensitive to visible and infrared light were used to monitor bird behaviour. We videorecorded the birds during this half-hour period.

The pressure and temperature values we used (Table 1) simulated extreme but realistic weather events. For example, winter storms in eastern North America are often caused by fast-moving, low-pressure systems such as Alberta Clippers or Colorado Lows moving west to east, or by low-pressure systems moving up the east coast of North America, called nor'-easters (NOAA National Weather Service Glossary, http://forecast.weather.gov/glossary.php). Movement of air masses can cause rapid changes in temperature. For example, on 9 December 2009, the barometric pressure dropped by 2.6 kPa and the temperature increased by 7 °C during a 12 h period in London, Ontario (data from Environment Canada, http://weather.gc.ca/). Our manipulations involved changes in temperature of 8 °C to 10 °C and changes in barometric pressure of 1.2 kPa (Table 1), but over a much shorter period, and thus represent realistic changes in magnitude but at an extreme rate.

Testing was conducted from 26 November to 14 December 2009. Due to constraints of the wind tunnel schedule and the limited size of the plenum, we were limited in both the number of birds that we could test each day and the number of total number of test days available. Each test day we used seven to eight of the 23 birds, and individual birds were tested a minimum of 7 days apart. Thus, each bird was tested in the control condition, and in two of the four experimental conditions (randomly selected for each bird).

*Analysis*

For each bird we quantified the following behavioural measures during the control and test sessions: latency to move following lights on, latency to feed following lights on, the number of movements (flights and hops combined) per minute and the number of food-cup visits per minute. The observer scoring the videos was blind to experimental manipulation during scoring. Our testing schedule resulted in an unbalanced experimental design (not all birds were exposed to all conditions). We thus used linear mixed models that can accommodate such data. Subject was entered as a random effect to account for repeated measures. Pressure (no change, increase, decrease) and temperature (no change, increase, decrease) were entered as fixed factors. Statistical significance of fixed factors was assessed with type III tests and, if significant, pairwise comparisons among levels were assessed with least-squares differences. Intermittent failure of the IR cameras on a few trials reduced sample sizes for some trials; thus, final sample sizes varied and are indicated in Fig. 1 (see Results). All analyses were run using PASW v.18 (SPSS Inc., Chicago, IL, U.S.A.).

## *Experiment 2: Spring Migratory Condition*

*Animals and apparatus*

Sixteen of the birds used in experiment 1 were switched to a long-day photoperiod (LD 16:8 h) on 21 December 2009. All other housing conditions remained the same, as did the equipment arrangement.

*Procedure*

Testing was conducted between 18 and 24 January 2010, after birds had been photostimulated with a long-day photoperiod for about 3 weeks. Singing behaviour and an increase in cloacal protuberance length were observed following the experiment and confirmed that the birds were indeed photostimulated (data not shown). We tested eight birds per night, with all birds being tested in all conditions (Table 1) in random order. Each test day, eight birds were wheeled into the wind tunnel plenum in their home cages in the late afternoon and the air pressure was slowly reduced to the holding pressure of 96.0 kPa. Pressure and temperature manipulations were carried out over a 30 min period that ended about 15 min prior to lights out (2000 hours). We then used infrared cameras to record the birds' behaviour for 1 h following lights off.

*Analysis*

For each bird we quantified the percentage of time spent in migratory restlessness and the number of movements made during the control and test sessions. We scored the percentage of time in migratory restlessness as the proportion of the recording session during which the bird showed beak-up behaviour and/or beak-up flight (Agatsuma & Ramenofsky 2006; Ramenofsky et al. 2008). Number of movements was the number of flights and hops per minute, regardless of beak-up posture. The observer scoring the videotapes was blind to experimental manipulation during scoring. Both behaviours were analysed with linear mixed models, with bird ID as a random effect, as in experiment 1.

# RESULTS

## *Experiment 1: Wintering Condition*

Birds exposed to decreases in barometric pressure moved more quickly and more often and visited the food cup more quickly following lights on (Fig. 1) than birds in the other treatments. Control birds typically remained on their perch longer (mean ± SE = 32 ± 6 s) following lights on and visited the food cup about 11 s later (43 ± 6 s after lights on). Movement latency was significantly shorter when barometric pressure was decreased ($F_{2,31.4} = 5.0$, $P = 0.01$); post hoc comparisons revealed that the two treatments where pressure decreased were significantly different from the other treatments, which did not differ from each other (Fig. 1). Movement rate showed a similar pattern. Birds exposed to decreasing pressure moved more during the observation period than birds exposed to increasing or stable pressure ($F_{2,43.3} = 4.4$, $P = 0.018$). There was no effect of temperature change on either movement latency ($F_{2,32} = 1.4$, $P = 0.26$) or movement rate ($F_{2,42.1} = 0.14$, $P = 0.87$). All of the movements were qualitatively similar across conditions, with birds hopping along the perches and flying back and forth to their food cup.

Feeding behaviour was affected by pressure treatment as well. Changes in barometric pressure affected latency to feed ($F_{2,31.4} = 5.0$, $P = 0.01$), and post hoc comparisons indicated that feeding latency was significantly shorter following decreases in barometric pressure compared to control conditions, and that feeding latency was significantly longer following increases in barometric pressure compared to control conditions (Fig. 1). Birds also tended to visit the food cup more often following decreases in barometric pressure; there was a significant main effect of pressure ($F_{2,41.6} = 3.5$, $P = 0.04$) but no significant pairwise comparisons among treatments (all $P > 0.05$). There was no effect of temperature change on either feeding latency ($F_{2,28} = 1.9$, $P = 0.16$) or feeding rate ($F_{2,40.4} = 2.8$, $P = 0.08$).

## *Experiment 2: Spring Migratory Conditions*

Most birds showed extensive beak-up behaviour and movement during the observation period following lights out. However, five of the 16 birds showed very little beak-up behaviour, less than 60 s sum total across the five observation periods for all treatment conditions. These birds were excluded from further analysis;

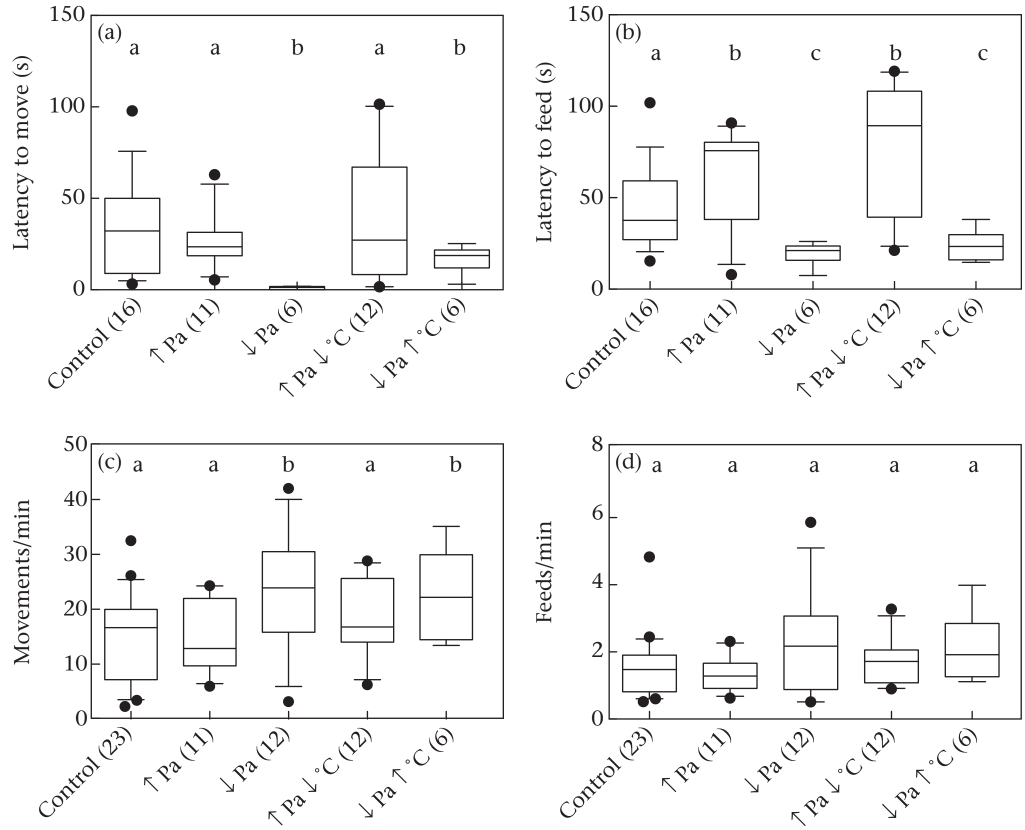


**Figure 1.** Effects of experimentally increased (↑) and decreased (↓) barometric pressure (Pa) and temperature (°C) on white-throated sparrows in wintering condition: (a) latency to move and (b) latency to feed from the food cup following lights on; (c) number of movements and (d) number of feeds from the food cup per minute. Box plots indicate 25th, 50th and 75th percentiles; whiskers indicate 10th and 90th percentiles; filled circles indicate outliers; number of birds per treatment is indicated in parentheses for each treatment. Different letters above box plots indicate a significant effect of pressure between treatments.

presumably they had not yet entered migratory condition or were inhibited from exhibiting migratory restlessness in captivity. All birds had large fat deposits, so we could not distinguish migratory condition based on body mass. We thus excluded the five nonmigratory birds based on lack of nocturnal activity.

Birds exposed to decreasing temperatures combined with increasing pressure reduced migratory restlessness compared to birds in the other treatments (Fig. 2). There was a significant effect of temperature change on migratory restlessness (percentage of time in beak-up behaviour: $F_{2,37.2} = 3.3$, $P = 0.049$). Post hoc comparisons indicated that following a decrease in temperature birds showed significantly less migratory restlessness than following no change in temperature ($P = 0.003$) or an increase in temperature ($P = 0.003$), which did not differ from each other ($P = 0.45$). There was no main effect of barometric pressure on migratory restlessness ($F_{2,37.3} = 1.4$, $P = 0.27$). Movement rates exhibited a similar pattern, with a significant effect of temperature change ($F_{2,36.7} = 3.5$, $P = 0.043$) but not of barometric pressure change ($F_{2,36.9} = 1.3$, $P = 0.28$). Birds experiencing a decrease in temperature moved less than birds experiencing an increase in temperature ($P = 0.027$), but neither of these differed from trials where temperature was constant (both $P > 0.05$).

## DISCUSSION

Overall, our results indicate that white-throated sparrows directly respond to changes in barometric pressure and air temperature. Birds in wintering condition altered their movement and feeding behaviour following decreases in air pressure regardless of temperature manipulations. Birds in spring migratory condition showed less migratory restlessness following decreases in temperature combined with increasing pressure. These results are consistent with the idea that birds use barometric pressure and temperature as environmental cues to cope with, and perhaps even predict, inclement weather and/or wind direction, as predicted from observational studies (Bagg et al. 1950; Richardson 1978; Carey & Dawson 1999).

For birds in wintering condition, there was a profound effect of decreasing pressure on latency to feed and move. At the time of lights on in the morning, the pressure manipulations had been occurring for about 15 min. Compared to the other test conditions, decreasing pressure led to the birds almost immediately leaving their roost perch and beginning to feed (Fig. 1). Similar results have been reported for congeneric white-crowned sparrows, *Zonotrichia leucophrys leucophrys*. Breuner et al. (2013) found that experimentally decreasing air pressure over 3 h during the day resulted in increased feeding by captive birds, similar to our results. Decreasing barometric pressure is often associated with precipitation. In the northern part of the white-throated sparrows' wintering range, such precipitation would come in the form of snow. Precipitation can limit foraging time, and snow cover can make food unavailable to ground-foraging species such as white-throated sparrows. Thus, more rapid and increased foraging prior to the onset of storms might increase the probability of overwinter survival.

Increasing barometric pressure did not affect movement latency but did increase feeding latency. This provides some evidence that the birds perceived increasing barometric pressure as indicating improving conditions under which rapid foraging is less important.

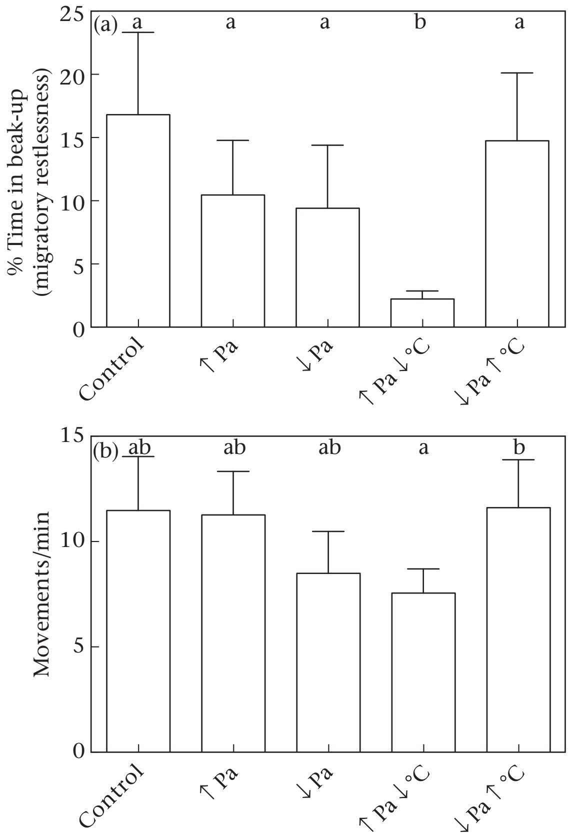


**Figure 2.** Effects of experimentally increased (↑) and decreased (↓) barometric pressure (Pa) and temperature (°C) on white-throated sparrows in spring migratory condition. $N = 11$ birds per group. Mean ± SE (a) percentage of time in beak-up behaviour (migratory restlessness) and (b) rate of other movements (hops and flights) in the hour following lights off. Different letters above bars indicate a significant effect of temperature between treatments.

High-pressure cold fronts can cause snow squalls downwind of large bodies of water such as the Great Lakes of North America, called 'lake-effect snow'. However, cold high-pressure air masses are often characterized by clear skies away from such large bodies of open water, and high-pressure air masses may thus create more favourable conditions in which to forage (Ahrens 2008).

It is notable that rapid changes in temperature did not affect movement or feeding behaviour in the wintering birds above and beyond the observed effects of pressure change. That is, there was no significant difference in the birds' behaviour when barometric pressure remained the same and temperature was varied or held constant. This suggests that barometric pressure (i.e. precipitation) poses a greater threat to birds foraging in winter, and thus is a more important cue, than is temperature. However, further experiments that manipulate temperature in a more fully balanced experimental design are required to confirm this.

When birds were in spring migratory condition we found that a simulated high-pressure cold front (increased pressure and decreased temperature), but not changes in pressure alone, reduced the birds' migratory restlessness at the beginning of the night. This is consistent with a delay in northward migration in the spring in the face of impending cold weather and northerly winds typically associated with the approach of high-pressure systems from the west, and is similar to results observed in free-living thrushes, which do not depart from migratory stopovers following cold days (Cochran & Wikelski 2005). Unfortunately, we could not include constant-pressure, changing-temperature treatments in our experiment and we can thus not fully disambiguate the effect of decreasing temperature from the effect of changing air pressure. Further experiments are required to isolate the effects of changing temperature alone.

We measured migratory restlessness in the first hour of the night to potentially infer how a bird's decision to depart on a nocturnal migratory bout might be influenced by atmospheric conditions. Birds might choose to not depart that night and stay at the stopover site, or to delay departure later into the night. Field studies have shown that migratory behaviour is influenced by a variety of such conditions, including barometric pressure (Richardson 1978; Walther & Bingman 1984; Hein et al. 2011). That we did not find a direct effect of pressure does not rule out the possibility that birds would respond to pressure under different conditions, or later during the night. The effect of temperature that we observed, however, adds to experimental data from other songbirds that birds' nocturnal migratory behaviour is responsive to a variety of environmental cues (Ramenofsky et al. 2008). Further work with longer-term experimental manipulations of environmental cues may shed light on the relative importance of such cues on migratory and stopover behaviour.

It is now clear that birds can sense changes in air pressure (Kreithen & Keeton 1974; Breuner et al. 2013; this study). However, the sensory and perceptual mechanisms of this ability require further study. It has been speculated that the inner ear paratympanic organ (PTO) plays a role in flight and sensation of air pressure (von Bartheld 1994). Homing pigeons with bilateral PTO lesions did not exhibit deficits in homing, suggesting that the PTO does not function as an altimeter (Giannessi et al. 1996). However, this does not rule out the possibility that the PTO functions as a barometer. Further work is required to determine whether and how the PTO functions in the perception of weather-related changes in barometric pressure.

In this study we have, for the first time, measured responses of birds in both wintering and migratory condition to experimentally increased and decreased air pressure and temperature that simulated changes during approaches of high- and low-pressure air masses. These techniques open the door to further understand the neural and endocrine mechanisms that allow birds to modify their wintering and migratory behaviour in response to changes in the weather.

## Acknowledgments

We thank Brendan McCabe, Pralle Kriengwatana, Tara Farrell, Yong Seok An and Thom Luloff for assistance. Funding was provided by the Natural Sciences and Engineering Research Council of Canada, the Canada Foundation for Innovation, and the Ontario Ministry for Research and Innovation.

## References

**Agatsuma, R. & Ramenofsky, M.** 2006. Migratory behaviour of captive white-crowned sparrows, *Zonotrichia leucophrys gambelii*, differs during autumn and spring migration. *Behaviour*, **143**, 1219–1240.

**Ahrens, C. D.** 2008. *Meteorology Today.* 9 edn. St Paul, Minnesota: Brooks Cole.

**Ankney, P.** 1984. A note on barometric pressure and behavior in *Drosophila pseudoobscura*. *Behavior Genetics*, **14**, 315–317.

**Bagg, A. M., Gunn, W. W. H., Miller, D. S., Nichols, J. T., Smith, W. & Wolfarth, F. P.** 1950. Barometric pressure patterns and spring bird migration. *Wilson Bulletin*, **62**, 5–19.

**von Bartheld, C. S.** 1994. Functional morphology of the paratympanic organ in the middle ear of birds. *Brain Behavior and Evolution*, **44**, 61–73.

**Breuner, C. W., Sprague, R. S., Patterson, S. H. & Woods, H. A.** 2013. Environment, physiology and behavior: can birds use barometric pressure to predict storms? *Journal of Experimental Biology*, **216**, 1982–1990.

**Carey, C. & Dawson, W. R.** 1999. A search for environmental cues used by birds in survival of cold winters. In: *Current Ornithology* (Ed. by V. Nolan Jr, E. D. Ketterson & C. F. Thompson), pp. 1–31. New York: Plenum.

**Cochran, W. W. & Wikelski, M.** 2005. Individual migratory tactics of new world thrushes: current knowledge and future tracking options from space. In: *Birds of Two Worlds: the Ecology and Evolution of Migration* (Ed. by R. Greenberg & P. P. Marra), pp. 274–289. Baltimore, Maryland: Johns Hopkins University Press.

**Dvorak, R. A.** 1978. A note on the relationship between barometric pressure and calving incidence. *Animal Reproduction Science*, **1**, 3–7.

**Falls, J. B. & Kopachena, J. G.** 2010. White-throated sparrow (*Zonotrichia albicollis*). In: *The Birds of North America Online. No. 128* (Ed. by A. Poole). Ithaca, New York: Cornell Lab of Ornithology. http://bna.birds.cornell.edu/bna/species/128doi:10.2173/bna.128.

**Giannessi, F., Fattori, B., Ruffoli, R. & Gagliardo, A.** 1996. Homing experiments on pigeons subjected to bilateral destruction of the paratympanic organ. *Journal of Experimental Biology*, **199**, 2035–2039.

**Hahn, T. P., Sockman, K. W., Breuner, C. W. & Morton, M. L.** 2004. Facultative altitudinal movements by mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*) in the Sierra Nevada. *Auk*, **121**, 1269–1281.

**Hein, C. M., Zapka, M. & Mouritsen, H.** 2011. Weather significantly influences the migratory behaviour of night-migratory songbirds tested indoors in orientation cages. *Journal of Ornithology*, **152**, 27–35.

**Kreithen, M. L. & Keeton, W. T.** 1974. Detection of changes in atmospheric pressure by the homing pigeon, *Columbia livia*. *Journal of Comparative Physiology*, **89**, 73–82.

**Leskey, T. & Prokopy, R.** 2003. Influence of barometric pressure on odor discrimination and oviposition by adult plum curculios (Coleoptera: Curculionidae). *European Journal of Entomology*, **100**, 517–520.

**Li, J. & Margolies, D. C.** 1994. Barometric pressure influences initiation of aerial dispersal in the twospotted spider mite. *Journal of the Kansas Entomological Society*, **67**, 386–393.

**Muller, R.** 1976. Effects of weather on the nocturnal activity of white-throated sparrows. *Condor*, **78**, 186–194.

**Ramenofsky, M., Agatsuma, R. & Ramfar, T.** 2008. Environmental conditions affect the behavior of captive, migratory white-crowned sparrows. *Condor*, **110**, 658–671.

**Richardson, W. J.** 1978. Timing and amount of bird migration in relation to weather: a review. *Oikos*, **30**, 224–272.

**Roitberg, B. D., Sircom, J., Roitberg, C. A., van Alphen, J. J. & Mangel, M.** 1993. Life expectancy and reproduction. *Nature*, **364**, 108.

**Sapir, N., Wikelski, M., Avissar, R. & Nathan, R.** 2011. Timing and flight mode of departure in migrating European bee-eaters in relation to multi-scale meteorological processes. *Behavioral Ecology and Sociobiology*, **65**, 1353–1365.

**Shamoun-Baranes, J. & van Gasteren, H.** 2011. Atmospheric conditions facilitate mass migration events across the North Sea. *Animal Behaviour*, **81**, 691–704.

**Théau, J. & Ferron, J.** 2000. Influence des conditions climatiques sur le comportement du Liévre d'Amérique (*Lepus americanus*) en semi-liberte. *Canadian Journal of Zoology*, **78**, 1126–1136.

**Walther, V. Y. & Bingman, V. O.** 1984. Orientierungsverhalten von Trauerschnäppern (*Ficedula hypoleuca*) während des Frühjahrszuges in Abhängigkeit von Wetterfaktoren. *Die Vogelwarte*, **32**, 201–205.

**Wingfield, J. C., Moore, M. C. & Farner, D. S.** 1983. Endocrine responses to inclement weather in naturally breeding populations of white-crowned sparrows (*Zonotrichia leucophrys pugetensis*). *Auk*, **100**, 56–62.

**Zajac, D. M., Cerasale, D. J., Landman, S. & Guglielmo, C. G.** 2011. Behavioral and physiological effects of photoperiod-induced migratory state and leptin on *Zonotrichia albicollis*: II. Effects on fatty acid metabolism. *General and Comparative Endocrinology*, **174**, 269–275.