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BODY CONDITION VARIES WITH MIGRATION AND COMPETITION IN MIGRANT AND RESIDENT SOUTH AMERICAN VULTURES

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ABSTRACT.—We investigated seasonal changes in the body condition of migrant and resident Turkey Vultures (*Cathartes aura meridionalis* and *C. a. ruficollis*), as well as Black Vultures (*Coragyps atratus brasiliensis*), in the Llanos of central Venezuela. Although the condition of adult migrants was below average in October and November following migration from the breeding grounds, it increased through the dry season to reach a peak before northward migration in March and April. Juvenile (FY; first-year) migrant Turkey Vultures followed a similar trend, but their condition improved more slowly than adults, perhaps due to intraspecific competition. The condition and mass of Black Vultures also increased through the dry season. This suggested that abundant carrion was available for vultures in the Llanos during the dry season. However, the condition of resident Turkey Vultures was below average when sympatric with migrants, whereas they were in above-average condition when migrants were absent. Unlike the linear relationship between condition and date in migrants, this relationship for residents was quadratic (second-order polynomial). Strikingly, condition of resident Turkey Vultures was negatively correlated with the density of *Cathartes* vultures (almost entirely migrants) during the study period. Migrant Turkey Vultures were significantly larger than resident Turkey Vultures in the majority of body measurements, explaining why they were dominant to residents in agonistic interactions at carcasses. These results may reflect the detrimental consequences of competition between migrant and resident Turkey Vultures on the condition of residents, and the physiological effects of migration on the condition of migrant Turkey Vultures. *Received 17 May 1993, accepted 5 January 1994.*

MANY NEARCTIC MIGRANT birds feed in mixed foraging flocks with tropical residents during the nonbreeding season (e.g. Willis 1966, Leck 1972, Fitzpatrick 1980, Hutto 1994). However, little is known about interspecific or intraspecific competition among migrants (Greenberg 1986), or between ecologically similar tropical residents and long-distance migrants; also, possible effects of dominance in the two groups have not been investigated in detail (see Leisler 1990). Recent studies of migrants in the tropics suggest that the dominance status of individuals might relate to their habitat use and, potentially, their survival. For example, Winker et al. (1990) showed that territorial (i.e. dominant) "wintering" Wood Thrushes (*Hylocichla mustelina*) inhabiting mature forest had lower mortality than subordinate flocking birds, which occupied secondary habitats and were subjected to increased predation. In such species, "wanderers" may have higher fat levels than sedentary individuals due to unpredictable food supplies (Rappole and Warner 1980).

In flocking species, dominant individuals can directly reduce the food intake of subordinates. Dominant individuals may have higher fat levels than subordinates in some short-distance migrants (e.g. Dark-eyed Junco, *Junco hyemalis*, Ketterson [1979]; White-throated Sparrow, *Zonotrichia albicollis*, Piper and Wiley [1990]), but there are few data for flocking long-distance migrants. One western race of the North American Turkey Vulture (*Cathartes aura meridionalis*) is a long-distance migrant that spends the boreal winter, between October and April, in the Llanos of central Venezuela, where it coexists with a small resident subspecies (*C. a. ruficollis*; Koester 1982). Migrants are larger than resident Turkey Vultures and dominate them in agonistic encounters at carcasses (Kirk and Houston in press). In other cathartids, intraspecific dominance hierarchies also reflect differences in

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body mass (Wallace and Temple 1987), although despite their smaller mass, migrant Turkey Vultures generally win one-to-one conflicts with Black Vultures (*Coragyps atratus brasiliensis*) in Venezuela (Kirk 1988). That migrants might restrict residents' access to food through interference competition is suggested by two important findings: (1) resident Turkey Vultures foraged almost exclusively in gallery forest, where there were relatively few migrants between November and late March, but foraged in both forest and savanna after migrants had left (Kirk 1988, Kirk and Currall in press); and (2) increased group size of migrants but not residents depressed feeding rates in residents through interference competition at carcasses placed in gallery forest (Kirk and Houston in press).

If migrant Turkey Vultures restrict residents' access to food through dominance, it follows that residents may have reduced fat levels during the period of sympatry with migrants. In contrast, one would predict that migrant Turkey Vultures would be in poorest condition on arrival in the study area following their southward migration during which some birds apparently do not feed (see Smith 1980, 1985). They should be in good condition during premigratory fattening prior to northward migration to the breeding grounds (March–April). In this paper, we report on seasonal variations in body condition of resident and migrant Turkey Vultures to test the above predictions. We also examine the condition of Black Vultures (resident in the study area) to see if these followed the same pattern as resident Turkey Vultures.

Intraspecific dominance is a correlate of age in cathartids (Wallace and Temple 1987). If we assume that the relative dominance of individuals affects their fat levels, then immature vultures might differ from adults in their condition. Therefore, we also examined seasonal changes in the condition of immature Turkey and Black vultures, and compared them with those of adults.

METHODS

We conducted our study at Fundo Pecuario Masaguaral, a private ranch and wildlife refuge of 7,500 ha in the middle Llanos of central Venezuela, Guárico state, 45 km south of Calabozo at 8°34′N, 67°35′W. The vegetation, described in detail by Troth (1979), consists of a mosaic of habitats from closed canopy gallery forest bordering the Rio Guárico to open palm savanna, shrub woodland, and marshes. The topography is typically flat, the highest elevation being only 60 to 75 m above sea level. A dry season occurs for four months from December to March, and a wet season from May to October. April and November are transitional months. Although the onset of the rainy season is highly variable from year to year, little rain fell during our study in either November or April; therefore, we included these transitional months in the dry season for data analyses. Average rainfall over a 20-year period was 1,400 to 1,500 mm; the annual temperature range is 17.5° to 38.5°C (Troth 1979). Three separate visits were made to Masaguaral: 17 November 1984 to 10 July 1985; 28 November 1985 to 21 June 1986; and 6 October 1986 to 27 March 1987. Thus, we examined vulture condition for the dry season and part of the wet season. During most of the wet season, with the Llanos flooded, fieldwork was logistically difficult.

Resident Turkey Vultures were easily distinguished from migrants by the yellowish, gold or greenish-white bands on their bare napes (see Brown and Amadon 1968). First-year (FY) Turkey Vultures could be distinguished by their brown heads and dark bills, compared to the red heads and white bills of adults (Jackson 1988a). Following southward migration, FY birds were easily identified, but late in the dry season this was more difficult as FY birds developed full adult head coloration. Only one FY resident Turkey Vulture was captured. We distinguished immature from adult Black Vultures by the degree of light-colored rugosity on the unfeathered head or neck (Rabenold 1984). The heads of FY birds generally were smooth, and the birds were rarely in molt (basic plumage lasts about a year in North American Black Vultures; Jackson 1988b). We also recognized possible second-year (SY) birds, but because wrinkling of the head skin is subject to individual variation (P. G. Parker pers. comm.) and because of small sample sizes, we pooled these age classes as immatures. As we did not have a sample of birds of known age (only two nestlings were wing-tagged), we could not reliably age older birds (>2 years). Therefore, we pooled data for those individuals that might have been adults with those of true adults. Small cathartid vultures are sexually monomorphic (Brown and Amadon 1968), and we were unable to use laparoscopy (Fry 1983) on trapped birds. Thus, we could not determine the sex of resident vultures, a factor that would affect their condition during breeding. We also found that the regression equations of Gaby (1982) did not separate sexes of the races that we examined.

To collect biometric data, vultures were caught in walk-in funnel (ca. 20 × 50 cm entrance) cage traps of dimensions 2.5 × 2.5 × 2.5 m (P. G. Parker and K. N. Rabenold pers. comm.). Traps were positioned in the shade, and water was provided to prevent heat stress in captured vultures. Traps were moved frequently to different habitats and baited with carcasses collected from the highway from Calabozo to San Fernando that bisects the ranch. The significance of locating traps in various habitats was that vulture taxa show differences in densities among habitats in this area (Kirk and Currall in press). In order to trap Turkey Vultures we used small mammal carcasses, whereas, for Black Vultures the highest success was achieved with large domestic livestock. We replenished food during trapping sessions because often it took several days to over a week for vultures to enter traps. Decoy individuals were sometimes left in traps to entice other vultures to enter, but this generally was unsuccessful.

The following body measurements were taken (all by D.A.K.): (1) Body mass. In all cases vultures vomited stomach contents during or right after initial handling. Mass was the last measurement taken on each bird and, thus, did not include gut contents. (2) Wingspan. Vultures were placed on their backs, with wings fully outstretched. The measuring tape was placed over the neck for one measurement (2a) or behind the neck for the other (2b). (3) Flat wing chord was taken on the flattened and straightened closed wing. (4) Wing breadth was measured from the leading edge to the trailing edge of the wing at the position of the humerus with the ulna/radius joint (4a, "ulna"), and from the leading edge to the trailing edge at the position of the ulna/radius with the carpus/metacarpals joint (4b, "wrist"). (5) Head and bill. This was measured from the base of the skull to the bill tip. (6) Head width was taken as the greatest head width posterior to the eyes. (7) Bill depth. (8) Bill length. One measurement was taken from the tip to the distal edge of nostril (8a), and another from the tip to proximal edge of nostril (8b). (9) Tarsus length was taken as the distance between the intertarsal joints flexed at right angles. (10) Head and body. Vultures were placed on their backs with neck outstretched and measured from the tip of bill to the tip of tail. (11) Tail length was measured from the shaft base of the central pair of rectrices to the tip of the longest tail feather.

Measurements were made on 132 adult migrant Turkey Vultures, 70 adult resident Turkey Vultures, and 118 adult Black Vultures. In addition, we caught 25 FY migrant and 1 FY resident Turkey Vultures, as well as 38 FY and possibly SY Black Vultures. However, smaller sample sizes were available for some analyses because an incomplete set of measurements was taken for some birds. We discarded data from birds that showed signs of injury or sickness; several birds had extended upper mandibles, low fat levels, and abundant lice. Two Turkey Vultures had broken femurs, possibly as a result of being caught in traps baited with carrion set by poachers.

A principal-components analysis (PCA) was carried out on the correlation matrix to extract a size factor using the following measurements: 2b, 3, 4a (right wing only), 4b (right wing only), 5, 6, 7, 9, and 10. Principal component I (PC I) has been used or recommended as an index of body size in many studies (see Rohwer 1972, Zink 1982, Rising 1988, Rising and Somers 1989). We excluded some measurements from the PCA because they contained identical skeletal components, because only small sample sizes were available, or in order to standardize the nine variables for all taxa.

As a measure of condition (probably largely a reflection of fat level), we used the residuals of a regression of mass on size (PC I). This provided a measure of relative mass that takes into account the effects of structural size. We subjected measurement data to log transformation to reduce skewness and used parametric statistics throughout (Sokal and Rohlf 1981), except when comparing condition with densities of vultures. We compared PCA results from both the log-transformed and original data, and found little difference. The data we present here are from the log-transformed measurements.

We examined two temporal effects in the changing condition of taxa: (1) the relationship between condition and season (dry and transitional or wet); and (2) the relationship between condition and numbers of migrant Turkey Vultures present in the study area. Given that group size of migrants has an effect on foraging behavior and possibly habitat use of residents (Kirk 1988, Kirk and Houston in press), competition levels may vary in response to changing population densities of migrants. Therefore, we compared condition of resident Turkey Vultures between two periods: (1) when residents were sympatric with large numbers of migrants (November–March); and (2) when few or no migrants were present (October, April, May, and June). Based on point-count data given in Figure 1 (Kirk and Currall in press), we pooled data for three distinct periods for migrant Turkey Vultures: (1) postmigratory period when migrant Turkey Vultures were arriving in the study area (October–November); (2) wintering (hereafter tropical residence) period (December–February); and (3) period of northward migration in the late dry season and transition months (March–April). For data analysis we used MINITAB (Ryan et al. 1992) and SAS PC+ software (SAS Institute 1988).

RESULTS

Principal-components analyses.—All correlations (loadings) of univariate measures on PC I were substantial, demonstrating that it represented an axis of size in all vulture taxa (Table 1). PC I explained a large proportion of the total variance in Turkey Vulture migrants (49.8%), Turkey Vulture residents (37.3%), and Black Vultures (34.4%), whereas PC II explained relatively little variation (12.0%, 14.1%, and 16.5% of total character variance for migrants, resi-

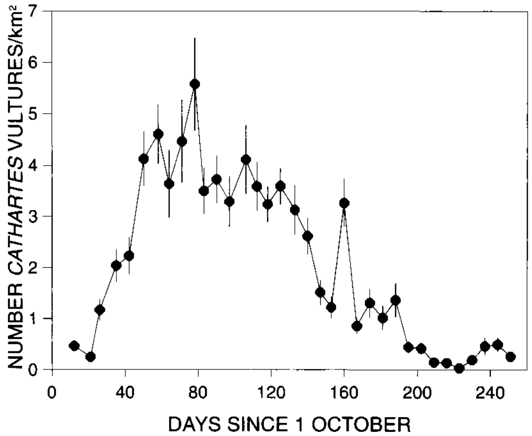

Fig. 1. Pattern of change in densities of *Cathartes* (mostly migrant Turkey) vultures over nine-month period (1986–1987) at Masaguaral. $\bar{x}$ ± SE of five point counts per day on 43 counts days. Day 0 = 1 October (Kirk and Currall in press).

dents, and Black Vultures, respectively). In all taxa, PC I was significantly correlated with mass (migrants, $r = 0.48$, $P < 0.001$; residents, $r = 0.45$, $P < 0.001$; Black Vultures, $r = 0.64$, $P < 0.001$). In the case of migrants, measurements with the highest loadings on PCI were wingspan, and head and body (Table 1). Wingspan also was the variable with the highest loading on PC I in resident Turkey and Black vultures; flat wing chord had the second highest loading (rather than head and body).

Variation in condition with migration and season.—When we examined the condition of migrant and resident Turkey Vultures from October (when migrants first arrived at study site) to April (when migrants had left) or June (for residents), some striking differences were found. As expected, following southward migration the condition of adult migrants was below average, but it increased with the number of days spent on the nonbreeding grounds (linear regression, $F_{1,116} = 6.98$, $P = 0.009$; Fig. 2A). Although the mean condition index did not differ significantly between migration periods (one-way ANOVA, $F_{2,115} = 2.26$, $P = 0.10$), there was a significant difference between the mean condition index following southward migration compared to that of tropical residence and northward migration combined (southward migration, $\bar{x} = -0.491$ ± SE of 0.11, $n = 16$; tropical residence and northward migration, $\bar{x} = 0.08 \pm 0.10$, $n = 102$; t-test, $t_{45} = 3.70$, $P < 0.001$). Like adults, the condition of FY migrant Turkey Vultures increased with time spent in the tropics (linear regression, $F_{1,20} = 13.02$, $P = 0.002$). However, there was some evidence that the rate of improvement in condition was lower than in adults because FY birds were in poorer condition following southward migration ($\bar{x} = -0.800 \pm 0.32$, $n = 6$) and the tropical residence period ($\bar{x} = -0.600 \pm 0.27$, $n = 10$) than prior to northward migration ($\bar{x} = 0.588 \pm 0.27$, $n = 6$; one-way ANOVA, $F_{2,19} = 5.73$, $P = 0.011$). Overall, FY birds tended to be in poorer condition than adults (adults, 0.06 ± 0.09, $n = 118$; FY, -0.331 ± 0.20, $n = 22$; $t_{30} = 1.76$, $P = 0.08$). However, when birds trapped on or before northward migration (period 3) were excluded, the difference was highly significant (adults, $\bar{x} = 0.034 \pm 0.10$, $n = 88$; FY, $\bar{x} = -0.675 \pm 0.20$, $n = 16$; $t_{23} = 3.13$, $P = 0.005$).

TABLE 1. Correlations with principal component I and nine characters for adult migrant Turkey Vultures ($n = 120$), resident Turkey Vultures ($n = 66$), and Black Vultures ($n = 49$).

Variable	Turkey Vulture		Black Vulture
	Migrant	Resident	
Wingspan b	0.41	0.47	0.48
Flat wing chord	0.35	0.45	0.43
Right wing wrist	0.37	0.25	0.15
Right wing ulna	0.36	0.27	0.35
Head and bill	0.28	0.32	0.38
Head width	0.22	0.08	0.15
Bill depth	0.22	0.21	−0.06
Tarsus	0.33	0.35	0.34
Head and body	0.40	0.40	0.39

In contrast to migrants, the relationship between condition of adult residents and days since the beginning of October was not linear but quadratic ($F_{1,59} = 11.49$, $P = 0.001$, with a significant interaction [$F = 12.64$, $P = 0.001$]; Fig. 2B). This indicated that residents were in better condition before migrants arrived in large numbers (ca. day 40; 9 November) and after most migrants had departed (day 180; 29 March; Fig. 2B). However, during the period of sympatry, the condition of residents was generally below average (Fig. 2B). The pattern of condition in residents followed almost exactly the reverse trend of the density of *Cathartes* vultures (mostly migrants) given in Figure 1 (Spearman rank correlation coefficient $r_{s60} = -0.352$, $P = 0.006$; Fig. 3; for statistical comparison, we used count closest to trapping date).

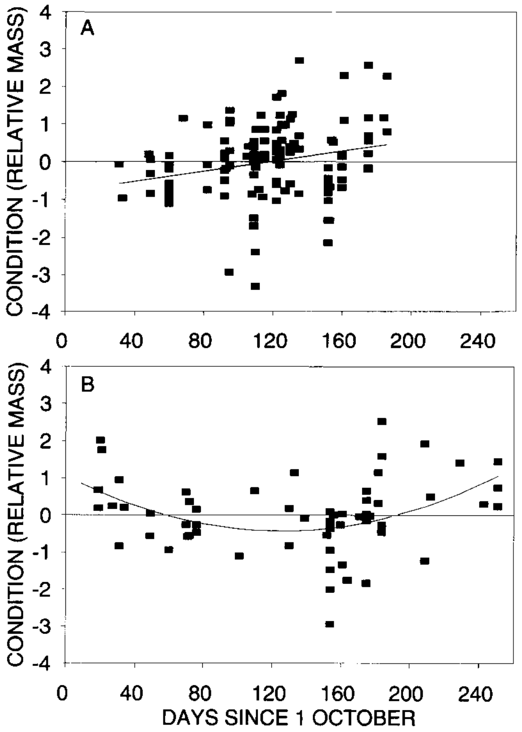

Fig. 2. (A) Relationship between condition (relative mass) of adult migrant Turkey Vultures and time since arrival on nonbreeding grounds (regression equation: condition = $-0.777 + 0.00665$[days since arrival]). (B) Relationship between condition (relative mass) of adult resident Turkey Vultures and days since 1 October (quadratic regression equation: condition = $1.0574 - 0.023589$ day $+ 0.000094$ day^2).

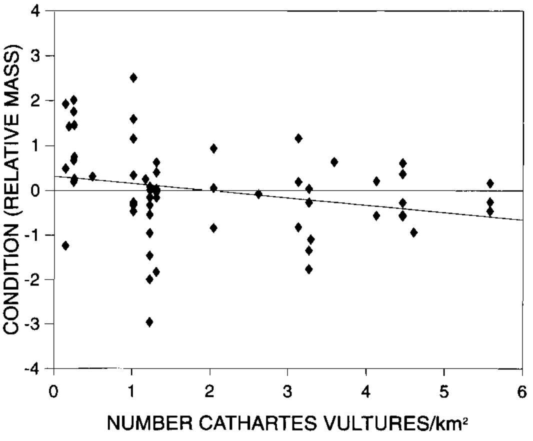

Fig. 3. Relationship between number of *Cathartes* vultures and condition of resident Turkey Vultures. Line indicates general trend.

Few data were available from adult Black Vultures to calculate condition indices, but 45 birds showed a pattern approaching statistical significance (linear regression, $F_{1,43} = 3.73$, $P = 0.06$) that was similar to that of migrant Turkey Vultures, with a positive correlation between the number of days since October and condition. This suggested that food for vultures was abundant during the dry season since Black Vultures were largely resident in the area (based on resightings of wing-tagged birds; Kirk 1988). Interestingly, immature Black Vultures were in significantly better condition than adults in the dry season (immatures, $\bar{x} = 0.42 \pm 0.24$, $n = 18$; adults, -0.164 ± 0.14, $n = 45$; $t_{30} = -2.10$, $P = 0.044$), which could be attributed to the fact that many of these were fledged young being fed or defended by their parents (see Rabenold 1986; 24 were identified as FY birds in March-April) or, more likely, that most adults were measured earlier in the season when their condition was lower. Supporting the latter assertion is the observation that the condition of adults did not differ significantly from immatures during the same period (March-April; $t_{32} = -1.69$, $P = 0.10$).

Variation in mass with migration and season.—We tested whether body mass for each taxon differed by season and migratory status. Except for adult migrant Turkey Vultures, which showed no significant trend, these mass changes substantiated patterns of change in the condition indices. As in the small sample of Black Vultures for which condition indices were derived, there was a positive linear relationship between mass and number of days since October (linear regression, $F_{1,117} = 30.98$, $P < 0.001$).

Relationship of numbers of vultures trapped and condition.—Variation in trap samples can cause biases in assessing condition indices of birds, because small catches are more likely to contain birds in poor condition (see Weatherhead and Greenwood 1981, Dufour and Weatherhead 1991). Because our goal was to determine whether such biases might affect the interpretation of seasonal variation in condition, we examined the effect of catch size (Fig. 4) on condition while controlling for time of year. To do this we performed an analysis of covariance (ANCOVA), the results of which are presented in Table 2. Because the relationship between condition and time of year was not linear in resident Turkey Vultures, we examined two periods of changing condition: (1) from arrival of

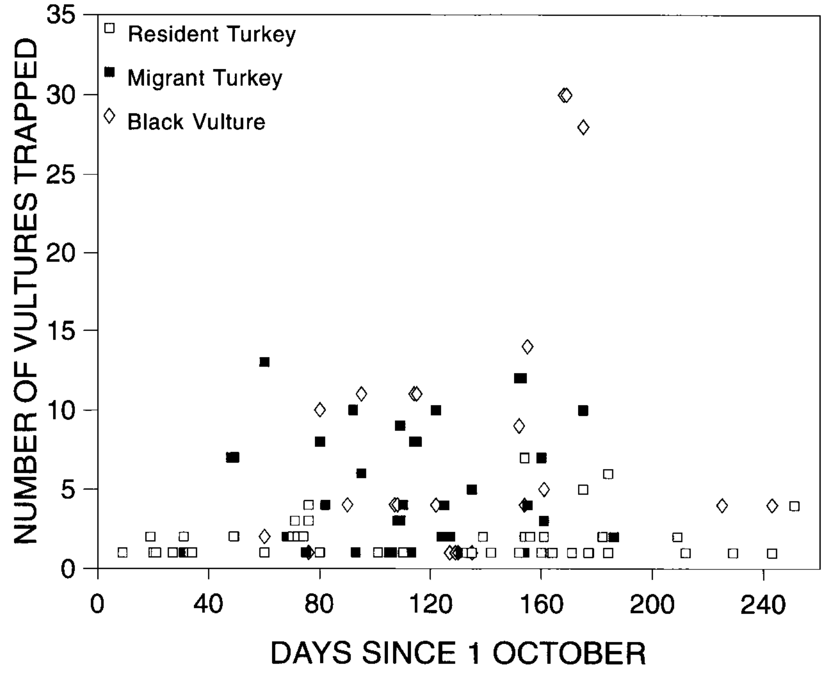

Fig. 4. Numbers of vultures of trapped on different days. For large catches (>25), number of vultures trapped is number of birds processed because many birds escaped or were released.

migrants to when most had departed; and (2) from departure of most migrants until June. These analyses showed that for period 1, when time of year was controlled, the effect of catch size on condition was not quite significant (Table 2). No effect on condition was detected in period 2 for either variable, but this could be due simply to small sample size and the short duration involved (84 days). For migrant Turkey Vultures, when time of year was controlled, catch size did not have a significant effect on condition (Table 2). In the case of Black Vultures there was a significant interaction between catch size and time of year so we could not perform an ANCOVA.

Morphological differences between subspecies and age classes.—Adult migrant Turkey Vultures were significantly larger than adult residents in the majority of body measurements, with the exception of three wing characters, bill length b and tail length (Table 3). To classify known birds into resident and migrant categories based

TABLE 2. Analysis of covariance to evaluate effect of catch size, while controlling for days since 1 October.

Taxon	Source	df	*F*	*P*
Resident Turkey Vulture[a]				
Period 1 (1 October–15 March)	Error	33		
	Catch size	2	3.17	0.055
	Covariate (day number)	1	5.30	0.028
Period 2 (16 March–June)	Error	19		
	Catch size	2	0.77	0.478
	Day number	1	0.01	0.928
Migrant Turkey Vulture	Error	105		
	Catch size	2	1.80	0.170
	Covariate (day number)	1	5.55	0.020

[a] Two separate analyses were performed for resident Turkey Vultures because relationship between days since 1 October and condition was not linear. Black Vultures were excluded because there was significant interaction between catch size and time of year. Catch-size groups were 1-5, 6-25, and >25. Data presented for adults only. Type III sums of squares (SAS Institute 1988).

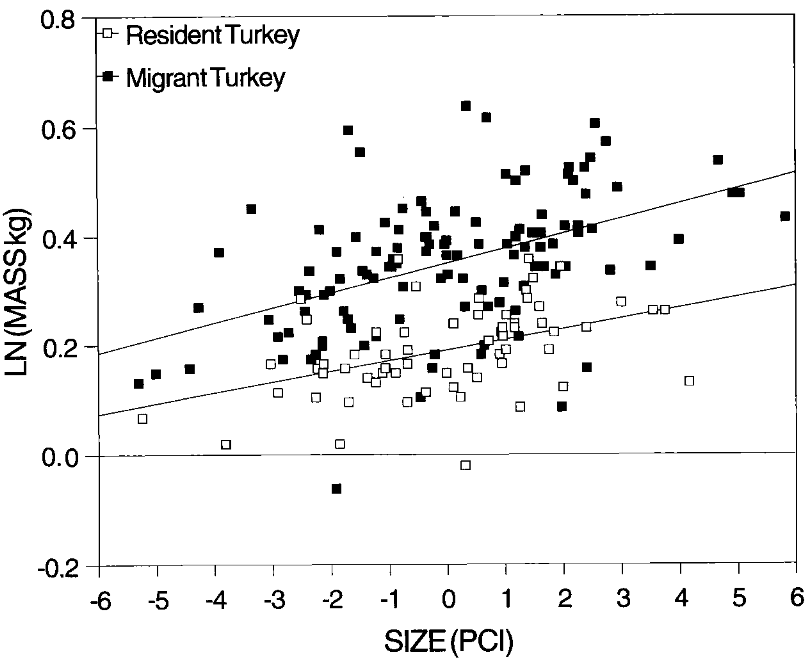

Fig. 5. Relationship between size (PC I) and natural log of mass (kg) in migrant and resident Turkey Vultures. Regression equation for residents: natural log of mass = 0.190 + 0.0198 size, $F_{1,60} = 15.19$, $P < 0.001$. Regression equation for migrants: natural log of mass = 0.349 + 0.0276 size, $F_{1,116} = 34.06$, $P < 0.001$. Separate PCAs performed for the two races.

on their mass and size, we performed a linear discriminant analysis. For 180 individuals (118 migrants and 62 residents), 76% were classified correctly as migrant or resident (87 migrants and 50 residents). To compare further the body size and mass of migrants and residents, we performed separate PCAs on measurement data from both resident and migrant Turkey Vultures, and then plotted body mass on PC I. The result (Fig. 5) demonstrated that migrants generally were larger and heavier than residents, but there was considerable overlap. Part of the reason for this overlap may be mixing of large-sized northern migrants with smaller-sized mi-

TABLE 3. Comparison of measurements between migrant and resident Turkey Vultures ($\bar{x}$ ± SE, with *n* in parentheses). Mass in kilograms and other measurements in centimeters.

Variable	Migrant	Resident	P^a
Mass	1.43 ± 0.02 (130)	1.22 ± 0.01 (65)	***
Wingspan a	169.01 ± 0.51 (66)	163.93 ± 0.88 (18)	***
Wingspan b	168.34 ± 0.37 (124)	164.49 ± 0.46 (67)	***
Flat wing chord	50.02 ± 0.18 (130)	49.73 ± 0.15 (69)	ns
Left wing wrist	29.57 ± 0.10 (131)	29.46 ± 0.13 (69)	ns
Left wing ulna	28.85 ± 0.11 (131)	28.10 ± 0.13 (69)	***
Right wing wrist	29.53 ± 0.09 (129)	29.22 ± 0.18 (70)	ns
Right wing ulna	29.05 ± 0.11 (129)	28.59 ± 0.14 (70)	*
Head and bill	9.59 ± 0.03 (131)	9.36 ± 0.03 (70)	***
Head width	3.84 ± 0.01 (130)	3.64 ± 0.02 (70)	***
Bill depth	1.60 ± 0.01 (130)	1.51 ± 0.01 (70)	***
Bill length a	3.65 ± 0.02 (65)	3.47 ± 0.03 (18)	***
Bill length b	2.32 ± 0.02 (66)	2.29 ± 0.02 (50)	ns
Tarsus	7.40 ± 0.03 (131)	7.23 ± 0.03 (70)	***
Head and body	64.61 ± 0.19 (121)	63.21 ± 0.17 (69)	***
Tail	25.03 ± 0.14 (63)	25.16 ± 0.10 (51)	ns

[a] *t*-test; ns, $P > 0.05$; *, $P < 0.05$; ***, $P < 0.001$.

TABLE 4. Comparison of measurements between age classes of migrant Turkey and Black vultures ($\bar{x}$ ± SE, with n in parentheses). Mass in kilograms and other measurements in centimeters. See text for significant differences.

	Turkey Vulture		Black Vulture	
Variable	Adult migrant	FY migrant	Adult	Immature
Mass	1.43 ± 0.02 (130)	1.38 ± 0.04 (23)	1.64 ± 0.01 (119)	1.64 ± 0.03 (36)
Wingspan a	169.01 ± 0.51 (66)	169.77 ± 1.15 (11)	135.04 ± 0.52 (60)	134.82 ± 0.88 (20)
Wingspan b	168.34 ± 0.37 (124)	170.09 ± 1.03 (22)	134.11 ± 0.57 (50)	133.77 ± 0.94 (19)
Flat wing chord	50.02 ± 0.18 (130)	50.75 ± 0.29 (24)	39.08 ± 0.16 (100)	38.78 ± 0.22 (29)
Left wing wrist	29.57 ± 0.10 (131)	29.81 ± 0.18 (24)	26.71 ± 0.10 (63)	26.89 ± 0.24 (20)
Left wing ulna	28.85 ± 0.11 (131)	29.01 ± 0.26 (24)	27.79 ± 0.12 (63)	27.69 ± 0.19 (20)
Right wing wrist	29.53 ± 0.09 (129)	29.77 ± 0.20 (23)	26.67 ± 0.12 (62)	26.57 ± 0.21 (20)
Right wing ulna	29.05 ± 0.11 (129)	29.32 ± 0.19 (23)	28.06 ± 0.11 (62)	27.83 ± 0.33 (20)
Head and body	9.59 ± 0.03 (131)	9.56 ± 0.06 (24)	10.69 ± 0.04 (62)	10.53 ± 0.08 (20)
Head width	3.84 ± 0.01 (130)	3.81 ± 0.02 (24)	4.03 ± 0.03 (62)	3.88 ± 0.03 (20)
Bill depth	1.60 ± 0.01 (130)	1.60 ± 0.03 (24)	1.50 ± 0.02 (62)	1.42 ± 0.02 (20)
Bill length a	3.65 ± 0.02 (65)	3.69 ± 0.05 (11)	4.45 ± 0.03 (62)	4.39 ± 0.06 (20)
Bill length b	2.32 ± 0.02 (66)	2.25 ± 0.03 (13)	2.53 ± 0.05 (36)	2.40 ± 0.03 (9)
Tarsus	7.40 ± 0.03 (131)	7.34 ± 0.07 (23)	8.98 ± 0.03 (99)	8.93 ± 0.05 (30)
Head and body	64.61 ± 0.19 (121)	65.36 ± 0.38 (22)	58.20 ± 0.27 (51)	58.01 ± 0.38 (19)
Tail	25.03 ± 0.14 (63)	25.38 ± 0.21 (11)	—	—

grants from southern parts of North America on the nonbreeding grounds (Wetmore 1964).

Dominance hierarchies in cathartid vultures often are related to body mass or age (Wallace and Temple 1987). Given that juveniles generally lost conflicts to adults (Kirk unpubl. data), we tested whether they had smaller dimensions. Immature (FY and tentative SY) Black Vultures were significantly smaller than adults in most cranial measurements: head width ($t_{53} = 4.16$, $P < 0.001$), bill length b ($t_{41} = -2.14$, $P = 0.039$), and bill depth ($t_{57} = 3.18$, $P = 0.002$; Table 4). No difference was found in overall size (PC I; $t_{26} = 1.47$, $P > 0.10$). However, in the case of migrant Turkey Vultures, FY birds were significantly larger than adults in wing chord ($t_{46} = 2.19$, $P = 0.033$; Table 4); no difference was found for any other characters, including overall size (PC I, $t_{29} = -0.79$, $P > 0.10$).

DISCUSSION

Our results provide evidence of the consequences of competition between migrant and resident Turkey Vultures on the physical condition of residents. Resident birds were in "poorer" condition during the period of sympatry with migrants, and their condition was negatively correlated with the density of *Cathartes* (mostly migrant) vultures in the study area. By contrast, the condition of both adult and FY migrants was low following their southward migration, improved with time spent in the tropics, and reached a peak prior to northward migration. The condition and mass of adult Black Vultures also followed a similar temporal trend, suggesting that food for vultures was abundant during the dry season. Black Vultures were not believed to be migratory in our study area, so their mass trends could not be related to migration. Although Eisenmann (1963) and Skutch (1969) suggested that Black Vultures were migratory in Panama, the movements they observed are not now regarded as true migrations (Jackson 1988b).

We did not attempt to measure carrion abundance at Masaguaral, but our observations, as well as domestic livestock counts (D. A. Kirk, pers. obs.) and research on two vertebrate species with a high biomass in the Llanos (capybara [*Hydrochaeris hydrochaeris*], Ojasti [1978]; spectacled caiman [*Caiman crocodilus*], Thorbjarnarson [1991]), suggest that animal mortality is highest in the dry season. Although both migrant Turkey and Black vultures show the same trends in condition indices, these two species specialize on carcasses of different animal species (Stewart 1978, Coleman and Fraser 1987). Black Vultures feed primarily on carcasses of domestic livestock, a more predictable and abundant food source at Masaguaral than the small carcasses of wild mammals preferred by Turkey Vultures. Also, Black Vultures forage in groups, may use communal roosts for information transfer, and show a high degree of kin association (Rabenold 1986). Conversely, Turkey Vultures forage singly or by local enhancement (Kirk 1988), lack food sharing, and show relatively little kin association (Prior and Weatherhead 1991). These foraging and social differences, and the shorter period over which Black Vultures were caught, might explain why more of the variability in body mass was statistically accounted for by body size in Black Vultures than in migrant Turkey Vultures. Despite having the same food preferences as migrant Turkey Vultures, residents did not show the same temporal trends in condition. There are several possible alternative explanations for such differences.

First, the body condition of migrant Turkey Vultures caught during the periods October-November and March-April is primarily affected by physiological changes associated with migration (see Blem 1990). Loss of accumulated fat during migration, when some Turkey Vultures apparently do not feed (Smith 1980, 1985), accounted for the low condition of migrants caught in November and December. In the months that follow, the average condition of birds was better, indicating that they had obtained sufficient food to restore fat reserves. The finding that the condition of immature birds improved more slowly than that of adults might indicate age-related differences in foraging efficiency or competitive ability (for review, see Wunderle 1991), or may simply be due to the small sample sizes of immatures involved. Adult migrant Turkey Vultures sometimes were displaced from carcasses by FY birds once the former were satiated (Kirk unpubl. data), but generally FY birds were subordinate to adults in conflicts. Premigratory Turkey Vultures were of average or above-average condition given that they were storing fat to prepare for migration. Thus, the metabolism of migrant Turkey Vultures may differ from that of residents because of the physiological changes associated with long-distance migration.

A second explanation is that one would expect adult female resident Turkey Vultures to be in above average condition before or around the time of egg laying, while the condition of both sexes might decline later in the breeding season when they are incubating (both sexes brood in North America; Davis 1983, Jackson 1988a,b) and feeding dependent young. In studies of Ruppell's Griffons (*Gyps rueppellii;* Houston 1976), Common Griffons (*G. africanus;* Houston 1976), and Tawny Owls (*Strix aluco;* Hirons et al. 1984), body condition declined markedly during the breeding season. If resident Turkey Vultures breeding at our study site followed the same schedule as in Panama (egg laying commenced between February and April; Smith 1980) and a similar duration to that in North America (Davis 1983, Jackson 1988a), they could have well-grown young by the late dry season or early wet season. While the stage of breeding might explain the poor condition of birds in the middle to late dry season (February-March), it does not account for those in poor condition caught in November-January, or those in good condition caught in April, May, and June, unless the latter were postbreeding or nonbreeding birds, which we doubt. No Turkey Vulture nest sites were found at Masaguaral, implying that breeding birds were extremely secretive, nested outside the ranch, or most likely bred during months when migrants were absent. Possibly supporting the latter hypothesis is the observation of a juvenile bird by Thomas (1979) in August. Other resident bird species might alter their breeding seasons to avoid the period of sympatry with migrant congeners, although evidence for such a pattern is limited (e.g. Miller 1963). The fact that only one FY resident Turkey Vulture was trapped during our study suggests that breeding was irregular, or that juveniles were spatially segregated from adults. Gaby (1982) found that immature migrant Turkey Vultures differed from adults in their resource utilization and, thus, their habitat use.

Condition trends in resident Turkey Vultures are entirely consistent with the consequences of competing with larger-sized and numerically dominant migrants. During the dry season, resident Turkey Vultures (identified in flight by their conspicuous nape bands) foraged almost exclusively over gallery forest, where the number of migrants was on average three to four times lower than in open savanna (Kirk and Currall in press). This suggests either that open savanna held the highest densities of carrion or that carcasses were easier to find there due to better visibility (Kirk and Houston in press). Support for the former hypothesis comes from estimates of mammalian densities (Eisenberg et al. 1979), which imply that mammalian biomass (including domestic livestock, which are largely restricted to savanna) is three to five times higher in open savanna than in gallery forest. Also, large populations of fewer species predominate in savanna, while the more structurally complex gallery forest has greater species richness (August 1983). When migrants departed in March and April, radio-tagged and marked residents apparently shifted their ranges to forage in all habitats, including the open savanna (Kirk 1988, Kirk and Houston unpubl. data). Some local movement of residents also may have occurred into savanna habitats from elsewhere when migrants left. Second, residents arrived first at carcasses placed in the gallery forest, and fed quickly before migrants arrived. The feeding rate of residents decreased significantly in response to group size of migrants, but was not affected by increased group size of other residents, suggesting that migrants competed directly with residents (Kirk and Houston in press). Finally, in conflicts at carcasses, migrants won all but 1 of 471 encounters they initiated against residents (Kirk and Houston in press).

Thus, the restricted habitat use by resident Turkey Vultures during the dry season could cause them to lose mass. In small passerines, subordinate individuals may be restricted to suboptimal habitats or foraging areas (e.g. Baker et al. 1981, Alatalo and Moreno 1987), requiring them to carry larger fat reserves than dominants (Ekman and Lilliendahl 1993). It could be argued that resident Turkey Vultures carry less fat in the dry season when carrion may be abundant, whereas in the wet season it would be adaptive for birds to store fat because food is more spatially or temporally patchy (see Blem 1990, Ekman and Hake 1990). Vultures with higher fat levels would be better able to survive longer periods without food, an advantage for birds with an ephemeral and patchy food supply (Houston 1976). However, this idea is not supported by the data for Black Vultures, which also were resident at Masaguaral and showed a linear increase in condition with time since 1 October. Clearly, the constraints affecting fat storage in large birds are very different from those affecting small passerines. We suggest that food supply is always unpredictable and patchy for vultures and, therefore, all individuals benefit from storing fat.

Some potential biases affected the measurement of body condition in vultures. First, we pooled data for all years because of small sample sizes. Second, we found some evidence that condition was related to the number of vultures trapped at any one time. Catch size showed an effect on condition of resident Turkey Vultures that approached statistical significance, even when time of year was controlled. However, we believe that condition of trapped birds genuinely reflected condition in the population of vultures. Independent measures of condition using other capture techniques are needed to evaluate whether condition biases occur in vultures caught in baited cage traps.

In conclusion, given the lack of evidence that residents breed during the period of sympatry with migrants, changes in their condition appear to be a consequence of interference competition for food from migrants, while the condition of migrants is influenced by physiological changes associated with migration. Thus, the endogenous programs, physiological states, and environmental conditions affecting fat storage and metabolism likely are different in the two subspecies. Further studies are needed to determine the breeding cycle of resident Turkey Vultures and to measure seasonal changes in carrion availability.

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