The Condor 87:350–355

SPREAD-WINGED POSTURE OF TURKEY VULTURES: SINGLE OR MULTIPLE FUNCTION?

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ABSTRACT.—The behavior and spread-winged postures of Turkey Vultures (*Cathartes aura*) were examined at a communal roost near Superior, Arizona, from April–June, 1979. The temporal occurrence of wing-spreading during the morning pre-departure period was positively correlated with the intensity of the sun's rays, but was independent of the ambient low overnight temperature. Wing-spreading was more common when vultures were wet than when they were dry. Turkey Vultures appear to spread their wings for at least two reasons: (1) to dry feathers, and (2) to ameliorate the thermal gradient between themselves and their environment, although the two functions are not mutually exclusive. Spreading the wings to realign feathers or to increase the mobility of ectoparasites seems unlikely.

Nocturnal body temperature (T_b) of captive Turkey Vultures (*Cathartes aura*) varies by as much as 4°C (Heath 1962), and from 0.4 to 2.6°C (Hatch 1970), below normothermic levels (39°C) for periods of many days. Diurnal fluctuations in T_b are apparently unrelated to food consumption, night-time low temperature, size or weight of the bird, age, or photoperiod (Hatch 1970). Because these vultures exhibit shallow regulated hypothermia, it has been proposed that their wing-spreading postures are energy-conserving behaviors; the birds may warm themselves or modify their thermal gradients by absorbing solar radiation (Heath 1962, Curry-Lindahl 1970, Ohmart and Lasiewski 1971, Kushlan 1973). Owing to their dark coloration, vultures would be expected to absorb much solar radiation (Hamilton and Heppner 1967, Lustick 1969, Marder 1973) at low wind speeds (Walsberg et al. 1978), even without spreading their wings. By adopting this posture, however, they may absorb much more sunlight, as suggested from the work of Lustick et al. (1980) with Herring Gulls (*Larus argentatus*).

In Little Cormorants (*Phalacrocorax niger*), spreading the wings dries them efficiently; the wetter the bird, the longer it spreads its wings after swimming (Winkler 1983). Anhingas (*Anhinga anhinga*) also dry quickly when spreading their wings (Hennemann 1982, 1983). Their wings are often spread even when dry, enabling the birds to increase rates of heat gain by enhancing absorption of sunlight. Anhingas spread their wings most frequently when solar radiation is intense and when ambient temperatures are low (Hennemann 1982).

Much is known about the wing-spreading behavior of aquatic birds, but the reasons why vultures spread their wings are far less certain (e.g., Clark 1969, Mueller 1972, Grier 1975). We therefore examined the behavior of Turkey Vultures in order to determine the significance of wing-spreading. We asked the following: (1) is wing-spreading independent of overnight low ambient temperature, or is wing-spreading by free-living vultures more frequent during cold weather, as shown for Anhingas? (2) is wing-spreading more common following rain than following dry conditions, owing to the heat-draining effects of wet plumage (Kennedy 1970, Mahoney 1984)? and, (3) is the occurrence of wing-spreading during the morning related to the intensity of solar radiation? Answers to these questions would allow us to address other hypotheses advanced to explain the occurrence of wing-spreading by various birds (e.g., Kennedy 1969, Mueller 1972, Houston 1980).

METHODS

Observations reported here were recorded at the Boyce Thompson Southwestern Arboretum, Superior, Arizona, from 7 April to 24 June 1979. Vultures perched in one to three *Eucalyptus* spp. trees overnight and then glided to two cliffs from the trees at dawn. At sunrise, sunlight shone directly on the vultures perched on these cliffs. The roost had been active from about 7 March to 7 October for at least 14 years (C. Crosswhite, pers. comm.).

We systematically sampled the vultures' behavior after nocturnal roosting on 18 mornings. The period which began 30 min before sunrise and ended about 10 min after the first flock of vultures flew was designated the "post-roost period." We chose that period because: (1) it represented the time when the behavior of most vultures could be accurately deter-

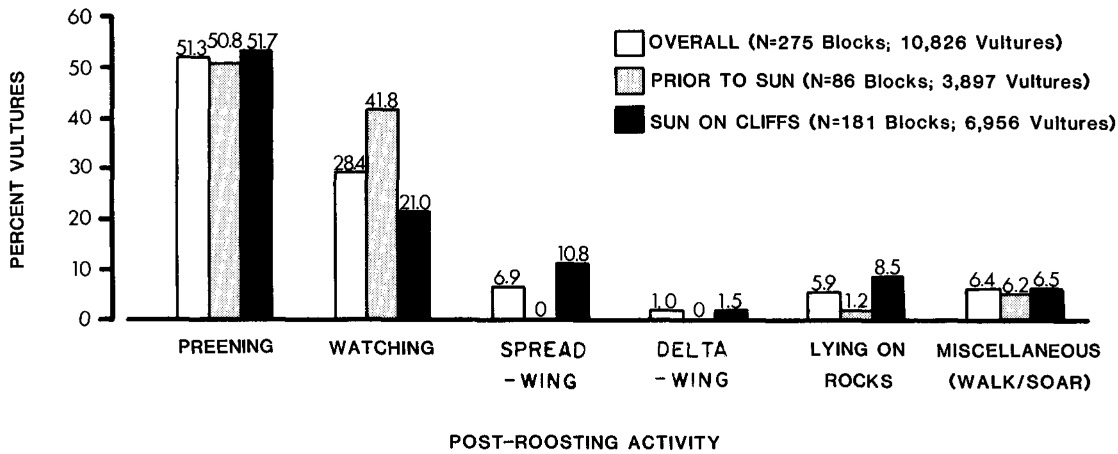

FIGURE 1. Distribution of Turkey Vulture behaviors during the morning post-roosting period, overall, before, and after, sun's rays strike post-roosting sites on cliffs. Percentage of all vultures seen based on group scans.

mined; (2) vultures tended to leave the roost synchronously; and, (3) we sought to determine the incidence of wing-spreading relative to sunrise.

We watched the vultures (with the aid of a spotting scope and binoculars) from two locations: a burlap blind placed on a prominent rock outcrop < 100 m from most vultures, and from a road about 300 m from the cliffs. Using a group scan, we recorded the instantaneous behavior of each vulture at 10-min intervals during the post-roosting period (Altman 1974). Behaviors were categorized as follows: *Preening*—preening with only brief (<5 sec) interruptions; *Watching*—loafing, looking about, not performing any other activity described here; *Spread-winged posture*—with wings and tail feathers fully spread, and the head clearly visible (Kushlan 1973). The dorsum was *always* oriented perpendicular to and facing towards the sun's rays. Vultures appeared to be alert, although they did occasionally close their eyes. The posture was held for up to 19 min, but it was usually not held that long (details below); *Delta-winged posture* (Kahl 1971)—was similar to the spread-winged posture, but wing tips dropped and the vulture usually preened. It often followed in sequence from the spread-winged posture, so that the dorsum was oriented (but not always) in the same manner as the spread-winged posture; *Lying down*—on the rocks (cliffs), either parallel or perpendicular to the sun's rays; and, *Miscellaneous*—which included primarily flapping while on the ground, and walking, but also brief flights. Using the frequency of occurrence of these behaviors, we calculated the proportions of vultures in various postures every 10 min, every morning (18) and for the entire study.

Temperature (°C) and rainfall were measured at about 1 m above ground within 100 m of the roost trees, using a max/min thermometer (in a Stevenson screen) and a standard rain gauge. During observation periods, cloud cover was estimated on a scale of 0 to 10 (10 being 100% cloud cover). The time when the sun's rays struck the cliffs was recorded, as were the periods during which clouds obscured the sun. The number of individuals using the roost was estimated by counting the vultures as they left the roost area.

To determine if the vultures spread their wings more frequently as ambient temperatures fell, we examined the relationship between overnight low temperature and the frequency of the spread-winged posture. When we investigated the relationships between wing-spreading and either the overnight low temperature or the intensity of solar radiation, we used only data from clear mornings following rainless nights. This precluded possible confounding effects due to wetting or cloud cover.

Statistical tests employed are described by Zar (1974). The probability level chosen for significance was 0.05.

RESULTS

Roost size varied seasonally from an estimated spring (late March, early April) maximum of ca. 90 vultures to a minimum of ca. 45 in early May, then gradually increased to a pre-migration peak of ca. 150 in late August. At first light, usually <20 min before sunrise, vultures left the roost tree(s) and soared <100 m to perch sites on the two cliffs. Some vultures remained in the trees until sunrise; others occasionally stayed in the trees during the entire post-roosting period as long as the perch was exposed to direct sunlight.

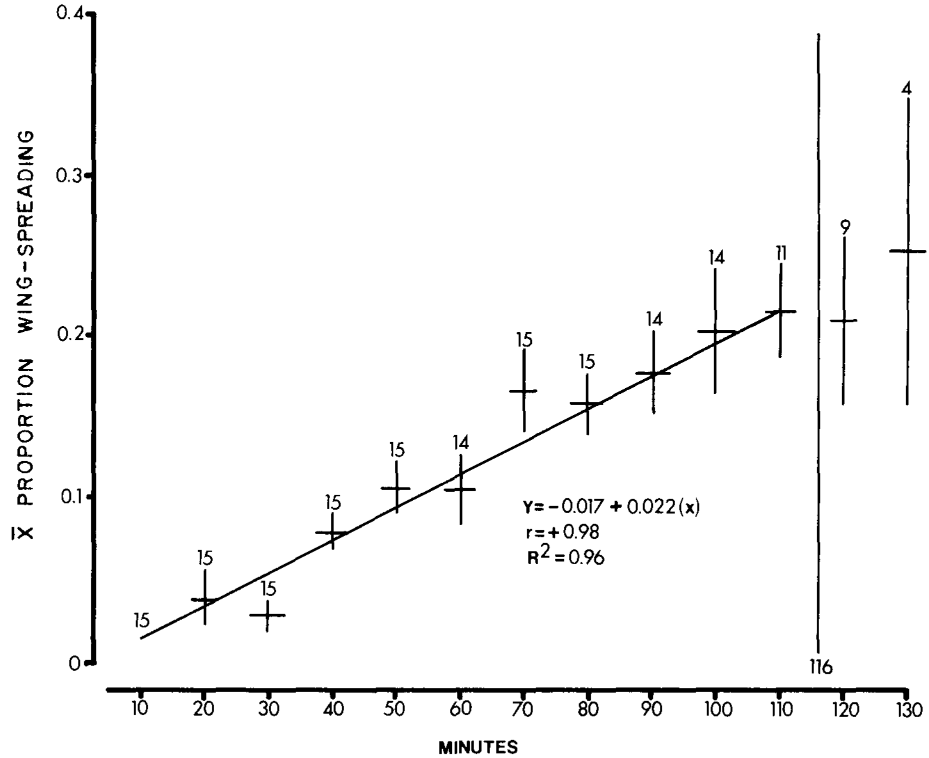

FIGURE 2. The relationship between the mean proportion of Turkey Vultures in the spread-winged posture after the sun's rays struck post-roosting sites on cliffs. On average, vultures departed 116 min (SD = 20 min, range = 80–160 min) after the sun's rays struck the cliffs. The simple linear regression was calculated using the 11 means prior to 116 min (see text). Horizontal bars are means, vertical bars are one SE; the numbers above vertical bars are sample sizes.

Vultures spent most of their time preening and watching (Fig. 1). Spread-winged posturing was more common than lying down on the rocks, which, in turn, was more common than delta-winged posturing. We observed birds in the spread-winged posture only when the sun was shining directly on them. The proportion of vultures lying on rocks increased when the sun's rays struck the cliffs, whereas the proportion watching or performing miscellaneous activities declined. The proportion of vultures preening before and after the sunlight struck them did not change ($\bar{x}^2 = 0.01$, 1 df, $P > 0.05$).

The mean proportion of vultures in spread-winged posture was significantly positively correlated ($r_s = +0.97$, $n = 11$, $P < 0.01$, Spearman rank correlation) with the number of minutes after the sun's rays struck post-roosting sites (Fig. 2). Fewer than 8% of the vultures spread their wings for the first 40 min, probably because the intensity of the first sunlight (05:00–06:30) was weak. The proportion increased to about 22% just before the mean departure time, about 76 min later (Fig. 2). Even with the data points for 120 and 130 min included, the rank correlation remained highly significant ($r_s = +0.98$, $n = 13$, $P < 0.01$), as did the simple linear regression ($r = +0.98$, $n = 13$, $P < 0.01$).

Based on the time-activity data (Fig. 1), and from 76 to 116 min between the start of potential basking conditions and departure from the cliffs, vultures spent from 8 to 12.5 min with their wings spread and from 1 to 2 min in delta-winged posture. On two mornings without sun, no vultures spread their wings or lay on rocks, and on one of these mornings having 100% cloud cover and following overnight rain, all vultures departed directly from the roost trees about 30 min after sunrise. On two other mornings when clouds intermittently obscured the sun, vultures stood with wings spread only during sunny periods.

The observed times of 9–14.5 min devoted to the spread-winged and delta-winged postures are much less than most values derived from theoretical and observed warming rates within the reported range of hypothermia in Turkey Vultures (Table 1), assuming an ambient temperature (T_a) of 20–25°C with very light wind and in the absence of solar radiation.

Minimum low temperatures averaged 9°C and ranged from 3.9 to 12.9°C during the study. These temperatures were well below the lower critical temperature (T_{lc}) calculated for captive

TABLE 1. Times for which Turkey Vultures could warm to normothermia in the absence of solar radiation at different levels of hypothermia, assuming T_a between 20–25°C with negligible wind.

Hypothermia	Warming rates	
	0.095°C/min[a]	0.050°C/min[b]
1.0°C	10	20
2.5°C	26	50
4.0°C	42	80

[a] Theoretical warming rate from Heinrich and Bartholomew (1971): °C/min = 2.03 $m^{-0.40}$, where m = body mass in grams (2,100 g).
[b] Observed warming rate for a 2,200 g Turkey Vulture, reported by Heath (1962).

TABLE 2. The effect of overnight rainfall and T_a on the proportion of Turkey Vultures in spread-winged postures. Observations were recorded between 130 and 160 min after sunlight struck post-roosting sites.

Date	Number of minutes[a]	$\bar{x}$ proportion wing-spreading	Overnight	
			Rainfall (mm)	Low temperature (°C)
23 April	130, 140	0.24 (6–28)[c]	0	10
21 May[b]	140, 150	0.56 (27–28)	TR[d]	11.7
10 May	140, 150, 160	0.52 (13–16)	4.1	3.9
24 May[b]	140, 150	0.36 (12–21)	3.8	18.9

[a] Number of minutes after sunrise.
[b] Clouds obscured the sun's rays so that only these two scans had wing-spreading vultures on these mornings.
[c] Range in number of vultures recorded during scans.
[d] Vultures were wet because trace rainfall was accompanied by heavy condensation this night and early morning.

Black Vultures (*Coragyps atratus*) by LaRochelle et al. (1982). Consequently, if a relationship existed, one would expect it under these conditions. The proportion of vultures with wings did not increase, however, as overnight low temperature decreased ($r_s = -0.25$, $n = 14$, $P > 0.05$, Spearman rank correlation).

On the morning of 20 May, following overnight rain (26 mm), 22 vultures (73% of birds still present) spread their wings simultaneously at 08:20, despite 100% thin cloud cover. They all folded their wings abruptly, however, when heavy clouds obscured the sun's rays several minutes later.

The proportion of vultures spreading (spread- and delta-winged postures) their wings following overnight rain (3.5 mm and heavy condensation) on 6 June ($\bar{x} = 0.16$, SD = 0.09, $n = 9$) was greater ($z = -1.79$, $T = 9$, $n = 9$, $P < 0.04$, one-tailed Wilcoxon matched-pairs test) than that of 23 June ($\bar{x} = 0.11$, SD = 0.07, $n = 9$) when there was no rain or condensation. We matched these two mornings for similarity in overnight low temperature (6 June = 15.7°C, 23 June = 16.1°C), and conducted the Wilcoxon test on proportions commencing 40 min after sun's rays struck post-roost sites (i.e., when spread-wing posture was first observed on both mornings). Information from two additional pairs of mornings that varied in overnight low temperatures and rainfall showed further increases in the proportion of wing-spreading when vultures were wet (Table 2). Considerably more vultures spread their wings when wet (21 May) than when dry (23 April). On 10 and 24 May, when birds were wet, the proportions of vultures in the spread-winged posture were generally much larger than average values computed from mornings following dry nights, shown in Figure 2 (e.g., 120, 130 min). On the morning of 10 May, substantially more vultures were spreading their wings during similar time periods than on 24 May, when the overnight low was 15°C warmer, but rainfall was virtually the same.

DISCUSSION

The spread-winged posture of the Turkey Vulture has been reported from Arizona (this study), Florida (Kushlan 1973), New Jersey (E. Henckel, pers. comm.), Ontario (F. Phelan, pers. comm.), and elsewhere (Clark 1969). If these birds spread their wings to increase heat gain and extend their thermoneutral zone, or combine shallow regulated hypothermia with absorption of solar radiation to increase deep T_b (Ohmart and Lasiewski 1971, Hennemann 1982, 1983), then most regions of North America offer conditions conducive to wing-spreading. Abiotic factors that promote this behavior certainly include nocturnal temperatures usually well below normothermy (ca. 39°C), and even below T_{lc}s of ca. 25°C (LaRochelle et al. 1982, for a Black Vulture averaging 2.1 kg), as well as rain. For example, in the hot Sonoran Desert, minimum temperatures during May, June, July, and August, 1979, fell to an average of 12.5, 19.0, 21.8, and 20.3°C, respectively, and measurable rain fell on 19 of 123 (15%) days. Thus, the potential for nocturnal hypothermia, and the consequent need for drying feathers, are evident even in a desert environment.

Turkey Vultures probably do not spread their wings at first sunlight because temperatures are low and solar radiation is relatively weak. Since the surface area available for heat exchange increases when vultures spread their wings, heat loss likely exceeds heat gain from insolation absorption at first sunlight on cool mornings (Grier 1975). Vultures can therefore gain heat most efficiently by spreading their wings when the temperature moderates and when solar radiation intensifies (Fig. 2).

Our study suggests that Turkey Vultures spread their wings to dry and to warm themselves, but we do not know that they actually elevate their deep T_b by using solar radiation.

Indeed, drying and warming probably occur concurrently when vultures are wet. The lack of correlation, in our study, between nocturnal low temperature and the number of wing-spreading vultures concurs with Hatch's (1970) experimental study in which the pattern of heterothermy was not affected by changes in ambient temperature or food. Since nocturnal hypothermia appears to be unrelated to overnight low temperature, perhaps the vultures have to re-warm to the same degree each morning. We suggest that any adaptation that conserves energy and promotes survival is important, especially where food supplies are temporally and spatially variable. For example, hypothermic Greater Roadrunners (*Geococcyx californianus*) are able to absorb solar radiation, an ability which helps them conserve considerable energy (Ohmart and Lasiewski 1971). Some investigators have inferred that vultures and other (desert-dwelling) scavengers encounter highly variable food supplies (e.g., Heath 1962, Ohmart and Lasiewski 1971, LaRochelle et al. 1982); perhaps the most efficient method of energy conservation by vultures is for them to become hypothermic every night. Reducing nocturnal T_b would result in substantial energy savings to vultures, as suggested from the work of Chaplin et al. (1984) with Red-tailed Hawks (*Buteo jamaicensis*). Hatch (1970) reported Turkey Vultures remaining at their roost for two days during inclement weather. In our study, vultures were forced to remain at the roost at least one day during a rain storm in March.

The increase in the proportion of vultures seen lying on rocks during sunny periods suggests that this behavior may have thermoregulatory significance. Furthermore, on mornings with 100% cloud cover we rarely saw this posture. Further research must examine the thermal characteristics of this (passive basking?) behavior to determine whether vultures absorb heat from sun-baked rocks.

The spread-winged posture was also noted during >14 evenings of random observation (many vultures also sought shade). Theoretical (Calder and King 1974) and experimental (LaRochelle et al. 1982) work has shown that hyperthermy (i.e., heat storage) can help conserve metabolic water. Furthermore, mild hyperthermia in the evening may decrease the extent of nocturnal hypothermia, thereby reducing the amount of warming needed the following morning. Because of their soaring flight, vultures may not be subject to much heat loading (Marder 1973) and, in fact, heat may be dissipated if the thermal gradient between vultures and their environment is reversed when flying (Walsberg et al. 1978).

Restoration of feather shape (Houston 1980) may also be an attribute of wing-spreading, but not during the post-roosting period. Whereas Houston proposed that sunning serves to straighten primaries in large soaring birds, this notion does not account for our results since, assuming that the phenomenon is applicable to Turkey Vultures, feathers would realign within a few hours (i.e., overnight). Furthermore, the morning "sunning" behaviors that we observed were never associated with soaring.

We cannot directly test the hypothesis that vultures warm their feathers to increase the mobility of parasites and make subsequent removal easier (Kennedy 1969, Mueller 1972). Our time-activity data show, however, that preening did not increase after the sun's rays struck post-roosting sites and vultures began wing-spreading. Preening was no more common before than after this time.

The morning wing-spreading of Turkey Vultures appears to serve at least two functions which have rather clear adaptive values. By maximizing heat gain in the morning in a passive rather than an active manner, hypothermic vultures may conserve energy. Also, drying of feathers serves to reduce heat loss (Hennemann 1982, 1983, 1984; Mahoney 1984) and possibly results in more efficient flight capability.

ACKNOWLEDGMENTS

We are grateful to B. Hennemann, R. MacMillan, W. Spofford, and especially S. Mahoney for their constructive reviews of early versions of this manuscript. We also thank C. Crosswhite, R. McKitrick, and other staff members of the Boyce Thompson Southwestern Arboretum for their generous hospitality and cooperation. H. Greenwood, D. Bird, J. Durham, and S. Cook criticized earlier drafts of the paper. We thank T. Clark for his help with field work, B. Thompson and S. Tomkiewicz for their helpful discussion, and E. Henckel and F. Phelan for their observations of the spread-winged posture. C. Zisner kindly typed drafts of the manuscript, and S. Lewis provided the illustrations. This study was funded by a Macdonald-Stewart Post-graduate Fellowship (McGill University) and a Department of Education pre-doctoral scholarship (Quebec) to R. Clark.

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