Movement Ecology

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Balancing opposing cues: seasonal shifts in push–pull drivers of migration in a temperate waterfowl species

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Abstract

Background Migration in birds results from a complex interplay of internal and environmental cues that shift across seasons. A push–pull framework conceptualizes migration as driven by external "push" cues, such as deteriorating weather, and internal "pull" cues associated with photoperiod and reproductive readiness. Understanding how these cues interact seasonally can inform predictions about migratory behavior under changing climatic conditions.

Methods We applied the push–pull framework to assess drivers of seasonal migration in mallards (*Anas platyrhynchos*), a behaviorally plastic waterfowl species. We analyzed GPS data from 414 individuals tracked across the Mississippi Flyway from 2019 to 2024. Monthly migration direction and distance were modeled as functions of minimum temperature, wind direction, barometric pressure change, and photoperiod. We examined how cue influence varied between autumn and spring migration periods.

Results By December 31, ~92% of southward migrations had occurred, with ~50% completed by mid-November. Autumn migration was primarily influenced by environmental push cues—declining temperatures, favorable wind direction, and falling barometric pressure all increased the likelihood and distance of migration. Migration distances peaked in November and December, when these push conditions were strongest. In contrast, spring migration was driven more by internal pull cues. Northward movements initiated in January and intensified through April, with photoperiod overriding weather as the primary driver. Weather still affected migration distances, e.g. warmer minimum temperatures in February increased distances by 62%, while strong north winds in March reduced movement by up to 213%. Barometric pressure had opposing effects by season: falling pressure promoted movement in autumn but inconsistently influenced spring migration.

Conclusions Our findings reveal a seasonal shift in the relative influence of environmental and internal cues on mallard migration. Weather exerts stronger influence during autumn, whereas photoperiod dominates in spring. These results highlight the utility of a push–pull framework for understanding migratory behavior and suggest that climate change may disproportionately disrupt the reliability of migration cues across seasons.

Keywords Behavior, Mallard, Migration, Photoperiod, Waterfowl, Weather

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Background

Migration is a widespread and highly adaptive phenomenon that has evolved in response to seasonal fluctuations in resource availability [1],. Migration timing reflects both immediate environmental cues and internal mechanisms that synchronize movements with favorable conditions [2–4]. Multiple drivers influence migratory behavior across different temporal and spatial scales, with their relative importance varying among species and populations [5–7]. Photoperiod provides a reliable cue that triggers physiological changes preparing birds for migration, while local climatic and landscape conditions fine-tune the precise timing of movements [8]. Weather patterns serve as crucial drivers of migration, with birds often adjusting their departure and arrival times in response to temperature, precipitation, and wind conditions [9–12].

Drivers of avian migration can be conceptualized within a "push-pull" framework [13–15]. Originally used to describe human settlement patterns [16], the push-pull hypothesis describes attractive or aversive forces that influence migration patterns. For birds, weather, resource scarcity, or disturbance may pressure individuals to leave a given area (push factors). Conversely, changing photoperiod may serve as proximate cues that guide birds toward seasonal destinations (pull factors). In autumn and winter, migratory birds are primarily pushed south as temperatures decline and resources are depleted or otherwise inaccessible. As spring commences, longer days act as strong pull factors directing movement northward [6, 17]. Thus, migration behaviors reflect trade-offs between internal and environmental cues. For example, temperature thresholds and advancing winter conditions in northern latitudes often determine the timing and rate of southward movements [18, 19], but the effect of these push factors may deteriorate as photoperiod begins to 'pull' migrators back to their breeding destinations [20, 21]. Ultimately, the interaction between push and pull forces shapes the timing, direction, and extent of migratory movements.

While studies such as Schummer et al. [22] have advanced our understanding of waterfowl migration by emphasizing temperature and snow cover, a more unified push–pull framework that also incorporates key variables like wind conditions [23] may help reconcile variation in study results and expand insight into migratory behavior. Furthermore, studies relying on bird counts often suffer from detection bias and sampling inconsistencies, whereas radar-based migration assessments present challenges in species identification and behavioral interpretation [24]. While Weller et al. [25] largely corroborated Schummer et al. [22] findings on weather-driven migration, Pearse et al. [26, 27].

Mallards (*Anas platyrhynchos*) represent a well-studied, flexible migrant whose responses to environmental cues can provide insight into more general migratory strategies across temperate-zone birds. Understanding how individuals balance conflicting cues (i.e., push vs. pull) across seasons has broad implications for predicting animal movement under climate change. Mallards, undertake complex seasonal migrations, often navigating vast distances across diverse landscapes. While migration strategies in waterfowl have been documented at broad spatial scales [28–30], fine-scale migratory movements and the environmental factors influencing migration initiation remain less understood. Previous studies have demonstrated that weather conditions, particularly temperature, wind patterns, and barometric pressure, can influence migratory behavior in waterfowl [22, 24, 31–33]. However, quantifying the relative importance of these factors in shaping migration timing and direction across different temporal and spatial scales remains a challenge.

The purpose of our study was to investigate the role of weather variables in shaping migratory behavior of mallards across both autumn and spring. Specifically, we assessed how weather conditions may push individuals southward during autumn migration and potentially inhibit or delay northward movements during spring, while also examining how these effects interact with seasonal progression and increasing photoperiod, which theoretically pulls birds toward their breeding grounds [6, 17, 20]. Through this integrated approach, we quantified the relative influence of weather and photoperiod on the timing, distance, and directionality of mallard movements and evaluated how these relationships shift throughout the migratory cycle. We hypothesized that mallard migration is governed by dynamic interactions between environmental (push) and internal (pull) cues, with their relative strength changing over time [4, 13]. We expected weather to exert greater influence during autumn as birds respond to deteriorating conditions (i.e., push) [22, 32], while photoperiod would increasingly drive northward migration in spring as day length extends and the pull toward breeding areas intensifies (i.e., pull) [3, 14, 21].

Methods

Mallard capture and auxiliary marking

We captured adult and juvenile male and female mallards using a combination of swim-in traps, confusion traps, and rocket-nets at eight locations in Tennessee from November through January 2019–2024 [34, 35]. We banded all mallards with a United States Geological Survey (USGS) federal aluminum tarsal band. We determined age and sex of mallards based on cloacal inversion, wing plumage, and bill color [36].

We attached 20-g solar rechargeable and remotely programmable, OrniTrack Global Positioning System-Global

System for Mobile transmitters (GPS-GSM; Ornitela, UAB Švitrigailos, Vilnius, Lithuania) to mallards weighing ≥1,000 g (i.e., ≤ 2.5% of total body mass) to ensure deployment package remained below recommended body weight limits (3–5% [37]). We attached transmitters via dorsally-mounted body harnesses made of automotive moisture-wicking elastic ribbon [38, 39]. Completed harnesses had two body loops which were knotted and sealed with cyanoacrylic glue above the keel and across the abdomen of the bird [38, 39]. Total package of GPS-GSM transmitter and harnesses at time of deployment weighed approximately 17–22 g. Transmitters were programmed to collect GPS data hourly over a 24-hour period. We processed and cleaned the raw GPS data by removing fix locations that had dilution of precision values > 7 which is considered error in the positional fix due to the geometry of the satellite signal received [40]. All capture and handling procedures of ducks were in accordance with Institutional Animal Care and Use Committee protocols for Tennessee Technological University #19–20-002 and 22–23-003.

Telemetry data processing

We interpreted the spatial scale of migration events by first estimating a probability-density function of cumulative log-transformed step-lengths and then identifying natural breaks in the smoothed distribution of step-lengths [41]. We interpreted step-lengths < 0.25 km as movement within wetland complexes, step-lengths 0.25–50 km as local-regional movements, and step-lengths ≥50 km as migration events, distances similar to previous research [30, 42, 43]. For our analyses we only used step-lengths ≥50 km considered migration events.

We defined spring migration as the period beginning when an individual initiated a directed flight > 50 km northward from its wintering area and exceeded a pre-specified latitude determined by its wintering origin [44–46]. Departure latitudes were calculated as the northernmost GPS location recorded for each mallard during January, when individuals were no longer migrating southward [14, 22]. Spring migration was considered complete when a bird (1) exceeded 43° N and (2) established residency, defined as remaining within a 50 km diameter circular area for ≥ 10 days [39, 44, 47]. The earliest GPS location within this residency period was used to denote the end of migration and the onset of breeding activities (e.g., wetland prospecting). Following the same criteria, we identified autumn migration events. Autumn migration began when individuals initiated a directed flight > 50 km southward and ended when they (1) moved south of 37° N and (2) established residency within a 50 km diameter circular area for ≥ 10 days [39, 44, 47]. We examined how environmental variables may stimulate migration based on known bird responses to weather [22, 24, 33]. Specifically, we used the RNCEP package in R [48] to interpolate minimum surface temperature (°C), north-south and east-west wind speeds (m/s), and change in barometric pressure (Pascals) to all GPS locations. Specifically, we calculated tailwind speed (m/s) for each location (day of), assuming a preferred direction of 150°, based on the horizontal and vertical windspeed [48–50]. The 150° direction was the relative direction of most autumn migrations and has been used previously, demonstrating a strong correlation between migration initiation of dabbling ducks to tailwinds in the Central and Mississippi Flyway [24, 30]. We also calculated changes in barometric pressure from the previous day (ΔPascals), where increasing barometric pressures (i.e., positive values) suggested windy but improving to clear weather conditions following a storm while decreasing pressure indicated balmy, windy conditions and impending severe weather [38, 51]. Prior to our analyses, we tested for collinearity between each of our covariates and excluded covariates using Pearson's correlation with an $r > 0.60$ [52].

Statistical analyses

We fitted two Bayesian hierarchical models using the brms package in R [53, 54] to assess the influence of photoperiod (month; pull cues) and weather (push cues) on migration in mallards. The first model evaluated the directionality of migratory movements (directional model), classifying each step as northward (1) or southward (0) using a Bernoulli distribution with a logit link.

$$\begin{aligned} directionality_i = {} & \beta_0 + \beta_1\,(month_i) \\ & + \beta_2\,(minimumsurfacetemperature_i) \\ & + \beta_3\,(tailwindspeed_i) \\ & + \beta_4\,(\Delta barometricpressure_i) \\ & + \beta_5\,(month_i * minimumsurfacetemperature_i) \\ & + \beta_6\,(month_i * tailwindspeed_i) \\ & + \beta_7\,(month_i * \Delta barometricpressure_i) \\ & + \varepsilon\,[individual_i] + \delta\,[year_i]\,, \end{aligned}$$

The second model assessed the magnitude of migration (magnitude model) by modeling step length as a continuous response using a Gamma distribution with a log link, with photoperiod and weather as covariates.

$$\begin{aligned} magnitude_i = {} & \beta_0 + \beta_1\,(month_i) \\ & + \beta_2\,(minimumsurfacetemperature_i) \\ & + \beta_3\,(tailwindspeed_i) + \beta_4\,(\Delta barometricpressure_i) \\ & + \beta_5\,(month_i * minimumsurfacetemperature_i) \\ & + \beta_6\,(month_i * tailwindspeed_i) \\ & + \beta_7\,(month_i * \Delta barometricpressure_i) \\ & + \varepsilon\,[individual_i] + \delta\,[year_i]\,, \end{aligned}$$

Because mallards did not migrate directly east or west, only northward and southward directions were retained for analysis. To account for individual variability and avoid pseudoreplication, we included random intercepts for each individual and migration year [55, 56].

For the directional model, prior distributions were informed by seasonal migration patterns. Southward movements predominated from October through December, both directions were observed in January, and primarily northward movements occurred from February through May. To reflect these expectations and stabilize model estimation, we applied informative normal priors to the main effects and interaction terms involving month and weather. Months with limited northward migration, such as October and December, were given strong negative priors (e.g., Normal($\mu = -4$, $\sigma = 1$)), while transitional months like January and September received moderately positive priors ($\mu = 4$, $\sigma = 1$). Months with predominantly northward migration, including February through May, received increasingly strong positive priors (e.g., $\mu = 8$, $\sigma = 1$). Similar priors were applied to interaction terms between month and weather variables (minimum temperature, tailwind, and change in barometric pressure), with signs and magnitudes of μ aligned to reflect biologically relevant expectations of movement propensity under seasonal and meteorological conditions.

We evaluated priors using prior–posterior overlap with the MCMCvis package [57], applying a 35% overlap threshold to identify potential identifiability issues [58]. Because we used informative priors and expected some degree of overlap, we also calculated the data–agreement criterion (DAC), based on Kullback–Leibler divergence [58]. A DAC ≤ 1 indicated that the prior was in agreement with the data, whereas a DAC > 1 suggested prior–data conflict. In such cases, we inflated the prior standard deviation by 25% to reduce prior influence. October was the only month that required this adjustment ($\sigma = 2$), based on evidence of prior–posterior conflict exceeding the 35% overlap threshold. This approach was applied across both models to ensure that priors were neither overly influential nor misaligned with the data.

For the magnitude model, we used weakly informative priors that were biologically plausible but minimally restrictive. The prior for the intercept was set as normal ($\mu = 5.3$, $\sigma = 1$), corresponding to the natural log of the mean observed migration distance (~200 km). Fixed-effect slopes were assigned normal ($\mu = 0$, $\sigma = 0.5$) priors to permit moderate effects on the log-transformed distance scale while avoiding extreme estimates. We also specified a Student's t prior (df = 3, $\mu = 0$, $\sigma = 2.5$) on the Gamma shape parameter to regularize the residual variance without imposing strong assumptions [59]. All continuous predictors were standardized by subtracting the mean and dividing by one standard deviation to improve model fit and interpretability [60].

For both models, we ran four MCMC chains with 5,000 iterations each (2,000 warm-up) and confirmed convergence using the Gelman–Rubin statistic ($\hat{R} < 1.1$). We summarized posterior distributions using 95% credible intervals (CrIs). Effects were considered statistically meaningful when CrIs did not overlap zero. If the CrI was centered near zero with substantial overlap and the probability of direction (pd) was < 89%, we interpreted the result as strong evidence for no effect. Moderate evidence for an effect was defined as CrIs that did not overlap zero and pd ≥ 89% [61]. Regardless of statistical significance, we defined biological relevance a priori as any model estimate associated with a ≥ 10% change in predicted movement probability [62, 63].

Results

We monitored 414 individuals that made autumn, winter, and spring migrations during 2019–2024. Of the 414 individuals, 62 had multiple years of migrations. Autumn mallard migration occurred as early as September 4, with ~50% of southward migrations occurring by November 17 and ~92% occurring by December 31 (Fig. 1). Spring migrations began as early as January 1, with ~50% of spring migrations occurring by April 3 (Fig. 1). Of all migration events included in the analyses ($n = 7{,}229$), 1.0% occurred in September, 3.7% in October, 12.1% in November, 3.7% in December, 1.3% in January, 5.0% in February, 28.4% in March, 32.6% in April, and 12.2% in May. Southward migration was the most common direction from September through December ($\bar{x} = 81.7\%$, SD = 18.7%), with January showing a lower proportion of southward movements (55.4%, SD = 4.9%; Fig. 2). Northward movements were most common from February through May ($\bar{x} = 96.0\%$, SD = 2.5%; Fig. 2). Average migration distances also varied across months, with the longest occurring in November ($\bar{x} = 326.5$ km, SD = 254.7 km) and the shortest in January ($\bar{x} = 134.5$ km, SD = 88.9 km; Fig. 2).

From September through January, the probability of northward movement remained low, indicating consistent southward migration, whereas from February through May, migrations northward increased (Table 1; Fig. 3). Increases in minimum temperature were associated with greater probabilities of northward movement in September (16%, 9 °C to 23.9 °C), January (57%, −5.9 °C to 15.2 °C), February (18%, 4.6 °C to 18.6 °C), March (18%, 6.4 °C to 20.6 °C), and April (27%, 4.3 °C to 25.9 °C). In contrast, decreases in minimum temperature were linked to reduced northward movement in February (−80%, −12.4 °C to 4.6 °C), March (−71%, 14.4 °C to 6.5 °C), and April (−28%, 16.8 °C to 4.3 °C), indicating birds remained farther south. However, a decrease in

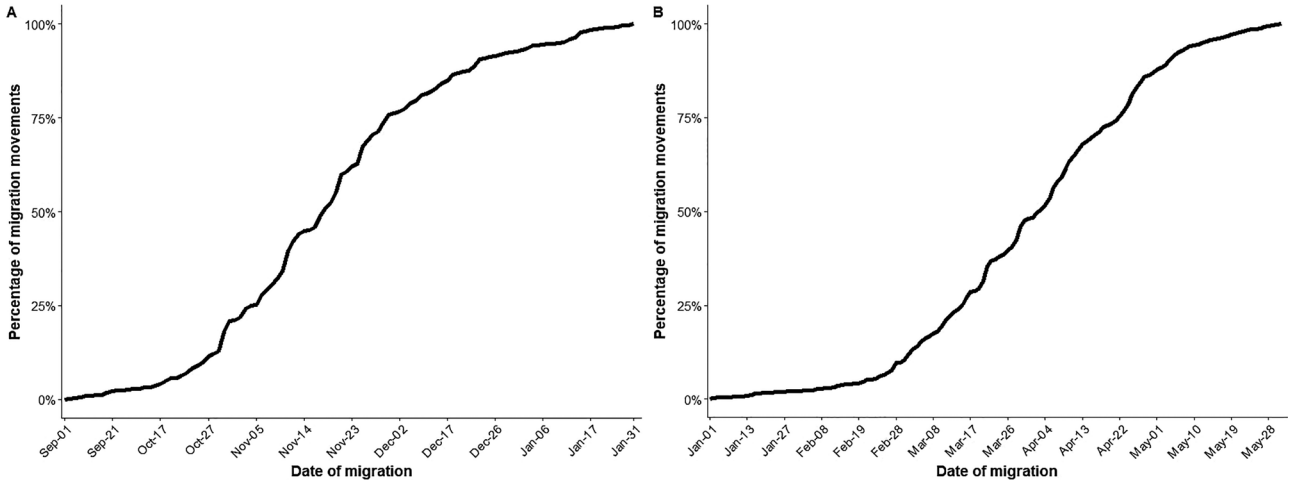

Fig. 1 Cumulative proportion of migratory movements for mallards (*Anas platyrhynchos*) during (**A**) autumn/winter migration (1 September–31 January) and (**B**) spring migration (1 January–31 May; 2020–2024). Each curve represents the cumulative percentage of total migration movements over time, providing a visual summary of the phenology and timing of directional movements across seasons

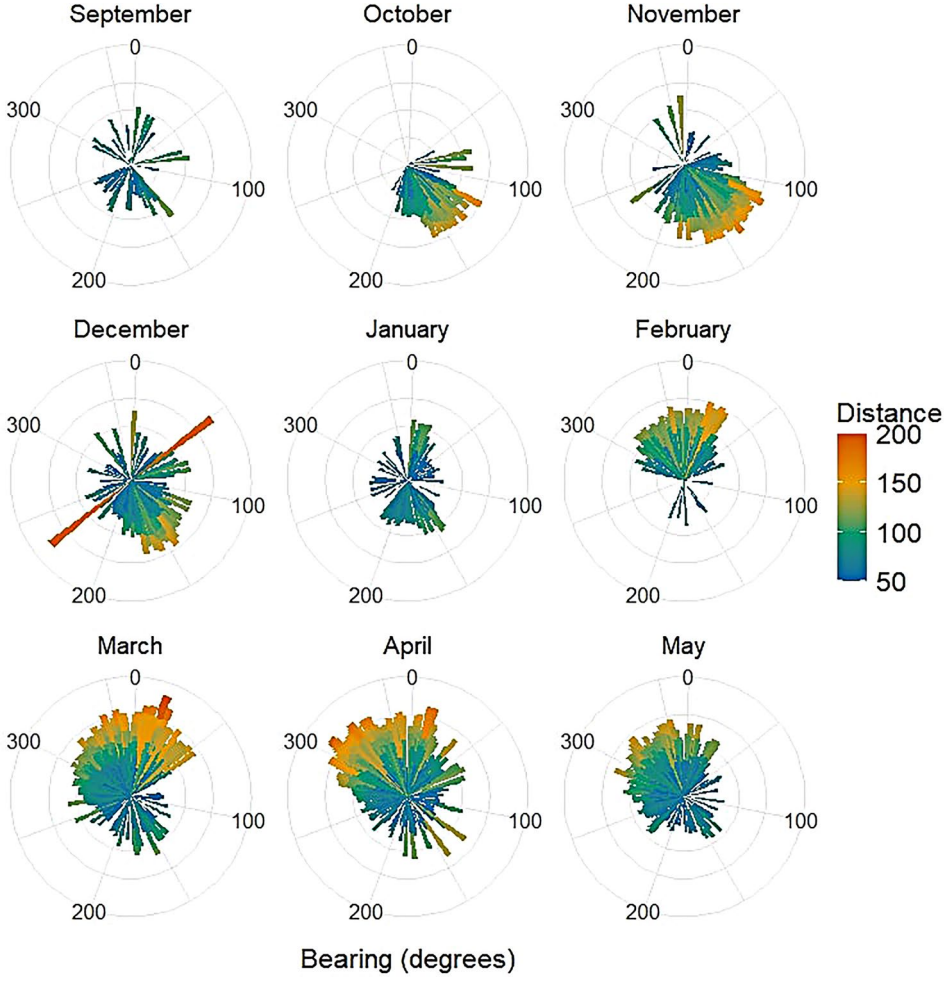

Fig. 2 Monthly distribution of mallard (*Anas platyrhynchos*) migratory movements by compass bearing and distance (km). Each polar plot represents directional movement patterns from September to May (2020–2024), with bearings indicating the direction of movement and color of the bar denoting step length (distance traveled)

Table 1 Parameter estimates, standard errors (SE), lower and upper credible intervals (CRI), and probabilities of direction (pd) for northward and southward movements of mallards (*Anas platyrhynchos*) during fall, winter, and spring migrations from 2020 to 2024. November served as the reference month

Parameter	Estimate	SE	Lower CRI	Upper CRI	pd
(Intercept)	−7.11	1.23	−9.40	−4.65	100%
September	2.52	0.75	1.06	4.00	99.93%
October	−3.27	1.12	−5.60	−1.21	100%
December	2.25	0.55	1.19	3.34	100%
January	4.55	0.52	3.54	5.58	100%
February	8.74	0.62	7.57	9.99	100%
March	7.92	0.42	7.10	8.77	100%
April	6.83	0.37	6.12	7.55	100%
May	5.72	0.40	4.95	6.49	100%
Minimum temperature	−1.42	0.24	−1.88	−0.94	100%
Tailwind	−5.03	0.37	−5.76	−4.33	100%
Change in barometric pressure	−4.30	0.37	−5.03	−3.58	100%
September × minimum temperature	2.27	0.61	1.06	3.46	99.98%
October × minimum temperature	−0.01	0.84	−1.65	1.67	98.67%
December × minimum temperature	0.74	0.49	−0.22	1.71	91.75%
January × minimum temperature	3.41	0.45	2.57	4.30	100%
February × minimum temperature	4.95	0.66	3.66	6.25	100%
March × minimum temperature	3.11	0.36	2.41	3.82	100%
April × minimum temperature	1.99	0.31	1.38	2.60	100%
May × minimum temperature	1.57	0.32	0.94	2.19	100%
September × tailwind	4.43	0.74	2.96	5.87	100%
October × tailwind	−3.03	1.73	−6.56	0.28	99.99%
December × tailwind	−0.38	0.70	−1.80	0.93	70.38%
January × tailwind	4.96	0.54	3.86	6.03	100%
February × tailwind	4.91	0.57	3.79	6.01	100%
April × tailwind	2.66	0.41	1.86	3.47	100%
March × tailwind	2.52	0.43	1.68	3.37	100%
May × tailwind	2.90	0.47	1.99	3.83	100%
September × change in barometric pressure	1.74	0.67	0.43	3.03	99.58%
October × change in barometric pressure	−1.94	1.39	−4.82	0.69	99.98%
December × change in barometric pressure	0.03	0.66	−1.29	1.30	50.47%
January × change in barometric pressure	3.91	0.52	2.90	4.93	100%
February × change in barometric pressure	4.34	0.60	3.16	5.51	100%
March × change in barometric pressure	4.40	0.42	3.59	5.23	100%
April × change in barometric pressure	4.04	0.40	3.25	4.84	100%
May × change in barometric pressure	3.71	0.42	2.87	4.54	100%

minimum temperature in December corresponded with increased northward movement (28%, 5.5 °C to 17.8 °C; Fig. 4). Southward winds were associated with decreased northward movement in February (−13%, −4.1 m/s to 19.9 m/s), March (−81%, −4.2 m/s to 16.2 m/s), April (−65%, −4.3 m/s to 15.4 m/s), and May (−29%, −2.5 m/s to 10.8 m/s), suggesting that northernly wind directions promote continued southward migration. Conversely, northward winds were linked to increased northward movement in October (13%, 4.7 m/s to 15.4 m/s), November (71%, 5.5 m/s to 19.2 m/s), March (18%, −4.2 m/s to 16.2 m/s), April (32%, −4.3 m/s to 15.4 m/s), and May (64%, −2.5 m/s to 10.8 m/s; Fig. 4). Decreasing changes in barometric pressure were associated with increased northward movement in October (94%, 0.39 ΔPa to 1.95 ΔPa), November (54%, 0.56 ΔPa to 3.47 ΔPa), April (12%, −0.38 ΔPa to 2.47 ΔPa), and May (32%, −0.12 ΔPa to 2.14 ΔPa), whereas increasing pressure changes in April (−19%, −2.27 ΔPa to −0.38 ΔPa) and May (−20%, −2.28 ΔPa to −0.12 ΔPa) were linked to southward movement (Fig. 4)

From September through December, predicted migration distances increased steadily, peaking in December before declining sharply in January (Table 2, Fig. 5). Distances rose again from February through April, followed by a decrease in May. Increases in minimum temperature were associated with longer migration distances in February (62%, 7.5 °C to 18.6 °C; Fig. 6). Northward winds were associated with shorter migration distances in January (−30%, 1.9 m/s to 12.0 m/s), February (−82%, −4.3 m/s to 19.9 m/s), March (−213%, −3.9 m/s to 14.3 m/s), April (−91%, −4.3 m/s to 14.7 m/s), and May (−105%, −2.3 m/s to 10.6 m/s). Rising changes in barometric pressure increased migration distances in February (145%, −0.35 ΔPa to 1.6 ΔPa) but decreased them in September (−32%, 0.44 ΔPa to 1.96 ΔPa; Fig. 6). Migration distances increased by up to 81% under warmer minimum temperatures in February (7.5 °C to 18.6 °C), but declined by as much as 92% with strong northerly wind directions in February and 166% in March. Drops in changes of barometric pressure also decreased migration distances in February (91%, −0.35 ΔPa to 1.6 ΔPa), while higher pressure changes in September continued to reduce distance by 33% (0.44 ΔPa to 1.96 ΔPa;Fig. 6).

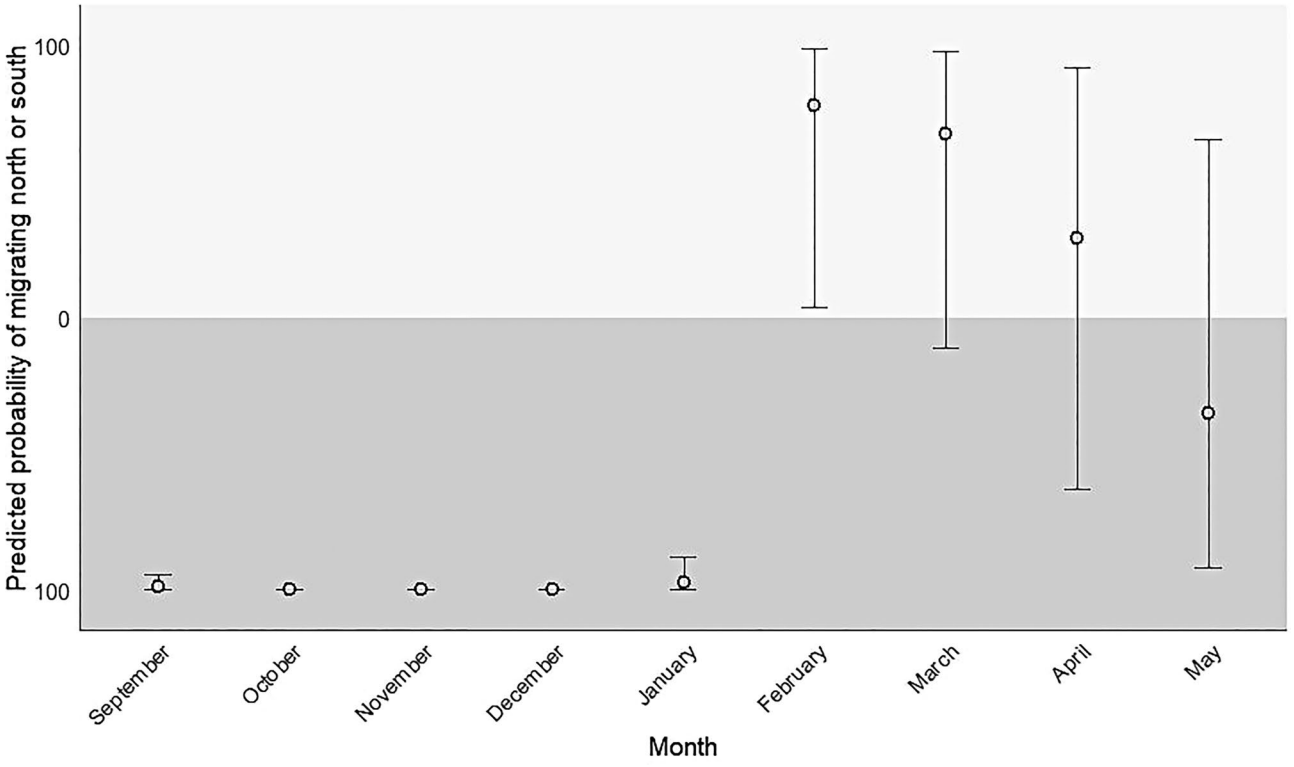

Fig. 3 Predicted probability of directional migration (northward or southward) for mallards (*Anas platyrhynchos*) across months (September–May; 2020–2024), based on a Bayesian regression model. To improve interpretability, predicted probabilities were rescaled such that a value of 0 indicates a 50% probability of either direction (i.e., random or no directional bias). The light gray background represents northward migration, while dark gray background represents southward migration. Points indicate posterior mean estimates, and error bars represent 95% credible intervals

Discussion

Our findings provide empirical support for a dynamic push-pull framework of migration in mallards, whereby external weather conditions act as "push" factors and internal photoperiod-driven cues operate as "pull" signals. During autumn migration, southward movements were strongly associated with declining minimum temperatures, supportive southward winds, and falling barometric pressure. These environmental indicators likely signaled deteriorating foraging conditions [22, 24, 64], increased thermoregulatory costs [65, 66], or advancing storms, prompting individuals to migrate away from higher latitudes [67, 68]. Migration distances peaked in November and December, with ~50% of all southward migrations completed by mid-November and ~92% completed by December 31, suggesting that birds maximized displacement when push cues were strongest. These patterns are consistent with other studies in migratory birds showing that autumn departures are often triggered by temperature thresholds and wind conditions that affect habitat accessibility and energetic efficiency [23, 33, 69].

In contrast, spring migration was primarily characterized by strong northward directionality that aligned closely with increasing day length (month). Although warming temperatures and wind conditions continued to influence movement decisions, the overall predictive strength of weather variables diminished compared to autumn. Northward departures began as early as January and intensified through April, even under variable weather conditions, indicating that internal physiological processes possibly mediated by photoperiod and reproductive readiness acted as stronger "pull" cues as spring advanced [70, 71]. Photoperiod is known to trigger endocrine responses [72], gonadal development [73–75], and increased migratory restlessness in many species [76–78], even when external environmental conditions remain suboptimal. This shift suggests a seasonal reversal in cue dominance, with photoperiod increasingly overriding weather signals as the breeding season approaches [79–81].

The interactions between weather and photoperiod were not always intuitive, emphasizing the complexity of migratory decision-making. For example, northward wind directions were unexpectedly associated with increased southward movement during spring, suggesting birds may have used these favorable conditions to reposition locally or delay northward movements when faced with temporarily unfavorable conditions [81–83]. Similarly, changes in barometric pressure had opposite effects across seasons, with decreasing pressure

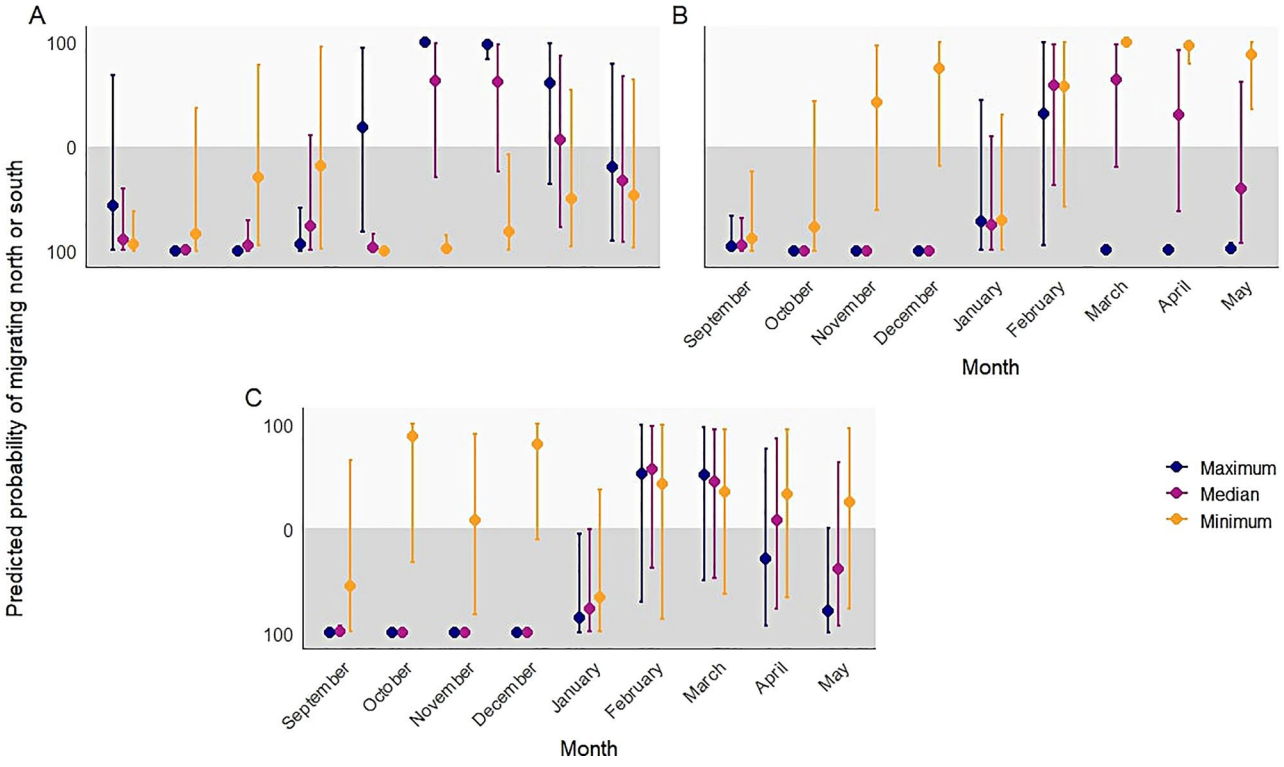

Fig. 4 Predicted probability of directional migration (northward or southward) for mallards (*Anas platyrhynchos*) from September to May (2020–2024) under three environmental conditions. Probabilities are rescaled where values above 0 (gray background) reflect northward migration and values below 0 (dark gray background) reflect southward migration. Colored points represent predicted migration probabilities at the minimum (gold), median (pink), and maximum (blue) observed values of (**A**) temperature (°C), (**B**) wind direction (m/s; negative values 330° southernly positive values 150° northernly), and (**C**) change in barometric pressure (δPa). Points indicate posterior median estimates, and error bars represent 95% credible intervals

promoting movement in autumn but producing mixed responses in spring. These results highlight that birds likely weigh multiple, sometimes conflicting cues simultaneously, and that migratory responses are shaped by the temporal context in which cues are received [84–86]. Additionally, some of the variability in migratory timing and distance we observed may reflect differences in breeding latitude. Birds bound for higher latitudes experience delayed spring green-up and require longer day lengths to initiate reproductive development, consistent with variation in photoperiodic thresholds among populations [87]. Such latitudinal differences suggest that endogenous circannual clocks, entrained by photoperiod, may influence strength or timing of pull cues during migration. Individuals migrating to northern breeding sites may therefore delay departure relative to conspecifics wintering at similar latitudes but breeding farther south, resulting in the broad range of migration timing observed across individuals [21, 87]. These complex responses to stimuli reinforces the need for integrative models that account for dynamic cue prioritization, rather than static threshold-based triggers [88, 89].

Our results demonstrate that mallard migration reflects context-dependent integration of environmental and endogenous cues across the annual cycle. In autumn, external environmental pressures dominate decision-making, driving movements to avoid inhospitable conditions. By spring, internal readiness associated with photoperiod increasingly governs timing and directionality, even when weather conditions are imperfect. This temporal cue switching supports broader theory suggesting that migration timing results from balancing risk avoidance with reproductive urgency [5, 90]. The push-pull framework thus offers a mechanistic explanation for the variability often observed in migratory behavior and provides a flexible conceptual model for assessing how multiple factors interact to influence movement strategies [88, 91, 92].

As climate change alters the timing, frequency, and intensity of weather events, the relative strength and reliability of push cues may shift, potentially leading to mismatches between environmental conditions and internal migratory programs [3, 93]. For example, delayed onset of severe winter weather could result in prolonged staging and collectively result in more northernly distributions of some wintering waterfowl [14, 94, 95]. Species with narrow migratory windows or strict habitat dependencies may be more vulnerable to such mismatches

Table 2 Parameter estimates, standard errors (SE), lower and upper credible intervals (CRI), and probabilities of direction (pd) for migration movement distances (km) of mallards (*Anas platyrhynchos*) during fall, winter, and spring migrations from 2020 to 2024. November served as the reference month

Parameter	Estimate	SE	Lower CRI	Upper CRI	pd
(Intercept)	5.25	0.09	5.09	5.42	100%
September	−0.13	0.24	−0.59	0.36	70.96%
October	0.01	0.15	−0.28	0.31	53.22%
December	−0.33	0.12	−0.57	−0.09	99.60%
January	−0.48	0.13	−0.75	−0.21	99.97%
February	−0.02	0.1	−0.22	0.18	56.56%
March	0.1	0.09	−0.07	0.26	87.21%
April	−0.06	0.08	−0.23	0.1	75.72%
May	−0.15	0.09	−0.33	0.02	95.27%
Minimum temperature	−0.08	0.05	−0.17	0.02	94.73%
Tailwind	0.21	0.05	0.11	0.31	100%
Change in barometric pressure	0.08	0.04	−0.0	0.16	97.30%
September × minimum temperature	−0.06	0.2	−0.44	0.34	61.84%
October × minimum temperature	0.05	0.09	−0.12	0.22	71.12%
December × minimum temperature	0.1	0.09	−0.07	0.27	86.72%
January × minimum temperature	−0.03	0.1	−0.23	0.16	62.55%
February × minimum temperature	0.26	0.09	0.08	0.44	99.81%
March × minimum temperature	0.03	0.06	−0.09	0.15	69.40%
April × minimum temperature	0.03	0.06	−0.08	0.14	71.49%
May × minimum temperature	0.01	0.06	−0.11	0.14	56.16%
September × tailwind	0.1	0.27	−0.41	0.63	64.41%
October × tailwind	−0.05	0.1	−0.25	0.15	68.69%
December × tailwind	0.07	0.09	−0.1	0.24	78.52%
January × tailwind	−0.31	0.14	−0.58	−0.05	98.88%
February × tailwind	−0.37	0.1	−0.56	−0.18	100%
March × tailwind	−0.54	0.06	−0.67	−0.41	100%
April × tailwind	−0.44	0.06	−0.56	−0.33	100%
May × tailwind	−0.43	0.08	−0.59	−0.27	100%
September × change in barometric pressure	−0.28	0.22	−0.7	0.15	90.42%
October × change in barometric pressure	−0.02	0.09	−0.19	0.16	58.19%
December × change in barometric pressure	0.07	0.09	−0.11	0.24	76.83%
January × change in barometric pressure	0.04	0.11	−0.16	0.25	66.03%
February × change in barometric pressure	0.14	0.08	−0.02	0.3	96.06%
March × change in barometric pressure	−0.02	0.06	−0.13	0.09	63.27%
April × change in barometric pressure	−0.07	0.05	−0.17	0.03	91.75%
May × change in barometric pressure	−0.07	0.07	−0.2	0.07	84.15%

[39, 96–98]. For waterfowl, delayed or weakened push cues could result in birds remaining farther north where weather remains tolerable but habitat quality declines as wetlands freeze or food resources become depleted. Individuals occupying these marginal areas may face higher energetic costs to thermoregulate or commute between remaining foraging and roosting sites, and prolonged exposure to suboptimal conditions could reduce body condition or subsequent reproductive investment [64, 65]. Mallards, as a generalist and behaviorally plastic facultative migrant may be buffered to some extent through their ability to exploit agricultural landscapes, waste grains, and urban wetlands even when natural habitat deteriorates [28, 39]. However this flexibility has limits, if warming reduces the frequency of push cues without sustain habitat quality, individuals could experience increased density-dependent competition or heightened predation risk as they concentrate in fewer suitable areas [32, 38, 99]. In a push–pull framework, partial migration reflects individual, state-dependent thresholds for departure. The same external pushes and internal pulls can lead one bird to migrate and another to remain resident because thresholds vary with condition, prior experience/site fidelity, and local habitat quality [100]. Future efforts to model migratory behavior and prioritize conservation actions should incorporate both environmental push and internal pull cues in temporally explicit frameworks that reflect the dynamic nature of migration [88, 101, 102].

Conclusions

Our study demonstrates that mallard migration is governed by seasonally shifting cue hierarchies, with environmental push factors predominating in autumn and internal photoperiodic pull cues driving spring migration. Declining temperatures, wind direction, and barometric pressure collectively stimulate long-distance southward movements in fall, while the influence of weather diminishes as photoperiod intensifies reproductive urgency during spring migration. These findings highlight the dynamic and interactive nature of cues during migration and provide a mechanistic understanding of how animals navigate annually. The push–pull framework offers a powerful lens to interpret migratory behavior and has important implications for predicting avian responses to climate change. As anthropogenic pressures continue to alter environmental cue reliability, understanding how species prioritize and respond to competing signals will

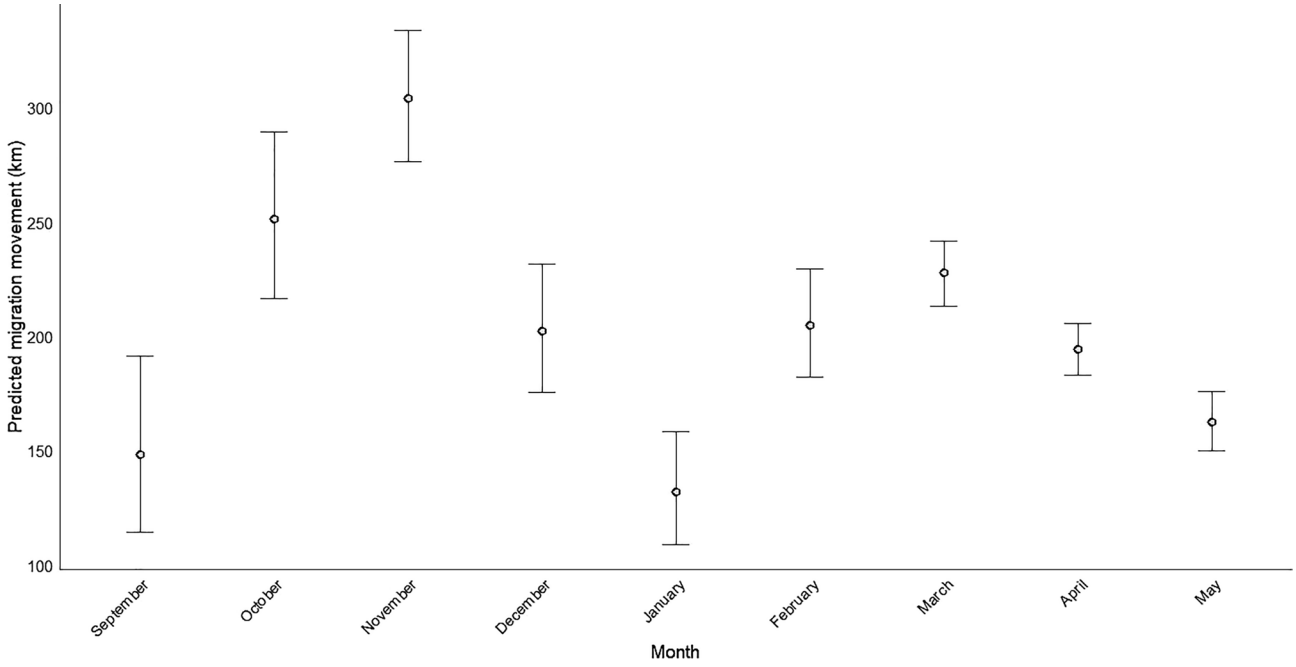

Fig. 5 Predicted probability of migration distance (km) for mallards (*Anas platyrhynchos*) across months (September–May; 2020–2024), based on a Bayesian regression model. Points indicate posterior mean estimates, and error bars represent 95% credible intervals

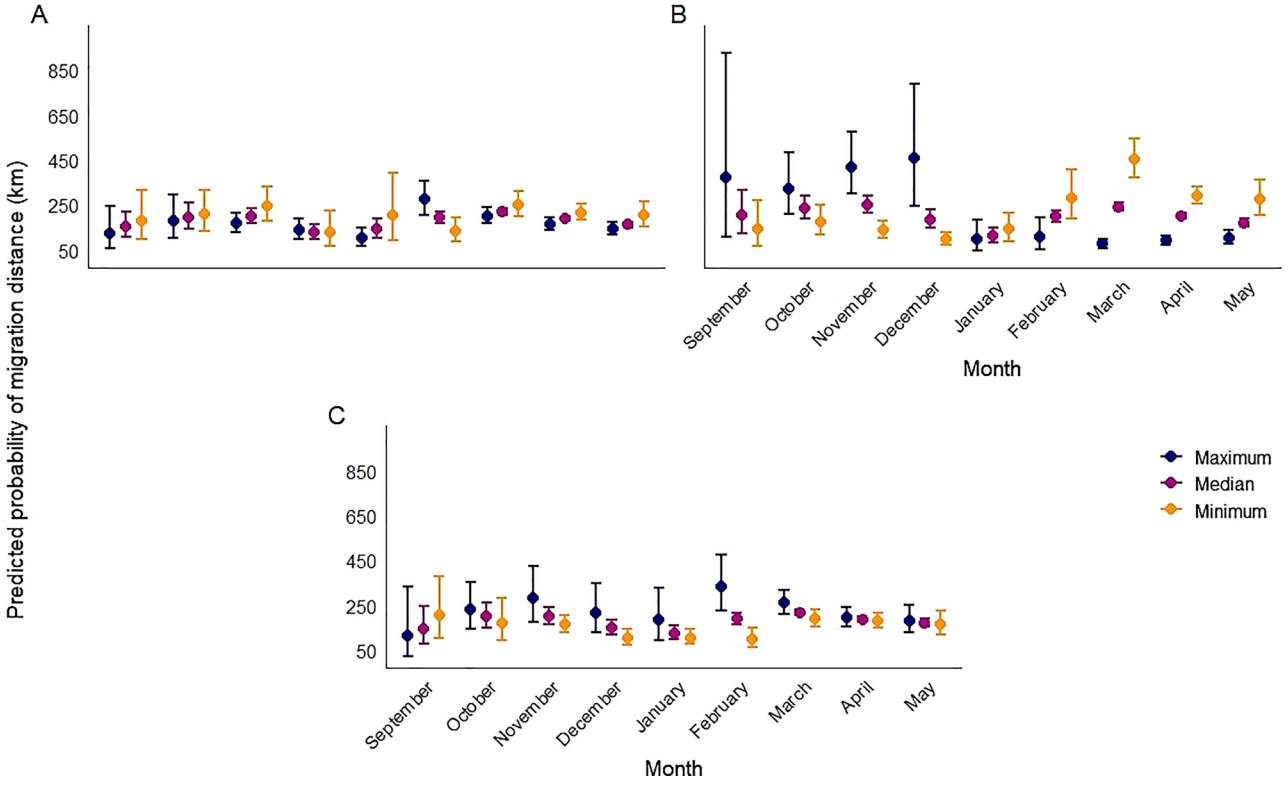

Fig. 6 Predicted probability of migration distance (km) for mallards (*Anas platyrhynchos*) from September to May (2020–2024) under three environmental conditions. Colored points represent predicted migration probabilities at the minimum (gold), median (pink), and maximum (blue) observed values of (**A**) temperature (°C), (**B**) wind direction (m/s; negative values 330° southernly positive values 150° northernly), and (**C**) change in barometric pressure (δPa). Points indicate posterior median estimates, and error bars represent 95% credible intervals

be vital for informing conservation strategies for migratory waterfowl and other mobile taxa.

Abbreviations

GPS	Global Positioning System
GSM	Global System for Mobile Communications
USGS	United States Geological Survey
RNCEP	R National Centers for Environmental Prediction
MCMC	Markov Chain Monte Carlo
DAC	Data–Agreement Criterion
CrI	Credible Interval
pd	Probability of Direction
SD	Standard Deviation
SE	Standard Error

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Data availability
The data that support the findings of this study are openly available in GitHub at Data and code are provided on a GitHub repository and archived on Zenodo: https://doi.org/10.5281/zenodo.15659563.

Declarations

Ethics approval
All capture and handling procedures of ducks were in accordance with Institutional Animal Care and Use Committee protocols for Tennessee Technological University #19–20-002 and 22–23-003.

Competing interests
The authors declare no competing interests.

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