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RESEARCH ARTICLE

In-flight turbulence benefits soaring birds

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ABSTRACT

Birds use atmospheric updrafts to subsidize soaring flight. We observed highly variable soaring flight by Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*) in Virginia, USA, that was inconsistent with published descriptions of terrestrial avian flight. Birds engaging in this behavior regularly deviated vertically and horizontally from linear flight paths. We observed the soaring flight behavior of these 2 species to understand why they soar in this manner and when this behavior occurs. Vultures used this type of soaring mainly at low altitudes (<50 m), along forest edges, and when conditions were poor for thermal development. Because of the tortuous nature of this flight, we describe it as "contorted soaring." The primary air movement suitable to subsidize flight at this altitude and under these atmospheric conditions is small-scale, shear-induced turbulence, which our results suggest can be an important resource for soaring birds because it permits continuous subsidized flight when other types of updraft are not available.

Keywords: Cathartes aura, contorted soaring, *Coragyps atratus*, flight behavior, turbulence, updraft

La turbulencia en vuelo beneficia a las aves planeadoras

RESUMEN

Las aves usan las corrientes atmosféricas ascendentes para subsidiar los vuelos de planeo. Observamos una gran variación en los planeos de *Coragyps atratus* y *Cathartes aura* que era inconsistente con las descripciones publicadas de los vuelos de las aves terrestres. Las aves que presentaron este comportamiento generalmente se desviaron vertical u horizontalmente de las trayectorias lineales del vuelo. Observamos los comportamientos de planeo de estas dos especies para entender por qué planean de esta manera y cuándo se manifiesta este comportamiento. Los buitres utilizaron este tipo de planeo principalmente a baja altura (<50 m), a lo largo de los bordes del bosque y cuando las condiciones fueron pobres para el desarrollo de térmicas. Debido a la naturaleza tortuosa de este vuelo, lo describimos como "planeo contorsionado". El principal movimiento de aire adecuado para subsidiar el vuelo a esta altura y bajo estas condiciones atmosféricas es la turbulencia inducida pura de pequeña escala. Nuestros datos sugieren que la turbulencia inducida pura de pequeña escala puede ser un recurso importante para las aves planeadoras debido a que permite vuelos subsidiados continuos cuando no están disponibles otros tipos de corrientes ascendentes.

Palabras clave: Cathartes aura, comportamiento de vuelo, *Coragyps atratus*, corrientes ascendentes, planeo controlado, turbulencia

INTRODUCTION

Atmospheric updrafts are important resources for soaring birds (Berthold 2001). By soaring instead of flapping, birds save energy and reduce the metabolic costs of movement (Baudinette and Schmidt-Nielsen 1974). Terrestrial soaring flight is limited to periods when weather promotes development of updrafts (Kerlinger 1989). Flight generalists (i.e. birds that routinely switch between soaring and flapping flight; Rayner 1988) use flapping when conditions are unsuitable for soaring (Sapir et al. 2011, Klaassen et al. 2012, Vansteelant et al. 2015). By contrast, obligate soaring birds require updrafts to fly long distances because the flapping flight of these species is energetically constrained (Bildstein et al. 2009). To extend their flight activity, some obligate soaring species are anatomically adapted to soar using weak updrafts (Pennycuick 1975) or to use multiple types of updraft.

Vultures are obligate soaring birds (Ruxton and Houston 2004) that use both thermal (DeVault et al.

TABLE 1. Site ID, location, land cover type, approximate forest edge length, area, and distance to nearest weather station for sites used in this study.

Site ID	Latitude	Longitude	Land cover	Edge (m)	Area (m^2)	Weather station distance (km)
1	37.317	−76.88085	Riparian	5,555	3,956,997	10.4
2	37.30003	−76.8992	Riparian	3,275	424,072	10.1
3	37.31692	−77.0985	Riparian	3,269	2,256,137	7.4
4	37.25775	−76.88047	Riparian	3,069	855,659	6.6
5	37.26237	−76.95368	Field	3,389	443,521	16.6
6	37.37288	−77.00505	Field	1,173	167,630	5.9
7	37.4065	−77.11957	Field	1,215	115,533	6.4
8	37.33937	−77.01922	Field	5,660	1,249,779	13.9
9	37.42132	−77.01572	Field	2,116	236,680	4.5
10	37.43843	−77.02217	Road	1,085	66,698	3.5
11	37.48272	−76.91247	Road	666	18,694	19.3
12	37.31652	−76.73442	Road	1,314	59,205	4.8
13	37.49377	−77.15702	Road	721	43,116	3.9

2005) and orographic (or slope-soaring; Pennycuick 1983, Bohrer et al. 2011) updrafts to subsidize flight. However, several species of vultures (Houston 1988) soar in a flight pattern characterized by numerous vertical and horizontal deviations from a straight-line path. Although Turkey Vultures (*Cathartes aura*; Houston 1988) and Black Vultures (*Coragyps atratus*; J. M. Mallon et al. personal observation) are known to engage in this type of soaring, little is known about the mechanisms or conditions of its use. Studying the context in which vultures engage in this flight behavior can provide insight into constraints and evolutionary drivers of avian soaring flight.

To understand the possible proximate (e.g., weather, habitat) and ultimate (e.g., evolutionary) drivers of this flight behavior, we studied flights of Turkey and Black vultures in eastern North America. Data collection involved the well-established approach of linking visual classification of flight behavior to the landscapes and aeroscapes that soaring birds experienced (Pennycuick 1972, Bildstein et al. 2009). We evaluated whether use of this behavior was (1) restricted to low altitudes and (2) typically associated with specific weather and land-cover types. We evaluated whether the behavior was (3) used to different extents by the 2 species.

METHODS

Flight Behavior

We observed 4 types of flight: (1) thermal soaring (circling while gaining altitude); (2) gliding (linear flight, losing altitude); (3) linear soaring (no change in direction or altitude); and (4) the flight pattern we describe here, with numerous vertical and horizontal deviations from a straight-line path. Linear soaring, described elsewhere (Spaar and Bruderer 1996), was observed far less frequently than the other soaring types and is omitted from our results. The vultures we watched also flapped intermittently (Ferland-Raymond et al. 2005), but we almost never observed sustained flapping flight (i.e. >20 flaps min^{-1}).

Data Collection

Turkey and Black vultures are locally abundant, year-round residents of southeastern Virginia, USA. The region has little topographic relief, which simplifies classification of flight behavior because vultures can't use orographic updrafts. We measured the behavior of flying vultures at 13 open sites that were surrounded by forest (Table 1). We selected sites with high visibility and that represented 3 common land-cover types in the study region. "Field" sites ($n = 5$) were agricultural (corn, wheat, or fallow). "Riparian" sites ($n = 4$) were combinations of deciduous forest, wetland, and human-use lands (e.g., boat docks) near bodies of water. Roads ($n = 4$) were ≥4 lanes across (≥15 m wide) and included surrounding parking lots and structures. Whenever possible, we observed 1 site of each land-cover type (field, riparian, or road) each day. Observation sessions lasted 2 hr. We collected data at each site 4 times during morning (0900–1130 hours), early afternoon (1130–1400 hours), and late afternoon (1400–1700 hours), for a total of 12 observations at each site.

Two observers followed focal birds using binoculars. We selected focal subjects when they entered our field of view and observed them until they flew out of sight. We recorded the focal bird's flight type (see below), altitude above ground level (AGL), and the amount of time the focal bird spent in each flight type and at each altitude. We estimated flight altitudes in the following ranges: <10, 11–25, 26–50, 51–100, or 101–200 m AGL (Bildstein et al. 2007).

Local meteorological stations (http://www.wunderground.com) provided temperature, humidity, and wind speed data

FIGURE 1. Illustration of a Turkey Vulture engaged in contorted soaring near tree height. The flight path, ~10 s in duration, deviates horizontally and vertically from a linear flight path while maintaining both altitude and general direction.

at intervals of ≥5 min for our study. We paired behavioral observations with weather data by temporally interpolating weather parameters from the nearest meteorological station available (Table 1). Furthermore, at 15-min intervals we estimated cloud cover as clear (<20% clouds), partly cloudy (20–80% clouds), or overcast (>80% clouds).

Data Analysis

We calculated mean flight altitudes by averaging the highest value in each altitude range recorded (<10 = 10 m, 11–25 = 25 m, etc.), and we log transformed these values so that they more closely approximated a normal distribution. For each flight type used, we calculated the duration and mean altitude at which it occurred. We used only observations that lasted ≥30 s. We linearly interpolated meteorological-station data to the time of each observed flight and averaged those data by hour.

We used Wilcoxon rank-sum tests in R version 3.0.2 (R Development Core Team 2013) to evaluate whether there was an interspecific difference in flight altitude and the frequency with which birds engaged in each flight behavior.

We used beta-binomial mixed models (package aod; Lesnoff and Lancelot 2012) for overdispersed data in an information-theoretic framework to determine whether flight behavior was associated with specific weather characteristics. Our modeled response variable was the proportion of time we observed each species engaged in each flight behavior. Fixed effects were cloud cover, wind speed, temperature, humidity, and land cover, and site was a random effect. We centered our nominal variables to reduce multicollinearity. We found the combination of weather variables that were most influential to the flights of vultures by using the "dredge" function (package MuMIn; Bartón 2015). For each species and for the 2 main soaring behaviors, we present model averages of highly competitive models (ΔAIC < 4).

RESULTS

We observed flights of Black Vultures ($n = 107$) and Turkey Vultures ($n = 464$) during 161 observation sessions (2 hr each) on 45 days at 12 sites in May–July 2013 and on 7 days at 1 site in June 2014.

Description of Contorted Soaring

The flight pattern we describe here occurred when a focal bird flew with numerous vertical and horizontal deviations from a straight-line path (Figure 1). In spite of these small-scale deviations characteristic of the behavior, focal subjects generally maintained a mostly linear flight path with little net change in altitude or direction.

During periods of high wind gusts, we observed birds in high, banking flight in which they appeared to turn perpendicular to the wind and were swept sideways. We sometimes observed individuals engaging in this flight behavior for several minutes, sustaining flight by repeatedly flying back and forth in a small area and appearing to "surf" in air. In these instances, vultures were likely propelled by a combination of momentum and wind gusts.

We call this behavior "contorted soaring" because it is characterized by inherently variable flight paths. Contorted soaring by Turkey Vultures, which hold their wings in a dihedral, was often accompanied by rocking or teetering motions. Although Black Vultures normally hold their wings flat, we occasionally observed individuals engaged in contorted soaring also holding a slight dihedral and teetering slightly.

Use of Contorted Soaring

Ninety-nine percent of vultures observed using contorted soaring flew at <50 m AGL. When engaged in contorted soaring, there was no difference in flight altitude between the 2 species (Black: 31 m AGL, 95% CI: 14.5–66.4; Turkey: 29 m AGL, 95% CI: 14.4–56.8; $U = 13$, $z = -0.18$, $P = 0.85$; Figure 2A), even though Black Vultures flew substantially higher than Turkey Vultures overall (Black: 52.9 m AGL, 95% CI: 18.2–154.1; $U = 13$, $W = 3{,}409$; Turkey: 36.4 m AGL, 95% CI: 16.4–80.8; $P < 0.001$; Figure 2B). For comparison, when thermal soaring, Black Vultures flew at 62 m AGL (95% CI: 19.3–199.5) and Turkey Vultures flew at 44 m AGL (95% CI: 14.8–132.3).

Turkey Vultures engaged in contorted soaring during a greater proportion of time than Black Vultures (29% vs. 10%; $U = 13$, $z = -3.41$, $P < 0.001$). Correspondingly, Black Vultures used thermal soaring a greater proportion of time than Turkey Vultures (51% vs. 32%; $U = 13$, $z = 3.67$, $P < 0.001$; Figure 3).

Conditions Associated with Contorted and Thermal Soaring

Both species engaged in contorted soaring during similar weather conditions and over specific land-cover types (Table 2A). Turkey Vultures were less likely to engage in contorted soaring during clear conditions; they were more likely to engage in contorted soaring when temperature

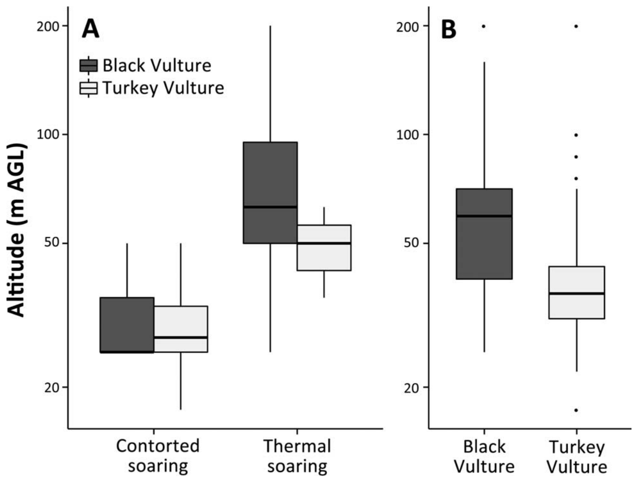

FIGURE 2. Altitude, in meters above ground level (m AGL), of vultures in flight in Virginia, USA, by (**A**) flight type and (**B**) species. (**A**) There was no difference in mean flight altitudes of species using contorted soaring ($P > 0.05$), but Black Vultures flew significantly higher than Turkey Vultures when using thermal soaring ($P = 0.04$). (**B**) On average, and across all flight types, Black Vultures flew higher than Turkey Vultures ($P < 0.001$).

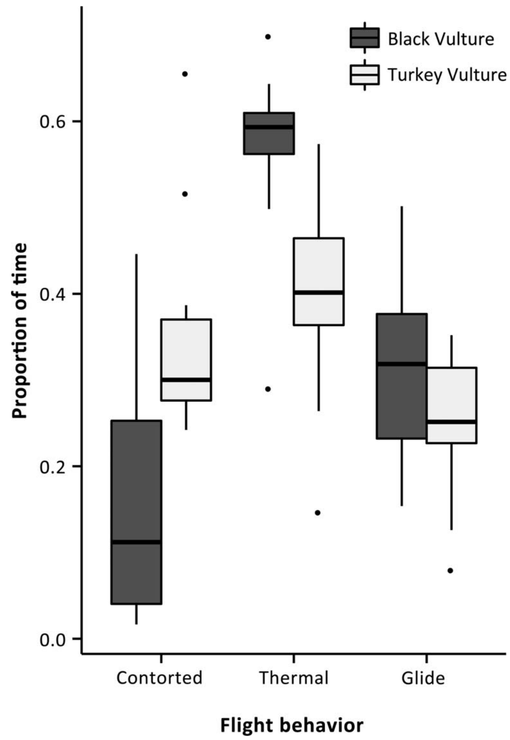

FIGURE 3. Observed proportion of time vultures spent using contorted soaring, thermal soaring, or gliding at 13 observation sites in Virginia, USA. Box plots show median, quartiles, and outliers.

was below average, when humidity and wind speed were above average, and during overcast or partly cloudy conditions. Turkey Vultures engaged in contorted soaring over riparian land cover more frequently than over road or field covers. Black Vultures were less likely to engage in contorted soaring during clear conditions; they were more likely to engage in contorted soaring when temperature was below average and during overcast or partly cloudy conditions. Use of contorted soaring by Black Vultures was not predicted by humidity or wind speed. Black Vultures engaged in contorted soaring over riparian and road cover more frequently than over fields.

Turkey and Black vultures engaged in thermal soaring under specific weather conditions that were different from those that occurred when they used contorted soaring (Table 2). Turkey Vultures were less likely to engage in thermal soaring when humidity was above average and during overcast conditions, and more likely to engage in thermal soaring when temperature and wind speed were above average and during partly cloudy or clear conditions. Turkey Vultures engaged in thermal soaring more often over riparian and road cover and less often over fields. Black Vultures were more likely to engage in thermal soaring during clear conditions and when temperature was above average, but were less likely to engage in thermal soaring when humidity was above average and during overcast or partly cloudy conditions. Use of thermal soaring by Black Vultures was not predicted by wind speed. Black Vultures engaged in thermal soaring more often over field cover than over riparian or road cover.

DISCUSSION

Despite previous work suggesting that cathartid vultures subsidize flight almost exclusively with thermal soaring (e.g., DeVault et al. 2005, Mandel et al. 2008) or with a combination of slope and thermal soaring (Pennycuick 1983, Bohrer et al. 2011), our results indicate that vultures also frequently use contorted soaring to subsidize flight. Observations of this flight behavior are not unprecedented (Pennycuick 1972, Kerlinger and Gauthreaux 1985, Houston 1988), but we know of no study that either proposes a mechanism for this behavior or distinguishes this flight type from other soaring types.

Atmospheric turbulence occurs at many spatial scales and is generated strongly near the ground (Stull 1988). In a region with flat terrain such as southeast Virginia, USA, the only subsidy that would support contorted soaring at low altitudes (Figure 2A) is small-scale, shear-induced turbulence. Horizontal air flow interrupted by a barrier such as a forest or tree line produces an area of uplift above and near the leading edge (Chatziefstratiou et al. 2014). In environments with limited topography where orographic updrafts are minimal or nonexistent, shear-induced turbulence provides an alternative source of atmospheric energy available to soaring birds.

TABLE 2. Soaring response variables evaluating hourly proportionate use of (A) contorted soaring and (B) thermal soaring of Turkey Vultures and Black Vultures across 13 sites in Virginia, USA. Weather and land cover were used to fit betabinomal mixed models. Cloud conditions were estimated in the field as clear, partly cloudy, or overcast in the field; and other weather data were collected from the nearest meteorological station (http://www.wunderground.com). Land cover was described at the site level as field, riparian, or road. Relative variable importance is indicated for each averaged model.

Species	Variable	Estimate	SE	*z*	*Pr*(>*z*)	Variable importance
(A) Contorted soaring						
Turkey	Intercept	−0.849	0.168	5.055	<4e-07	–
	Temperature	−0.029	0.010	2.894	0.004	0.82
	Humidity	0.014	0.005	2.699	0.007	0.62
	Wind speed	0.023	0.026	0.883	0.377	0.53
	Cloud: overcast	0.332	0.206	1.615	0.106	0.47
	Cloud: partly cloudy	0.294	0.182	1.612	0.107	0.47
	Land cover: riparian	0.314	0.162	1.934	0.053	0.12
	Land cover: road	0.148	0.239	0.620	0.535	0.12
Black	Intercept	−2.872	0.407	7.060	<2e-16	–
	Temperature	−0.024	0.020	1.193	0.233	0.35
	Land cover: riparian	1.539	0.558	2.760	0.006	1.00
	Land cover: road	1.464	0.479	3.053	0.002	1.00
	Cloud: overcast	0.359	0.332	1.082	0.279	0.30
	Cloud: partly cloudy	0.665	0.357	1.864	0.062	0.30
(B) Thermal soaring						
Turkey	Intercept	−0.903	0.112	8.027	<2e-16	–
	Temperature	0.019	0.009	2.013	0.044	0.79
	Humidity	−0.005	0.005	1.004	0.315	0.30
	Wind speed	0.046	0.024	1.898	0.058	0.30
	Cloud: overcast	−0.229	0.180	1.276	0.202	0.21
	Cloud: partly cloudy	0.114	0.160	0.710	0.478	0.21
	Land cover: riparian	0.300	0.169	1.776	0.044	0.49
	Land cover: road	0.125	0.222	0.563	0.976	0.49
Black	Intercept	−0.076	0.1925	0.391	0.696	–
	Temperature	0.033	0.016	2.071	0.038	0.68
	Humidity	−0.008	0.009	0.903	0.367	0.77
	Cloud: overcast	−0.517	0.348	1.487	0.137	0.23
	Cloud: partly cloudy	−0.206	0.304	0.676	0.499	0.23
	Land cover: riparian	−0.399	0.420	0.950	0.342	0.09
	Land cover: road	−0.354	0.283	1.247	0.212	0.09

Both of our study species increased their use of contorted soaring (Table 2A) when weather conditions were not optimal for thermal development (Table 2B). By using both types of soaring (i.e. thermal and contorted), vultures can presumably increase the amount of time they can spend on the wing. We suspect that contorted soaring occurs only in areas of predictable wind shear and turbulence. Furthermore, it is probable that contorted soaring, like slope soaring, is less time-efficient than thermal soaring (Duerr et al. 2012). Therefore, we do not expect birds to use contorted soaring for cross-country soaring or during migration. Instead of being used by birds that are time constrained, we anticipate that contorted soaring is primarily used by foraging birds that are energy constrained.

Turkey Vultures, in particular, may benefit from contorted soaring because they use olfaction to detect carrion (Bang 1960) in forested environments (Houston 1986). For this species, flying near tree height thus produces 2 benefits. First, small-scale, sheer-induced turbulence occurs at this altitude; second, because carrion is difficult to detect at high altitudes, being low should maximize the vulture's chances of detecting carrion olfactively (Smith and Paselk 1986). We suspect that using contorted soaring provides a third benefit in Turkey Vultures: By flying near tree height, individual Turkey Vultures minimize competition for resources by avoiding alerting Black Vultures to the presence of carrion. Black Vultures, which are not known to use olfaction to detect carrion (Bang 1964), rely heavily on local enhancement to find carrion and frequently usurp carcasses from Turkey Vultures (Stewart 1978).

The 2 species we observed are likely able to use contorted soaring because they are lightly wing loaded (Turkey Vulture: 40.6 N m^{-2}; Black Vulture: 57.6 N m^{-2}; Houston 1988). Low wing loading allows birds to fly more slowly without losing altitude. The Turkey Vulture's low wing loading is accompanied by other morphological features that enhance soaring flight. In particular, they have a long tail and hold their long, narrow wings in a dihedral. We suspect that the Turkey Vulture's dihedral wing structure is a "key innovation" (Bock 1965) that, paired with low wing loading, increases their agility in soaring flight (Pennycuick 1975) and enables them to remain buoyant close to the ground (Mueller 1972).

Understanding the proximate and ultimate reasons why Turkey and Black vultures use contorted soaring helps to interpret and predict flight behavior of other soaring species. Other lightly wing-loaded, obligate and nonobligate soaring species that forage on the wing or hold their wings in slight dihedrals are likely to use turbulent updrafts to subsidize their flight. For example, Lesser Yellow-headed Vulture (*Cathartes burrovianus*; Houston 1988), Greater Yellow-headed Vulture (*C. melambrotus*; Houston 1988), Egyptian Vulture (*Neophron percnopterus*), Black Kite (*Milvus migrans*; Pennycuick 1972), Bateleur (*Terathopius ecaudatus*; Pennycuick 1972), and Zone-tailed Hawk (*Buteo albonotatus*; Mueller 1972) all fly in a slight dihedral, and all engage in low-altitude, tortuous flight patterns consistent with the contorted soaring we describe here. Recent advancements in animal tracking technology (Williams et al. 2015) may provide further insight into how birds use contorted soaring or other undiscovered types of subsidy in flight.

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Ethics statement: No handling of vultures was necessary for this work; thus, no animal care protocols were required.

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