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Creagh W. Breuner

University of Montana - Missoula, creagh.breuner@umontana.edu

Rachel Seabury Sprague

The University of Montana

Stephen Harold Patterson

The University of Montana

H. Arthur Woods

University of Montana.edu, art.woods@mso.umt.edu

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RESEARCH ARTICLE

Environment, behavior and physiology: do birds use barometric pressure to predict storms?

Creagh W. Breuner^{1,2,*}, Rachel S. Sprague^{1,3}, Stephen H. Patterson² and H. Arthur Woods²

¹Wildlife Biology Program, The University of Montana, 32 Campus Drive, Missoula, MT 59812, USA, ²Organismal Biology and Ecology, The University of Montana, 32 Campus Drive, Missoula, MT 59812, USA and ³Pacific Islands Regional Office, NOAA National Marine Fisheries Service, Honolulu Hawaii 96814, USA

*Author for correspondence (creagh.breuner@umontana.edu)

SUMMARY

Severe storms can pose a grave challenge to the temperature and energy homeostasis of small endothermic vertebrates. Storms are accompanied by lower temperatures and wind, increasing metabolic expenditure, and can inhibit foraging, thereby limiting energy intake. To avoid these potential problems, most endotherms have mechanisms for offsetting the energetic risks posed by storms. One possibility is to use cues to predict oncoming storms and to alter physiology and behavior in ways that make survival more likely. Barometric pressure declines predictably before inclement weather, and several lines of evidence indicate that animals alter behavior based on changes in ambient pressure. Here we examined the effects of declining barometric pressure on physiology and behavior in the white-crowned sparrow, *Zonotrichia leucophrys*. Using field data from a long-term study, we first evaluated the relationship between barometric pressure, storms and stress physiology in free-living white-crowned sparrows. We then manipulated barometric pressure experimentally in the laboratory and determined how it affects activity, food intake, metabolic rates and stress physiology. The field data showed declining barometric pressure in the 12–24 h preceding snowstorms, but we found no relationship between barometric pressure and stress physiology. The laboratory study showed that declining barometric pressure stimulated food intake, but had no effect on metabolic rate or stress physiology. These data suggest that white-crowned sparrows can sense and respond to declining barometric pressure, and we propose that such an ability may be common in wild vertebrates, especially small ones for whom individual storms can be life-threatening events.

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INTRODUCTION

Organisms use environmental cues to time annual cycles, fine-tune breeding and make daily behavioral decisions. In the long term, predictable changes in photoperiod, rainfall and temperature help organisms correctly time life history transitions to maximize fitness. In the short term, organisms use a broader array of cues for predicting near-term weather. Here we focus on the latter class, asking whether sparrows use declining barometric pressure as a cue to prepare for oncoming storms.

Storms can profoundly affect foraging success, metabolic requirements, body condition and parental behavior. For example, heavy rains can flood nest sites and limit foraging opportunities, and high winds can decrease foraging efficiency and increase heat loss. Storms can also include low temperatures and snow. Cold temperatures can increase metabolic costs of thermoregulation and directly threaten survival. Snow can limit activity and cover food resources. Are there predictable components to these rapid abiotic changes? In principle, organisms could use storm-related cues over several time scales. The most proximate are derived from the storm itself – increasing cloud cover, high winds, falling temperatures and heavy precipitation. However, cues in advance of the storm may be more useful, because they potentially give organisms more time to prepare by appropriately altering physiology and behavior.

One well-known predictor of impending storms is falling barometric pressure. As inclement weather approaches, barometric pressure can decline by 2–12 kPa over 24 to 72 h [depending on the severity of the storm (Saucier, 2003)]. This phenomenon is well documented and could be a reliable cue used by vertebrates. Studies from a variety of taxa indicate that animals use barometric pressure to time behavioral transitions. Frogs may call more when barometric pressure is low and rain is likely (Brooke et al., 2000; Oseen and Wassersug, 2002); fish move into salt marshes (possibly to forage) as barometric pressure declines (Crinall and Hindell, 2004); and bats and birds can sense changes in barometric pressure (Kreithen and Keeton, 1974; Lehner and Dennis, 1971; Paige, 1995), and may alter migratory behavior to avoid poor weather (Blokpoel and Richardson, 1978; Cryan and Brown, 2007; Maransky et al., 1997; Matthews and Rodewald, 2010; Panuccio et al., 2010; Pyle et al., 1993; Sapir et al., 2011; Shamoun-Baranes et al., 2006). The majority of studies, however, examine correlations among behavioral patterns and naturally varying barometric pressure. Direct manipulation of barometric pressure itself is rare.

We also do not yet understand the mechanisms by which vertebrates integrate pressure information into physiological and behavioral responses. One likely candidate is the endocrine system, especially the adrenocortical axis, which is a well-known integrator of stress information in other contexts. Endocrine systems commonly

translate environmental cues into organismal responses; for example, elevated androgens promote migratory behavior in response to longer days. Glucocorticoids are secreted from the adrenal gland, and are thought to redirect physiology and behavior so that animals can cope with deteriorating or unpredictable situations (Wingfield and Sapolsky, 2003). From a life history perspective, glucocorticoids are thought to redirect energy expenditures from reproduction to self-maintenance, increasing the likelihood of survival during sub-optimal conditions (Breuner et al., 2008; Wingfield et al., 1998). Several lines of evidence suggest that corticosterone (CORT; the primary avian glucocorticoid) regulates behavioral responses to storms. Animals captured during snow and rainstorms can have elevated CORT (Astheimer et al., 1995; Bize et al., 2010; Rogers et al., 1993; Smith et al., 1994; Wingfield et al., 1983). Extreme temperatures can increase circulating CORT (Bize et al., 2010; de Bruijn and Romero, 2011; Dunlap and Wingfield, 1995; Tyrrell and Cree, 1998). Glucocorticoids can increase activity in both laboratory and field settings, and have been shown to increase food intake in several vertebrates (e.g. Arvaniti et al., 1998; Astheimer et al., 1992; Breuner et al., 1998; Breuner and Hahn, 2003; Crespi et al., 2004; Nasir et al., 1999). And finally, glucocorticoid implants alter responses to inclement weather in white-crowned sparrows (Breuner and Hahn, 2003). Overall, these studies suggest that glucocorticoids could become elevated as barometric pressure changes and storms begin, and that rising glucocorticoids cause changes in physiology and behavior that enable animals to withstand deteriorating conditions.

Here we examine the relationships between barometric pressure, physiology and behavior in free-living and captive white-crowned sparrows. In a field study of wild sparrows, we used a 7 year data set to evaluate both how much barometric pressure declines before snowstorms, and the relationships between pressure and CORT physiology. In a laboratory study, we exposed birds experimentally to declining barometric pressure and evaluated changes in their metabolic rates, foraging behavior, activity and stress physiology.

MATERIALS AND METHODS

Field study

Birds

White-crowned sparrows *Zonotrichia leucophrys oriantha* Oberholser 1932 were sampled as part of a long-term field study on stress physiology (Breuner and Hahn, 2003; Breuner et al., 2006; Crino et al., 2011; Hahn et al., 2004; Lynn et al., 2007). White-crowned sparrows are an ideal species to use for studies of environment–physiology–behavior interactions. Four of the subspecies (*gambelii*, *oriantha*, *leucophrys* and *pugetensis*) breed in habitats where spring storms are common, and individual birds often must redirect physiology and behavior to breed successfully (Addis et al., 2011; Breuner and Hahn, 2003; Romero, 2002; Wingfield et al., 1983; Wingfield and Ramenofsky, 2011). We have studied behavioral and physiological response to spring storms in *Z. l. oriantha* (the mountain white-crowned sparrow) since 1997.

Male *Z. l. oriantha* arrive at the high elevation breeding grounds in early May. Females arrive ~2 weeks later and often begin laying eggs in early June (Morton, 2002). During this period, snow cover recedes from 100 to ~50%, with frequent new snow. Birds were caught at Tioga Pass Meadow, Inyo National Forest, CA, USA (37°54'53"N, 119°15'18"W, ~3000 m elevation), with seed-baited potter traps. The majority of blood samples were collected between early May (when males first arrive at the breeding site) and mid-June (when nesting is underway and we no longer use seed-baited trap lines to catch birds). Blood was collected into heparinized capillary tubes from the alar

vein after puncture with a 26 gauge needle, within 3 min of disturbance in the trap [sitting and eating in a potter trap does not alter baseline or <30 min CORT levels in white-crowned sparrows (Romero and Romero, 2002)]. Birds were held in a cloth bag, and serial blood samples were taken after 15 and 30 min [termed a 'stress series' (e.g. Wingfield, 1994)]. Blood was kept on ice until centrifuged (within 5 h), and plasma was removed and frozen until assayed. CORT levels were measured using enzyme immunoassay (EIA) as per Wada et al. (Wada et al., 2007). All assays were completed in the Breuner laboratory, using corticosterone EIA kits from Assay Designs (ADI-901-097, Enzo Life Sciences, Farmingdale, NY, USA). The data presented here are collated from over 8 years of assays; on average detectability levels were between 0.5 and 1.5 ng ml⁻¹, average intra-assay variation was 6.6%.

Barometric pressure

Barometric pressure was measured in Tuolumne Meadows, Yosemite National Park (37.9°N, 119.4°W), by Dr Jessica Lundquist (Department of Civil and Environmental Engineering, University of Washington) as part of a long-term environmental study [~1 km from Tioga Pass Meadows (Lowry et al., 2010)]. Barometric pressure was logged every 30 min from 2001 to present.

Storms

To evaluate the barometric pressure change prior to snowfall, we identified six storms from 2002 to 2008 when first snowfall was detected at the meadow. We then graphed barometric pressure from the previous 12+h.

Corticosterone

To determine the relationship between barometric pressure and stress physiology in free-living birds, we calculated the change in barometric pressure over the 12 h prior to each stress series sampled. Both baseline CORT (endogenous level of CORT measured on capture, $N=773$), and maximum CORT (highest CORT measured in response to handling stress, $N=452$) were compared with the rate of barometric pressure decline during the preceding 12 h. This analysis evaluates barometric pressure effects on both (1) resting levels of CORT and (2) the animals' ability to respond to subsequent stressors.

Barometric pressure *versus* mass and fat scores

If sparrows respond to approaching storms by eating more, they may also gain mass or fat. However, it is also possible that the declining environmental conditions would require greater energy expenditure to maintain body temperature. We evaluated the direction of the relationship between barometric pressure change and mass or fat scores using linear mixed-effects (lme) models (Pinheiro and Bates, 2000), with days before the first egg lay of the season as a covariate, and individual ID as a random factor (R2.11.1, package nlme).

Laboratory experiment

Birds

White-crowned sparrows *Zonotrichia leucophrys leucophrys* (Forster 1772) were caught in seed-baited potter traps at the Center for Environmental Research at Hornsby Bend in Travis County, TX (30°20'00"N, 97°48'00"W). Birds were captured during February and March 2005 ($N=6$) for experiments completed in April and May 2005, and during February and March 2006 ($N=8$) for experiments completed in April and May 2006. Birds were brought into captivity and housed in individual cages (33×38×43 cm) on an 8h:16h light:dark cycle for at least 3 weeks before the experiment began.

Chambers and pressure manipulation

Birds were put into custom-built Plexiglas chambers (32×30.5×32 cm outside, 30.5×29×30.5 cm inside; University of Texas machine shop, Austin, TX, USA) fitted with several doors (for entry into the cage and for food and water) and several ports for gas flow and pressure measurements. All doors were sealed with O-rings and ports with airtight bulkhead fittings.

The experimental setup is shown in Fig. 1A. Chambers were ventilated by ~3 l min⁻¹ CO₂-free air, which was pulled by a vacuum system and controlled by an upstream solenoid valve. CO₂-free air was produced by a gas generator (PureGas, Broomfield, CO, USA) at 3.5–4 l min⁻¹ and pushed to an overflow bypass. The vacuum pulled air from the overflow through the bird chamber and then through a Venturi flow tube, which we used as a flow meter. The Venturi tube consisted of two copper tubes soldered together with a short, conical copper connector; the upstream tube was larger (7.2 mm diameter) than the downstream tube (4.5 mm). Each section had a port drilled into it to which short pieces of small brass tubing were fitted. These two lines were then connected to a differential pressure meter (PT-100B, Sable Systems, Las Vegas, NV, USA).

The arrangement was calibrated by simultaneously measuring flow rate of air (with a calibrated fixed rotameter, max. 10 l min⁻¹) and differential pressure in the Venturi tube (with the differential pressure meter). As expected, the relationship between flow and differential pressure was exponential (Fig. 1B); to linearize, we log transformed both sides (Fig. 1B, inset). The relationship was highly repeatable across days (the calibration includes measurements from multiple days). Once the calibration curve was obtained, we used only differential pressure to estimate flow rates, as this was more easily logged onto a computer.

We manipulated pressure in the bird chamber by controlling the degree of opening of a solenoid valve placed upstream. A vacuum pulled air through the system at an approximately constant rate;

therefore, greater resistance upstream led to a greater drop in pressure from room to chamber. The solenoid valve was under computer control, and we therefore could automatically ramp down the chamber pressure to mimic an approaching storm (Fig. 1C). Absolute pressure in the chambers was monitored continuously (PT-1000, Sable Systems).

Metabolic measurements

We estimated metabolic rates from rates of CO₂ emission. Outgoing air from the Venturi air tube was sub-sampled at 200 ml min⁻¹ (MFS-1, Sable Systems). To remove water vapor, the sub-sampled stream was pushed through a tube of Drierite. CO₂ content of the stream was then measured by an infrared gas analyzer (CA-2A, Sable Systems), with data logged at 12 Hz onto a computer *via* an analog-digital converter (UI-2, Sable Systems). The gas analyzer was calibrated frequently (zero gas was pure N₂ and span gas was 2800 p.p.m. CO₂ in N₂).

Because each bird was kept for several days in its Plexiglas chamber, baselining was performed in two stages. Before and after each run, the analyzer was baselined with pure N₂ (to measure drift in the analyzer). To obtain baseline levels of CO₂ leaking into the rest of the system (chamber + other parts), chambers were sealed as in an experiment, but without birds, and then ramped through typical pressure changes. Leaks were large enough that chambers had background levels of 50–60 p.p.m. CO₂. However, the levels were not significantly affected by pressure ramping. Moreover, levels of CO₂ from chambers containing birds were much higher, from 600 to 1300 p.p.m. To adjust metabolic traces from each bird, we subtracted its chamber background value from measured experimental values. These baseline-adjusted values were then converted to rates of CO₂ emission by multiplying the molar fraction of CO₂ by the molar flow rate. We did an additional transformation to account for the large chamber volume (28.3 l) compared with the

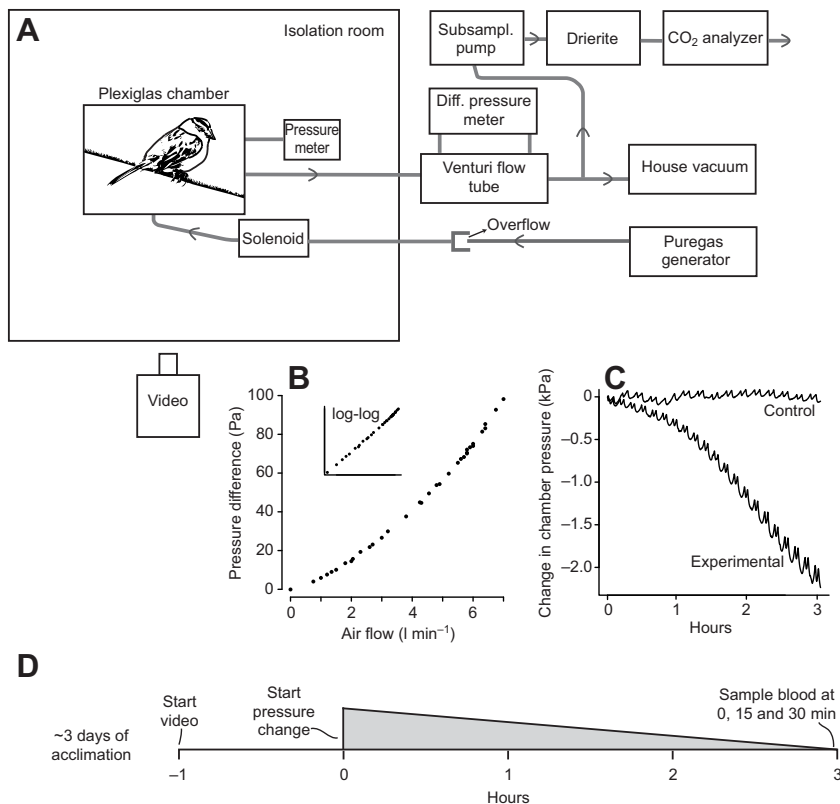


Fig. 1. Arrangement of hardware for producing the pressure change, typical traces, and a schematic of the experimental protocol. (A) Schematic showing the arrangement of parts in the respirometry system, as well as of the bird, the isolation room and the video camera. (B) Calibration curve for the Venturi tube. Rate of air flow was measured independently by a rotameter, and the corresponding pressure difference in the Venturi tube was measured with a differential pressure meter. (C) Typical pressure traces for control and experimental (pressure change) treatments. The high-frequency noise in the traces originated in the house vacuum supply and was, for our purposes, unavoidable. (D) Schematic of the experimental protocol, showing timing of major events.

overall flow rate ($\sim 31 \text{ min}^{-1}$), which has the effect of integrating metabolic events over long periods of time (the half-life of CO_2 in the chamber was $9.4 \text{ min} = 28.31 \text{ min}^{-1} / 31 \text{ min}^{-1}$). To obtain instantaneous rates of CO_2 emission, we used eqn 3 from Bartholomew et al. (Bartholomew et al., 1981), with effective chamber volume set to 28.31 and the other parameters (actual flow rate, CO_2 levels) measured during the experiments. The equation calculates future equilibrium levels of CO_2 from the short-term kinetics of change at any instant.

Experimental protocol

Birds were housed in the Plexiglas housing chamber 3 days prior to running the experiment to allow acclimation to the new housing. The testing room held two Plexiglas chambers, each holding one bird; birds were visually isolated from each other during this time. Only one bird was tested each day, and each bird was tested two days in a row (control and pressure change, order of treatment randomized across birds). Birds were videoed from outside the testing room, through a one-way mirror. On testing day, the video was started at $\sim 10:00 \text{ h}$. One hour later, the computer program was activated to begin barometric pressure decline. After 3 h of barometric pressure decline, the video was stopped, blood samples were collected and birds were returned to the housing chamber. On control testing days the exact protocol was followed, but barometric pressure levels were left at ambient (see Fig. 1D).

Behavior

Videos were scored for five behaviors: (1) activity: the number of times the bird crossed the vertical midline of the cage; (2) foraging: the number of pecks made into the covered food dish; this was not precisely food intake, as ingestion of food was not ascertained with each peck; (3) water intake: the number of drinks taken from the water dish; (4) bill swipe: each set of two swipes (brushing the bill against the perch or other object, once left to right and once right to left) was counted as one bill swipe; and (5) random peck: any peck to a surface other than inside the covered food dish.

We also analyzed videos using an automated technique, which provided higher temporal resolution (1 s) at the cost of less behavioral detail. Raw digital videos (30 frames s^{-1}) were processed in a VLC media player (v. 2.0.4, <http://www.videolan.org/vlc/>) to extract 1 frame s^{-1} . The image sequences were then imported into ImageJ (v. 1.46r, National Institutes of Health, Bethesda, MD, USA) and processed, using a set of differencing operations, to produce a video containing only white and black pixels, with white corresponding to the difference between successive images (see ImageJ script in supplementary material Appendix S1). The mean pixel value of each frame was then outputted to a text file for further processing in R. This analysis provided detailed information about overall movements of birds within each single run, but could not identify particular movements (as was done by eye). Examples of raw and processed videos and a plot of the outputted behavioral data are available in supplementary material Movies 1, 2 and Fig. S1).

CORT sampling

At the end of the 4 h, we obtained a blood sample from the focal bird within 3 min of entering the room. Birds were then held in a cloth bag, and serial blood samples were taken 15 and 30 min after initial sampling. Blood was immediately placed on ice until it was centrifuged (within 1–2 h). Plasma was removed and assayed with EIA as described above for the field samples.

Statistical analysis

Field data (barometric pressure change and CORT) were analyzed using lme models (Pinheiro and Bates, 2000) (R2.11.1, package nlme) with individual as a random factor. CORT values from the field study were \ln transformed, and statistical outliers (mean +2 s.d., $N=32$ of 805 total data points) were removed from the baseline CORT data. Inclusion of outliers did not change the reported relationship. CORT values in the laboratory study were $\log+1$ transformed to account for heteroscedasticity and then analyzed with lme, with individual as a random factor.

Metabolic data also were analyzed using lme models implemented in R, with hour and treatment (control or pressure) as main effects and individual as a random factor. In this analysis, the key statistic of interest is whether there is a significant interaction between time and treatment, which (if present) could indicate that the metabolic rates of birds in the two treatments change in different ways over time. We followed a standard protocol for model identification (Crawley, 2007). In brief, metabolic rate was modeled as a function of the main effects of activity, treatment and hour, with individual specified as a random effect. The metabolic data were extensively autocorrelated, reflecting that metabolic rate at a given time more closely resembled other metabolic rates nearby in time compared with metabolic rates at more distant times. An initial model not accounting for autocorrelation had residuals that were significantly autocorrelated up to lags of many minutes. A subsequent set of mixed-effects models were specified with different autocorrelation structures (including autoregressive moving averages of orders 2–5, and autoregressive of order 1), and those models were compared using the Akaike's information criterion (AIC). Once the best model was identified (lowest AIC), it was validated by examining residual structure. The total size of the data set ($>32,000$ observations) required memory allocation far in excess of what was available to us; we therefore subsampled every 10th data point.

Behavioral data were analyzed in two main ways. Visually scored data were binned into hours for each bird. Data were then corrected for day-to-day variation in individual behavior (e.g. food pecks in hour 1 subtracted from food pecks in hours 2, 3 or 4 on that day), so that elevations or declines in behavior over baseline levels were analyzed. Baseline-corrected values were compared across treatments using paired t -tests (GraphPad Prism, GraphPad Software, La Jolla, CA, USA). Effect size (Hedges' d) was calculated using MetaWin 2.1 <http://www.metawinsoft.com/> (Hedges and Olkin, 1985). All data were normally distributed, except for activity, which was \log transformed before analysis.

The pixel-based data were analyzed using measures of cumulative activity, considered between treatments within birds. The null expectation is that cumulative activity increases linearly with the same slope between treatments. If pressure change leads to changes in activity levels, this will be reflected as a shift in the slope toward the end of the curve in the pressure treatment (e.g. if activity increases during pressure change, the cumulative activity will curve upward). A secondary consideration, which emerged from visual inspection of the behavioral data, was whether bouts of activity were periodic; we analyzed this, for all behavioral traces, using autocorrelation functions.

Finally, to examine whether activity influenced metabolic rate, we used cross-correlation analysis between the time series of metabolic rates and their associated time series of high-resolution (pixel-based) behavior. The behavioral data were first averaged into 5 s bins (so that their frequency would match that of the metabolic data obtained at 12 Hz) and then pre-whitened by differencing once, which removed small-amplitude shifts in baseline but kept the spikes.

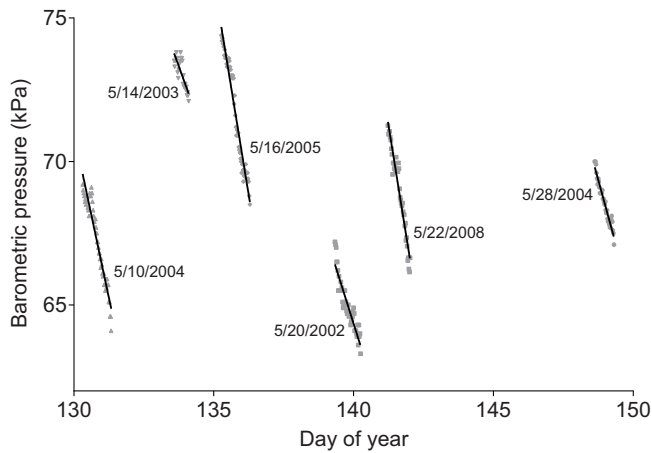


Fig. 2. Barometric pressure up to 24 h before snowfall at Tioga Pass.

RESULTS

Field data

Barometric pressure and storms

During the 12 h prior to snowfall, barometric pressure declined on average by 2.31 ± 0.22 kPa (range 2.88 to 1.34, $N=6$; Fig. 2). The slope (pressure change per hour) for each storm was significantly different from zero (linear regression, $P < 0.0001$ in each case, average $F=449 \pm 129$).

There was no relationship between barometric pressure change over 12 h and endogenous CORT secretion in free-living white-crowned sparrows (lme model with individual as a random effect, to correct for multiple samples taken from a proportion of individuals; baseline CORT: $F_{1,409}=0.077$, $P=0.79$; maximal CORT: $F_{1,409}=0.702$, $P=0.403$; Fig. 3).

There was no effect of barometric pressure decline on mass in the free-living population (lme: $F_{1,362}=0.06$, $P=0.8$). However, there was a relationship between fat score and barometric pressure change (lme: $F_{1,370}=15.26$, $P < 0.0001$, significant interaction with days before first egg lay: $F_{1,370}=96.07$, $P < 0.0001$). The relationship was positive, in that birds sampled when the barometric pressure has been declining had lower fat scores; however, the r^2 was very low (0.014).

Laboratory experiment

Metabolic rate

We measured metabolic rates continuously during 4 h trials in the first year ($N=6$). Metabolic rate during each run (second, third and fourth hours) did not change from baseline (first hour) rates in either the control or barometric pressure change treatments (Fig. 4A,B, supplementary material Figs S2, S3). These data were analyzed using

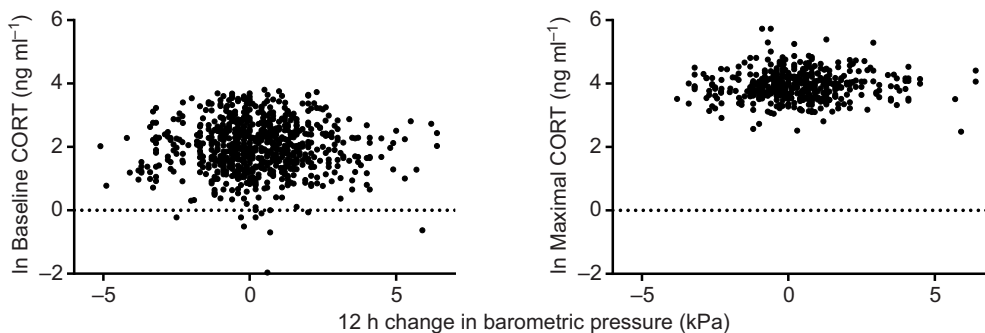


Fig. 3. Baseline and maximal corticosterone as a function of barometric pressure decline over the previous 12 h.

lme models, with individual as the random factor. The key test was whether there was a significant interaction between hour and treatment, which would indicate that the metabolic rates in one treatment group changed (over time) differently than those in the other treatment group. In fact, that term was insignificant (Table 1), so we concluded that there was no effect of pressure on metabolic rate. The significant effect of treatment does not reflect real differences arising as a cause of the treatments; rather, it reflects that by chance the birds had statistically different metabolic rates during the first hour (before the treatments commenced). With no effect of pressure evident in the first year, we decided against measuring metabolic rates in the second year.

Stress physiology

Blood samples were taken at 0–3, 15 and 30 min after the experiment ended. There was a significant increase in CORT over the 30 min, but no effect of treatment, and no interaction between time and treatment (lme with individual as a random factor; time: $F_{2,65}=495$, $P < 0.0001$; treatment: $F_{1,65}=1.49$, $P=0.23$; interaction: $F_{2,65}=0.33$, $P=0.72$; Fig. 5). Integrated CORT (the entire amount of CORT secreted over the 30 min) also did not vary by treatment (paired t -test; $t_{13}=1.20$, $P=0.25$; Fig. 5, inset).

Behavior

Visually scored behavioral results (sum of counts per hour, corrected for baseline behavior that day) are shown in Table 2. A positive number indicates that behavior increased from hour 1, a negative number indicates a decrease. There was no significant effect of treatment on activity, random pecks (not to food), water intake or bill swipe ($P > 0.25$, $P > 0.14$, $P > 0.27$ and $P > 0.21$, respectively).

Foraging increased significantly during the third hour of pressure treatment ($t_{1,13}=2.611$, $P=0.02$; Fig. 6B), but levels were not significantly different during hours 2 or 4 ($t_{1,12}=0.51$, $P=0.62$ and $t_{1,13}=0.94$, $P=0.36$, respectively).

The high-resolution (1 Hz) video analyses showed no effect of treatment on activity. Most of the cumulative activity traces (supplementary material Fig. S4) rose approximately linearly, indicating that rate of large movements did not change with time. Two of six birds had cumulative activity traces whose slopes became shallower during the pressure change, indicating reduced movement late in the session. One of the six birds had a cumulative activity trace that became shallower as the session progressed during the control treatment.

The pixel-based analyses also suggested that bird movements were periodic (see Fig. 4A,B, supplementary material Figs S2, S3). We analyzed this periodicity quantitatively using fast Fourier transforms implemented in R. All periodograms had the shape of the one shown in Fig. 4C, with most of the power concentrated at low frequencies (corresponding to long periods between bouts of

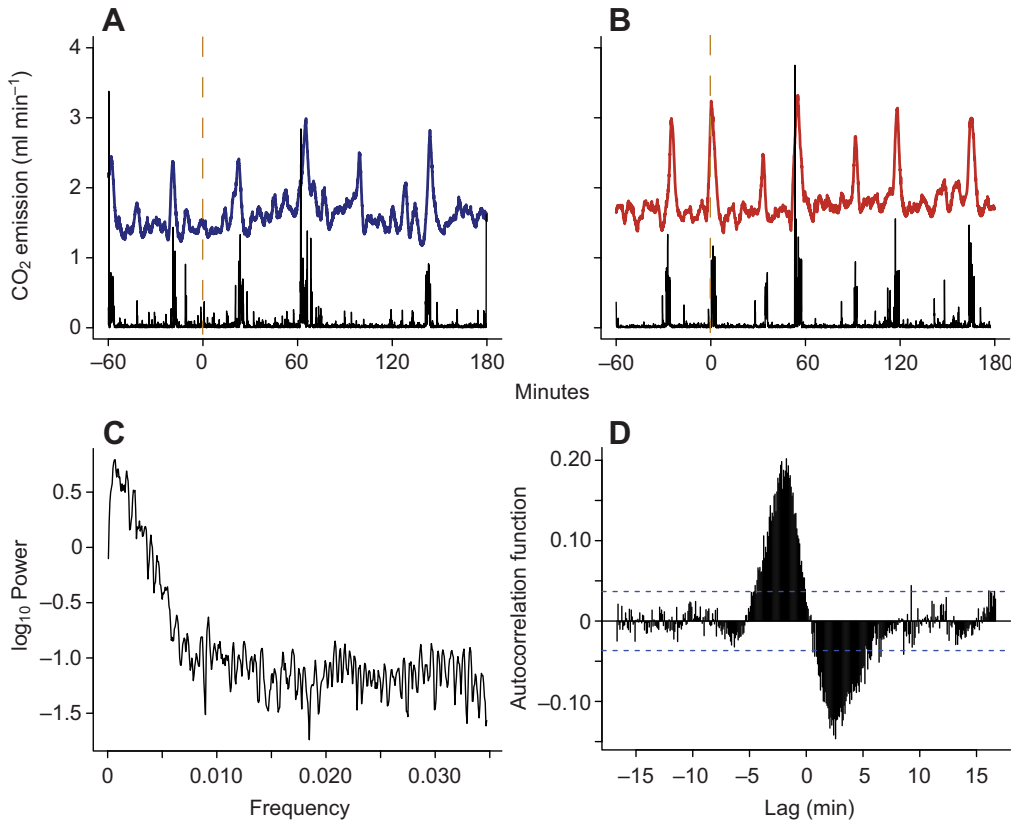


Fig. 4. CO₂ emission (blue and red lines) and behavior (black lines; arbitrary units) during the control run (A), in which chamber pressure was not ramped down, and during the pressure change treatment (B). Pressure was ramped starting at time 0. These traces are for bird number 5; plots for the other birds are available in supplementary material Figs S2, S3. (C) Power spectrum from fast Fourier transformed behavioral data of bird 5 (pressure run). The highest power occurs at low frequencies, about 0.00069 Hz. This frequency corresponds to 24 min, which describes the spacing of major behavioral bouts visible in B. (D) Cross correlation of behavioral and metabolic data, indicated by the major positive and negative peaks around lag=0 min. The cross correlation is also apparent visually in A and B: whenever bouts of activity occur, metabolic rate increases.

activity). In all periodograms, we picked out the single frequency containing the highest power, for each bird × treatment combination, and converted those frequencies to periods in minutes. The mean value was 31.52 min (range 17.35–48.00), and there was no difference according to pressure treatment.

Correlations between activity and metabolic rate

Although neither metabolic rate nor activity changed significantly as functions of time or treatment, inspection of the traces together (Fig. 4A,B, supplementary material Figs S2, S3) suggested that the two measures were strongly correlated. Cross-correlation analysis of the time series confirmed this impression (example in Fig. 4D). Of the 12 pairs of time series (two pairs per bird × six birds), nine showed major peaks of cross-correlation centered around lags of zero. Of the remaining three that did not show strong cross-correlation, two were pressure treatments and one was a control. The larger bouts of activity raised instantaneous rates of CO₂ emission by 35–100% (see supplementary material Figs S2, S3).

DISCUSSION

Declining barometric pressure reliably signals approaching storms. We examined whether, in anticipation, sparrows altered their behavior or physiology. We predicted that glucocorticoid hormones

Table 1. Summary of linear mixed-effects model of the metabolic data shown in Fig. 4A,B and in supplementary material Figs S2, S3 (all metabolic data)

Source	<i>F</i> _{1,3272}	<i>P</i>
Intercept	3514	<0.0001
Treatment	33.4	<0.0001
Hour	0.64	0.43
Hour × Treatment	0.13	0.71

(CORT in birds) would respond to this environmental change, possibly mediating the behavioral and physiological reactions. In white-crowned sparrows, declining barometric pressure indeed altered behavior. Compared with control birds, those in the pressure treatment increased foraging behavior. However, those birds showed no changes in metabolic rate or CORT physiology.

Our data thus provide modest support for the hypothesis that animals can use changing barometric pressure to predict the onset of inclement weather. Several studies indicate that birds can detect changes in barometric pressure (Kreithen and Keeton, 1974; Lehner and Dennis, 1971), and may alter behavioral patterns as a result

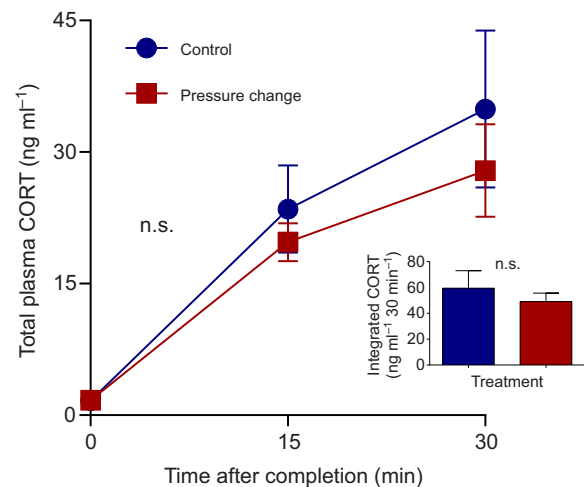


Fig. 5. Corticosterone (CORT) levels 0–3, 15 and 30 min after completion of the barometric pressure experiment. Data shown are means ± s.e.m. Inset: integrated CORT over the entire 30 min. Birds were held in cloth bags between sampling times.

Table 2. Behavioral data for the control and pressure decline treatment groups

Behavior	Second hour	Third hour	Fourth hour
Activity			
Control	-30.8±32.9	-39.4±24.7	-23.9±33.4
Pressure decline	-23.0±13.4	-1.14±23.7	-41.0±15.4
Foraging			
Control	15.7±14.8	-8.43±12.4*	9.79±6.60
Pressure decline	-0.92±16.9	12.5±16.2	40.71±36.5
Water intake			
Control	-0.14±0.98	-0.71±0.91	-0.65±0.64
Pressure decline	0.62±0.90	-0.86±0.77	-0.50±0.82
Random peck			
Control	11.0±26.0	-1.87±4.34	9.50±14.2
Pressure decline	-10.2±17.4	-25.4±12.8	-17.2±16.5
Bill swipe			
Control	8.93±13.0	-14.1±9.21	-11.0±6.83
Pressure decline	-18.2±9.48	-8.43±7.86	-13.6±8.04

Data are means ± s.e.m. of the sum of behaviors over the hour, corrected for baseline ($N=13$ for second hour, $N=14$ for third and fourth hours).

* $P<0.05$ with paired t -test.

(especially during migration) (Blokpoel and Richardson, 1978; Maransky et al., 1997; Matthews and Rodewald, 2010; Panuccio et al., 2010; Pyle et al., 1993; Sapir et al., 2011; Shamoun-Baranes et al., 2006). However, this is the first study to experimentally test this idea. The behavioral change could benefit animals as a storm approaches. Higher food intake is a logical step toward increasing energy stores before the storm prevents further foraging. With increased food intake in our laboratory experiment, we may expect that free-living birds caught after pressure decline in the field may weigh more or have greater fat stores. Our data indicate that although there is no relationship between barometric pressure and mass, sparrows have lower fat scores when sampled after barometric decline in the wild. This indicates that sparrows may be spending energy at a higher rate as conditions decline. However, the r^2 for this value is exceptionally low (0.014), indicating a weak relationship between factors.

Our experiments contained a 2 kPa decline in barometric pressure over 3 h. The absolute decline in barometric pressure before a storm is difficult to predict: the relationship between barometric pressure decline and storms is specific to altitude, geography, wind and temperature (Saucier, 2003). However, we can use the barometric pressure change from the California data to evaluate what an environmentally relevant change in barometric pressure would be. On average, barometric pressure declined 2.33 kPa over 13 h. Thus, our experiments provided an average pressure change for a storm, but over a compressed time frame. This short time frame was required so that ambient pressure changes did not override our

experimental manipulations. It is possible, therefore, that birds in the laboratory would have shown more dramatic physiological and behavioral changes if we had imposed longer-term pressure changes. Alternatively, the rapid barometric pressure decline over 2 h may have been a super-stimulus, and our behavioral measures are overestimates of possible change. Unfortunately, longer-term experiments simply were not feasible with the equipment available.

Birds probably detect barometric pressure using the paratympanic organ (PTO). The PTO is located in the middle ear and is mechanoreceptive (von Bartheld and Giannessi, 2011). It may be homologous to the mechanoreceptive scale sensory organ found in fish (Baker et al., 2008). The PTO is thought to function as both a barometer and an altimeter, helping birds to detect changes in both weather and altitude during migration. Although the PTO was first discovered by Vitali (Vitali, 1911), we still know little about its function. The only ablation experiments, which examined homing ability in pigeons, showed no reduction in performance (Giannessi et al., 1996). However, homing requires a map and a compass [vision and magnetic detection (Kramer, 1953)], but not a barometer. Several other studies have hypothesized that the PTO detects barometric pressure (Paige, 1995; Shamoun-Baranes et al., 2006; von Bartheld and Giannessi, 2011), but none have tested it directly.

CORT physiology did not correlate with barometric pressure change in the field, and experimental barometric pressure decline in the laboratory did not affect circulating or inducible glucocorticoids. This is surprising, given the role glucocorticoids play in shifting time and energy allocation towards survival during unpredictable or stressful events (Breuner et al., 2008; Wingfield et al., 1998; Wingfield and Sapolsky, 2003). However, there was clearly no relationship between barometric pressure and CORT in free-living sparrows, and CORT levels were highly overlapping in the laboratory experiment.

Metcalf et al. (J. Metcalf, K. L. Schmidt, W. Bezner Kerr, C. G. Guglielmo and S. A. MacDougall-Shackleton, submitted) have also recently tested the behavioral and physiological responses to barometric pressure change in laboratory sparrows. Their experimental design differed substantially from ours, but the results were similar. In white-throated sparrows (*Zonotrichia albicollis*, a sister species to the white-crowned sparrow), a rapid decline in barometric pressure decreased the latency to feed, but had no effect on glucocorticoid physiology.

Few studies have evaluated correlations between environmental barometric pressure and endogenous glucocorticoids. Frigerio et al. (Frigerio et al., 2004) discovered a significant relationship between barometric pressure and CORT metabolites appearing in the feces of graylag geese (*Anser anser*). Given the arguments presented here, we would expect that low barometric pressure is associated with elevated CORT. However, Frigerio et al. found the opposite effect: low barometric pressure during the preceding morning was

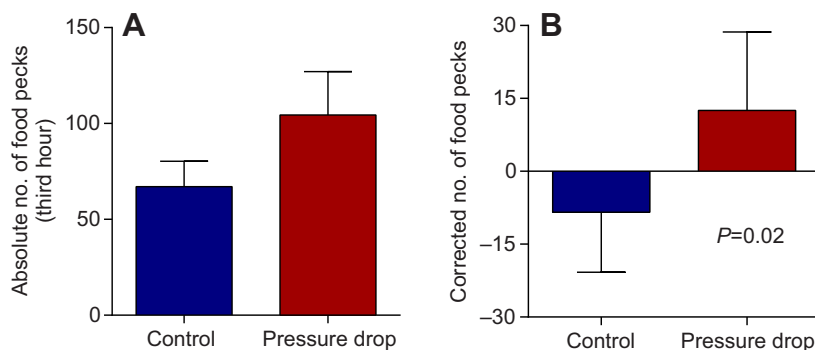


Fig. 6. Foraging behavior was elevated during the third hour of declining barometric pressure change as compared with the control treatment. (A) Absolute number of food pecks during the third hour. (B) The same data corrected for hour 1 behavior.

associated with low CORT metabolites in the feces the next morning. The authors hypothesized that low barometric pressure promoted a 'sit and wait' strategy, which in turn resulted in lower levels of CORT (activity promotes CORT secretion). It is also possible that barometric pressure decline increased food intake, thereby diluting the concentration of CORT in the feces. This is the only field CORT–barometric pressure paper that we have identified. Romero et al. (Romero et al., 2000) examined correlations between CORT secretion and several weather variables in three species of arctic passerine, but did not consider barometric pressure.

In summary, our data demonstrate that white-crowned sparrows respond to declining barometric pressure by altering their behavior in ways that appear to prepare them for inclement weather. We found no association between barometric pressure and CORT-driven stress physiology in either the field or the laboratory. It is possible that other neuro-hormonal systems [e.g. orexin, neuropeptide Y, agouti-related peptide (e.g. Thorpe and Kotz, 2005) (for a review, see Arora and Anubhuti, 2006)] drive this system. A more neurological approach to appetite and activity would be required to ascertain a role for these peptides in pressure-induced changes in behavior.

LIST OF ABBREVIATIONS

AIC	Akaike's information criterion
CORT	corticosterone
EIA	enzyme immunoassay
lme	linear mixed effects
PTO	paratympanic organ

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AUTHOR CONTRIBUTIONS

C.W.B. ran all of the field studies, with contributions from R.S.S. and S.H.P. C.W.B. and H.A.W. devised the laboratory experiments. H.A.W. designed and calibrated the barometric/metabolic chamber design; he also developed the video analysis technique and ran the statistical analyses on the metabolic and pixelated behavioral data. R.S.S. and C.W.B. ran the laboratory experiments, with support from H.A.W. S.H.P. collated, proofed and analyzed the field corticosterone data.

COMPETING INTERESTS

No competing interests declared.

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