SHORT COMMUNICATIONS

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SOCIAL STRUCTURE OF ANDEAN CONDOR ROOSTS: INFLUENCE OF SEX, AGE, AND SEASON

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Abstract. We examined how Andean Condors (*Vultur gryphus*) segregate by sex and age in summer and autumn at a communal roost in the Patagonian Andes. Preferred roosting places received earlier sun at sunrise (summer) and later sun at sunset (autumn); sheltered crevices were also selected. Individuals strongly competed for preferred places: adults dominated juveniles and within each age class males dominated females. Although individuals preferred roosting places independent of their dominance status, fighting and subsequent relocating led to a defined social structure at the roost. Sunny exposures may allow occupants to maximize time available for foraging, plumage care, and maintenance, and to avoid cold stress. Irregularity in the spatial distribution and aggregation patterns of Andean Condors may be the result of requirements for roosting. Availability of adequate roost places should be considered in conservation programs.

Key words: age, Andean Condor, dominance, roost, sex, social structure, *Vultur gryphus*.

Estructura Social en Dormideros de *Vultur gryphus*: Efectos de la Edad, Sexo y Estación

Resumen. Examinamos la segregación de individuos de *Vultur gryphus* en un dormidero communal en los Andes patagónicos con relación a la edad, el sexo y la estación del año. Los lugares preferidos para dormir fueron aquellos que recibieron la luz del sol más temprano al amanecer (verano) o temprano al amanecer y tarde al anochecer (otoño). Las oquedades abrigadas fueron también seleccionadas. Las aves compitieron por los lugares preferidos: los adultos dominaron a los jóvenes, mientras que dentro de cada clase de edad dominaron los machos. Aunque los lugares

preferidos eran seleccionados inicialmente por aves de cualquier sexo y edad, las peleas y recolocaciones subsiguientes dieron lugar a una estructuración social en el dormidero. La preferencia por exposiciones soleadas puede reportar ventajas en la maximización del número de horas disponible para volar en busca de alimento, en el cuidado y mantenimiento del plumaje y en la reducción del estrés térmico derivado de las bajas temperaturas. Los requerimientos asociados a los dormideros pueden determinar patrones irregulares en la distribución y agregación de la especie a lo largo de su área de distribución. La disponibilidad de dormideros adecuados debe ser considerada en programas de conservación.

Ecological pressures leading to grouping in communal roosts have been widely discussed in avian literature (Andersson et al. 1981, Giraldeau 1997, Beauchamp 1999). Apart from the large-scale potential benefits of information gathering and mate acquisition (Blanco and Tella 1999), immediate rewards derived from day-to-day site selection within a roost have been related to factors such as individual survival, thermoregulation, avoidance of damage caused by the droppings of birds roosting above, and social status (Yom-Tov 1979, Draulans and Vessen 1986, Summers et al. 1987, Bishop and Groves 1991, Buckley 1998). Individual placement in roosts is usually regulated by social structure, a central question in the study of adaptive value of communal roosting behavior. Studies carried out with passerines reveal that subordinate individuals, as determined by age, sex, and body condition, are relegated to less-preferred places (Still et al. 1987, Bishop and Groves 1991, Jenni 1993).

Large communally roosting species such as birds of prey may encounter different selective pressures because of their body size. Large eagles and vultures that typically roost in cliffs, trees, and large human-made structures are apparently constrained by the availability of safe places to take off and land (Ceballos and Do-

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názar 1990, Thompson et al. 1990, Ferrer and Janss 1999). In situations where preferred roosting places are limited, competition among individuals is expected and adjustments in social structure should occur. Information about social structure of roosts in large species is, however, scarce since most research has been descriptive. Investigations are also complicated by the absence of unambiguous sexual dimorphism in many large raptor species.

We examined individual segregation by sex, age, and season in a communal roost occupied year round by Andean Condors (*Vultur gryphus*), a sexually dimorphic scavenger species. Males are 36–37% heavier than females and show a head comb (del Hoyo et al. 1994, Wallace and Temple 1987, Houston 2001). If quality of roosting places differs, competition should be higher for good sites. Quality was evaluated as the degree of insulation of the roosting place, as longer exposure to the sun enables large vultures to spend more time flying (Hiraldo and Donázar 1989) and preening (Houston 1980). Sex and age asymmetries were expected on the basis of the previous observation in intraspecific competitive situations: males feeding at carcasses dominate females and, within sex, younger individuals are subordinate (Donázar et al. 1999). Finally, we expected to find seasonal patterns: selective behavior and competitive pressures should increase during cold seasons, when weather conditions are worse and the number of hours of sun diminishes.

METHODS

STUDY AREA

The study was carried out in Condorito National Park (31°37'S, 64°42'W, 2300 m elevation), Province of Córdoba, Argentina. This area is a great depression 800 m deep, with two large vertical cliffs separated by 1400 m. The cliffs receive direct sun during most of the day, especially during the austral summer. Winds are irregular, but thermal lifts predominate throughout the year. The climate is temperate cold, with average annual temperature 8°C (minimum records of -15°C in August). Rainfall varies from 800–900 mm year⁻¹ (Capitaneli 1979). Grasses (*Alchemilla pinnata*, *Festuca hieronymi*) dominate vegetation; scattered trees (*Polylepis australis*, *Maytenus boaria*) can be found in humid ravines (Luti et al. 1979).

The Andean Condor population in the Condorito region is approximately 30 breeding pairs. In the roost study area the number of roosting condors varies between 80 (summer) and 100 (winter). The proportion of age classes (see below for plumage characteristics) is roughly constant between the two seasons: adult males: 20–25%, adult females: 18–20%, subadult and juvenile males: 26–29%, subadult and juvenile females: 29–33% (Feijóo 1999).

FIELD PROCEDURES

Andean Condors occupy a roosting cliff (400 × 700 m) located in the center of the study area. Between 1995 and 1998 we made observations from a blind situated approximately 1100 m from the roosting area. Each year, observations were carried out for 8 days in each of two seasons: summer (January–March) and autumn (April–June); thus, the total number of field days

was 64. In summer condors were feeding growing chicks, whereas in autumn the postfledging period was finishing and a new breeding season (courtship) beginning. Observations lasted from dawn (when condors began to depart) to dusk (when the last individuals arrived to roost). Each potential roost site had previously been numbered and characterized on the basis of the following variables: (a) *arrival of sunlight*, expressed as the difference (in min) between sunrise and the moment that direct sunlight reached the roost place; (b) *departure of sunlight*, the difference (in min) between the moment that direct sunlight left and the sunset; (c) *roost characteristics*, placed into four categories: (1) ledge without vegetation; (2) ledge with vegetation; (3) sheltered crevice; and (4) cave. We recorded each occasion that a condor landed on each roost site.

The age and sex of the individuals were determined on the basis of morphological and plumage characteristics following del Hoyo et al. (1994) and Donázar et al. (1999). We distinguished six categories on the basis of the two sexes and three age classes: adult, subadult, and juvenile (<1 year). Males and females were identified by size and the presence or absence of a comb. Adult birds have pure-white upperwing coverts; these feathers are gray in subadult individuals, and brown in juveniles. During each observation day we recorded the age and sex of the first and last condor occupying each roost site.

If a condor tried to displace another individual from a roost site we recorded the incident as an interaction; the sex and age of each bird was noted as well as the result (winner and loser) of the fight. Thus, for each roost site we recorded the total number of interactions during each season of the study period. All the considered confrontations involved two birds; we never observed condors trying to displace two or more individuals. There are 3–5 nests in the roosting area; we did not include data from these sites to avoid behavioral patterns related to nest defense.

STATISTICAL ANALYSES

As an initial step to data analyses, we determined for each roost place the most frequent sex-age category detected at the first and last occupation for the entire observation period (per season and year). Roost places were characterized as high quality if they were occupied by condors in >50% of our visits, and as low-quality places if they were occupied in <50% of visits.

Apart from some nonparametric statistics (Siegel and Castellan 1988) we performed generalized linear models (GLM; Nelder and Wedderburn 1972, Dobson 1983, McCullagh and Nelder 1983) to identify those features determining the frequency of selection of roost sites. Separate analyses were performed for summer and autumn. For both seasons, the response variable was the frequency of use of the roost site (number of occasions that the site was occupied by condors in relation to the total number of observation days). Explanatory variables were those described above, plus the year of observation. We used binomial distribution of errors (denominator = 8) and logistic link function (equivalent to a logistic regression; McCullagh and Nelder 1983). Model fitting was done through a modification of the traditional forward stepwise procedure,

TABLE 1. Results of displacement attempts by Andean Condors at roost sites. Figures reflect percentage of attempts won, with the number of observed attempts in parentheses. Figures are pooled from 8 days of observation each summer and autumn from 1995–1998, after tests for effect of season and year were nonsignificant ($P > 0.25$ in all cases).

Actor	Receiver						Total
	Adult male	Adult female	Subadult male	Subadult female	Juvenile male	Juvenile female	
Adult male	36.5 (159)	97.5 (244)	100 (255)	100 (289)	100 (283)	100 (255)	(1485)
Adult female	7.5 (53)	60 (95)	37.5 (104)	76.3 (152)	75.9 (145)	100 (222)	(745)
Subadult male	8.8 (34)	27.5 (69)	51.7 (89)	66.9 (142)	81.1 (169)	77.8 (248)	(725)
Subadult female	5.9 (17)	3.7 (27)	14.6 (41)	42.7 (75)	41.9 (86)	93.9 (196)	(371)
Juvenile male	0 (6)	8.3 (36)	0 (39)	14.4 (125)	58.7 (189)	70.4 (125)	(643)
Juvenile female	0 (2)	0 (0)	0 (1)	0 (12)	0 (30)	48.2 (114)	(114)

which derives, through the principle of parsimony, the least complicated model able to describe the data set (Bustamante et al. 1997). Values reported are means $\pm$ SD.

RESULTS

Andean Condors used a greater number of roost sites in summer than in autumn (1995: 112 in summer vs. 91 in autumn; 1996: 110 vs. 83; 1997: 108 vs. 93; and 1998: 114 vs. 79). We observed strong competition for roosting places. During summer, the number of interactions in relation to the number of occasions that the roost site was used was similar for places of high and low quality (1.0 ± 0.9 , $n = 216$ vs. 1.1 ± 0.6 , $n = 228$, respectively; Mann-Whitney U -test: $Z = -1.2$, $P = 0.24$). In contrast, during autumn low-quality roost places registered a significantly lower rate of interactions than those of high quality (0.8 ± 0.8 , $n = 157$ vs. 1.3 ± 0.7 , $n = 189$ respectively; $Z = -1.3$, $P < 0.001$).

Dominance patterns at roost sites were clearly established by sex and age (Table 1). A strong hierarchy was established by age, with adults being the most dominant birds followed by subadults and juveniles. Within each age category males dominated females. Number of interactions initiated by each sex-age category was strongly related to dominance (Table 1). The most dominant birds (adult males) initiated 38% of the observed aggressive interactions. Subordinate individuals (juvenile females) initiated only 4% of encounters.

We examined whether there was interannual variation in the frequencies of occupation of roost sites of high and low quality by the different age-sex categories between summer and autumn. We did not detect significant differences ($P > 0.25$ in eight tests performed), so we pooled data for further exploratory analyses (Fig. 1). In summer, those birds occupying low-quality places early in the day were mostly young females and, to a lesser extent, young males whereas high-quality places were occupied mainly by adult and

subadult birds of the two genders ($\chi^2_5 = 47.4$, $P < 0.001$). When we tested individual last positions during summer we also detected significant differences ($\chi^2_5 = 268.3$, $P < 0.001$): adult males and females and subadult males appeared more frequently in high-quality places; on the contrary, subadult females and juvenile males and females were relegated to low-quality places. The same trends were apparent in autumn (Fig. 1, initial positions: $\chi^2_5 = 33.5$, $P < 0.001$; last positions: $\chi^2_5 = 211.3$, $P < 0.001$).

The GLM for summer occupation of roosting sites accounted for 35% of the initial deviance, and showed low overdispersion (residual deviance/df = 965.1/442 = 2.2). Only one variable included in the model was negatively related to occupancy: the number of minutes passed between sunrise and the first direct sunlight (Table 2). Thus, Andean Condors more frequently occupied those places receiving the sun early in the morning. The GLM for autumn occupation of roosting sites accounted for 44% of the initial deviance, and showed low overdispersion (647.5/340 = 1.9). Three variables were included in the model (Table 2). The birds selected roost sites receiving sun earliest in the morning and latest in the afternoon. In addition, condors showed preference (in descending order) for sheltered crevices, ledges with vegetation, caves, and ledges without vegetation.

DISCUSSION

Roosting Andean Condors clearly segregated by sex and age: dominant individuals occupied the best places in the roosting area. Thus, peripheral places, more prone to predation and hypothermia, were more commonly occupied by subordinate individuals as in other vulture species (Buckley 1998). Invariably, active competition is the main mechanism determining individual segregation. Andean Condors fought for roosting places, and more interactions were recorded in high-quality sites. Roost structure changed during the last hours of the day: subordinate birds were forced to abandon the places preferred by dominant individuals.

FIGURE 1. Seasonal variation in the frequency of occupation of roost sites of low quality (black bars) and high quality (gray bars) by Andean Condors. Each day, we recorded the age-sex class of the first and last individual to occupy each roost site. Sample sizes (n) are the number of occupied low-quality and high-quality roost sites, respectively. Age-sex categories: A = adult; S = subadult; J = juvenile; M = male; F = female.

TABLE 2. Generalized linear models explaining summer and autumn frequency of occupation of roosting sites by Andean Condors. In the autumn model, three levels of the roost characteristics variable were included in the model.

	Parameter estimate	SE	P
Summer occupancy			
Constant	1.2	0.1	
Arrival of sunlight ^a	-0.5	0.0	<0.001
Residual deviance	965.1		
df	442		
Autumn occupancy			
Constant	1.9	0.1	
Arrival of sunlight ^a	-0.6	0.0	<0.001
Departure of sunlight ^b	-0.2	0.0	<0.001
Ledge with vegetation	0.3	0.1	<0.05
Sheltered crevice	0.5	0.2	<0.05
Cave	0.2	0.2	<0.05
Residual deviance	645.7		
df	340		

^a Difference (in min) between sunrise and the moment that direct sunlight reached the roost place.

^b Difference (in min) between the moment that direct sunlight left the roost place and the sunset.

In our study, intraspecific dominance was determined primarily by age and, within age classes, by sex: older birds and males dominated. This pattern is somewhat different than that found by Donazar et al. (1999) in scavenging Andean Condors in Patagonia, where dominance was determined by sex and, within each sex, by age. In sum, dominance status of females is not similar between breeding and foraging areas. Breeding-area defense may determine their higher status in the study site since there were some nests within the roost (although interactions at nest sites were not recorded). Thus, adult females would successfully expel males (other than their mate) from good resting sites near nests. In other birds of prey, the subordinate sex has been observed collaborating in territorial defense against individuals of the opposite gender (Newton 1979). On the contrary, at carcasses, dominance is established only on the basis of body size, as occurs in many scavenger species (see Donazar et al. 1999).

Quality of roosting sites was determined by the number of sunny hours. Places receiving sun early in the morning were clearly preferred during summer, and Andean Condors used even more sunny exposures during autumn, and interference between individuals was higher as a consequence of lower resource availability (adequate places). Condors selected places receiving not only early morning sun, but also late-afternoon sun. Several nonexclusive hypotheses could explain this trend. First, by selecting sunny exposures Andean Condors maximize the number of hours available for foraging activities, especially in autumn (see also Hiraldo and Donazar 1989). Andean Condors are very heavy birds needing strong thermals or slope winds to gain altitude. In fact, bad soaring conditions can render

them unable to take off and vulnerable to hunting by humans. Second, benefits from sunning can be related to the maintenance of plumage and elimination of ectoparasites (Houston 1980). Finally, occupation of sunny exposures may reduce the energy lost by cold stress (Yackel Adams et al. 2000). Following this last argument, the observed selection of sheltered roost places probably permits some protection from bad weather in rainy or foggy conditions.

Requirements for good roosting places could somewhat limit the spatial distribution and aggregation patterns of the Andean Condor in large parts of its range. In fact, it has been suggested that variations in soaring conditions may be responsible for the disappearance during the Quaternary Period of this species from some parts of South America (Tonny and Noriega 1998, Houston 2001), and for the absence of large vultures in parts of Eurasia (Haller 1983). In addition, stringent roosting requirements, especially during cold seasons, should be taken into account when conservation strategies (including reintroduction) are planned. If natural conditions are not met, birds can be forced into suboptimal habitats with a higher risk of mortality.

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