

1 **Sustained hovering, head stabilization and vision through the water surface in the Pied**  
2 **kingfisher (*Ceryle rudis*)**

3

4 Gadi Katzir\*, Department of Evolutionary and Environmental Biology, Faculty of Life Sciences,  
5 University of Haifa, Mt Carmel, Haifa 3498838, Israel. Email: [katgad@gmail.com](mailto:katgad@gmail.com)

6

7 Dotan Berman, Department of Marine Sciences, Faculty of Life Sciences, University of Haifa, Mt Carmel,  
8 Haifa 3498838, Israel. [dotiberman@gmail.com](mailto:dotiberman@gmail.com)

9 Moshe Nathan, Faculty of Life Sciences, Bar Ilan University, Ramat Gan, 52900, Israel. Email:  
10 [moshen70@gmail.com](mailto:moshen70@gmail.com)

11

12 Daniel Weihs, Faculty of Aerospace Engineering and Autonomous Systems Program, Technion, Haifa,  
13 3200003, Israel. Email: [dweihs@tx.technion.ac.il](mailto:dweihs@tx.technion.ac.il)

14

15

16

17

18 \* Corresponding author

19

20 **Abstract.** Pied kingfishers (*Ceryle rudis*) capture fish by plunge diving from hovering that may last  
21 several minutes. Hovering is the most energy-consuming mode of flight and depends on active wing  
22 flapping and facing headwind. The power for hovering is mass dependent increasing as the cube of  
23 the size, while aerodynamic forces increase only quadratically with size. Consequently, birds above  
24 a certain body mass can hover only with headwind and for very short durations. Hummingbirds are  
25 referred to as the only birds capable of hovering without wind (sustained hovering) due to their  
26 small size (ca. 2-20 gr), high wing-beat frequency and unique anatomy.

27 We studied the hovering characteristics of pied kingfishers in relation to wind and sun orientation,  
28 in 139 hovers. Furthermore, plunge diving necessitates the coping with the visual effects of light at  
29 the air/water interface. The kingfishers oriented their body axis towards the wind more than towards  
30 the sun. Hovering in little or no wind was common. With increased wind speed (a) orientation  
31 precision increased, (b) wing beat amplitude did not change, (c) wing beat frequency decreased and

32 (d) body tilt became more horizontal. The head was highly stabilized and with orientations that  
33 indicated monocular viewing of prey.

34 We conclude that pied kingfishers achieve sustained hovering. This is despite their being  
35 significantly heavier than the theoretical maximum and showing ordinary kinematics and  
36 morphology. Head stabilization is a means of aiding viewing of submerged prey across the  
37 interface.

## 38 **Introduction**

39 Many fish eating (piscivorous) birds plunge-dive into water from perches, (e.g., kingfishers) or  
40 from a flapping flight, to capture fish. Of the latter, most plunge dive from a direct flight (e.g.,  
41 brown pelicans, *Pelecanus occidentalis*, gannets, *Sula* spp. and *Morus* spp., terns, *Sterna* spp.),  
42 while only a handful (e.g., Osprey, *Pandion haliaetus*) plunge dive from a hovering flight, i.e., from  
43 a relatively stable position in the air, maintained by wing motion (Cramp et al., 1977).

44 Of the ca. 100 species of kingfishers (Aves, Alcedinidae), the majority prey predominately on  
45 terrestrial prey while only ca. 20 species prey predominately on fish. In both terrestrial and aquatic  
46 habitats the kingfishers employ “perch-diving” as a common mode to capture prey (Fry & Fry,  
47 1992). A foraging pattern that is distinctly different is observed in the piscivorous pied kingfisher  
48 (*Ceryle rudis*, Cerylinae; Reyer & Westerterp, 1985; Reyer et al., 1988 ). Pied kingfishers (PKF)  
49 typically forage using flapping flight with intermittent hovering episodes, during which position is  
50 unchanged for a given duration and from which they plunge dive (Fig. 1; Cramp et al., 1977; Fry &  
51 Fry, 1992). Hover duration ranges between several seconds and several minutes and hover heights –  
52 from less than one to more than eight meters above the water.

53 The use of lengthy hovers is uncommon in birds and raises questions especially as to their capacity  
54 for sustained hovering – i.e., keeping a fixed spatial position without aid of wind. The forces  
55 required for hovering are provided by wing flapping and by utilizing wind, when available ( Videler  
56 et al., 1983; Daan et al., 1990; Pennycuick, 1990; Pennycuick, 2008). The power required for  
57 hovering is mass dependent, increasing as the cube of the size, while the aerodynamic forces  
58 increase only quadratically with size, being dependent on wing dimensions. Sustained hovering is  
59 the most energy-consuming mode of flight, being ca. 4-5 times more energy demanding than  
60 regular flapping flight, because the weight of the bird has to be fully supported by its muscle power.

61 Consequently, for birds above a certain body mass, hovering is very much wind dependent and  
62 birds such as kestrels, short toed eagles or osprey can hover in still air only for several seconds, yet  
63 perform significantly longer hovers in the wind (Grubb, 1977a,b; Machmer & Ydenberg, 1990).  
64 The contribution of wind to lift, however, becomes negative at high wind velocities, due to the  
65 increased drag and the destabilization by wind bursts.

66 Sustained hovering is mostly associated with hummingbirds (Trochilidae). This group shows  
67 extreme morphological, anatomical and physiological adaptations (Altshuler & Dudley, 2002 ;  
68 Tobalske, 2010) reaching peak aerodynamic performances that exceed present technical capabilities  
69 (Videler et al., 1983; Pennycuick, 2008). The notion prevailing in the literature is that  
70 hummingbirds are the only birds capable of sustained hovering (Chai & Millard, 1997), due to their  
71 small size, high wing-beat frequency and anatomy (Tobalske, 2010). We show that the much  
72 heavier pied kingfishers are capable of sustained hovering.

73 Plunge diving for fish requires coping with multiple visual effects of light at the air/water interface  
74 (Katzir & Intrator, 1987; Labinger et al., 1991). Wind is a major factor affecting vision through  
75 creating of water surface ripples and determining ripple direction, frequency and amplitude. Ripples  
76 and wavelets constantly change patterns of reflected and refracted sunlight and skylight that, in turn,  
77 affect image formation. We posit that a hovering PKF will attempt to place itself, and to orientate,  
78 so as to maximize the quality of the information gained on its underwater prey prior to the plunge  
79 dive that, once begun, is ballistic. The positioning is determined by the interaction between  
80 aerodynamic needs to produce lift and decrease drag, as well as by the visual needs to reduce the  
81 effects of light refraction and reflection and the detection by the prey. Thus, for example, wind  
82 direction will result in a given 3D body orientation while concurrent visual requirements will result  
83 in a different 3D orientation of the head (Fig.1&10).

84 To answer the hypotheses above, we conducted field observations and discuss the results in the light  
85 of the potential pros and cons of hovering and of head stabilization.

## 86 **Materials & Methods**

87 Field observations were conducted at the fisheries of Kibbutz HaMa'apil, Israel (Lat. 32.367348  
88 Lon. 34.975555) in an area comprising 15 rectangular fish-ponds (width range 30-47m, length  
89 range 65-97m). Pied kingfisher foraging in the ponds was frequent and the surrounding low-lying

90 vegetation (< 50cm) allowed direct observations over long distances. We conducted observations  
91 from December 2014 to July 2015 and the data analyzed was selected from 50 hours of  
92 observations performed over 13 days, between 06:00 and 20:00 so as to cover a range of wind,  
93 temperature and sun conditions.

94 A foraging sequence comprised one or more forward flight episodes interspersed with hovering  
95 flight episodes. Hovering episodes are defined as periods in which the bird moved less than one  
96 body length horizontally or vertically over many seconds. A sequence was analyzed from first  
97 sighting of a PKF to its leaving of the pond area. Most plunge dives commenced from stationary  
98 hovers (Douthwaite, 1976; Cramp et al., 1977; Reyer et al., 1988).

99 Hovering episodes were video recorded using a Canon© Powershot SX-50 camera on a tripod ca.  
100 2.0m above the water surface, with an optical zoom of 50X and filming at 24, 120 or 240 fps. A  
101 PKF was selected as a focal individual if it flew within ca. 50m of the observer. It was first tracked  
102 freely with the camera and once a hovering episode began, the camera was locked and the lens  
103 zoomed in on the subject. Overall, 375 sequences were acquired. Of these, 139 were selected as  
104 suitable for analysis in terms of duration and image quality. Video analysis was performed using a  
105 semi-automatic / manual tracking software developed by SIPL of the Technion and by “Kinovea©”  
106 software (version 0.8.15).

107 **Wind and sun.** We recorded wind velocity immediately following the video recording of each  
108 foraging sequence. Measurements were performed using a handheld digital anemometer (Skywatch-  
109 Xplorer1), ca. 3m above the ground and ca. 4m above water surface. Wind direction was estimated  
110 from the compass direction of maximum wind velocity. Sun azimuth and elevation at each foraging  
111 bout was obtained from a web-available chart (<http://www.sunearthtools.com/>).

112 **Wing beat amplitude and frequency.** For wing beat amplitude, we analyzed 33 hovering episodes.  
113 For the proximal wing, wingtip peak positions (highest / lowest) were marked in up to 11  
114 consecutive cycles, and the vertical distance (in pixels) between any two consecutive peaks was  
115 measured. We used published measurements of PKFs (wingspan 46cm, wing length 19 cm; Cramp  
116 et al., 1977) to compute the angular displacement from stroke amplitude and the wing length. For  
117 wing beat frequency, we analyzed one sequence from each of 42 again randomly chosen episodes.  
118 We marked a frame at the very beginning of the first clearly measurable sequence and recorded the  
119 consecutive (up to a maximum of 10) wing beat cycles. Wing beat frequency was calculated from

120 the number of frames required to complete a full cycle, at filming rates of 24, 120 and 240 frames  
121 per second (fps).

122 **Body orientation and tilt.** To determine body orientation, (i.e., azimuth, in the horizontal plane)  
123 and tilt (in the vertical: see Fig.2) we selected 35 sequences in which the sagittal plane of the  
124 kingfisher as approximately perpendicular to the camera's optical axis. From each sequence we  
125 selected a single episode and the orientation of the body (sagittal plane) was determined as follows:  
126 A single frame was captured from the beginning, middle and end of each selected episode. The  
127 body orientation relative to the camera was determined by eye, based on the shape of the body and  
128 the wing overlap, as viewed from the direction of the camera (Figs. 2 & S1). Body orientation was  
129 determined using rough blocks of ca.  $22^\circ$ , with  $0^\circ$  defined as viewing the PKF at right angles with  
130 its bill to the right. The absolute body orientation was calculated from the known azimuth of the  
131 camera's optical axis. The orientation of the body relative to the wind and to the sun was calculated  
132 by subtracting the wind or sun values from body values.

133 In hovering, the body underwent periodic changes in tilt, corresponding with wings' down strokes.  
134 From 29 episodes, selected each from a different sequence, the orientation was analyzed for up to  
135 10 consecutive cycles in which there was no apparent displacement of the center of gravity. Body  
136 tilt was determined from the angle of the imaginary line connecting the tip of the tail and the neck,  
137 with the horizon, (Figs. 2 & S1). The frames sampled were from points at which the body was  
138 closest to vertical. The absolute body tilt was calculated from the known azimuth of the camera's  
139 optical axis as above. For each sequence sampled, the average of the body tilt angles was  
140 calculated.

141 **Movements of the head and body.** For the analysis of movements and stabilization only sequences  
142 in which the sagittal plane of the PKF was approximately perpendicular to the camera's optical axis  
143 were selected. Analyses were based on three points on the PKF's body: The eye, the breast  
144 (approximately the rostral point of the sternum) and the proximal wingtip (Fig. 2). For six episodes  
145 we analyzed the change of vertical position of all three points while for the eye, horizontal change  
146 was also tested. For each episode, up to 10 wing beat cycles were sampled, from recordings taken  
147 at 120 fps, and the number of frames analyzed ranged between 90-240. For each of the points, the  
148 x-y coordinates of the first reading was taken as the origin (0,0) and subsequent readings were  
149 relative to it.

150 The angle of viewing of the PKF by the camera, in different hovering episodes, varied as a function  
151 of the relative 3D positions of the camera and the bird at the onset of each episode. To correct for  
152 these differences we used a photographic analysis of a mounted PKF. The PKF was secured  
153 horizontally on a stand, with its wings half open and its bill pointing down (Fig. S1). The origin  
154 (0,0) was the point in which the optical axis of the camera was horizontal, at the level of the PKF  
155 breast, and perpendicular to the sagittal plane of its body, at its center. Subsequent photographs  
156 were taken of the PKF from the predetermined intersection nodes of latitude lines (ventrally, 0°, -  
157 30°, -60°) and longitude lines (rostral, 0°, +30°, +60°; caudal, 0°, -30°, -60°). From the real  
158 dimensions of the PKF and the photographic dimensions we calculated a correction factor for each  
159 viewing angle, using Kinovea™. The absolute tilt angle and bill length were taken from the images  
160 that were perpendicular to the bird's sagittal plane.

161 The orientation of the PKF was analyzed using circular statistics of non-parametric angular-angular  
162 correlation (Zar, 1996). All other statistical tests were performed using SPSS (version 21). AIC  
163 ranking was used to determine models of best fit. Weather conditions during the research period  
164 ranged from hot, sunny days with little or no wind to stormy days with winds reaching 18 m/sec.

165

## 166 **Results**

167 **Flight patterns in foraging.** The kingfishers captured fish mostly by plunge diving from hovering  
168 flight or, infrequently, by diving from a perch. A typical foraging bout comprised episodes of level  
169 flight and episodes of stationary hovering (Fig. 1). The durations of individual hovering episodes  
170 ranged from a few seconds to more than a minute and the durations of entire bouts, from entering a  
171 pond area to leaving, ranged between a few seconds and over two minutes. Typically, a PKF would  
172 fly several meters above the pond in a fast, level flight, at an average speed of 10-12m/sec. It would  
173 then halt abruptly and hover in midair, at heights ranging between 0.5-12m, mostly with its bill  
174 pointing down (overall relative to the horizon  $76.4^\circ \pm 9.2^\circ$ ; mean $\pm$ sd). Flight segments between  
175 hovering bouts frequently were of a shallow u-shape. Following a plunge-dive it would either  
176 resume hovering, or land on a perch or leave the area (Cramp et al., 1977; Douthwaite, 1976; Reyer  
177 et al., 1988).

178 **Body orientation.** In each hovering episode, the body orientation of the PKFs in the horizontal  
179 plane remained virtually unchanged (variance ca. 0 over 35 episodes). Thus, once a position has  
180 been adopted, the PKF minimized positional changes.

181 Body orientation was significantly correlated with wind direction (Fig. 3;  $\alpha=0.05$ ,  $N=35$ ) and there  
182 was a trend, although not reaching significance, of a decrease in relative body orientation with  
183 increased wind velocity (Fig. 5). In other words, the higher the wind velocity the higher the  
184 precision of facing it directly.

185 Body orientation was related to sun position, yet the correlation did not reach significance (Fig. 4;  
186  $\alpha>0.05$ ,  $N=35$ ).

187 **Motion of the wings, body and head.** During a given hovering episode, the tilt angle of the body,  
188 the head-bill and the tail were roughly unchanged. The bill in most hovering episode pointed down  
189 (i.e., pitch) with the head partially rotated (Fig. 10) so that one eye gazed downwards. In the  
190 transition from a stationary hovering position to flight, the orientation of the head - bill first  
191 changed so that the bill first pointed in the direction of the ensuing flight, and the body followed.

192 **Wing beat amplitude and frequency.** Wing beat angular amplitude (range  $9^{\circ}$ - $134^{\circ}$ ) was not  
193 correlated with wind velocity (Fig. 6) while wing beat frequency (range 5.4-9.5Hz) was  
194 significantly and negatively correlated with wind velocity (Fig. 7;  $N=42$ ,  $R^2=0.725$ ,  $P<0.05$ ). In  
195 other words, the higher the wind velocity, the lower the wing beat frequency. Wing beat amplitude  
196 was minimal at wind velocity of ca. 7m/sec and wing beat frequency was minimal at ca. 12-14m/s  
197 (Figs 6 & 7).

198 During a hovering episode, the kingfishers' body tilt underwent periodic changes with wing beat  
199 cycles, as the majority of the lift during the entire cycle is produced during the down stroke so that  
200 the body is moved upwards. The tilt serves to reduce the body drag during this upward motion of  
201 the cycle. The maximal vertical extent of body tilt was significantly correlated with wind velocity  
202 (Fig. 8) so that with increased wind velocity (up to ca. 12 m/s) the tilt became more horizontal. At  
203 wind velocities higher than 12 m/s, body tilt became more vertical again ( $N=29$ ,  $R^2=0.851$ ,  
204  $P=0.003$ ).

205 **Stabilization of the head and body.** The vertical displacements of the wingtips, body and head  
206 during a hover episode differed significantly, with the head (eye) undergoing the smallest



207 displacements and the wingtip – the highest. In the example given (Fig. 9) the wingtip displacement  
208 ( $172.6 \pm 72.7\text{mm}$ ) were ca. two orders of magnitude greater than that of the breast or eye  
209 (respectively  $8.4 \pm 4.6\text{mm}$  and  $4.3 \pm 2.7\text{mm}$ ). Eye horizontal displacement was of similar magnitude  
210 ( $3\text{-}5.9\text{mm}$ ). The periodicity of wingtip position differed from that of the eye and breast by  $180^\circ$   
211 (Fig. 9).

## 212 **Discussion.**

213 Pied kingfishers are exceptional in making extensive use of hovering from which they plunge dive  
214 for fish, sometimes from heights well over 10m above the water (Cramp et al., 1977; Labinger et  
215 al., 1991; Fry & Fry, 1992). This falls within the general pattern of birds that hover near potential  
216 prey that mostly leads to a rapid strike, dive or plunge-dive (e.g., kestrel, *Falco tinnunculus*; short-  
217 toed eagle, *Circaetus gallicus*; osprey, *Pandion haliaetus*)

218 Hovering is considerably more energy demanding than level flight so it is much less used. This is  
219 especially apparent in relation to hovering in still air (“sustained hovering”) a task that most birds  
220 are unable to perform as they cannot produce enough lift through muscle power (Videler et al.,  
221 1983) and must gain additional lift by flying into moderate wind (Videler, et al. 1983; Daan et al.,  
222 1990). The frequent and lengthy hovering episodes of kingfishers in still air prove their capacity for  
223 sustained hovering. This finding revises the prevailing view that sustained hovering is confined to  
224 extremely small birds. Previous theoretical and experimental approaches have led to the conclusion  
225 that maximal body size for sustained hovering is that of hummingbirds (5-10gr). Indeed they are  
226 regarded as “...the *only birds that can sustain hovering...*” ( Pennycuick, 1978; Chai & Millard,  
227 1997; Altshuler & Dudley, 2002; McNeill Alexander, 2005; Tobalske, 2007; Pennycuick, 2008;)  
228 due to “.. their small size, high wing beat frequency, ... wing anatomy that enables them to ..  
229 supinate during upstroke so that they can generate lift on both up - and down-strokes ...” (Chai &  
230 Millard, 1997; Tobalske et al., 2003; Tobalske, 2010; Goller & Altshuler, 2014). Pied kingfishers  
231 (ca. 80-100 gr) are considerably heavier than hummingbirds, their wing-beat frequencies are lower  
232 (ca. 7-10 Hz. Vs. 70-80Hz) and they do not exhibit morphological or motor specializations of the  
233 wings (e.g., unique aspect ratio or wing-load). Also, their flight kinematics seems most similar to  
234 non- hovering, flapping flight including wing-beat frequency and amplitude that are correlated with  
235 wind velocity and direction. Thus, it is not possible at this stage to point to specific aspects of the



236 hovering flights that enable these capacities, unobserved in other species This leaves open questions  
237 of size limits for sustained hovering.

238 Hovering in the kingfishers was sensitive to wind and with increased wind velocity the birds  
239 orientated increasingly more closely into the wind, most probably to decrease the drag coefficient.  
240 As wind speed increases, the need to stay in a horizontally fixed position becomes more demanding,  
241 because drag increases quadratically with wind speed and so becomes more dominant. This turning  
242 point in the relative importance of drag is related to the volitional speed of the pied kingfisher  
243 forward flight. With increased wind velocity, body tilt became increasingly more horizontal, to  
244 reduce drag by reducing body frontal area. As wind velocity increased from zero to roughly 12 m/s,  
245 wing beat frequency decreased but wing-beat amplitude did not. We attribute this to the increasing  
246 contribution of wind energy to the production of the lift required to stay at a fixed altitude. At the  
247 higher wind velocities, hovering was infrequent and rather chaotic, as expected, because at these  
248 velocities every deviation due to local turbulence is of the order of the bird size. There seem to be  
249 two ranges of wind velocities, in which hovering have different characteristics, with the change  
250 occurring at about 12 m/s (Figs 3 and 4). These patterns are expected if the pied kingfishers were  
251 attempting to maximize lift while minimizing their own active contribution.

252 In hovering, the kingfishers kept their torso and their head fixed to different degrees. While the  
253 wings underwent displacements of up to ca. 120deg, the torso motion was reduced by an order of  
254 magnitude and the head movement was further reduced so that eye perturbation was of order 5mm.  
255 These results are similar to head stabilization of kestrels (Videler et al., 1983, pied kingfishers,  
256 unpublished) and herons on a moving perch (Katzir et al., 2001) While body tilt changed with wind  
257 speed, the orientation of the stabilized head was kept with the bill pointing downwards (Fig. 1, top  
258 center).

259

260 As to the pros and cons to hovering, one potential disadvantage is increased conspicuousness: To  
261 the fish, the kingfisher presents a high contrast silhouette against the sky mostly perpendicularly  
262 above, which is at the center of the fish Snell's window, where optical distortions are minimal. Add  
263 to the attractiveness is wing motion. On the advantage side, hovering releases the kingfishers from  
264 the need to use vegetation to perch on, thus extending their foraging to several km offshore (Fry &  
265 Fry, 1992). Also, hovering provides a stable "springboard" that enables a rapid re-positioning in 3D  
266 to improve visual detection of prey under the visually complex air/water interface. Being

267 perpendicular to the fish may reduce optical problems while dynamic re-positioning may reduce the  
268 problem of the rapid escape responses of fishes (Katzir & Camhi, 1993). So why is the pied  
269 kingfisher's hovering so dominant among piscivorous birds? One factor may be the prey. Cichlids  
270 (Cichlidae), the most species-rich fish group, evolved in the African lakes and are a main prey of  
271 pied kingfishers. Many cichlids nest in shallow waters and the males keep a position above the  
272 substrate built nests making them conspicuous and vulnerable to avian predation. It may well be  
273 that pied kingfishers have evolved to cope with single, relatively large prey, requiring high  
274 precision. In comparison, species such as terns or gannets prey on fish in schools with large  
275 numbers of fish in motion, and where precise estimates can only be made at close range.

276 While hovering the kingfishers stabilize their eyes/head. Birds are known to stabilize their eyes  
277 extremely well even under marked perturbations, while flying or when walking. In the case of the  
278 PKF hovering can be performed w/o head stabilization ( Videler et al., 1983; Troje & Frost, 2000;  
279 Warrick, 2002; McArthur & Dickman, 2011). Gaze stabilization of minimal duration is required to  
280 reduce image slippage on the retina and hence reduce blur (Land, 1999; Zeil et al., 2008). The  
281 sensory information for stabilization may be visual, such as optic flow (e.g., hummingbirds, Goller  
282 & Altshuler, 2014) or mechanical (inertial, vestibular, e.g., swans, Pete et al., 2015). As for using  
283 vision, there are several potential difficulties: Visually distinct “anchor points”, both beneath and  
284 lateral to the hovering bird, are relatively distant and most probably do not provide the precision  
285 provided by a nearby object such as a flower several cm from the eye of a hovering hummingbird.  
286 Moreover, the water surface provides dynamic patterns and unlikely to be used reliably. Thus a  
287 more probable source is the vestibular.

288 A clue to the constraints on the kingfishers' vision may be found in the marked 3D tilt/roll  
289 orientation of head during the hovers (Figs. 1,10) that may stem from preferred gaze directions. In  
290 many birds, including kingfishers, each retina has a temporal fovea that “looks forward” and  
291 provides for close range binocular vision and a central fovea that “looks sideways” and provides for  
292 long distance, monocular, high resolution vision (Moore et al., 2015). Consequently, when faced  
293 with a distant target, such birds tilt their head to direct their monocular gaze at the target (Moroney  
294 & Pettigrew, 1987; Tucker, 2000). The pronounced head tilt / roll of the pied kingfisher allows  
295 monocular viewing of the prey while minimizing the aerodynamic negative effects of body  
296 orientation.

297 It may be useful to view a kingfisher as comprising two rigid units that interact, a larger torso and a  
298 smaller head, with three flexible units, the neck, wings and tail (Katzir et al., 2001). The body,  
299 wings and tail perform mainly the flight tasks and need to maximize lift, while affecting vision and  
300 the head orientates so as to maximize visual input yet also affects flight.

301 **Acknowledgements.** We thank Kibbutz Ha-Maapil and the operators of the kibbutz fish ponds.

302 **Competing interests.** There are no competing interests.

303 **Funding.** The research was funded by the ISF-Israel Science Foundation grant no. 2005/16 to GK  
304 and by the National Geographic Society grant no. 9720-15 to GK and DW.

305

306 **References**

- 307 Altshuler, D. L., & Dudley, R. (2002). The ecological and evolutionary interface of hummingbird  
308 flight physiology. *The Journal of Experimental Biology*, 205(Pt 16), 2325–2336.
- 309 Chai, P., & Millard, D. (1997). Flight and size constraints: hovering performance of large  
310 hummingbirds under maximal loading. *The Journal of Experimental Biology*, 200, 2757–2763.
- 311 Cramp, K. S. et al., (1977). *Handbook of the birds of Europe, the Middle East and North Africa.*  
312 *The birds of the Western Palearctic.* Oxford University Press: Oxford. ISBN 0-19-857506-8. 913  
313 pp.
- 314 Daan, S., Masman, D., & Groenewold, A. (1990). Avian basal metabolic rates: their association  
315 with body composition and energy expenditure in nature. *The American Journal of Physiology*, 259,  
316 333–340.
- 317 Douthwaite, R. J. (1976). Fishing techniques and foods of the pied kingfisher on lake Victoria in  
318 Uganda. *Ostrich*, 47(4), 153–160.
- 319 Fry, C. H., & Fry, K. (1992). *Kingfishers, Bee-Eaters, & Rollers.* London: Bloomsbury.
- 320 Goller, B., & Altshuler, D. L. (2014). Hummingbirds control hovering flight by stabilizing visual  
321 motion. *Proceedings of the National Academy of Sciences*, 111(51), 18375–18380.
- 322 Grubb, T. C. (1977a). Weather-Dependent Foraging in Ospreys, 206(744), 793–794.
- 323 Grubb, T. C. (1977b). Why osprey hover. *Wilson Bulletin*, 89, 149–150.
- 324 Katzir, G., & Camhi, J. M. (1993). Escape Response of Black Mollies ( *Poecilia sphenops* ) to  
325 Predatory Dives of a Pied Kingfisher ( *Ceryle rudis* ). *Copeia*, 1993(2), 549–553.
- 326 Katzir, G., & Intrator, N. (1987). Striking of underwater prey by a reef heron, *Egretta gularis*  
327 schistacea. *Journal of Comparative Physiology A*, 160, 517–523.
- 328 Katzir, G., Schechtman, E., Carmi, N., & Weihs, D. (2001). Head stabilization in herons. *Journal of*  
329 *Comparative Physiology - A Sensory, Neural, and Behavioral Physiology*, 187(6), 423–432.
- 330 Labinger, Z., Katzir, G., & Benjamini, Y. (1991). Prey size choice by captive pied kingfishers,

- 331 Ceryle rudis L. *Animal Behaviour*, 42(6), 969–975.
- 332 Land, M. F. (1999). The roles of head movements in the search and capture strategy of a tern (Aves,  
333 Laridae). *Journal of Comparative Physiology - A Sensory, Neural, and Behavioral Physiology*,  
334 184(3), 265–272.
- 335 Machmer, M. M., & Ydenberg, R. C. (1990). Weather and Osprey foraging energetics. *Canadian*  
336 *Journal of Zoology*, 68(1), 40–43.
- 337 McArthur, K. L., & Dickman, J. D. (2011). State-dependent sensorimotor processing: gaze and  
338 posture stability during simulated flight in birds. *Journal of Neurophysiology*, 105(4), 1689–700.
- 339 McNeill Alexander, R. (2005). Models and the scaling of energy costs for locomotion. *Journal of*  
340 *Experimental Biology*, 208(9), 1645–1652.
- 341 Moore, B. A., Pita, D., Tyrrell, L. P., & Fernandez-Juricic, E. (2015). Vision in avian emberizid  
342 foragers: maximizing both binocular vision and fronto-lateral visual acuity. *Journal of Experimental*  
343 *Biology*, 218, 1347-1358.
- 344 Moroney, M. K., & Pettigrew, J. D. (1987). Some observations on the visual optics of kingfishers  
345 (Aves, Coraciformes, Alcedinidae). *Journal of Comparative Physiology A*, 160(2), 137–149.
- 346 Pennycuick, C. J. (1978). Fifteen Testable Predictions about Bird Flight. *Oikos*, 30(2), 165-176. pp  
347 Pennycuick, C. J. (1990). Predicting wingbeat frequency and wavelength of birds. *The Journal of*  
348 *Experimental Biology*, 150, 171–185.
- 349 Pennycuick, C (2008). Modelling the flying bird. *Theoretical Ecology Series*, (5), 1–480.
- 350 Pete, A. E., Kress, D., Dimitrov, M. A., & Lentink, D. (2015). The role of passive avian head  
351 stabilization in flapping flight. *Journal of The Royal Society Interface*, 12(110),
- 352 Reyer, H. U., & Westerterp, K. (1985). Parental energy expenditure: a proximate cause of helper  
353 recruitment in the pied kingfisher (Ceryle rudis). *Behavioral Ecology and Sociobiology*, 17(4), 363–  
354 369.
- 355 Reyer, H.U., Migongo-Bake, W., & Schmidt, L. (1988). Field studies and experiments on the  
356 distribution and foraging of pied and malachite kingfishers at lake Nakuru (Kenya). *Journal of*

357 *Animal Ecology*, 57, 595–610.

358 Tobalske, B. W. (2007). Biomechanics of bird flight. *Journal of Experimental Biology*, 210(18),  
359 3135–3146.

360 Tobalske, B. W. (2010). Hovering and intermittent flight in birds. *Bioinspiration & Biomimetics*,  
361 5(4).

362 Tobalske, B. W., Hedrick, T. L., Dial, K. P., & Biewener, A. A. (2003). Comparative power curves  
363 in bird flight. *Nature*, 421(6921), 363–366.

364 Troje, N. F., & Frost, B. J. (2000). Head-bobbing in pigeons: how stable is the hold phase? *The*  
365 *Journal of Experimental Biology*, 203(Pt 5), 935–940.

366 Tucker, V. a. (2000). The deep fovea, sideways vision and spiral flight paths in raptors. *The Journal*  
367 *of Experimental Biology*, 203, 3745–3754.

368 Videler, J., Weihs, D., Daan, S., (1983). Intermittent gliding in the hunting flight of the kestrel,  
369 *Falco tinnunculus* L. *The Journal of Experimental Biology*, 102, 1–12.

370 Warrick, D. R. (2002). Bird Maneuvering Flight: Blurred Bodies, Clear Heads. *Integrative and*  
371 *Comparative Biology*, 42(1), 141–148.

372 Zeil, J., Boeddeker, N., & Hemmi, J. M. (2008). Vision and the organization of behaviour. *Current*  
373 *Biology*, 18(8), 320–323.

374

## 375 **Figure Legends**

376 Fig 1. A schematic foraging path of a pied kingfisher. A hovering episode terminated if the  
377 kingfisher either (i) plunge-dived, or (ii) made a sharp vertical or horizontal change of position or  
378 (iii) landed, or (iv) left the area altogether.

379 Fig. 2. Parameters used in this study.

380 Fig 3a: Body azimuth relative to sun azimuth. Vector diagram: Radius - highest number of  
381 observations in any sector (each sector - 22.5°). Azimuth 0° - facing the wind. Arrow - mean  
382 relative orientation (N=35 sequences). Fig. 3b. Difference between orientations to wind and to sun.

383 Fig. 4. Body azimuth relative to wind azimuth. Vector diagram: Radius - highest number of  
384 observations in any sector (each sector - 22.5°). Azimuth 0° - facing the wind. Arrow - mean  
385 relative orientation (N=35 sequences).

386 Fig 5: Body azimuth relative to wind velocity. Each column represents the mean  $\pm$ SD of the relative  
387 body to wind azimuth in a given wind velocity category (N=35).

388 Fig. 6: Wing beat amplitude relative to wind velocity. Each solid circle is the mean  $\pm$ SD of between  
389 3-10 wing beat cycles per sequence (N=33 sequences).

390 Fig. 7: Wing beat frequency relative to wind velocity. Each solid circle is the mean  $\pm$ SD of between  
391 3-10 wing beat cycles per sequence (N=42 sequences).

392 Fig. 8: Body tilt relative to wind velocity (in categories). Each solid circle is the mean  $\pm$  SD of the  
393 smallest angle of body tilt in each of 5-10 wing beat cycles (N=26 sequences).

394 Fig. 9: Stabilization of the head and body. Example of wingtip, breast and eye vertical position  
395 over seven wing beat cycles. Elements are drawn to the same scale. The smaller chart is in  
396 independent scales.

397 Fig. 10a. Head position relative to the torso and wings in a hover and a dive (inset). A clear roll and  
398 tilt are observed.

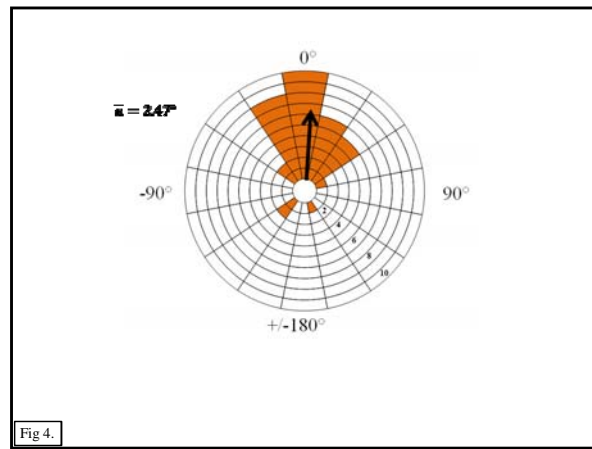
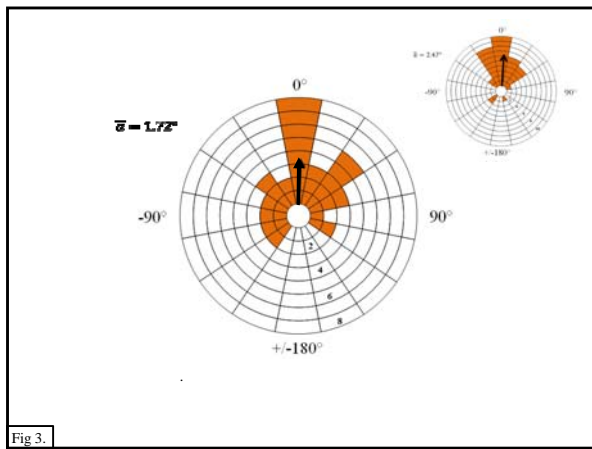
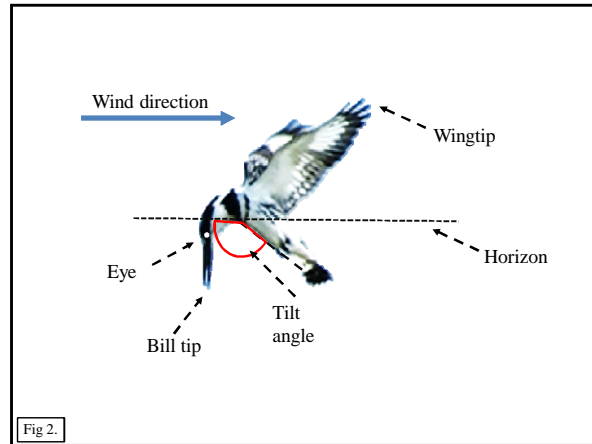
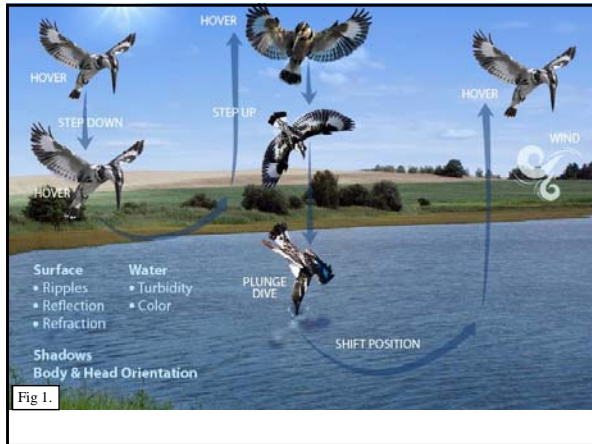
399 Fig. 10b. Bill tip-eye angle relative to wind velocity. Each solid circle is the mean  $\pm$  SD of bill tip-  
400 eye-horizon the (smaller) angle in each of 6-10 wing-beat cycles (N=18 sequences).

#### 401 **Supplement**

402 S1. Correction method. A set of images were made of a stuffed PKF. The photographs were from  
403 different angles that were calculated by positioning the camera at measured distance. from the  
404 object.



9/6/2018



9/6/2018

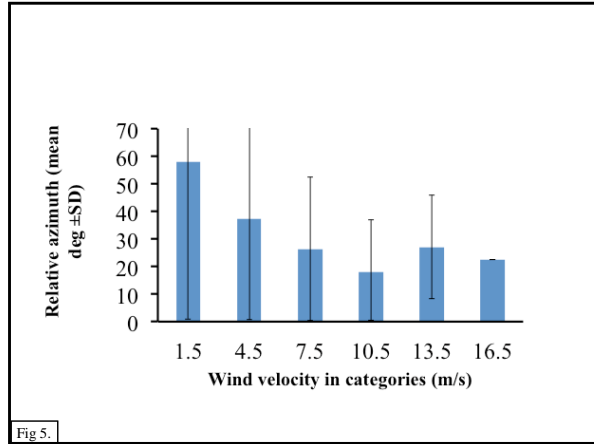


Fig. 5.

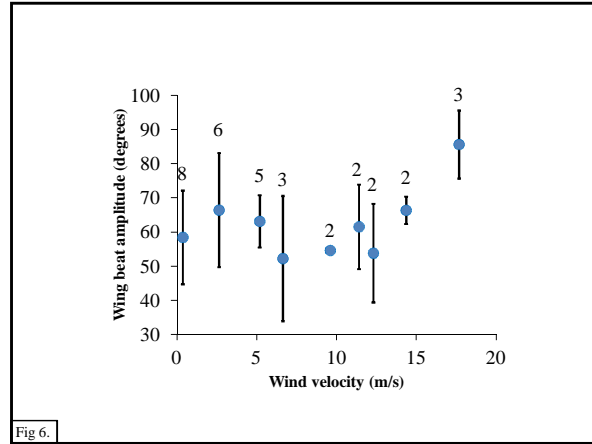


Fig. 6.

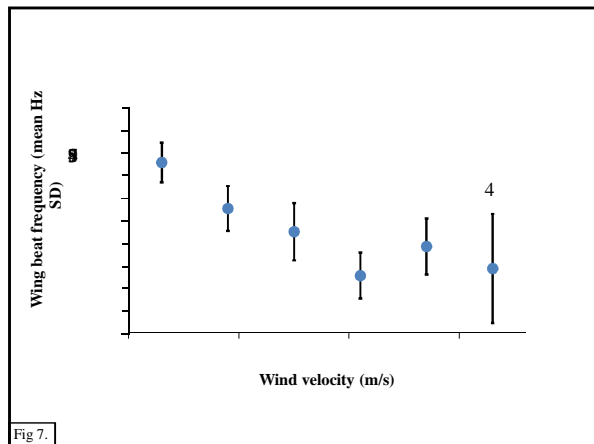


Fig. 7.

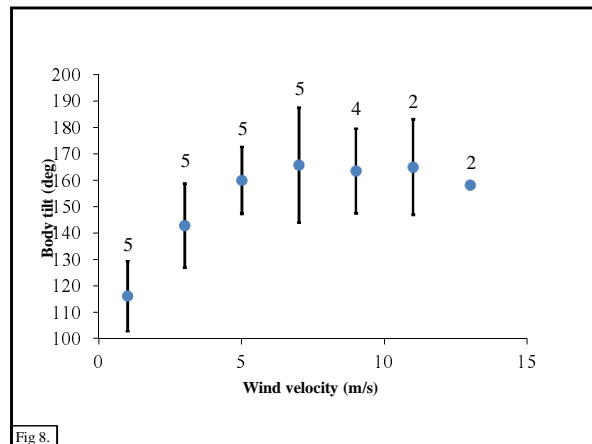


Fig. 8.

9/6/2018

