Analysis of California Condor (*Gymnogyps californianus*) Activity Using Satellite Telemetry Data

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Abstract: We describe new methods for quantifying specific in-situ activities of wildlife, in this case the endangered California condor (*Gymnogyps californianus*). These methods extract information from hundreds of thousands of temporally continuous and spatially explicit satellite telemetry reports. Visual observations and ground-based telemetry can provide behavioral data, although the information is often spatially and temporally limited and sample sizes can be small for wide-ranging species. Automated satellite telemetry offers continuous position reporting and unbiased spatial coverage, but to date has lacked thematic content such as the time, place, and duration of particular activities. Procedures developed for this study use a combination of models and geographic information systems (GIS) to identify condor transit flight, perching, roosting, and nesting activity based only on hourly telemetry position reports. This approach combines the temporal and spatial advantages of automated telemetry with increased thematic quality from activity models. The analytical methods were applied to 340,694 satellite-based position records from 51 California condors which were collected from June 2005 to April 2012. We identified 31,268 extended perch locations and an additional 15,483 overnight roost locations by translating basic location, speed, and time data into characterizations of bird activities. This approach correctly identified nine of the ten known nest sites occupied by condors outfitted with telemetry transmitters based only on the telemetry data. The spatial locations of these activities were mapped using GIS. This represents a significant advantage over simple location and movement data normally associated with wildlife telemetry, and is applicable to a wide range of species.

Keywords: California condor, Satellite telemetry, GIS, Wildlife activity model.

INTRODUCTION

The use of satellites to track individual animals through space and time is revolutionizing our understanding of animal movements and habitat use [1-3]. Research on cryptic species that move long distances or inhabit remote or inaccessible areas has been especially aided by satellite telemetry, as the vantage point from space can provide a relatively unbiased look at how these individuals move and conduct activities [4]. Satellite telemetry is also well suited to the study of endangered species, where a timely and clear understanding of habitat needs and threats is often essential to apply effective management [5].

The California condor (*Gymnogyps californianus*) is an iconic endangered species, having received international attention by scientists, policy makers, and the general public for the last five decades [reviewed by 6]. The condor is

considered a flagship endangered species, representing a considerable range of conservation challenges, and serves as an example of how science, captive breeding, reintroductions, and intensive management can save a species from the brink of extinction [6]. The condor is also a good candidate for investigating how we might mine satellite telemetry data for additional information useful for applied conservation because: (1) a large number of individuals in the population are outfitted with satellite telemetry, (2) condors use a wide variety of habitats and range over large areas, and (3) the population is expanding, meaning that it will be useful to managers if we can identify where condors are performing specific activities (e.g., nesting, perching, roosting).

California condors are one of the largest soaring birds on the planet [7]. With a massive wingspan, condors rarely use flapping flight; instead, they are masters of soaring flight. This is a critical adaptation, because as obligate scavengers they must be able to efficiently search vast areas for medium- to large-sized mammal carcasses [8, 9]. Condors are not considered habitat specialists [7], but they do have specific habitat requirements for certain activities. Nests are generally in mountainous areas in caves located on cliff faces, alt-

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hough sometimes in large trees [10]. Condors will typically roost in trees or on rock ledges. They forage primarily in grasslands or open woodlands where they can more easily locate food and scan for potential predators. California condors generally do not successfully breed until they are 6-8 years old (median age at first reproduction for females = 8.6; males = 8.1), but can live >50 years in captivity [11]. Breeding pairs generally fledge less than two chicks in three years due to their exceptionally long breeding cycle and the need for extended post-fledging parental care [12]. Their slow maturation, long breeding cycle, and low fecundity make populations sensitive to increases in adult mortality [12].

The California condor's historical range once extended from southern British Columbia to Baja California, but contracted to a relatively small area encompassing the mountains of southern California by the 1960s due to wanton shooting and contaminated food resources [6, 13]. The species was one of the first to be placed on the list of endangered species by the U.S. Fish and Wildlife Service in 1967, under the predecessor to today's U.S. Endangered Species Act. A recovery plan was formulated for the declining condor population in 1975 (U.S. Fish and Wildlife Service 1975) and following a series of reports that called for development of captive breeding strategies [14, 15], an intensive research program was initiated in the 1980s [6, 10]. As part of that research program condors were captured and fitted with radio transmitters for ground-based telemetry tracking [8]. This effort greatly improved our knowledge of condor movements and the habitats they used [16, 17]; however these telemetry studies were largely limited to line-of-sight radio signal reception. The California condor remains a critically endangered species and the primary threat to its continued survival is lead toxicosis [18, 19]. The pathway for lead ingestion is through gut piles left in the field by hunters after they remove the meat, or through animals that are shot and unrecovered [19, 20].

The condor population suffered further losses in the winter of 1984-1985 with a 40% decrease in the remaining wild population. Additional condor mortality in 1986 prompted a decision to remove all remaining condors from the wild to prevent substantial losses and to maximize the genetic diversity of the small captive flock [6]. All condors had been trapped and placed in captivity by 1987, with the world population numbering only 27 individuals. A successful captive breeding program and newly developed release techniques led to the first releases to the wild of captive bred condors in January, 1992. Released condors were outfitted with telemetry to monitor their movements.

Ground-based radio tracking of condors continues to be an essential tool for management of the species after nearly three decades of telemetry use. Field personnel have been able to use telemetry-derived location data to: (1) identify whether birds are stationary for long periods (which might indicate that they have been poisoned and are in need of assistance, or that they are deceased); (2) identify areas of seasonal or traditional use; (3) identify areas of potential conflict, where the birds and specific threats occur at the same locale; and (4) assess patterns of habitat expansion as the wild population increases.

By 2005, reliable satellite-based telemetry that integrated global positioning systems (GPS) began to offer an additional type of management information for condors. Satellite telemetry complemented the ground-based telemetry, offering precise hourly position reports during daytime that provided vastly superior temporal and spatial resolution. The satellite telemetry generated improved position reports, just as the growing population made thorough visual monitoring of each bird's activities more difficult. The application of ground-based radio telemetry data and visual observations effectively resulted in *high* thematic resolution (observed behavioral data) whereas the GPS telemetry program with a rarity of visual observations reverses the character of the data to have high spatial and temporal resolution but *low* thematic resolution.

Condor GPS data have already provided insights on bird movements and habitat occupancy [21, 22]. Here we present new methods for extracting more information from telemetry data. We describe the California condor satellite telemetry dataset for southern California and present a series of algorithms to increase the thematic resolution of GPS data. We also explore how this additional thematic resolution might improve our understanding of condor habitat use and we assess the management implications of these methods. Then we report on what is effectively a new population of condors formed in the years following captive breeding and release to the wild. This population may have activity patterns that differ from those of past decades. Our dataset is also unique, being the largest dataset of condor locations ever analyzed. We restrict our analysis to satellite telemetry data to explore its potential as a sole information source, as well as to minimize any bias from ground-based observation. Whereas our focus is on the California condor, we anticipate that these methods will have applications for other species where satellite telemetry monitoring is used.

MATERIALS AND METHODOLOGY

From 16 June 2005 through 3 April 2012, 51 condors released in southern California were fitted with patagial mount GPS telemetry units (Argos/GPS PTT, Microwave Telemetry, Inc., Columbia, MD) which upload condor movement data to the Argos satellite network. Approximately 40% of the released birds were equipped with satellite telemetry, with monthly and annual variation in the number of birds transmitting data. The specified horizontal accuracy of the solar powered GPS units is 18 meters, with a position recorded every hour during daytime (approximately 06:00 – 19:00). Vertical accuracy is specified as 22 m, however values roll over to restart with one meter at an altitude of 2048 m. We did not include altitude data in our models because of insufficient resolution to discriminate activities near the ground. Spatial resolution of the data is approximately 0.00017 degrees horizontal, or about 19 m latitude. The dataset for this analysis includes 340,694 point localities (Fig. **1**), with data volume and number of birds increasing since 2005 (Fig. **2**). Six of the 51 condors were newly outfitted with satellite telemetry in December 2009. Ten of the 51condors were not outfitted until December of 2011. These large end-of-year additions mask the summer data emphasis noted in annual summaries from other years (Fig. **2**). The transmitters are programmed to shut down at night to con-
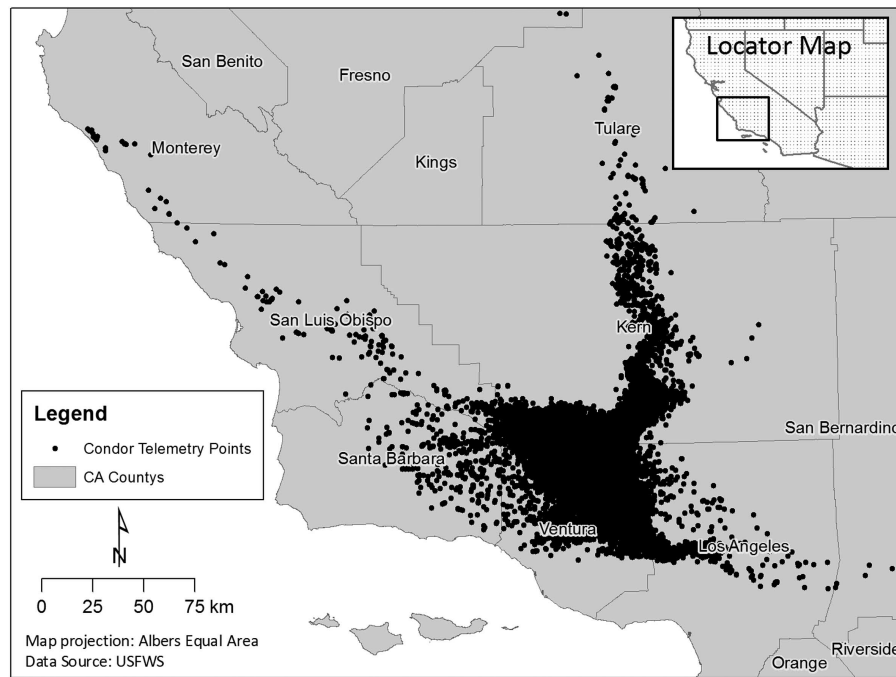
Fig. (1). California condor GPS telemetry locations in Southern California counties from 16 June 2005 through 3 April 2012.
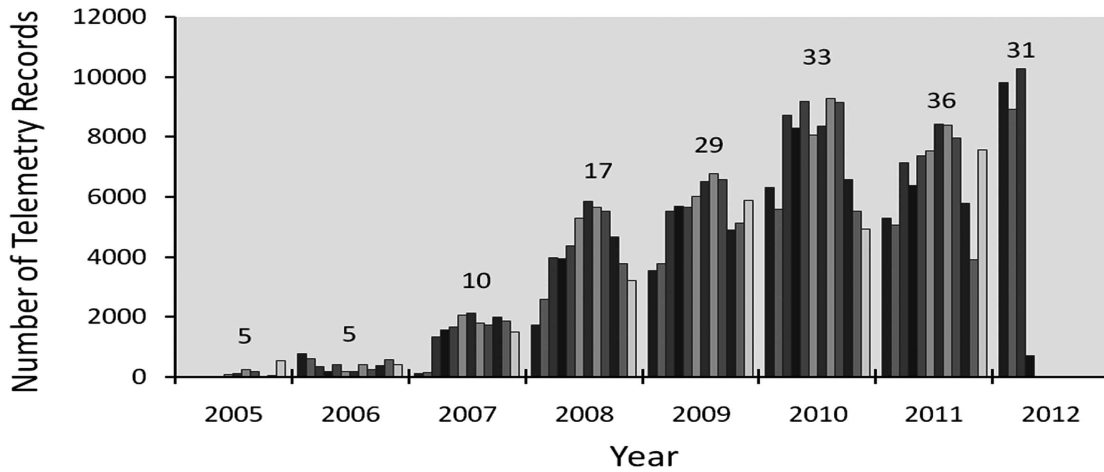
Fig. (2). Frequency distribution for number of condor telemetry records by year and month, 16 June 2005 – 3 April 2012. Each grey-shade bar represents one month. Values at the top of the bars are the total number of birds with satellite telemetry in each year. Some condors were equipped with telemetry late in the year. Note that years 2005 and 2012 are partial.

serve battery power. Each hourly record includes a transmitter number, location (latitude, longitude, and altitude), flight speed, date, and time. Missing position reports are common, due to limitations with satellite telemetry reception. Once downloaded, each record was linked to the identity of an individual bird, and validated for logical consistency. The data are formatted for use with Geographic Information System (GIS) software.

We used ArcMap GIS software [23] for visualization, mapping, and spatial analysis. We also used the GIS software to export data for use with the C++ programming language for temporal analysis and modeling. Our focus was on the detection of certain condor activities from telemetry data rather than habitat use generalizations which require individual condors as sampling units. We developed algorithms

with four types of logical queries to detect spatio-temporal patterns in the data. One analysis looked at transit-only zones where condors fly over habitat but never land. We also analyzed the telemetry data to determine perch, roost, and nesting events to focus on stationary activities. We defined stationary birds as those remaining at one position within a 40 m radius, accommodating the precision and accuracy of the satellite telemetry and minor bird movements.

Our modeling approach is transcribed to language-independent pseudocode notation for brevity, and included as appendix material. Model inputs include all available satellite telemetry data, and output is a new GIS format map and database of specific activities. These four models categorized condor data according to the following criteria:

1). Transit Area Analysis Using Stationary vs. Non-Stationary Condor Activity Areas

We used the GPS speed value from each telemetry record to identify transit-only areas in contrast with locations where condors stop. We generated a 250 m map grid for the area of the southern California data, then assigned each grid cell a value equal to the minimum speed from all telemetry points within the cell. Grid cells with assigned values below 10 km hr^{-1} ($\sim$ 6 mph) were considered stationary records, allowing for GPS error and the need to include birds moving at less than flight speeds as "stationary."

2). Perching – Condor Activity where the Bird is Stationary

We defined perching in a general sense as stationary, non-flight activity in daytime that does not extend overnight. This activity was indicated in the telemetry data as two or more consecutive hourly reports from the same location, with GPS speed less than 10 km·h^{-1}. Detecting the sequential stationary records allowed us to tally the number of hours associated with each perch event. See Appendix **A** for our perch activity pseudocode.

3). Roosting – Condor Activity where the Bird Remains Stationary Over Night

Our criteria for roosting assumed an individual condor has a position record in the evening matched within a 40 m radius by the first record the next day. Roosting duration is unlimited (unlike perching), including multi-day stationary periods with GPS speed less than 10 km·h^{-1}. Our roost analysis was intended to produce two types of records: "matched" or "unmatched". The matched records have the last afternoon location coincident with the first morning position, yielding a high confidence roost report. The unmatched records have afternoon and morning (before 12:00) position reports, but in two locations. The unmatched records were labeled as "overnight events." We did not consider the overnight event records as roosts; however, they were useful indicators of condor movement during periods when telemetry was inactive in the late evening and early morning hours. Both matched and unmatched data were summarized for overall perspective, and additionally subdivided by month to reveal seasonal patterns. Our roost activity pseudocode is presented in Appendix **B**.

4). Nesting

We characterized nesting activity as courtship behavior by pairs of birds, followed by nest site selection, egg laying, and a chick hatching from the egg. Courtship involves a pair's frequent flights together and investigations of potential nest sites, so our initial focus was on synchronized locations involving two birds. Once the condors selected a nest site we looked for the continuous presence of one of the adults at a single location ($\pm$ 40 m), with the two adults repeatedly exchanging nest duties. Nesting pairs were assumed monogamous within each season, so the identities of the two birds were expected to remain consistent with few other condors perching or roosting at the same location. Condor nest caves can easily block satellite telemetry signals, so we anticipated frequent data dropouts for birds on a nest. If a nest site was abandoned, frequent telemetry for both birds was expected to resume.

We began our nest analysis by building this general characterization into a logic that could be applied to satellite telemetry data. We then developed the nest logic into an algorithm to detect early courtship behavior, nest site activities, and failed nesting attempts. This analysis did require both nesting adults to have working telemetry units. Our nesting activity pseudocode is presented in Appendix **C**.

Identify Potentially Nesting Condor Pairs:

Our first task was to identify possible pairs of nesting birds that spent time together in a courtship period, using telemetry data from the first four months of the nesting season (1 January through 30 April). Our algorithm began with a search for all possible pairs of birds that had a position report at the same moment (independent of location). For each pair of birds we tallied the number of times there was a position report at the same time, referred to as the temporal sum ($\sum_T$). Next, we looked through all possible pairs of birds that were within 200 m of each other and summed the number of spatially matching records for the pair. This became our spatial sum ($\sum_S$). We based the 200 m distance for members of the pair on observations of courting birds in the field. To identify condor pairs that spend a proportionally large amount of time together, we calculated a "proximity ratio" by dividing the spatial sum by the temporal sum ($\sum_S$) / ($\sum_T$). There are many reasons why a pair of birds will travel together (e.g., feeding efficiency), so a large proximity ratio is not sufficient evidence to label a pair as nesting. Thus, we only used this ratio as a first filter to identify possible pairs. We required $\sum_T$ to be at least 50 telemetry reports in a given month to remove false positives from small dataset sizes. The proximity ratio needed to be greater than 0.40 to qualify as a possible breeding pair, indicating the pair was spending at least 40% of their time together. The 40% rule is a conservative value for condor pairs in courtship based on our field observations.

Identify Active Condor Nests:

After identifying pairs of condors that spent more than 40% of their time together, we looked for signs that a nest location had been selected. With one condor on the nest with poor telemetry, we looked for the other member of the pair to have a lone telemetry signal as it moved about to feed and roost. We identified this behavior by the rapid decrease in the temporal sum value for the pair. If the temporal sum from our identified pair of birds dropped by at least 80% (a major decrease in paired telemetry records), we predicted these birds to be nesting.

Locate the Nests:

For each nesting pair of condors, we looked for the single most common location for both birds. This point became our predicted nest location, rounded to the nearest 100 m. Courting birds will occasionally continue to investigate several potential nests in the days before final site selection. We

included each of the potential nest locations in our results when the data indicated this behavior.

Detect Nest Failure:

Typical nest duty exchanges by the adults will keep the proximity ratio low in the four months following the peak values associated with courtship. If that ratio increased to above 40%, we considered the birds to be together and outside the nest cave, indicating that they had abandoned the nest.

Accuracy Assessment for Nesting Model:

We compared our nest activity results with known nests from 2005-2012 to assess our telemetry data model. We measured accuracy in terms of the proportion of nests correctly predicted from the telemetry data, and in terms of the distance between the predicted location and the actual location as measured by biologists in the field.

Cartographic Methods Used for Presentation of Results:

Our perch, roost, and nesting output maps were based on point density in order to best visualize large numbers of data points. Density maps avoid the problem whereby large numbers of map points obscure themselves and introduce perception bias. These maps were derived using a convolution filter with an output raster cell size of 1 km and a kernel radius of 8 km for smoothing. The kernel radius determines the size of the area used to calculate an average point density, with larger areas generally resulting in lower values. We used an 8-class geometric interval classification on our final maps to discriminate a range of values, reporting density as the number of condor records per square kilometer.

RESULTS

We used hourly telemetry reports and logical algorithms based on our knowledge of condor ecology to identify transit-only zones and three condor activity types. Our results are presented here as a series of maps and charts, featuring transit, perching, roosting, and nesting activities.

Transit Area Analysis

The transit area analysis identified a central range area where all of the telemetry records were of condors in flight (Fig. **3**). Southern Kern County and central Ventura County were identified as areas of stationary activity, with additional non-stop (transit) areas on the outer fringes of the range. San Luis Obispo and Santa Barbara Counties were areas of mixed use. With this type of analysis, each 250 m grid cell was strictly classified as stationary or transit.

Perching

Our analysis detected 31,268 perch events that included 54,820 hourly telemetry records (16 % of all records) recorded between 16 June 2005 and 3 April 2012. All 51 condors in the dataset had perch events. The density values of perch locations ranged from zero (where no perch activity was detected) to 324 h/km^2 in areas with many perch events (Fig. **4**).

The perch records revealed that stationary activities were dominant in three main areas. The southern area is centered on the Hopper Mountain National Wildlife Refuge, to the northwest is the Bitter Creek National Wildlife Refuge, and to the northeast is the private Tejon Ranch Company. The highest density of perch locations was found at the Bitter Creek Refuge, where condors have been released from cap-
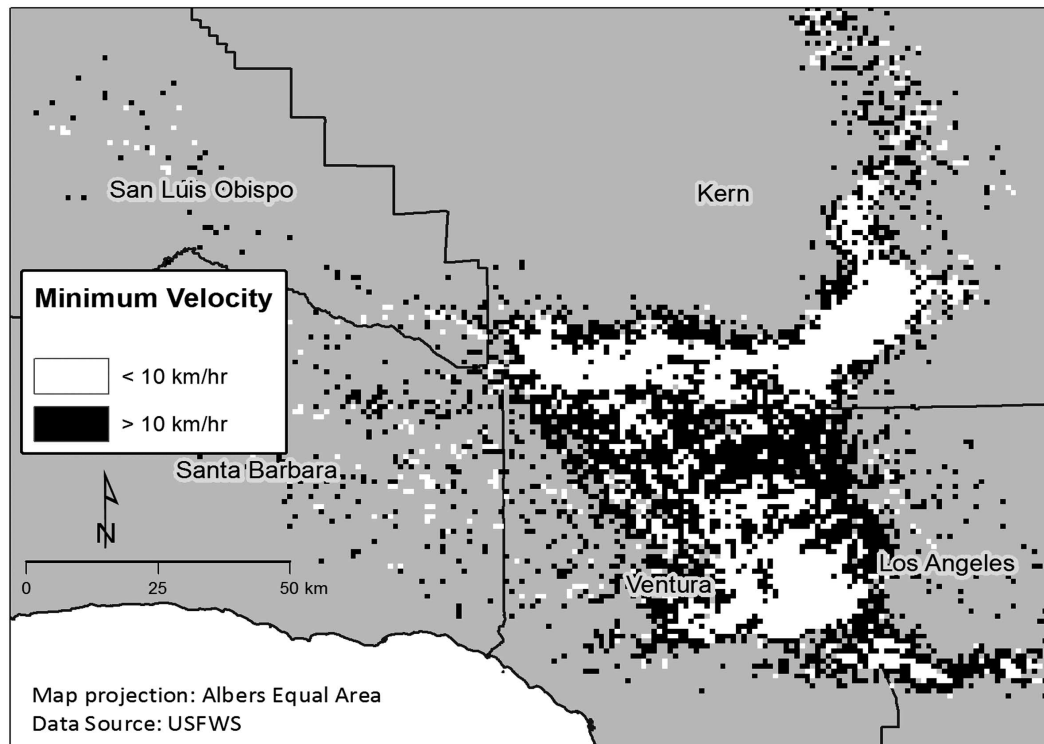

Fig. (3). Transit area analysis comparing stationary vs. non-stationary California condor activity in southern California. White areas represent 250 m grid cell locations that include stationary birds and black areas represent transit areas where speed was always greater than 10 km·h−1.

tivity and feeding operations occurred. Less frequent perch activity was found farther north in Monterey and Tulare Counties and as far south as central Los Angeles County. The northern perch locations in central Kern and Tulare Counties were recent range expansions dating from 2010 and 2011.

Roosting

We identified 15,483 roost events with matching evening and morning locations. All 51 condors with satellite teleme-

try had roosting events. The number of combined roost and non-matching overnight events records was 27,653. The majority of roost locations were in the same three areas where high density perch records occurred, with additional low densities of roost locations spread broadly across the range (Fig. **5**).

The 15,483 roost events represent 56% of the 27,653 combined roost and non-matching overnight events, and reflect limitations in the operational hours of the telemetry data. Proportions of roost events vs. the combined total of
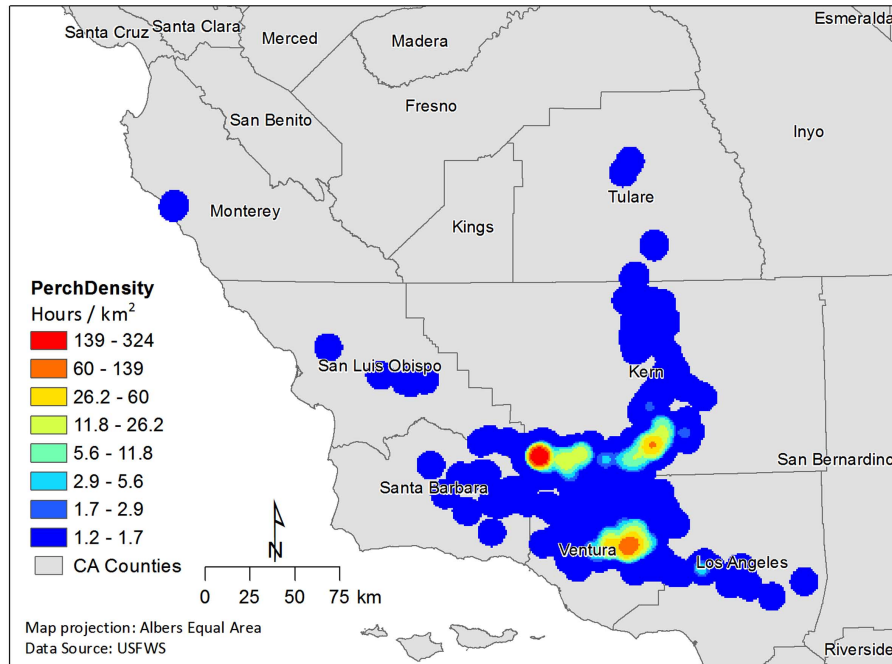

Fig. (4). California condor perch locations in southern California, 2005-2012, as determined by analysis of satellite telemetry data. Perch points from GPS positions are represented as a density field reflecting hours of perching per square km compiled over a seven-year period.
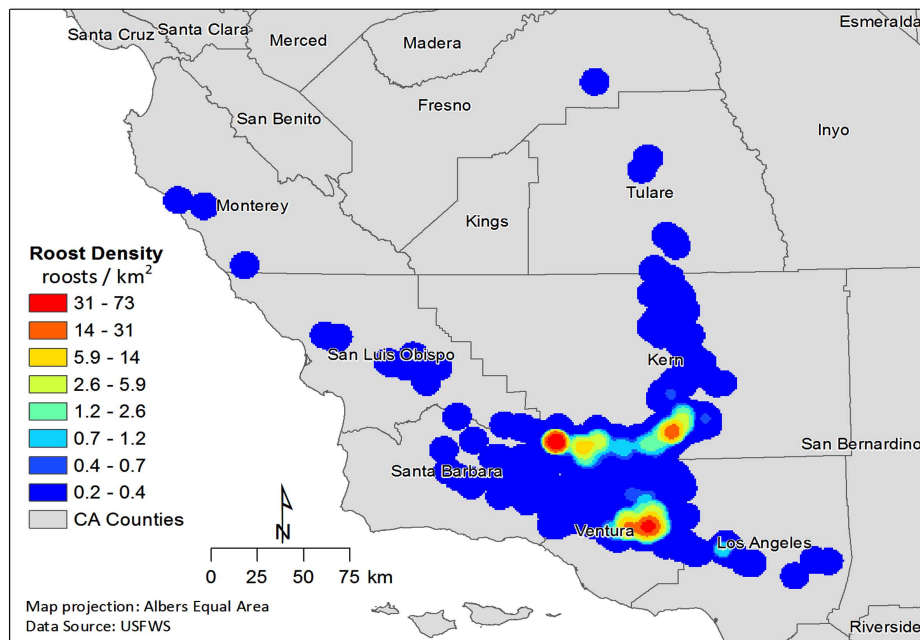

Fig. (5). California condor roosts in southern California, 2005 – 2012, as determined by analysis of satellite telemetry data. Roosts are represented as a density field of condor roost events with values ranging from zero to 73 roost events per square km using an 8 km density distribution kernel for smoothing.
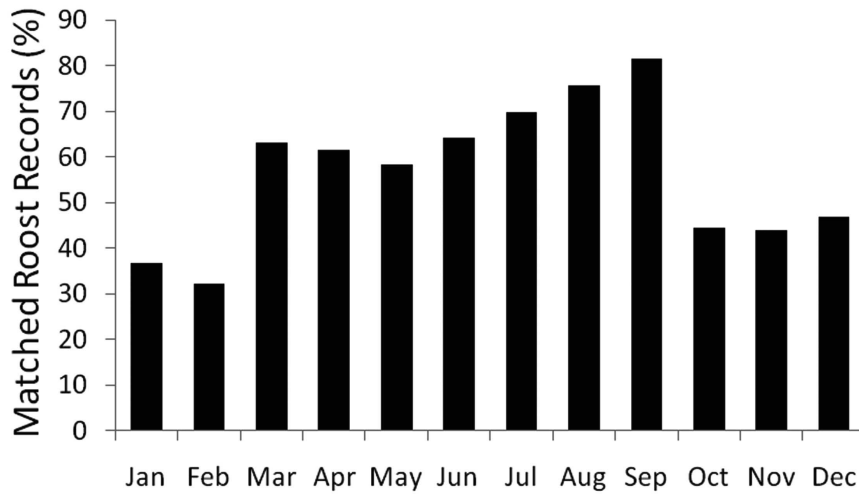
Fig. (6). Monthly proportions of condor matching roost events vs. the combined total of roost and overnight events. Average value over all months is 56%, based on 15,483 roost events from 2005 – 2012.
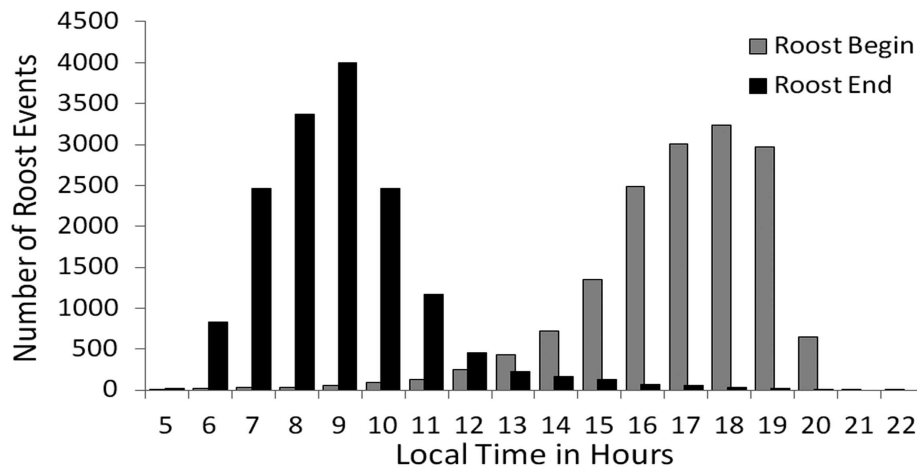

Fig. (7). Distribution of California condor roost end times (time of 1st morning flight) in black and roost begin times (time when birds stop flying for the day) in gray. Time of day as Pacific Standard Time for all records. Based on 15,483 roost events from 2005 – 2012.

roost and overnight events varied with season, with a higher proportion of the matching roosts occurring in summer months (Fig. **6**).

The roost start and end time analysis determined that the most common beginning time for roosting was 18:00 (local time) and the most common ending time was 09:00 (Fig. **7**). Monthly reporting of roost activity revealed a seasonal trend in the data, with 17:00 the most common roost begin time in January, shifting to 19:00 in July when days are longer (Fig. **8**).

Nesting

Our analysis independently detected nesting activity for nine of the 10 nesting condor pairs associated with satellite telemetered birds in southern California between 16 June 2005 and 3 April 2012. Other condors were also nesting, but they were not birds with functioning satellite telemetry. The single undetected nesting pair involved an egg that failed to hatch in 2009. The analysis identified an additional 11 potential condor pairs through our first-filter proximity analysis and then correctly classified these as non-nesting birds. Nest

locations were also detected for all nine condor pairs. Five of the nests were detected with each having a single location. For the other four nests, the data indicated that each had 2-3 probable locations without a clear single candidate. Accuracy of the detected nest locations compared to field verified nests ranged from 16 to 681 m, with an average distance of 191 m. Alternate nest locations where nesting birds spent time during courtship but did not adopt the site were recorded as potential future nest locations. The maximum distance from true nests to the alternate locations investigated by the birds in courtship was 6.2 km; the minimum distance was 423 m, with an average of 2.9 km. The egg failed to hatch at two of the nine nests. The nest failure analysis using the $(\sum_S)$ / $(\sum_T)$ proximity ratio correctly identified one of these as a failed nest, however the second failed nest also had the female of the adult pair die so the paired bird telemetry data were unavailable.

DISCUSSION

Several condor activities are associated with particular habitat requirements. These include foraging, perching, feed-
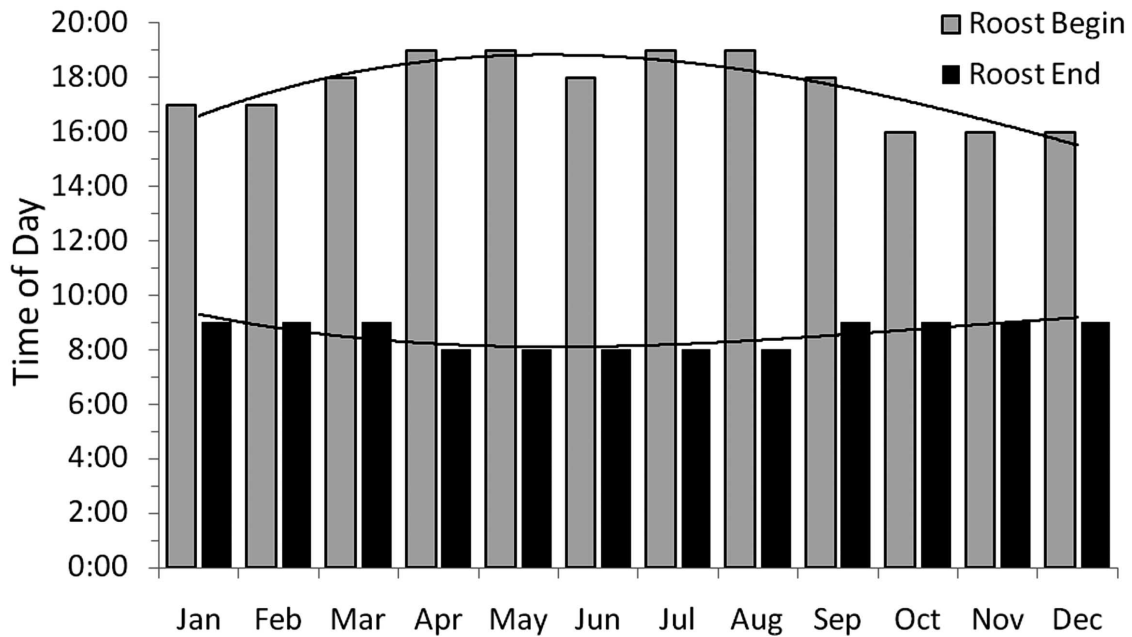
Fig. (8). Frequency distribution of the most common roost begin and end times by month. The curved trendlines indicate seasonal changes in roost activity. Time of day as Pacific Standard Time for all records. Based on 15,483 roost events from 2005 – 2012.

ing, nesting, roosting, bathing, and drinking [24]. When considering crucial habitat needs, condor biologists and land use managers have long recognized the importance of a holistic habitat picture [13], ensuring each required habitat type is available and protected for the species. For the condor, this habitat mosaic is often fragmented and distributed across many kilometers, making habitat identification and protection a challenge.

Ground-based animal sighting data can help to evaluate habitat use, however these studies are often plagued by at least three basic problems: (1) observations are typically not random or independent, (2) observation sample size is typically small (especially for rare or cryptic species), and (3) error or uncertainty in sighting data [17]. Satellite telemetry holds promise for addressing these issues by providing a large number of observations on a regular cycle with a high degree of positional accuracy. Our analysis indicates that if one can associate specific activities with the voluminous location information from satellite telemetry, an even clearer understanding of how animals use space is likely to emerge. Our analysis focused on these challenges, detecting specific locations for individual transit, perching, roosting, and nesting activities.

Transit analysis and perch detection

We identified transit zones and perch locations, finding overflight (transit) zones and 31,268 perch events (Fig. **4**). Whereas a condor could pause on a tree branch for a few moments then fly away, our perch model identified birds in the same location for two or more consecutive hourly reporting periods. Because our perch model was only based on stationary positions and hourly telemetry points, actual condor activity was probably varied, including possible drinking or feeding events. These "extended stationary" records revealed areas where individual condors spend more time on the ground. Our transit area analysis (Fig. **3**) also identified areas where condors were stationary; however this activity was determined using only speed data so was less sensitive to the duration of the stopover compared to perch detection. With both approaches we had similar results, finding that each condor used the far northern Ventura County more for transit and less for stationary activities. Both analytical approaches characterized central Ventura County and southern Kern Counties as habitat where stationary activities occur.

Any area where condors stop is an area of interest for condor management. Locations where condors spend the most time have additional needs for monitoring existing land use practices and proposed changes in land use. Two of the high density perch areas are currently in the vicinity of the Bitter Creek and Hopper Mountain National Wildlife Refuges where provided food attracts the birds. A third area is on the private Tejon Ranch Company recently recolonized by condors [22] where habitat protection measures are yet to be determined.

Roosting

The roost analysis identified locations where condors stay overnight. This analysis was sensitive to the daily operating hours of the telemetry transmitters, as some transmitters were programmed to stop transmitting before the individual condor reached a roost site for the evening. With adjustments for the season, most transmitters were programmed to begin transmitting at 06:00 or 07:00 and continue until 19:00 or in some cases 20:00 each day. If a condor continues to fly after transmitter shutdown, there will be no record of the roost site until the first record the next morning. Without matching evening and morning records, our analysis took the conservative approach and rejected these locations as confirmed roost sites. Our roost analysis serves management needs in three ways:

1) We identified and mapped high confidence roost events (Fig. **5**), identifying specific areas for further habitat assessment.

2) For mismatched overnight events we highlighted seasonal patterns, to identify inadequate transmitter settings for daily operating hours (Fig. **6**). These results suggested the operational hours for telemetry should be extended in January and February.

3) We generated statistics on start and end times for the overall roost activities (Fig. **7**), and categorized the data by month (Fig. **8**). The trendline for monthly roost times was consistent with day length in southern California. This provides a long-term perspective on roost schedules, and is particularly useful when there is a need to prioritize field observation hours.

Our analysis of roost activities provides critical data to support additional research using formal habitat use models. Records from 2012 and 2011 in northern Kern and Tulare Counties suggested a continuing range expansion into these historic habitats. Likewise, roost records in the remote Santa Barbara County wilderness areas suggested these historic nesting and roosting areas may be repopulated in the near future. From the perspective of endangered species management, increasing roost records in Santa Barbara County exemplify valuable information to assist with revised habitat assessments and interagency planning.

Nesting

Our nesting analysis was perhaps the most challenging, because of inherent limitations in nest site telemetry. Condors tend to nest in shallow caves on rock cliffs – locations that often shield the telemetry antenna from contact with Argos satellites. A condor shielded at a nest site can be characterized as much by an unusual lack of signal as by the multi-hour stationary signal that would otherwise be expected. Telemetry is also problematic when condors are approaching a nest, as they tend to enter a limited transmission zone as they descend into the canyons associated with the cliff sites. Detecting nine of the 10 nests associated with telemetry equipped condors presents a good case to expand the telemetry program to include more birds. In particular, we were able to identify this critical activity early in the courtship phase, before the egg was laid.

The early detection of condor pairs in courtship allows heightened field monitoring of potentially nesting birds. It is also critical to determine the nest location as soon as possible, to assess the area for hazards and alert the field teams to begin nest management protocols. California condors typically spend the first month of the nesting season in courtship, involving paired flights and time spent investigating several potential nest locations. Experienced field biologists will often observe nest site selection narrowing down to two or three possible sites, however the final site is often unclear until the egg is actually laid. The potential nest sites can be formerly active nests, but may also indicate new sites that will be used in future years. In some cases, our analysis highlighted more than one option for a nest location. This last minute uncertainty for the final nest location is con-

sistent with field observations and represents valuable information to be saved as clues for future sites.

Two of our detected nest sites failed before the egg hatched. Our proximity ratio increased after a 2009 nest failure, correctly indicating both adults were away from the nest instead of incubating. A failed nest in 2011 did not result in the expected ratio increase, because the adult female had died near the time of the nest failure.

Implications for Telemetry Activity Models

Historically, condor researchers have used a variety of data and analytical techniques to detect and predict activity patterns. Functioning as a flagship species, and an endangered species, researchers have accumulated relatively large volumes of condor data presenting unique opportunities for the development and testing of telemetry activity models. Early work by Carl Koford [24] and others was based on field observations. Later researchers introduced new technologies such as photo surveys [25], GIS spatial analysis [16, 17], and habitat use analysis [22] to better understand the species. In this paper, we have analyzed both movement and specific activities for what is effectively a new population formed in the years following captive breeding and offspring release to the wild. Our telemetry analysis approach offers a methodology for comparing current habitat use to historic patterns, as well as for monitoring a growing population and an expanding range. This approach is uniquely suited to make best use of large volume satellite telemetry data that are growing daily.

Radio telemetry data such as the condor data analyzed here can be transitioned from basic locality report *data* to management-relevant *information* through a cautious interpretation of patterns. A challenge is to base the interpretation on sound knowledge of the species and a familiarity with the day-to-day activity patterns that are suggested by the telemetry data.

The Condor Recovery Program field teams use both ground-based and satellite telemetry for daily management operations. The ground-based data facilitate intermittent visual observations whereas the satellite data contributes frequent and precise location data. Combined, these data offer information on bird location, assist in the location of potentially injured birds, and offer clues to locations of critical interest such as nesting areas. These applications have transformed field operations for the condor, greatly increasing the ability of biologists to monitor and manage the reintroduced birds.

A second application of the telemetry data is the longer term retrospective, as a means to integrate months or years of data to build up a picture of activity patterns and habitat use. Biologists working in the field generally have an excellent sense of daily and seasonal patterns; however, is it difficult to formulate and maintain a synoptic overview of year to year patterns.

Our analysis methods have both short-term and long-term applications. Using only the satellite telemetry data, we have presented an analysis that achieves some of the advantage of visual observation, combined with the satellite-based ad-

vantage of vast volumes of long-term information with high accuracy GPS spatial data.

Information gained from satellite telemetry is invaluable for condor management. These data can guide us to improve decision making on a range of critical land use planning issues, such as zoning, lead exposure, recreation management, oil and gas extraction, wind farm placement, wilderness additions, and timber harvest planning. As intensive management operations diminish (and as the condor population increases), our ability to remotely monitor these birds will become increasingly important.

Using over 340,000 records of hourly telemetry data our analysis of the previous seven years of condor activity has provided insights to the key activities of transit flight, perching, roosting, and nesting. The results of our analysis are consistent with general knowledge of condor activities, but more importantly we can use these methods and the insights they provide to support and enhance decision making in specific habitat areas. Future research directions will likely include models for additional activities such as feeding, although currently this appears to be limited by GPS accuracy and precision. The activity analysis also enables additional research on habitat characterization, which can be accomplished by combining telemetry analysis with individual condors as sampling units, land cover data, and spatial analysis.

This analysis is designed to directly benefit the management of the California condor and its habitat. The work also serves as an example for other wildlife research on cryptic mobile species, with particular applications for intensive conservation management of endangered or threatened species. The combination of our spatio-temporal activity models and improving telemetry technology is well suited to better inform research and management for the increasing numbers of avian and mammalian taxa being studied using satellite telemetry. This advance allows us to move beyond basic animal movement tracking, and to refine our knowledge of animal activities through space and time.

CONFLICTS OF INTEREST

The authors confirm that this article content has no conflicts of interest.

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Appendix A. Pseudocode for Critical Programming Elements to Detect Condor Perch Activity from Satellite Telemetry Data.

```
for every bird (b1) in the database {

  for every record d[n] {              // possible start for a
perching sequence

    perch = false;
```

```
    overnight = false;

    site = position of d[n];

    for every record d[n+m] after d[n] {      // search for a
perching sequence

      // if bird is moving faster than 10 km/hr, this is the end of
the sequence

      if ( speed of d[n+m] > VelocityCutoff )    exit loop;

      // if bird has moved more than 40m, this is the end of the
sequence

      if ( site - position of d[n+m] > DistanceCutoff )    exit
loop;

      // if the sequence extends overnight, don't count it as a
perch event

      // don't exit the loop yet so that the we get the rest of the
overnight sequence

      if ( time of d[n+m] == next day)  overnight = true;

      // if two or more hourly records are missing then be con-
servative and assume the sequence has ended

      if ( time of d[n+m] > time of d[n+m-1] +
DiscontinuityCutoff ) exit loop;

      // if the bird has been at this location for at least one
hour, it's a perch

      if ( time of d[n+m] - time of d[n] >= DurationCutoff )
perch = true;

    }

    // is the sequence really a perch?

    if ( (perch == true) and (overnight == false) )    save this
as a perch record;

    // advance the loop to look for the starting point of a new
sequence...

    if ( (perch == true) or (overnight == true) ) {

      // next start is after this sequence has ended

      d[n] = d[n+m];

    } else {

      // bird may have moved >40m from original site, but
<40m from an intermediate point

      // start with intermediate point, use sliding window

      d[n] = d[n+1];

    }

  }

}
```

Appendix B. Pseudocode for Critical Programming Elements to Detect Condor Roost Activity from Satellite Telemetry Data.

```
for every bird (b1) in the database {

  for every record d[n] {              // possible start for a
roosting sequence
```

```
    overnight = false;

    site = position of d[n];

    for every record d[n+m] after d[n] {    // search for a roost-
ing sequence

        // if bird is moving faster than 10 km/hr, this is the end of
the sequence

        if ( speed of d[n+m] > VelocityCutoff )    exit loop;

        // if bird has moved more than 40m, this is the end of the
sequence

        if ( site - position of d[n+m] > DistanceCutoff )    exit
loop;

        // if the sequence extends overnight, then it is a roost

        // don't exit the loop yet so that the we get the rest of the
sequence

        if ( time of d[n+m] == next day)  overnight = true;

        // if two or more hourly records are missing in the middle
of the day

        // then be conservative and assume the sequence has end-
ed

        if (( time of d[n+m] is not the first record of the day)

            and   ( time of d[n+m] > time of d[n+m-1] +
DiscontinuityCutoff )) exit loop;

    }

    // is the sequence really a roost?

    if ( overnight == true )    save this as a roost record;

    // advance the loop to look for the starting point of a new
sequence...

    if ( overnight == true ) {

      // next start is after this sequence has ended

      d[n] = d[n+m];

    } else {

      // bird may have moved >40m from original site, but
<40m from an intermediate point

      // start with intermediate point, use sliding window

      d[n] = d[n+1];

    }

  }

}
```

**Appendix C. Pseudocode for Critical Programming Ele-
ments to Detect Condor Nesting Activity from Satellite
Telemetry Data.**

```
for every possible combination of birds (b1,b2) in the data-
base {

 for every year {

  for every month in the year {        // January-December

    // make a table:
```

```
    // there's one row for each daylight hour during the
month

    // there are two columns to hold the records for the two
birds

    table[hours,2]

    // align the records for the two birds

    for every record (r1) for bird (b1) in the month {

      table[time of r1,1] = r1;

    }

    for every record (r2) for bird (b2) in the month {

      table[time of r2,2] = r2;

    }

    // count up the number of table lines where both birds
have a record

    temporal_sum = 0;

    for every line in the table {

      if ((table[line,1] not empty) and (table[line,2] not emp-
ty))   temporal_sum = temporal_sum + 1;

    }

    // count up the number of table lines where we have a
record of the two birds being near each other

    spatial_sum = 0;

    for every line in the table {

      if ((table[line,1] not empty) and (table[line,2] not emp-
ty)) {

        // if birds are closer than DistanceCutoff (40m) we
consider them to be at the same place

        if ( position of table[line,1] - position of table[line,2] <
DistanceCutoff )    spatial_sum = spatial_sum + 1;

      }

    }

    // save these two metrics for each month

    saved_temporal_sum[month] = temporal_sum;

    saved_spatial_sum[month] = spatial_sum;

  }

  // done collecting the metrics, now analyze them...

  // filter 1: finding possible courtship behavior

  possible_courtship = false;

  max_proximity_ratio = 0;

  for every month in the mating season {          // January-
April

    // calculate the proximity ratio - what fraction of the time
the birds are together

    proximity_ratio    =    saved_spatial_sum[month]    /
saved_temporal_sum[month];
```

```
    // we require at least 50 data points to filter out small
sample errors

    // we set the threshold for possible courtship at 40%

    if ((saved_temporal_sum[month] >= 50) and (proximi-
ty_ratio >= 0.40)) {

        possible_courtship = true;

        if (proximity_ratio > max_proximity_ratio) {    // find
the month with the highest ratio

            max_proximity_ratio = proximity_ratio;

            courtship_month = month;

        }

    }

    }


    if (possible_courtship == false)    no courtship, go on to
the next year;

    // filter 2: look for nesting behavior

    nesting_behavior = false;

    for every month after courtship_month, max of four
months {

        // check if there has been a significant drop (80%+) in the
temporal sum since courtship

        temporal_sum_change = saved_temporal_sum[month] /
saved_temporal_sum[courtship_month];

        if (temporal_sum_change < 0.20)    nesting_behavior =
true;

    }

    if (nesting_behavior == true)    found a nesting pair for
this year;

    }  // end of year loop

}  // end of bird pairing loop
```

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