

Survivorship Patterns in a Population of Andean Condors *Vultur gryphus*

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The life-history strategy of every species can be viewed as lying somewhere along a continuum between extremes of r and K selection (Pianka 1970). Birds at the r-selected end of this continuum tend to have small body sizes, early sexual maturity, large clutches, brief parental care, frequent reproduction and little reliance on high adult survivorship. In contrast, birds at the K-selected end of the continuum tend to have large body sizes, delayed sexual maturity, small clutches, extended parental care, infrequent reproduction and great emphasis on high adult survivorship.

The Andean Condor (*Vultur gryphus*) lies about as far toward the K-selected extreme of the life-history continuum as any bird. Condors are among the largest flying creatures; they do not become sexually mature until at least eight years old; they lay a single-egg clutch; they care for their young for periods of up to a year; they can reproduce only in alternate years; and, at least in captivity, they are among the most long-lived of birds. It has been inferred that condors must have extraordinarily high survival rates in nature. However, there have never been any survival studies of wild condors to confirm this inference, and predictions of high survival rates have been based exclusively on predictive models which calculated survival rates needed to maintain stable populations, given the other assumed life-history traits (e.g. Mertz 1971, Verner 1978).

We studied a regional population of Andean Condors in Peru, and we are able to construct tentative schedules of age-specific survival on the basis of our observations of 58 marked individuals over a period of 51 months. With this information on survivorship, together with other information on reproduction, we can discuss the dynamics of this condor population and the prospects for its long-term maintenance.

STUDY AREA

From May 1980 to August 1982 and March 1984 to August 1984, we studied condors in two nearby areas of Northern Peru: the Cerro Illescas on the Sechura Peninsula and the Olmos and Naupe region in the western Andean foothills. Located at the tip of the Sechura Peninsula (6.00°S latitude x 81.00°W longitude), the Cerro Illescas is an isolated mountain range bordered on three sides by the Pacific Ocean and separated from the Andes Mountains to the east by over 150 km of sparsely vegetated desert. From a maximum elevation of 480 m, dry steep-walled canyons radiate to the periphery of the hills that cover an area of approximately 800 km². These canyons provide condors with ledges for roosting and nesting. There was little human activity in the area.

The second area was 150 km east of the Cerro Illescas in the western foothills of the Andes near the towns of Olmos (6.00°S x 79.46°W) and Naupe (5.35°S x 79.46°W), which are 75 km apart. Brushy vegetation and scattered trees cover the steep slopes and gorges in this area, which rises in

elevation to about 1,000 m. Precipitous escarpments in these Andean foothills provide secure roosting and nesting sites, isolating condors to some extent from the activities of ranchers living in the desert grasslands below. Additional details about the study areas are provided by Wallace and Temple (1987a,b,c).

These two study sites supported partially overlapping populations of condors. Individuals that roosted or held nesting territories in the Andean foothills made occasional foraging excursions across the desert to scavenge on the beaches of the Sechura Peninsula. The condors that roosted or held nesting territories in the Cerro Illescas were, however, less mobile and tended to range into the Andean foothills infrequently.

METHODS

We trapped 46 wild condors, using rocket nets baited with carcasses of domestic animals. Ages of the trapped condors were determined on the basis of their plumage and bill and eye colours, which change sequentially until birds are six years old and adult plumage is attained (Wallace & Temple 1987a, K.C. Lint, pers. comm. and J.W. Carpenter, pers. comm.). We attached numbered patagial tags (Wallace *et al.* 1980) to the wings of all trapped condors, and 15 of them were also fitted with solar-powered radiotransmitters. We radiotracked these condors using conventional radiotelemetry procedures (Mech 1983).

In addition to the 46 marked and radioed wild birds, we also monitored the survival of 11 marked and radioed condors that had been produced in captivity and released on the Cerro Illescas study site; see Wallace & Temple (1978b) for details on the release program. We assumed that the observed survival rate of these birds during their first year in the wild was equivalent to that of wild condors during the first year after fledging. Because of a severe drought in the study area, condor reproduction was impaired (Wallace & Temple 1987c), and there were too few wild yearlings for us to measure their survival rates.

Condors moult continuously at equatorial latitudes, and individual differences in their moult ing schedules allowed us to individually identify another 63 wild birds solely on the basis of patterns of loss and regrowth of flight feathers. Snyder & Johnson (1985) described this method of identifying individuals.

The total resident population of condors on the study areas was believed to be at least 120 individuals: 46 marked wild birds, 63 individually recognizable but unmarked resident wild birds, and 11 marked birds that we released from captivity. The age structure of this population is summarised in Table 1, which shows that our sample of 46 marked wild birds represented a substantial portion of the total population and had a representative age structure.

We used the analytical methods described by Heisey & Fuller (1985) to estimate age-specific survival rates for our 57 marked condors. We grouped these condors into three age categories: individuals less than a year old and hence not yet fully independent; individuals between one and six years old and hence not yet in the definitive plumage; and individuals more than six years old. For condors in each age category we accumulated a number of bird-months of observations by regularly resighting or relocating each marked individual.

Table 1. Age structure of the wild condor population on study areas.

Age in years ¹	Marked birds		Unmarked birds ²	
	Number ³	Percent of birds	Number ³	Percent of birds
6	33	72	48	80
4-5	5	11	3	5
3-4	0	0	2	3
2-3	2	4	3	5
1-2	6	13	7	11

1 Age determined by plumage and bill and eye colour.

2 Identified through moult patterns.

3 Differences in the age structure of the marked and unmarked groups were not significant ($\chi^2 = 2.98$, $df = 4$, $P = 0.56$).

These cumulative observations began when the bird was marked and ended either when the bird was known to have died or when we terminated our field studies. We estimated monthly survival rates (s_m) for each age category from the number of bird months of observations (x_m) and the number of mortalities (y_m), using the following formula:

$$\underline{s}_m = \frac{\underline{x}_m - \underline{y}_m}{\underline{x}_m}$$

We assumed monthly survival rates (s_m) were constant within each age category, and we calculated annual survival rates (s_y) as:

$$\hat{s}_y = \underline{s}_m^{12}$$

After obtaining estimates of age-specific survival for the population, we used the methods described by Henny *et al.* (1970) to estimate the reproductive rate that would be required to counterbalance mortality in the population. We assumed that condors begin breeding when eight years old and then breed in alternate years, that there is no reproductive senility in the population, and that the population has a stable age-distribution. We calculated "balancing productivity" as:

$$\underline{2m} = \frac{2(1-\underline{s}_a)}{\underline{s}_f \cdot \underline{s}_j^5 \cdot \underline{s}_a^2}$$

where $\underline{2m}$ is the number of offspring each adult female in the population must produce annually to counterbalance mortality and where estimated annual survival rates for cohorts are: s_f for dependent fledglings (0-1 years old), s_j for juveniles (1-6 years old), and s_a for adults (more than 6 years old).

RESULTS AND DISCUSSION

In Table 2 we present our estimates of annual survival rates for three age classes of Andean Condors. Our field observations and the analytical techniques of Heisey & Fuller (1985) produce survival estimates that increase with age, varying from 0.75 in the first year of life to 0.94 in fully mature adults. Survival rates of adult Andean Condors are, as suspected, among the highest estimated for any wild bird population (Ricklefs 1973). Our estimates from field studies are also remarkably close to those Verner (1978) calculated on the basis of a simple model of the dynamics of a population of California Condors (*Gymnogyps californianus*), a species with almost identical life-history traits. He calculated that a stable California Condor population must have an annual adult survival rate of 0.95 and sub-adult survival of 0.89.

Table 2. Estimated annual survival rates for a marked population of Andean Condors.

Age classes	Age (years)	Number of marked birds	Number of bird-months of observation	Number of deaths recorded	Annual survival rate with 95% confidence interval
Adults	6	33	367	2	0.94(0.85-1.02)
Independent juveniles	1-6	13	115	1	0.90(0.71-1.08)
Dependent juveniles ¹	0-1	11	175	4	0.76(0.55-.97)

¹ Inferred from data on captive-reared birds for 1 year after their release.

From these estimates of age-specific survival rates, we calculated "balancing reproduction", the rate of reproduction that exactly counterbalances mortality and thus stabilises population size. With annual survival rates of 0.94, 0.90 and 0.75 for each of the three age classes, the balancing reproductive rate for the population is 0.31 offspring per adult female per year. This means that adult female condors must rear at least one young during every three-year period. At best each female could rear no more than one young every two years, so somewhat less than the maximum rate of reproduction would be required to stabilise the size of our population under prevailing patterns of survivorship.

Wallace & Temple (1987c) have shown that the reproductive cycles of these condors are tied closely to periodic El Niño events that strongly affect rainfall patterns and hence productivity in the Peruvian coastal deserts. Condors are normally able to reproduce only during the two or three years during and after El Niño events, which occur at intervals that average five years but range from two to twelve. Wallace & Temple (1987c) have shown that these condors are therefore reproducing at near the absolute minimum rate needed to maintain their numbers.

This climatic restriction on their breeding activities means that these desert-inhabiting condors could not maintain their population size intrinsically if there were any increases in their mortality rates. It is noteworthy that few populations of condors have been able to survive in coastal deserts of South America where they come into frequent contact with human beings. Condors are persecuted in populated coastal areas (McGahan 1972), and we suspect that most coastal populations dwindled to extinction owing to elevated mortality rates resulting from persecution. Our study populations have so far been largely protected from heavy persecution by the remoteness of their habitat. It is alarming, however, that of the seven deaths that we recorded in the population, three were caused by man. The long-term prospects for the condor populations on our study areas may thus depend primarily on how well the birds are protected from human persecution. The construction of new roads and an oil pipeline through the Sechura Peninsula will, for example, increase human activities in the area and heighten the probability of human-induced mortality. We fear that without special protection the local condor populations could eventually be extirpated, following the fate of other coastal condor populations in the past.

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