Kinematics of flap-bounding flight in the zebra finch over a wide range of speeds

<table>
<thead>
<tr>
<th>Authors</th>
<th>Tobalske, Peacock, Dial</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>1999</td>
</tr>
<tr>
<td>Volume</td>
<td>202 (Pt 13)</td>
</tr>
<tr>
<td>Issue</td>
<td></td>
</tr>
<tr>
<td>Pages</td>
<td>1725-39</td>
</tr>
</tbody>
</table>

Abstract
It has been proposed elsewhere that flap-bounding, an intermittent flight style consisting of flapping phases interspersed with flexed-wing bounds, should offer no savings in average mechanical power relative to continuous flapping unless a bird flies 1.2 times faster than its maximum range speed (Vmr). Why do some species use intermittent bounds at speeds slower than 1.2Vmr? The 'fixed-gear hypothesis' suggests that flap-bounding is used to vary mean power output in small birds that are otherwise constrained by muscle physiology and wing anatomy to use a fixed muscle shortening velocity and pattern of wing motion at all flight speeds; the 'body-lift hypothesis' suggests that some weight support during bounds could make flap-bounding flight aerodynamically advantageous in comparison with continuous flapping over most forward flight speeds. To test these predictions, we studied high-speed film recordings (300 Hz) of wing and body motion in zebra finches (Taenopygia guttata, mean mass 13.2 g, N=4) taken as the birds flew in a variable-speed wind tunnel (0-14 m s⁻¹). The zebra finches used flap-bounding flight at all speeds, so their flight style was unique compared with that of birds that facultatively shift from continuous flapping or flap-gliding at slow speeds to flap-bounding at fast speeds. There was a significant effect of flight speed on all measured aspects of wing motion except percentage of the wingbeat spent in downstroke. Changes in angular velocity of the wing indicated that contractile velocity in the pectoralis muscle changed with flight speed, which is not consistent with the fixed-gear hypothesis. Although variation in stroke-plane angle relative to the body, pronation angle of the wing and wing span at mid-upstroke showed that the zebra finch changed within-wingbeat geometries according to speed, a vortex-ring gait with a feathered upstroke appeared to be the only gait used during flapping. In contrast, two small species that use continuous flapping during slow flight (0-4 m s⁻¹) either change wingbeat gait according to flight speed or exhibit more variation in stroke-plane and pronation angles relative to the body. Differences in kinematics among species appear to be related to wing design (aspect ratio, skeletal proportions) rather than to pectoralis muscle fiber composition, indicating that the fixed-gear hypothesis should perhaps be modified to exclude muscle physiology and to emphasize constraints due to wing anatomy. Body lift was produced during bounds at speeds from 4 to 14 m s⁻¹. Maximum body lift was 0.0206 N (15.9% of body weight) at 10 m s⁻¹; body lift:drag ratio declined with increasing air speed. The aerodynamic function of bounds differed with increasing speed from an emphasis on lift production (4-10 m s⁻¹) to an emphasis on drag reduction with a slight loss in lift (12 and 14 m s⁻¹). From a mathematical model...
of aerodynamic costs, it appeared that flap-bounding offered the zebra finch an aerodynamic advantage relative to continuous flapping at moderate and fast flight speeds (6-14 m s⁻¹), with body lift augmenting any savings offered solely by flap-bounding at speeds faster than 7.1 m s⁻¹. The percentage of time spent flapping during an intermittent flight cycle decreased with increasing speed, so the mechanical cost of transport was likely to be lowest at faster flight speeds (10-14 m s⁻¹).