RANGE USE AND MOVEMENTS OF CALIFORNIA CONDORS[1]

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Abstract. Between 1982 and 1987, photographic and telemetric tracking of California Condors (*Gymnogyps californianus*) yielded information on use of the last known range of the species by 23 individual birds. Except for yearlings, most and possibly all individuals in the population used all major foraging zones. Use of the foraging zones was not uniform among individuals, however. Breeding pairs tended to forage most frequently in zones close to their nests (usually within 70 km, occasionally as far away as 180 km). Immatures (at least older immatures), unpaired birds, and paired birds that were not breeding foraged more widely. Male and female adults used the foraging range in a similar manner. Although most portions of the foraging range received some condor use throughout the year, use varied seasonally in accord with recent and historical patterns of food availability.

Nesting areas were separated from foraging zones and were visited much less freely than foraging zones. Paired birds tended strongly to visit only their own and immediately adjacent nesting areas. Their nesting areas remained stable over the years. Unpaired adults and immatures ranged more widely among nesting areas.

Condors were sometimes documented flying more than 200 km and traversing the entire range of the species during a day. Birds were variably social in movements. Pair members tended to stay together during long-distance travels. Immatures and unpaired birds sometimes traveled with other condors but often moved singly. In years when the population still included many breeders, the largest observed aggregations included one-half to two-thirds of the total population.

The comparative strengths and weaknesses of photographic and telemetric methods are described for tracking and other research endeavors.

Key words: Gymnogyps californianus; scavenger; radio telemetry; photography; home range; foraging; endangered.

INTRODUCTION

In 1987, the last wild California Condor (*Gymnogyps californianus*) was brought into captivity. Captive breeding has been highly successful (Kiff 1990; Wallace and Wiley, in press), and the first captives were released to the wild in January, 1992. Because the demise of the wild condor population resulted mainly from mortality threats that were not uniformly distributed, such as poisoning and shooting (Snyder and Snyder 1989),

the success of releases will probably depend in large measure on what sorts of movement patterns develop in released birds. Thus, understanding what forces controlled the range use of the last wild population of California Condors may be crucial for successful reintroductions of the species. Such understanding may also contribute to conservation efforts with other large scavenging birds.

Animals that feed on sparse, patchily distributed food resources must travel extensively to forage successfully. How far they should travel and how far they actually do has received little theoretical (Andersson 1978, Pyke 1983, Green 1987) or empirical (Andersson 1981, Ott et al. 1985) attention. From information on flight speed and duration, Wilbur (1978b) suggested that con-

dors might be able to fly up to 165 km (100 miles) in a day. However, until the present study, the longest recorded flights within a day were only 110 km (70 miles) (Koford 1953).

Substantial ranges and daily movements have been reported for other large vultures. Bearded Vultures (*Gypaetus barbatus*) traveled up to 40 km in a day, and more when food was limited (Glutz et al. 1971). Pairs of Bearded Vultures observed in France used areas of roughly 300 sq km (Terrasse et al. 1961); pairs in southern Africa had overall home ranges of approximately 4,000 sq km (Brown 1991). European Griffon Vultures (*Gyps fulvus*) were observed using areas as far as 50–60 km from roosts or nests (Westernhagen 1962). Rueppell's Griffon Vultures (*Gyps rueppellii*), soaring at speeds of up to 47 km/hr, regularly traveled 150 km from their nests in search of food (Houston 1974b; Pennycuick 1972, 1983). In contrast, one radiotagged Cape Vulture (*Gyps coprotheres*) foraged only 10–15 km from its nest colony (Boshoff et al. 1984). Nonbreeding Andean Condors (*Vultur gryphus*) covered areas as large as 1,300 sq km during a year; adults foraged up to 200 km from nests (Wallace and Temple 1987). Despite these studies, seasonal, sex, and age-class variations in movements have not been described comprehensively for any large scavenging bird.

Koford (1953) and Wilbur (1978b) differed substantially in their descriptions of California Condor movements. Koford assumed that any condor not engaged in breeding might be seen anywhere in the range of the species on any day. In contrast, Wilbur believed that condor movements were more limited and that condors existed in two main subpopulations with a line of separation that was, at most, rarely crossed.

With the establishment of the Condor Research Center (CRC) in 1980, intensive research began on many aspects of California Condor biology. Two major approaches were adopted which permitted study of movements: (1) radio transmitters enabled observers to identify and follow some condors directly, and (2) a system of photographic identification of flying birds allowed the first complete censuses to be performed and provided additional data on ranging patterns of all condors (Snyder and Johnson 1985).

In this paper, we describe and discuss how individuals used their home ranges, how far they traveled from nests, and effects of factors such as age, breeding condition, and sex on movement patterns. In addition, we compare observed seasonal trends with patterns described by other researchers. Finally, we compare the data gathered by photographic and telemetric means and comment on the effectiveness of each technique.

STUDY AREA

During our investigations, condors ranged through the mountains and foothills of a six-county area in southern California (Fig. 1). Nest and roost sites were located in the Coast, Transverse, and Sierra Nevada mountain ranges. Most foraging took place in the southern San Joaquin Valley foothills (including the Hudson, Snedden, and San Emigdio ranches, the Tehachapi Mountain foothills, the western Sierra Nevada foothills), and in the Elkhorn Hills-Cuyama Valley-Carrizo Plain complex to the southwest of the San Joaquin Valley.

Nest sites in the Coast and Transverse ranges were situated in cliffs surrounded by chaparral habitat interspersed with conifers, mainly bigcone Douglas-fir (*Pseudotsuga macrocarpa*) (Snyder et al. 1986). Roost sites in these ranges were located in cliffs or in tall conifers. The two nests known in the Sierra Nevada were in giant sequoias (*Sequoiadendron giganteum*) in mixed-conifer stands. The major known roost site in the Sierra Nevada was on a rocky ridge with scattered ponderosa pines (*Pinus ponderosa*). All nest and major roost sites were on public lands, including the Los Padres National Forest (encompassing the Sespe and Sisquoc condor sanctuaries), Angeles National Forest, Sequoia National Forest, Blue Ridge Wildlife Habitat Area, and Hopper Mountain National Wildlife Refuge (HMNWR).

Major feeding areas were in foothill grassland and oak-savannah habitat. Supplemental feeding stations were located on Hudson Ranch (now the Bitter Creek National Wildlife Refuge), in the Tehachapi Mountain foothills, in the southern Sierra Nevada foothills, and on HMNWR. With the exception of HMNWR, the foraging areas were on private cattle-ranching lands.

For the purposes of this report, we subdivided condor feeding range into six major zones and segregated nest sites into eight nest areas (Fig. 1). The feeding zones were delineated by examination of feeding location data, which showed well-separated clusters of feeding sites. The nest areas
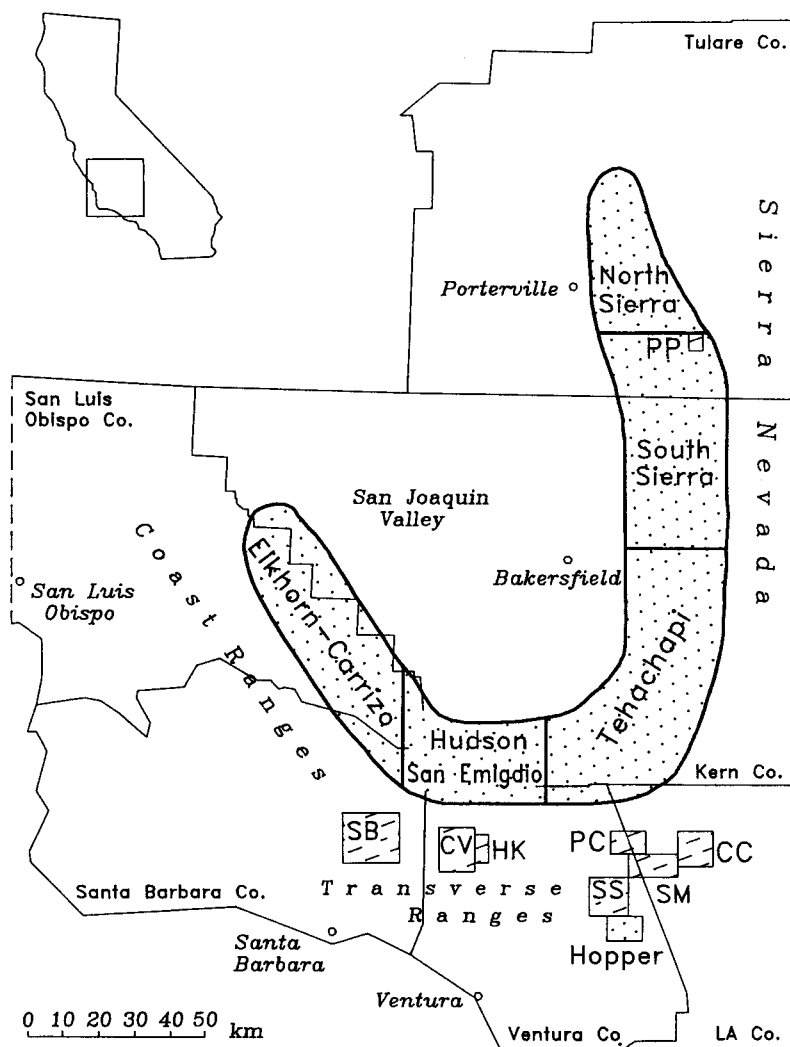
FIGURE 1.   Nest areas (hatching) and major feeding grounds (stippling) of California Condors, 1982–1987.

were delineated to include all nest sites used by given pairs. Pairs with scattered nest sites were assigned larger nest areas than pairs observed for only a single season or pairs with closely-spaced nest sites.

METHODS

Photographic records covered the period January 1982–December 1985, and included all 23 condors found alive during the study (Snyder and Johnson 1985). Observations of radiotagged birds covered October 1982–April 1987 and included locations of nine radiotagged condors (Table 1).

EQUIPMENT AND GENERAL PROCEDURES

For telemetry studies, California Condors were trapped with cannon nets or pit traps. Patagially mounted radio transmitters and tags were attached to both wings (Wallace et al. 1980). Blood samples were drawn for genetic analysis, sexing, blood chemistry, and contaminants studies. Weights and notes on condition and plumage were taken; birds usually were released within 1–2 hr of capture. Two birds were radiotagged in late 1982. Seven additional birds were tagged in late 1984; and by 1985, seven of nine surviving wild birds were radiotagged. Ground observers

TABLE 1. Dates for which photographic and visually-confirmed (v-c) telemetry data were collected for 23 California Condors. The fate of each bird (dead, disappeared, or captured) is also indicated. With the exception of UN1 and CCF, v-c telemetry observations began when birds were radiotagged (see text).

Condor[a]	Sex	V-c telemetry data	Photographic data	Fate
BFE	M		6/82–4/85	died 4/85
BOS	F		9/82–11/83	died 11/83
CCF	F	4/85–9/85[b]	1/82–9/85	captured 9/85
CCM	M		1/82–10/84	disappeared winter 84/85
CVF	F		2/82–11/84	disappeared winter 84/85
CVM (AC7)	M	12/84–1/85	2/82–1/85	disappeared early 1985
HIW (IC4)	M	11/84–6/85	6/82–6/85	captured 6/85
IC1 (IC1)	M	10/82–3/84	8/82–3/84	died 3/84
PAX	M		5/82–12/82	captured 12/82
PCA (AC6)	M	11/84–7/86	1/82–10/85	captured 7/86
PCB	?		1/82–11/83	disappeared late 1983
PPF	F		5/82–10/84	disappeared winter 84/85
REC (AC9)	M	12/84–4/87	1/82–11/85	captured 4/87
SBF (AC3)	F	11/84–1/86	5/82–11/85	died 1/86
SBM (AC2)	M	11/82–12/86	2/82–10/85	captured 12/86
SMA	?		1/82–3/82	disappeared spring 1982
SMM (AC5)	M	12/84–2/87	1/82–12/85	captured 2/87
SSF (AC8)	F	10/84–6/86	5/82–11/85	captured 6/86
SSM	M		5/82–11/84	disappeared winter 84/85
UN1	F	3/85–8/85[b]	5/82–7/85	captured 8/85
UN2	?		2/82–4/82	disappeared spring 1982
UN3	?		9/83	disappeared fall 1983
WGI	?		2/82–8/82	disappeared summer 1982

[a] Birds who were members of known pairs at the beginning of the photocensusing study were assigned names beginning with a two letter abbreviation for their general nest area and ending with M for the male and F for the female (Snyder and Johnson 1985). Telemetric names are given in parentheses.
[b] These birds were never radiotagged but were identified visually by major plumage characteristics and lack of radiotags after the wild flock was reduced to fewer than 10 birds.

used receivers equipped with hand-held Yagi antennas to detect transmitter signals. Aerial tracking was conducted from a light plane using an omnidirectional whip antenna and paired Yagi antennas. Transmitters were routinely detected at distances of 150 km when the line of sight was unobstructed.

Visual observations were made with binoculars and spotting scopes. Photographic data were collected with 35 mm cameras equipped with telephoto lenses with focal lengths of 300 to 1,000 mm (Snyder and Johnson 1985).

CATEGORIES OF OBSERVATION

Telemetry observations were recorded by ground and aerial observers. Those observations in which birds were visually confirmed or were accurately pinpointed by aerial overflights are referred to as "v-c telemetry observations" for the rest of the paper. Individual radiotagged birds were identified by transmitter frequency. When several birds were present, changes in signal intensity could often be matched to changes in posture or flight path to allow observers to distinguish among the birds at a distance. Toward the end

of the study, telemetry also aided the identification of two untagged birds (UN1 and CCF) by process of elimination. These two birds could be identified by their lack of transmitters and by distinctive feather patterns. When observers identified these birds visually, the locations were recorded as v-c telemetry data.

Ground observers also used telemetry to detect radiotagged birds that were not visually confirmed. These telemetric observations consisted of single bearings from observer locations. Due to signal bounce in rough terrain, signal strength variation during circling, and various problems with early transmitters, triangulations from telemetry data proved too imprecise for most levels of investigation. Fortunately, triangulations were seldom the only form of data available for a bird on a given day. Since v-c telemetry and photographic locations were the most accurate data available, we have limited our analyses to these data.

Photographic data were originally collected to census the condor population, but also were used to record condor locations (Snyder and Johnson 1985). Ground observers at nest sites and feeding

sites photographed birds whenever they were within range (< 1 km). Comparisons of molt condition and feather damage patterns permitted birds to be identified rigorously.

DATA COLLECTION

Location data were not gathered using a formal sampling scheme. Under the conditions of the study, neither a random nor a systematic sampling effort was feasible. Neither were such sampling schemes considered a high priority in relation to other research needs. The major goal of field workers was to track as many birds as possible as closely and frequently as possible. Ground observers concentrated their efforts at known nesting areas and feeding grounds. To avoid redundant observations, the pilot avoided tracking birds near sites under constant ground observation. Thus, most aerial tracking data were collected along condor travel routes and away from monitored nest sites and foraging grounds.

Several factors affected the way in which condor location data were collected. Differences in transmitter performance, differences in level of effort temporally and spatially, and differences in the use and effectiveness of photographic and v-c telemetry techniques all biased data collection.

Data inconsistencies resulting from transmitter malfunctions occurred most often during 1985. As failed transmitters were replaced with improved versions, signal detection became more reliable. Birds carrying malfunctioning transmitters could often be identified by patagial tag number, by process of elimination, or by their behavior toward an identifiable mate.

Photographic and v-c telemetry observations were emphasized to varying degrees during the study, in part due to changes in numbers of observers. Observers continuously attended all known active nest sites during the study and took photographs at every opportunity. Use of photography at feeding grounds increased substantially after 1984. Photography ceased after December 1985, at which time the remaining wild birds were all radiotagged.

V-c telemetry was biased towards foraging zones overall, and until late 1984 represented only a small fraction of age and sex classes in the population. Except at the SB nest area, nest observers did not have telemetry receivers until 1985 (of the nesting birds, only SBM was radiotagged before this time).

Throughout the study, nest areas were observed during all daylight hours when birds were breeding, but only sporadically when they were not. Feeding zone observations varied greatly among areas. The Hudson-San Emigdio zone was the most consistently monitored foraging ground in all years. The Tehachapi zone was monitored closely after 1984 but not earlier. The Elkhorn-Carrizo zone and the Southern Sierra zone were monitored erratically throughout the study. The Hopper zone received little coverage except during spring 1985. The Blue Ridge roost area in the Northern Sierra zone was observed daily during the summers of 1983–1985, but much less intensively at other times.

Use of other sites was observed when birds traveled away from known nest, roost, and feeding areas and when ground or air observers were available to track. In general, areas that were not suited to nesting, roosting or feeding received relatively little coverage. Aerial coverage of these parts of the range, and of the Sierra zones, was much better than ground coverage, especially after 1984.

Before spring 1985, five feeding sites were stocked on an irregular basis: one each in the southern Sierras, Tehachapis, Elkhorn Plains, Hudson Ranch, and HMNWR. After spring 1985, the Hudson and Tehachapi sites were stocked daily, and the site in the southern Sierras was stocked when birds were known to be in the area. Stocking at the HMNWR and Elkhorn sites stopped after spring 1985. Stocking was used to attract birds to trap sites, and later, to provide uncontaminated food sources, although condor use of stocked carcasses was highly variable.

DATA PREPARATION

V-c telemetry and photographic observations were recorded as locations on an X,Y grid overlaid on a map of condor range. Photographic locations were recorded as the photographer's position. V-c telemetry observations were recorded to the nearest kilometer and less often to the nearest 500 m. Bird locations were analyzed by grouping them in the zones and areas shown in Figure 1. Locations along travel corridors between feeding zones and nest areas are not discussed in this paper.

Birds were categorized in age/breeding groups as immature, adult unpaired, adult paired not breeding, and adult breeding (Appendix). A bird was considered immature if it exhibited any im-

mature feathering or coloration characteristics (Snyder 1988) and if it had not yet shown signs of courtship or breeding. A bird was considered paired if it showed courtship behavior toward and consistently accompanied a second bird. Two possibly homosexual pairs were observed during the study period (SMA and SMM; PCA and PCB). They were considered paired because they displayed courtship, copulatory, and nest-inspection behaviors, although they never produced eggs.

Breeding observations covered periods of courtship, copulation, nest-site inspection, incubation, nesting care, and post-fledging dependency. Suspected homosexual pairs were considered to be breeding as long as courtship, copulations, or nest-site inspections occurred. Heterosexual pairs whose eggs were taken for artificial incubation were considered to be breeding until their final egg of the season was taken, or until nest-site inspections ceased if these continued after the last egg was taken.

Immature birds were assigned to yearly age classes on the basis of fledging dates. The first year class extended until the first anniversary of fledging; birds moved into a new age class at each anniversary of fledging. Once birds showed breeding behavior of some kind or developed full adult coloration they were classified as adults. Since most adults could not be aged, we made no attempt to assign adults to age classes.

Nest areas were classified as own, adjacent, or unassociated. Observations of birds at their current or previously-used nest areas were classified as own. The SM and PC nest areas were contiguous, and birds using either of the two passed through the other regularly. Similarly, the CV and HK nest areas were contiguous, as were the SM and CC nest areas. Contiguous nest areas were classified as adjacent. In addition, the PC and SM nest areas were on flight paths from the SS nest area to foraging grounds in the San Joaquin Valley foothills (Fig. 1). Most occurrences of SS birds in the PC and SM nest areas were not true nest "visits," but simply transits on the way to and from foraging grounds. These occurrences were also classified as adjacent. Visits not classified as own or adjacent were considered unassociated.

Because many roost areas and travel corridors were not closely monitored, we have limited our analyses to data from nest areas and feeding zones. Due to the biases and irregularities in the data set, statistical techniques were not appropriate for most analyses. Several analyses were restricted to relatively unbiased subsets of the data to permit the most reliable conclusions.

Observations were reduced to one entry per bird per zone per day to standardize the data. Overall analyses of movements used both photographic and v-c telemetry data; the data sets were combined before standardization. Analyses of differences between photographic and v-c telemetry data were made after separately standardizing the two data sets.

RESULTS

Twenty-three condors were observed and their locations recorded during January 1982–April 1987 (Table 2). The number of observations varied widely among birds. More locations were recorded for radiotagged birds than for birds that were unmarked (location-days/month for nine tagged birds: $\bar{x} = 13.8$; location-days/month for 23 untagged birds: $\bar{x} = 2.41$, $t = 7.05$, $P < 0.01$).

ADULT USE OF FEEDING GROUNDS

Observers at feeding grounds recorded 16 of the 18 adult condors known during the study period (UN2 and SMA were observed only at nest areas before disappearing early in the study). Of the 16 adults sighted on feeding grounds, UN3 was observed only twice before disappearing. Use of the six feeding zones by the remaining 15 adult condors is presented in Table 3.

Eleven of the 15 adults were observed in the northern Sierra zone; thirteen were observed in the southern Sierra zone. Two birds were never observed in the Sierra zones; of these, CVM was observed once in the Tehachapi zone, and only PCB, a bird that disappeared relatively early in the study (late 1983), was never observed in any of the eastern zones.

The southern San Joaquin Valley foothills (Hudson-San Emigdio) were used by all 15 adults. Thirteen of these adults were documented in the Elkhorn-Carrizo zone, in the western part of condor range. Only five adults were recorded in the Hopper zone, but this zone was quite small in comparison to the other zones and was monitored only after 1984. Within the limitations with which observations were made, these data indicate that many, and very possibly all, adult condors were familiar with all major feeding zones used by the remnant population.

Effect of breeding status on use of feeding

TABLE 2. Data available for California Condors 1982–1987. One location on one day is one location-day.

Condor	Photo location-days	V-c telemetry location-days	Total days	Total location-days
BFE	76		76	76
BOS	35		35	35
CCF	122	37	141	142
CCM	71		70	71
CVF	80		80	80
CVM	83	5	87	87
HIW	81	64	117	123
IC1	28	225	184	240
PAX	17		17	17
PCA	128	245	300	337
PCB	49		49	49
PPF	89		88	89
REC	148	570	530	665
SBF	154	173	271	293
SBM	203	722	703	838
SMA	3		3	3
SMM	130	277	344	371
SSF	125	325	337	420
SSM	76		75	76
UN3	2		2	2
WGI	5		5	5
Totals	1,705	2,643	3,514	4,019

grounds. During the study, paired birds used 1–4 feeding zones while breeding and 2–5 zones while not breeding; unpaired adults used 2–6 feeding zones (Table 3). Apparent differences here may have been due in part to relatively limited coverage during the early breeding season; winter weather frequently prevented ground tracking in some foraging zones. Nevertheless, a close examination of the data confirms that nesting birds did restrict their travels. None of the birds that nested in the southern part of the range was ever detected in the North Sierra zone while breeding (Table 3). Further, the birds that visited the South Sierra zone while breeding were, in almost all cases, birds whose nests were closest to the Sierras (SSF, SSM and CCF, CCM) or were actually in the Sierras (PPF and SMM). Use of the Sierra zones was much more general among paired nonbreeding birds and among unpaired birds.

In a like manner, the one pair nesting in the Sierras (PPF and SMM) was never detected in the Elkhorn-Carrizo zone and rarely detected in the Hudson-San Emigdio zone while breeding, despite intensive coverage of the Hudson-San Emigdio zone during this period. These same birds used the Hudson-San Emigdio zone with

frequency when they were unpaired and while paired but not breeding.

The tendency of paired birds to favor foraging zones close to their nest sites can be analyzed more rigorously by limiting analysis to photographic data from 1982 to 1984 and comparing use of foraging zones by the four pairs that were active throughout this period: SB, CV, SS1, and CC (Table 4). For this analysis we combined the two Sierra foraging zones with the Tehachapi zone, as coverage of these eastern zones was relatively low in these years and numbers of observations in these zones were relatively few. Although absolute levels of photographic coverage of the feeding zones varied greatly, one can argue that all birds present within a zone had equal probabilities of being photographed. If so, the overall proportions of records of various pairs in a zone should give a good indication of the relative extent to which the pairs emphasized the zone in their foraging activities. This assumption of equal probabilities of being photographed may have been violated to some extent by the fact that SBM was radioed during part of this period; this may have inflated the number of photographs obtained of the SB pair.

The data suggest that the various foraging zones were used most heavily by the nearest nesting pairs (Table 4). Thus, the largest proportions of photographs in the Hudson-San Emigdio zone were of the SB and CV pairs, the closest nesting pairs. Also, the SB pair was photographed more frequently in the Elkhorn-Carrizo zone than the CV pair and was correspondingly closer to this zone than the CV pair. In a similar manner, the largest proportions of photographs in the Tehachapi and Sierra zones were of the SS1 and CC pairs, the closest pairs, and use of the Hudson-San Emigdio zone was predictably greater by the SS1 pair than by the CC pair. Note, however, that the CC pair was photographed in the Elkhorn-Carrizo zone somewhat more frequently than the CV and SS1 pairs.

Overall, the records in Table 3 suggest that breeding pairs did not normally move more than 50–70 km from their nesting areas when foraging. For example, the SS2 pair (SSF and REC) commonly foraged in the Tehachapi zone some 40–50 km from their nest during the breeding season. More distant movements by pairs were generally limited to periods when they were not breeding. However, exceptions occurred. One particularly well documented long-distance trip

TABLE 3. Adult condor use of feeding grounds (location-days) as a function of breeding status. Birds shown here were observed at least ten times at feeding grounds. An empty column indicates the bird was not in that condition during the study.

	Condor														
	SBM	SBF	CVM	CVF	PPF	SMM	PCA	PCB	CCF	CCM	SSF	SSM	REC	BFE	UNI
Total visits															
North Sierra	1	1	0	0	33	12	4	0	0	2	2	4	23	8	1
South Sierra	5	1	0	2	9	29	7	0	4	2	40	5	34	18	11
Tehachapi	55	8	1	0	1	87	61	0	5	5	56	0	158	0	1
Hudson–San Emigdio	404	179	66	61	26	177	163	21	79	17	70	25	184	45	87
Elkhorn–Carrizo	53	17	1	4	1	0	5	1	3	3	1	1	2	0	3
Hopper	0	0	0	0	0	7	3	0	2	0	31	0	62	0	0
Months observed	58	44	34	33	29	61	52	23	44	34	49	31	18	16	39
Unpaired															
North Sierra	0		0		2	8	4	0	0		1		8	4	1
South Sierra	4		0		0	20	6	0	2		28		8	10	11
Tehachapi	46		0		1	85	60	0	0		13		87	0	1
Hudson–San Emigdio	107		5		15	163	146	0	67		45		41	18	87
Elkhorn–Carrizo	10		1		0	0	4	1	0		1		0	0	3
Hopper	0		0		0	7	3	0	2		16		19	14	0
Months observed	12		2		11	41	28	23	10		12		11	14	37
Paired, nonbreeding															
North Sierra	1	1	0	0	11	4	0	0	0	2	1	4	0		
South Sierra	1	1	0	1	7	8	1	0	1	1	10	3	4		
Tehachapi	7	8	1	0	0	2	0	0	5	5	23	0	33		
Hudson–San Emigdio	195	140	55	53	11	12	17	21	12	17	14	15	6		
Elkhorn–Carrizo	23	12	0	0	1	0	1	1	3	3	0	0	1		
Hopper	0	0	0	0	0	0	0	0	0	0	2	0	5		
Months observed	24	24	12	12	10	10	14	13	21	21	15	13	4		
Paired, breeding															
North Sierra	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0
South Sierra	0	0	0	1	2	1	1	0	1	1	2	2	0	1	0
Tehachapi	2	0	0	0	0	0	1	0	0	0	20	0	23	0	0
Hudson–San Emigdio	99	39	6	8	0	2	0	0	0	0	11	10	0	0	0
Elkhorn–Carrizo	20	5	0	4	0	0	0	0	0	0	13	1	14	0	0
Hopper	22	20	20	0	9	0	0	0	0	0	22	0	4	2	2[a]
Months observed	22	20	20	21	9	11	10	10[a]	13	13	22	18	4	2	2[a]

[a] These birds were observed in this breeding status, but not on the feeding grounds.

TABLE 4. Proportional use of feeding grounds by four pairs of California Condors, 1982–1984, as determined from photographic data. Proportions are the fractions of visits to the zone made by given pairs.

Feeding zones	SB pair	CV pair	SS1 pair	CC pair	Total
Sierra and Tehachapi					
Proportional use	0.05	0.08	0.48	0.40	
Location-days	2	3	19	16	40
Hudson-San Emigdio					
Proportional use	0.46	0.33	0.13	0.08	
Location-days	168	122	47	30	367
Elkhorn-Carrizo					
Proportional use	0.61	0.15	0.06	0.18	
Location-days	20	5	2	6	33

was made by CVF at a time when she was tending a chick. Seen at her nest in midmorning, she was photographed in the southern Sierra zone by midafternoon of the same day, a distance of approximately 150 km. Similarly, the male of the PP pair, SMM, made two journeys of approximately 180 km between his active nest in the Sierras and the Hudson-San Emigdio zone.

The longest observed daily travels were for unpaired and immature condors. Several months after losing his mate, SBM traveled from the SB nest area, through the Hudson-San Emigdio zone to the Tehachapi zone and back to his nest area within a day, a distance of about 200 km. IC1, an immature, was recorded traveling the full length of the condor range in a day, from the northern Sierra zone, through the Tehachapi zone, across to a roost just north of the SB nest area, a distance of approximately 225 km. Not only did data suggest that all condors in the remnant population were familiar with the entire range of the species, it appeared they were at least sometimes capable of moving between any two points in that range in a single day.

Sex differences in use of feeding grounds. Of the adult condors listed in Table 3, six were female, eight were male and the sex of one bird was undetermined. Overall, both males and females were observed in 3–6 feeding zones. Four unpaired females were observed in 3–6 feeding zones; six unpaired males were observed in 2–6 feeding zones. Five paired, nonbreeding females were observed in 2–5 feeding zones; seven males of the same status also were observed in 2–5 feeding zones. Six breeding females were observed in 0–4 feeding zones, while eight breeding males were observed in 1–3 feeding zones. Thus, there was no gross evidence to suggest that the sexes used different numbers of feeding zones.

Similarities between male and female foraging patterns were especially apparent within pairs (Table 5). For example, the proportional use of

TABLE 5. Use of feeding zones (location-days) by members of pairs of California Condors, 1982–1986. Observations cover the entire period the pairs existed. SBM was radiotagged in 1982, SBF was radiotagged in 1984; SSF and REC were radiotagged throughout the period they were paired.

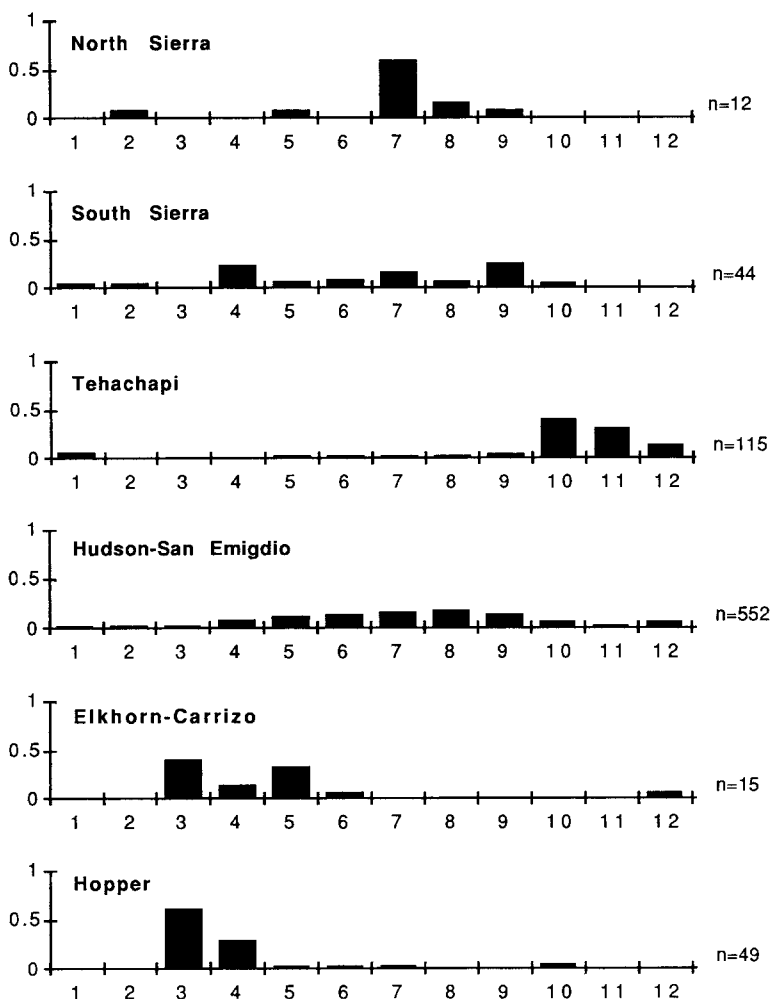| Feeding zone	Pair											
	SB		CV		PP		CC		SS1		SS2	
	SBM	SBF	CVM	CVF	SMM	PPF	CCM	CCF	SSM	SSF	REC	SSF
North Sierra	1	1	0	0	4	31	2	0	4	2	0	0
South Sierra	1	1	0	2	9	9	2	2	5	9	4	5
Tehachapi	9	8	1	0	2	0	5	5	0	1	55	42
Hudson-San Emigdio	300	177	61	61	13	11	17	13	25	22	6	3
Elkhorn-Carrizo	43	17	1	4	0	1	3	3	1	1	1	0
Hopper	0	0	0	0	0	0	0	0	0	0	19	15
Observed as a pair:	Feb 82–Dec 85		Feb 82–Nov 84		Apr 83–Oct 84		Jan 82–Oct 84		May 82–Nov 84		Nov 85–Jun 86	

FIGURE 2.   Seasonal use of six feeding zones by six California Condors (SBF, SBM, SMM, PCA, SSF, REC) during 1985. Of these birds, only SBF and SBM bred in 1985 (Jan–Apr). Bars show proportion of yearly use that occurred during the given month. Sample sizes are number of location-days at the site during the year.

various feeding grounds was almost identical in the SB male and SB female. Likewise, males and females of the CC pair, the CV pair, and both SS pairs (SSF and SSM; SSF and REC) used the foraging grounds similarly. In part, the within-pair similarities resulted because pair members tended to forage and travel together during much of the year. Only during incubation and early chick rearing was it necessary for pair members to forage alone.

However, despite the overall similarities in foraging patterns of pair members, the PP male and female (PPF and SMM) may have used somewhat different foraging grounds while breeding (Tables 3 and 5): the female was frequently observed at a roost in the northern Sierra zone but the male was almost never observed in any known foraging zone during the same period.

Seasonal changes in foraging. To obtain the most unbiased evaluation of seasonal patterns, we limited our analyses to those birds for whom telemetry data were available throughout 1985 or 1986, the years of most intensive aerial and ground tracking. Photographic efforts were strongly biased seasonally, and photographic data were difficult to obtain at seldom-used sites.
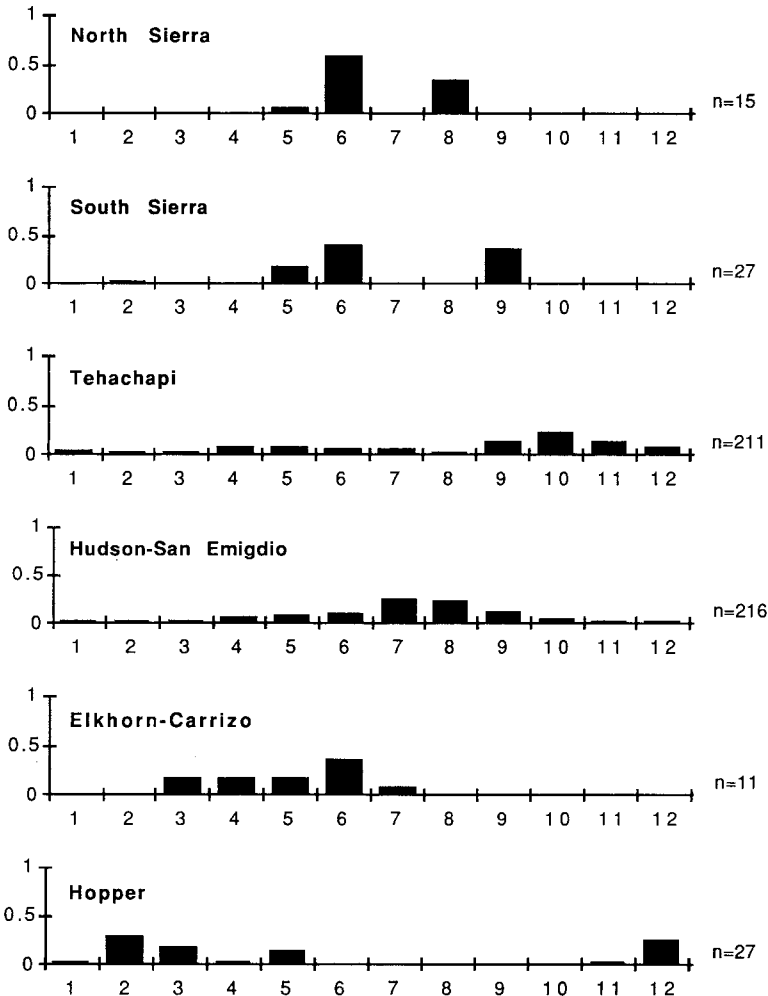
FIGURE 3.   Seasonal use of six feeding zones by three male California Condors (SBM, SMM, REC) during 1986 (only REC bred, Jan–Apr). Bars show proportion of yearly use that occurred during the given month. Sample sizes are number of location-days at the site during the year.

Condors in less usual locations were generally located with telemetry, and often could not be photographed due to limited access.

Use of foraging zones varied seasonally, but was quite similar in the two years of intensive tracking (Figs. 2, 3). For example, the Hudson-San Emigdio zone was used throughout much of the year but most heavily between July and September while the Elkhorn-Carrizo zone was used most between March and June. Significant use of the Hopper zone for feeding was only detected during the spring of 1985. Most Hopper records in 1986 represented tangential overflights by REC, the male of the nearby nesting SS2 pair (the female was captured during 1986 and her location data are not included in Fig. 3).

ADULT VISITS TO NESTING AREAS

Data on visits to nest areas by 17 adult condors were analysed by breeding status (Table 6). We observed ten unpaired adults in nest areas. Of these, UN2 was never observed paired, BFE was unpaired before finding a mate, and UN1 was unpaired both before and after she paired with BFE. The remaining seven birds were observed unpaired only after losing mates (CVM disap-

peared shortly after becoming unpaired). Of the unpaired adults, CVM, CCF, SSF and REC were observed only in their own or adjacent nest areas. The remaining six adults were all observed in at least one unassociated nest area while unpaired; SMM was observed in all possible unassociated nest areas.

Paired and breeding birds were almost never observed visiting unassociated nest sites. Twelve adults were observed while paired but not breeding; none was observed to visit an unassociated nest area. Sixteen adults were observed while breeding. Of these, only PPF was observed visiting an unassociated nest area; just prior to egg laying, she once visited her mate's previous nest with him. All other breeding birds were documented visiting only own or adjacent nest areas.

Among unpaired birds, the reasons for apparent individual differences in tendencies to visit unassociated areas were unclear but may have included the lengths of associations with own nest areas, previous unknown breeding histories, and gender differences. Birds losing mates tended to remain associated with former nest areas. Among females, neither CCF nor SSF bred the season after losing their mates, despite the presence of unpaired males. CCF was taken captive before the second breeding season after her mate's death. SSF paired with REC in the second season after losing her earlier mate, and the new pair used her previous nest area. Both SSF and CCF had histories of at least five breeding seasons at their own nest areas and both continued to frequent their own nest areas after their mates died. In contrast, after losing her mate late in courtship, UN1 left her briefly-used nest area within a few days and roosted elsewhere until her capture later that year. None of these females was recorded visiting unassociated nest areas following losses of their mates.

Among males who lost mates, SMM remained at his 1982 nest area for at least two months after SMA disappeared. The following spring he was observed at his 1982 nest area once, but also visited one adjacent and one unassociated nest area. By late spring, he was observed in association with PPF, and the following year they nested at the PP site, 140 km away from his 1982 nest area (her history at PP was unknown). When PPF was lost, SMM moved to a roost area 37 km from SM and 150 km from PP. SBM, REC and PCA continued to roost in their nest areas following the loss of their mates, although SBM and PCA also visited other nest areas. When

SBM lost his mate of five plus years in 1986, there were no unpaired females remaining in the population; nevertheless he was observed visiting three unassociated nest areas. Shortly thereafter, REC lost his mate of one year. There were no females remaining in the population and he was not observed visiting any unassociated nest areas. PCA continued to roost in the area he had shared with his possibly homosexual mate until he was captured three years after his mate disappeared; during these three years, he was observed visiting four unassociated nest areas.

USE OF CONDOR RANGE BY IMMATURE CONDORS

Observations of immature condors were classified by year class (Table 7). Data for BOS, PAX and WGI were limited mainly to the year following fledging (age class 1). These birds were observed in their natal nest areas, and in 1–3 feeding zones each. They were not observed on the foraging grounds until late in their first years.

HIW, REC, IC1 and BFE were observed later in their development. Observations suggested that these birds visited more areas as they aged (note: IC1 died early in his fifth year). However, this trend was probably at least partly due to increased coverage through the years and the progressive radiotagging of birds.

IC1 and REC were documented visiting nonnatal nest areas as four-year-olds, while HIW was first detected in nonnatal nest areas as a five-year-old. BFE was not observed in any nest area as an immature, possibly because he was never radiotagged. Of these birds, only IC1 was radiotagged as a four-year-old. HIW and REC were radiotagged as five-year-olds. Since no birds were radiotagged as two- or three-year-olds, we cannot exclude the possibility that visits to nonnatal nests sometimes occurred at these ages. Similarly, while most older immatures visited all major foraging zones, the ages at which they began traveling extensively were not determined.

COMPARISON OF PHOTOGRAPHIC AND V-C TELEMETRY DATA COLLECTION METHODS

For all radiotagged birds, photographic efforts resulted in fewer location-days than did v-c telemetry efforts (Table 8). In addition, photography consistently documented fewer foraging and nesting areas for these birds than did v-c telemetry. Only data from January–November 1985 were considered for these comparisons be-

cause both types of data collection were used extensively during this period.

Feeding grounds. For each bird, photography recorded bird attendance at all feeding zones for which eight or more v-c telemetry locations were recorded. Eighteen bird-feeding zone combinations had fewer than eight v-c telemetry observations (Table 8); photography recorded 10 of these.

Nest areas. Photography recorded use of unassociated and adjacent nest areas less completely than use of feeding zones. Of 23 bird-nest area combinations recorded with v-c telemetry, only six were also recorded photographically.

SBM and SBF were the only breeding birds during 1985, and both v-c telemetry and photographic data recorded their presence in their nest area. All three of the unpaired adult birds of this year had attempted breeding in previous years. V-c telemetry and photographic data recorded the presence of two of them in their previous nest areas; SMM was recorded once in his old SM nest area by v-c telemetry, but was not photographed there. Of three bird-adjacent nest area combinations recorded with v-c telemetry, one was recorded photographically. Of 15 bird-unassociated nest area combinations recorded with v-c telemetry, one was recorded photographically.

DISCUSSION

The recent range of the California Condor included roughly two million ha, much of it inaccessible because of rugged terrain or because it was privately owned and not open to CRC personnel. There was no possibility of obtaining condor movement data that were not biased by such geographic constraints. This problem was most pronounced with photographic data and with ground tracking data. Tracking data from airplanes were also biased, especially because relatively few birds were radiotagged until late in the study, but also because the logistics of aerial tracking dictated biased patterns of data gathering. Despite the substantial biases, it was still possible to determine many important aspects of condor movements from the data.

INDIVIDUAL FAMILIARITY WITH FORAGING ZONES

The data in Tables 3 and 7 indicate that all condors may have been familiar with all major feeding zones by their fourth or fifth year. Although some adults were not observed in all feeding

zones, the holes in the data are few, and most can be explained or eliminated by considering other data. For example, of ten birds who were not recorded in the Hopper zone, seven were dead or dying before any systematic coverage occurred in that zone. Of the remaining three, two were detected at the SS nest area only 2 km away. Of the four birds who were not recorded in the Tehachapi zone, three visited the Sierra zones, and almost surely passed through the Tehachapis en route (only once did we document a condor moving directly across the San Joaquin Valley, rather than through foothills and mountains around the valley).

Because only two adults observed in this study were ever observed as immatures, we could not determine how widely most condors ranged in their lifetimes. Nevertheless, the especially wide-ranging habits of older immature condors (Table 7) suggested that the few zones in which some adults were not observed may well have been visited when these birds were younger. Also, because the few feeding zones where we did not record certain adults tended to be zones where our coverage was least thorough, and because most of the holes in the data were for birds that were never radiotagged or were radiotagged only briefly, many of the apparent failures of birds to visit zones may only have represented missed observations.

Condors often feed socially and roost communally (Koford 1953, Wilbur 1978b, Johnson et al. 1983). They frequently circle high above carcasses for long periods before landing and obviously are attracted to flying conspecifics from distances up to several kilometers. Such behavior permits condors to use one another as guides to food and explains, at least in part, why they should be familiar with all feeding zones. Similar attraction to conspecifics has been observed in other large scavenging birds (Houston 1974a, Mundy 1982, Wallace and Temple 1987).

AGGREGATIONS ON FEEDING GROUNDS

Despite the mutual attraction of conspecifics, we never observed all members of the population simultaneously in a feeding zone until the population had been reduced to 3–5 birds. In earlier years, the largest groups observed were 14 birds of 21 known alive in 1982, 13 of 19 birds in 1983, 10 of 15 birds in 1984, and 7 of 9 birds in 1985. Through 1984, most adults in the population were paired and breeding (Snyder and Snyder 1989), limiting their opportunities to join

TABLE 6. Adult condor visits (location-days) to nest areas as a function of breeding status. An empty column indicates the bird was not in that condition during the study. Boldface text indicates own nests; asterisks indicate adjacent nests. For UN1, who was unpaired before and after having a mate, all unpaired observations occurred before breeding. All unpaired observations of other birds (except UN2, who was never known to be paired) occurred after mate loss.

	Condor																
	SBM	SBF	CVM	CVF	PPF	SMM	SMA	PCA	PCB	CCF	CCM	SSF	SSM	REC	BFE	UN1	UN2
All visits																	
SB nest area	**312**	**87**	0	0	0	3	0	2	0	0	0	0	0	0	0	2	2
CV nest area	1	0	**19**	**13**	0	4	0	10	0	0	0	0	0	0	0	0	0
PP nest area	0	0	0	0	**18**	18	0	0	0	0	0	0	0	0	0	1	0
SM nest area	1	0	0	0	1	**13**	**3**	*6	*1	0	*1	*20	*1	*10	0	0	1
PC nest area	1	0	0	0	0	*3	0	**61**	**26**	*1	0	*17	0	*16	0	0	0
CC nest area	0	0	0	0	0	2	0	0	0	**48**	**41**	0	0	0	1	0	1
SS nest area	2	0	0	0	0	11	0	4	0	0	0	**183**	**40**	160	0	1	0
HK nest area	0	0	0	0	0	5	0	11	0	0	0	0	0	0	**4**	**4**	0
Months obs'd	58	44	34	33	29	61	2	52	23	44	34	49	31	18	16	39	2
Unpaired																	
SB nest area	**66**		0			3		2		0		0		0	0	2	2
CV nest area	1		**5**			4		10		0		0		0	0	0	0
PP nest area	0		0		**0**	**0**		0		0		0		0	0	1	0
SM nest area	1		0			**9**		*4		0		*13		*2	0	0	1
PC nest area	1		0			*3		**31**	**21**	0		*6		*4	0	0	0
CC nest area	0		0			*1		0		0		0		0	1	0	1
SS nest area	2		0			11		4		0		**57**		63	0	1	0
HK nest area	0		0			5		11		0		0		0	0	0	0
Months obs'd	12		2		11[a]	41		28	13	10		12		11	14	37	2
Paired, nonbreeding																	
SB nest area	**68**	**32**	0	0	0	0		0	0	0	0	0	0	0			
CV nest area	0	0	**2**	**1**	0	0		0	0	0	0	0	0	0			
PP nest area	0	0	0	0	**0**	**0**		0	0	0	0	0	0	0			
SM nest area	0	0	0	0	0	**0**		*1	0	0	0	0	0	*3			
PC nest area	0	0	0	0	0	*1		**8**	**3**	*1	0	*2	0	*4			
CC nest area	0	0	0	0	0	0		0	0	**6**	**10**	0	0	0			
SS nest area	0	0	0	0	0	0		0	0	0	0	**28**	**1**	31			
HK nest area	0	0	0	0	0	0		0	0	0	0	0	0	0			
Months obs'd	24	24	12	12	10[a]	10		14	13	21	21	15	13	4			

TABLE 6. Continued.

	SBM	SBF	CVM	CVF	PPF	SMM	SMA	PCA	PCB	CCF	CCM	SSF	SSM	REC	BFE	UNI	UN2
Paired, breeding																	
SB nest area	178	55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
CV nest area	0	0	12	12	0	0	0	0	0	0	0	0	0	0	0	0	
PP nest area	0	0	0	0	18	18	0	0	0	0	0	0	0	0	0	0	
SM nest area	0	0	0	0	1	4	3	*1	*1	0	*1	*7	*1	*5	0	0	
PC nest area	0	0	0	0	0	0	0	22	23	21	0	*9	0	*8	0	0	
CC nest area	0	0	0	0	0	0	0	0	0	0	31	0	0	0	0	0	
SS nest area	0	0	0	0	0	0	0	0	0	0	0	98	39	66	0	0	
HK nest area	0	0	0	0	0	0	0	0	0	0	0	0	0	4	4	4	
Months obs'd	22	20	20	21	9	11	2	10	10	13	13	22	18	4	2	2	

a These birds were observed in this breeding status, but not in nest areas.

large flocks. In early breeding stages, nest duties usually required one pair member to remain at the nest while the other foraged; in addition, pairs usually foraged close to their own nests and often did not overlap greatly with other pairs in their use of foraging grounds while breeding. After 1984, the population was composed mostly of unpaired birds who were freer to join one another on the foraging grounds.

In the early 1980s, when the fraction of the population breeding was substantial, the largest flocks comprised about two-thirds of the total population. Similar but somewhat smaller proportions appeared to characterize earlier decades. For the late 1960s, the largest flock observed was 27 birds, when the total number of condors was estimated at 50–60 (Wilbur 1978b). The largest reported flock in the early 1960s was 63 birds, when the total population was probably on the order of 100 birds; and the largest flock reported in the 1940s was 85 birds, when the total population may have been about 150 birds (Johnson 1985, Snyder and Snyder 1989). As discussed in Snyder and Snyder (1989), the latter high counts and population estimates are in some dispute, but regardless, it is interesting that they indicate an apparently similar ratio of high flock counts to population sizes as in more recent data.

SEASONAL USE OF FEEDING GROUNDS

The seasonal patterns of use of foraging grounds (Figs. 2, 3) were reasonably consistent with use patterns reported historically for these zones. Thus, our observations indicated principal use of the Sierra zones occurred during the summer, matching historical reports (Koford 1953, Miller et al. 1965, Wilbur 1978a). Observations indicated that the Tehachapi foraging grounds were used most heavily in the fall, and that use of the Hudson-San Emigdio zone peaked in late summer and early fall, matching the historical patterns reported by Wilbur (1978b) and Johnson et al. (1983). The strong spring peak in use of the Elkhorn-Carrizo zone during our study may also have matched historical patterns reasonably well, judging from sightings listed in Koford (1953), Miller et al. (1965), and Wilbur (1978b), although this correspondence is less certain. Lastly, our observations of spring condor activity in the Hopper zone (formerly the Percy Ranch) match reports of winter and spring activity in this region (Koford 1953, Miller et al. 1965, Wilbur 1978a).

TABLE 7. Use of condor range (location-days) by seven immature condors, as a function of age. Of the birds shown, IC1 was radiotagged as a four-year old, and HIW and REC were radiotagged as five-year olds. Boldface text indicates natal nest, when known.

Feeding zones/ Nest areas	BOS 1	BOS 2[a]	PAX 1[b]	WGI 1[a]	HIW 2	HIW 3	HIW 4	HIW 5[b]	REC 2	REC 3	REC 4	REC 5[c]	IC1 3	IC1 4	IC1 5[a]	BFE 4	BFE 5[c]
North Sierra					2	3	5	1		1	4	10		24	6	2	2
South Sierra	2					6	5	4	1	6	4	11		65	32		7
Tehachapi						2						15		24	11		
Hudson-San Emigdio	19	9	15	3	8	7	7	50	12	12	19	94	4	15	18	10	17
Elkhorn-Carrizo	3					5	1	5				1		6	6		
Hopper								1				24					
SB nest area	2							7			1			6	3		
CV nest area			2					2						3	1		
SM nest area											1						
PC nest area												3		2			
CC nest area									1			1		1			
SS nest area				2										1			
PP nest area												8		5			
HK nest area								1				1		3			
Total	26	9	17	5	10	23	18	72	14	19	29	168	4	156	77	12	26

[a] Individual died during this year.
[b] Individual was captured during this year.
[c] Individual became an adult in the next year.

For the most part, seasonal shifts in foraging appeared to coincide with local changes in food availability, although condor traditions may also have played a role. The fall peak in condor use of the Tehachapi zone appeared, at least in part, to be correlated with deer-hunting season, with many records of birds feeding on deer gut piles or on crippling-lost deer (often in clear preference to the calf carcasses stocked at the feeding site). The late summer peak in condor use of the Hudson-San Emigdio zone appeared to be tied to high availability of aborted calves (Johnson et al. 1983, Studer 1983). Historically, the main food supply in the Hopper zone was calving mortality, which peaked in winter and spring (Koford 1953). In 1985, when condors were again discovered using the zone, they were feeding on a naturally-occurring calf carcass. Reasons for the spring peak

TABLE 8. Comparison of photographic (ph) and visually-confirmed telemetric (vct) location-days for seven condors observed during January–November 1985. HIW was only observed during January–June. Boldface text indicates own nest areas, and asterisks indicate adjacent nest areas of adults.

	SBM (paired male) vct	ph	SBF (paired female) vct	ph	HIW (immature male) vct	ph	SMM (unpaired male) vct	ph	PCA (unpaired male) vct	ph	SSF (unpaired female) vct	ph	REC (immature male) vct	ph
North Sierra	0	0	0	0	0	0	1	1	0	0	1	0	8	2
South Sierra	1	0	1	0	2	2	5	3	3	0	24	3	5	3
Tehachapi	7	0	7	1	0	0	11	2	29	2	19	3	23	3
Hudson-San Emigdio	95	51	71	37	41	26	68	44	96	42	39	23	76	59
Elkhorn-Carrizo	5	1	7	1	7	2	0	0	1	0	0	0	1	0
Hopper	0	0	0	0	1	0	3	4	1	2	8	8	15	16
SB nest area	**47**	**18**	**58**	**21**	6	0	3	0	1	0	0	0	0	0
CV nest area	0	0	0	0	2	0	1	0	1	0	0	0	0	0
SM nest area	0	0	0	0	0	0	1	0	*2	*2	*12	0	2	1
PC nest area	0	0	0	0	0	0	0	0	6	1	*6	0	1	0
SS nest area	0	0	0	0	0	0	7	0	2	0	**46**	**17**	12	0
HK nest area	0	0	0	0	1	0	3	0	10	0	0	0	1	0
Total	155	70	144	60	60	30	103	54	150	47	137	54	144	84

in use of the Elkhorn-Carrizo zone and the broad summer peaks in use of the Sierra zones were less clear.

Despite the good overall correlation of seasonal use of various foraging zones with food supplies, the seasonal shifts in emphasis from one zone to another during our studies sometimes took place contrary to "apparent" food-availability considerations. Thus, although the CRC provided a steady supply of food in the Hopper zone in late spring 1985, the birds abandoned the zone by summer in accordance with historical patterns. Wilbur (1978a) similarly found strong seasonality in use of artifically-provided carcasses in the Hopper zone in spite of steady availability of food. Also in 1985, condors made their traditional shift from the Hudson-San Emigdio zone in late summer and early fall to the Tehachapis in midfall, despite continued provisioning of food on Hudson-San Emigdio. Since there continued to be natural foods available in unprovisioned zones (in addition to the carcasses provided at artificial feeding sites), this persistence of seasonal shifts in foraging should not be surprising. As Wilbur et al. (1974) and Wilbur (1978a) found in earlier years, feeding programs were only partly successful in controlling foraging activities of the wild population.

FACTORS FAVORING RANGING BEHAVIOR

Despite the stability of seasonal foraging patterns, one of the most striking results overall of the study was the fact that most birds continued to travel quite widely among feeding zones throughout the year. Maintaining familiarity with food supplies through much of the foraging grounds may be adaptive for several reasons. Even relatively reliable food sources are not completely predictable. Timing and abundance of carcasses may vary substantially from year to year within a zone, and mammalian scavengers or Golden Eagles (*Aquila chrysaetos*) may often prevent condors from feeding at some sites. In addition, unpredictable carcasses can be found throughout the foraging range at any time during the year. And in exceptional cases, unexpected local abundances of food occur, such as are created by disease outbreaks (Miller et al. 1965). These food supplies can only be discovered with a foraging strategy that emphasizes monitoring of large areas. Birds accustomed to a food supply that is unpredictable spatially and temporally can

be expected to retain wide-ranging prospecting behavior and to be quite slow to abandon such behavior in the face of the development of a constant food supply at a fixed location.

The relatively confined movements of breeding condors were very likely a result of the constraints on foraging imposed by the need to return frequently to nests. Similarly, Brown (1991) found that Bearded Vultures foraged less widely when breeding; overall ranges averaged 4,000 sq km, in comparison to 600 sq km during the early nestling period and 1,300 sq km later in the breeding cycle.

It is also important to note that evidence from Andean Condor and European Griffon Vulture studies (Wallace and Temple 1987; Terrasse 1988; M. P. Wallace, pers. comm.) indicates that under some circumstances the wide-ranging behavior of large scavenging birds can be modified to very confined foraging patterns. On the northwest coast of Peru, a region with a remarkably constant food supply of washed-up seabirds and marine mammals, Wallace found several pairs of Andean Condors that limited their foraging activities to stretches of beach only several kilometers long. Similarly, in release experiments with captive-bred Andean Condors in nearby regions, Wallace found that birds were generally content to remain dependent on provided food and were induced to adopt wider-ranging foraging behavior only by positioning food in unpredictable locations. Experience (traditions) may be important in influencing the willingness of birds to exploit new foraging sites. Birds that mature knowing only a constant, predictable food supply in one area may be reluctant to feed at multiple sites. In part, they may hesitate to land at carcasses in new foraging areas because of possible dangers from hidden mammalian predators in unfamiliar sites. Such an effect could also explain the general reluctance of released European Griffon Vultures to land at new feeding stations (Terrasse 1988).

FORAGING MOVEMENTS OF IMMATURE CONDORS

Immature condors had no ties to mates or chicks and did not exhibit any consistent associations with nest areas after reaching independence. Immatures were not constrained in their choices of feeding sites, and, being subordinate to adults and Golden Eagles at carcasses, may have needed significantly more feeding opportunities than

adults to get enough food. While a majority of the observations for a given immature were usually in a single feeding zone, immatures (at least older immatures) visited most feeding zones several times during the year, with a relatively even distribution among zones (Table 7).

COMPARISONS WITH EARLIER RESEARCH

Koford (1953) assumed that most California Condors using the northern foraging zones in summer were nonbreeders, presumably because most known nest sites were in the southern portion of the range and because of the commuting costs entailed for birds foraging at great distances from their nests. Our data support this conclusion in that during the entire study we never recorded any members of actively breeding pairs from the southern areas using the northern Sierra zone. The only nesting bird recorded in the northern Sierras was PPF whose nest was at the southern boundary of that zone.

In his discussion of condor numbers, Koford (1953) implicitly assumed that condors seen in the Sespe Sanctuary (nest area SS) on one day might be the same individuals seen in the Sisquoc Sanctuary (near nest area SB) on the next day. However, data in Tables 6 and 7 indicate that such movements between nest areas did not normally occur for paired birds and were relatively uncommon for unpaired and immature birds. Wilbur (1978b) similarly called attention to a general absence of condor movements along the mountain ranges between the Sisquoc and Sespe nesting areas. In our observations, normal movements of paired adults involved direct flights from their respective nesting areas to the nearest portions of the feeding grounds, and thence up and down the foraging grounds to a greater or lesser extent, followed by direct flights back to their respective nesting areas from the foraging grounds. While condors did mix quite fluidly on the foraging grounds, they showed little tendency to move from one nest area to another. At least in recent years, counts of birds in the Sespe Sanctuary could be added to counts in the Sisquoc Sanctuary the next day with near total confidence that different birds would be involved. Koford's assumption of potential synonymy of birds in the Sespe and Sisquoc sanctuaries was one factor leading to his relatively low population estimate for condors (Wilbur 1978b, Johnson 1985, Snyder and Johnson 1985, Snyder and Snyder 1989).

We found no evidence to support a division of the condor population into two or more subpopulations, as postulated by Wilbur (1972, 1978b). Wilbur proposed a dividing line between subpopulations along the Ventura Co.-Santa Barbara Co. border, an unlikely place for such a division (Fig. 1). The Elkhorn-Carrizo feeding zone lies immediately to the west, while the Hudson-San Emigdio zone lies immediately to the east. These zones have been major condor foraging grounds for many years and are not separated by any significant barriers. Condors using one of these zones readily moved to the other throughout the duration of our studies. For example, the normal foraging activities of the SB pair took them across Wilbur's line on a near-daily basis.

It was clear as a generality that all condors saw all other condors in the population with frequency. There is no evidence that individuals in the remnant wild population might have had difficulty locating members of the opposite sex for reproductive purposes.

MATE SELECTION AND INVESTIGATION OF NEST AREAS

Among adult condors, unpaired birds were the most common visitors at unassociated nest sites (Table 6). Sometimes breeding pairs drove visitors from their nest areas, but there were frequent exceptions. For example, in 1982 the CC pair once landed and copulated near the SM nest site without provoking any hostile reaction from the resident pair. In contrast, the SM pair frequently engaged in vigorous aggressive interactions with the adjacent PC pair. IC1, an immature male, and SMM, an unpaired male, visited the active SS nest area together in 1983. At one point, they even landed at the entrance to one of the nest caves together with the resident pair without eliciting any appreciable aggression from the pair. Similarly, UN1 was tolerated at the PP nest site in 1984 with only mild aggression from the resident male. Conceivably, the tendencies to attack or tolerate intruders were related in part to kinship factors, but we have too little information on the relatedness of the condors to draw any firm conclusions.

Very probably, unpaired adults visited unassociated nest areas primarily to seek mates. Mate seeking was especially apparent in a series of nest visits by UN2 in 1982. Within two months this bird made five visits to four nests areas and flew in "pair flights" (Snyder 1988) with single members of the resident pairs in several cases. Shortly thereafter this bird disappeared.

While unpaired adults and immature birds were the most common visitors to unassociated nest areas, we observed considerable variation in the extent to which they visited nests. In the breeding season after SSF and CCF lost their mates, all the unpaired males in the population visited the SS nest area and flew with SSF at least once, but only SMM visited the CC nest area (for him an adjacent area). Interestingly, SSF readily re-paired in the wild and in captivity, while CCF has been so aggressive to prospective captive mates that she was resexed to verify her gender in 1989 (C. Cox, S. Kasielke, pers. comm.). The possession of a nesting area may not be the only criterion by which condors select or search for mates.

The way in which immature birds learned the location of nests was not documented although it seems likely that they followed other birds in most cases. Immature birds were occasionally observed visiting historic nests alone (for example, REC at the PP nest in 1984) but these may not have been first visits. In one of the most intriguing instances of nest visitation, documented visually in 1984 from a helicopter, three birds were observed flushing from the branches immediately adjacent to the sequoia nest studied by Koford (1953). This site was not known to have been active since 1950 (although it was not monitored in many of the intervening years). The birds involved were believed to have been SMM and PPF, whose active nest was only 5 km away, and REC, a four-year-old immature, although identity of these birds could not be rigorously confirmed. Clearly the Koford nest, a very inconspicuous site, was still known to the condor population although it may have been unused for as long as 34 years. Knowledge of its location may have been transmitted from bird to bird through the generations. Conceivably, we witnessed REC's first visit to the site.

COMPARISON OF DATA COLLECTION METHODS

The combined photographic and v-c telemetry data permitted us to describe development of range-use patterns in young condors, seasonality in use of feeding grounds, and condor use of nesting and feeding grounds in relation to breeding status. Each of the data sets contributed to the analyses, but the two techniques had different strengths and weaknesses depending on the topic under investigation.

Both forms of documentation adequately detected condors on their most frequently used feeding grounds and at their own nest sites (Table 8). Both indicated that young and unpaired condors tended to make wider use of the feeding range than did paired condors.

V-c telemetry identifications, especially from aerial tracking, recorded rare events better than did photographic identifications (Table 8). Rare events included visits to less-frequently used feeding grounds (e.g., Elkhorn-Carrizo), and visits to adjacent or unassociated nest sites.

Observers generally entered infrequently-used areas only when they tracked birds to them. Thus, data from such areas were usually v-c telemetry data, often from aerial observers. Because observers did not have off-road access in many feeding grounds, photographs from secondary feeding grounds were often difficult to obtain unless a bird flew near a road.

Telemetry revealed that birds often visited unassociated and adjacent nest areas when observers were not present to photograph them. In general, ground observers in nest areas monitored nest sites only when they were active. In addition, visiting birds sometimes did not fly near enough to photographers to allow clear photographs. Telemetric identification of radiotagged nest visitors was straightforward, even at a distance.

Flight paths (not discussed in this paper) were determined primarily by aerial tracking mainly because this technique permitted the birds to be followed continuously. Telemetry was also especially useful for tracking immature birds, whose movements were often relatively unpredictable.

While photography was less useful than telemetry for recording unpredictable or rare events, it was the only technique that provided movement and range-use data for all the individuals in the population. Furthermore, it was photography, primarily, that revealed that condors seen at a nest site in a given year were the same condors that had used the site in previous years. And it was photography, primarily, that determined the identity of members of new pairs (Snyder and Johnson 1985).

Currently, the cost of one set of basic telemetry equipment is several times the cost of an adequate SLR camera and telephoto lens. Telemetry also necessitates substantial investments in trapping equipment and efforts. For telemetry studies, each additional observer requires an additional set of tracking equipment and each additional bird followed requires an additional transmitter and additional trapping effort. For

photographic work, an additional observer requires an additional set of camera equipment, but each additional bird requires only additional photographs.

While the usefulness of telemetry is limited by equipment costs, the usefulness of photography is limited by species characteristics and population size. Photographic identification requires differences in molt patterns or markings among individuals. Both cues were used to identify condors, although the bulk of identifications were based on molt condition which is highly irregular and individually idiosyncratic in condors (Snyder et al. 1987). Individuals of species with more regular molt may be much more difficult to identify photographically unless they commonly have individual feather-damage markings large enough to be visible at a distance. Patagial tags can be used as individual markings on species that lack them, but patagial tags are often harder to discern or photograph at a distance than plumage patterns.

Photographic identification requires that differences between individuals be reliable and discernable. As the number of individuals being identified increases, the likelihood that some individuals will resemble each other closely also increases. For a system of plumage identification such as was used for condors, the upper feasible limit to analysis may be about 50 birds.

Other limitations of the photographic method include substantial investments in darkroom time and analysis effort. In addition, there is an unavoidable delay between photographing a bird and identifying it. For studies in which locations of individual animals must be constantly monitored, or when dead individuals must be recovered to determine causes of mortality, telemetry is essential. Similarly, if rare events are of interest, or if movement patterns are unpredictable, telemetry can be immensely useful. But the data presented here clearly demonstrate that photography can provide adequate movement information for some species and at a substantially lower cost than telemetry.

The photographic method also has the considerable advantages of rapid startup time, immediate coverage of all individuals in a population, avoidance of investments in capturing birds, avoidance of artifacts of behavior resulting from capture and handling of birds, and greater safety, because birds do not have to be captured and handled (unless markers are to be used). Cen-

susing and mortality-rate determinations for the condor were made primarily from photographic data (Snyder and Johnson 1985, Snyder and Snyder 1989). Telemetry replaced photography in these roles only after all condors were radio-tagged.

LITERATURE CITED

ANDERSSON, M. 1978. Optimal foraging area: size and allocation of search area. Theor. Popul. Biol. 13: 397–409.

ANDERSSON, M. 1981. Central place foraging in the Whinchat, *Saxicola rubetra*. Ecology 62:538–544.

BOSHOFF, A. F., A. S. ROBERTSON, AND P. M. NORTON. 1984. A radio-tracking study of an adult Cape griffon vulture *Gyps coprotheres* in the south-west-

ern Cape Province. S. Afr. J. Wildl. Res. 14:73–78.

BROWN, C. J. 1991. Bearded vultures in southern Africa. WWGBP Newsletter 14:17.

GLUTZ VON BLOTZHIEM, U. N., K. BAUER, AND E. BEZZEL. 1971. Handbuch der Vögel Mittel-Europas, Bd. 4. Akademische Verlagsgesellschaft, Frankfurt.

GREEN, R. F. 1987. Stochastic models of optimal foraging, p. 273–302. In A. C. Kamil, J. R. Krebs, and H. R. Pulliam [eds.], Foraging behavior. Plenum Press, New York.

HOUSTON, D. C. 1974a. Food searching in griffon vultures. E. Afr. Wildl. J. 12:63–77.

HOUSTON, D. C. 1974b. The role of griffon vultures Gyps africanus and Gyps ruppellii as scavengers. J. Zool. (Lond.) 172:35–46.

JOHNSON, E. V. 1985. Commentary, California Condor population estimates. Condor 87:446–447.

JOHNSON, E. V., D. L. AULMAN, D. A. CLENDENEN, G. GULIASI, L. M. MORTON, P. I. PRINCIPE, AND G. M. WEGENER. 1983. California Condor: activity patterns and age composition in a foraging area. Am. Birds 37:941–945.

KIFF, L. 1990. To the brink and back: the battle to save the California Condor. Terra 28(4):6–18.

KOFORD, C. B. 1953. The California Condor. Natl. Audubon Soc. Res. Report No. 4:1–154.

MILLER, A. H., I. McMILLAN, AND E. McMILLAN. 1965. The current status and welfare of the California Condor. Natl. Audubon Soc. Res. Report No. 6:1–61.

MUNDY, P. J. 1982. The comparative biology of southern African vultures. Vulture Study Group, Johannesburg, South Africa.

OTT, J. R., L. A. REAL, AND E. M. SILVERFINE. 1985. The effect of nectar variance on bumblebee patterns of movement and potential gene dispersal. Oikos 45:333–340.

PENNYCUICK, C. J. 1972. Soaring behavior and performance of some East African birds, observed from a motor-glider. Ibis 114:178–218.

PENNYCUICK, C. J. 1983. Effective nest density of Ruppell's Griffon Vulture in the Serengeti-Rift Valley area of northern Tanzania, p. 172–184. In S. R. Wilbur and J. A. Jackson [eds.], Vulture biology and management. Univ. California Press, Los Angeles.

PYKE, G. H. 1983. Animal movements: an optimal foraging approach, p. 7–31. In I. R. Swingland and P. J. Greenwood [eds.], The ecology of animal movements. Clarendon Press, Oxford, England.

SNYDER, N.F.R. 1988. California Condor, p. 43–66. In R. S. Palmer [ed.], Handbook of North American birds. Vol. 4. Yale Univ. Press, New Haven, CT.

SNYDER, N.F.R., AND E. V. JOHNSON. 1985. Photographic censusing of the 1982–1983 California Condor population. Condor 87:1–13.

SNYDER, N.F.R., E. V. JOHNSON, AND D. A. CLENDENEN. 1987. Primary molt of California Condors. Condor 89:468–485.

SNYDER, N.F.R., R. R. RAMEY, AND F. C. SIBLEY. 1986. Nest-site biology of the California Condor. Condor 88:228–241.

SNYDER, N.F.R., AND H. SNYDER. 1989. Biology and conservation of the California Condor, p. 175–267. In D. M. Powers [ed.], Current ornithology. Vol. 6. Santa Barbara Museum of Natural History, Santa Barbara, CA.

STUDER, C. D. 1983. Effects of Kern County cattle ranching on California Condor habitat. M.S.thesis. Michigan State Univ., East Lansing, MI.

TERRASSE, M. 1988. Réintroduction du vautour fauve dans les Grands Causses. Colloque "Réintroductions d'espèces animales," Saint-Jean du Gard. Fonds d'Intervention pour les Rapaces, Saint Cloud, France.

TERRASSE, J.-F., M. TERRASSE, AND Y. BOUDOINT. 1961. Observations sur la reproductions du vautour fauve, du percnoptère et du gypaète barbu dans les Basses-Pyrénées. Alauda 29:1–24.

WALLACE, M. P., P. G. PARKER, AND S. A. TEMPLE. 1980. An evaluation of patagial markers for cathartid vultures. J. Field Ornithol. 51:309–314.

WALLACE, M. P., AND S. A. TEMPLE. 1987. Releasing captive-reared Andean condors to the wild. J. Wildl. Manage. 51:541–550.

WALLACE, M. P., AND J. WILEY. In press. Use of Andean Condors to enhance success of California Condor reintroduction to the wild. Proc. Int. Orn. Cong. 20.

WESTERNHAGEN, W. VON. 1962. Greifvögel in Andalusien. Ornithol. Mitt. 14:41–48.

WILBUR, S., W. CARRIER, AND J. BORNEMAN. 1974. Supplemental feeding program for California Condors. J. Wildl. Manage. 38:343–346.

WILBUR, S. R. 1972. Food resources of the California Condor. U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, MD.

WILBUR, S. R. 1978a. Supplemental feeding of California Condors, p. 135–140. In S. A. Temple [ed.], Endangered birds: management techniques for preserving threatened species. Univ. of Wisconsin Press, Madison, WI.

WILBUR, S. R. 1978b. The California Condor, 1966–1976: a look at its past and future. U.S. Fish Wildl. Serv. North Am. Fauna 72:1–136.

APPENDIX.   Breeding status of 23 California Condors during 1982–1987. Information in parentheses following the condor ID includes sex, natal nest area, hatching year and mate ID(s) when these are available. Dashes within the parentheses indicate missing data. For birds that were radiotagged, the month in which they were radiotagged is given in parentheses following the appropriate year.

Condor	Immature	Unpaired	Paired, not breeding	Breeding
BFE (M, –, 1978, UN1)				
1982	Jun–Dec	—	—	—
1983	Jan–Dec	—	—	—
1984	—	Jan–Dec	—	—
1985	—	Mar–Apr[a]	—	Jan–Feb
BOS (F, SB, 1982,–)				
1982	Sep–Dec	—	—	—
1983	Jan–Nov[a]	—	—	—
CCF (F, –, –, CCM)				
1982	—	—	May–Dec	Jan–Apr
1983	—	—	Jun–Dec	Jan–May
1984	—	Nov–Dec	May–Oct	Jan–Apr
1985	—	Jan–Sep[b]	—	—
CCM (M, –, –, CCF)				
1982	—	—	May–Dec	Jan–Apr
1983	—	—	Jun–Dec	Jan–May
1984	—	—	May–Oct[a]	Jan–Apr
CVF (F, –, –, CVM)				
1982	—	—	May–Dec	Feb–Apr
1983	—	—	5 Aug–Dec	Jan–4 Aug
1984	—	—	9 May–Nov[a]	Jan–8 May
CVM (M, –, –, CVF)				
1982	—	—	May–Dec	Feb–Apr
1983	—	—	5 Aug–Dec	Jan–4 Aug
1984 (Dec)	—	Dec	9 May–Nov	Jan–8 May
1985	—	Jan[a]	—	—
HIW (M, –, 1980, –)				
1982	Jun–Dec	—	—	—
1983	Jan–Dec	—	—	—
1984 (Nov)	Jan–Dec	—	—	—
1985	Jan–Jun[b]	—	—	—
IC1 (M, –, 1979, –)				
1982 (Oct)	Aug–Dec	—	—	—
1983	Jan–Dec	—	—	—
1984	Jan–Mar[a]	—	—	—
PAX (M, CV, 1981, –)				
1982	May—Dec[b]	—	—	—
PCA (M, –, –, PCB)				
1982	—	—	24 Jun–Dec	Jan–23 Jun
1983	—	Dec	4 May–Nov	Jan–3 May
1984 (Nov)	—	Jan–Dec	—	—
1985	—	Jan–Dec	—	—
1986	—	Jan–Apr[b]	—	—
PCB (–, –, –, PCA)				
1982	—	—	24 Jun–Dec	Jan–23 Jun
1983	—	—	4 May–Nov[a]	Jan–3 May
PPF (F, –, –, ???[c], SMM)				
1982	—	Jun–Dec	May	—
1983	—	Jan–26 Apr	27 Apr–Dec	—
1984	—	—	16 Sep–Oct[a]	Jan–15 Sep

APPENDIX. Continued.

Condor	Immature	Unpaired	Paired, not breeding	Breeding
REC (M, CC, 1980, SSF)				
1982	Jan–Dec	—	—	—
1983	Jan–Dec	—	—	—
1984 (Dec)	Jan–Dec	—	—	—
1985	Jan–Oct	—	Nov–Dec	—
1986	—	6 Jun–Dec	16 Apr–5 Jun	Jan–15 Apr
1987	—	Jan–Apr[b]	—	—
SBF (F, –, –, SBM)				
1982	—	—	—	May–Dec
1983	—	—	27 Apr–Dec	Jan–26 Apr
1984 (Nov)	—	—	May–Dec	Jan–Apr
1985	—	—	24 Apr–Dec	Jan–23 Apr
1986	—	—	1–3 Jan[a]	—
SBM (M, –, –, SBF)				
1982 (Nov)	—	—	—	Feb–Dec
1983	—	—	27 Apr–Dec	Jan–26 Apr
1984	—	—	May–Dec	Jan–Apr
1985	—	—	24 Apr–Dec	Jan–23 Apr
1986	—	4 Jan–Dec[b]	1–3 Jan	—
SMA (–, –, –, SMM)				
1982	—	—	—	Jan–Mar[a]
SMM (M, –, –, SMA, PPF)				
1982	—	Apr–Dec	—	Jan–Mar
1983	—	Jan–26 Apr	27 Apr–Dec	—
1984 (Dec)	—	Nov–Dec	16 Sep–Oct	Jan–15 Sep
1985	—	Jan–Dec	—	—
1986	—	Jan–Dec	—	—
1987	—	Jan–Feb[b]	—	—
SSF (F, –, –, SMM, REC)				
1982	—	—	14 Aug–Dec	May–13 Aug
1983	—	—	9 Nov–Dec	Jan–8 Nov
1984 (Oct)	—	Dec	22 May–Nov	Jan–21 May
1985	—	Jan–Oct	Nov–Dec	—
1986	—	—	16 Apr–Jun[b]	Jan–15 Apr
SSM (M, –, –, SSF)				
1982	—	—	14 Aug–Dec	May–13 Aug
1983	—	—	9 Nov–Dec	Jan–8 Nov
1984	—	—	22 May–Nov[a]	Jan–21 May
UN1 (F, –, –, BFE)				
1982	—	May–Dec	—	—
1983	—	Jan–Dec	—	—
1984	—	Jan–Dec	—	—
1985	—	Mar–Aug[b]	—	Jan–Feb
UN2 (–, –, –, –)				
1982	—	Feb–Apr[a]	—	—
UN3 (–, –, –, –)				
1983	—	Sep[a]	—	—
WGI (–, SS, 1981, –)				
1982	Feb–Aug[a]	—	—	—

[a] Individual died or disappeared during this month and year.
[b] Individual was captured during this month and year.
[c] PPF was seen with an apparent mate on one occasion. The second bird was not identified and she was never again seen with it.