

A wing-assisted incline running exercise regime during rearing increases initial flight velocity during descent in adult white- and brown-feathered laying hens

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ABSTRACT Domestic laying hens rely primarily on their hindlimbs for terrestrial locomotion. Although they perform flapping flight, they appear to use maximal power during descent and thus may lack control for maneuvering and avoiding injuries on landing. This in turn may result in injury in open rearing systems. Wing-assisted incline running (**WAIR**) requires a bird to use its wings to assist the hindlimbs during climbing of an incline, and training in WAIR may therefore provide a useful method to increase a hen's power reserve and control for flight. We subjected hens to an exercise regimen involving inclines to induce WAIR for 16 wk during rearing. We then measured wing and body kinematics during aerial descent from a 155 cm platform. We hypothesized that birds reared with

exercise would be better able to modulate their wing and body kinematics for making slower, more-controlled descent and landing. Brown-feathered birds exhibited greater wing beat frequencies than white-feathered birds, which is consistent with the higher wing loading of brown-feathered birds and WAIR-trained birds exhibited greater initial flight velocities compared to control birds. This may indicate that WAIR training provided an improved capacity to modulate flight velocity and strengthen the leg muscles. Providing incline exercises during rearing may therefore improve welfare for adult laying hens as greater initial flight velocity should reduce the power required for supporting body weight in the air and allow a hen to direct her excess power toward maneuvering.

Key words: body kinematics, chickens, flight, wing kinematic, aerial locomotion

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INTRODUCTION

Chickens and their relatives (Galliformes) are primarily terrestrial birds and many of these species are not adept fliers (Tran et al., 2022). In addition to their use in terrestrial locomotion, the hindlimbs play an important role in bird flight as they provide the main force and work for acceleration and the initial velocity for take-off (Provini et al., 2012). Following the hindlimb's contribution to the initial acceleration in take-off, the wings are the main provider of the subsequent forces required for maintaining aerial locomotion (Provini et al., 2012). The slow flight speeds immediately after

takeoff and before landing require high power output from the wing muscles (Tobalske et al., 2003).

Domestic chickens kept for egg laying (laying hens) appear to be at maximal capacity for flight even when descending a short distance (León et al., 2021). Lacking power in excess of the minimum required for descent means that the birds are unlikely to have capacity to maneuver, or modulate their velocity and descent angle (Pennycuik, 1975; Warrick et al., 1998). This lack of excess power therefore limits the laying hen's ability to orchestrate a safe landing. The poor flight ability of laying hens is attributed to the high energetic cost of slow flight and the laying hen's high wing loading (large body mass to wing area ratio) (Greenewalt, 1962). As laying hens and other Galliformes seek elevated refuges only when threatened or to roost (Appleby and Duncan, 1989), the ability to perform successful take-off is especially important to avoid predators and competitors (Harlander-Matauschek et al., 2015). Additionally, they have to be able to return to the ground after flight.

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Laying hens land at 2 to 3 times the landing speed of more skillful fliers (León et al., 2021), such as pigeons (*Columba livia*), zebra finches (*Taeniopygia guttata*), and diamond doves (*Geopelia cuneata*) (Green and Cheng, 1998; Berg and Biewener, 2010; Provini et al., 2014). With such high landing speeds, it is crucial that laying hens are able to make appropriate landings, otherwise they increase the risk of muscle and bone damage including deformation or breakage of their keel.

A safe descent is dependent on appropriate deceleration and lowering the steepness of descent angles (Provini et al., 2014). Within backyard chicken coops and commercial aviary housing systems, birds are provided with ramps or inclines to ease their transition between elevated structures (Stratmann et al., 2015; Heerkens et al., 2016; Norman et al., 2021). Chickens are able to anticipate and modulate the force production of their hindlimbs depending on the steepness of the incline to navigate the varying slope safely (LeBlanc et al., 2018). On steeper inclines, both the wings and legs contribute in a type of locomotion termed wing-assisted incline running (WAIR) where the wings produce forces to aid in propelling the body toward the substrate and upward (Tobalske and Dial, 2007; LeBlanc et al., 2016). WAIR is also a common behavior seen in wild, juvenile birds to help develop their flight abilities, muscles and the visuomotor system needed for flapping flight in adult life (Tobalske and Dial, 2007). Laying hens accustomed to ramps as chicks demonstrate less hesitancy behavior prior to ascending or descending ramps and use elevated structures more frequently from an earlier age and into adult life (Stratmann et al., 2015, 2022; Norman et al., 2021).

We hypothesized that when chicks and pullets perform a combination of leg and wing exercises through WAIR training over a period of 16 wk, adult birds would have an improved ability to modulate their wing and body kinematics to accommodate take-off, flapping-flight, and landing from an elevated height. To test this hypothesis, we used white- and brown-feathered laying

hens, which differ in wing-loading and body weight, to specifically ask 1) how are take-off velocities, decent angles, acceleration and other flight kinematic variables affected by a WAIR training program and 2) do white- and brown-feathered birds exhibit different wing and body kinematic responses to a WAIR training program?

MATERIALS AND METHODS

Animals and Housing

This experiment was approved by the University of Guelph Animal Care Committee (Animal Utilization Protocol Number 4828). A total of 82 hens, 41 white-feathered (Dekalb White) and 41 brown-feathered (Hyline Brown), were used in this study. Birds were housed in 8 identical floor pens (183 cm L × 244 cm W × 290 cm H) within a room at the Poultry Research Centre (Guelph, Canada). Each pen housed 10 to 11 hens with an approximately equal number of hens from each strain. All pens included a feeder, automatic nipple drinkers, 3 nest boxes, 2 platforms (122 cm L × 31 cm W) at 92 cm and 74 cm above ground, a high perch (163 cm L × 4 cm W) 181 cm above ground and a low perch (153 cm L × 4 cm W) 15 cm above ground. A 14:10 h light-dark cycle with a 30-min dawn/dusk period was implemented and the room was kept at 21°C.

WAIR Exercise Program and Control

At 1 wk of age (WOA), each pen was assigned to 1 of 2 treatment groups: WAIR or CONTROL. The WAIR group was introduced and habituated to the ramp apparatus (150 cm L × 10 cm W × 115 cm H; Figure 1) from 2 to 4 WOA. The exercise regime began when chicks were 5 WOA. A ramp incline of 60 degrees was used between 5 and 9 WOA and increased to 65 degrees from 10 WOA until 21 WOA (LeBlanc et al., 2018). Chicks were required to exercise twice a week with at least 1 d of

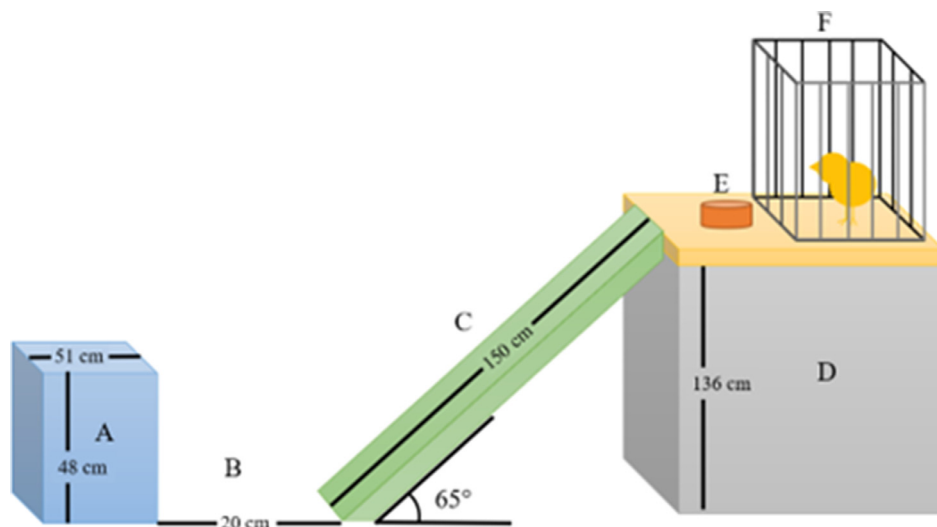


Figure 1. Chicks/pullets begin the WAIR exercise program at the start box (A), make their way down the walkway (B) to the ramp (C). Chicks/pullets then ascend the ramp on to the ramp apparatus (D) where highly desirable food rewards (E) and social rewards (conspecifics; F) were provided. The ramp is in this diagram is set to an angle of 65° with a corresponding height of 136 cm. Diagram not to scale.

rest in between. During exercise, all chicks began each run in a start box (Figure 1A) and made their way through a walkway (Figure 1B) to the base of the ramp. Time (in seconds) to ascend the ramp (Figure 1C) was recorded once chicks had both feet off the ground (i.e., both feet on the ramp) and ended when both feet reached the top of the ramp. The time to ascend the ramp was used to calculate velocity and loss of velocity in real time. Daily exercise ended and chicks were returned to their pen for the day when they had completed 10 runs up the ramp and the exercise criterion was met. The exercise criterion was based on a human study by Pareja-Blanco et al. (2017) where sprinters ran until a 40% loss in velocity was seen from their fastest run. For the chicks, the exercise criterion was met if, after the minimum 10 runs were completed, 2 consecutive runs had a 40% decrease in velocity relative to the fastest run.

The CONTROL group underwent a handling procedure as part of a larger experiment (Hong, 2023) and to ensure all birds received similar handling to minimize effects of human interaction. The CONTROL group was introduced to the handling procedure at 3 and 4 WOA, while the WAIR group was introduced to the ramp apparatus and underwent similar handling. The handling treatment began at 5 WOA where chicks were moved across 3 transport crates. First, an entire pen of birds was caught and kept in the first crate. One chick from the CONTROL group was moved to the second crate once exercise began for one of the chicks in the WAIR group and into the third crate once exercise was completed. Once all chicks from the pen completed the

handling treatment for the day, they were released into their home pen and received a food reward, similar to the WAIR birds.

Room Setup and Flight-Testing Apparatus

A 155 cm high testing apparatus (jump tower; León et al., 2021) was used to determine wing and body kinematics. The jump tower was set-up in an alleyway (335 cm L × 155 cm W × ~280 cm H, Figure 2) in an empty room, between furnished cage structures at the Poultry Research Centre (Guelph, Canada). White curtains were used to cover the cage structures to minimize distractions while hens performed the jumping procedure. Two layers of foam mats (approximately 2.55 cm total thickness) lined the testing room floor with additional foam mats (1.30 cm thick) lining the cage structures behind the curtains to decrease the risk of injury from potential collisions. The foam mats covering the floor were marked with tape, separating the landing area into a 6 by 3 grid (~63.5 cm L × 63.5 cm W). Each square within the grid was numbered (1–18) and used to track where the bird landed after each jump.

Ten flood lights (8 at 5,000 lumens, 2 at 2,000 lumens) were added to brighten the room and ensure clear visuals for video recording and analysis. Two cameras were set-up to ensure frontal and lateral views of the bird's flight trajectory. Cameras were placed so that clear recordings (min. 3 wingbeats per video) of the hen's flight trajectory were captured regardless of where the hens landed.

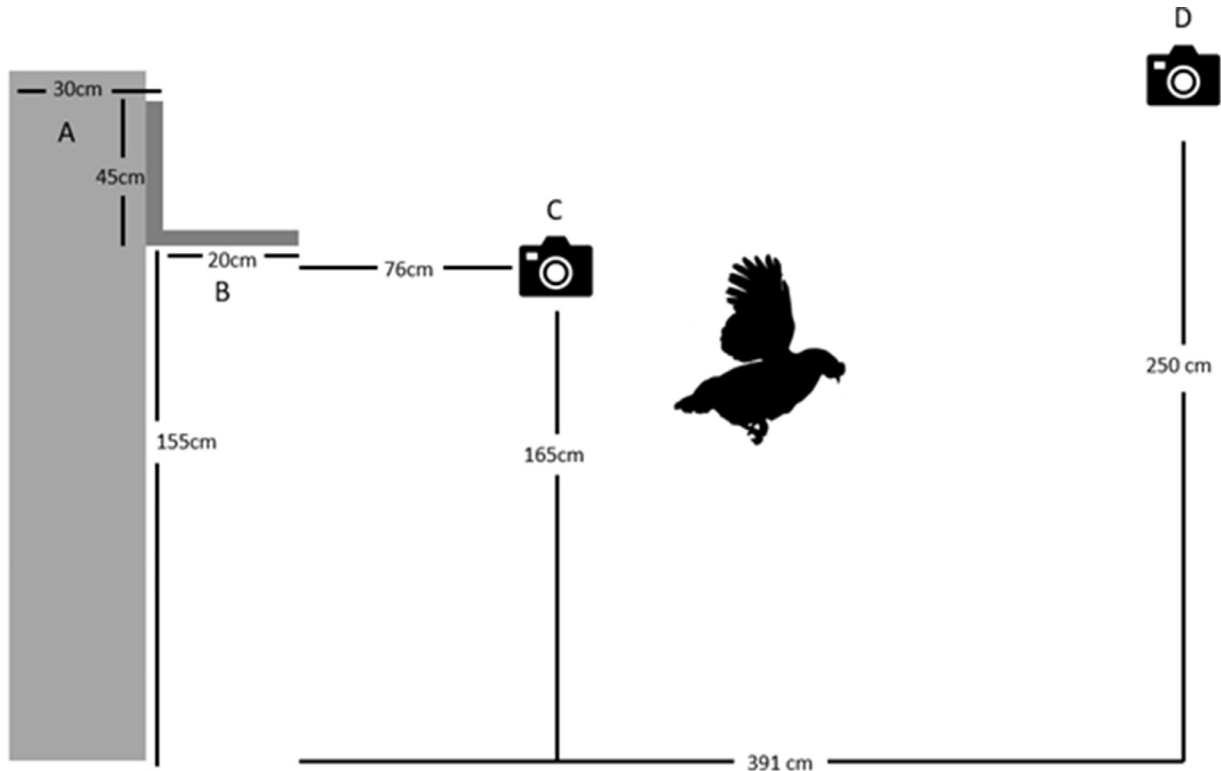


Figure 2. The jump tower apparatus is composed of a start box (A) and a platform (B) where birds are placed prior to jumping. The lateral camera (C) was mounted on the right side of the jump tower apparatus, 165 cm above ground and 76 cm away from the jump tower platform. The frontal camera (D) was mounted 250 cm above ground and 391 cm away from the jump tower platform. Diagram not to scale.

The lateral view camera (GoPro Hero7 Black, GoPro, San Mateo, CA) was mounted 76 cm away from the jump tower platform and 165 cm above the ground, on the cage structure (Figure 2). The frontal view camera (GoPro Hero5 Black, GoPro, San Mateo, CA) was mounted 391 cm away from the jump tower platform and at a height of 240 cm from the ground (Figure 2). A meter stick was shown to the lateral camera from a distance of 155 cm to calculate the conversion factor (see video analysis) for the body kinematics analysis.

Flapping-Flight Testing

A subsample of birds was euthanized at 21 WOA for dissection as part of another experiment (Hong, 2023). All remaining hens from both WAIR ($n = 30$) and CONTROL ($n = 31$) groups were gradually trained to jump from a 155 cm height a week prior to testing. Hens had 3 training sessions in which they jumped off the apparatus in pairs. In each progressive session, the jump tower height increased from 55 cm to 115 cm to the final height of 155 cm. In each session, hens jumped from the jump tower 5 times before moving on to the next session. Highly desirable food rewards (dish full of corn) were placed on the floor at the end of the testing room to entice the hens to jump from the tower.

The flapping-flight test (excluding training) was conducted over a period of 4 d when the hens were 37 WOA. All birds were examined for health and soundness of feet, legs, and wings prior to testing. Thirteen hens showed signs of severe footpad dermatitis during the training period and were excluded from the study. A final group of 48 hens composed of 23 birds from the WAIR group (10 white- and 13 brown-feathered) and 25 birds from the CONTROL group (12 white- and 13 brown-feathered) underwent the flight test. Hens were always placed onto the jump tower platform facing the tower and were allowed 15 s to turn around and an additional 30 s to jump from the tower platform. If hens did not turn around within 15 s or did not jump from the

platform within the allotted 30 s, an observer gently turned the bird around, and if still needed gently pushed the hen off the platform. The floor grid system was used to record the bird's landing location after each jump.

Video Analysis

During the flight test, hens jumped from a height of 155 cm 3 times to increase the likelihood of having at least one clear recording of their flight trajectory. One video per hen, that is, the first recording with the straightest jump with a minimum of 3 wingbeats, was chosen to be analyzed for wing and body kinematics. To determine the straightest jump, recordings were evaluated using landing location data and the direction in which they landed (turned body vs. facing the frontal camera). Videos were analyzed by 1 trained and blinded researcher.

All wingbeat visualizations, video analysis, and calculations were conducted using MatLab v2021a (2022, The MathWorks Inc., Natick, MA). The frontal camera videos were used to assess wing kinematics, including wingbeat frequency (Hz), wingbeat amplitude (rad) and angular velocity (rad/s) of the proximal wings. The lateral camera recorded the right side of the bird and was used to assess body kinematics, including resultant velocity 1 (RV1, m/s), resultant velocity 2 (RV2, in m/s), descent velocity (m/s), descent angle ($^{\circ}$), and acceleration (m/s^2).

Frontal View Video Analysis for Wing Kinematics

Frontal view video analysis tracked the 10 to 11 frames surrounding the highest point of the upstroke (Figure 3A) and the 10 to 11 frames surrounding the lowest point of the downstroke (Figure 3B) of both shoulders and wrists as the hen descended from the jump tower. The upstrokes and downstrokes of the first and last wingbeats were used for analysis. The first wingbeat was defined as the first complete wingbeat after the hen's feet had left the jump tower platform and

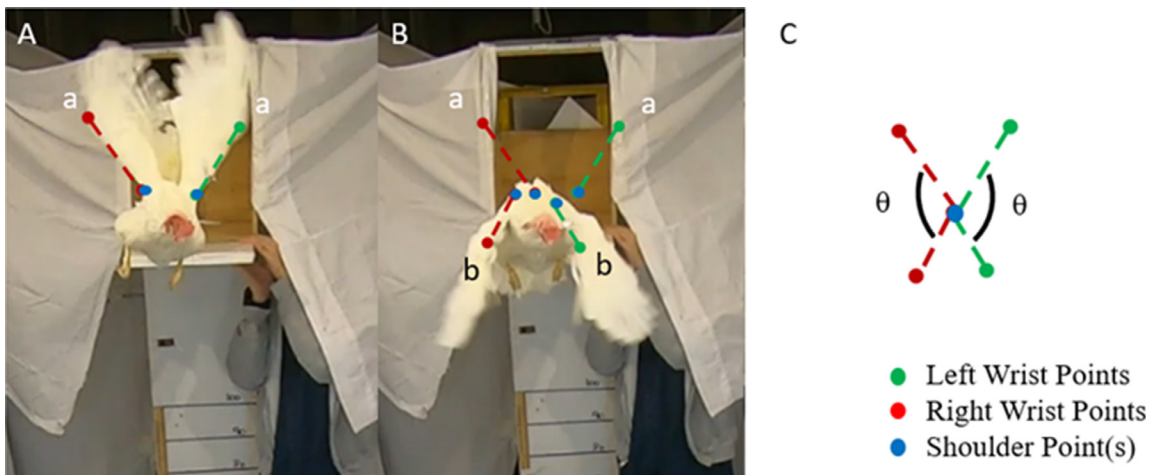


Figure 3. Examples of the top of the upstroke (A) and the bottom of the downstroke (B) for the same wing beat. Visualization of wing beat amplitude (C) using position vectors rooted at the shoulders and extending to the wrists at the top of the upstroke (a) and bottom of the downstroke (b).

the observer's hand was no longer touching the hen. The final wingbeat was defined as the last complete wingbeat before the hen went out of view or before both feet touched the ground.

Wing beat frequency, wing beat amplitude, and angular velocity of the left and right wings were calculated separately, as described in León et al. (2021), and averaged for analysis. In brief, wing beat frequency was calculated as the frame rate (frames/second) divided by the number of frames between the first and final downstroke, multiplied by the number of complete wing beats present between the first and final wingbeats. Wing beat amplitude was calculated as the angle (radians; θ) between the top of the upstroke and bottom of the downstroke of a single wingbeat, using position vectors rooted at the shoulder points and extending to the wrist points (Figure 3C). Angular velocity was calculated by dividing the amplitude in radians by the duration of the downstroke (in seconds). The difference in frames between the start and end of the downstroke divided by the frame rate was considered the duration of the downstroke. Using the averages of the first and final wing beat, asymmetries of wing beat frequency (**WBF** asymmetry, in Hz), wing beat amplitude (**WBA** asymmetry, in rad), and angular velocity (**AV** asymmetry, in rad/s) were calculated as the absolute difference between the left and right wings.

Lateral View Video Analysis for Body Kinematics

For the body kinematics, the tip of the upper beak was tracked using 3 single frames (Figure 4); 1) the highest

point of the first upstroke, 2) the highest point of the second upstroke or the highest point of the third upstroke, and 3) the lowest point of the final downstroke. A meter stick was placed in the middle of the hen's flight path to obtain a pixels-to-metric conversion factor, which was used to calculate the body kinematic variables.

Body kinematic measurements were calculated as described in León et al. (2021). In brief, to calculate the resultant velocities (RV1 and RV2) of the bird's wing beats, the horizontal and vertical velocities were determined first (Figure 4). The position of the upper beak point at the highest point of the upstroke (i.e., beginning of the downstroke) during the first and second wing beats were compared to a standardized point in the field of view. This was then used to measure the distance traveled. The traveled distance was divided by the total number of frames between the 2 beak points to calculate velocity (m/s). When applied to the horizontal and vertical planes, this calculation provides the horizontal and vertical velocities (m/s).

Horizontal velocity 1 and vertical velocity 1 were calculated using the first and second upstroke beak points and then used to calculate RV1 (m/s) by applying the Pythagorean theorem (Figure 4A, B). RV2 (m/s) was calculated similarly using the beak points of the bird at the beginning of the second upstroke and third downstroke, obtaining horizontal and vertical velocity 2 before applying the Pythagorean theorem (Figure 4B, C). Descent velocity (m/s) was calculated by averaging RV1 and RV2 (m/s). Descent angle ($^{\circ}$) was the dot product between the first beak position vector subtracted from the final beak position vector and a horizontal position vector. Resultant acceleration (m/s^2)

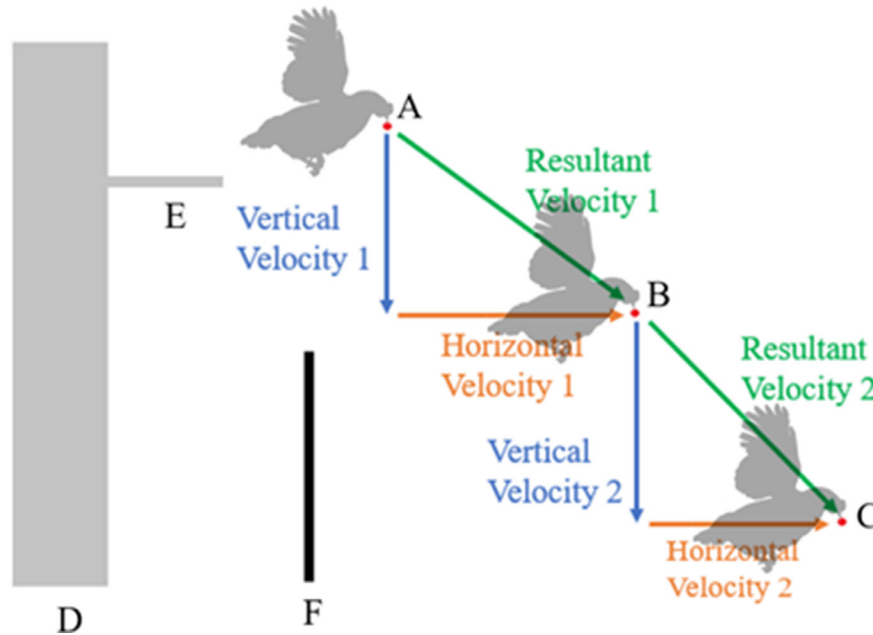


Figure 4. Schematic depicting the calculation of vertical and horizontal velocities between downstrokes for the purpose of calculating resultant velocity 1 and 2 (RV1, RV2, in m/s). Beak of the hen is indicated by a red dot in the diagram on the right. The lower beak is tracked in 3 different frames as the hen descends from the jump-tower apparatus (D), when the beak of the hen is at the beginning of the first downstroke (A) after both feet have left the platform (E), when the beak of hen is at the beginning of the second downstroke (B) and when the beak of the hen is at the beginning of the third downstroke (C). Before hens make their descent, a meter stick (100 cm; F) is shown in view of the camera to later determine the pixels-to-metric conversion factor. Diagram not to scale.

was calculated using the horizontal and vertical acceleration (m/s^2) applied to the Pythagorean theorem. To calculate vertical acceleration (m/s^2), the difference in vertical velocity (m/s) between the second to final beak positions and the first to second beak positions was divided by the difference in average time between the second to final beak positions and the first to second beak positions. Horizontal acceleration (m/s^2) was calculated similarly using horizontal velocity (m/s) (León et al., 2021).

Statistical Analysis

We tested for significant effects of exercise and strain upon all outcome variables using generalized mixed models (PROC GLIMMIX) in SAS (v.9.04, SAS Institute INC., Cary, NC). Distributions were assessed using the Akaike information criterion (**AIC**) to find the best fitting distribution for each outcome variable. There were 11 outcome variables analyzed in this study; 6 associated with wing kinematics (wing beat frequency, wing beat amplitude, angular velocity, WBF asymmetry, WBA asymmetry, AV asymmetry) and 5 associated with body kinematics (descent angle, acceleration, RV1, RV2, descent velocity).

Wing beat frequency (Hz), angular velocity (rad/s), WBA asymmetry (rad), decent angle (°), acceleration (m/s^2), RV1 (m/s), RV2 (m/s), and decent velocity (m/s) were analyzed using lognormal distributions to meet normality assumptions, whereas wing beat amplitude (rad), WBF asymmetry (Hz), and AV asymmetry (rad/s) were analyzed using a Gaussian distribution. Back transformed least-square (**LS**) means and standard errors (**SE**) are presented, unless otherwise specified. Pen (12 levels: 1 to 12) was added as a random effect and body weight was added as a covariate into all models. Treatment (2 levels: WAIR, control), strain (2 levels: white, brown) and their interaction were used as fixed effects. A Tukey-Kramer *P* value adjustment was used to account for multiple comparisons. *P* values less than 0.05 were considered significant.

RESULTS

Descriptive statistics such as means \pm standard deviations (**SD**) of the wing kinematic measurements (wing beat frequency (**WBF**), wing beat amplitude (**WBA**), angular velocity (**AV**), WBF asymmetry, WBA asymmetry, AV asymmetry), and body kinematic measurements (descent angle, acceleration, resultant velocity 1 (**RV1**), resultant velocity 2 (**RV2**), descent velocity) are presented in [Table 1](#) for white- and brown-feathered laying hens according to their exercise regime.

We did not observe significant interactions between exercise and strain for any wing or body kinematic variables (all $P > 0.05$). Among the wing kinematic variables, there were significant differences in WBF between strains where brown-feathered birds were about 0.4 Hz faster than white-feathered birds ($F_{1,41.89} = 4.42$, $P = 0.0417$; Figure 5). The mean values for the other

Table 1. Descriptive statistics (N , mean \pm SD, minimum, maximum) for the wing kinematic variables (wing beat frequency (WBF), wing beat amplitude (WBA), angular velocity, wing beat frequency asymmetry (WBF asymmetry), wing beat amplitude asymmetry (WBA asymmetry) and angular velocity asymmetry (AV asymmetry)) and the body kinematic variables (descent angle, descent acceleration, resultant velocity 1 (RV1), resultant velocity 2 (RV2) and descent velocity) of white- and brown-feathered laying hens that had been trained to perform wing-assisted incline running (WAIR) during 16 wk or not (CONTROL).

Kinematic variable	White-feathered						Brown-feathered					
	WAIR			CONTROL			WAIR			CONTROL		
	N	Mean (SD)	Min	Max	N	Mean (SD)	Min	Max	N	Mean (SD)	Min	Max
Wing kinematics												
WBF (Hz)	10	9.1 ± 0.67	8.0	10.4	12	9.3 ± 0.47	8.4	10.2	12	9.7 ± 0.50	8.9	10.6
WBA (rad)	10	103.0 ± 13.40	79.4	120.1	12	97.9 ± 14.31	78.6	122.1	13	106.1 ± 7.94	92.1	117.5
Angular velocity (rad/s)	10	34.6 ± 7.26	23.0	44.5	12	34.7 ± 4.18	27.5	40.8	13	39.5 ± 3.92	33.0	44.5
WBF asymmetry (Hz)	9	0.1 ± 0.16	0.0	0.3	12	0.1 ± 0.16	0.0	0.4	13	0.3 ± 0.29	0.0	0.9
WBA asymmetry (rad)	10	13.5 ± 11.64	2.1	32.1	11	20.0 ± 11.23	9.8	39.0	12	10.6 ± 7.12	2.1	23.8
AV asymmetry (rad/s)	10	4.8 ± 3.94	0.7	8.2	11	4.4 ± 2.43	2.1	9.8	13	3.1 ± 2.42	0.7	8.2
Body kinematics												
Descent angle (°)	10	37.0 ± 4.73	31.8	44.6	12	34.1 ± 5.17	26.1	43.6	13	30.2 ± 5.75	18.5	37.8
Descent acceleration (m/s ²)	10	2.0 ± 0.63	1.2	2.8	12	2.9 ± 0.86	1.8	4.5	13	3.3 ± 1.12	1.8	2.8
RV1 (m/s)	10	2.4 ± 0.30	1.8	2.8	12	2.3 ± 0.35	1.7	2.8	13	2.6 ± 0.26	2.2	3.1
RV2 (m/s)	10	2.5 ± 0.41	1.6	3.0	12	2.6 ± 0.42	1.9	3.3	13	2.8 ± 0.38	2.3	3.7
Descent velocity (m/s)	10	2.5 ± 0.35	1.7	2.9	12	2.4 ± 0.38	1.8	3.1	13	2.73 ± 0.31	2.2	3.4

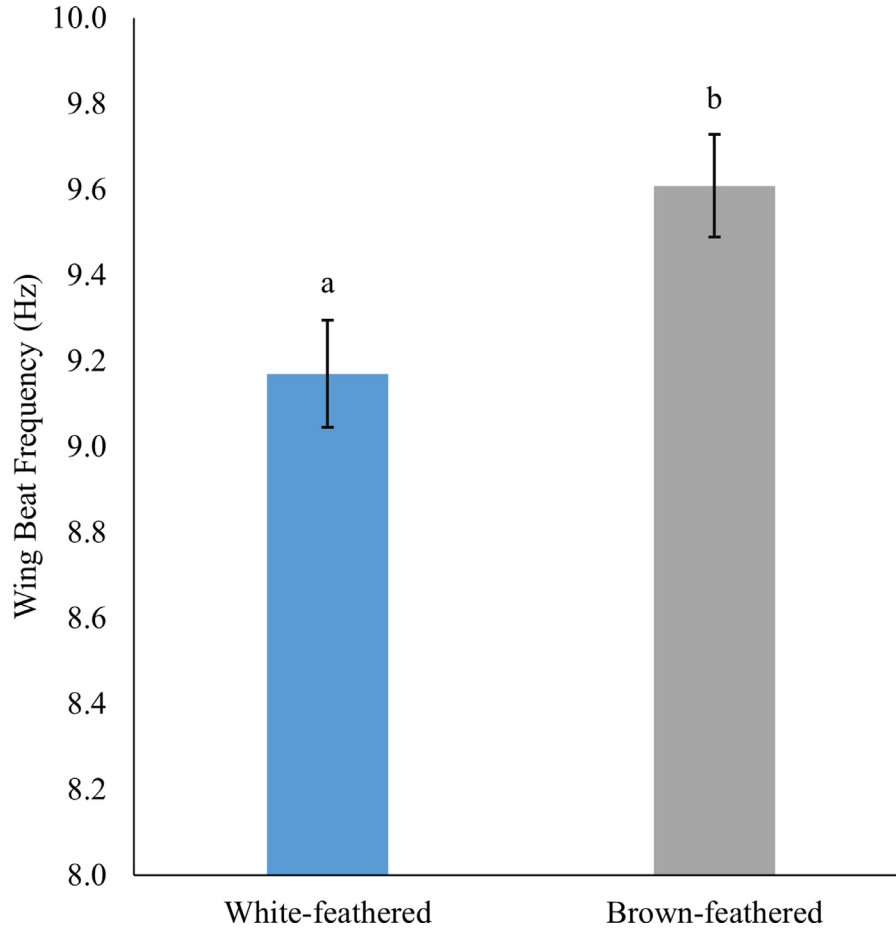


Figure 5. LS means \pm SE for wing beat frequency (WBF, Hz) of white- and brown-feathered laying hens. Note that the y -axis of the figure does not start at 0 Hz due to the biology of the trait (WBF of 0 Hz is not biologically relevant) to allow for a better visual comparison of the variance between the strains. Columns that do not share a letter superscript are significantly different ($P < 0.0$).

wing kinematics variables we measured did not exhibit significant differences according to exercise or strain (all $P > 0.05$, [Supplementary Table 1](#)).

Within the body kinematic measurements, resultant velocity 1 (RV1) was significantly greater in the WAIR groups than in the CONTROL groups ($F_{1,43} = 4.75$, $P = 0.0348$, [Figure 6](#)). As RV1 was defined as the first half of their descent, from jumping off the jump tower platform until about midway through their flight path, this reflects their take-off velocity. The WAIR birds therefore, had faster take-off velocities by about 0.2 m/s in both strains of laying hens in comparison to the CONTROL group. There was also an overall trend toward slower descent accelerations in WAIR (2.46 ± 0.20 m/s²) vs. CONTROL (3.11 ± 0.25 m/s²) groups ($F_{1,5.603} = 4.19$, $P = 0.0901$). Remaining body kinematic variables were not affected by exercise, strain or their interaction (all $P > 0.05$, [Supplementary Table 1](#)).

Body weight as a covariate did not significantly impact any of the wing kinematic measurements ($P > 0.05$). It, however, significantly affected the body kinematic measurements, specifically RV1, RV2, descent velocity and descent angle. Generally, as body weight increased, RV1, RV2 and descent velocity increased by 0.4 ± 0.10 m/s ($F_{1,43} = 15.66$, $P = 0.0003$), $0.5 \pm$

0.13 m/s ($F_{1,39.91} = 17.39$, $P = 0.0002$) and 0.5 ± 0.11 m/s ($F_{1,43} = 16.54$, $P = 0.0002$), respectively, and descent angle decreased by $0.4^\circ \pm 0.17^\circ$ ($F_{1,41.82} = 4.50$, $P = 0.0399$).

DISCUSSION

Our results provide partial support for our hypothesis that training using WAIR would have an effect on the flapping flight in laying hens. In particular, trained birds exhibited higher initial flight velocity. Contrary to our hypothesis, however, overall descent velocity and angle did not vary with training. In addition, we found that brown-feathered birds used greater wingbeat frequencies than white-feathered birds, which is consistent with their higher wing loading ([LeBlanc et al., 2017](#)).

Effects of WAIR on Wing and Body Kinematics

Take-off velocities (RV1) were significantly greater in WAIR-trained birds (+6.5%) compared to CONTROL birds. During take-off, birds mainly rely on their hindlimbs as jumping into flight is a more efficient means of

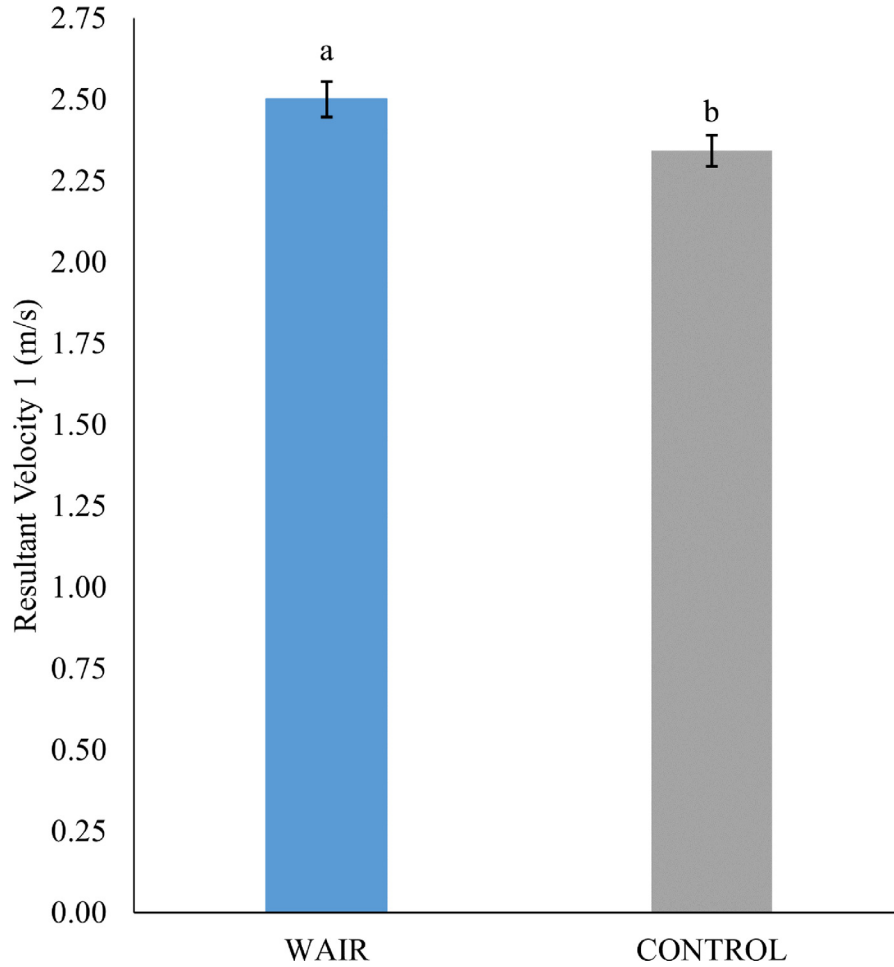


Figure 6. LS means \pm SE of the resultant velocity 1 (RV1; m/s) of white- and brown-feathered laying hens in WAIR and CONTROL groups. RV1 is the take-off velocity, representing the first half of the descent of the bird. Columns that do not share a letter superscript are significantly different ($P < 0.05$).

creating propulsion than wing flapping alone (Parslew et al., 2018). The hindlimbs can be responsible for up to 94% of the initial flight velocity in zebra finches (*Taeniopygia guttata*) and up to 95% in diamond doves (*Geopelia cuneata*) (Provini et al., 2012). Consequently, it is possible that strengthening of the hindlimb muscles through the WAIR exercise contributed to the significantly higher take-off velocities observed as no differences were found in the overall descent velocity or in RV2, meaning birds landed at approximately the same speeds. The ability of the hindlimbs to produce enough force during take-off is extremely important for conserving energy as flapping flight is very energetically demanding (Provini et al., 2012). This is also essential for making quick and efficient transitions to the air to successfully escape predators in the wild or negative social interactions such as aggressive or severe feather pecking in a commercial setting. A tendency toward less acceleration in WAIR-trained birds was observed. It is reasonable to hypothesize that laying hens are able to anticipate declines as past studies have shown success in anticipating inclines (LeBlanc et al., 2018) and birds reared with access to vertical structures display less hesitancy to cross visual cliffs (Jones et al., 2023). Therefore, WAIR birds may have been able to practice these skills during the exercise training to make

better judgments and decelerate during their descent from the jump tower, however this needs to be explored further in future studies.

Body weight significantly increased RV1, RV2, and descent velocity. Any characteristic speed of a flying animal is expected to scale proportional to the square root of wing loading (Ellington, 1991). Increasing body weight probably increased wing loading, although we cannot test for this as we did not measure wing area (León et al., 2021), with hens flying in similar conditions as in our study, report that increasing body weight increased the asymmetry of angular velocity (i.e., the difference of angular velocity produced between the left and right wings), but did not have significant effects body velocity. Reconciling these different results will require further study of the effects of wing loading on wing kinematics and flight velocity in hens.

While significant differences in take-off velocity (and a tendency for less acceleration during descent) between WAIR and CONTROL groups are reported in this study, many other wing and body kinematic variables remained similar between groups. It is noteworthy that many characteristics of the home pens were significantly different from the testing arena. For example, the amount of space that the testing arena provided for

descent was much larger than their home pens. Although birds were allowed a period of time to habituate to the jump tower apparatus and testing room, future studies can investigate how rearing environments of varying space may affect the flight kinematic measurements analyzed in the present study. This line of research is especially relevant since aviaries vary vastly in the amount of space available for aerial descent.

Effects of Strain on Wing and Body Kinematics

Brown-feathered birds had 1.05 times faster WBF than their white-feathered counterparts. While white- and brown-feathered laying hens share many similarities, there are some key differences in body shape and behavior between the strains which may account for this difference (Silversides et al., 2012; de Haas et al., 2013; Ali et al., 2016; Garant et al., 2022). White-feathered birds tend to have lower wing loading (body weight per unit wing area (León et al., 2021) and spend more time on elevated equipment compared with brown-feathered birds (Ali et al., 2016; Garant et al., 2022) who generally have higher wing loading. Thus, brown-feathered hens may have needed to increase their WBF to create sufficient power output and achieve similar descent velocities as the white-feathered hens (Provine et al., 1984; Garant et al., 2022).

No other differences were found in the remaining wing and body kinematics despite strain differences being reported in the musculoskeletal system and behavior. Although similar in many aspects, many studies have found that white- and brown-feathered hens respond differently to the provision of equipment such as perches, more complex housing options (ramps, multiple tiers/platforms, and perches) and additional space for locomotion (Kozak et al., 2016; Ali et al., 2019; Chew et al., 2021; Pufall et al., 2021; Garant et al., 2022). Even as pullets, white-feathered birds exhibit increased rates of locomotion, higher bone breaking strength of the tibiae and heavier pectoralis-to-body mass ratios when reared with more space and elevated equipment (Chew et al., 2021; Pufall et al., 2021). Taken together, these studies indicate that white-feathered strains benefit and respond more positively to rearing in more complex environments, while little effect is seen in brown-feathered strains (Pufall et al., 2021; Rentsch et al., 2023a,b). It is possible, however, that the lack of similar effects in brown-feathered birds seen in these past studies may reflect their natural space usage, preference, and motivation rather than their potential to benefit from the addition of these equipment and/or increased locomotion. In contrast, the present study used a more structured and routine approach where both strains ultimately finished the trial with performing equal amounts of locomotion and ramp usage. It appears that under the used exercise regime white- and brown-feathered birds did not respond differently in regards to wing- and body-kinematics. Possibly, the early exercise programmed the white- and brown-feathered birds to be

more similar, however, some strain differences were still observed. Further research should therefore continue to consider strain differences to help inform the design of housing systems.

CONCLUSIONS

An exercise regime of WAIR increased initial flight velocity during descent in white-feathered and brown-feathered birds, which we interpret as evidence of leg strengthening. This may contribute to improving hen welfare if increased takeoff velocity reduces the power requirement for supporting their weight and thus enhances their power available to maneuver. The key variables of total descent velocity and angle were not significantly affected by exercise. Brown-feathered birds had greater wing beat frequencies which we interpret to be due to compensation for higher wing loading.

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DISCLOSURES

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in the present study.

SUPPLEMENTARY MATERIALS

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.psj.2023.103375](https://doi.org/10.1016/j.psj.2023.103375).

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