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1 **Title**

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

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16

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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 O₂. 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 (μ 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 μ 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). 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 ± 2.8 deg at the beginning of phase 1 to 178.6 ± 3.4 deg at
307 the beginning of phase 2. In Zebra Finch, *angle_neck* went from 144.58 ± 4.6 deg at the
308 beginning of phase 1 to 178.01 ± 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_{tz} (the difference between the maximum and the minimum of H_{tz}), 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_{tz} 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 ± 3.6 deg in Diamond Dove and of 179 ± 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 ± 3.8 mm/s in Diamond Dove, and of 3.1 ± 2.9
327 cm/s in Zebra Finch. Translations of the trunk were mostly caudocranial with a magnitude of
328 Tr_{tx} (10.3 ± 1.0 cm in Diamond Dove and 4.1 ± 2.6 in Zebra) relatively higher than the
329 magnitude of Tr_{tz} (2.4 ± 1.7 in Diamond Dove and 1.3 ± 1.3 cm in Zebra Finch) or of Tr_{ty}

330 (0.8 ± 1.0 in Diamond Dove and 1.4 ± 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 ± 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 ± 10.7 mm/s in Diamond Dove, and
338 28.2 ± 8.8 cm/s in Zebra Finch. In both species, caudocranial translations of the trunk remained
339 important (magnitude of 21.7 ± 2.9 cm in Diamond Dove and 11.9 ± 7.2 cm in Zebra Finch) but
340 went with an increase of trunk vertical upward translations (magnitude of 13.0 ± 2.7 cm in
341 Diamond Dove and 8.2 ± 2.0 cm in Zebra Finch). Upward pitch of the trunk was high in
342 Diamond Dove (magnitude of 14.5 ± 1.1 deg), which was not the case in Zebra Finch
343 (magnitude of 2.5 ± 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 ± 2.9
347 deg in Diamond Dove and 4.5 ± 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 ± 3.0 deg in Diamond
351 Dove and 20.4 ± 7.9 deg in Zebra Finch) (Fig.4). In Diamond Dove, abduction increased
352 (magnitude of 5.2 ± 2.8 deg), whereas adduction increased in Zebra Finch (magnitude of
353 6.5 ± 3.3 deg). Long axis rotation became higher in Zebra Finch (magnitude of 10.7 ± 6.2 deg),
354 which was less noteworthy in Diamond Dove (magnitude of 4.4 ± 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 ± 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 ± 11.9 deg in Diamond Dove and 15.8 ± 8.4 deg in Zebra Finch). This went with a rise of
363 the tibiotarsus long axis rotation (magnitude of 13.7 ± 6.7 deg in Diamond Dove and 7.0 ± 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 ± 4.8 deg in Diamond Dove and 6.6 ± 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 ± 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 ± 16.0 deg in
373 Diamond Dove and 39.8 ± 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 ± 8.3 deg in Diamond Dove and
376 11.1 ± 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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621

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