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How do birds' tails work? Delta-wing theory fails to predict tail shape during flight

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Birds appear to use their tails during flight, but until recently the aerodynamic role that tails fulfil was largely unknown. In recent years delta-wing theory, devised to predict the aerodynamics of high-performance aircraft, has been applied to the tails of birds and has been successful in providing a model for the aerodynamics of a bird's tail. This theory now provides the conventional explanation for how birds' tails work. A delta-wing theory (slender-wing theory) has been used, as part of a variable-geometry model to predict how tail and wing shape should vary during flight at different airspeeds. We tested these predictions using barn swallows flying in a wind tunnel. We show that the predictions are not quantitatively well supported. This suggests that a new theory or a modified version of delta-wing theory is needed to adequately explain the way in which morphology varies during flight.

Keywords: delta-wing theory; aerodynamic models; birds' tails

1. INTRODUCTION

From casual observations of birds in flight it seems obvious that birds use their tails as part of their flight apparatus. However, while a bird's tail seems to play an important aerodynamic role, the precise aerodynamic functions of the tail have been the subject of considerable speculation (Maynard Smith 1952; Pennycuick 1975; Norberg 1990). Most of the suggested roles for the avian tail have been aimed at explaining the observation that the tail is principally used in slow flight and during manoeuvres. The most widely used theoretical models of bird flight (all concerned with steady-state flight) ignore any forces that could be produced by the tail (Pennycuick 1975, 1989; Rayner 1979a,b,c). Recently, a novel explanation for the function of the furled tail during flight has been proposed. Maybury & Rayner (2001) have shown that the furled tail of a starling (*Sturnus vulgaris*) appears to function as a splitter plate, reducing parasite drag by controlling vortex shedding at the distal end of the bird, where the dorsal and ventral airflows must rejoin. This is an interesting idea but is unlikely to provide a complete explanation for the aerodynamics of a bird's tail. If the tail solely acted as a splitter plate the tail should never be spread or held at an angle of attack to the airflow.

However, in order to understand the diversity of tail shapes seen in birds, or the different ways in which tails might work, it is necessary to have a model of the aerodynamics of the tail. In 1993, Thomas made the imaginative suggestion that a bird's tail could be regarded as a low-aspect-ratio delta wing (a triangular wing that is relatively short from side-to-side compared with its length), similar to the wings of modern high-performance aircraft like Concorde and many fighter aircraft. If this were true then the theories that have been developed to predict the lift

forces on such aircraft could be applied to predict the aerodynamic forces generated by a bird's tail (Thomas 1993). Thomas adapted theories from the aerospace literature, principally slender-lifting surface theory, to develop a theory for the aerodynamics of birds' tails. A theory that provided a model of the aerodynamics of birds' tails allowed new areas of investigation to be instigated. Thomas and co-workers initially used this theory to examine the effects of sexually selected tail shapes on bird flight (Balmford *et al.* 1993, 1994), and this has subsequently been taken up by others (Møller 1994; Cuervo *et al.* 1996; Fitzpatrick & Price 1997). Delta-wing theory has also been applied in aerodynamic considerations of flight (Norberg 1995; Tucker 1995; Pennycuick 1997; Warrick *et al.* 1998; Tobalske *et al.* 1999), fluctuating asymmetry (Evans *et al.* 1994), and the evolution of early birds (Gatesy & Dial 1996). In total, Thomas's delta-wing theory has been cited in over 60 papers in the last 8 years.

In a series of experiments on model starlings mounted in an airflow, Maybury *et al.* (2001) recently demonstrated that the lift produced by the tail does not change as predicted by the specific version of delta-wing theory used by Thomas (1993). This was the first empirical test of delta-wing theory as applied to bird's tails, but suffers from the fact that the experiments were conducted on model birds mounted with wings removed. It remains possible that live birds can behave in a manner that permits delta-wing theory to be applied.

In an explicit attempt to provide testable predictions for the application of delta-wing theory to the tails of birds, Thomas used a simple aerodynamic model to examine the way tail and wing shape should change with airspeed if the tail produced lift, as suggested by a specific version of delta-wing theory: slender-wing theory (Thomas 1996). It should be noted that these predictions may only apply for the specific version of delta-wing theory (slender-wing theory) used by Thomas. He predicted that the tail and wings should be well spread at low airspeeds with the tail

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at a high angle of attack. As speed increases, both the spread and angle of attack of the tail should decrease until the tail is completely furled, and is parallel to the airflow. It is important to note that, although these qualitative effects could have been described by any competent ornithologist and were precisely the observations that the earlier ideas about tail function were designed to explain (Maynard Smith 1952; Pennycuick 1975; Norberg 1990), they were emergent properties of Thomas's model. In addition to predicting qualitative changes in morphology, Thomas's model predicted that, for a swallow, these changes should occur in a specific order: with increasing airspeed, tail angle of attack should decrease first followed by a decrease in tail spread, and only then a reduction in wingspan. Finally, Thomas's model also made quantitative predictions about the way in which these changes in morphology should occur (Thomas 1996). Predictions can therefore be produced for three levels of analysis. The objective of this work was to test these predictions and thus provide the first, to our knowledge, direct, empirical test of the variable-geometry application of delta-wing theory on live birds.

2. MATERIAL AND METHODS

The experiment was conducted in a low-turbulence, closed-circuit design wind tunnel at Lund University, Sweden (Pennycuick *et al.* 1997). Two male swallows were filmed while flying in the wind tunnel by using two, synchronized, high-speed Redlake video cameras (Motionscope PCI 500, USA) at 125 frames s^{-1}. The swallows were filmed in steady flight at 1 m s^{-1} intervals between 4 and 14 m s^{-1}, and five replicate flight sequences of posterior, ventral and lateral views of the swallows were obtained at each airspeed. This range represents the minimum and maximum flight speeds at which the swallows appeared able to maintain steady forward flight in the wind tunnel. Wingspan, body tilt angle, tail spread angle and angle of attack were analysed using Redlake Imaging Motionscope 2.16 and Mapinfo Professional 4.5. Wherever possible, for each swallow, $n = 5$; however, some datapoints represent less than this. Further methodology details and additional wingbeat kinematic data from this experiment are published elsewhere (Park *et al.* 2001).

The theoretical predictions were made using Thomas's variable-geometry model (Thomas 1996). The original paper suffered from a few typographical errors that we corrected. The geometry of a forked tail has been added to replace the rounded tail used in the default model. Predictions are representative for a bird the size of barn swallows used in the wind tunnel, i.e. body mass of 0.019 kg, wingspan of 0.32 m, wing area of 0.01365 m^2, mean chord 0.0429 m, body frontal area of 0.00094 m^2, central tail feathers 0.0455 m and streamer length of 0.115 m, flying at sea level with a body drag coefficient of 0.2 (Hedenström & Liechti 2001). To minimize total power, three morphological parameters were allowed to vary within a defined window: wingspan (maximum to 1/3 of maximum; Rosén & Hedenström 2001), tail spread angle—120° to 0° (Norberg 1994) and tail angle of attack—28.6° to 0° (Thomas 1996).

In any process of hypothesis testing, predictions derived from a null hypothesis must be tested against those from an alternative hypothesis. We considered that the appropriate null hypothesis was that the lift produced by the tail should be zero. We
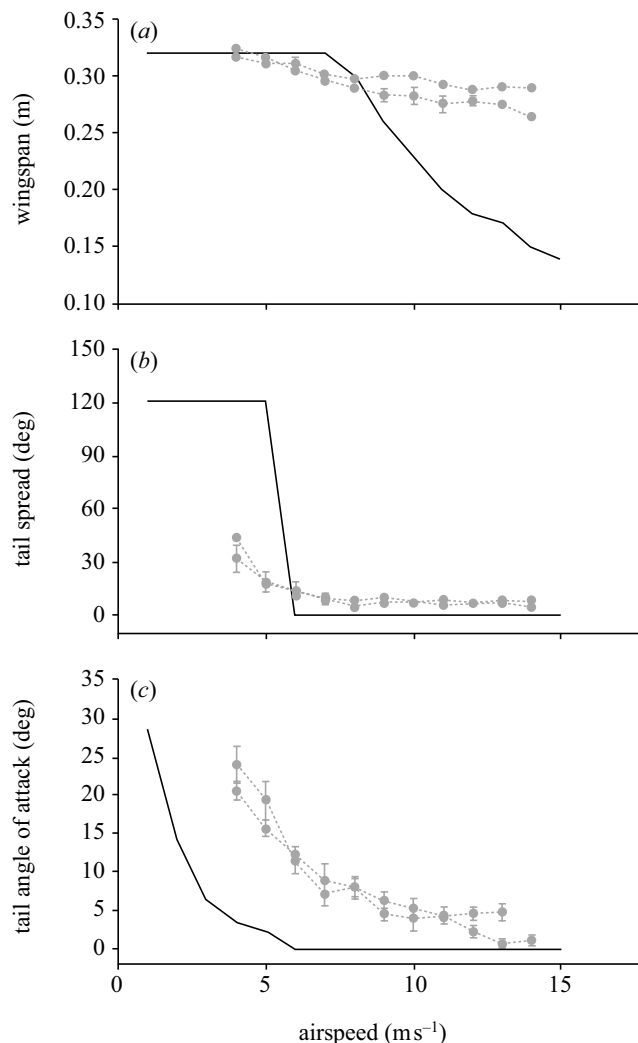
Figure 1. (*a*) Wingspan, (*b*) tail spread angle and (*c*) tail angle of attack, in swallows flying at different airspeeds. The solid black line represents predictions obtained for a swallow using Thomas's (1996) model. The grey and dotted lines are the observed data from the two swallows flying in a wind tunnel.

derived predictions for the way in which tail spread and angle of attack and wingspan should change with airspeed, assuming tail lift to be zero and using power minimization as our currency. We used a modified version of Thomas's (1996) variable-geometry model to generate our null predictions, setting tail lift to zero.

In order to determine whether our results were reasonable representations of the way in which morphology changes with airspeed, we compared the swallow data with previously published results on black-billed magpies (*Pica pica*) and pigeons (*Columbia livia*) (Tobalske & Dial 1996).

3. RESULTS

(a) *Predictions*

The variable-geometry model predicts a sequence of changes in morphology with tail angle of attack changing at lower airspeeds than tail spread, which should be furled before wingspan starts to decrease. The way in which tail angle of attack, tail spread and wingspan are predicted to change with airspeed are shown as the solid black lines in figure 1.

Our null hypothesis assumes that tail lift will be zero independently of morphology. We need to make predictions about tail and wing morphology variation under this null hypothesis. As tail angle of attack is only used to calculate lift (and consequently induced drag), if tail lift is zero, then tail angle of attack has no effect and can take any value. The most parsimonious value is a tail angle of attack of zero, which would involve the muscles of the tail doing the least work to maintain tail position. Therefore, we predict that under the null hypothesis, tail angle of attack is zero. Tail spread is used to calculate lift (and so induce drag) and profile drag and therefore should be zero if power is being minimized. Therefore, tail spread will also be zero at all airspeeds if tail lift is zero. The relationship between wingspan and airspeed if tail lift is zero is predicted to be the same as when the tail is assumed to produce lift. Figure 1 shows that under the variable-geometry model, even if the tail is assumed to produce lift, reduction in wingspan is only predicted to start after tail spread has reached zero, so the tail is no longer producing any lift above an airspeed of 6 m s^{-1}. The predicted changes in wingspan are therefore occurring in the absence of tail lift.

(b) *Observations*

At low airspeeds the tail was spread, was held at a high angle of attack to the airflow and the wingspan was large. At high airspeeds the tail was furled at a low angle of attack, and the wingspan was smaller than at low airspeeds. These results from the two birds used in our experiments are shown as the grey and dotted lines in figure 1. These data suggest that the mean deviation of the observed wingspan from that predicted was 5.1 cm (*ca.* 17% of wingspan) across the speeds used here; for the reasons already outlined this was the same for the null model as well as the delta-wing model. The mean deviation of the observed tail spread from that predicted by the variable-geometry model was 23.5°, while the mean deviation from the null model was 11.9°. There was no significant difference between the deviation of the observations from the predictions of the null model or the predictions of the variable-geometry model ($t_{11} = 0.41$, $p = 0.19$). Similarly the mean deviation between the observed tail angle of attack and that predicted by the variable-geometry model was 7.6° and from the null model 8.2°. Once again, there was no significant difference between the deviation of the observations from the predictions of the null model or the predictions of the variable-geometry model ($t_{11} = 0.45$, $p = 0.18$).

(c) *Comparative data*

Data on the way in which black-billed magpies and pigeons change wingspan and tail spread with airspeed, taken from Tobalske & Dial (1996), are shown in figure 2. The swallows used in our experiments changed their tail and wing morphology in a similar way to that seen in these other two species. Generally, wingspans change little with airspeed, while tail spread gradually moves from fully spread to furled as airspeed increases. For both of these variables magpies and pigeons change morphology in a more gradual manner than do swallows.
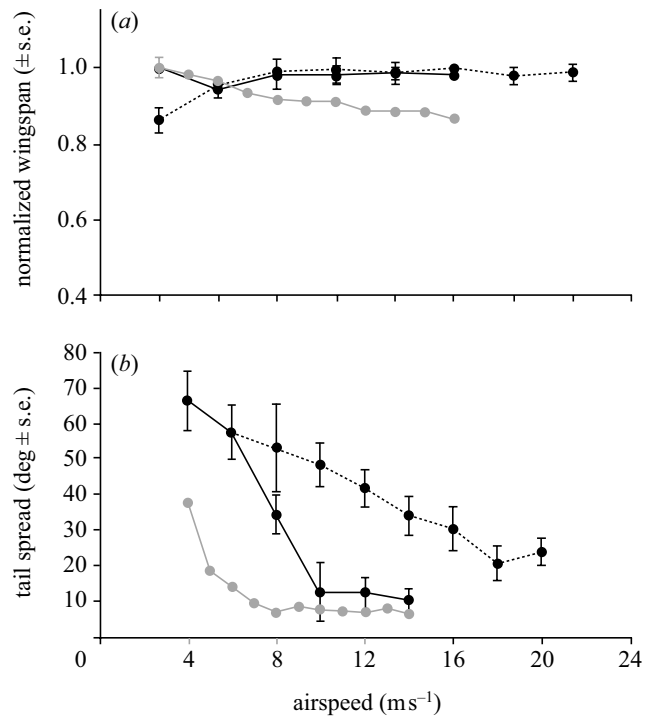
Figure 2. Changes in (*a*) normalized wingspan (proportional to maximum wingspan) and (*b*) tail spread angle with airspeed in swallows (data were averaged from the two swallows (grey line), magpies (black line) and pigeons (dotted line). Data from magpies and pigeons have been redrawn from Tobalske & Dial (1996).

4. DISCUSSION

Our observations of flying swallows show that at low speeds the tail was spread and held at a high angle of attack, and wingspan was maximized. At high airspeeds the tail was furled, held parallel to the airflow and wingspan was reduced. Therefore, there is a good qualitative match between the theory and observation, which is better than the qualitative match with our null hypothesis that the tail produces no lift. It would seem reasonable to conclude that the tail is producing some lift.

The variable-geometry model predicts a sequence of changes in morphology with tail angle of attack changing at lower airspeeds than tail spread, which should be furled before wingspan starts to decrease (Thomas 1996). This sequence is not seen in the swallows flying in the wind tunnel, in which there is a more gradual change in all three parameters over a wider range of airspeeds. These data suggest that wingspan changes continuously across the range of airspeeds at which the swallows would fly, while tail spread and angle of attack reach their minima at higher airspeeds than predicted by the variable-geometry model. In our data, tail angle of attack reaches its minimum at a higher airspeed than does tail spread. This is not what is predicted by the variable-geometry model.

For a robust theory, there should be a good quantitative match between prediction and observation. The results in figure 1 demonstrate that any quantitative match between prediction and observation is very small. Wingspan varies much less than predicted, the swallows in our experiment varied their wingspan by less than 10%, whereas the model predicts that wingspan should vary by over 60%.

It should be noted that as described above, the predictions for changes in wingspan are the same whether or not the tail produces lift. These changes are not due to delta-wing theory and are in fact due to other aspects of Thomas's (1996) model, which is based on a variant of Pennycuick's momentum jet model (Pennycuick 1975, 1989). The maximum tail spread during level flight was about one-third of the maximum value observed in turning flight (95°; seen during manoeuvres filmed in the wind tunnel), and declined much more gradually with airspeed than predicted. If the mean deviation between the observed tail spread and the prediction is taken as a measure of match between theory and prediction, then Thomas's (1996) variable-geometry model, which assumes that the tail produces lift, makes predictions that are no better than those produced by the null model, which assumes that the tail produces no lift. While tail angle of attack never reaches the high levels predicted there is a better match between prediction and observation for this variable, although observed tail angles of attack start to decline at higher airspeeds than those predicted by Thomas (1996). The prediction is that the tail should be parallel to the airflow by an airspeed of 5 m s^{-1}, while the tails of the swallows in our experiment were almost at maximal angle of attack at this airspeed. The mean deviation between the observed tail angle of attack and the predictions from the null model are similar to those of Thomas's (1996) variable-geometry model, suggesting that they are similarly good quantitative predictors of tail angle of attack.

Our comparison with changes in morphology in magpies and pigeons show that the swallows used in our experiments changed their tail and wing morphology in a similar way to that seen in these other two species (figure 2). In all three species wingspans change little with airspeed, while tail spread gradually moves from fully spread to furled as airspeed increases.

None of these comparative data show the abrupt changes in shape predicted by this application of delta-wing theory. The similarity in the way the three species considered here change their morphology, and the consistent lack of match between empirical data and prediction, suggest that delta-wing theory, as used in this variable-geometry model, may not be an adequate description of the aerodynamics of the avian tail.

The theoretical bird used in Thomas's work could adopt any morphology up to certain prescribed maximum values. In reality, any animal is constrained by its anatomy; a swallow cannot change its wingspan during flight by a factor of three. It is possible that the theory could be modified to accommodate the fact that in real life, animals are not infinitely plastic, even though virtual animals may be. In addition, the variable-geometry model uses an optimization routine that assumes that the bird will adopt a morphology that minimizes the power required to fly (Thomas 1996). While intuitively attractive and mathematically tractable, the currency of power minimization may not be appropriate to a flying bird. Power minimization implies that the bird is attempting to spend as little energy on locomotion as possible. Flying birds, however, are invariably trying to achieve something during flight. In the case of a swallow this could include foraging for self and young, migration, predator avoidance or mate attraction. A number of alternative and probably more biologi-

cally reasonable currencies could be envisaged, such as maximizing distance travelled per unit energy or unit time or even maximizing manoeuvrability. Consideration of alternative currencies may prove to be a fruitful way of progressing and may produce more biologically relevant predictions (Hedenström & Alerstam 1995).

This is the first test, to our knowledge, in live birds of the predictions made by delta-wing theory as applied to birds' tails. The work presented here suggests that the tail is likely to be producing lift: our null model that predicted no change in tail shape and angle of attack was a worse qualitative predictor of changes in morphology during flight than delta-wing theory. However, our empirical observations failed to provide robust support for the variable-geometry application of delta-wing theory—the order of morphological changes and the way in which morphology changes with flight speed were not well predicted. It is possible that the use of delta-wing theories other than slender-wing theory (e.g. leading-edge vortex theory) would improve the predictions. However, taking the results reported here with the results of Maybury *et al.* (2001) and in the absence of direct tests of the applicability of delta-wing theory, we would conclude that caution should be used when applying delta-wing theory as a model for the aerodynamics of birds' tails.

REFERENCES

Balmford, A., Thomas, A. L. R. & Jones, I. L. 1993 Aerodynamics and the evolution of long tails in birds. *Nature* **361**, 628–630.

Balmford, A., Jones, I. L. & Thomas, A. L. R. 1994 How to compensate for costly sexually selected tails: the origin of sexually dimorphic wings in long-tailed birds. *Evolution* **48**, 1062–1070.

Cuervo, J. J., de Lope, F. & Møller, A. P. 1996 The function of long tails in female barn swallows (*Hirundo rustica*): an experimental study. *Behav. Ecol.* **7**, 132–136.

Evans, M. R., Martins, T. L. F. & Haley, M. 1994 The asymmetrical cost of tail elongation in red-billed streamertails. *Proc. R. Soc. Lond.* B **256**, 97–103.

Fitzpatrick, S. & Price, P. 1997 Magpies' tails: damage as an indicator of quality. *Behav Ecol. Sociobiol.* **40**, 209–212.

Gatesy, S. M. & Dial, K. P. 1996 From frond to fan: *Archaeopteryx* and the evolution of short-tailed birds. *Evolution* **50**, 2037–2048.

Hedenström, A. & Alerstam, T. 1995 Optimal flight speeds of birds. *Phil. Trans. R. Soc. Lond.* B **348**, 471–487.

Hedenström, A. & Liechti, F. 2001 Field estimates of body drag coefficient on the basis of dives in passerine birds. *J. Exp. Biol.* **204**, 1167–1175.

Maybury, W. J. & Rayner, J. M. V. 2001 The avian tail reduces body parasite drag by controlling flow separation and vortex shedding. *Proc. R. Soc. Lond.* B **268**, 1405–1410. (DOI 10.1098/rspb.2001.1635.)

Maybury, W. J., Rayner, J. M. V. & Couldrick, L. B. 2001 Lift generation by the avian tail. *Proc. R. Soc. Lond.* B **268**, 1443–1448. (DOI 10.1098/rspb.2001.1666.)

Maynard Smith, J. 1952 The importance of the nervous system in the evolution of animal flight. *Evolution* **6**, 127–129.

Møller, A. P. 1994 Differential costs of a secondary sexual character: an experimental test of the handicap principle. *Evolution* **48**, 658–670.

Norberg, R. Å. 1994 Swallow tail streamer is a mechanical device for self-deflection of tail leading edge, enhancing aerodynamic efficiency and flight manoeuvrability. *Proc. R. Soc. Lond.* B **257**, 227–233.

Norberg, U. M. 1990 *Vertebrate flight: mechanics, physiology, morphology, ecology and evolution.* Berlin: Springer.

Norberg, U. M. 1995 How a long tail and changes in mass and wing shape affect the cost for flight in animals. *Funct. Ecol.* **9**, 48–54.

Park, K. J., Rosén, M. & Hedenström, A. 2001 Flight kinematics of the barn swallow (*Hirundo rustica*) over a wide range of speeds in a wind tunnel. *J. Exp. Biol.* **204**, 2741–2750.

Pennycuick, C. J. 1975 Mechanics of flight. In *Avian biology*, vol. 5 (ed. D. S. Farner & J. R. King), pp 1–75. London: Academic.

Pennycuick, C. J. 1989 *Bird flight performance: a practical calculation manual.* Oxford University Press.

Pennycuick, C. J. 1997 Actual and 'optimum' flight speeds: field data reassessed. *J. Exp. Biol.* **200**, 2355–2361.

Pennycuick, C. J., Alerstam, T. & Hedenström, A. 1997 A new low-turbulence wind tunnel for bird flight experiments at Lund University, Sweden. *J. Exp. Biol.* **200**, 1441–1449.

Rayner, J. M. V. 1979a A vortex theory of animal flight. I. The vortex wake of a hovering animal. *J. Fluid Mech.* **91**, 697–730.

Rayner, J. M. V. 1979b A vortex theory of animal flight II. The forward flight of birds. *J. Fluid Mech.* **91**, 731–763.

Rayner, J. M. V. 1979c A new approach to animal flight mechanics. *J. Exp. Biol.* **80**, 17–54.

Rosén, M. & Hedenström, A. 2001 Gliding flight in a jackdaw: a wind tunnel study. *J. Exp. Biol.* **204**, 1153–1166.

Thomas, A. L. R. 1993 On the aerodynamics of birds' tails. *Phil. Trans. R. Soc. Lond.* B **340**, 361–380.

Thomas, A. L. R. 1996 The flight of birds that have wings and a tail: variable geometry expands the envelope of flight performance. *J. Theor. Biol.* **183**, 237–245.

Tobalske, B. W. & Dial, K. P. 1996 Flight kinematics of black-billed magpies and pigeons over a wide range of speeds. *J. Exp. Biol.* **199**, 263–280.

Tobalske, B. W., Peacock, W. L. & Dial, K. P. 1999 Kinematics of flap-bounding flight in the zebra finch over a wide range of speeds. *J. Exp. Biol.* **202**, 1725–1739.

Tucker, V. A. 1995 Drag reduction by wing tip slots in a gliding harris hawk, *Parabuteo unicinctus*. *J. Exp. Biol.* **198**, 775–781.

Warrick, D. R., Dial, K. P. & Bienwener, A. A. 1998 Asymmetrical force production in the slow maneuvering flight of pigeons. *Auk* **115**, 916–928.