ARTICLES

King Vultures (Sarcoramphus papa) follow jaguar in the Serranía de la Cerbatana, Venezuela

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Summary

I collected data over six field seasons (34 ½ wks) between 1994-2000 at Hato Las Nieves in northwestern Bolívar state, Venezuela. A mean of 6.4 King Vultures (Sarcoramphus papa) \pm 4.9 SD (range = 2-15) searched in flight for jaguar (Panthera onca) or remains of kills and were present at or seen going directly to kills. Jaguarrelated activities took place on 27 of the 162 days on which the vultures were not feeding on livestock carcasses. On 16 days only vultures presumed to be local to the area (n = 2-4 adults, 1 young) were involved. The presence of a jaguar was confirmed by tracks and/or known kills on livestock. Vulture behaviours were correlated with dates and locations of tracks and kills as well as with direction of travel of tracks. After sighting a jaguar, King Vultures perched to monitor the feline, or showed prolonged circling overhead, and then focused searching to specific areas, indicating they knew the routes it used and the areas most likely to have kills. Searching often alternated, from one day to the next or from morning to afternoon, with monitoring the ranch refuse dump, feeding on remains of former carcasses or foraging in palm stands. King Vultures also monitored large terrestrial mammals that were potential big-cat prey, especially white-tailed deer (Odocoileus virginianus), often when a jaguar was or had been present. A small number (n = 1-8) of American Black Vultures (Coragyps atratus) and/or Turkey Vultures (Cathartes aura ruficollis), the only other Cathartidae in the area, joined the King Vultures in searching on only 9 days and did not go into the mountains with them. Searching for jaguar and/or kills along the presumed travel routes of the feline was mainly a King Vulture activity, but the smaller vulture species were present (n = 26 and 10 birds, respectively) at kills within the valley. Few published data are available on the use of big-cat kills by vultures in the Neotropics, and further study is needed on the proportion of such kills, notably those of jaguar, in the food supply of King Vultures.

Introduction

Vultures in many areas of the Neotropics likely obtain part of their food from big-cat kills, especially those of jaguar (Panthera onca) which often abandon prey without feeding or leave substantial remains of large items without attempting to cache them (Schaller & Vasconcelos 1978. Schaller & Crawshaw 1980). Published data on the use of kills by Neotropical vultures, however, are scarce. I found accounts on American Black Vultures (Coragyps atratus) following jaguars to use the remains of kills in Venezuela (Humboldt & Bonpland 1820) and in Argentina (Gallardo 1987); Greater Yellow-headed Vultures (Cathartes melambrotus) were seen at the remains of a big-cat kill in closed rainforest in the Brazilian Amazon (Hero et al. 1992) and Andean Condors (Vultur gryphus) have been reported to gather at daytime puma (Puma concolor) kills in the Andes (Bank & Franklin 1998). Here, I report on a foraging association I observed between King Vultures (Sarcoramphus papa) and jaguar in the northwest uplands of the Venezuelan Guayana.

Study area and methods

My observations were part of a long-term study conducted over six field seasons (34 ½ wks) between 1994 and 2000 at Hato Las Nieves (6°34'80"N, 66°12'17"W), a ranch set up in 1976 in the southeast section of the Serranía de la Cerbatana.

Estado Bolívar, Venezuela. The valley, ca. 20 km long (northwest-southeast) and 9-10 km wide, is dominated by lowland shrub and tree savanna (Figure 1) having chaparrales of Curatella americana (Dilleniaceae), Mauritia flexuosa palm stands (morichales) and numerous watercourses lined by narrow bands of gallery forest. The central part, modified for ranching, is mainly 220-260 m elevation with high points up to 297-310 m; bordering mountains reach 1600 m (west) and 1880 m (north). Most observations took place early June to mid-August during the rainy season, which usually lasts from April through October or November.

Apart from monitoring vulture activity at livestock carcasses (74 days), using 10 x 50 binoculars I made daily observations from outcrops and other high points from 06h15 - 19h00. The length of observation bouts (up to five consecutive hours) and number of bouts per day varied depending on weather and logistics. I investigated vulture activity whenever possible and explored the valley on foot when the King Vultures were absent. Identification of felid tracks was based on Emmons & Feer (1990). Time of passage was estimated from dryness of tracks, especially in relation to mine, and number of hours from last rains. The large tracks (n = 9 occurrences)corresponded to jaguar - the only big cat known to hunt at Las Nieves (Y.

Carbonell & A. Mendoza pers. comm.). Here, the term "follow jaguar" includes searching in flight for the feline or remains of kills, perching to monitor the cat or circling overhead as well as direct flight to or feeding at a kill.



Figure 1. Valley of Las Nieves in the Serranía de la Cerbatana, Estado Bolívar, Venezuela. View to south-southwest (December 1999). The mountains in the background form the watershed divide for the extreme south-southwest reaches of the Caño Las Nieves basin, the northwest reaches of the Río La Plata basin south of Las Nieves and the Caño Las Siete Lomas basin to the west. (Photo: Marsha A. Schlee).

Results

Known or presumed jaguar-related activities took place on 27 of the 162 days on which the vultures were not feeding on livestock carcasses or inedible parts of slaughtered animals. No carcasses of native fauna, other than the presumed jaguar kills cited below, were known to have been consumed by King Vultures during my study periods. A mean of 6.4 King Vultures (± SD 4.9, range: 2-15,

including three young) were involved in following jaguar, but on 16 days only the presumed local birds (n=2-4 adults, four times with an immature) were present. The non-local vultures were already following the feline from another part of its range when it came to Las Nieves (LN). The highest number of King Vultures was recorded in 1996 when carrion was abundant (26 of 48 days), which may have induced the vultures to

remain close to LN; the lowest, in 1999-2000 when carrion was scarce (7 days) and the King Vultures were absent 26 of 47 days, presumably feeding (16 days) at Hato Los Espejos (HLE), a ranch located ca. 8 km east of the southeast boundary of LN, and at an indigenous community much farther to the south (A. Mendoza pers. comm.). At LN most livestock had been removed by May 1997. A small number of American Black Vultures (n = 2-7) and/or Turkey Vultures (Cathartes aura ruficollis: n = 1-8), the only other cathartids in the area, joined the King Vultures in searching on 9 days but did not go with them into the mountains. As many as 26 Black and 10 Turkey Vultures were present at kills. Searching for jaguar or remains of kills was often interspersed with monitoring the ranch refuse dump, picking over remains of former carcasses or foraging in palm stands (Schlee 2005), the activity changing from morning to afternoon or from one day to the next. Some King Vultures also monitored (n = 18 occurrences) large terrestrial mammals that were potential big-cat prey, mainly white-tailed deer (Odocoileus virginianus; n = 16 of 18: based on sightings, tracks and/or excrement).

1994 field season

A jaguar may have been responsible for the death of a pig before dawn on 13 July, but not enough remained of the carcass to verify predation. During this study period I found no evidence of a big cat being present in the valley and observed no King Vultures carrying out the behaviours seen in other periods when a jaguar was known to have been present.

1995 field season

On 18 July a jaguar killed a cow at HLE while I was monitoring a carcass at LN (16-21 July). From 27 July through 1 August the King Vultures (n = 1-5)started soaring very high, presumably looking for carrion elsewhere, sometimes being seen near midday southeast or south of LN, over areas without livestock, and twice returning in late afternoon to forage in the valley. On 2 August at 10h45, one adult ascended in the northwest and went directly to the southeast boundary where it spent over 30 min foraging while another, with three Black Vultures, was far to the south-southwest. The latter foursome worked their way to the southwest slopes near Caño Agua Fria (CAF) and at 11h55 were joined by the first and two more with an immature that had spent the morning perched along the central section of Caño Las Nieves (CLN) near the refuse dump; only the King Vultures continued northward over the higher slopes, going into the mountains at 12h30 toward the Río Túriba (RT) watershed northwest of LN. At ca. 17h00 I saw the presumed same five circling south

of CLN near the southeast boundary. Since the vultures did not return the next morning, I explored the savannas in south-central LN. The presence of a jaguar was confirmed at 11h40 when I found fresh tracks near a creek, ca. 7 km from the presumed kill, and heading toward a wooded area over which two Turkey Vultures were carrying out low inspective flight. That afternoon at 16h40, Black and Turkey Vultures (n = 12 and 8, respectively) were seen circling intensively over a rocky, somewhat wooded area with remnant morichales to the east of central CLN. (This area was ca. 4 km north of the jaguar tracks.) Afterwards the vultures returned to the southeast zone. At 09h30 on 4 August the vultures started ascending from the presumed kill; 45 min later all three species suddenly glided across LN from the southeast and went down in the northwest where two King Vultures were circling. (I did not have access to either area.) The vultures were absent all day. I believe the King Vultures might have witnessed another kill, prolonged circling overhead not having been observed when they discovered dead or dying livestock. After an interlude of monitoring monkeys (Cebus olivaceus: Schlee 2005), the King Vultures (n =2-4) resumed searching, briefly visiting the southeast zone and then focusing on the north-central foothills and west to the RT drainage.

1996 field season

A jaguar killed two calves at an interval of 23 days, the first on 2 June at the edge of a morichal in the northeast while I was monitoring activity at a carcass (30 May - 4 June) in western LN. At 10h00 on 7 June a lone adult King Vulture soared from the calf site and worked its way south in low foraging flight to the CLN-CAF confluence and on toward the southwest ridges where it was joined by three others (11h52). The foursome spent three hours much farther south, returned to the southwest slopes and finally worked their way east over the savannas (15h29). The next day they foraged in a morichal (Schlee 2005), but on 9 June two adults searched the entire eastern sector of the valley south of the kill site (07h55 - 09h09) and one also checked the far northwest, their behaviours suggesting that the feline might still have been in the valley. On 10 June one adult King Vulture was again in the far south-southwest and at 10h52 was joined by seven more over the Caño Las Siete Lomas (CLSL) watershed divide farther west. Four went south to the Río La Plata drainage and were joined by three more, all finally going west and lost from sight over the CLSL basin (12h15). The next three mornings King Vultures (n = 2-5) monitored whitetailed deer in the northeast and spent \leq 90 min searching the area before going high and out of sight. On 14 June the

King Vultures (n = 9) soared at 08h02and disappeared very high, being seen again at 11h47 with five more as well as Black Vultures (n = 22) and Turkey Vultures (n = 10) circling south of CLN near the southeast boundary. Most of the vultures returned in mid-afternoon and several went through rubbish at the camp refuse dump. They roosted in that area and went southeast the next morning at 09h22, returning again only in early morning on 16 June and dispersing at 10h40. The behaviours and movements of the vultures suggest they had witnessed a kill and when the predator had finished feeding, returned to eat the remains

The next episode started on 23 June, the day after a carcass was finished and the King Vultures (n = 21) had left the valley. From 09h41 - 11h56, four adults were seen in low searching flight over the gallery forests in various parts of central LN. When they reached the north-central foothills, north of Caño La Danta (CLD), six more ascended ca. 4 km farther west and all went west to the RT basin. The next day at 11h55, the King Vultures (n = 6) that had roosted near north-central CLD started moving eastward from tree to tree as if following something north of the stream while eight Turkey Vultures circled intensively over the same area. The King Vultures soared at 12h07 and were joined by eight more ascending ca. 2.5 km farther west. All soared high, along with Black and Turkey Vultures, and split up; some remained in view over the valley. At 12h47 the presumed same birds were again cruising low over the initial area. At 13h25, more than 25 vultures suddenly circled over an area farther south and landed. From 14h39, King Vultures with full or partially filled crops (n = 7) started showing up along CLD south of the second site. Presumably a kill had been made and the King Vultures had been following the predator from the RT drainage. The presence of a jaguar was confirmed the next day (25 June) when 47 vultures (n = 12 King) were sighted (06h55) at the edge of a morichal near the fresh remains of a calf ca. 3.5 km south of the presumed kill the day before. I found jaguar tracks coming from the north, heading toward a fence, which the feline jumped, and then toward the calf. Torrential rains washed out the tracks in mid-afternoon, and I was not able to determine the feline's direction of travel. The next morning from 09h37-13h15, King Vultures (n = 11) perched in the gallery forest along north-central CLD and ca. 0.5 km to the south along CLN, apparently monitoring a female white-tailed deer that was running and browsing on the range between the streams.

1997 field season

Four foraging episodes, in which tracks confirmed the presence of a jaguar, were observed.

(1) On 7 July, the day after finishing a cow carcass, four of the 15 King Vultures that had gathered at the site in early morning remained in the valley (09h53) and searched the southsouthwest lowlands, slopes and ridges from 10h40-16h00, finally disappearing over the CLSL drainage farther west. Two searched the same area the next morning but later picked over remains at the previous carrion site. On 9 July, from 07h19 until soaring at 09h52, eight King Vultures congregated near the CLN-CAF confluence (south-central LN) and appeared to be monitoring the ranges to the south and/or east. Suddenly at 11h13 some 24 vultures (n = 14 King) circled intensively over the far south-southwest lowlands, while another King Vulture searched more to the east, until 11h40. Six of the King Vulture group continued northward over the western slopes and at 12h30 went into the mountains toward the RT watershed. The others disappeared southwest over the CLSL basin while the smaller species dispersed in the valley. I suspected a jaguar had been sighted.

The next two mornings (10-11 July) the King Vultures (n = 2-5) monitored three white-tailed deer, and once, a giant anteater (Myrmecophaga tridactyla), in the northeast. On 12 July three King Vultures appeared at the top of a tree on the western range near CAF at 07h35 and 20 min later, two more in the gallery forest farther south. All were still perched

at 09h35 when I started crossing the range to investigate. Two were cruising over the area at 10h50 when I located the first tree. Numerous jaguar tracks were underneath, some headed toward the second tree and more were near the gallery forest. I found no prey remains, but jaguars often completely consume small items (Rabinowitz & Nottingham 1986). At 12h11 one King Vulture was still searching the southwest piedmont near CAF while the others were much farther south, all disappearing over the CLSL basin at 13h30. The next day the King Vultures (n = 7) split up to search the entire valley; three were still over the southwest section at 13h08 but were lost from sight over CLSL (13h20).

(2) Over the next 7 days (14-20 July) King Vultures were rarely present, but on the mornings of 17, 19 and 20 July, four to six gathered on the eastern range in the vicinity of an old carrion site, once monitoring a large boxer dog that was on visit to LN and running loose. Upon soaring, all went south to the Rio La Plata drainage, and on 20 July one adult was seen later to the south-southwest. being lost from sight over CLSL at 12h54. On 21 July the King Vultures (n = 9) ascended at 10h07 in southern LN and went west, their behaviour being reminiscent of that observed in the northwest the year before. Later, three foraged over the southwest slopes and ridges (10h49-11h55), one going high over southern LN and finally to the far

northwest. Black (n = 15) and Turkey Vultures (n = 10) soared from along central CLN at ca. 11h00. Neither joined the King Vultures, but the Black Vultures spent considerably time cruising over an area on the east side of the stream. That evening at dusk I found fresh jaguar tracks near the eastern bend of CLD north of the central camp. The tracks were ca. 9 km from the southern site, came from the east side of CLN and were ca. 1.5 km north of the area over which the Black Vultures had been circling earlier. The tracks headed into the CLD gallery forest, from where the feline could go west by following CLD and its tributaries for over 6 km and on toward the RT basin. The next day at 10h22, three King Vultures, after soaring, suddenly perched near the tracks. I went to investigate and found fresh tracks of red-brocket deer (Mazama americana), and one was killed near there by a jaguar three months later. On 23 July only one King Vulture was in the valley. At 09h45 another soared in and circled several times over the first without trying to land. The first immediately took off to join it, making a wild zigzag ascent against the winds, and both glided out westnorthwest. Just then another soared in and, while craning its neck down, circled low over the same area, presumably also looking for its partner. Not finding it, this one went southwest, where the vultures had been foraging previously. The King Vultures were gone all day, most likely

to a kill in the RT drainage where a jaguar appeared to have headed two days earlier. Over the next two days the King Vultures were seen gliding around on wind currents rather than foraging, and on 26-28 July, five or six picked over remains at former carrion sites.

(3) On 29 July two adult King Vultures were soaring over the southern savannas when suddenly at 12h09 they perched along CAF in the southwest sector. One sat for 20 min and the other for ca. 90 min while the first, joined by two more, searched the southwest slopes. Jaguar tracks went south on the road and cut across the range toward the tree. The next morning at 09h02 two King Vultures, joined at 09h50 by a third, searched the entire southwest sector, one finally going to the northwest (12h55) and later (13h50) high over LN while the others disappeared over the CLSL basin.

(4) On 13 August the King Vultures (n = 8) that had returned to roost along CLN near the last carcass site (ca. 1.3 km northwest of the central camp), after soaring, went directly west-northwest in low flight (11h10). Two more ascended along western CLD and before going west as the others, spent ca. 45 min soaring over the northwest ranges, where a female white-tailed deer was browsing, and another 20 min circling, along with a Turkey Vulture, over a flat area in the western foothills along CAF where something suddenly attracted their

attention. At 16h37 as I was going west on the range between CLD and CLN to photograph vegetation, I noticed one Black and six Turkey Vultures circling over the southern bank of CLN ca. 3.5 km east of the earlier sighting. When I came back through the same area at dusk, I found jaguar tracks coming from the gallery forest, crossing mine on the road-both sets showed similar dryness-and heading north toward CLD, the two streams being ca. 500 m apart in that section. I concluded the vultures had sighted the jaguar in both areas and that the King Vultures were returning in late morning to a known kill or to search the area where they had last seen the feline. Two roosted along CLD north of the tracks the next evening and on 15 August (09h16) inspected the foothills to the north, slowly making their way west before being lost from sight over the northern reaches of CLN. On 16 August the King Vultures that had roosted at LN (n = 5 adults, 1 young)went directly west-northwest at 09h52. When they returned at 10h05 on 17 August, in low flight, one adult and the immature continued south to the Río La Plata drainage while the other four adults, paired in twos, engaged in a tandem-flight display (Schlee 2001) and finally went southwest to the CLSL basin. The King Vultures' behaviours indicated they were no longer foraging and I concluded they had most likely returned from a kill near the RT watershed divide

northwest of LN.

1998 field season

This was the first dry-season visit (March: 13 days) and it was much shorter than originally planned. The King Vultures (n = 1-4 adults) monitored white-tailed deer on eight days, but I do not know if a big cat was or had been present. The deer had come from the northwest and were travelling over the northern foothills to central LN, then south along the eastern banks of CLN or across the eastern ranges to a large morichal along Caño Quitoní not far from the CQ-CLN confluence. During the last six days of my visit, a thick haze, induced from fires in the area, cut off visibility to the foothills and mountains.

1999-2000 field season

A pig found dead near the central camp in early morning on my day of arrival (24 November) might have been a jaguar kill. Four Turkey Vultures were already feeding when King Vultures (n = 4 adults, 2 young) started arriving (14h45-15h44); the latter left LN the next day at 08h48 and did not return for 11 days, presumably feeding elsewhere. During their absence I found tracks of an adult jaguar (30 November: 11h42) in a remnant morichal southeast of the camp, which lends support to the possible kill six days earlier, and smaller ones (6 x 7 cm wide) in the west near

CAF (1 December), presumably made by a young jaguar. Tracks of an ocelot (Leopardus pardalis) were also seen. HLE reported two kills on livestock during the same time periods.

On 15 December at 17h09 an adult King Vulture perched conspicuously at the summit of a hill in the southwest near CAF. It disappeared at 18h00 and re-appeared there the next morning at 07h47, a second adult being sighted farther north at 08h08. Upon soaring (09h00), the pair was joined by a juvenile with remnants of down, presumed to be their offspring, that disappeared near the CLSL ridge and did not join in foraging. The two adults searched the entire southwest zone and continued west into the CLSL basin. On 17 December I followed the disused road south of CAF near the hill. Both adults had been foraging over the southwest ridges since 09h48 and at 12h35 were over the upper slopes on the LN side when I found 6 x 7 cm wide feline tracks at a waterhole along the road. The tracks resembled those found farther north 16 days earlier. The waterhole was clearly in view from the hill, and presumably the King Vultures had been monitoring the feline. Over the next 24 days the King Vultures (n = 1-3)were seen only six times at LN-gliding overhead, foraging in the southeast or going directly to the CLSL basin after having roosted in the valley.

Discussion

Since jaguar and puma are sympatric throughout most of the jaguar's range south of the Río Orinoco (Linares 1998), I cannot rule out that some presumed kills near LN could have been made by pumas. The latter, however, rarely leave large amounts of wastage and minimize loss to scavengers by caching large kills under leaves and debris and feeding mainly at night (Beier et al. 1995, Bank & Franklin 1998). The locations of the tracks I found (attributed to jaguar) in relation to direction of travel and King Vulture searching behaviour lead me to believe the observations reported here concerned jaguar. The kills on livestock reported by HLE were also attributed to jaguar. It was assumed that the same cat(s) visited both ranches, which may or may not be the case depending on the locations of kills. Some jaguars are primarily nocturnal (Rabinowitz & Crawshaw 1980) but others are more active during the day, travelling and hunting most at dawn, noon and dusk (Crawshaw & Quigley 1991), the level of daytime activity being higher in the wet season (Scognamillo et al. 2003). The jaguars at LN showed high diurnal activity during my study periods and thus would have been visible to vultures. Moreover, the northwest uplands of the Venezuelan Guayana, which include the Cerbatana massif, have both evergreen and semi-deciduous forests as well as isolated patches of shrublands and savannas (Huber 1995a,b) which should allow an aerial scavenger to receive more visual cues indicating the presence of jaguars, kills or carrion than it would when foraging over a vast tract of dense rainforest. Several jaguar home ranges may overlap at LN; however, except for the simultaneous presence in 1999 of a young jaguar and an adult, only one big cat was known to be in the valley at any one time during my study periods. The two presumed kills made at opposite ends of the valley in 1995 could have been made by the same cat, the second kill being ca. 14 km from the tracks I found and taking place almost 24 hours later. Jaguar movement patterns at LN can only be inferred, but elsewhere radio telemetry studies have shown that a jaguar may stay with a kill for 2-3 days, sometimes transporting it to a new site (Schaller & Crawshaw 1980), and also remain in small areas (2.5 km²) from 4-14 days before shifting to another part of its range (Rabinowitz & Nottingham 1986), travelling up to 10.4 km in a single night (Crawshaw & Quigley 1991).

King Vulture foraging behaviours included perching to monitor jaguar and circling overhead, especially when the cat was on the hunt or presumed to be feeding, as do African vultures when following large carnivores (reviewed in Mundy et al. 1992). The King Vultures also monitored large domestic dogs that occasionally ran loose (sightings and

tracks) but not ocelot or savanna fox (Cerdocyon thous: tracks and sightings throughout central LN). After sighting a jaguar, the King Vultures searched specific zones, indicating they knew the routes travelled by the feline(s) and also the areas most likely to have kills. In some instances searching may have been triggered by the unusual presence of large-sized potential prey, particularly white-tailed deer, rather than the sight of the predator. The King Vultures also perched to monitor the deer and sometimes briefly cruised overhead. The interest taken in whitetailed deer corresponded in 8 of 16 sightings to periods when a jaguar was present or had recently come through the valley (not known for remaining eight sightings). White-tailed deer seem to be fairly common in the southeast part of the Cerbatana massif, and at LN they often came from the northwest, travelled over the northern footbills to central LN, crossed to the southeast or went south along CLN and on to the south-southwest lowlands. Hoogesteijn et al. (1993) did not cite white-tailed deer among the mammalian prey taken by big cats in the Venezuelan llanos, but recently Scognamillo et al. (2003) found evidence of such predation there by both jaguar and puma (5% and 10% of scats, respectively). Also, large carnivores are known to change dietary preferences when a major food source becomes

less abundant (Leopold & Krausman 1986), and type of habitat influences prey spectra so certain prey are thus taken more, or less, often than expected (Scognamillo et al. 2003). Further study is needed on the use of big-cat kills by vultures in the Neotropics.

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predation, Venezuelan Guayana. King Vulture Sarcoramphus papa.

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