Natural take-off flight performance is repeatable and scalable in mixed flock tit species

Kyu Min Huh[1]*, Marco KleinHeerenbrink[1], Steven J Portugal[1] and Graham K. Taylor[1]

[1]Department of Biological Sciences, The University of Oxford, Oxford, OX1 3SZ, UK

Modelling small bird flights is challenging, as small birds (< 20 g) rarely engage in steady-state flights, as assumed by traditional flight models. Additionally, their flights are difficult to measure in the field due to the mass of high-resolution GPS loggers and the low resolution in lightweight geolocators. This study aimed to measure and model spontaneous, non-steady-state take-off flights of wild tit species that forage in mixed flocks during winter, despite differences in body sizes and ecological niches. We recorded 1434 spontaneous flights from 49 individuals of great tits (*Parus major*), blue tits (*Cyanistes caeruleus*), and marsh tits (*Poecile palustris*) in the Paridae family using two automated RFID-infrared tunnels. We developed a power margin model to predict in-flight acceleration based on initial velocity, scaled by species-specific wing loading. Lastly, we tested the repeatability of flight metrics to assess whether flight may be interpreted as an individual behavioural trait. We found significant differences in initial velocity ($p = 0.004$) and in-flight acceleration ($p < 0.001$) between species. The observed difference in the in-flight acceleration aligned with the power margin model prediction. Finally, we found significant individual repeatability in both initial velocity ($R = 0.21$) and in-flight acceleration ($R = 0.11$). Our findings suggest that the flight performance of small birds can be consistently measured in the field, modelled beyond steady-state assumptions, and interpreted as an individual behavioural trait.

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Author for correspondence:

Kyu Min Huh

kyumin.huh@biology.ox.ac.uk

1. Introduction

Flight performance is essential for foraging and predator escape in most birds [1,2]. Therefore, it is important to model flight performance at the individual and species level to fully understand their ecology. Studying flight performance of small passerine birds in the natural environment provides an opportunity to assess how morphology and performance shape the ecology of these highly adaptable and manoeuvrable species [3,4]. However, small birds (<20g) often deviate from mathematical predictions of flight speed, as such models assume steady-state flight; in equilibrium at constant velocity, such as cruising flight [5,6]. Small birds rarely fly in steady-state, either accelerating or decelerating [7,8]. This capacity to shift acceleration within split seconds can determine survival during escape in the natural environment [1,9].

Measuring small bird flight in the wild is challenging. Small birds in captivity have been studied in wind tunnels or under multiple high-speed cameras at take-off, landing, foraging flight, and cruising flight [10–13]. However, studying performance in the laboratory environment inevitably excludes the ecological context in which the flight performance naturally occurs [14]. In the field, durable, bird-attached accelerometers, magnetometers, and satellite GPS tags continue to reveal fine-scale behavioural plasticity in flight performance [15–19]. Yet, these sensors are nearly as heavy as small passerine birds (12-90g), and have been size-limited to medium to large birds ranging from pigeons (*Columbidae*) to condors (*Cathartidae*) and albatrosses (*Diomedeidae*) [16,20,21]. Light-sensitive geolocators are now light enough to be deployed on arctic warblers (*Phylloscopus borealis*, 8.5 - 10g), but lack the resolution required to quantify local movements of resident birds [22,23]. A recent development in accelerometer technology has reduced the device mass to 0.5-0.8g, enabling deployment on great tits (*Parus major*, ca 18g) and pine siskins (*Spinus spinus*, ca 15g) to quantify daily activities [24,25]. This opens opportunities to estimate flight activity in small birds over 10 grams over extended periods, but its use remains limited by the 5% body-mass rule for birds under 10g [26].

Small birds such as zebra finches (*Taeniopygia* sps.) and hummingbirds (*Trochilidae*) have been frequently studied in the laboratory due to their characteristic flight modes, such as flap-and-bounding flight [13,27] and hovering [28–30]. As two of the most widely studied passerine species in the wild [31], great tits (*Parus major*) [32] and blue tits (*Cyanistes caeruleus*) [33] have been recorded for their take-off flight speed in the field, in addition to laboratory measurements [34,35]. These studies show that flight performance depends on morphology, sex, age, and context. Blue tits with higher wing loading (bodyweight relative to wing area) exhibited lower acceleration [34], and egg-laying female blue tits were 14% heavier and flew 20% slower [33]. Sex and age potentially have interaction effect on flight performance, as adult male great tits flew faster than juvenile females with higher body mass [32]. Lastly, birds most likely modify their flight performance depending on the situation, as great tits flew faster during escape take-offs than during spontaneous take-offs [35].

Yet, individual repeatability in flight performance remains unmeasured in these species. This may be due to the difficulty in acquiring a large number of repeated flight recordings of the same individuals, particularly among small passerines. Other bird families demonstrated high individual repeatability in flight metrics, such as in leg force at take-off (R = 0.60) and landing (R = 0.72) in starlings (*Sturnis vulgaris*), power (R = 0.75) and acceleration 0.17 seconds after take-off (R = 0.72) in least auklets (*Aethia pusilla*), and route efficiency (R = 0.86) and mean distance travelled (R = 0.86) in homing pigeons (*Columba livia*), but the sample sizes were limited to 35 flights of 16 auklets [36] and 54 flights of 9 pigeons [37] in the field, and 202 take-offs and 213 landings from 14 starlings in a laboratory setting [38].

Tits in the Paridae family are promising candidates for repeated measurements of natural flight performance of multiple species due to their affinity with artificial feeders and nest boxes, and their tendency to forage with other tit species [39,40]. Tits of various niches, body sizes and bod masses form mixed-species flocks while foraging [40,41]. Great tits (ca 18g) are nearly twice as heavy as blue tits (*ca* 10g) [42,43]. Blue tits are similar in size to marsh tits, but exhibit more erratic movements, and forage on more arthropods [31]. Marsh tits (*Poecile palustris*, ca 10g) are subordinate to more abundant great tits and blue tits and rely on caching seeds [43]. The mixed-species flock, despite the size difference and dominance hierarchy between its members, is known to benefit from increased foraging efficiency and dilution of predation risk during predator escape [40,41,44–46]. This suggests that the members of the mixed-species flock may demonstrate appreciable similarity in flight speed, as a notable difference from the group norm would be disadvantageous during predator escape [47,48]. However, when a bird is foraging alone while a predator is not immediately visible or inferred, the following submaximal take-off performance may reflect morphological constraint more directly [35].

Take-off is initiated by the legs, which serve as the primary accelerators, contributing 80% of kinetic energy exerted during this crucial step [10]. Birds with equal proportions of leg muscles relative to their body mass should take off at the same speed, regardless of size [49], as the muscle work exerted in a single contraction is proportional to muscle mass. Assuming equal proportions of leg muscles to their body mass, all species in this study are expected to show similar leg acceleration while feet are in contact with the ground. Once the feet lose contact from the ground, species-specific differences in wing loading and body length should begin to affect flight speed. Whether these morphological differences result in biologically meaningful variation in flight speed among ecologically similar mixed-species group, however, is unknown.

To model non- steady-state take-off of small birds in the natural environment, firstly, we automatically recorded 1434 spontaneous take-off flights of 34 blue tits, 12 great tits, and 4 marsh tits. We used two custom-made infrared tunnels paired with RFID feeders to measure individual take-off flight velocities and accelerations. Since great tits have the highest wing loading and blue tits the lowest among the three species [50], we predicted that great tits would exhibit lower in-flight acceleration compared to the other species. In addition, assuming similar leg muscle proportions relative to their respective body mass [51], we expected similar leg acceleration, reflected in initial velocity, across all species. Secondly, we developed a power margin model to predict in-flight acceleration from the measured initial velocity, scaled by species-specific wing loading. We used the concept of power margin to predict in-flight acceleration from the observed initial velocity, based on the premise that birds can accelerate when their available muscular power exceeds the power required for the observed initial velocity. Lastly, we assessed individual repeatability in initial velocity and in-flight acceleration to assess whether flight performance in tit species is consistent within individuals to allow ecologically meaningful interpretations.

2. Methods

Study systems and data collection

This study is set in the long-term study population in Wytham Woods, Oxford (51°46’N, 1°20’W) in 385 ha of woodland. Since 2007, all nestbox-breeding great tits, blue tits, marsh tits, and their 14-day-old hatchlings have been fitted with a plastic passive-integrated transponder

(PIT) ring containing a unique identifier code (IB-technology), in addition to a metal British Trust for Ornithology (BTO) ring fitted since the 1960s [32,34]. We used 2.3mm diameter EM4102 PIT bird tags for blue tits and 2.6mm EM4102 tags for great tits (both 2.3mm and 2.6mm tags ~0.1 g, Eccel technology Ltd). The metal rings used for all tits were below 0.07 g. The PIT tag and metal ring together comprise approximately 1.6 % of blue tit's body mass and 0.9 % of great tit's body mass. Immigrant birds and other birds undetected in the breeding season are mist-netted and fitted with both rings in the autumn and winter months. Birds captured during mist-netting are aged and sexed based on plumage, morphology, and breeding records, and their body mass, wing chord length, fat score, and muscle score are recorded [54–56].

We measured the flight speed and acceleration of PIT-tagged birds following spontaneous take-off from a feeder-perch with a radio frequency identification (RFID) antenna at the end of a 0.75 m long flight tunnel (figure S1). The flight tunnel was equipped with three rows of infrared emitters and receivers located 0.03 m, 0.26 m and 0.56 m from the feeder-perch. As a bird flew out of the tunnel after feeding, the start and end times of the passage event were recorded using a microcontroller (Arduino Mega 2580) logging the exact times at which each beam was broken and restored (figure S1). The feeder logged a time-stamped RFID for any visiting bird with a PIT tag, triggered by the bird's weight on the perch (figure S1, custom-made by NatureCounters).

We calculated the bird's initial flight speed and end flight speed by dividing the distance between the rows of infrared beams by the duration of flight between those rows, based on the time each beam was restored. The margin of error was estimated to be 3cm, corresponding to the spacing between each infrared sensor pair in a row. Assuming that the tit individuals may reach flight speeds around 3 m/s during spontaneous take-offs [33,57], the temporal precision of our measurement system was estimated at 0.01s. Flight metrics were reported to two decimal places to reflect this level of precision. The initial flight velocity served as a proxy to leg acceleration as the very first performance metric collected at each take-off. We calculated the in-flight acceleration by the difference between the end flight speed and initial flight speed, divided by the half duration of the flight from the first row to the third row assuming constant acceleration.

We accounted for weather conditions in our analyses (for measurement methods, see supplementary methods), as other studies have shown that these can affect flight performance. For example, wind velocity and direction influenced flight speed [6,15,58,59], low ambient temperature increased fat reserves [42,60,61], and high humidity may correlate with high aerodynamic drag and the metabolic cost of flight [52,62].

Power margin model

The maximum horizontal acceleration of a flying bird can be predicted from the difference between the power available from the muscles and the power required for steady flight. This difference is known as the power margin [52], usually referred to in the context of climbing flight [53]. To compare between different species within the same family great tits, blue tits, and marsh tits , we normalised the power curve based on the hover condition. We show that differences in acceleration should be expected due to differences in wing loading and due to any variation in muscle fraction, i.e. variation in fat load.

The forward acceleration (a) that a bird can achieve in flight depends on how much excess power a bird has available (ΔP) over that required to maintain steady horizontal flight (P_{req}) at the current flight speed (U):

$$a = \frac{\Delta P(U)}{mU}$$

where m is the bird's mass. We can manipulate this equation (see Appendix [sec:DerivationPowerMarginModel]) to the form:

$$a = \frac{1}{\hat{U}}\left[c_1 \frac{\mu}{\sqrt{W}} - c_2 \hat{P}_{req}(\hat{U})\right]$$

where $\hat{U}$ is the normalised flight speed, $\hat{P}_{\mathrm{req}}$ the normalised power required for steady flight, and c_1 and c_2 are positive constants representative for the members of the tit family Paridae. The ratio $\mu / \sqrt{W}$ is the muscle fraction (μ; muscle mass to total body mass) to the square root of the wing loading (W, weight per wing area). Here, all velocities are normalised by the hover-induced velocity: $v_{\mathrm{h}} = \sqrt{2W/\rho\pi A}$ (with ρ is the air density, and A the wing aspect ratio).

Equation [eq:acceleration_proportionality] shows that birds with a higher muscle fraction μ or a lower wing loading W will achieve a higher acceleration a at any normalized airspeed $\hat{U}$. Moreover, as $\hat{P}_{\mathrm{req}}(\hat{U})/\hat{U}$ is a U-shaped function of airspeed, peak acceleration will be achieved at some unique normalized airspeed $\hat{U}^{¿}$ for a given ratio $\mu / \sqrt{W}$. The actual airspeed $U^{¿}$ at which this occurs will be lower in birds with lower wing loading because $U^{¿} = \hat{U}^{¿} v_h \propto \sqrt{W}$. Hence, if individual birds lower their fat reserves in response to perceived predation pressure, then this will increase their muscle fraction and decrease their wing loading, enhancing their acceleration in flight and causing them to reach their peak acceleration at a lower airspeed and hence sooner after take-off. Likewise, as great tits have a higher wing loading than blue tits, we would always expect them to achieve lower accelerations in flight unless their higher wing loading were compensated by a higher muscle fraction.

Furthermore, even if the ratio $\mu/\sqrt{W}$ were the same for both species, we would still expect blue tits to achieve the same acceleration at a lower actual airspeed. Species with a higher wing loading will therefore require a more powerful contribution from their leg muscles at take-off to avoid being left behind in collective escape flight.

Power margin model simulation

To compare the simulation results to our observed metrics time to travel a set distance, we integrated the acceleration model twice using an Ordinary Differential Equations (ODE) solver. We used the initial velocity in this simulation as a free parameter to achieve a best fit with the observed timings of birds flying through the tunnel. We calculated wing loading from body mass and wing area of blue tit and marsh tit obtained from Greenwalt (1962)[63] and those of great tit from Alerstam et al (2007)[64].

Model analysis

To detect the between-species variation in flight speed, we used linear mixed models with species, sex, age, and headwind as fixed effects, and ring identification as a random effect to control for individual variation. To distinguish which pair of species showed a significant difference in flight speed in linear models, we performed pair-wise comparisons using least means with package “emmeans” [65]. Response variables for both datasets were initial velocity, end velocity, average velocity, and in-flight acceleration.

Before fitting full models, we checked the collinearity of covariates and outliers using the “PerformanceAnalytics” and “Envstats” packages [66,67]. Day and hour variables were excluded from the baseline models as they were correlated with climate variables. Model assumptions of linearity of continuous variables, heteroskedasticity, independence, and normality of fixed and random effect residuals were assessed with the “redres” package [68, 69]. We chose headwind as the representative climate variable as air temperature and humidity were both correlated to headwind. Headwind also better explained the data than others as a single climate term.

We conducted model averaging to identify the best supported model for each of the response variables using the “MuMIn” package [70,71]. The best supported model was identified with the lowest Akaike Information Criterion (AIC) and highest Akaike weight among multiple candidate models within the $\Delta AIC < 5$ threshold [71]. For in-flight acceleration, the top two models, one including species alone and the one with species and sex together, produced identical Akaike weights (0.18). We chose species and sex as the best model predictors for in-flight acceleration to fully assess their effects. The best models for end velocity and average velocity both included headwind as the sole predictor. We report the effects of headwind in the end velocity and average velocity models with full data with outliers, but caution is required in interpreting the results as both models still violated the normality of residuals assumption after omitting outliers and applying logarithmic transformations to the response variables. Lastly, the best models that fulfilled model assumptions were evaluated with type III Wald test with Kenward-Roger approximation for degrees of freedom [72] using “car” package [73] and false discovery rate to minimise Type I error [74,75]. The best models included outliers as these made little difference to model assumptions.

The individual repeatability and variance for initial velocity and in-flight acceleration were assessed on the best models using the "rptR" package [76]. The significance of repeatability was assessed using likelihood ratio tests and 10,000 parametric bootstraps. We reported standard errors for repeatability values to reflect variability across bootstrap samples, and standard deviations for the number of flights per individual and flight metrics per species to capture variability within each species population.

3. Results

We found significant differences in initial velocity (type III Wald test; $F_{2,45.7} = 6.39$, $p = 0.004$) and in-flight acceleration ($F_{2,39.1} = 12.8$, $p < 0.001$) between species (figure 1, 2). Species alone best explained variation in initial velocity (Akaike weight = 0.60), whereas the combination of species and sex best explained in-flight acceleration (weight = 0.18). Headwind as the sole predictor best explained both end velocity (weight = 0.92) and average velocity (weight = 0.89).

Great tits showed higher initial velocity and lower in-flight acceleration compared to blue tits (figure 1). Estimated initial velocity (mean ± SE) was highest in great tits at 2.83 ± 0.081 m/s, followed by marsh tits at 2.65 ± 0.119 m/s, and blue tits at 2.51 ± 0.042 m/s. Estimated in-flight acceleration (mean ± SE) was highest in blue tits at 3.98 ± 0.43 m/s², followed by marsh tits at 1.30 ± 1.15 m/s², and great tits at 0.70 ± 0.74 m/s² (table S2). This agreed with the power margin model, which predicted lower in-flight acceleration of great tits compared to blue tits (figure 2). Marsh tits did not differ in flight performance from other species and were omitted from the power margin model due to a large variance in data collected from four individuals (figure 1,2).

Predictions from the power margin model for tunnel transit times and for relative velocity and acceleration between blue tits and great tits closely aligned with the observed flight performance (figure 2). However, the power margin predicted line fell below the measured initial velocity means for great tits, and this discrepancy was larger than for blue tits (figure 2B). The wing loading used in the power margin model for blue tits and great tits was expected to represent our study population as the body mass means used for wing loading per species (19g for great tits 11g for blue tits) matched with the measured body mass means (18.5 ± 0.70 g for greats tit 10.8 ± 0.60 g for blue tit). It could be possible that great tits have morphological attributes in addition to their wing loading that enable them to outperform what is expected of them from wing loading, such as leg morphology more adapted for ground-up take-off compared to blue tits and marsh tits that often forage in canopies [41, 51].

Flight performance metrics were significantly repeatable within individuals for initial velocity ($R = 0.21 \pm 0.04$ (s.e.), $p < 0.001$, figure S2) and in-flight acceleration ($R = 0.11 \pm 0.03$ (s.e.), $p < 0.001$, figure S2). The raw flight data points reflect the difference between the species and individual repeatability shown in the model means of initial velocity and in-flight acceleration (figure S3). The individual differences accounted for 21% and 11% of variance in the best models of initial velocity and in-flight acceleration, respectively (table S3).

End velocity and average velocity each increased by 5% ($F_{1,1431.2} = 21.4$, $p < 0.001$) and 4% ($F_{1,1412.4} = 13.4$, $p < 0.001$) for each unit increase in headwind (m/s; table S2). However, headwind only explained 1% of variance in these response variables, while individual differences accounted for 23 % and 25 %, respectively (table S2). Caution is required when interpreting these results, as both models did not satisfy assumption of residual normality.

Blue tits visited the tunnels (7 flights per individual per day) significantly more often than great tits (2.5 flights per individual per day, table 1). Marsh tits did not show a difference in visits to either species. In the raw data before model fitting, the three species exited the tunnel in 0.21 ± .05 seconds on average. Great tits were significantly faster in the first 0.26-metre section (Welch two sample *t*-test, $t = 3.94$, df = 192, $p < 0.001$) but similar with blue tits in the second 0.30-metre section (Welch two sample *t*-test, t = -1.61, df = 207, $p = 0.11$, table 2). The average weather estimates during the study period were 11 ± 1.6 Celsius, 3.2 ± 1.0 m / s to the southwest and 78 ± 10 % humidity.

Table 1. Number of individuals and number of flights per individual by species, sex and age in Mean ± SD.

species	category	no. of individuals	no. of flights per individual
Blue tits	female	15	33.7 ± 18.9
	male	17	32.8 ± 26.2
	unsexed	2	54.5 ± 17.7
	first-year	22	33.6 ± 24.6
	adults	12	36.0 ± 20.0
	total	34	34.5 ± 22.8
Great tits	female	4	15.8 ± 17.4
	male	8	10.6 ± 10.5
	first-year	10	11.4 ± 11.5
	adults	2	17.0 ± 22.6
	total	12	12.3 ± 11.0
Marsh tits	total	4	28.5 ± 11

Table 2. Mean ±SD of the raw flight metrics between species in speed (m/s), acceleration (m/s^2), and exit time (s).

	Blue tits	Great tits	Marsh tits
Initial velocity (m/s)	2.53 ± 0.45	2.84 ± 0.62	2.62 ± 0.51
End velocity (m/s)	2.94 ± 0.41	2.87 ± 0.48	2.85 ± 0.41
In-flight acceleration (m/s^2)	3.89 ± 4.43	-0.02 ± 5.30	1.96 ± 3.91
average velocity (m/s)	2.71 ± 0.38	2.83 ± 0.49	2.71 ± 0.44
First section exit time (ms)	107 ± 30	97 ± 28	106 ± 44
Second section exit time (ms)	105 ± 27	108 ± 22	108 ± 19
Total exit duration (ms)	212 ± 47	206 ± 45	214 ± 53

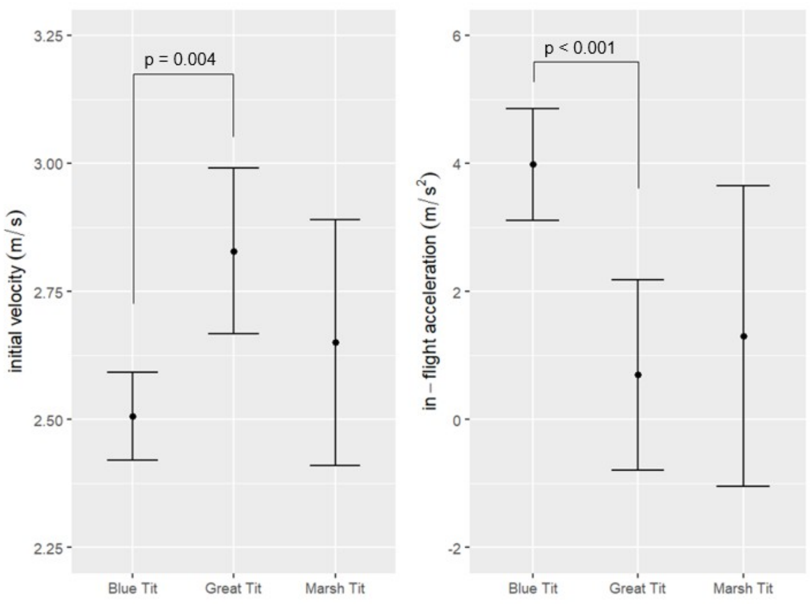

Figure 1. Comparison of model means of initial velocity and in-flight acceleration among three species (number of individuals, number of flights): Blue tits (33, 1172), great tits (12, 148), and marsh tits (4,114). Least square means and 95% confidence intervals are calculated from linear mixed models of initial velocity and acceleration with individual variation as random effects. Pairs with significant values are linked. The model structure and candidate models can be found in table S1.

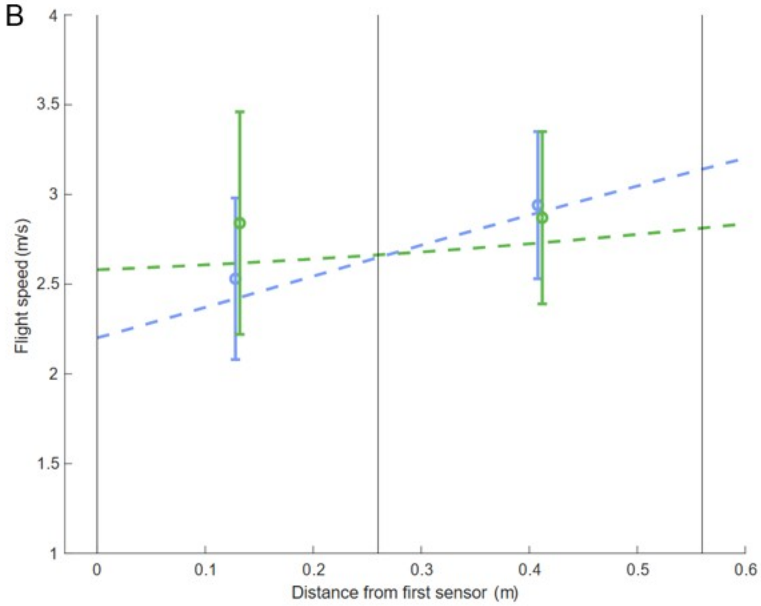

Figure 2. A) Simulation of the timing of blue tits (blue) and great tits (green) along the tunnel using the power margin model. B) Simulation of blue Tit (blue) and great tit (green) speed along the tunnel using the power margin model. Solid circles and whiskers indicate Mean ± S.D. from the measured data (table S1). Dashed lines are predictions by the power margin model given initial velocities measured per species.

4. Discussion

We found that natural take-off flight performance is repeatable and scalable by species-specific wing loading in mixed tit species flocks. Our custom infrared tunnels successfully detected between-species differences in natural flight performance. The observed differences in initial velocity and flight acceleration between great tits and blue tits, consistent with the power margin model, highlight that flight performance in small birds can be scaled by wing loading under the assumption of non- steady-state flight. Great tits, which have higher wing loading than blue tits, exhibited lower in-flight acceleration despite having higher measured initial velocity. Our flight measurements between great tits and blue tits correspond with the prediction from the power margin model. Intraspecifically, blue tits with higher wing loading also demonstrated lower instantaneous acceleration in a laboratory setting [34].

Admittedly, the observed 0.013 s difference in the exit time over the first 0.26 m between blue tits and great tits is close to the infrared tunnel's expected temporal resolution of 0.01 s, based on a 0.03 m spacing of infrared sensors and assumed initial velocity of 3 m/s. Since temporal resolution is calculated as spatial resolution divided by velocity, a 0.013s timing difference in the exit time can only be reliably detected at flight velocity of 2.30 m/s or higher. To test whether this 0.013 s difference reflects a true biological signal rather than measurement noise, we repeated the analysis using only flights with initial velocities ≥ 2.30 m/s (1035 flights of 48 individuals), with species, sex, age, and headwind as predictors and individual as random effects. The results still showed a significant species effect on initial velocity (type III Wald test; $F_{2, 36.6} = 13.12$, $p < 0.001$) and in-flight acceleration ($F_{2, 36.9} = 7.76$, $p < 0.001$).

The significant repeatabilities of initial velocity and in-flight acceleration suggest that flight performance can be studied as a consistent individual behavioural trait. The repeatability values of 0.21 and 0.11 found in initial velocity and in-flight acceleration, respectively, align with the previously reported values in this family for risk-taking behaviour ($R = 0.26$, great tits; $R = 0.18$, blue tits), exploratory behaviour ($R = 0.27 - 0.48$, great tits), and reproductive behaviour ($R = 0.18$, marsh tits) [76,77]. The proportions of variance explained by individuals (23% and 25%) overshadow those by headwind (both 1%) to the end velocity and average velocity models. The violation of residual normality assumption in these models and yet the significant positive association between headwind and the measured flight speeds together, suggest that the wind effect may have carried over to the flight performance in the tunnel, which was relatively sheltered from the wind. Although results from this study cannot confirm this hypothesis, further study may test this potential carry-over effect more robustly by experimentally exposing birds to different wind speed and then flying them in the same environment without wind.

The higher initial velocity observed in great tits contrasts with our prediction of similar initial velocity across species, which was based on the assumption of equal leg muscle proportions. One possibility is that great tits are equipped with leg muscles better suited for standing take-off, contributing to greater leg force at take-off. Great tits are more frequently observed on the ground with their longer legs more adapted to standing, while blue tits prefer upper canopy with better developed leg flexor muscles and shorter legs suitable for hanging [41,51]. Earls (2000) [78] found that common quails (*Cortunix cortunix*), ground-nesting birds about twice the body mass of common starlings (*Sturnis vulgaris*), produced higher leg force at take-off relative to body mass in a more vertical trajectory. Similarly, great tits may achieve higher initial acceleration driven by legs compared to blue tits, due to leg morphology better suited for standing take-off.

Secondly, given the measurement system of the tunnel, great tits may have been able to accelerate over a longer distance between the first two rows of infrared sensors. The mean tarsometatarsus length of great tits in this study was 23.0 ± 0.4 mm, compared to 19.2 ± 0.7 mm in blue tits. Since the first infrared row was positioned 0.03 m from the perch, both species may have crossed the first row while still in contact with the perch. Longer legs provide longer lever, which will produce larger torque and higher initial velocity when the same magnitude of leg force is applied. This extended leg launch may have allowed great tits to further accelerate during take-off than hypothesized from the higher wing loading compared to blue tits [63, 64]. Although our results are primarily concerned with solo foraging flights, this higher moment of arm would be advantageous compensating for the larger body and high wing loading compared to other tit species in case of synchronous predator escape [50].

Here, we identified natural flight performance in small birds as a consistent, individual behavioural trait. In addition, we developed a power margin model that explains the observed differences in the measurements of in-flight acceleration, given a known initial velocity and wing loading. The higher initial velocity observed in great tits compared to blue tits suggests that the morphology and kinematics of legs may strongly influence real-life take-off flight performance. Now that flight performance can be tested as an individual trait, more comprehensive and automated measurements of leg-driven take-off in the natural environment may offer insights into the variability in flight performance, actively employed by individuals in a wide range of ecological scenarios.

Ethics. All work was conducted under BTO licence and UK standard requirements to ring and PIT-tag birds as pulli, when caught at breeding nest-boxes or when caught using mist nets. Field risk assessments were subject to review by the Department of Biology (University of Oxford) health and safety committee.

Data accessibility. Code and data files to reproduce all analyses are available at https://github.com/kyubird/wytham-tits-fly

Declaration of AI use. We have not used AI-assisted technologies in this article.

Author contributions. K.M.H.: conceptualization, formal analysis, investigation, methodology, validation, visualisation, project administration, writing— original draft, writing—review and editing. M.K.H.: formal analysis, resources, software, writing —review and editing. S.J.P.: funding acquisition, validation, visualisation, project administration, writing—review and editing. G.K.T.: conceptualization, funding acquisition, investigation, methodology, resources, supervision, validation, visualisation, project administration, writing—review and editing.

Conflict of interest declaration. We declare we have no competing interests.

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