

1 How Turkey vultures tune their airspeed
2 to environmental and behavioral factors

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9

10 Abstract

11 Animals must tune their physical performance to changing environmental conditions,
12 and the breadth of environmental tolerance may contribute to delineating the species'
13 geographic range. A common environmental challenge that flying animals face is the reduction
14 of air density at high elevation and a reduction in the effectiveness of lift production that
15 accompanies it. Turkey vultures (*Cathartes aura*) inhabit a >3000 m elevation range, and fly
16 considerably higher, necessitating that they compensate for air density differences through
17 behavior, physiology, or biomechanics. We predicted that birds flying at high elevation would
18 demonstrate higher median flight speeds while maintaining similar glide angles. We used 3-
19 dimensional videography to track Turkey vultures flying at three elevations and found a
20 negative relationship between median airspeed and air density that matched our prediction.
21 Additionally, neither the ratio of horizontal speed to sinking speed nor flapping behavior varied
22 with air density. These results were robust to varying flight behavior (climbing vs. level flight).
23 Finally, we derived a glide polar from the free-flying vultures and showed that they are
24 proficient at tuning their flight speed to minimize their cost of transport during straight-line
25 flight, but transition to a minimum power strategy during gliding turns.

26 Keywords

27 Air density, Equivalent airspeed, Glide polar, computer vision, 3D tracking, Cathartidae

28 Introduction

29 The breadth of environmental conditions that species tolerate and exploit may, in large
30 part, determine their geographic extent. Intuitively, species that can tolerate only a narrow set
31 of environmental variables may be expected to have smaller geographic distributions than
32 species that thrive in more diverse conditions [1]. Thus, exploring how species whose ranges
33 span broad environmental gradients or inhabit variable environments compensate for
34 environmental challenges, and what prevents others from reacting similarly, may shed light on
35 how geographic range is constrained.

36 Life at high elevation, and the correspondingly reduced air density, presents a two-fold
37 challenge to locomotor performance in flying animals [2]. First, a physiological challenge of low
38 air density stems from the reduction of available oxygen for respiration [2,3], which can lead to
39 hypoxia and decreased metabolic power output. Secondly, reduced air density poses a physical
40 challenge to fliers, as it decreases the effectiveness of lift generation [2,4]. However, birds can
41 be found at the highest elevations [5,6], suggesting that some species are able to compensate
42 for these hardships. A variety of cardiopulmonary adaptations allow high flying birds, such as
43 bar-headed geese [5,7] and several lineages of Andean waterfowl [6,8], to obtain the oxygen
44 that they need for aerobic respiration. There are a variety of mechanisms that fliers can use to
45 compensate for the aerodynamic consequences of flight in low air density. As was documented
46 in tropical hummingbirds by Feinsinger et al. [9], high elevation species tend to have larger
47 wings relative to their body mass than their low-elevation counterparts. Additionally, birds can
48 adapt to flight in low air density by increasing power output [9], flapping more than they would
49 in higher density air [10], or by using higher amplitude wing strokes [11]. One question that has

50 received less attention, though, is whether birds are capable of compensating for reduced air
51 density at high elevation behaviorally, such as through modulation of airspeed. While not
52 applicable to hovering flight or to landing and takeoff, modulation of airspeed may otherwise
53 offer a low to no cost method for maintaining flight performance across air density gradients.
54 Modern techniques that facilitate high-resolution tracking of birds in the field, either via GPS
55 technology [e.g.: 12], or by high-definition videography [13,14], can be used to look for
56 differences in flight speed among bird populations living at different elevations.

57 Bird species with broad geographic ranges may be exposed to large elevation gradients,
58 and this provides an opportunity to study how they tune their locomotor performance to
59 different environmental conditions. Turkey vultures (*Cathartes aura*) are common throughout
60 North America, inhabit an elevation range of >3000 m [15], and have been reported flying at
61 much higher altitude [16–18]. No evidence is available to suggest that any morphological
62 differences in wing area or flight muscle mass exist among *C. aura* throughout their range,
63 though this has not been addressed explicitly. However, they could alter their power output via
64 increased flapping frequency or higher amplitude wing strokes when challenged by low air
65 densities. Vultures are primarily gliding fliers [19–22], and could also adopt a strategy where
66 they maintain the same true airspeed (which is the same as ground speed in still air) by
67 increasing their glide angle, effectively increasing their power output by cashing in potential
68 energy at a greater rate. Furthermore, *C. aura* consume almost exclusively carrion, which is a
69 food resource that is sparsely distributed and highly ephemeral [23,24]. Thus, it would seem
70 advantageous for *C. aura* to minimize their energetic expenditure while foraging, and suggests
71 that increased flight power output is an unlikely adaptation to high elevation life. Thus, we

72 hypothesized that vultures accommodate flight at varying air densities by changing their true
73 (i.e. observed) airspeed, increasing it as air density decreases. Mathematically, this is identical
74 to the vultures maintaining the same equivalent airspeed (i.e. airspeed corrected for air
75 density) at all air density conditions they experience. We further predicted that vultures would
76 avoid activities that increase their cost of flight: that they would not increase flapping in low air
77 density, and that they would maintain similar glide angles throughout the elevation range.

78 We addressed these hypotheses by recording vultures flying at three sites along a ~2000
79 m elevation gradient to examine how they tune their flight performance to compensate for the
80 air density gradient. As expected, and regardless of the recorded vulture flight behavior, there
81 was a negative relationship between observed airspeed and air density. Vultures did not flap
82 more frequently in lower density air, and the observed change in speed was a near perfect
83 match to that theoretically required to maintain lift, suggesting that other factors such as wing
84 morphing are also unimportant in this case. This study demonstrates how field studies can
85 illuminate the relationship between biomechanical performance and ecology.

86 **Methods**

87 **Vulture recordings**

88 We recorded vultures returning to roost sites on 22 separate afternoons in May, June,
89 and July 2015, and September 2016 at three locations: the Orange County Landfill, Chapel Hill,
90 NC, USA (35°58'9.23"N, 79° 4'54.71"W), the University of Wyoming campus, Laramie, WY, USA
91 (41°18'44.15"N, 105°35'1.04"W, see Fig. 1) and the Alcova Lakeside Marina, Alcova, WY, USA
92 (42°31'45.99"N, 106°46'44.21"W). Each roost colony was comprised by >50 individuals. We
93 were unable to identify and track identities of individual bird and birds readily transited into

94 and out of the camera field of view multiple times during recording bouts, so to
95 pseudoreplication of these individuals, the resulting data were primarily analyzed by reducing
96 each recording session to the median airspeed of all birds in that recording. Subsequent
97 analyses of airspeed were conducted on those medians. There were multiple recordings per
98 day, however we treated each of these separately because ambient temperature and humidity
99 change throughout the day, so air density also varied among recordings.

100 Video data were collected with three digital SLR cameras (Canon OES 6d, Canon inc.,
101 Ōta, Tokyo, Japan) at 29.97 Hz and images had dimensions of 1920 by 1080 pixels. The cameras
102 were arranged in a staggered setup, with intersecting views of the tops of roost trees and
103 airspace above and around them (Fig. 1). Due to the altitude at which the vultures approached
104 the roost trees, and the requisite upward angle of the cameras, we were unable to use a
105 standard wand calibration [e.g.: 13,14]. Instead, we obtained a preliminary calibration using
106 shared views of the flying vultures, digitized using the MATLAB (The MathWorks, Natick, MA,
107 USA) package DLTdv5 [25]. After the initial calibration was complete, we automated tracking of
108 the vultures using a computer vision workflow adapted from that used in Evangelista et al. [26].
109 In brief, birds were detected in each video file by using a 30-frame moving average background
110 subtraction routine plus a fixed background mask for the trees. The resulting background-
111 subtracted images were cleaned with an erosion-dilation operation. The $[u,v]$ pixel coordinate
112 of each remaining foreground object was recorded as a possible vulture detection. These 2D
113 detections from the three cameras were combined to compute a 3D point by searching the
114 possible 2D point combinations for ones that produced a 3D reconstruction residual of less than
115 3 pixels. Points generated from either two or three cameras were accepted. Once the sets of 3D

116 points for all video frames were generated, we joined the resulting 2D+3D datasets across time
117 using a set of Kalman filters to predict the expected position of the birds from frame n in frame
118 $n+1$ and then a Hungarian assignment operation to match the observations in frame $n+1$ to
119 these predicted positions. Unmatched observations started new tracks, and tracks with more
120 than 20 missed detections in sequence were discontinued. Tracks with fewer than 300 data
121 points were dropped from the dataset. The calibration was refined using the complete set of
122 digitized points from the vulture tracks for each recording session, and we used the distances
123 between the cameras to scale the scene. The cameras were aligned to gravity using their
124 onboard roll-leveling feature, and we measured their pitch inclination using a digital
125 inclinometer affixed to the hot-shoe mount on the top of the base camera body. Finally, the
126 scene was oriented to a geographic frame of reference by aligning to the compass vector
127 between the base camera and the roost tree.

128 Individual bird 3D tracks in the scaled and aligned dataset were smoothed using a zero-
129 lag digital Butterworth low-pass filter with an 8 Hz cutoff frequency. Velocity vectors were
130 calculated from this position time-series by fitting a quintic spline polynomial and
131 differentiating it. We added the wind speed vector (see below) to this ground reference frame
132 velocity vector to get each bird's observed airspeed.

133 [Air density and airspeed](#)

134 Wind and weather conditions during the recording sessions were recorded from the
135 closest National Oceanic and Atmospheric Administration (NOAA) weather station for all
136 locations, and from a rooftop-mounted weather station atop the University of Wyoming
137 Biological Sciences building, adjacent to the roost. Because of the distance between the

138 recording sites and the weather stations, and because ground-level wind conditions may not
139 reflect the conditions experienced by the birds, we estimated the magnitude and direction of
140 wind conditions during each recording session from the ground speeds of the birds as they flew
141 in different directions, following the methods of Sherub et al. [27]. Absent any wind or other
142 directional factors, bird ground speeds are not expected to vary with flight direction such that a
143 plot of the two components of their horizontal velocity vector form a circle centered on [0,0]. A
144 wind alters the center of the circle. For example, a 5 ms⁻¹ wind in the +X direction moves the
145 center to [5,0]. Thus, we estimated the wind speed and direction experienced by the vultures as
146 the center point of a circle fit to the X and Y components of their measured groundspeeds over
147 a recording session. This method depends on having a sample of flights headed in all compass
148 directions. Consequently, we omitted trials with vulture tracks comprising less than 90% of the
149 full circle. Ground speed was calculated as the first derivative of vulture position with respect to
150 time (see above). Vulture airspeed was then obtained by subtracting the X and Y components of
151 the estimated wind speed from their respective ground speed components of the vulture
152 tracks. No sustained thermal soaring behavior was observed during the recording periods, and
153 we were unable to assess vertical movement of the air, so we assumed that non-flapping tracks
154 represented gliding flight.

155 Air density (ρ) was calculated from mean barometric pressure, ambient air temperature,
156 and dew point readings from the NOAA weather stations during the recording periods using the
157 formula for density of moist air from [28, pg. 37]:

$$158 \quad \rho = \left(\frac{Pressure}{Gas\ constant_{dry\ air} * T} \right) * \left(1 - \frac{0.378 * Pressure_{vapor}}{Pressure} \right) \quad (1)$$

159 We calculated median airspeeds for each track, and from those the median airspeed of vultures
160 during the entire recording session. Because we were unable to assign individual identifiers to
161 birds and track them beyond the camera field of view, it is highly probable that individual
162 vultures contributed multiple tracks to the dataset by appearing during successive recording
163 sessions at the same site. However, these individual replicates would have been collected at
164 separate points in time and thus represent flight under different conditions (e.g. air density,
165 wind direction relative to flight direction, and even body mass).

166 We hypothesized that vulture airspeed would decrease as a function of air density (ρ) in
167 the sample (predicted slope = -5.22) based on a linear approximation of the theoretical
168 relationship between airspeed and ρ and the median airspeed of vultures at the maximum ρ in
169 the sample ($\rho = 1.227$):

$$170 \quad m_{pred} = \frac{V_1 - V_1 \sqrt{\frac{1}{\rho_1}}}{\rho_1 - \rho_2} \quad (2)$$

171 where m_{pred} is the predicted linear approximation slope, ρ_1 is the highest air density in the
172 sample, ρ_2 is the lowest air density in the sample, and V_1 is the median airspeed of vultures
173 flying in the highest ρ conditions in the sample. The estimate of airspeed at ρ_2 is based on
174 equation 5 in Pennycuick [29]. Although the theoretical relationship between V and ρ is non-
175 linear, because the range of ρ is small, a linear approximation provides a convenient and easily
176 testable hypothesis.

177 We tested a set of multiple linear regression models to evaluate the relationship
178 between median airspeed and ρ as well as the impact of wind speed on the relationship. We

179 used AICc to select the best fit among these candidate models. Additionally, to assess whether
180 flight behavior (i.e. climbing, descending, or level flight) might influence the relationship
181 between air density and airspeed, we parsed the data into climbing, descending, and level flight
182 tracks using vertical speed thresholds of ($V_{z,med} > 0.25$ m/s), ($V_{z,med} < -0.25$ m/s), and (0.5 m/s
183 $> V_{z,med} > -0.5$ m/s) respectively, and used ordinary least-squares (OLS) regression to evaluate
184 the relationship between V and ρ in each set. We used a Wald χ^2 test to assess whether the
185 model slopes differed from m_{pred} .

186 Air density and flapping behavior

187 The automatic tracking algorithm detects and tracks the visual centroid of the vultures
188 in each video frame (as opposed to a fixed point on the body, such as the head). Because of
189 this, and due to the large size of the birds' wings, their tracks appear as a sinusoidal wave
190 pattern when the birds flap, contrasting with comparatively smooth gliding tracks. We
191 exploited this to assess whether the vultures flapped more in lower air density, a sign that they
192 might be compensating for decreased lift by modulating power output. We used a custom
193 MATLAB program to detect that characteristic sinusoidal track pattern and coded each video
194 frame of each track with a binary (0) gliding, or (1) flapping. We then used the mean to quantify
195 the proportion of the track the bird spent flapping vs. gliding. Further analyses of flapping
196 behavior were restricted to tracks closer than 350 m from the cameras, as this appeared to be
197 the maximum distance at which flapping is detectable (see Fig. 3). We also excluded tracks
198 within 50 meters of the roost to avoid tracks in which the birds were making their final landing
199 approach, which was characterized by a large amount of flapping not necessarily related to the
200 density of the air. Data were again collapsed to medians for each recording bout. We used OLS

201 regression to look for a relationship between incidence of flapping and ρ . Finally, we assessed
202 whether the proportion of flapping in tracks using OLS regression on the mean, or the
203 probability of detecting flapping (binary logistic regression) varied with wind speed.

204 **Glide polar calculation**

205 Finally, we also constructed a glide polar from the vulture tracks by fitting the
206 observations to the following equation [30]:

$$207 \quad \dot{Z}_{fit} = \frac{P}{g} = k_1 \frac{1}{2} \rho_0 S (U_e)^3 + k_2 \frac{2(mg)^2}{\rho_0 S U_e} \quad (3)$$

208 Where \dot{Z}_{fit} is the sinking rate that expends potential energy at the same rate as the
209 overall kinematic power P (i.e. the instantaneous rate of change in kinetic and potential
210 energy), g is the magnitude of gravitational acceleration, k_1 is a coefficient for parasite and
211 profile power, ρ_0 is standard air density, S is wing area, U_e is equivalent airspeed (i.e. airspeed
212 adjusted for air density), and k_2 is the induced power coefficient. See Hedrick et al. (2018) for
213 further details on this calculation. Literature values of 0.456 m² and 2.18 kg [31] were used for
214 S (wing area) and m (body mass), respectively. However, these values have no effect on the
215 resulting glide polar, only on the numerical values for k_1 and k_2 arrived at by the statistical
216 fitting process, a general linear model.

217 Reducing each vulture flight track to its median values, as was done for the air speed
218 versus air density analysis results in a dataset with a compressed range of equivalent airspeeds
219 whereas fitting a glide polar requires a wide range of airspeeds. Thus, for the glide polar
220 calculations we created an alternative dataset by sampling individual data points from the
221 entire set of flight tracks. In constructing this dataset, we first established the following criteria

222 for possible inclusion: 1) non-flapping, 2) instantaneous turn radius > 20 m, 3) non-landing, 4)
223 negative P (i.e. negative instantaneous summed rate of change in kinetic and potential energy),
224 5) $P > 5^{\text{th}}$ percentile, and 6) distance to cameras < 350 m. From the resulting set of
225 approximately 473,000 data points, we selected approximately 3000 equally spaced points,
226 matching the number of vulture flight tracks.

227 For comparison with the dataset used to compute the glide polar, we produced a
228 “gliding turns” dataset that might reflect brief thermal use or other aerial behaviour beyond
229 straight gliding. For this dataset we used the following criteria: 1) non-flapping, 2)
230 instantaneous turn radius < 15 m, 3) non-landing, 4) P in the 5th to 95th percentile range, and 5)
231 distance to cameras < 350 m, the limit of flapping detection. From the resulting set of
232 approximately 218,000 data points, we again selected approximately 3000 equally spaced
233 points for inclusion in the dataset.

234 Results

235 Vulture tracks, air density, and flight speeds

236 We collected 3027 vulture flight tracks representing 18 hours of vulture flight time.
237 Median vulture airspeeds, summarized by recording bout, ranged from 7.5 to 12.58 ms^{-1} with
238 an overall median airspeed of $10.12 \pm 0.87 \text{ ms}^{-1}$. There was a large amount of variation in
239 airspeed among vulture flight tracks in each recording session, median absolute deviations
240 (MAD) ranged from 16% to 68% of the median (Fig. 2). After correcting for ambient
241 temperature and relative humidity, ρ ranged from 0.890 to 1.227 kg m^{-3} (see Fig. 2).

242 The best performing model, via AICc, included effects of ρ and wind speed (AICc weight
243 = 0.67). Median vulture airspeed (V_{med}) decreased with ρ (estimated slope $m_{\rho} = -3.73$, $F_{3,27} = 7.82$,

244 slope $\rho = 0.003$; see Fig. 2) and increased with wind speed ($m_{wind} = 0.24$, slope $\rho = 0.004$). Full model
245 results are presented in Table 1. Similar relationships existed when the data were subset into
246 vultures that were climbing (slope = -4.63, $F_{1,29} = 7.57$, $p = 0.01$, adj. $r^2 = 0.18$) and flying
247 approximately level (slope = -4.52, $F_{1,29} = 7.51$, $p = 0.01$, adj. $r^2 = 0.18$), however the relationship
248 between V_{med} and ρ was not significant when the birds were descending (slope = -2.72, $F_{1,29} =$
249 2.81, $p = 0.10$, adj. $r^2 = 0.06$).

250 The estimated slope of the relationship between V_{med} and ρ was not statistically
251 distinguishable from the predicted slope (m_{pred}) in the best performing model, which included
252 both ρ and wind speed (Wald χ^2 test, $F_{2,28} = 2.04$, $p = 0.16$), the runner-up model with the wind
253 speed-by- ρ interaction ($F_{3,27} = 0.15$, $p = 0.70$), or the model which included only ρ ($F_{1,30} = 0.67$, p
254 = 0.42). Similarly, the slopes of the tests of climbing and level flight were indistinguishable from
255 m_{pred} (Wald χ^2 test, all $p > 0.65$).

256 Flapping analysis

257 We were only able to detect flapping in tracks that were in close proximity to the
258 cameras, so we restricted analysis of flapping behavior to tracks that were within 350 m of the
259 roost, and at least 50 m away from it to avoid analyzing landing tracks. Fortunately, 84% of the
260 tracks in the overall dataset fit these criteria (see Fig. 3). There was no relationship between the
261 proportion of flapping in the tracks and ρ (OLS regression, $F_{1,29} = 1.91$, $p = 0.18$), however, the
262 proportion of flapping in tracks decreased steeply away from the roost (Fig. 3). There was also
263 no relationship between wind speed and the proportion of tracks where flapping was detected
264 ($p = 0.59$), but the probability of detecting flapping did increase ($p < 0.01$) with wind speed (see
265 Fig. 4).

266 **Glide polar**

267 Our kinematic analysis of vulture flight tracks produced a glide polar with a minimum
268 sinking speed of 0.74 ms^{-1} at a flight speed of 7.9 ms^{-1} (Fig. 5). Coefficients k_1 and k_2 were both
269 highly significant ($p < 0.001$) and had respective values of -0.0134 and -0.0260 with standard
270 errors of $4.58e^{-4}$ and $1.00e^{-3}$. The maximum range speed was 10.3 ms^{-1} with a sinking speed of
271 0.84 ms^{-1} . The maximum lift to drag ratio was 12.2. The mean flight speed in the dataset
272 constructed for fitting the glide polar (i.e. straight, descending glides) was 10.1 ms^{-1} , nearly
273 identical to the maximum range speed expressed by the polar. However, the comparison
274 dataset of “gliding turns” had a mean airspeed of 8.0 ms^{-1} , nearly identical to the minimum
275 power speed in the glide polar.

276 **Discussion**

277 **Summary of results**

278 We predicted that median airspeed in vultures flying across a range of elevations and
279 ambient conditions would increase in response to decreasing air density (ρ). Based on a simple
280 linear approximation of the relationship between airspeed and ρ , we predicted a slope of -5.22
281 across the sampled range of ρ . We found that median vulture airspeed (V_{med}) largely conformed
282 with this prediction, despite a large amount of variation among individual tracks. Furthermore,
283 this relationship was largely invariant with flight behavior; climbing and level tracks also
284 followed the predicted relationship. These results agree with prior observations of Himalayan
285 vultures (*Gyps himalayensis*) tracked via GPS [27].

286 Increased airspeed compensates for decreased air density

287 Drag forces also decrease with air density [32], and is a likely mechanism for the
288 observed increase in airspeed. However, this assumes that birds among the different
289 populations are geometrically similar, having roughly the same wing loading and wing shape,
290 and that morphological disparity (the variation in body shape and size) is roughly equivalent
291 across populations. Local adaptation of wing morphology to high elevation in the sample would
292 likely have manifested in less change in V_{med} relative to ρ , or a difference in the ratio of sinking
293 speed (V_z) relative to horizontal speed (V_{xy}). There was no difference in the relative
294 contribution of horizontal vs. sinking speed in the sample ($p = 0.99$). This, plus the agreement
295 between the predicted and estimated slopes of the V_{med} vs. ρ relationship suggest no localized
296 adaptation in wing morphology or loading. Further, if the increase in airspeed is simply a
297 passive effect related to the reduction of drag, it implies that birds do not alter their flapping
298 behavior [10] or increase their glide angle in low density air. Vultures in the recordings
299 examined here flapped more as they neared their roost trees, perhaps as part of their approach
300 and landing maneuvers. Flapping also increased in response to greater wind speed, but did not
301 vary with ρ . Taken together, these results do not indicate any localized behavioral or
302 morphological adaptations to maintain similar airspeed among populations of Turkey vultures
303 residing at different elevations.

304 Our sample sites, which encompass a 27% reduction in air density, captured the
305 variation of flight conditions that vultures experience during typical flight bouts across their
306 geographic range, but may not reflect extreme conditions that vultures sometimes experience.
307 Vultures have been recorded at altitudes exceeding 1000 m [16], and anecdotal reports suggest

308 that their maximum flight altitudes may be much higher (up to perhaps 6000 m). Air density
309 decreases exponentially as altitude increases, necessitating disproportionately greater airspeed
310 increases to maintain lift as birds climb higher, so it is possible that the relationship that we
311 have described between V_{med} and ρ might change for vultures flying at especially high altitudes,
312 requiring that they modify their flapping behavior or glide angle. Despite some observations of
313 extremely high vulture flight, tracking data suggest that typical vulture flight altitudes are much
314 lower, around 150 m above ground level [16,17], well within our sampled elevation range.

315 Wind effects

316 Wind conditions on our sample days varied from calm to heavy, gusty winds. The best
317 performing model included both air density and wind speed as predictors for vulture airspeed.
318 Our estimate of wind speed is based upon its influence on the measured groundspeeds of the
319 birds flying at different angles relative to the wind (see Methods), and we would expect no
320 lingering relationship between wind speed and airspeed if this correction is consistent across all
321 wind velocities. However, we found a positive relationship between wind speed and airspeed.
322 This relationship was largely driven by the windiest day in our sample, with an average wind
323 speed of 7.8 ms^{-1} . The linear regression between median vulture airspeed and estimated wind
324 speed was significant ($p < 0.01$) with that day included but was non-significant when we
325 removed it ($p = 0.08$). Our overall multiple regression model results predicting vulture airspeed
326 were robust to inclusion, or not, of that particularly windy day. We interpret this result as the
327 vultures modifying their flight behavior to maintain forward progress toward their destination
328 in the face of strong headwinds. The wind speed on that day was nearly equal to the minimum
329 power speed (Fig. 5) and thus sufficient to noticeably influence bird airspeed [33]. Despite the

330 wind effect, the relationship between vulture airspeed and air density is statistically
331 indistinguishable from the slope that we predicted based on the elevation and ambient
332 temperature and humidity at our sample sites. Therefore, though the vultures clearly reacted to
333 windy conditions, air density was still the dominant influence on their flight speed.

334 **Glide polar and gliding performance**

335 Our analysis of the vulture flight trajectories produced a glide polar (Fig. 5) with
336 characteristic minimum power and maximum range speeds of 7.9 and 10.3 ms⁻¹, respectively.
337 While no published glide polars exist for Turkey vultures, several exist for Black vultures
338 (*Coragyps atratus*), which are of similar body mass and sympatric with Turkey vultures for much
339 of their range. However, Black vultures have significantly higher wing loading (i.e. smaller wings
340 relative to body mass) compared to Turkey vultures [31,34], and these morphological
341 differences are expected to manifest as differences in flight performance. Specifically, gliding
342 Turkey vultures are expected to have a smaller magnitude minimum sinking speed than Black
343 vultures and achieve that sinking speed at a slower airspeed than Black vultures [35,36]. Our
344 results support these predictions; Parrot [37] studied the gliding flight of a Black vulture in a
345 wind tunnel and reported a minimum sinking speed of approximately 1.1 ms⁻¹ at an airspeed of
346 11.5 ms⁻¹, compared with the respective values of 0.74 and 7.9 ms⁻¹ for Turkey vultures in this
347 study.

348 The Turkey vultures studied here were also strikingly proficient at modulating their flight
349 speed toward different biomechanical optima for different behaviors. Straight, descending
350 gliding flight (instantaneous turn radius > 20 m) had a mean equivalent (i.e. air density

351 adjusted) airspeed of 10.1 ms^{-1} , similar to the maximum range speed of 10.3 ms^{-1} on the glide
352 polar. Thus, during straight glides the vultures were using a flight speed that maximizes distance
353 traveled per unit energy expended. We did not observe any sustained circling behavior in the
354 vulture flights recorded here, but did record some turning flight, and even instances where the
355 vultures achieved an instantaneous gain in their summed kinetic and potential energy, a result
356 consistent with brief use of rising air currents for energy gain. Birds gaining energy from rising
357 air should fly at an airspeed close to that which minimizes sinking speed thus maximizing the
358 elevation gain from the rising air. Birds turning for other reasons may also slow their airspeed
359 to minimize centripetal acceleration during turning, and flying at the minimum sinking speed
360 minimizes energy losses to induced, parasite, and profile drag leaving more lift available for
361 turning. Both these effects suggest birds engaged in gliding turns should fly near their minimum
362 power speed. In this case, turning Turkey vultures (instantaneous turn radius $< 15 \text{ m}$) flew at an
363 airspeed of 8.0 ms^{-1} , nearly identical to the minimum power speed of 7.9 ms^{-1} from their glide
364 polar. Thus, Turkey vultures conform surprisingly closely to the separate biomechanical optima
365 for gliding for distance and gliding while turning.

366 **Concluding remarks**

367 Animals interact with their physical environment to move, forage, migrate, and a host of
368 other functions, and their ability to do so effectively can be limited by physical constraints
369 imposed by their environment. We showed that Turkey vultures respond to a fundamental
370 environmental gradient that could impact their flight performance, the decrease of air density
371 at high elevation by increasing their flight speed and adjust their flight speed to optimize their
372 gliding flight. The tool that we used was developed for field studies of biomechanics

373 [13,14,25,38], but this study also demonstrates that tools from the biomechanics toolchest can
374 be successfully applied to ecological questions.

375 Data availability

376 Vulture tracks and associated metadata are available along with the R and MATLAB data
377 processing scripts used to perform the analyses and generate the figures in this manuscript will
378 be made publicly and permanently available upon manuscript acceptance.

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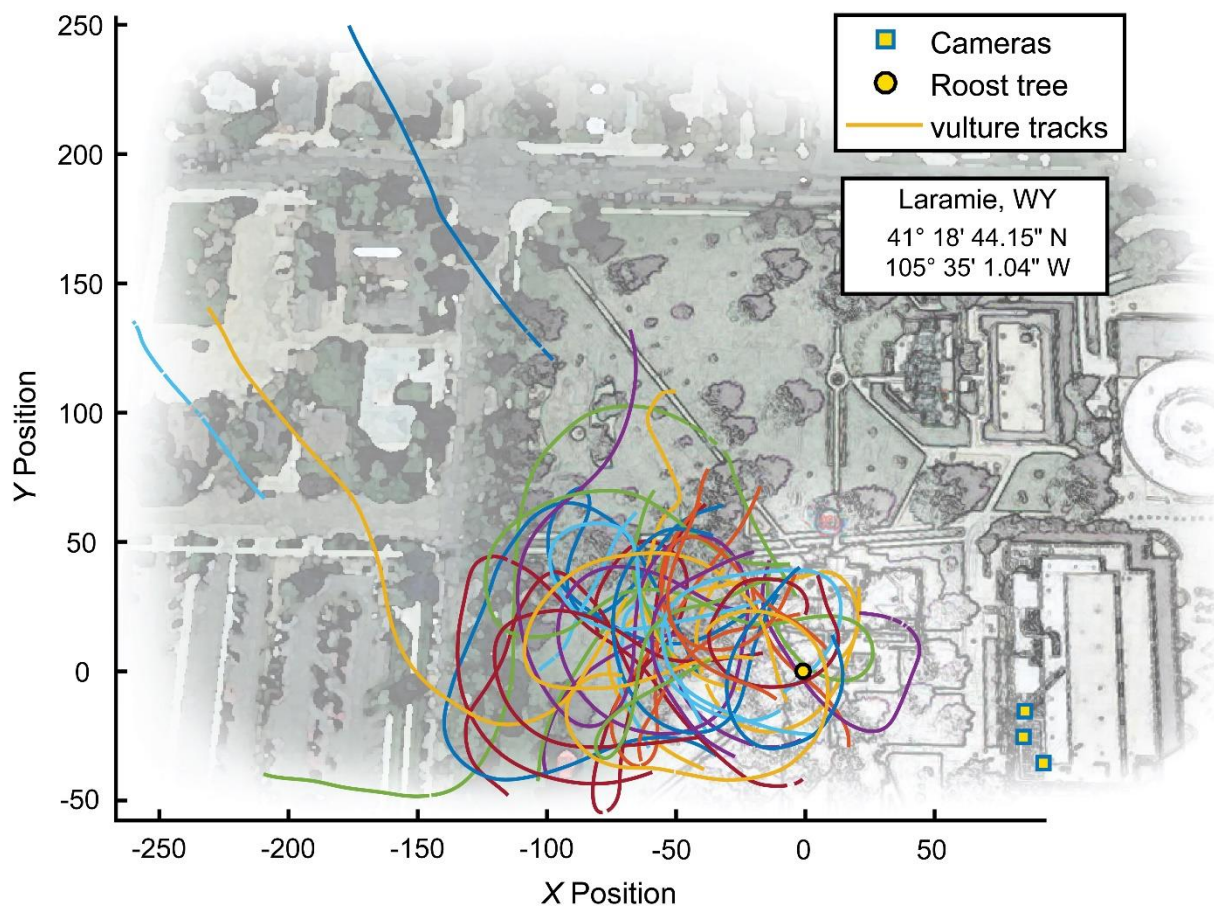
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- 477

478 **Figure 1**

479 Overhead view of the Laramie, WY recording site. Blue squares denote camera locations atop the
480 Biological Sciences building at the University of Wyoming, and the black circle shows the center of the
481 roost trees. The multicolored tracks depict a sampling of the vulture tracks recorded from one recording
482 bout.

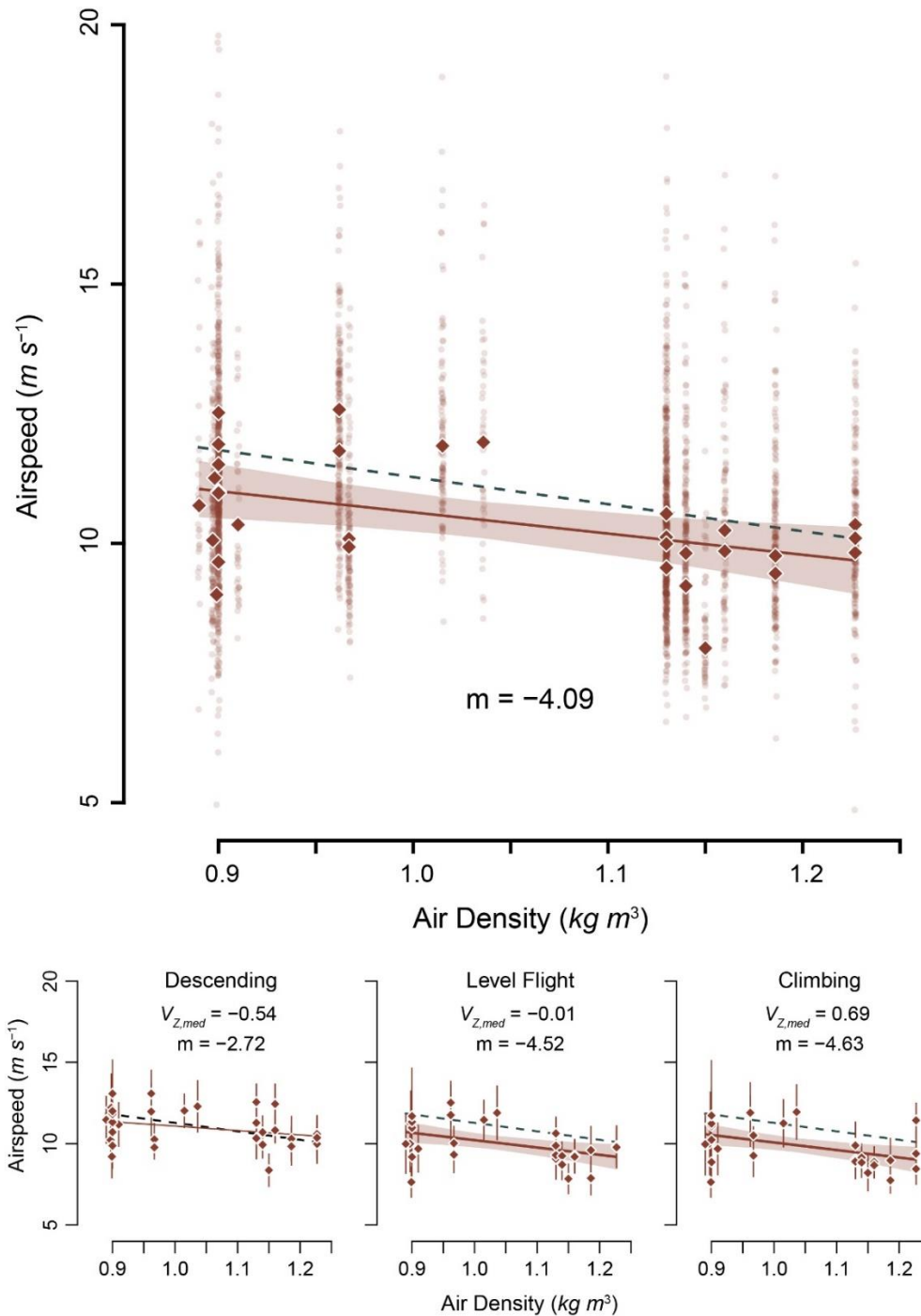


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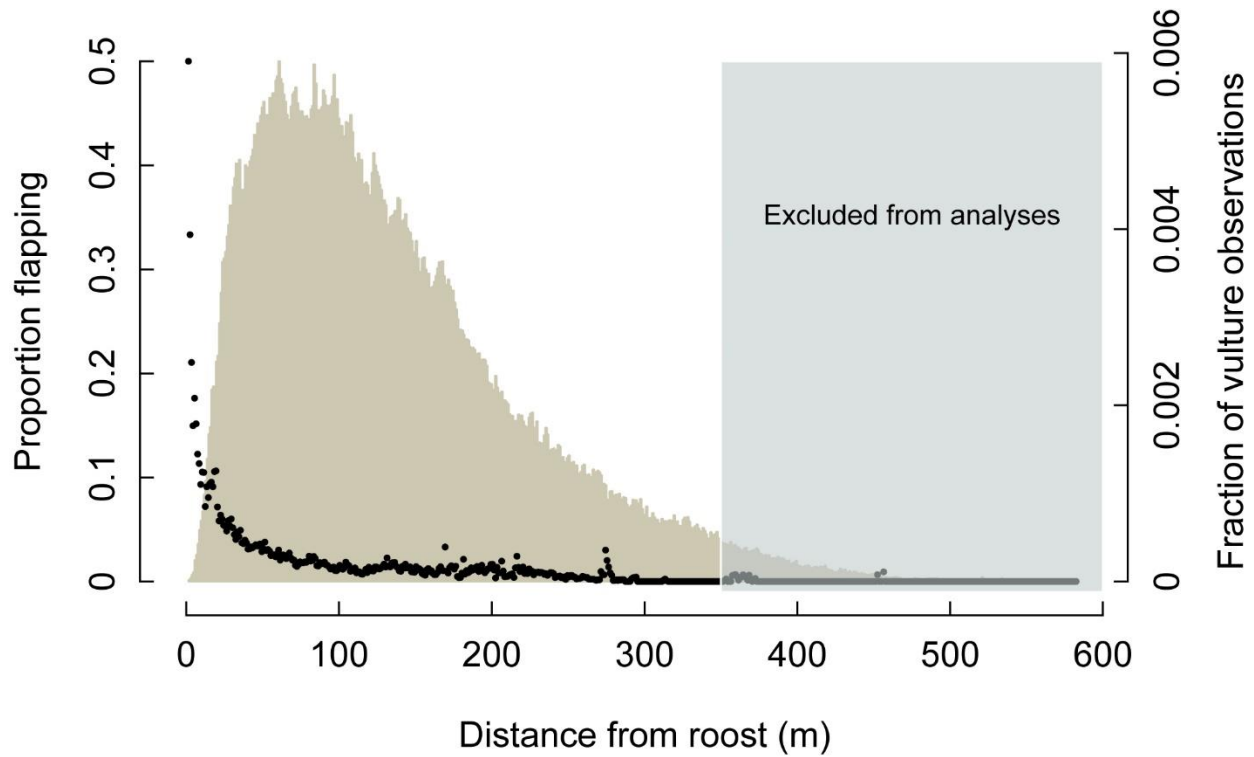
485 **Figure 2**

486 Median airspeed decreased with increasing air density. Transparent data points show median values for
487 each track, highlighting the large variation in the sample. Analyses were conducted on median values for
488 each recording session, depicted by solid diamonds. The dashed green line shows the predicted slope (-
489 5.22), while the solid brown line shows the modeled slope with its 95% confidence interval (shaded
490 region)



492 **Figure 3**

493 Proportion of detected flapping events, indicated by black points, decreased with distance from the
494 roost trees. The histogram depicts distribution of tracked birds, relative to the roost position. The ability
495 to detect flapping diminished with distance from the cameras, so tracks greater than 350 m from the
496 roost were excluded from further analyses.

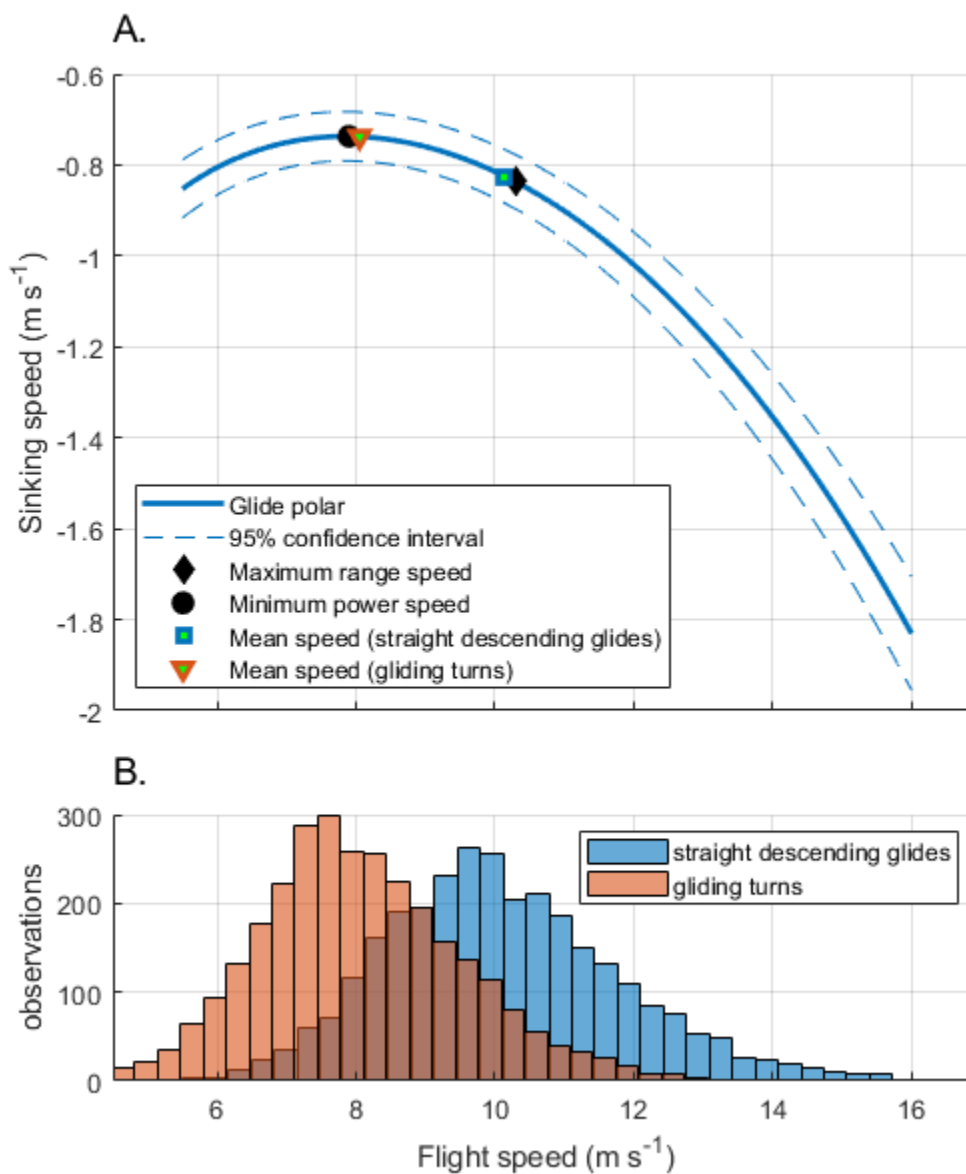


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508 **Figure 5**

509 The Turkey vulture glide polar measured from the recorded trajectories. A) shows the glide polar itself,
510 along with a 95% confidence interval, two biomechanically interesting points (black symbols) and the
511 mean flight speed of the vultures during two different types of flight behavior (colored symbols). B)
512 expands the mean speed results for straight glides and gliding turns into histograms to fully illustrate the
513 difference between the two categories. The two distributions have significantly different means
514 ($p < 0.0001$, 2-sample t-test) and these means correspond almost precisely to the two biomechanical
515 optimal for transport over distance (i.e. maximum range speed) during straight glides and minimum
516 descent speed for turning glides. Flying at minimum descent speed will both facilitate the vulture taking
517 advantage of a column of rising air and minimize aerodynamic costs of turning.



519 **Table 1. Model selection results**

Model	Model Statistics	AICc	AICc.w	m_ρ m_{wind} m_{int}
$V \sim \rho + \text{Wind}$	$F_{2,28} = 11.09, p = 0.003, \text{adj. } r^2 = 0.40$	82.77	0.67	-3.73** 0.24**
$V \sim \rho + \text{Wind} + (\rho \cdot \text{Wind})$	$F_{3,27} = 7.82, p < 0.001, \text{adj. } r^2 = 0.41$	84.34	0.31	-6.64* -0.81 1.07
$V \sim \rho$	$F_{1,29} = 8.80, p = 0.006, \text{adj. } r^2 = 0.21$	89.99	0.02	-4.09**

520 Significance codes for estimated slope coefficients: * $p < 0.05$, ** $p < 0.01$