

1 **Title**

2 Whole-body 3D kinematics of bird take-off: key role of the legs to propel the trunk

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## 30 **Abstract**

31 Previous studies showed that birds primarily use their hindlimbs to propel themselves into the  
32 air in order to take-off. Yet, it remains unclear how the different parts of their musculoskeletal  
33 system move to produce the necessary acceleration. To quantify the relative motions of the  
34 bones during the terrestrial phase of take-off, we used biplanar fluoroscopy in two species of  
35 birds, Diamond Dove (*Geopelia cuneata*) and Zebra Finch (*Taeniopygia guttata*). We  
36 obtained a detailed 3D kinematics analysis of the head, the trunk, and the three long bones of  
37 the left leg. We found that the entire body assisted the production of the needed forces to take-  
38 off, during two distinct but complementary phases. The first one, a relatively slow preparatory  
39 phase, started with a movement of the head and an alignment of the different groups of bones  
40 with the future take-off direction. It was associated with a pitch down of the trunk and a  
41 flexion of the ankle, of the hip and to a lesser extent of the knee. This crouching movement  
42 could contribute to the loading of the leg muscles and store elastic energy that could be  
43 released in the propulsive phase of take-off, during the extension of the leg joints. Combined  
44 with the fact that the head, together with the trunk, produced a forward momentum, the entire  
45 body assisted the production of the needed forces to take-off. The second phase was faster  
46 with mostly horizontal forward and vertical upward translation motions, synchronous to an  
47 extension of the entire lower articulated musculo-skeletal system. It led to the propulsion of  
48 the bird in the air with a fundamental role of the hip and ankle joints to move the trunk  
49 upward and forward. Take-off kinematics were similar in both studied species, with a more  
50 pronounced crouching movement in Diamond Dove, which can be related to a large body  
51 mass compared to Zebra Finch.

52

## 53 **3-6 key words**

54 3D kinematics, X-ray Reconstruction Of Moving Morphology, trunk, hindlimbs, Zebra Finch,  
55 Diamond Dove.

57 Take-off is a challenging phase of flight as it allows the transition between two environments  
58 with different physical constraints. The animal must move from a standing position with a  
59 very low speed, to an efficient flying posture with enough velocity to stay in flight. Therefore,  
60 take-off involves significant transitional motions of the articulated system between two  
61 locomotor positions, combined with the production of enough acceleration to propel itself into  
62 the air. In small animals, such as insects or small birds, take-off generally starts with a jump  
63 (Alexander 1995; Dudley 2002; Manzanera and Smith 2015), consisting in a crouching  
64 movement followed by a rapid extension of the legs. It has been observed that the first wing  
65 downstroke starts after lift-off (Brackenbury 1992; Card and Dickinson 2008; Earls 2000;  
66 Manzanera and Smith 2015; Provini et al. 2012b; Zumstein et al. 2004), suggesting that the  
67 legs produce most of the acceleration needed to become airborne. In birds, ground reaction  
68 force measurements during take-off (Bonser and Rayner 1996; Earls 2000; Heppner and  
69 Anderson 1985; Tobalske et al. 2004) and a quantification of wings' and legs' contribution in  
70 the small columbid Diamond Dove (*Geopelia cuneata*) and the passerine Zebra Finch  
71 (*Taeniopygia guttata*) (Provini et al. 2012b) confirmed this hypothesis. Interestingly, despite  
72 large discrepancies between the different studied species in terms of body size, terrestrial  
73 locomotion strategy, wing morphology, and slow-flight kinematics, the most important  
74 differences were not observed in the production of aerodynamic forces during the first  
75 wingbeats, but in the ground reaction forces, when the bird is still in contact with the perch.  
76 Indeed, both the magnitude and the timing of the forces generated by the two species of birds  
77 were different (see SM1 and Provini et al. (2012b)). Here, we aim to understand how the  
78 different parts of the avian musculoskeletal system moved in relation to each other to produce  
79 the necessary force to take-off and what in the kinematics could explain the differences  
80 observed in the ground reaction forces between Diamond Dove and Zebra Finch.

81 In spite of the obvious importance of take-off to flight only few studies have investigated bird  
82 take-off kinematics (Berg and Biewener 2010; Earls 2000; Provini et al. 2012b; Tobalske et  
83 al. 2004). On the one hand, the fact that take-off is a non-cyclic transitional motion makes it  
84 relatively difficult to study. Contrary to walking, running, hopping, swimming or flying, for  
85 which a high number of cycles can be recorded, it is more challenging to obtain a great  
86 number of take-off trials. Moreover, the lack of data could be explained by several technical  
87 factors. First, the rapidity of take-off requires high-speed video cameras to capture the  
88 movement of the animal. Furthermore, as feathers hide most of the body in birds, it is  
89 impossible to infer accurately the skeleton motions of the proximal parts of the limbs solely  
90 with the use of light cameras; thus, X-ray imaging has to be included in the data acquisition.

91 Third, motions of the head, the trunk, and the hindlimbs are not truly planar. Recent studies in  
92 birds have demonstrated the importance of long-axis rotations in hindlimbs kinematics  
93 (Kambic et al. 2014) which can only be quantified with an accurate 3D analysis of the bones  
94 motions. Until recently, it was nearly impossible to acquire high-speed 3D X-ray data, but  
95 thanks to the combination of X-ray imaging and computational process (X-ray Reconstruction  
96 of Moving Morphology, XROMM), we are now able to record precise and accurate 3D  
97 skeletal movement (Brainerd et al. 2010; Gatesy et al. 2010) and have access to relatively  
98 concealed motions. The present study took advantage of these technical advances and used  
99 XROMM methods to carry out a 3D kinematics analysis during the terrestrial phase of take-  
100 off, finishing when the bird loses contact with the perch at lift-off.

101 We chose Zebra Finch (*Taeniopygia guttata*) and Diamond Dove (*Geopelia cuneata*) for their  
102 compatibility in terms of size and behaviour with our experimental protocol and because of  
103 the ground reaction forces data previously obtained from a similar experiment (Provini et al.  
104 2012b), allowing us to draw a biomechanical comparison between these two species.

105 We carried out a kinematic analysis of the lower appendicular skeleton, *i.e.* the legs' three  
106 long bones (femur, tibiotarsus, and tarsometatarsus) and the pelvis. Including the pelvic girdle  
107 in our kinematics analysis, in addition to the leg bones, was motivated by the fact that the  
108 trunk participates in the crouching movement of the first phase of take-off and also because  
109 the trunk is known to play an important role to guide the entire body trajectory in bird  
110 locomotion (Abourachid et al. 2011; Berg and Biewener 2010; Gatesy 1999; Provini et al.  
111 2012a). Finally, we included the head kinematics in our study as its position differs from a  
112 standing to a flying posture (Maurice et al. 2006) and to investigate its potential role in take-  
113 off kinematics. Because the role of the wings is not determinant to propel the centre of mass  
114 during this phase (Provini et al. 2012b) we did not include the wing motions in our study,  
115 however, the two light cameras allowed us to follow their general motions.

116

## 117 **Materials and methods**

### 118 **1. Animals**

119 Two *Taeniopygia guttata* (mean+s.d mass: 15.4±1.2g) and two *Geopelia cuneata* (mean+s.d  
120 mass: 52.0±3.2g) were purchased from commercial dealers, housed in flight cages, and  
121 provided with food and water *ad libitum* at the Concord Field Station in Bedford, MA, USA.  
122 They were trained to take-off from a wood perch in the scope of two C-arms and two visible-  
123 light video cameras (Fig. 1).

124

## 125      2. Surgical and experimental protocols

126 Prior to videographic recording, birds were implanted with 0.5 mm diameter tantalum beads.  
127 For this purpose, birds were anesthetized with isoflurane in O<sub>2</sub>. Anaesthesia was induced  
128 using a custom constructed facemask and maintained for the duration of the surgery through  
129 an endotracheal tube. Then, feathers overlying the implantation sites were removed and a  
130 small cutaneous incision was made. Connective tissue and muscle were incised and 0.5 mm  
131 diameter tantalum beads were implanted on the head, the pelvis and left hindlimb bones  
132 (femur, tibiotarsus, and tarsometatarsus). We implanted one to three markers per bones: one  
133 marker on the beak, one on the pelvis, two on the left femur, two on the left tibiotarsus, and  
134 three on the left tarsometatarsus (SM2). When two or three markers were implanted on the  
135 same bone, we spaced them as far apart as possible to maximise the accuracy of bone 3D  
136 reconstruction (Brainerd et al. 2010). Finally, after all tissues were sutured closed, birds were  
137 allowed to recover until a normal locomotion behaviour had resumed. All experiments were  
138 conducted in accordance with international and institutional guidelines for the care and use of  
139 the animals.

140 Birds were recorded while taking-off at a resolution of 1080 x 1024 pixels and a speed of  
141 1000 frames per second (fps) using two X-ray videography systems, each composed of a  
142 Photron 1024 PCI camera (Photron USA Inc., San Diego, CA, USA) coupled to an X-ray C-  
143 arm system (Model 9400, OEC-Diasonics Inc., remanufactured by Radiological Imaging  
144 Services). The two X-ray C-arms were set in a lateral and a dorsoventral positions and set to  
145 emit at 60 kVp and 100 mA (Fig. 1). Two visible-light video cameras were added to the  
146 experimental setup: a Photron 1024 PCI (Photron, Inc., San Diego, CA, USA) recording at a  
147 resolution of 1024 x 1024 pixels and 1000 fps a Phantom MiroEx4 (Vision Research Inc.,  
148 Wayne, NJ, USA) recording at 800 x 600 pixels and 1000 fps (Fig. 1). We followed  
149 recommendations regarding distortion correction and calibration of the space during the  
150 experiment (Brainerd et al. 2010; Gatesy et al. 2010). We use both a perforated steel sheet  
151 with precise hole size and spacing for distortion correction and a calibration object for  
152 accurate camera 3D placement for each video. We selected trials where birds kept a relatively  
153 straight trajectory during take-off.

154

## 155      3. Bone models and XROMM analysis

156 To obtain the bones models, needed for the XROMM analysis, animals were sacrificed via an  
157 overdose of isoflurane inhalant and scanned in a micro computed tomography ( $\mu$ CT) system  
158 (XRA-002 X-tek microCT scan available at the Center for Nanoscale Systems at Harvard  
159 University; 66kV, 130mA and a resolution of 0.04mm on each axis). We used Avizo (version

160 6.3; FEI Visualization Sciences Group) to reconstruct bones models from the  $\mu$ CT scans.  
161 Then, models were imported in obj file format into Maya (version 2013; Autodesk). For  
162 bones with less than three markers, we used rotoscoping methods (Gatesy et al. 2010) or a  
163 combination of rotoscoping and marker-based methods (Brainerd et al. 2010), with marker  
164 positions digitized and reconstructed in 3D, using the program XrayProject 2.2.4 in MATLAB  
165 (Brainerd et al. 2010) ([www.xromm.org](http://www.xromm.org)). We obtained a 3D animation of the head, the trunk,  
166 and the three long bones of the left hindlimb (femur, tibiotarsus, and tarsometatarsus) for two  
167 take-off trials in two Zebra Finches and two Diamond Doves (Figs 2a, 2b, SM3).

168

#### 169 4. Kinematics analysis

##### 170 a. Three-dimensional coordinate systems

171 The XROMM analysis provided the 3D motion of five rigid bodies: head, trunk (pelvis, keel  
172 and rib cage considered as one rigid body), femur, tibiotarsus (tibia and fibula considered as  
173 one rigid body), and tarsometatarsus. To quantify the 3D motion of joints and bones, we used  
174 a combination of two sets of coordinate systems: Anatomical Coordinate Systems (ACSs) and  
175 Joint Coordinate System (JCS) (Grood and Suntay 1983) that were previously proposed as a  
176 common framework, established for guineafowl hindlimbs, to facilitate comparisons among  
177 individuals and different avian species (Kambic et al. 2014).

178 The relative motions between a bone and a global coordinate system can be measured with  
179 one ACS and one global coordinate system. The construction of the ACSs was exclusively  
180 based on skeletal anatomy. We defined a global coordinate system to quantify the 3D motions  
181 of both the trunk and the head. Its origin was defined as the point on the perch intersecting  
182 with the sagittal plane of the trunk at the beginning of the take-off trial, with a horizontal X-  
183 axis in the direction of the trunk motion pointing backwards, a vertical Z-axis pointing up, and  
184 a horizontal Y-axis perpendicular to the two previous axes pointing to the right. For the trunk,  
185 we used the pelvis ACS previously described (Kambic et al. 2014) (SM4), for the head, we  
186 built a specific ACS, following a similar rationale. To establish the head ACS origin, we  
187 isolated the two orbits in the head 3D model and fitted them with spheres in Geomagic Studio  
188 2013 (3D Systems, Morrisville, NC, USA). The midway between sphere centroids was used  
189 as the origin, the Y-axis ran through the right and left orbit centres, positive to the right, the  
190 X-axis ran orthogonally down the midline, intersecting the middle of the beak tip and the  
191 occipital region, positive pointing caudally, the Z-axis was set orthogonal to both Y-axis and  
192 X-axis, positive dorsally (SM4a).

193 Moreover, the relative motions between two adjacent bones can be measured with a  
194 combination of two ACSs, one on each bone, enabling the definition of a JCS for the  
195 corresponding joint. The characteristics of the ACSs (origin and orientations) were previously  
196 defined for the trunk, femur, tibiotarsus and tarsometatarsus (Kambic et al. 2014), allowing us  
197 to build the JCSs corresponding to the hip, knee, and ankle. We built a specific JCS for the  
198 head. Z-axis rotations (Yaw and flexion-extension) measured rotation of the head ACS about  
199 a fixed, global vertical Z-axis, positive to the left. X-axis rotation (roll and long-axis rotation)  
200 designated rotation about the local head X-axis, raising to the right orbit relative to the left  
201 being positive. Y-axis rotations (pitch and abduction-adduction) quantified rotation about a  
202 floating JCS Y-axis (always orthogonal to the yaw and roll axes), head up being positive  
203 (SM4).

204 A reference pose (SM4) was also built following Kambic et al. (2014) recommendations. All  
205 translations and rotations were set to zero, each pair of ACS contributing to the JCS was  
206 perfectly aligned. The head JCS was aligned on the pelvis JCS, head and pelvis  
207 interpenetrating (SM4g).

208 Thereby, for each trial of each species of birds, we obtained a dataset of 6 variables,  
209 corresponding to the six degrees of freedom motions, of the left hip, left knee, and left ankle,  
210 as well as of the trunk and the head, relative to a global coordinate system. Translations along  
211 the X-axis ( $t_x$ ), the Y-axis axis ( $t_y$ ), and the Z-axis ( $t_z$ ) were measured for the head, trunk, left  
212 hip, left knee and left ankle. Roll ( $r_x$ ), pitch ( $r_y$ ) and yaw ( $r_z$ ) were obtained for the head and  
213 the trunk. Long-axis rotation ( $r_x$ ), abduction/adduction ( $r_y$ ), and flexion/extension ( $r_z$ ) angles  
214 for the left hip, left knee and left ankle (Figs 3, 4) were also calculated. We followed previous  
215 similar analysis for notations (Gidmark et al. 2012). We defined letters to refer to each rigid  
216 body or joint: head (H), trunk (Tr), hip (Hip), knee (Kn), ankle (Ank). These letters were  
217 followed by either “t” for translation along or “r” for rotation about, and “x”, “y”, or “z” to  
218 denote the specific axis. Therefore, translation about the x-axis of the head would be  $H_{t_x}$ .

219

## 220 **b. Trials synchronisation and space adjustment**

221 As birds did not perform take-off exactly at the same rate, trials lengths differed. To be able to  
222 compare and average trials among a given species, we synchronized our data in both space  
223 and time. Our observations of all the take-off trials revealed that the minimum of head vertical  
224 translation ( $H_{t_z}$ ) corresponded to a repeatable event, thus we used it to set a synchronization  
225 time. The timing of each degree of freedom motions of rigid bodies or joints was  
226 synchronized to this instant. Then, trials were cropped to start at the beginning of take-off ( $t_0$ ),  
227 when the bird initiates the crouching movement and the alignment of the head with the rest of

228 the body, and to end at lift-off (LO), when the bird loses contact with the perch. We  
229 calculated a sequence percentage with 0% corresponding to  $t_0$  and 100% corresponding to lift  
230 off (LO).

231 Moreover, as the initial point of each take-off was slightly different among trials, we shifted  
232 the data to an arbitrary point. For each degree of freedom motions of rigid bodies or joints, we  
233 recorded the magnitude at synchronized time equals zero and subtracted this value to the  
234 corresponding data set (for example, if the magnitude of  $Tr_{tx}$  at synchronized time equals zero  
235 was equal to 2.1 for a given trial, we subtracted 2.1 to the  $Tr_{tx}$  data of the entire trial).  
236 Therefore, further of translations and rotations values were not absolute. The synchronized  
237 data adjusted in space allowed us to calculate an average of each degree of freedom motions  
238 of rigid bodies or joints within each species.

239

#### 240 **c. Take-off sequence**

241 We observed three key events during takeoff (SM3): 1) take-off start ( $t_0$ ), when the bird  
242 initiates the crouching movement and the alignment of the head with the rest of the body, 2)  
243 beginning of leg extension, also corresponding to the end of the crouching movement, 3) lift  
244 off, LO, when the bird loses contact with the perch (Fig. 2). These three events defined two  
245 distinct phases, previously named “phase 1” and “phase 2” (Provini et al. 2012b).

246 The beginning of the leg extension phase corresponded to a modification of rigid bodies  
247 trajectories. To extract the instant it occurred, we used the trunk trajectory ( $Tr_{tx}$ , and  $Tr_{tz}$ ),  
248 because the motions of the trunk, being the heaviest part of the body, was considered as a  
249 proxy for the motions of the center of mass. We performed a segmented linear regression,  
250 using the R package *segmented* (version 0.5-1.4) (R Development Core Team 2010). It  
251 provided a breakpoint for  $Tr_{tx}$ , and  $Tr_{tz}$  for each trial of each species of birds. We averaged the  
252 results and obtained an objective measure to divide the take-off sequence between the  
253 “crouching movement phase” and the “legs extension phase” for each species (SM5). Note  
254 that the timing of the breakpoint was not necessarily similar to the synchronization time.

255

#### 256 **d. Bones and joints motion quantification**

257 Using the R package *stats* (version 3.3.0) (R Development Core Team 2010) and with the  
258 previously synchronized and space adjusted data ( $tx$ ,  $ty$ ,  $tz$ ,  $rx$ ,  $ry$ , and  $rz$  for the head, trunk,  
259 left femur, left tibiotarsus and left tarsometatarsus), we averaged and calculated standard  
260 deviation at each time step for the four trials of Diamond Dove and the four trials of Zebra  
261 Finch. We calculated a magnitude, corresponding to the difference between the maximum



262 value and the minimum value of each variable. We calculated the mean and standard  
263 deviation associated to the magnitude of each previous variable, during phase 1 and during  
264 phase 2 (Table 1).

265 To quantify the change in velocity between the two phases of take-off, we derived  $Tr_{tx}$  and  
266  $Tr_{tz}$  on each trial (SM6). We calculated the mean and standard deviation associated to trunk  
267 velocity on the X and Z axes for phase 1 and phase 2 in each species of birds.

268 The head aligned with the trunk before the beginning of legs extension (Fig. 2, SM3). To  
269 quantify this alignment, we measured the angle formed between the head and the trunk. To do  
270 so, we used the 3D animation obtained from Maya (Autodesk, version 2013) and added  
271 virtual markers (*VM*), corresponding to small icons on the Maya scene that mark a point in  
272 space. We added one *VM* at the most caudal part of the sagittal plane of the trunk, at the level  
273 of the first caudal vertebrae ( $VM_{T1}$ ), and another one on the most cranial part of the sagittal  
274 plane of the trunk at the level of first thoracic vertebrae ( $VM_{T2}$ )(SM2). We measured the  
275 angle formed by these two virtual markers and the marker located on the beak during each  
276 trial. We named this variable *angle\_neck* and calculated mean and standard deviation for this  
277 variable for each species of birds at each time step.

278 In order to capture the neck flexion/extension, we measured the distance between the head  
279 and the trunk, between a virtual marker located at the level of the supraoccipital bone on the  
280 sagittal plane of the head ( $VM_{H1}$ ) and  $VM_{H2}$ . We named this variable *dist\_neck* and calculated  
281 the mean and the associated standard deviation for each species of bird at each time step (Fig.  
282 5a). Following the same rationale, to capture the entire limb flexion/extension effect, we used  
283  $VM_{T2}$  and placed another virtual marker on the most distal part of the tarsometatarsus at the  
284 third digit trochlea level ( $VM_{Tmt1}$ ) (SM2). We named this variable *dist\_limb* and calculated the  
285 mean and the associated standard deviation for each species of bird at each time step (Fig.  
286 5b).

287 Considering the small number of trials and specimens, inter-species comparisons were only  
288 performed qualitatively for each variable, with the help of the figures (Figs 2, 3, 4, 5).

289

## 290 **Results**

### 291 **1. Take-off sequence**

292 Take-off was divided into two phases, phase 1 and phase 2, corresponding to a downward  
293 motion of the trunk followed by an upward motion of the trunk. The segmented linear  
294 regressions of the trajectory of the trunk showed that two linear regressions could fit the data  
295 for  $Tr_{tx}$  and  $Tr_{tz}$  as a function of the sequence percentage for both species of birds (SM5).

296 For Diamond dove, we found a breakpoint at  $63.6\pm 2.2\%$  of take-off sequence for  $Tr_{tx}$  and  
297  $65.5\pm 3.0\%$  for  $Tr_{tz}$ . We thus considered that the beginning of phase 2 occurred at  $64.5\pm 2.7\%$   
298 of take-off sequence. For Zebra finch, the breakpoint occurred at  $59.1\pm 4.3\%$  of take-off  
299 sequence for  $Tr_{tx}$  and  $64.6\pm 7.9\%$  for  $Tr_{tz}$ . Therefore, we considered that the beginning of  
300 phase 2 was at  $61.8\pm 6.6\%$  of take-off sequence.

301

## 302 5. 3D motions analysis

### 303 a. Head motions

304 During phase 1, the head aligned with the sagittal plane of trunk. This is visible on the  
305 dorsoventral view of Fig. 2a for Diamond dove and in Fig. 2b for Zebra Finch. In Diamond  
306 Doves, *angle\_neck* went from  $140.5\pm 2.8$  deg at the beginning of phase 1 to  $178.6\pm 3.4$  deg at  
307 the beginning of phase 2. In Zebra Finch, *angle\_neck* went from  $144.58\pm 4.6$  deg at the  
308 beginning of phase 1 to  $178.01\pm 2.6$  deg at the beginning of phase 2. Thus in both species, the  
309 head was in very close alignment to the trunk at the beginning of phase 2. This alignment was  
310 linked to a rotation of the trunk or of the head along the vertical axis (Figs 2, 3). As the  
311 magnitude of  $H_{rz}$  (the difference between the maximum and the minimum of  $H_{rz}$ ), during  
312 phase 1 was lower than  $Tr_{tz}$  for Diamond Dove, it suggested that the alignment was mostly  
313 due to a trunk rotation. In contrast, because the magnitude of  $H_{rz}$  was higher than of  $Tr_{tz}$  for  
314 Zebra Finch, the alignment was mostly due to the head rotation. At the same time, *dist\_neck*  
315 slightly decreased in Zebra Finch, equivalent to a flexion of the neck (Fig. 5a), whereas it was  
316 not the case in Diamond Dove. The magnitude of  $H_{tz}$  was higher compared to the magnitude  
317 of  $Tr_{tz}$  in both species, suggesting that the flexion was due to the vertical upward translation  
318 of the head downwards. The head also translated forward in both species during phase 1.

319 During phase 2, the head remained aligned with the sagittal plane of the trunk with a  
320 consistent value of *angle\_neck* of  $181\pm 3.6$  deg in Diamond Dove and of  $179\pm 2.5$  deg in Zebra  
321 Finch (Fig. 2). The head followed a linear trajectory in the direction of take-off with a similar  
322 shape of  $H_{tx}$ ,  $H_{ty}$ , and  $H_{tz}$  as  $Tr_{tx}$ ,  $Tr_{ty}$ , and  $Tr_{tz}$  respectively. The increase of *dist\_neck* during  
323 phase 2 corresponded to an extension of the neck.

324

### 325 b. Trunk motions

326 During phase 1, the velocity of  $Tr_{tz}$  was of  $4.2\pm 3.8$  mm/s in Diamond Dove, and of  $3.1\pm 2.9$   
327 cm/s in Zebra Finch. Translations of the trunk were mostly caudocranial with a magnitude of  
328  $Tr_{tx}$  ( $10.3\pm 1.0$  cm in Diamond Dove and  $4.1\pm 2.6$  in Zebra) relatively higher than the  
329 magnitude of  $Tr_{tz}$  ( $2.4\pm 1.7$  in Diamond Dove and  $1.3\pm 1.3$  cm in Zebra Finch) or of  $Tr_{ty}$

330 ( $0.8\pm 1.0$  in Diamond Dove and  $1.4\pm 0.3$  cm in Zebra Finch). This indicated a propulsion of the  
331 trunk in the forward direction during this phase. Trunk rotations predominantly corresponded  
332 to a downward pitch (Table 1 and Fig. 3). Trunk pitch was relatively higher in Diamond Dove  
333 compared to Zebra Finch (magnitude of  $17.5\pm 3.8$  deg and  $7.43$  deg respectively). In Diamond  
334 Dove, roll and yaw motions were still substantial during phase 1, (magnitude of  $Tr_{rx} = 7.1\pm 2.8$   
335 deg and  $Tr_{rz} = 7.6\pm 2.7$  deg), which was not the case in Zebra Finch (magnitude inferior to  $2.5$   
336 deg) (Table 1).

337 During phase 2, the velocity of  $Tr_{tz}$  increased to reach  $39.5\pm 10.7$  mm/s in Diamond Dove, and  
338  $28.2\pm 8.8$  cm/s in Zebra Finch. In both species, caudocranial translations of the trunk remained  
339 important (magnitude of  $21.7\pm 2.9$  cm in Diamond Dove and  $11.9\pm 7.2$  cm in Zebra Finch) but  
340 went with an increase of trunk vertical upward translations (magnitude of  $13.0\pm 2.7$  cm in  
341 Diamond Dove and  $8.2\pm 2.0$  cm in Zebra Finch). Upward pitch of the trunk was high in  
342 Diamond Dove (magnitude of  $14.5\pm 1.1$  deg), which was not the case in Zebra Finch  
343 (magnitude of  $2.5\pm 3.6$  deg).

344

#### 345 c. Hip motions

346 During phase 1, flexion of the hip was predominant in both species (magnitude of  $11.6\pm 2.9$   
347 deg in Diamond Dove and  $4.5\pm 9.9$  deg in Zebra Finch) (Fig.4), whereas abduction-adduction  
348 and long-axis rotations of the femur were low in both species (lower than 3 deg magnitude of,  
349 (Table 1).

350 During phase 2, extension of the hip was dominant (magnitude of  $36.3\pm 3.0$  deg in Diamond  
351 Dove and  $20.4\pm 7.9$  deg in Zebra Finch) (Fig.4). In Diamond Dove, abduction increased  
352 (magnitude of  $5.2\pm 2.8$  deg), whereas adduction increased in Zebra Finch (magnitude of  
353  $6.5\pm 3.3$  deg). Long axis rotation became higher in Zebra Finch (magnitude of  $10.7\pm 6.2$  deg),  
354 which was less noteworthy in Diamond Dove (magnitude of  $4.4\pm 5.6$  deg).

355

#### 356 d. Knee motions

357 During phase 1, flexion-extension motions were low (less than 2 deg in both species) (Table  
358 1). In Diamond Dove, we observed a relatively high adduction magnitude (magnitude of  
359  $8.4\pm 10.1$  deg), which was not true in Zebra Finch where the tibiotarsus remained static during  
360 this phase of take-off (magnitude lower than 4 deg) (Fig.4).

361 During phase 2, we observed an increase of knee extension in both species (magnitude of  
362  $31.9\pm 11.9$  deg in Diamond Dove and  $15.8\pm 8.4$  deg in Zebra Finch). This went with a rise of  
363 the tibiotarsus long axis rotation (magnitude of  $13.7\pm 6.7$  deg in Diamond Dove and  $7.0\pm 2.7$   
364 deg in Zebra Finch). In Diamond Dove, adduction stopped during phase 2, whereas abduction

365 increased in Zebra Finch (magnitude of  $3.4\pm 4.8$  deg in Diamond Dove and  $6.6\pm 4.4$  deg in  
366 Zebra Finch).

367

#### 368 e. Ankle motions

369 During phase 1, flexion of the ankle was predominant in Diamond Dove (magnitude of  
370  $8.9\pm 4.8$  deg), which was not the case in Zebra Finch, with a relatively low rotation  
371 magnitudes in all three directions (Fig. 4).

372 During phase 2, the ankle extension became dominant (magnitude of  $72.4\pm 16.0$  deg in  
373 Diamond Dove and  $39.8\pm 16.6$  deg in Zebra Finch) compared to adduction-abduction  
374 (magnitude inferior to 3 deg in both species). We can note that long axis rotation was  
375 relatively important in both species (magnitude of  $11.0\pm 8.3$  deg in Diamond Dove and  
376  $11.1\pm 7.1$  deg in Zebra Finch).

377

#### 378 f. Timing of joint flexion-extension

379 In both species, *dist\_limb* mostly increased during the take-off sequence, although in  
380 Diamond Dove, this augmentation was preceded by a reduction of *dist\_limb* during phase 1  
381 (Fig. 5).

382 In Diamond Dove, we observed a clear sequence of joint extension. First, the hip extension  
383 began at around 45% of the take-off sequence, followed by the ankle extension at around 60%  
384 of the take-off sequence, and finally the knee extension at around 75% of the take-off  
385 sequence. In Zebra Finch, the sequence was not as obvious, with a synchronous extension of  
386 the hip, knee and ankle at 50% of the take-off sequence.

387

## 388 Discussion

389 Our 3D kinematics analysis revealed a stereotyped behaviour during perch take-off in two  
390 species of birds, *Taeniopygia guttata* and *Geopelia cuneata*. Indeed, considering the small  
391 number of recorded sequences, the relatively low standard deviations of translation and  
392 rotation motions in both species (Table 1) demonstrates a consistency of motions among take-  
393 off trials. Overall, the kinematics is similar in the two studied species, although we observed  
394 differences in motion magnitudes that could be linked to differences in size and long bone  
395 proportions between the two species. In both species, take-off could be divided into two  
396 phases. Phase 1 corresponds to a preparatory phase, including both an alignment of the  
397 different parts of the skeleton into the direction of the future motion and a crouching motion.

398 Phase 2 was described as a propulsive phase, with an extension of the lower appendicular  
399 skeleton, propelling the entire body into the air.

400 During phase 1, we observed relatively slow motions, with a trunk vertical velocity  
401 corresponding to only 8.3% and 6.5% of the velocity at Lift off in Diamond Dove and Zebra  
402 Finch, respectively. The head is aligning with the sagittal plane of the trunk, which is  
403 demonstrated by *angle\_neck*, reaching 180 deg at the end of phase 1. This alignment is  
404 produced by both latero-medial translation and rotation of the head along the vertical axis  
405 (Fig. 3). In this respect, the high variability of  $H_{rz}$  in Zebra Finch (Table 1) is linked to the fact  
406 that some animals were looking to the right and others to the left at the beginning of the  
407 sequence. By aligning with the future direction of take-off, the head anticipates the global  
408 motion of the animal. This can be compared to what is observed in human locomotion where  
409 the eyes and the head anticipate the change in trajectory during turning, with a delay of the  
410 trunk (Imai et al. 2001). This alignment phase could contribute to reduce the aerodynamic  
411 drag, one of the forces resisting the forward motion. Although drag dominates at higher  
412 speeds than those observed during the terrestrial part of take-off, the frontal area remains an  
413 important factor in the drag coefficient calculation (Pennycuick 1975) and a streamlined  
414 profile contributes to reduce drag. Simultaneously with the head alignment, roll and yaw  
415 motions of the trunk are relatively important in Diamond Dove, also suggesting a  
416 reorientation of the trunk to align with the future motion of the animal. This motion could also  
417 help to reach take-off velocity by aligning the joints in the take-off direction.

418 The crouching motion observed in phase 1 goes with a trunk pitch down, as well as with  
419 flexions of the hip, knee and ankle (Fig. 4, Table 1). This leads to a decrease of *dist\_limb* in  
420 both species (Fig. 5) and contributes to lowering down the entire body. Previous studies in a  
421 variety of birds (Earls 2000; Heppner and Anderson 1985; Tobalske et al. 2004) suggested  
422 that a continuum exists in the take-off strategies, where tiny birds (3-5 g) show a crouching  
423 movement less exaggerated than the one displayed in small birds (15-90 g), which is itself  
424 less pronounced than in medium birds (100 g to 1.5 kg) who exhibit a motion similar to a  
425 squat (Manzanera and Smith 2015). Zebra Finch and Diamond Dove fall at the two sides of  
426 the small bird category, with a less pronounced pitching movement in Zebra Finch compared  
427 to Diamond Dove. This classification suggests that the size of the bird is correlated to the  
428 intensity of the crouching movement. A heavier bird needs more force output to take-off, per  
429 unit time compared to a smaller bird. However, because muscular force is proportional to  
430 muscular cross-section (a squared measurement), whereas weight is proportional to a volume  
431 (a cubed measurement), the potential muscular force generated by a heavy bird is lower than  
432 in a lighter bird. A higher flexion of the ankle and the hip in a heavier bird, such as in

433 Diamond Dove compared to Zebra Finch (Fig. 4, Table 1), contributes to a more pronounced  
434 crouching movement. Because stretched muscle tendon units could store elastic energy, a  
435 more pronounced flexion of the ankle and the hip could lead to the loading of the associated  
436 muscles and tendons, and generate more force than if they simply shortened (Henry et al.  
437 2005; Roberts 2016). Then, this elastic energy could be released during phase 2, the  
438 propulsive phase of take-off. The heavier the bird is, the more efficient this phenomenon  
439 could be and the more pronounced crouching movement it should display. Ground reaction  
440 forces, recorded with a similar protocol in the same two species (Provini et al. 2012b) (SM1)  
441 revealed a higher maximum vertical force magnitude in Diamond Dove, compared to Zebra  
442 Finch. If we standardize this value, taking the bird's body weight into account, maximal  
443 hindlimbs force produced by Diamond Dove corresponds to 3 times body weight compared to  
444 around 5 times body weight in Zebra Finch (Provini et al. 2012b). This means that a Diamond  
445 Dove, with a more pronounced crouching movement needs proportionally less forces to  
446 accomplish the same task as a Zebra Finch. This is coherent with the previous hypothesis and  
447 the potential use of elastic energy in Diamond Dove.

448 In addition to the crouching motion, we observed an importance of the forward motions, *i.e.*  
449 antero-posterior translations of the head and trunk. Therefore, the global motion of the  
450 skeleton tends to move the animal downwards and forwards. Given that in birds, the centre of  
451 mass is located in the trunk (Abourachid 1993; Allen et al. 2009), a forward translation of the  
452 head and trunk can generate a forward momentum. This momentum could also contribute to  
453 the initial acceleration in the forward movement and could assist take-off.

454

455 The second part of the terrestrial phase of take-off allows the propulsion of the entire body in  
456 the direction of flight. The alignment of the different body parts persists during this phase.  
457 The yaw, pitch and roll of the head are low (Fig. 4, Table 1) and the head rotations are close  
458 to zero at lift-off, corresponding to a stabilisation of the head, previously documented during  
459 flight (Warrick et al. 2002). We also observed a low and stable abduction-adduction of the  
460 hip, knee and ankle in both species (Table 1) with symmetrical and synchronous latero-medial  
461 motions of the limb joints that allow an adjustment of the limb position. It is interesting to  
462 note that long-axis rotations are higher than abduction-adduction (Table 1). This result  
463 confirms the importance of 6 degrees of freedom kinematics analysis and justify the use of  
464 XROMM to quantify such motions, especially because long-axis rotations of a proximal bone  
465 have effect on distal bones (Hutchinson 2000; Kambic et al. 2014); a small motion of the  
466 femur can have drastic consequences on the motions of the foot (Fischer et al. 2002).

467 Phase 2 of take-off is associated with a dominance of antero-posterior (tx) and ventro-dorsal  
468 translations (tz). The head is protracted as demonstrated by the increase of *dist\_neck* (Fig. 5b).  
469 An extended neck is typical during flight and has been related to vestibular and optical  
470 reflexes (Bilo and Bilo 1983; Maurice et al. 2006). As the head hold the sensory organs,  
471 especially the eyes and the vestibular system, we can hypothesis that its position at the  
472 beginning of the take-off triggers the beginning of the propulsive phase. Therefore, even if it  
473 does not participate to propulsion, its kinematics is essential for a successful take-off.  
474 Because the foot is immobile on the perch, upward and forward translations of the trunk are  
475 the result of the flexion-extension of the leg joints: the trunk is pitching upwards as the hip  
476 extends. More generally, the entire lower limb is extended, mainly due to the extension of the  
477 ankle, hip, and to a lesser extent of the knee (Table 1). It is true for both species of birds,  
478 although the timing of motions slightly differs. In Diamond Dove, the beginning of hindlimb  
479 joint extension is not synchronous, starting with the hip, followed by the ankle and finally by  
480 the knee, whereas in Zebra Finch, the extension of the three joints is synchronous. Only  
481 tendinous parts of muscles cross the ankle in birds (Baumel 1993) which are known to  
482 contribute to mechanical energy storage and recovery. This has been demonstrated during  
483 running (Alexander 1988; Alexander 1984; Cavagna et al. 1964) and can easily be applied to  
484 take-off, especially given the previous assertions regarding crouching movement and the  
485 probable loading of muscles in Diamond Dove. Such a system is energetically efficient, as  
486 this passive mechanism contributes to decrease both muscular work and metabolic cost  
487 (Roberts 2002; Roberts 2016). Overall, during this first phase of take-off, the trunk and the  
488 hindlimb segments can be seen as a spring (Henry et al. 2005). Incidentally, bioinspired  
489 jumping robots often use a spring to copy a biological leg structure, because it produces good  
490 jumping performances (Zhang et al. 2017) as it is a simple structure with a strong energy  
491 storage capacity and a potential of fast energy release.

492

493 Take-off is a transition between a static state to a dynamic state, and in contrast to terrestrial  
494 locomotion, inertial forces do not contribute to the propulsion. All the motions of the centre of  
495 mass are generated by the leg muscles, especially the thigh muscles, which are the main part  
496 of the leg musculature (Baumel et al. 1993). The first leg joint extended during take-off is the  
497 hip, demonstrating that thigh muscles primarily move the trunk. During take-off from a perch,  
498 all of the leg joints are flexing during crouching and then, all the joints are extending during  
499 the propulsion. These similar and successive motions of all the leg joints contribute to the  
500 propulsion of the centre of mass because the feet are immobile on the perch. This situation is  
501 different in other locomotor conditions, which are cyclic, with dissimilar joint motions within

502 the legs, and highly mobile feet. During bird bipedal locomotion, depending on the propulsion  
503 mechanics, the thigh musculature can have different functions. During take-off, the thighs  
504 mainly move the trunk, participating to the propulsion of the centre of mass. During walking,  
505 they move the trunk to guide the centre of mass path (Abourachid et al. 2011). During  
506 paddling, the thighs stabilize the hip (Provini et al. 2012a). During running, which is a  
507 bouncing mechanics (Hancock et al. 2007) the thighs participate to the increase of the stride  
508 length (Gatesy 1999). If we consider the leg joints participation, during take-off, knee  
509 extension is the lowest among leg joints whereas during the propulsive phase of terrestrial  
510 locomotion, knee extension is high at low as well as high speeds (Gatesy 1999). During take-  
511 off, the ankle extension magnitude is twice as high as the hip and knee extensions. The ankle  
512 is supporting the animal forward motion, similarly to what is observed in semi-aquatic birds,  
513 during paddling, where the tarsometatarsus associated with the webbed-foot displays a high  
514 amplitude of motions and plays the role of the paddle, responsible for most of the propulsion  
515 (Provini et al. 2012a). Therefore, depending on the locomotion mode, the function of the  
516 joints changes, participating to the versatility of the avian body plan.

517

518 Our 3D kinematics analysis revealed the importance of studying the entire body and not only  
519 the limbs of the animal while studying locomotion. In that sense, a detailed kinematics  
520 analysis of the forelimbs motion would be helpful to understand take-off completely. Another  
521 key moment in bird flight is landing, where forces are also transmitted between the substrate  
522 and the rest of the body through the hindlimbs, it would be interesting to compare the  
523 kinematics of take-off with the one of landing in the same species of birds, also with a whole  
524 body approach.

525

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622

## 623 **Figure legends**

624 **Fig. 1** Experimental protocol sketch, showing the orientation of the two X-ray sources and the  
 625 two light cameras. Examples of the pictures recorded, with rotoscoped 3D model of a  
 626 Diamond Dove are shown for each source of data

627

628 **Fig. 2** Images of the 3D reconstruction of the skeleton of a Diamond Dove (a) and a Zebra  
 629 Finch (b) during a sequence of take-off on the lateral view, dorso-ventral view, latero-frontal  
 630 view, and latero-dorsal view.

631

632 **Fig. 3** Plots of translations (a, c) along the antero-posterior (red), left-right (green), and  
 633 ventro-dorsal (blue) axes, and roll (red), pitch (green), and yaw (blue) rotations (b, d) of the  
 634 head and trunk in Diamond Dove and Zebra Finch. In each plot, means calculated at each  
 635 time step are represented with a solid line, the envelop represents standard deviation, for

636 Diamond Dove (n=4) on the left and Zebra Finch (n=4) on the right. Note that the values are  
637 not absolute as the data have been adjusted to in each trial in order to be averaged (see  
638 Material and Methods section for further details). The orientation and direction of the motions  
639 are represented on the drawings of the head and trunk, with a coloured arrow for translations  
640 and a black arrow for rotations.

641

642 **Fig. 4** Plots of hip (a), knee (b) and ankle (c) rotations, showing long-axis rotations (red),  
643 abduction-adduction (green), and flexion-extension (blue) in Diamond Dove and Zebra Finch.  
644 In each plot, means calculated at each time step are represented with a solid line, the envelop  
645 represents standard deviation, for Diamond Dove (n=4) on the left and Zebra Finch (n=4) on  
646 the right. Note that the values are not absolute as the data have been adjusted to in each trial in  
647 order to be averaged (see Material and Methods section for further details). The orientation  
648 and direction of the motions are represented with a black arrow on the drawings of the axes  
649 located on the femur, tibiotarsus and tarsometatarsus, the proximal bone of the joint is  
650 represented with a semi-transparent model whereas the distal bone is represented with an  
651 opaque model.

652

653 **Fig. 5** Mean distances between two bones in Diamond Doves in blue and Zebra Finches in  
654 green during take-off, between the head and the trunk, corresponding to *dist\_neck* (a),  
655 between the most proximal part of the trunk and the most distal point of the tarsometatarsus,  
656 corresponding to *dist\_limb* (b). On the right side, drawings of the skeleton position at the  
657 beginning and at the end of a take-off sequence showing the measured distances. Shading  
658 illustrates the variability, defined as standard deviation across all trials

659

660 **Table 1** Translations and rotations magnitudes in Diamond Doves (a) and Zebra Finches (b),  
661 for each phase of take-off (mean and standard deviations)

662

663 **Supplementary Material 1** Resultant forces profiles in Diamond Dove (a) and Zebra Finch  
664 (b) during take-off, modified from Provini et al. (2012b).

665

666 **Supplementary Material 2** Location of the implanted markers (in black) and virtual markers  
667 (in red) on the head (a), the pelvis (b), the left femur (c), left tibiotarsus (d) and left  
668 tarsometatarsus (e). The size of the markers has been magnified to facilitate their identification  
669 on the figure.

670

671 **Supplementary Material 3** Video of the terrestrial phase of take-off of a Diamond Dove and  
672 a Zebra Finch

673

674 **Supplementary Material 4** ACS (a-f), JCS conventions (h) for each bones and reference  
675 pose (g). Craniolateral and lateral view of the head ACS (a), craniolateral and lateral view of  
676 the trunk ACS (b), craniolateral and lateral view of the left acetabular ACS (c), craniolateral  
677 and dorsal view of the femur ACSs (d), craniolateral and dorsal view of the tibiotarsus ACSs  
678 (e), craniolateral and dorsal view of the tarsometatarsus ACSs (f). Craniolateral and dorsal  
679 views of the reference pose (g), showing the JCSs axes when all translations and rotations are  
680 0. To differentiate the bones that are overlapping we used several colours (orange for the  
681 head, light yellow for the trunk, yellow for the femur, white for the tibiotarsus, light yellow  
682 for the tarsometatarsus). Anterolateral view of the head, trunk and hindlimbs showing the  
683 joint coordinate systems (JCSs) (h) by which flexion-extension (blue), abduction-adduction  
684 (green) and long-axis rotations (red) were measured at the hip, knee and ankle and by which  
685 antero-posterior (red), left-right (green) and ventro-dorsal (blue) translations, as well as yaw  
686 (blue), pitch (green) and roll (red) were measured at the head and pelvis.

687

688 **Supplementary Material 5** Segmented regressions calculated on  $Tr_{tx}$  (red) and  $Tr_{tz}$  (blue)  
689 through take-off sequence in each trial of Diamond Dove take-off (a) and Zebra Finch (b).  
690 Breakpoint value is indicated as well as the  $r^2$  of the segmented regression for each trial.

691

692 **Supplementary Material 6** Mean velocities calculated on the Trunk vertical and horizontal  
693 translations. Means are represented with a solid line, the envelop represents standard  
694 deviation, for Diamond Dove (a) on the left and Zebra Finch (b).

695