© 2017. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2017) 220, 2908-2915 doi:10.1242/jeb.154039

RESEARCH ARTICLE

Homing pigeons (*Columba livia*) modulate wingbeat characteristics as a function of route familiarity

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ABSTRACT

Mechanisms of avian navigation have received considerable attention, but whether different navigational strategies are accompanied by different flight characteristics is unknown. Managing energy expenditure is critical for survival; therefore, understanding how flight characteristics, and hence energy allocation, potentially change with birds' familiarity with a navigational task could provide key insights into the costs of orientation. We addressed this question by examining changes in the wingbeat characteristics and airspeed of homing pigeons (*Columba livia*) as they learned a homing task. Twenty-one pigeons were released 20 times individually either 3.85 or 7.06 km from home. Birds were equipped with 5 Hz GPS trackers and 200 Hz tri-axial accelerometers. We found that, as the birds' route efficiency increased during the first six releases, their median peak-to-peak dorsal body (DB) acceleration and median DB amplitude also increased. This, in turn, led to higher airspeeds, suggesting that birds fly slower when traversing unfamiliar terrain. By contrast, after route efficiency stabilised, birds exhibited increasing wingbeat frequencies, which did not result in further increases in speed. Overall, higher wind support was also associated with lower wingbeat frequencies and increased DB amplitude. Our study suggests that the cost of early flights from an unfamiliar location may be higher than subsequent flights because of both inefficient routes (increased distance) and lower airspeeds (increased time). Furthermore, the results indicate, for the first time, that birds modulate their wingbeat characteristics as a function of navigational knowledge, and suggest that flight characteristics may be used as 'signatures' of birds' route familiarity.

KEY WORDS: Airspeed, Flight, Navigation, Route learning, Wingbeat amplitude, Wingbeat frequency

INTRODUCTION

Forward flapping flight is the most energetically demanding form of vertebrate locomotion (Norberg, 1990; Schmidt-Nielsen, 1972). To reduce the energetic cost of flight, birds utilise behavioural mechanisms, such as intermittent flight patterns (Rayner, 1985; Tobalske and Dial, 1996), formation flight (Weimerskirch et al., 2001) and modulation of their wingbeat frequency and amplitude (Greenewalt, 1962; Lilienthal, 2001). Whilst energy-saving mechanisms have been identified, little is known about the extent to which birds employ these mechanisms in relation to navigation, for example, as a function of familiarity with a given landscape. Until now, avian navigation research has primarily focused on the sensory and cognitive underpinnings of orientation (Wiltschko and Wiltschko, 2009) and the total cost of a flight (Flack et al., 2016). However, a bird navigating from a familiar location, such as a roost or foraging site, may utilise different flight patterns compared with when flying over less familiar terrain where the distance to be covered and the route to be taken are less well known. Energy is frequently considered the currency of life (Butler et al., 2004), which means that managing energy expenditure is a key aspect of survival. Thus, energy allocation is likely to play a pivotal role in dictating the flight patterns utilised whilst navigating. Investigating whether birds modulate, for example, their wingbeat patterns in relation to their familiarity with a navigational task could provide key insights into the cost of orientation.

Homing pigeons (*Columba livia* Gmelin 1789) are an ideal model species for studies investigating flight characteristics in relation to navigational knowledge because of their innate homing ability, amenability to experimental manipulation, and body size permitting the attachment of state-of-the-art tracking devices. For research subjects, this means we can ensure that the full navigational experience of a given individual is known and can be characterised over successive flights. Although the finer details are still debated, it is generally accepted that over unfamiliar terrain, pigeons navigate by utilising a combination of olfactory cues for position fixing (Gagliardo, 2013), and a solar and magnetic compass for directional guidance (Kramer, 1957; Schmidt-Koenig, 1990; Wiltschko and Wiltschko, 2005). In addition, over familiar terrain, pigeons are also able to utilise visual landmarks (Meade et al., 2005). Meade et al. (2005) found that homing pigeons released repeatedly from the same site gradually developed stereotypical routes, with each individual having their own, slightly indirect, route. The results of this study and others indicate that pigeons reliably adopt such individually idiosyncratic routes as familiarity with the local landscape increases, and rely more on visual landscape features as they become more experienced (Biro et al., 2004; Guilford and Biro, 2014; Meade et al., 2005). Correspondingly, birds' route efficiency (the straight line distance between the start and end of the route divided by the distance travelled by the bird) increases steadily during the early stages of training and then plateaus once the birds have developed stable idiosyncratic routes (Guilford and Biro, 2014; Meade et al., 2005). Recapitulating a familiar but less direct route, rather than increasing route efficiency further, suggests that there could be a higher energetic and/or cognitive cost associated with navigating in an unfamiliar landscape for homing pigeons, relative to following a familiar route. However, whether different navigational strategies during route learning are accompanied by the same or different flight characteristics (e.g. wingbeat frequencies and amplitudes) is still unknown.

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Received 25 November 2016; Accepted 30 May 2017

Our study addresses this question by quantifying changes in the flight characteristics of homing pigeons as they learn a homing task. Recent technological advances have led to the introduction of miniature GPS devices, which provide highly accurate geographical position fixes over the full duration of a flight (Steiner et al., 2000), and high-frequency tri-axial accelerometers, which can measure the acceleration of an animal in three different planes, or dimensions, of movement (Halsey et al., 2009; Wilson et al., 2006). In turn, the combination of GPS and accelerometers allows us to simultaneously reconstruct birds' routes, speeds, wingbeat frequencies and amplitudes of dorsal body (DB) displacement. Although the precise relationship between the DB amplitude and the amplitude of wing motions is unclear, the former can nevertheless be used as an indirect measure of the latter (Hedrick et al., 2004; Usherwood et al., 2011). Together, wingbeat frequency and amplitude are related to the variation in power and speed of flapping flight, and thus can be used as a proxy for energy expenditure and/or work rate. By varying wingbeat frequency and amplitude, a bird is able to adjust the costs of flight. Reducing wingbeat frequency reduces the inertial power cost of the flight (i.e. power required to move the wings), as the power requirement of horizontal steady flight is proportional to the square of wingbeat amplitude but the cube of wingbeat frequency (Greenewalt, 1962; Lilienthal, 2001). By contrast, increasing wingbeat frequency and decreasing amplitude reduces the drag of the wings and body and increases lift, thereby optimising aerodynamic efficiency (i.e. optimising the forces acting on the bird relative to the air for efficient flight parameters) (Usherwood, 2009; Usherwood et al., 2011). Thus, analysing variation in wingbeat characteristics and speed in relation to navigational knowledge could shed new light on the costs of navigation and the energetic strategies employed by birds as they learn a route to a target.

MATERIALS AND METHODS

Subjects

Twenty-one homing pigeons aged either 1 or 3 years were used. All birds had prior homing experience, but had not been released at or near the sites used in the present study. The subjects were housed with ∼120 other pigeons in two neighbouring lofts at the Oxford University Field Station, Wytham, UK (51°46′58.2″N, 1°19′2.7″W). Access to water, grit and a standard pigeon feed mix were available *ad libitum* at all times in the loft. All subjects were able to perform free flights around the loft on a daily basis throughout the year. In addition, in the month immediately preceding the start of the experiment, all subjects participated in a minimum of 24 solo or flock releases from four different release sites 1–3 km from home, as basic homing training, to familiarise the birds with the catch-and-release procedures and with being flown from an unfamiliar location. The protocols outlined in this paper were approved by the Local Ethical Review Committee of the University of Oxford's Department of Zoology.

Experimental protocols

Two release sites, both on a bearing of 282 deg from the lofts, were selected. The 'far' site (Barnard Gate; 51°47′48.1″ N, 1°25′3.3″W) was 7.06 km from the lofts and the 'near' site (Mill Lane, Eynsham; 51°47′24.2″N, 1°22′19.5″W) was located 3.85 km from the lofts. Subjects were randomly assigned to two groups in an approximately even age distribution. Individuals in group 1 (10 pigeons; five 1-year-old and five 3-year-old birds; mean±s.d. body mass=471±39 g) were released 20 times individually from the 'far' site, and individuals in group 2 (11 pigeons; six 1-year-old and five 3-year-old birds; 471±20 g) were released 20 times individually from the 'near' site. Releases were conducted between May and July 2015, on days when the sun was visible and the wind speed was <7 m s^{-1} when measured 5.5 m above the ground. Subjects participated in a maximum of two releases per day, with a minimum of 3 h between each release. All birds were released individually. Initially, releases occurred at 10-min intervals; this was later reduced to a minimum of 4 min if it could be visually confirmed that the previously released bird had left the vicinity of the release site. If, at any point, a bird accidentally paired up with another subject, the release was excluded for both birds (18 flights). Four additional tracks were removed from the analysis. One bird failed to return home before the GPS battery ran out on its first release from the far site; a GPS fault occurred for two birds, one during the fifth release and one during the 14th release; and the devices could not be accurately synchronised for a bird on its 10th release. In addition, four birds landed during their first release. For these landings, the entire descent, stationary and ascent sections were removed from the track data from the point of first descent to the peak of ascent.

Data logging

The birds were tracked using 5 Hz GPS loggers (BT-Q1300ST, Qstarz International Co., Taipei, Taiwan; 15 g) and 200 Hz tri-axial accelerometers (AX3, Axivity, Newcastle upon Tyne, UK; ±16 ***g***; 11 g). The loggers were attached to the pigeons using Velcro strips, which were glued to trimmed feathers on the back (Fig. 1; Biro et al., 2002). In total, the loggers and fastenings weighed 27 g (less than 7% of the subjects' mean body mass). Two weeks prior to the start of the experiment, clay weights (27 g) were attached to the birds' back via Velcro to accustom them to flying with the additional mass. These were exchanged for GPS devices and accelerometers immediately prior to each release. GPS and accelerometer data were downloaded using QTravel [Qstarz International Co.; version 1.48(T)] and Open Movement (Om) GUI Application (Newcastle University; version 1.0.0.28), respectively.

The weather, including mean wind speed per minute and a running mean of the wind bearing over the previous 10 min, was

Fig. 1. A homing pigeon with an Axivity AX3 accelerometer (front) and QStarz BT-Q1300ST GPS logger (case removed; back) attached to the back via Velcro strip, which was glued to trimmed feathers.

recorded using a WS2083 Professional Wireless Weather Station with USB upload (Aercus Instruments, Doncaster, UK) situated 5.5 m above the pigeon lofts. Weather data was logged using Cumulus Weather Station Software (Sandaysoft, Sanday, Orkney, UK; version 1.9.4).

Data processing

GPS and accelerometer data were synchronised to an accuracy of ±0.2 s (GPS frequency) using the point of take-off in both the GPS and accelerometer loggers, which were identified using the marked increases in GPS speed and dorsal acceleration peaks produced during take-off. The weather data were combined with the GPS and accelerometer data using the timestamps from the weather station and the GPS loggers. For each GPS point, the orthodromic (great-circular) distance travelled and birds' final bearing from the previous point were calculated using the haversine formula and forward azimuth, respectively. For each flight, route efficiency was calculated as the ratio between the total straight-line (great-circular) distance between release and home, divided by the sum of the direct (great-circular) distances between each successive GPS point (straightness index; Batschelet, 1981). Wind support and crosswind were calculated using the methods described in Safi et al. (2013): wind support represents the length of the wind vector in the direction of the bird's flight and crosswind represents the absolute speed of the wind vector perpendicular to the bird's direction of travel (Fig. S1). Airspeed, the speed of the bird relative to the wind, was then calculated using the speed derived from the GPS devices while taking into account wind support and crosswind (Safi et al., 2013).

The dorsal (*Z*-axis) accelerometer measurements were filtered by taking a running mean over five data points (0.025 s). Static acceleration (or gravity) was removed by subtracting a running mean over 15 wingbeat cycles (>2 s). The running mean was calculated over wingbeat cycles rather than over specific time periods, because variation in wingbeat frequencies would have meant including varying quantities of partial wingbeat cycles in a time-based running mean. The dorsal acceleration signal was then used to detect each wingbeat using the upper reversal point in acceleration (Fig. S2) (Norberg, 1990; Portugal et al., 2014). The peak-to-peak DB acceleration (***g***) and wingbeat frequency (number of wingbeats per second; Hz) were calculated for each individual wingbeat. The amplitude of the DB displacement (mm), which is the amount the body is displaced per wingbeat, was then calculated by the double integration of dorsal accelerometer measurements (Usherwood et al., 2011). After the first integration, a running mean over 15 wingbeat cycles was removed from velocity to remove drift. The data were then filtered using a fourth-order high-pass Butterworth filter with a cut-off frequency of 1 Hz. The procedure was repeated after the integration for displacement but with a cut-off frequency of 2.5 Hz in the Butterworth filter. The cut-off frequencies were determined by visualising the data using fast Fourier transforms. A more conservative estimate of the amplitude of the DB displacement was also calculated by passing the raw accelerometer measurements through fourth-order Butterworth filters prior to integration instead of running means, but this led to no significant difference in the results (Fig. S3).

In order to only compare sections of steady flight, the data were trimmed in a 1000 m radius around the release site (start point) and the pigeon lofts (end point). The shortest straight-line distance of the entire steady flight therefore measured 5.08 km for the far site and 1.85 km for the near site. In addition to comparing the entire steady flight, the data were also trimmed to remove sections with lower wingbeat frequencies (≤3.0 Hz) and sections of tortuous flight to remove any effect of gliding, idling or circling from the dataset. Tortuosity was calculated by taking a running mean of the change in the birds' bearing over every 1 s of data (five GPS points), with changes in direction of ≥3.0 deg removed in order to discard circling and keep only active straight-line powered flight.

Data analyses

Piecewise linear mixed effects (LME) models were used investigate the effect of repeated releases on route efficiency, median peak-to-peak DB acceleration per wingbeat (***g***), median DB amplitude per wingbeat (mm), median wingbeat frequency (Hz) and median airspeed ($\mathrm{m\ s^{-1}}$). Piecewise, or segmented, regression identifies an abrupt change of the dependent variable (or breakpoint) with respect to the independent variable, which allows one to fit pre- and post-event slopes (Naumova et al., 2001). We used this approach to determine whether changes in wingbeat characteristics corresponded to changes in route efficiency and to identify the trends in the data either side of this change. Breakpoints were objectively estimated using one-dimensional optimisation. Piecewise LME models were fitted using the fixed effects of release number less than the breakpoint (breakpoint – release number), release number greater than the breakpoint (release number – breakpoint), median wind support, median crosswind and group. Individual was also added as a random slope on both release number effects.

To establish the effect of wingbeat characteristics on airspeed, two LME models were used. Firstly, with median peak-to-peak DB acceleration and median wingbeat frequency as fixed effects, and secondly with median DB amplitude per wingbeat, which is dependent on peak-to-peak DB acceleration (force exerted on the dorsal body) and wingbeat frequency (duration of the wingbeat), as a fixed effect. Group was added as a fixed effect to both models but was insignificant. Individual was added as a random effect on the intercept. In addition, LME models were used to directly relate route efficiency with wingbeat characteristics and airspeed between releases 1 and 6 using the fixed effects of route efficiency, median wind support, median crosswind and group, and the random effect of individual.

Route efficiency was negatively skewed, and was therefore transformed before analysis by directly inverting values and taking the logarithm using the formula $\log_{10}(1-x)$. From the full models, simpler models were obtained by stepwise deletion of non-significant terms. Likelihood ratio tests were used to test the statistical significance of each fixed effect in the best-fitting model. LME models were calculated using maximum likelihood and the models were checked for assumptions of linearity, normality, homoskedasticity and autocorrelation by visual inspection of plotted residuals. Model fit was assessed by calculating conditional *R*-squared values ($R^2_{\mathrm{LME}(c)}$) using the methods described in Nakagawa and Schielzeth (2013).

Data processing and analysis were conducted using MATLAB (MathWorks, Natick, MA, USA; version R2015a) and the open-source software R (version 3.2.3; R Foundation for Statistical Computing, Vienna, Austria) using the packages lme4 (Bates et al., 2015; version 1.1-8) and MuMIn (version 1.15.1; https://cran.r-project.org/package=MuMIn).

RESULTS

Route efficiency improved as the birds became more experienced (Fig. 2). Over the first five releases, route efficiency increased significantly from 0.46±0.27 (mean±s.d.) for release 1 to 0.82±0.18

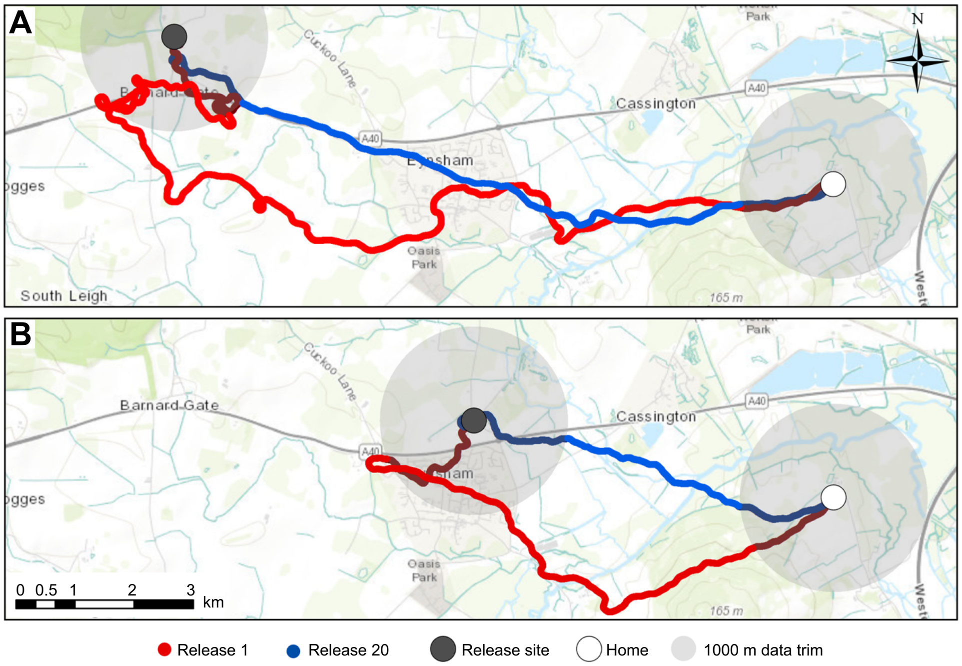

Fig. 2. Examples of routes flown during the first (red; release 1) and last release (blue; release 20). (A) From the far site; (B) from the near site. Note the increase in route efficiency at both sites. Map designed using ArcGIS 10.4.1 using the World Topographic Map (http://services.arcgisonline.com/ArcGIS/rest/services/World_Topo_Map/MapServer).

for release 5 (piecewise linear mixed model parameter estimate=0.287; likelihood ratio test for the model without release number: χ^2_1=32.9, P<0.001). A breakpoint, which denotes a change of the dependent variable (route efficiency) in respect to the independent variable (release number), was then automatically detected between releases 5 and 6 {5.5, 95% confidence interval (CI)=[4.3, 6.2]; Fig. 3}. No significant difference in route efficiency was detected among releases ranging from release 6 (0.88±0.10) to release 20 (0.87±0.10; χ^2_1=0.7, P=0.390). Group (i.e. release distance) also had a significant effect on route efficiency, with birds released at the nearer site (group 2) flying significantly more efficient routes than those released at the far site (group 1; estimate=0.316, χ^2_1=4.8, P=0.029). However, group had no significant effect on wingbeat characteristics or speed, thus the results from the two groups were pooled for the remainder of the analyses (Table 1). Route efficiency was also significantly affected by both median wind support (estimate=−0.05, χ^2_1=14.8, P<0.001) and median crosswind (estimate=0.10, χ^2_1=7.9, P=0.005), with greater wind support and lower crosswinds associated with higher route efficiency.

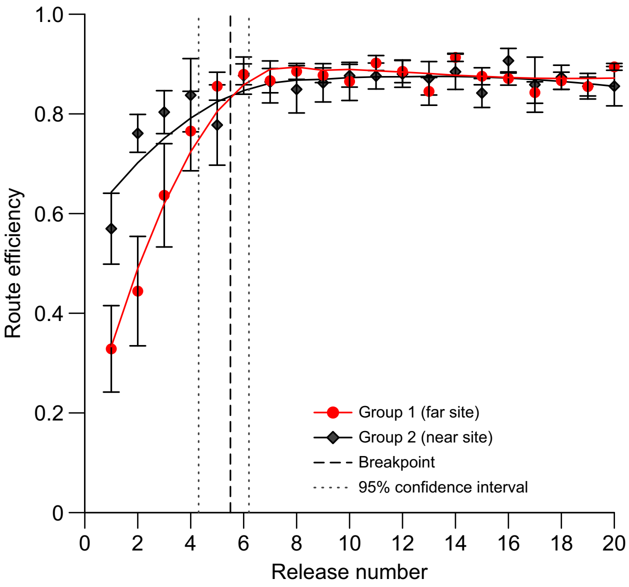

Fig. 3. Route efficiency (mean±s.e.m.) as a function of release number for group 1 (far site, *n*=10) and group 2 (near site, *n*=11). The dashed line indicates a computationally optimised piecewise linear mixed model breakpoint (±95% CI indicated by dotted lines) denoting a change in response function in respect to release number. Solid lines correspond to local polynomial regression fitting.

A breakpoint was detected in the median peak-to-peak DB acceleration (5.6, 95% CI [4.1, 6.8]) and in the median DB amplitude (5.99, 95% CI [4.6, 6.9]) between the same release numbers (5 and 6) as route efficiency (5.5, 95% CI [4.3, 6.2]). Both the DB acceleration and amplitude significantly increased prior to the breakpoint (acceleration: estimate=0.038, χ^2_1=7.4, P=0.007; amplitude: estimate=0.295, χ^2_1=8.5, P=0.004) before decreasing (acceleration: estimate=−0.006, χ^2_1=8.5, P=0.004; amplitude: estimate=−0.123, χ^2_1=16.4, P<0.001; Fig. 4A,B). By contrast, the breakpoint for median wingbeat frequency appeared later, between releases 9 and 10 (9.6, 95% CI [4.5, 12.6]), with no significant change prior to the breakpoint (χ^2_1=2.0, P=0.159). Upon visual inspection, one might argue that there is a breakpoint in the median wingbeat frequency around release 6 (Fig. 4C). Indeed, manually moving the breakpoint to the breakpoints of DB acceleration (5.6) and amplitude (5.99) revealed that wingbeat frequency significantly decreased during the early releases (breakpoint 5.6: estimate=−0.03, χ^2_1=2.83, P=0.007; breakpoint 5.99: estimate=−0.02, χ^2_1=6.89, P=0.009). However, the resultant models were weaker and accounted for less of the variability, which is why the objective breakpoint is situated slightly later between releases 9 and 10. The visual ambiguity in the breakpoint is reflected in the confidence interval, which is large for median wingbeat frequency (95% CI [4.5, 12.6]). After the objective breakpoint, wingbeat frequency increased significantly (estimate=0.02, χ^2_1=18.6, P<0.001).

Median wind support also had a significant effect on both median wingbeat frequency and median DB amplitude, with higher wind support associated with lower wingbeat frequencies

Table 1. Comparison of the piecewise linear mixed effects models for efficiency, wingbeat characteristics and airspeed for releases 1–20

	Breakpoint (95% CI)	Release number<breakpoint		Release number>breakpoint		Wind support		Crosswind		Group		$R^2_{\mathrm{LME}(c)}$
		P	Est.	*P*	Est.	*P*	Est.	*P*	Est.	*P*	Est.	
Efficiency (transformed)	5.5 (4.3, 6.2)	**<0.001**	**0.287**	0.390	–	**<0.001**	**–0.049**	**<0.001**	**0.099**	**0.029**	**0.316**	0.69
Median peak-to-peak DB acceleration (***g***)	5.6 (4.1, 6.8)	**0.007**	**0.038**	**0.007**	**–0.006**	0.487	–	0.679	–	0.286	–	0.65
Median DB amplitude per wingbeat (mm)	5.99 (4.6, 6.9)	**0.004**	**0.294**	**<0.001**	**–0.123**	**<0.001**	**0.195**	0.430	–	0.288	–	0.70
Median wingbeat frequency (Hz)*	9.6 (4.5, 12.6)	0.159	–	**<0.001**	**0.016**	**<0.001**	**–0.025**	0.302	–	0.735	–	0.68
Median airspeed (m s^{-1})	5.2 (3.9, 7.8)	**<0.001**	**0.527**	**0.001**	**–0.065**	N/A	–	N/A	–	0.281	–	0.22

Fixed effects with *P*-values and parameter estimates (Est.) denoted in **bold** are included in the final model. Conditional *R*-squared values ($R^2_{\mathrm{LME}(c)}$) are calculated using the methods described in Nakagawa and Schielzeth (2013).

*Note: manually moving the breakpoint for wingbeat frequency revealed a significant decrease in this variable during the early releases (breakpoint 5.6: estimate=−0.03, χ^2_1=2.83, *P*=0.007; breakpoint 6.0: estimate=−0.002, χ^2_1=6.88, *P*=0.009).

(estimate=−0.02, χ^2_1=26.5, P<0.001) and increased DB amplitude (estimate=0.20, χ^2_1=25.3, P<0.001). By contrast, median wind support had no effect on peak-to-peak DB acceleration, and median crosswind had no effect on any of the wingbeat characteristics.

Median airspeed (m s^{-1}) increased during the first five releases (breakpoint 5.2, 95% CI [3.9, 7.8]; estimate=0.53, χ^2_1=32.5, P<0.001) and thereafter decreased slightly (estimate=−0.07, χ^2_1=10.6, P<0.001; Fig. 4D). The means of the median flight airspeeds for the first three releases were particularly low (release 1: 20.1±1.6 m s^{-1}; release 2: 19.2±1.4 m s^{-1}; release 3: 19.7 ±1.0 m s^{-1}). However, the coefficient of determination for the relationship between median airspeed and release number was low, even when accounting for individual variation ($R^2_{\mathrm{LME}(c)}$=0.22). By analysing all 20 releases in an LME model with median peak-to-peak acceleration and median wingbeat frequency as fixed effects, we found that higher airspeeds were associated with higher peak-to-peak DB accelerations (estimate=1.57, χ^2_1=10.3, P=0.001) and lower wingbeat frequencies (estimate=−0.78, χ^2_1=3.9, P=0.048). Furthermore, in a model with DB amplitude (displacement) as a fixed effect, which is dependent on peak-to-peak DB acceleration (force exerted on the DB) and wingbeat frequency (duration of the wingbeat), DB amplitude was positively associated with airspeed (estimate=−0.24, χ^2_1=23.3, P<0.001).

The results thus far indicate that changes in wingbeat characteristics and airspeed correspond to changes in our route familiarity variable (i.e. route efficiency). To directly relate these findings, LME models were used with route efficiency as a fixed effect between releases 1 and 6. The results of these analyses

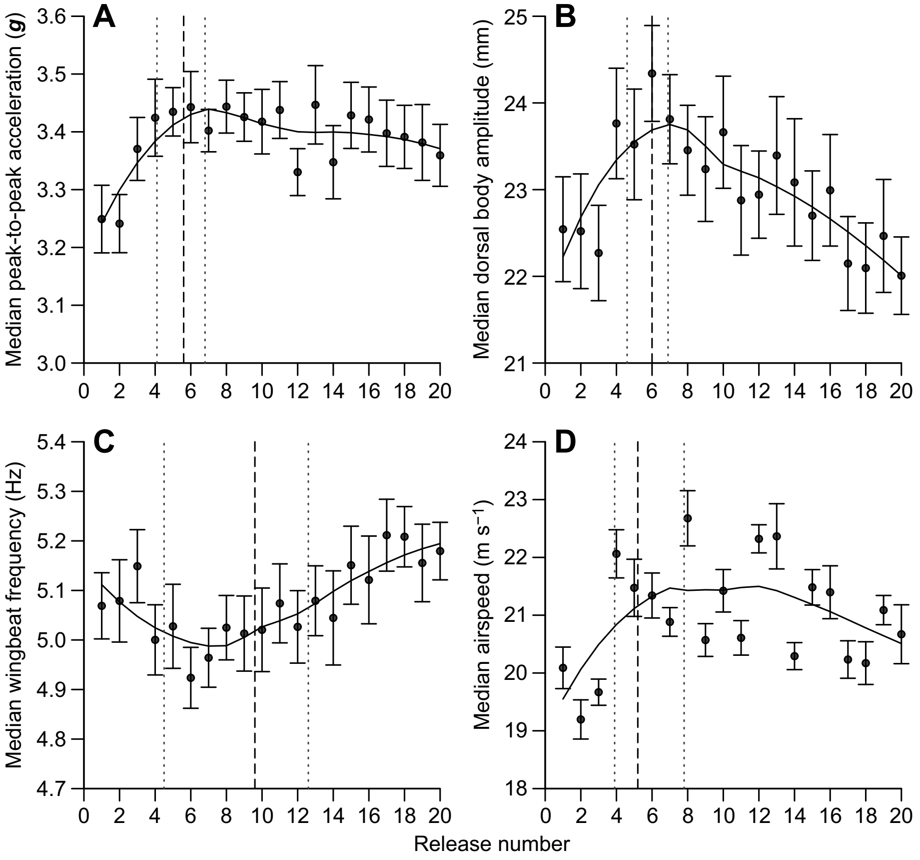

Fig. 4. Wingbeat characteristics and airspeed (mean±s.e.m., *n*=21) as a function of release number. (A) Median peak-to-peak acceleration, (B) median dorsal body amplitude, (C) median wingbeat frequency and (D) median airspeed. Dashed lines indicate computationally optimised piecewise linear mixed model breakpoints (±95% CI indicated by dotted lines) denoting a change in response function in respect to release number. Solid lines correspond to local polynomial regression fitting.

corroborate these findings, with median peak-to-peak DB acceleration (estimate=−0.11, χ^2_1=30.0, *P*<0.001), median DB amplitude per wingbeat (estimate=−0.86, χ^2_1=20.9, *P*<0.001) and median airspeed (estimate=−0.84, χ^2_1=20.2, *P*<0.001) all positively related to route efficiency (negatively related to the transformed route efficiency; Table S1, Fig. S4). As with release number, median peak-to-peak acceleration was only influenced by route efficiency, with no significant effect of median wind support, median crosswind or group (*P*>0.1). By contrast to DB acceleration, DB amplitude and airspeed, higher median wingbeat frequencies were associated with lower route efficiencies in releases 1–6 (estimate=0.06, χ^2_1=8.1, *P*=0.004). Although there was a significant difference between groups in route efficiency in the piecewise LME model (estimate=0.318, χ^2_1=4.8, *P*=0.029), there was no significant difference between groups when relating wingbeat characteristics and airspeed to route efficiency (*P*>0.1).

We hypothesised that one potential explanation for differences in wingbeat characteristics could be changes in wingbeat modes with navigational experience, such as additional circling behaviour and gliding in the early releases. Analysing only data with flap frequencies >3 Hz and tortuosity <3 deg (i.e. without gliding and circling segments, respectively) resulted in a shift in the breakpoint in wingbeat frequency from release 9.6 (95% CI [4.5, 12.6]) to release 6.2 (95% CI [4.6, 12.5]). In addition, the wingbeat frequencies significantly decreased prior to the breakpoint (estimate=0.02, χ^2_1=4.6, *P*=0.03). However, aside from the slight changes to median wingbeat frequency, removing circling and gliding had no other significant effect on the results other than decreasing median wingbeat frequency and median peak-to-peak DB acceleration, and increasing median DB amplitude and median airspeed (Fig. S5). Furthermore, it is important to note that the confidence interval in the breakpoint for wingbeat frequency remains approximately the same and that on visual inspection, one could place a breakpoint in the whole flight data at around release 6, as discussed above.

DISCUSSION

We investigated the effect of navigational experience in relation to wingbeat characteristics and airspeed in homing pigeons. The results indicate, for the first time, that gradual increases in the birds' route efficiency, observed as birds become more experienced with a given terrain, are also accompanied by changes in wingbeat characteristics and airspeed. As the birds' route efficiency improved during the first six releases, the median peak-to-peak DB acceleration, median DB amplitude and, consequently, median airspeed also increased. By contrast, after route efficiency stabilised, the birds' median DB acceleration and amplitude decreased, whereas median wingbeat frequency increased. However, decreasing DB amplitude, and hence wingbeat amplitude, in favour of increasing wingbeat frequency did not result in a higher airspeed. Taken together, our results suggest that birds may be modulating their flight characteristics as a function of navigational familiarity with the area through which they are travelling.

As with previous studies (reviewed in Guilford and Biro, 2014), route efficiency improved over consecutive releases. It increased significantly over the first five releases, with a breakpoint detected between releases 5 and 6. The breakpoint denotes a change in route efficiency (dependent variable) with respect to release number (independent variable), with the position of the breakpoint determined by where the slopes of the two segments join. We chose the piecewise linear mixed model approach to objectively identify a change of state because, as these results demonstrate, wingbeat characteristics and airspeed continue to change long after route efficiency stabilises. Whilst we could manually divide the data into segments, an automated approach enables us to objectively identify changes in wingbeat characteristics and airspeed as a function of release number and to identify whether these changes correspond to changes in route efficiency. In this study, we identified that route efficiency increases up to a breakpoint of 5.5 and thereafter stabilises. As expected, the near-site group (straight-line distance: 3.85 km) flew significantly more efficient routes home in the early stages of route learning than the far-site group (7.06 km), owing to the proximity of the near release site to the familiar area surrounding the pigeons' home lofts. However, despite these differences, no significant difference was found between groups in wingbeat characteristics and speed, and route efficiency still significantly increased over the first five releases for both groups. These results reinforce the idea that birds modulate their wingbeat characteristics in response to navigating an unfamiliar route, and that this effect is detectable even at short distances from home.

The aforementioned changes in route efficiency did correspond to changes in wingbeat characteristics, both in terms of the positioning of the breakpoint and when directly relating these factors during the first six releases. As route efficiency increased, the peak-to-peak DB acceleration and DB amplitude also increased, which indicates that the acceleration, or force, the dorsal body experienced increased over the first few releases. The median peak-to-peak DB acceleration per wingbeat was especially low during the first few releases. Although DB acceleration did decrease again after route efficiency stabilised, the DB accelerations the birds experienced during the first few releases were still much lower than in the last few releases, which could suggest that the overall flapping force was lower during the first few releases. Correspondingly, the airspeeds of the first three flights were also particularly low. By analysing the influence of peak-to-peak DB acceleration and wingbeat frequency on airspeed, we established that higher airspeeds were associated with higher peak-to-peak accelerations and lower wingbeat frequencies, with peak-to-peak acceleration having a slightly larger effect than wingbeat frequency. However, the amplitude of the DB displacement, which is dependent on the peak-to-peak acceleration (force exerted on the DB) and the wingbeat frequency (duration of the wingbeat), had the greatest overall effect on airspeed. For example, a wingbeat which is both high in force (peak-to-peak acceleration) and long in time (low wingbeat frequency) will result in a greater displacement, and hence higher airspeed, than one that is low in force or short in time. It should be noted, however, that this negative relationship between wingbeat frequency and airspeed is within the subtleties of active flight parameters, and may not represent the relationship over the entire range of the pigeons' wingbeat characteristics. Although DB amplitude is an indirect measure of wing amplitude, the two measures are likely to be related (Hedrick et al., 2004). An alternative explanation for the changes in wingbeat characteristics and airspeed could be changes in flight behaviour, such as increased circling and/or gliding. However, removing both wingbeat frequencies below 3 Hz and tortuous flight made no substantial difference to the results other than shifting the breakpoint of median wingbeat frequency, suggesting that the changes in wingbeat characteristics are occurring during straight-line powered flight. Flying at a slower speed from an unfamiliar location may be an advantage as it may enable the bird to gather more local ambient information.

Breakpoints in the median peak-to-peak acceleration (release: 5.7) and the median DB amplitude (5.99), which occur between the same release number as route efficiency (5.5), along with the fact that higher peak-to-peak acceleration and DB amplitude were associated with higher route efficiency in releases 1–6, indicate that DB movements change as a function of navigational knowledge. By contrast, during the first six releases, higher wingbeat frequencies were associated with lower route efficiencies. The large confidence interval and slightly later breakpoint in wingbeat frequency (9.6) suggest that it is likely that birds continue to learn routes home even after route efficiency initially plateaus. Indeed, removing circling and gliding behaviour resulted in a breakpoint in wingbeat frequencies being detected at release 6.2. Thus, changes in wingbeat characteristics shortly after the route efficiency breakpoint could still be related to the acquisition of navigational knowledge. An alternative explanation could be increases in the birds' physical fitness, or acclimatisation to the sensor mass or to the capture and release procedure. However, given the substantial number of releases immediately prior to the start of the experiment (≥24), the daily free flights around the loft and the fact that the birds were fitted with clay weights equal to the size and mass of the devices 2 weeks prior to the start of the experiment, this is unlikely to have been a factor. Furthermore, migratory species, such as barnacle geese (*Branta leucopsis*) undertaking 2500 km journeys, do not increase flight behaviour prior to migratory departure (Portugal et al., 2012), suggesting exercise is not a prerequisite for extended flight.

Shortly after route efficiency stabilised, changes in the birds' flight characteristics consisted largely of increases in wingbeat frequency as the birds' DB acceleration and amplitude decreased. The inertial power requirement, or cost, of horizontal steady flight is proportional to the square of wingbeat amplitude but the cube of wingbeat frequency (Greenewalt, 1962; Lilienthal, 2001), which means increasing wingbeat frequency would result in a higher inertial power cost. If this higher wingbeat frequency translated into higher airspeeds, then this strategy could be beneficial as the bird would then reach its destination in less time (Hedenström and Alerstam, 1995). However, as already highlighted, higher wingbeat frequencies were associated with lower airspeeds. Indeed, airspeed did decrease significantly from release 6, although variability in this was high and the effect size small. Albeit increasing wingbeat frequency would increase the inertial power costs, a higher wingbeat frequency would also result in a higher aerodynamic efficiency by reducing the drag from the wings and body and increasing lift (Greenewalt, 1962; Lilienthal, 2001), which may be advantageous once the total length of the journey is known. The median wingbeat frequency increased in this study from 4.9 (release 6) to 5.2 (release 18), i.e. by 5.8%. However, these wingbeat frequencies are still considerably lower than those reported for homing pigeons participating in flight that may require a higher degree of aerodynamic efficiency or stability, such as flock flight (∼6.6–7.0 Hz; Usherwood et al., 2011) and during ascending and descending flight (6.1–9.6 Hz; Berg and Biewener, 2008). Thus, the increases in wingbeat frequency exhibited in the present study are more likely to be related to birds optimising their flight patterns between inertial power requirements and aerodynamic efficiency.

Increasing aerodynamic efficiency, by increasing wingbeat frequency, could help conserve energy, particularly as the results of this study also indicate a strong effect of the wind on route efficiency and flight characteristics. The effect of wind on flight is well documented, particularly in relation to the timing and distance travelled during migration (Alerstam, 1979; Liechti and Bruderer, 1998). Liechti (2006) highlighted that wind speed can easily double or halve the bird's speed and thereby affect the overall cost of the flight. Weather data used in this study (mean wind speed and bearing) were recorded 5.5 m above the pigeon lofts, 7.06 km from the 'far' release site. Therefore, the accuracy of the readings decreased the further away the bird was from the lofts, which could explain some of the variation, particularly in airspeed, found in this study. Nevertheless, the results indicate that wind support, in particular, was a consistent and significant factor contributing to the work rate, with a higher wind support (tail wind) associated with a lower wingbeat frequency, which would decrease the inertial power costs. By contrast, the birds' peak-to-peak DB acceleration was not affected by the wind, which suggests that in winds under 7 m s^{-1}, birds compensate for the wind by modulating wingbeat frequency rather than the amplitude. Indeed, the change in breakpoint in the wingbeat frequency from the whole flight data to the active straight-line data from release 9.6 to release 6.2 could also be a reflection of the birds utilising circling and gliding behaviour to compensate for the effects of the wind. Furthermore, higher route efficiency was associated with higher wind support and lower crosswinds, which suggests that the birds may modify their route (and hence their route efficiency) depending on the wind conditions.

Regardless of the underlying cause for the changes in wingbeat characteristics, the results of this study indicate, for the first time, that pigeons modulate their wingbeat characteristics as a function of navigational knowledge, which suggests that navigation and the learning process may have physical manifestations in birds. In particular' peak-to-peak DB acceleration was especially low during the first few releases, which was unaffected by wind characteristics, and related to a lower airspeed. Thus, measuring flight characteristics could provide new insights into the cognitive state of the bird. For example, wingbeat characteristics may be used as 'signatures' of birds' route familiarity, which could be utilised in navigation research to identify how familiar a bird is with a given navigational task. Furthermore, the results of this study lead us to speculate that birds may be able to orient and learn more effectively at lower speeds, in which case the flight would then become a trade-off, or compromise, between optimal navigation and learning (accuracy), and vulnerability to predators and the total flight time (speed). Moreover, these results suggest that the cost of the first flight, such as the first migration or first route out in search of a novel foraging site, may be higher than that of subsequent flights, because of both inefficiencies in the route, which increase the total distance flown, and the increased flight time, owing to lower airspeeds. This, in turn, could impact on the total time available for foraging and reproduction, and other decisions, such as whether to fly with other individuals. For example, despite the additional energetic cost of flying in a close cluster flock (Usherwood et al., 2011), a naive individual may be able to conserve energy by flying with experienced individuals to reduce the total flight time, as well as gain protection from predators. Thus, studying intra-individual modulations of wingbeat characteristics and airspeed could provide new insights into the decision-making and navigational strategies of birds.

Acknowledgements

We thank Lucy Larkman, Dave Wilson and Phil Smith for animal husbandry and technical support, and Graham Taylor, Theresa Burt de Perera, Lauriane Rat-Fischer, Isobel Watts, Oliver Padget, Allert Bijleveld, Simon Taylor, Indira Nagesh, Marco Klein Heerenbrink and members of the navigation, flight and behavioural ecology research groups at Oxford's Department of Zoology for helpful discussions and comments on earlier versions of the manuscript. We would also like to thank two anonymous reviewers for their helpful comments on the manuscript.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: L.A.T., S.J.P., D.B.; Methodology: L.A.T., S.J.P., D.B.; Formal analysis: L.A.T.; Investigation: L.A.T.; Resources: L.A.T., D.B.; Data curation: L.A.T.; Writing - original draft: L.A.T.; Writing - review & editing: L.A.T., S.J.P., D.B.; Visualization: L.A.T.; Supervision: S.J.P., D.B.; Project administration: L.A.T., D.B.; Funding acquisition: L.A.T., D.B.

Funding

L.A.T. was funded by the Biotechnology and Biological Sciences Research Council (BBSRC) UK (grant number BB/J014427/1), D.B. by a Royal Society University Research Fellowship (grant UF110081).

Data availability

Data are available from the Dryad Digital Repository (Taylor et al., 2017): http://dx.doi.org/10.5061/dryad.37d5m

Supplementary information

Supplementary information available online at
http://jeb.biologists.org/lookup/doi/10.1242/jeb.154039.supplemental

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