

The energetic cost of variations in wing span and wing asymmetry in the zebra finch *Taeniopygia guttata*

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Summary

Asymmetry is a difference in the sizes of bilaterally paired structures. Wing asymmetry may have an effect on the kinematics of flight, with knock-on effects for the energetic cost of flying. In this study the ¹³C-labelled bicarbonate technique was used to measure the energy expended during the flight of zebra finches *Taeniopygia guttata*, prior to and after experimental manipulation to generate asymmetry and a change in wing span by trimming the primary feathers. In addition, simultaneous high-speed video footage enabled differences in flight kinematics such as flight speed, wing amplitude, up- and downstroke duration and wing beat frequency to be examined. In 10 individuals, the primary feathers on the right wing were trimmed first, by 0.5 cm, and then by an additional 0.5 cm in six of these individuals. In a separate 'control' group ($N=7$), approximately 0.25 cm was trimmed off the primary feathers of both wings, to produce the same reduction in wing span as 0.5 cm trimmed from one wing, while maintaining symmetry. When birds were manipulated to become asymmetric they

maintained flight speed. They also increased the left wing amplitude and decreased the right up- and downstroke durations to counteract the changes in wing shape, which meant that they had an increase in wing beat frequency. When the wing area was reduced while maintaining symmetry, birds flew with slower flight speed. In this case wing amplitude did not change and wing upstroke slightly decreased, causing an increased wing beat frequency. The mean flight cost in the pre-manipulated birds was 1.90 ± 0.1 W. There was a slight increase in flight cost with both of the asymmetry manipulations (0.5 cm, increase of 0.04 W; 1.0 cm, increase of 0.12 W), neither of which reached statistical significance. There was, however, a significantly increased flight cost when the wing span was reduced without causing asymmetry (increase of 0.45 W; paired t -test $T=2.3$, $P=0.03$).

Key words: flight cost, wing asymmetry, labelled bicarbonate technique, zebra finch, *Taeniopygia guttata*, kinematics.

Introduction

Small differences in the size of bilaterally paired structures, or asymmetry, are very prevalent in nature, occurring in structures as widely different as the fins of Siberian sturgeon *Acipenser baeri* (Ruben, 1992) to the horns of beetles *Onthophagus taurus* (Moller, 1992a) or the antlers for fallow deer *Dama dama* (Putman and Sullivan, 2000). It is thought that the degree of asymmetry observed between different individuals within a single population reflects the degree of stress encountered by each individual, either directly as an effect of the environment or previously during development. Genetic stress occurs during development due to problems such as inbreeding or mutation (Balmford et al., 1993), while environmental stresses may affect individuals at any life stage (Putman and Sullivan, 2000). These environmental stressors include disease, pollution, parasites and food deprivation. The

most commonly observed asymmetry in birds occurs in their plumage, particularly during moult. For example, after food deprivation in starlings *Sturnus vulgaris*, deprived birds had significantly higher levels of asymmetry in their primary feathers (Swaddle and Witter, 1994). The effects of stress on asymmetry are, however, not always clearcut. Out of 21 studies using experimental manipulations of stress, seven showed increasing asymmetry with stress, seven did not show any difference and seven showed an increase only with a specific type of stress or in a specific trait (Bjorksten et al., 2000). This has led to development of several alternative hypotheses to the stress hypothesis to explain the origins of asymmetry (Kellner and Alford, 2003), the best of which suggests that recent growth history is the most important factor.

It may be that traits used during courtship for sexual

selection express higher correlations with stress and therefore may be a reliable indicator of individual 'quality' (Moller and Pomiankowski, 1993; Grammer et al., 2003). Female birds often choose mates with the biggest, brightest and most symmetrical sexual ornaments. The handicap hypothesis (Zahavi, 1975) indicates that males with such ornamentation are more preferable to the opposite sex because the ornaments are costly to maintain, and by implication males that have survived such costs must have good genes to pass on to their offspring. If asymmetry causes an increased energy cost of flight or affects flight performance, then according to the handicap theory, females might be expected to select males that are the most asymmetrical, because these individuals would have a larger handicap. However, Moller's developmental stability model (Moller, 1992b) suggests that females should mate with more symmetrical males because symmetry is an indication of the genomes ability to buffer against environmental and genetic stresses.

It has been suggested that birds with bigger sexual ornaments must maintain a high degree of symmetry to reduce the costs of having the ornament (Evans et al., 1994). However, in horned beetles *Onthophagus taurus*, larger sexually selected traits are more asymmetrical (Hunt and Simmons, 1997). Consequently, it is possible that some traits are more important when choosing a mate than others, with size being selected over symmetry because the size of the trait depends highly on stresses affecting the individual (Hunt and Simmons, 1997; Bjorksten, 2000).

Wing feathers in birds show less extreme asymmetry than tail feathers, and natural asymmetries in wing feathers are lower in birds that spend a higher proportion of the day in flight (Balmford et al., 1993). If asymmetry occurs in the primary flight feathers, the consequences include a reduction in flight performance. Additionally there may also be raised energetic costs. If flight behaviour is affected there may be a change in flight parameters such as speed or wing beat frequency. If there is a cost for having asymmetrical wings, it may therefore be energetic, behavioural, or a direct impact on the fitness of the individual *via* mate choice.

The fitness and behavioural consequences of being asymmetrical are well documented. For example, zebra finches *Taeniopygia guttata* made asymmetrical by adding different coloured leg bands had significantly fewer offspring than symmetrically banded males (Swaddle, 1996). Birds can therefore suffer from a reduced reproductive success as a result of asymmetry (Forkman and Corr, 1996; Moller, 1992b). Behavioural consequences include increased predation due to a decreased flight performance (Moller, 1996; Moller and Nielsen, 1997; Swaddle, 1997), or increased mortality such as in laying hens *Gallus gallus domesticus*, where larger asymmetrical birds tend to be cannibals while smaller asymmetrical birds are cannibalised (Yngvesson and Keeling, 2001). Little is known about the energetic consequences. The energetic consequences of a reduction in wingspan, however, can be predicted using aerodynamic theory (e.g. Pennycuick, 1989; Pennycuick et al., 1996; Rayner, 1999). Pennycuick

(1989; Pennycuick et al., 1996) developed a simple computer program that allows predictions to be made of mechanical flight costs in individuals of known mass and wingspan. The program predicts that reducing wingspan by 5% in a 20 g bird will increase the mechanical flight cost by around 7.3%. This program, however, assumes that the reduction in wingspan is symmetrical, affecting both wings by the same degree, and cannot make any predictions about the energetic effects of asymmetry. The energetic cost of wing asymmetry therefore needs to be determined empirically.

In this study we aimed to investigate whether there are energetic and/or behavioural costs associated with artificially increasing wing asymmetry in zebra finches, and if energetic costs correspond with the predictions from aerodynamic theory based on span change alone. Natural asymmetries in wild animals do not lend themselves to testing ideas about energy costs of asymmetry, because natural asymmetries may involve other conflicting factors such as parasitism that may incidentally affect energy expenditure. Artificially manipulating asymmetry in healthy captive birds controls for the effects of natural stresses that cause asymmetry. We therefore examined the energetic cost of flight before and after a series of manipulations to the wing area and span, in addition to examining the time-averaged wing kinematics to evaluate any related change in behaviour.

Materials and methods

Calibration of the ¹³C-labelled bicarbonate technique

A calibration was conducted on five zebra finches *Taeniopygia guttata* Vieillot 1817 as described previously (Hambly et al., 2002). Isotope elimination rates (k_c), measured in breath samples after injection with ¹³C-labelled bicarbonate, were compared to simultaneous metabolic measurements by indirect calorimetry. The time interval 15–20 min after injection provided the following relationships for predicting metabolism from a measured isotope elimination rate (Hambly et al., 2002):

$$\dot{V}_{O_2} = 6.10k_c + 0.48 \quad (1)$$

and

$$\dot{V}_{CO_2} = 4.70k_c + 0.48, \quad (2)$$

where \dot{V}_{O_2} and \dot{V}_{CO_2} are in ml min⁻¹.

Wing manipulations

The energy cost of flight was measured in 17 zebra finches. Bird mass (± 0.01 g) was recorded prior to each flight and wing areas and spans were measured prior to and after manipulation, both by photography and drawing around the outstretched wings on graph paper. The wings were carefully stretched out to the same degree in all birds to maintain a comparable estimate of area across individuals. From the wing tracings, the squares were counted to measure the combined area of the two wings and body, excluding the head and tail. In addition, the birds were photographed using a Leitz Reprovit camera (GMBH Wetzlar, Germany) based around a Leica M3 camera

system. The wing outlines from the photographs (excluding the head and tail) were traced onto acetate and transferred onto a PC using PC Image for Windows, which was used to calculate the area after calibration using known areas. The area calculations were averaged for each bird. For the flight study the birds were placed in the same cylindrical Plexiglas® chamber as was used in the calibration. Dried air was pumped through the chamber at the same rate as used during the calibrations (485 ml min^{-1}). Unlabelled breath samples were taken every minute for 4 min prior to injection to obtain a basal enrichment level for ^{13}C . A weighed volume of 0.2 ml of the same $0.29 \text{ mol l}^{-1} \text{ NaH}^{13}\text{CO}_3$ solution as used in the calibration was then administered *via* an intraperitoneal injection. The bird was returned to the chamber and breath samples were collected 10–14 min after injection. At 15 min after injection the bird was released from the chamber and encouraged to fly between two perches, 20 m apart, for a timed period of approximately 2 min. The bird was then rapidly re-caught and placed back in the chamber where further breath samples were collected for the following 8 min. Flights were simultaneously filmed using a Hi-8 video camera (Sony CCD-V800E) to measure the total time in flight to the nearest second and mean flight speed. In addition a Kodak EM high-speed video camera was used to film each flight at a frequency of $500 \text{ frames s}^{-1}$. This recorded 19 s of footage for each flight. The video footage was used to examine mean wing beat frequency (F_b), wing amplitude and up- and downstroke duration during each flight. Three repeated flights were completed for each individual on separate days.

After completion of the initial flights, three different wing manipulations occurred. The birds were given a minimum of 4 days to adjust to the manipulation and were then involved in further flight measurements. The first two manipulations produced an artificial wing asymmetry as well as changes in wingspan and area. First, approximately 0.5 cm was trimmed off each primary feather of the right wing in ten individuals. Then a further 0.5 cm was trimmed from six of these birds, making the total feather loss up to 1.0 cm of the primary feathers of the right wing. The final manipulation controlled for the effects caused by changes in wingspan and area while still maintaining wing symmetry. To achieve this reduction approximately 0.25 cm was trimmed off the primary feathers of both wings in seven different individuals. Birds were photographed and traced again following manipulation, and the flight procedure and filming was repeated three further times on each bird. High-speed video footage was examined to calculate wing kinematics by slowing the 19 s of footage recorded to individual frames. The exact time for each wing beat or up- and downstroke duration could be calculated to the nearest 0.002 s. This was repeated for at least 20 beats throughout the film duration for F_b and at least three measurements for up- and downstroke duration for birds flying both towards and away from the camera. Wing amplitude was measured by freezing the frame at the top of the wing beat and tracing the wing angle on acetate. The point at the tip of the beak was also marked. The film was then forwarded to the point when the wing was at the bottom of the wing beat and

the acetate was placed over the bird with the beak in the same location and the wing retraced. The angle between the up- and downstroke was calculated. Flight speed was measured by slowing the normal high-8 video down to individual frames, and accurately measuring the time taken to fly between the perches located 20 m apart. A minimum of ten flights between perches were timed and these were spread over the whole 2 min flight interval consisting of flights both towards and away from the camera.

Data analysis

Values are means \pm standard error (S.E.M.) unless otherwise stated. Repeated one-way analysis of variance (ANOVA), multiple linear regression and paired *t*-tests were applied to our data using Minitab 11 software.

Results

Wing areas

The mean area was reduced by $2.6 \pm 0.4\%$ of the total wing area after 0.5 cm had been trimmed from the right wing primary feathers, which was significantly different from that of the pre-manipulated birds (paired *t*-test; $T=5.5$, $P<0.001$). This reduction was not significantly different from the reduction of area of $3.2 \pm 0.4\%$ that occurred when approximately 0.25 cm was removed from both wings (one-way ANOVA; $F_{1,16}=1.3$, $P=0.3$). Removing 0.25 cm from both wings also significantly reduced the wing area relative to that pre-manipulation (paired *t*-test; $T=6.56$, $P<0.001$). The manipulation where 1.0 cm of primary feathers were removed from the right wing caused an average reduction in area of $5.3 \pm 0.7\%$, which was significantly different from the pre-manipulated area (paired *t*-test; $T=7.75$, $P<0.001$).

Flight costs

Flight energy costs were calculated using the protocol described by Hambly et al. (2002). In brief, each flight was not continuous as the birds rested intermittently on perches at either end of the flight corridor. The time resting on the perches was calculated from the high-8 video footage, and the flight was assumed to have occurred continuously in the middle of the flight period, preceded and succeeded by rest time of equal duration. As with a previous study on zebra finches (Hambly et al., 2002) the relationship between the time since injection and the log-converted isotope enrichment was linear prior to the flight (Fig. 1). After flight the enrichment rose to a peak on average 4 min after the end of flight, and then declined. A second-order polynomial best fitted this pattern of elimination, in all cases. The resulting best-fit regression equations for the enrichment decline with time were extrapolated to the adjusted time when the flight began and ended, accounting for the time spent on the perches. This generated two estimated enrichments, the gradient between them being the isotope elimination rate during the flight (k_c). This k_c was interpolated onto the calibration equations (Equations 1 and 2) to predict the oxygen consumption and carbon dioxide production during

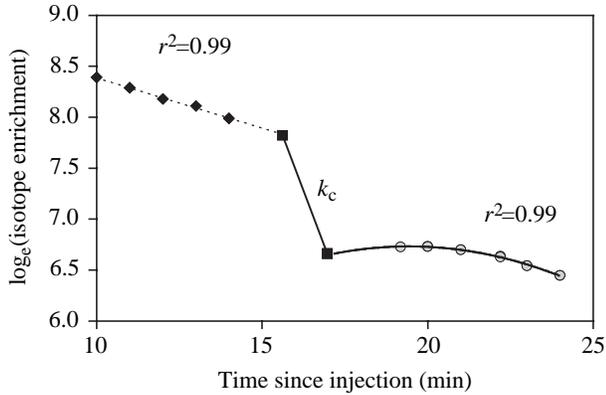


Fig. 1. Typical isotope enrichments from breath samples taken before (diamonds) and after flight (circles) in a zebra finch. In this example, depressed isotope enrichment occurred in the first breath sample collected at 3 min after flight. A linear regression was therefore fitted before flight and forward-extrapolated to predict the enrichment at the time when the bird first began to fly. A polynomial regression was fitted after flight and back-extrapolated to predict the enrichment at the time when flight ended (accounting for the time spent on the perches). This generated two points, the gradient between them being the elimination rate (k_c) during flight. k_c was substituted into Equations 1 and 2, to give predictions of \dot{V}_{O_2} and \dot{V}_{CO_2} , which were converted to energy expenditure in W.

flight, which was converted to energy expenditure in W using the measured respiratory quotient (RQ; Hambly et al., 2004).

Flight cost in the pre-manipulated individuals averaged 1.90 ± 0.1 W. There was a significant difference in the mean flight costs measured in different individuals (one-way ANOVA; $F_{16,47}=4.1$, $P<0.001$). Some individuals flew with a consistently higher flight cost than others. A multiple-linear regression model was used to examine the morphological and behavioural parameters that were related to flight cost (in the pre-manipulated birds). These parameters included mean flight speed, wing beat frequency, wing area and span, body mass, amplitude, up- and downstroke duration and wing loading. The only parameters that had a significant influence on flight cost were body mass (regression; $F_{1,47}=5.5$, $P=0.02$), mean wing amplitude (regression; $F_{1,43}=6.4$, $P=0.02$) and wing span (regression; $F_{1,47}=4.7$, $P=0.04$) (Fig. 2).

The differences between the flight energy costs (W) of the pre and post-manipulated birds were calculated (Table 1 and Fig. 3). After trimming approximately 0.5 cm of the right wing, all but one bird maintained normal flight between the perches. One individual (Pink 141) had difficulty maintaining flight and the flight cost after manipulation was $3\times$ that from before manipulation. This bird was removed from the study. Excluding this individual, the mean difference in flight cost when 0.5 cm was trimmed from the right wing was slightly increased from the pre-manipulated flight cost (0.04 ± 0.1 W). This difference was not significant (paired t -test; $T=0.3$, $P=0.8$). After removing a further 0.5 cm from six of these birds there was an increase in flight cost, with a difference from the pre-manipulated birds of 0.12 ± 0.2 W, which was

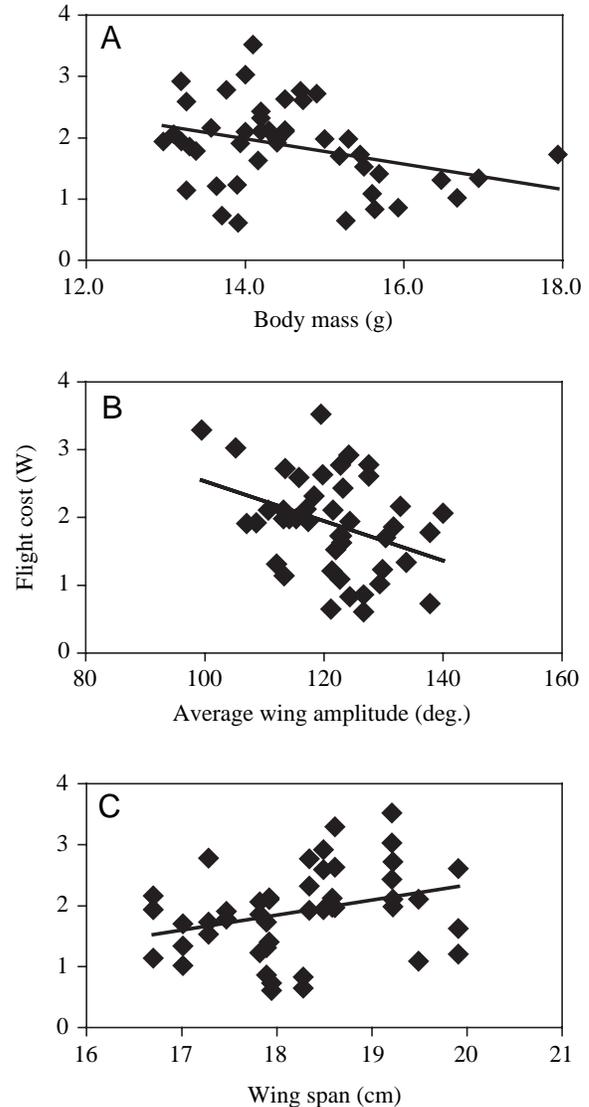


Fig. 2. Relationship between flight cost and (A) body mass ($y=4.86-0.21x$, $r^2=0.11$), (B) wing amplitude $y=5.45-0.029x$, $r^2=0.13$) and (C) wingspan ($y=0.25x-2.66$, $r^2=0.09$), which were the only parameters that had a significant influence on flight cost.

also not significantly different to the pre-manipulated cost (paired t -test; $T=0.6$, $P=0.6$). The birds used in the third 'control' manipulation, where 0.25 cm was trimmed from the primary feathers of both wings, had a significant increase in flight cost compared to the pre-manipulated birds (paired t -test; $T=3.8$, $P=0.01$) with a mean difference of 0.45 ± 0.2 W (Fig. 3).

The relationships between flight cost and wingspan and body mass in the pre-manipulated birds were significant, with flight cost decreasing with a larger body mass and increasing with a larger wingspan (Fig. 2). These results, however, were not consistent with our findings when wingspan was experimentally manipulated. Body mass remained the same in the experimentally manipulated birds (paired t -test; $P>0.05$), while wingspan was reduced and the resulting flight cost

Table 1. The difference in the energetic cost of flight (in W) compared to the pre-manipulated flight cost in each individual

Bird ID	Cost of flight (difference from pre-manipulated value) (W)					
	0.5 cm trimmed (one wing)	N	1.0 cm trimmed (one wing)	N	0.25 cm removed (both wings)	N
Black 1	-0.56	3	-0.48	3		
D Green 1	0.26	4	0.83	3		
D Green 4	0.01	3	0.51	3		
L Green 4	0.24	3	0.07	3		
Pink 141	[4.15*]	3		*		
Purple 31	-0.46	3	0.16	3		
Purple 32	-0.16	2		*		
Purple 37	0.88	3		*		
Purple 50	0.17	3	-0.41	3		
Purple 65	-0.01	3		*		
Average	0.04±0.1		0.12±0.2			
Black 5					0.13	3
D Green 3					0.52	3
L Blue 2					0.55	2
L Green 5					0.96	3
L Green 7					0.21	3
Pink 172					0.67	3
Purple 80					0.12	3
Average					0.45±0.1	

After 0.5 cm has been trimmed from the right wing, one bird (pink 141), failed to maintain normal flight patterns and subsequently increased its flight cost by 3× that of its normal pre-manipulated flight. The data from this bird was removed from the calculations (asterisk).

increased, which is opposite to the predictions of the multiple linear regression model. Flight cost differences with changes in wingspan within individuals due to our manipulations were, therefore, inconsistent with the natural differences observed between individuals.

Wing kinematics

Wing beat frequency (F_b) ranged between 19.6 and 28.7 beats s^{-1} and increased with the loss of wing area from each manipulation. The increase in mean F_b when 0.5 cm was trimmed from one wing, compared to pre-manipulated values, was 1.1 ± 0.6 beats s^{-1} . This increase was not significant (paired t -test; $T=1.8$, $P=0.1$). There was a larger increase (2.6 ± 0.6 beats s^{-1}) when 1.0 cm was removed from one wing, which was significantly different from the F_b of the same individuals prior to wing trimming (paired t -test; $T=4.0$, $P=0.01$). When 0.25 cm was trimmed from both wings the average difference in F_b from the pre-manipulated value was also significantly higher, by 1.87 ± 0.5 beats s^{-1} (paired t -test; $T=4.0$, $P=0.007$) (Fig. 4).

Wing amplitude in the pre-manipulated birds averaged $121.4 \pm 1.34^\circ$. When the right wing was trimmed to produce an asymmetry the mean wing amplitude of the right wing did not differ from the same individuals prior to manipulation ($P>0.05$) but the left wing increased in amplitude, with the change becoming larger and significant the greater the extent of asymmetry (paired t -test; 0.5 cm trimmed, $T=2.07$, $P=0.07$; 1.0 cm trimmed, $T=3.3$, $P=0.002$). However, when the wings

were altered by removing 0.25 cm off both wings but maintaining symmetry, neither the left nor right wing amplitude changed from the pre-manipulated value (paired t -test; left wing, $T=-0.29$, $P=0.78$; right wing, $T=-0.69$, $P=0.52$; Fig. 5)

In addition to the adaptations in wing amplitude and wing beat frequency there were changes in both up- and downstroke duration. The left wing up- and downstroke durations did not

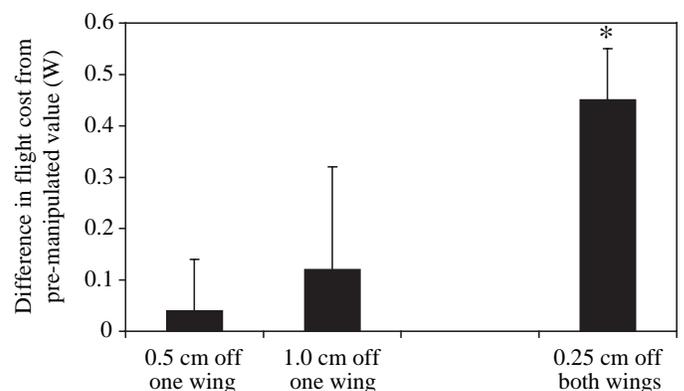


Fig. 3. The mean difference in flight cost (W) between birds with trimmed wings, and the pre-manipulated flight cost for each individual. *Increase in flight cost was significantly higher than in the pre-manipulated individuals. Values are means \pm S.E.M. For N values, see Table 1.

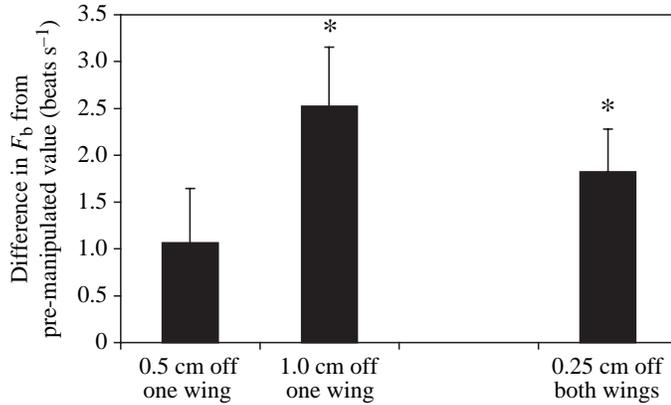


Fig. 4. The difference in mean wing beat frequency (F_b) between pre- and post-manipulated birds (beats s^{-1}). The largest increase in F_b from pre-manipulated levels occurs between the birds that had 1.0 cm removed from one wing. *Increase in F_b was significantly higher than in the pre-manipulated individuals. Values are means \pm S.E.M. For N values, see Table 1.

significantly differ from pre-manipulated values ($P>0.05$), but the right wing up- and downstroke durations significantly decreased (0.5 cm removed, paired t -test; upstroke $T=-3.32$, $P=0.01$, downstroke $T=-3.56$, $P=0.008$; 1.0 cm removed, paired t -test; upstroke $T=-4.31$, $P=0.008$, downstroke $T=-6.17$, $P=0.002$; Fig. 6). When the wings were trimmed on both sides wing stroke duration achieved a significant increase on both the left (paired t -test; $T=-2.80$, $P=0.031$) and the right upstroke (paired t -test; $T=-4.07$, $P=0.007$; Fig. 6).

Flight speed ranged between 4.7 and 7.6 $m s^{-1}$. The increase in flight speed from the speed recorded in the pre-manipulated individuals was $0.2\pm 0.2 m s^{-1}$ higher when 0.5 cm was trimmed (paired t -test; $T=1.3$, $P=0.2$) and $0.5\pm 0.3 m s^{-1}$ higher when 1.0 cm was trimmed (paired t -test; $T=2.2$, $P=0.1$), neither of which were significantly higher than pre-manipulation

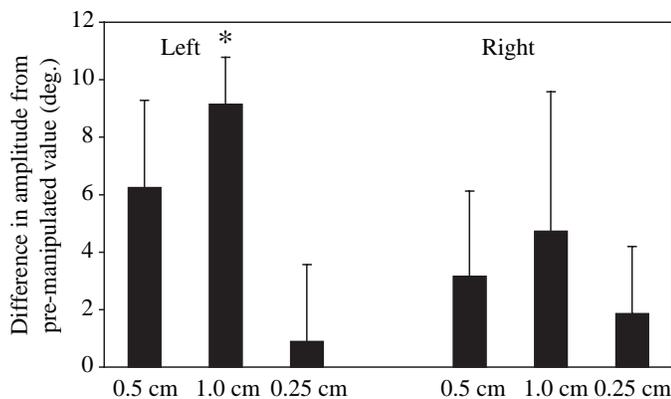


Fig. 5. Difference in mean wing amplitude between pre- and post-manipulated birds. In manipulated birds, left or right wings were trimmed, by 0.25, 0.5 or 1.0 cm. Asterisks indicate where the resulting increase in wing beat frequency F_b was significantly higher than the pre-manipulated individuals. Values are means \pm S.E.M. For N values, see Table 1.

values (Fig. 7). When both wings were trimmed to be symmetrical there was a significant decrease in flight speed of $0.6\pm 0.2 m s^{-1}$, compared to the pre-manipulated individuals (paired t -test; $T=3.3$, $P=0.02$).

In summary, when birds were manipulated to become asymmetric by trimming the primary feathers on one wing, there was no significant increase in flight cost. The birds responded to the change in wing area by maintaining flight speed. They also increased the left wing amplitude and decreased the right up- and downstroke durations to counteract the changes in wing shape, which meant that they had an increase in wing beat frequency. In contrast, when the wing area was reduced by 3.2% while maintaining symmetry, the birds had a significantly elevated flight cost combined with a slower flight speed. In this case wing amplitude did not change and wing upstroke slightly decreased causing an increased wing beat frequency.

Aerodynamic models

Two aerodynamic models were used to predict the effect that the change in wingspan would have on flight cost; the Pennycuick (1989) model, which is a simplistic model using wing span, area and body mass to predict flight costs, and the Rayner (1999) model, which uses other kinematic parameters of speed, wing beat frequency, amplitude, up/down stroke ratio and estimates for stroke plane angle relative to the horizon and the body, which were assumptions taken from Tobalske et al. (1999) for the appropriate average speed. These models predict mechanical power, which has to be converted to metabolic power using the measured efficiency. The efficiency was measured by dividing the measured flight cost in pre-manipulated birds by the mechanical flight cost prediction from the model. The efficiency for the pre-manipulated birds using the Pennycuick model was 13.01% while the Rayner model predicted an efficiency of 13.17%. These values were used to convert predicted mechanical power from the models to estimate total power for the future manipulations. The models did not predict a significant change in flight cost using the individual bird data, for any of the manipulations ($P>0.05$) with similar differences in flight costs compared to the pre-manipulated values.

Discussion

The results from the present study indicated that primary feather asymmetry does not significantly increase the energy cost of flight. The birds were found to alter their wing kinematics enabling them to continue to fly over the short distances we measured without an increase in their energetic cost.

Thomas (1993) stated that there are two possibilities that birds could use to overcome the impacts of asymmetry. The first is to pull the longer wing in to equal the length of the shorter one, which will be costly unless the bird flies above normal cruising flight speeds. As the cost did not increase dramatically with increasing asymmetry and the birds did not

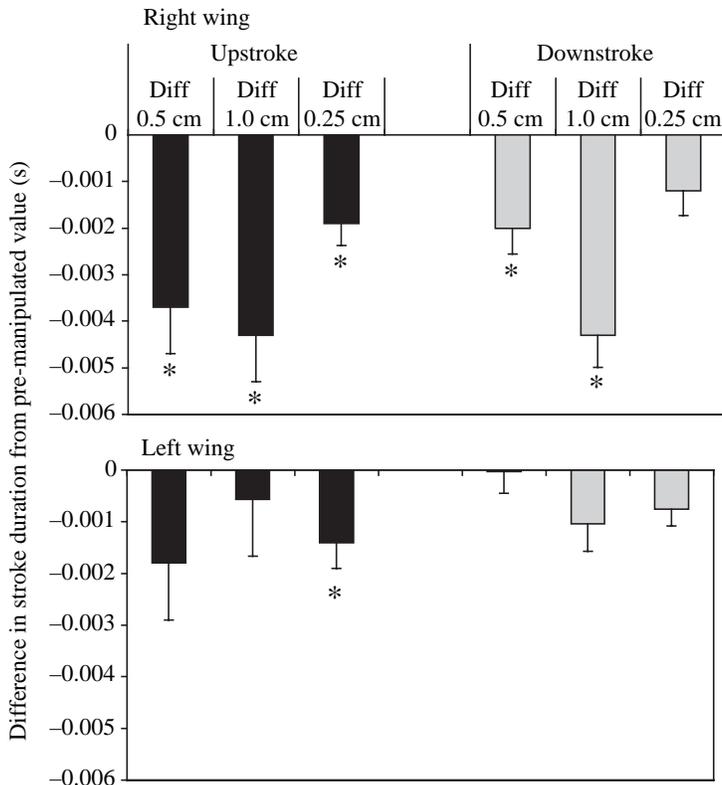


Fig. 6. Differences in mean up- and downwing stroke duration between pre- and post-manipulated birds. Asterisks indicate where the resulting increase in wing beat frequency F_b was significantly higher than the pre-manipulated individuals. Values are means \pm S.E.M. For N values, see Table 1.

significantly increase their flight speed in this study, they were unlikely to be using this method to compensate. In addition, when both wings were trimmed, reducing the span in the same way as pulling in one wing, there was a significant increase in flight cost. An alternative hypothesis (Thomas, 1993) was that the birds might counteract the spanwise distribution of lift

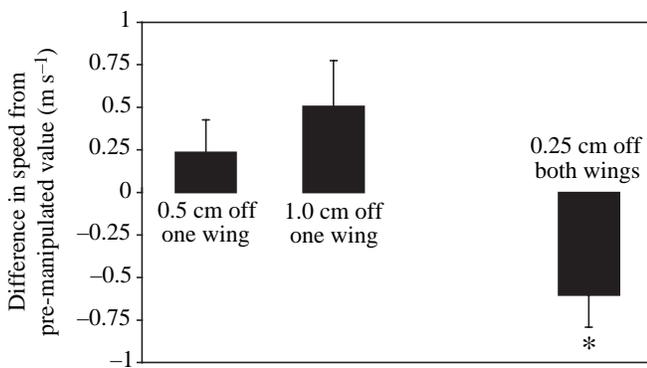


Fig. 7. The difference in the mean flight speed (m s^{-1}) with each manipulation compared to the pre-manipulated flight speed. There was a slight but not significant increase in flight speed between the manipulations when one wing only was trimmed. When both wings were trimmed there was a significant decrease in flight speed. *, $P=0.02$.

across the wings, by altering either the camber or the angle of attack independently in each of the wings. Our kinematic data indicated that the birds did alter the amplitude of the longer wing while reducing the stroke duration of the shorter wing, supporting this latter hypothesis.

In the control group, where the span and area were reduced without changing the symmetry, flight cost did increase. If Thomas' (1993) second hypothesis is correct, then when wing area was reduced while maintaining symmetry, the spanwise distribution of lift across the wings would be symmetrical and therefore, beating both wings independently could not compensate for the change in area.

Pennycuick's aerodynamic model (Pennycuick, 1989) predicted that using the mean wingspan, area and body mass in the pre-manipulated birds there would be an increase in flight cost of 7.3% with a reduction in wingspan of 5%. This does not account for asymmetrical changes in wingspan or adaptations to behaviour, which reduced the affect for the birds in this study. When flight costs are examined over a range of speeds, the resulting relationship tends to conform to either a U-shaped (Pennycuick et al., 1996) or J-shaped (Rayner, 1999) curve. These models predict that at low or high flight speeds the energetic cost would increase, with an optimum 'minimum power' speed (V_{mp}) where the bird flies at the lowest power requirement. Using the mean body mass and wingspan for the birds in the present study and keeping all other factors constant, the minimum power speed was predicted to be 5.7 m s^{-1} using the Pennycuick model and 4.3 m s^{-1} using the Rayner model. The pre-manipulated birds were initially flying, on average, above the minimum power speed at 6.3 m s^{-1} , which may be attributed to the short distance that they were flying over and the range of behaviours that are involved in repeated take-off and landings. When the primary feathers were asymmetrically trimmed, flight speed did not change and there was therefore no associated increase in flight cost. However, when the wings were trimmed symmetrically, the speed was reduced to be closer to V_{mp} and therefore flight cost should also have decreased. Instead, contradictory to the models, flight cost increased by 24.7%. Tobalske et al. (1999) examined the effect that changes in speed had on flight kinematics of zebra finches. A reduction in speed was associated with a reduction in wing beat frequency while increasing the wing amplitude. When symmetry was maintained while reducing wing span, speed reduced, but the expected associations were not present. Wing amplitude did not alter while wing beat frequency increased. This may explain why flight cost in these individuals did not follow the patterns predicted by the aerodynamic models and care must be taken when using models for birds that are in moult or have undergone stresses, which have a different wing shape from the norm.

In conclusion the birds observed in this study were able to modify their behaviour to respond to the imposed asymmetrical morphological changes minimising the impact on flight

energetics. Consequently any costs of asymmetry are likely to be manifested primarily as behavioural effects, which may affect the risk of predation (Moller, 1996; Moller and Nielsen, 1997; Swaddle, 1997).

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