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HUMAN IMPACTS ON THE GOLDEN EAGLE POPULATION OF SAN DIEGO COUNTY FROM 1928 TO 1981

A Thesis

Presented to the

Faculty of

San Diego State University

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by

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Approved by:

George W. Cox ______ 21 Nov. 1985

Date

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This thesis is dedicated to my parents
who taught me how to live,
and to the California Condor,
from whom we have yet much to learn.

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INTRODUCTION

Human activities vary greatly in their impact on wildlife. Unfortunate species suffer extinction, while opportunists expand their distributions and numbers. Most wildlife species, however, lie between these extremes, influenced in ways that are poorly understood. Nesting activities provide a focal point for investigating the effect of human activity on birds; they represent a time of great vulnerability for breeding birds and are the ultimate source of recruitment into the population. This vulnerability of nesting activity to human disturbance is particularly great for raptors, which have long breeding seasons, readily detectable nests, and elicit human reactions ranging from persecution to worship.

This thesis examines the relationship between nesting Golden Eagles (_Aquila chrysaetos_) and human disturbance in San Diego County, California, by comparing past and present conditions of areas that have been deserted with those that have remained active. Many authors have speculated about how human disturbance affects raptor populations, but no study has examined nesting conditions before and after abandonment.

This study was made possible by the wealth of data collected on Golden Eagles in San Diego County prior to rapid expansion of urban and agricultural areas in the 1950's. Notes and recollections of naturalists showed that comparisons could be made between historical and current conditions at Golden Eagle nest areas, and that shifts in the population could be related to the growth and development of the human population in the study area.

The objective of this study was to define the relationship between nest abandonment and a set of postulated disturbance variables. These included: distance to disturbance, intensity of disturbance, and type of disturbance. Historical data allowed comparison between the pre- and post-abandonment conditions at abandoned nest areas, and between the change at abandoned areas and that at areas that have remained active.

Species Description

Extensive descriptions of Golden Eagle natural history are given by Brown and Amadon (1968), Brown (1976), Haller (1982), and Newton (1979). The species is an opportunistic forager, taking a combination of medium-sized vertebrate prey and carrion (Olendorff 1976). Pairs typically nest in cliffs or trees, and forage over plains, grasslands, or low and open shrublands. The Golden Eagle has the widest distribution of the seven species in its genus, or in allied genera (36 species). Brown (1976) suggests that the worldwide population of Golden Eagles is about 500,000. Olendorff et al. (1981) estimated (from wintering population numbers) that approximately 65,000 Golden Eagles inhabit North America. Overall abundance and wide range, however, have not protected the Golden Eagle from local extirpation in the eastern United States (Spofford 1971), Britain (Brown 1976), and Europe (Haller 1982).

Golden Eagles in North America take a wide variety of prey (Olendorff 1976). The diet of Golden Eagles in California is dominated by lagomorphs (*Lepus californicus*, *Sylvilagus auduboni*, and *S. bachmanii*) and the California ground squirrel (*Spermophilus beecheyi*) (Carnie 1954, Hunsicker 1972, Bloom and Hawks 1982).

Golden Eagles appear to maintain stable densities of breeding pairs and often show similar densities under a variety of conditions (Table 1).

Golden Eagles in San Diego County begin courtship flights and nest construction in January. Egg records indicate that most eagles in San Diego County lay eggs between the first and third weeks of February (L. Kiff pers. comm.). Incubation appears to be close to the

Table 1. Published estimates of population densities of breeding Golden Eagles.

Study Area	Average Area per Pair (km)	Source
California	93	Dixon (1937)
Colorado	93	Arnold (1954)
Idaho	99	U.S. Dept. Inter. (1979)
Montana	142 to 272	Reynolds (1969)
Scotland	36 to 91	Brown and Watson (1963)
Switzerland	109	Haller (1982)
Utah	98	Camenzind (1969)
Utah	119	Edwards (1969)
Yukon, Canada	100 to 125	Nelson (1979)

estimates of Olendorff (42 days; pers. comm.). Fledging occurs nine to ten weeks after hatching, parental care continues into August. Family groups remain together into November.

Golden Eagles defend nest areas from conspecifics and appear to defend part of their home range (Haller 1982, Harmata 1984), but there can be substantial overlap between the home ranges of adjacent pairs (Brown and Watson 1963). Golden Eagles in San Diego County have been observed making undulating flights toward conspecific intruders near nests; in one case grasping talons with the intruder and forcing it to the ground.

Studies on Human Disturbance and Raptors

Studies on human disturbance and raptors can be grouped into three categories: (1) descriptive studies, including reports or case histories on patterns of disturbance or patterns of raptor behavior relative to disturbance, (2) comparative studies, in which disturbance factors were treated as independent variables for comparison against dependent variables, such as breeding success or behavioral response, and (3) manipulative studies, in which researchers created specific types of disturbance, and monitored dependent variables.

Descriptive studies. Descriptive research on human disturbance to raptors has been dominated by work on wintering Bald Eagles (*Haliaeetus leucocephalus*). Typically, this research correlated eagle behavior with some type of human disturbance. Coffey (1977) suggested that Bald Eagles could adjust to less than five persons near perches; greater number of persons would cause the eagles to leave the area. Detrich (1980) and Walter and Garrett (1981) found that observers were the most common cause of eagles leaving perches. Adults usually flushed at greater distances than immatures (Edwards 1969, Shea 1973, Stalmaster and Newman 1978, Detrich 1980, Goldberg 1980, Fisher et al., 1981, LaBonde 1981, Harmata 1984). Typical distances from human intruder to flushing eagles was near 200 m in nearly all the studies. Fisher et al. (1981), however, found that immatures flushed more often than adults presented with the same disturbance (low flying airplanes).

Vehicles traveling nearby roads did not necessarily disturb perching birds (Steenhof 1976, Beck 1980). Griffin (1978), LaBonde (1981), and Lish (1975) found that Bald eagles tended to flush if vehicles stopped, especially if the occupants got out of the vehicles. Alt (1980) found that individuals or boats lingering near nest location caused a greater response than if they passed without stopping.

McWhorter (1981) reported few Osprey (*Pandion haliaetus*) breeding-failures resulting from boat traffic near nest locations. She noted that Ospreys quickly adjusted to disturbance, but only if it was regular in nature and location. In contrast, Cape Vultures (*Gyps coprotheres*) are extremely susceptible to breeding failures if nests are visited even once during early incubation (J. Dobbs, pers. comm.). Furthermore, vultures reoccupy nests that were visited (only once during the breeding season) at a lower rate than nests that were not visited. Stahldecker (1975) reported that a nuclear detonation in Colorado caused the abandonment of two Red-tailed Hawk (*Buteo jamaicensis*) nests with eggs, but did little to 12 other nests within a radius of 16 km around the explosion. Nelson (1982) encouraged Golden Eagles to nest on power-line pylons, showing that they are capable of habituating to man-made structures and are tolerant of some forms of human disturbance.

Thompson et al. (1982) speculated that conversion of Great Basin scrublands to crested wheat-grass would substantially lower the breeding success of Golden Eagles by lowering the abundance of black-tailed jackrabbits (*Lepus californius*).

Comparative studies. Many studies have compared productivity among nests grouped by overall levels of disturbance. Mathisen (1968) and French (1972) ranked Bald Eagle nest locations into high, moderate, and low categories of surrounding disturbance, comparing productivity between the categories. Juenemann (1973) modified this sytem by giving each nest a numerical disturbance-score based on the severity and proximity rankings of a set of 8 disturbance variables. McEwan and Hirth (1979) used a system similar to Juenemann's, but ranked disturbance variables within concentric zones around Bald Eagle nests (rather than assigning proximity scores). Tjernberg (1983) used three ranks of overall disturbance around Golden Eagle nests in Sweden. None of these techniques yielded significant differences in productivity among disturbance categories. Wiley (1975) found that Red-tailed Hawks nesting within 0.25 mi (0.4 km) of roads had significantly lower breeding success than pairs nesting greater than 0.25 mi from roads. He attributed the difference to habitat change and human predation on the young. Juenemann (1973) found an increase in number of fledglings with decrease in disturbance when he regrouped his data into quartiles. However, there is no biological reason for the *a posteriori* grouping of data in this fashion.

Researchers often compared productivity and nesting location with land-use patterns. Newton and Moss (1981) found very little evidence that British land-use patterns in 1, 3, and 5 km concentric circles around nest sites affected Red Kite (Milvus milvus) breeding success. They did observe significantly more forestry activity within 1 km of nests that were abandoned without laying compared to those within 1 km of nests in which eggs were layed. Gargett (1979) found that Tribal Trust Lands in Zimbabwe had Black Eagle (Aquila verreauxi) densities that were one third those in the adjoining Matopos Park. Average fledging success on the Tribal Trust Lands was 20 percent lower than in the park. Decreased prey abundance in the Tribal Trust Lands was suggested as a probable cause for lower densities of eagles. Howard and Sather-Blair (unpublished) found that productivity of Golden Eagle pairs was lower in agricultural areas than in natural shrublands, even though the densities of nesting pairs were similar in the two vegetation types. Gaulshin et al. (1983) found that Rough-legged Buzzards (Buteo lagopus) were more numerous in semi-urban areas than in natural tundra in Russia. They suggested that higher vole populations in developed areas offset the negative aspects of human disturbances. Finally, Vincenty (1974) found that more raptors nested in riparian woodlands than in agricultural, urban, or residential areas along the American River near Sacramento, California. However, this distribution primarily resulted from nest habitat requirements rather than human disturbance. These comparative studies show that land-use patterns affect productivity or population densities of raptors, but do not reveal the causal relationships.

Stalmaster (1976) related Bald Eagle occurrence to levels of human activity within sample units of river in Washington. He found that eagles tended to frequent river areas with low to moderate human activity, and seldom used units with high activity. Russell (1980) noted that large flushing distances were more frequent in stretches of the Suak River (Washington) with low human-activity. Her study suggests that Bald Eagles habituate to disturbance in areas with high human-activity. Young (1980) compared nesting behavior between Bald Eagle pairs in high disturbance areas with those in low disturbance areas on the San Juan Islands, Washington. He observed lower nest attendance in the high disturbance area, but found no difference in breeding success.

Manipulative studies. Most manipulative studies have involved flushing distances of perched or nesting Bald Eagles. Methods consisted of duplicating a disturbance activity while monitoring the behavior of the eagles.

Stalmaster (1976), Fraser (1981), and Harmata (1984) experimentally disturbed Bald Eagles by walking toward them. Stalmaster observed that adults flushed at greater distances than immatures, and that flushed eagles typically remained near their original perch. Fraser (1981), working with nesting eagles, reported that flushing distance increased with habituation but decreased as the breeding season progressed. Harmata (1984) found that banded eagles were less tolerant of researchers and their vehicles after banding, and flushed at greater distances. Alt (1980) approached nests by boat, noting that the angle of approach affected the reaction of the nesting eagle; oblique angles caused less response than direct approaches.

Grier (1969) divided a group of Bald Eagle nests into two samples, climbed into the nests of one sample (after the young had hatched), and then compared the fledging success of the two groups. He found no significant difference in the breeding success between the two groups. Platt (1977), Ellis (1981), and White et al.

(1981) examined nesting behavior and success in response to disturbances other than human presence. White and Thurow (1985) found few nest failures that could be attributed to the experimental disturbances (discharge of firearms, engine noise, and approach of nests on foot and by vehicles). Ellis (1981) found very little reaction to noises simulating sonic booms, and found no significant difference between nest reoccupancy frequencies for experimentally disturbed and undisturbed raptors. Platt (1977) observed that Gyrfalcon nests disturbed by helicopter flights (51 flights conducted over 22 nests) had the same productivity rate as undisturbed nests. Disturbed nests, however, had a significantly lower rate of reoccupancy than undisturbed nests.

METHODS

Study Area

The study area covered the western half of San Diego County, from approximately 32° 30' to 33° 30' north latitude and from 116° 30' to 117° 45' west longitude (Figure 1). This area corresponds to the organizational units of local data systems rather than to the distribution of Golden Eagles in the region. Golden Eagles occur throughout the transverse and peninsular ranges of California, and into Baja California and the Sonoran Desert (Figure 2).

San Diego County contains four distinct geographic regions (Pryde 1984): coastal terraces, foothills (cismontane), mountains, and deserts (Figure 3). Zones of transition and interdigitation are typically broad between the coastal terraces, foothills, and mountains. The interface between the mountains and deserts is well defined and occurs along a narrow escarpment. The transition from mountains to desert occurs within 95 km of the coast along the entire length of the study area. Approximate proportions of each region in the study area were: 15 percent coastal terrace, 73 percent foothill, 7 percent mountain, and 5 percent desert.

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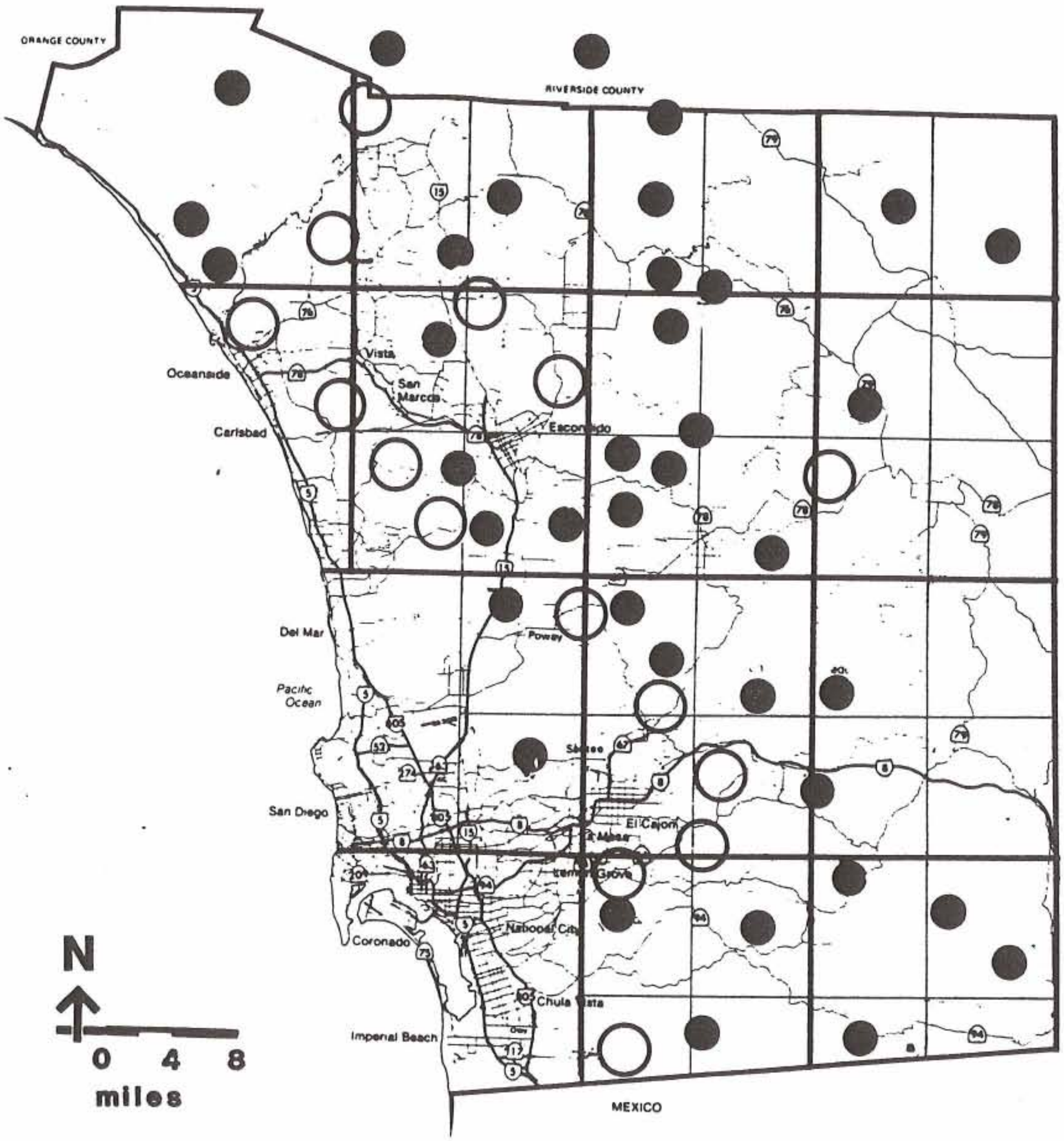

● Active pairs

○ Abandoned areas

Fig. 1. The configuration of the Golden Eagle study area in San Diego County, California. Grid lines represent the 15 (bold line) and 7.5 minute quadrangles used in population analyses.

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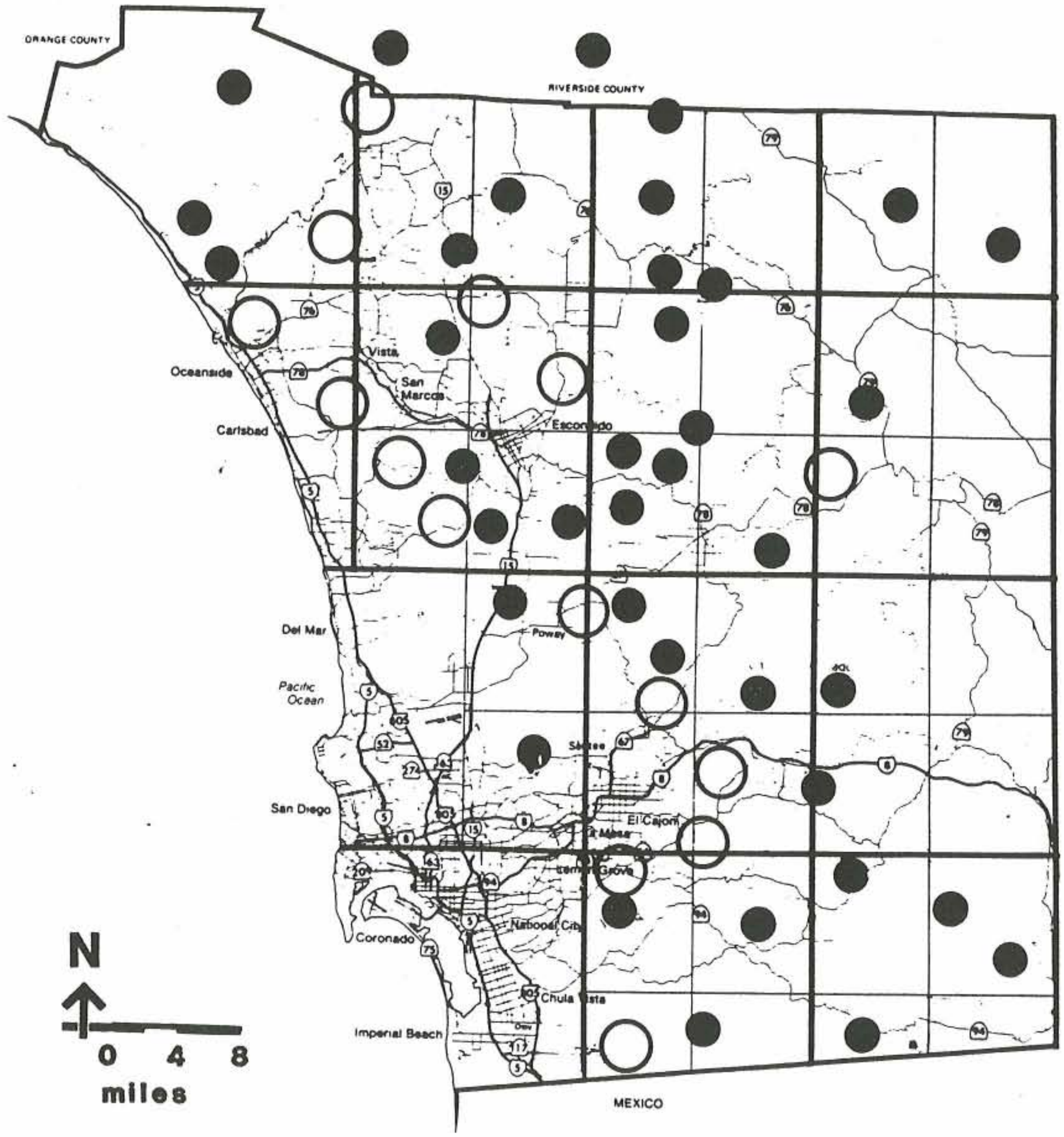


● Active pairs

○ Abandoned areas

Fig. 1. The configuration of the Golden Eagle study area in San Diego County, California. Grid lines represent the 15 (bold line) and 7.5 minute quadrangles used in population analyses.

Fig. 2. The location of the Golden Eagle study area in California.

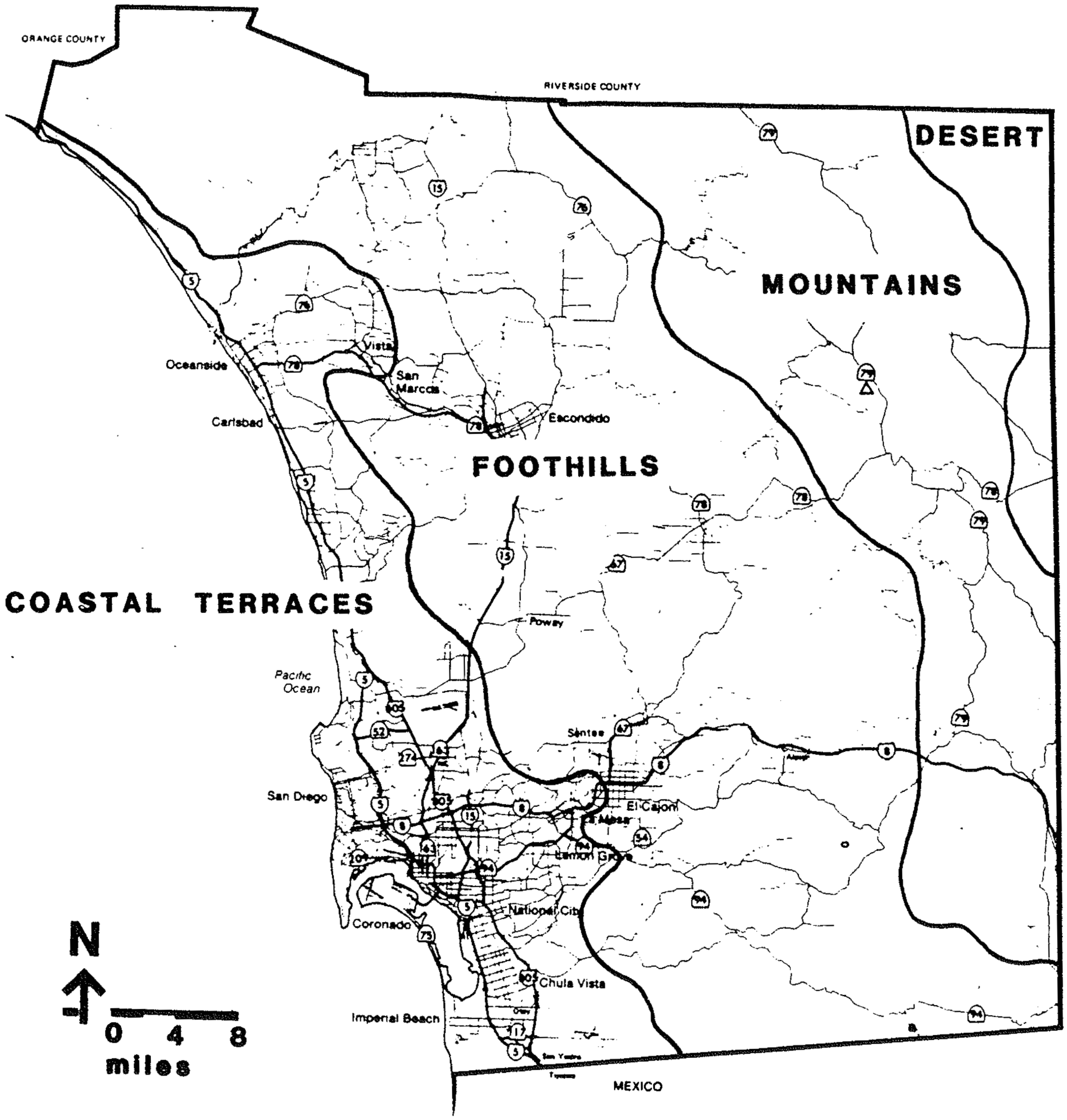


Fig. 3. Geographic regions of the Golden Eagle study area in San Diego County.

Vegetation in the study area is dominated by shrublands (62.1 percent of the total area and 75.2 percent of the vegetated area), with small proportions of grasslands (10.8 percent, 13.6 percent) and woodlands (8.9 percent, 11.2 percent) (Figure 4). Dominant and representative plant species of these vegetation types are listed in Table 2 (Thorne 1976). Coniferous, oak, and riparian woodlands provide tree nest sites for Golden Eagles in the study area. Coniferous woodlands are restricted to the mountains, oak woodlands are widely distributed from the mountains to the coast, and riparian woodlands occur primarily in the major canyons.

The temperate climate of San Diego County is typified by wet winters and warm, dry summers. Average precipitation ranges from 22 to 30 cm in the coastal areas, 30 to 50 cm in the foothills, 40 to 122 cm in the mountains, and 8 to 15 cm in the deserts (Pryde 1984).

The human population of San Diego County was approximately 1,862,000 in 1980 (Pryde 1984). Most of the population lives in or near the urbanized western portion of the study area, along the coast from the Mexican border to the City of Oceanside (population 75,000), and along the development corridor that extends

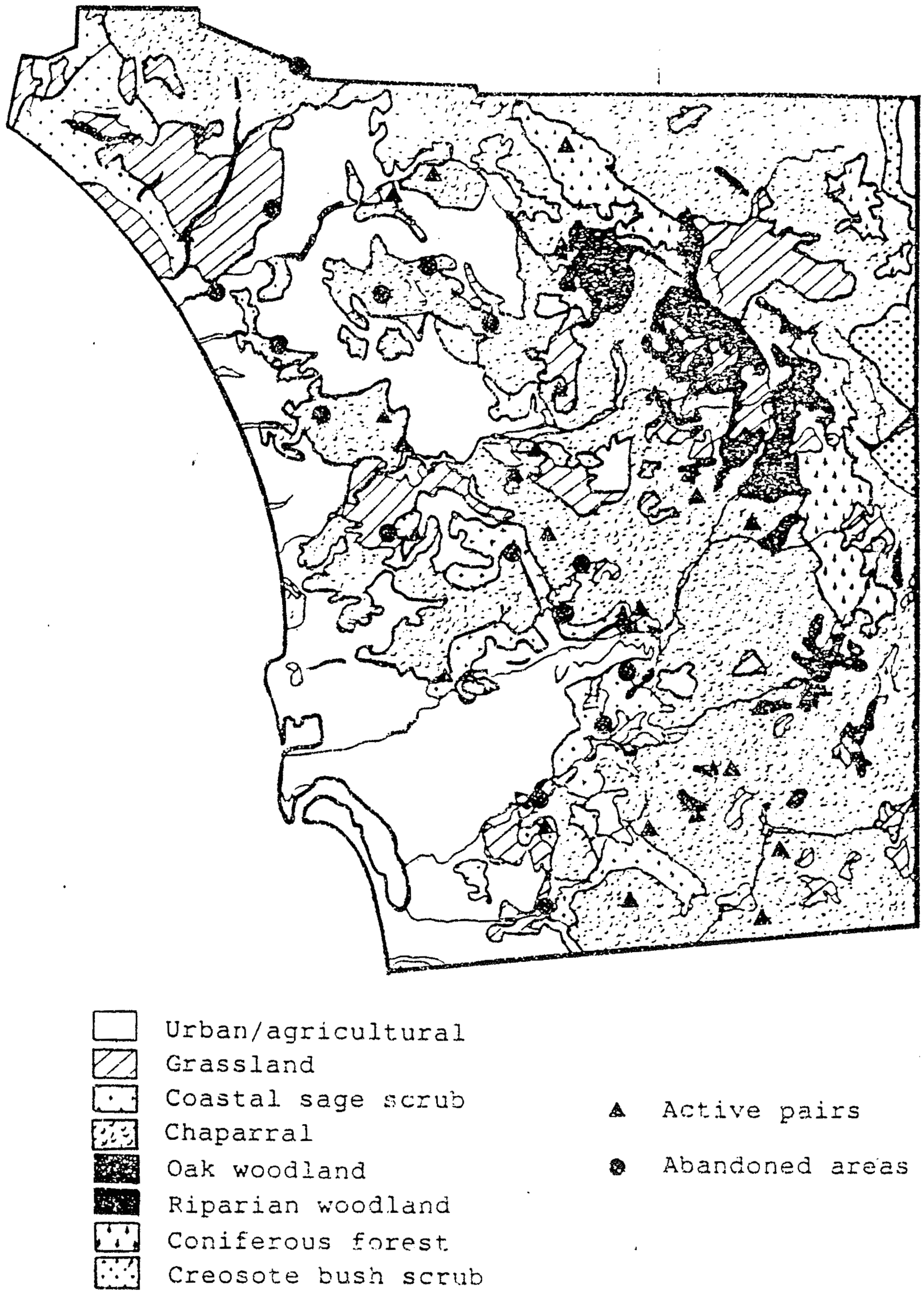


Fig. 4. Vegetation types occurring in the Golden Eagle study area in the western half of San Diego County, California. Adapted from Oberbauer (1979).

Table 2. Dominant and representative plant species of vegetation types in the Golden Eagle study area, western San Diego County.

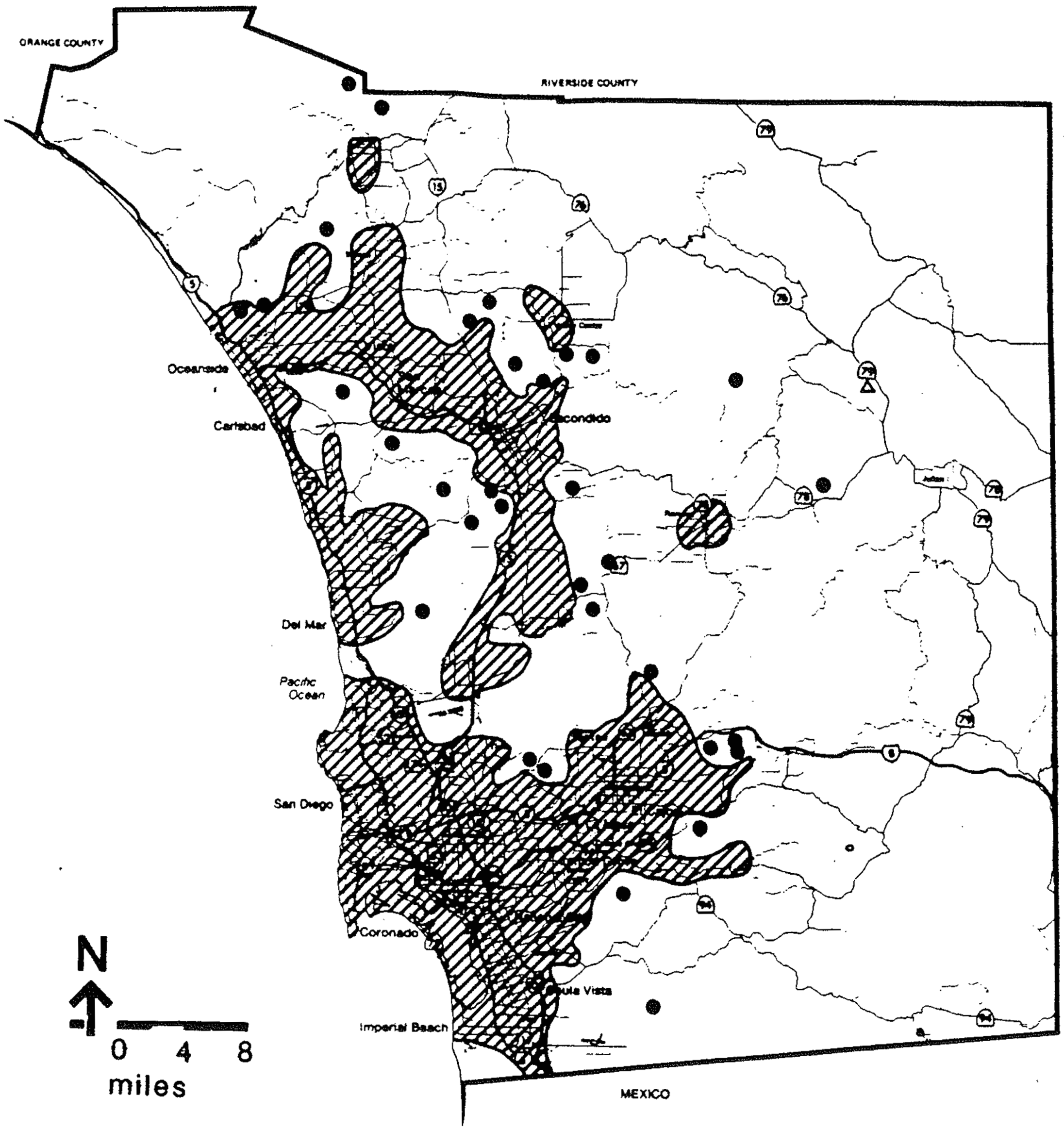
Vegetation Type	Dominant and Representative Species and Genera
Grassland	*Avena*, *Brassica*, *Bromus*, *Erodium*, and *Festuca*
Open Shrublands	
Island Sage Scrub	*Artemisia californica*, *Diplacus* spp., *Eriogonum fasciculatum*, *Haplopappus* spp., *Lotus scoparius*, *Lupinus* spp., and *Malosma laurina*
Creosote Bush Scrub	*Ambrosia dumosa*, *Atriplex* spp., *Encelia farinosa*, *Larrea divaricata*, and *Opuntia* spp.
Chamise Chaparral	*Adenostoma fasciculatum*
Dense Shrublands	
Mixed Chaparral	*Adenostoma fasciculatum*, *Arctostaphylos* spp., *Ceanothus* spp., *Quercus* spp., *Rhamnus* spp., and *Rhus* spp.
Woodlands	
Oak Woodlands	*Quercus agrifolia*, *Q. kelloggii*, and *Q. engelmannii*
Riparian Woodlands	*Platanus racemosa*, *Populus fremontii*, *Quercus agrifolia*, and *Salix* spp.
Coniferous Forest	*Pinus ponderosa*, *Pseudotsuga*, *Macrocarpa*, and *Quercus kelloggii*

from San Diego to Escondido (population 85,000) in the foothills (Figure 5).

Sample Units within the Study Area

Golden Eagles occupy home ranges, within which there are typically one or more nest areas and several nest sites. The terminology used in this study follows Newton (1979): (1) the nest site is the actual nest substrate and structure; (2) the nest area is the immediate vicinity of the nest site, e.g., the nest cliff or stand of trees (in the case of Golden Eagles, a nest area usually contains several nest sites); and (3) the home range is the area over which the birds forage.

The movements of eagles define their home range, making this area impossible to reconstruct for past populations. Breeding pairs are the most satisfactory sample unit when measuring population distribution and change, but it is more meaningful and, in most cases, more convenient to analyze disturbance by nest areas. These analyses can be complicated by the fact that some pairs have several nest areas. However, in nearly all cases a specific pair possessed a primary nest area that contained more nest sites than other nest areas, and could be used as a reference point for the pair. Unless



Limit of urbanization 1980

● Abandoned areas

Fig. 5. Distribution of the human population in the Golden Eagle study area in western San Diego County. Adapted from Pryde (1982).

otherwise stated, the present and past locations of eagle pairs were defined by primary nest areas.

Historical Data

Historical data on Golden Eagle nest locations were obtained from notes, records, and recollections of egg collectors, primarily from those active in the first 40 years of this century. Egg collectors visited or found nearly all nest areas of Golden Eagles within the study area, taking over 400 clutches of eggs from the late 1800's to the 1950's (L. Kiff, pers. comm.). This information provides a reliable, although somewhat punctuated, history of the breeding activity of Golden Eagles in the study area prior to the population decline after 1950.

Dixon's (1937) paper on the breeding Golden Eagle population near Escondido, California, provided a focal point for the collection of historical data. Using his paper and an unpublished map of Golden Eagle home ranges near Escondido (given to Ray Quiggley by Dixon in 1940), I was able to estimate the number of eagle pairs and their approximate locations in the northern half of the study area during the period 1900 to 1937. Data from other collectors were used to make similar estimates for areas outside that of the Dixon study.

Precise locations of historical nest sites were pointed out in the field or were plotted on maps through the verbal and written descriptions of oologists, professional and amateur ornithologists. Ralph Dixon provided photographs of 14 nest areas active prior to 1955.

Recent Data

Field work began in January 1977 and continued through the breeding season of 1981. Active nest areas in the study area were censused in 1977 and 1978 using a combination of road, foot, and helicopter surveys (helicopter surveys were conducted on U.S. Forest Service lands only). Once located, eagle pairs were observed until the nest areas were found. These active nest areas were checked three times during each breeding season: (1) during mating and nest construction, (2) during incubation, and (3) during brooding or at fledging. Nests in some areas could not be checked during the fledging. Historical nest areas were checked twice during each breeding season from 1978 to 1981: once during January and once during February, March, or April.

Golden Eagle Distribution and Abundance

Undisturbed populations of Golden Eagles are stable in total number and distribution of paired adults (Brown and Watson 1963, Newton 1979, Haller 1982). However, eagle pairs sometimes do not breed (although they occupy a home range with suitable nest areas). Thus, the number of breeding pairs in any given year may only be a portion of the total number of adult pairs in an area. My analyses were designed to account for these normal fluctuations and to test long-term changes in the abundance and occurrence of resident pairs. The distribution of nest areas was compared to a set of environmental variables in order to make sure that population changes were not the result of environmental change and to collect background information on nest habitat selection.

The hypothesis that the current population has a random spatial distribution over the study area was tested by dividing the study area into 50 rectangular quadrats (7.5 minutes in area, based on USGS topographic maps) and by comparing the observed distribution of eagle pairs among these quadrats to the expected Poisson distribution using a G-test for goodness of fit. The locations of eagle pairs were mapped (scale 1:128,000) by their primary nest area (or most frequently used nest location if the pair did not have a primary location). Mapping was done for both current and historical populations (Figure 5). Population density was estimated with the mean number and standard error of eagle pairs per quadrat.

The hypothesis that nesting eagles were nonrandomly associated with vegetation types was tested by comparing the distribution of pairs in the various types against an expected distribution based on the proportions of each type in the study area. The similar hypothesis that nesting pairs were nonramdomly associated with fire frequency categories was tested in the same manner. Vegetation categories were determined from the map presented by Oberbauer (1979), and fire frequency data were taken from fire maps prepared by Krausmann (1981). The proportions of vegetation and fire categories within the study area were measured using a polar planimeter.

The hypothesis that the location of nesting pairs was related to topographic heterogeneity was tested by comparing the topographic heterogeneity of nest areas to that of a set of randomly chosen areas. Data on slope categories were not available for the study area, and standard techniques do not exist for the measure of topographic heterogeneity. As a result, I established an index of topographic heterogeneity by counting the number of topographic contour lines intersecting two perpendicular (N-S and E-W) lines (each 1.60 km long) drawn through township and range sections (scale 1:128,000) in the study area. The number of contour lines intersected constituted the index of topographic heterogeneity. Of the 3,150 sections in the study area, 74 were chosen at random (approximately 2.3 percent of the total) to compare with the sections containing nest areas.

The hypothesis that the distribution of nesting pairs had changed from 1928 to 1978 was tested by comparing the distributions of the two time periods away from a fixed line (the coastline of the study area). The distances between nesting pairs and the coastline were measured for 1928 and 1978 distributions and then compared with a Kolmogorov-Smirnov test for contingency. The hypothesis that nesting pairs had moved away from foci of human activity was tested in the same way, except that the measured distance was from the nesting pairs to the closest focal point of human activity. Foci of human activity were defined as the centers of population clusters with more than 10,000 persons. The population data were taken from the Comprehensive

Planning Organization (CPO) report on the San Diego Region (San Diego 1977).

Selection of Sample Units for Disturbance Analyses

As stated earlier, nesting areas typically contain several nests, with the distance between nests varying from 3 meters to 2 km. Nests in close proximity create problems of lack of sample independence if each nest is treated as a single sample unit. Furthermore, the total sample becomes weighted towards pairs that build the most nests, and fails to treat the nest selection behavior of all pairs equally. At the other extreme, a sample unit large enough to encompass all nests of a given pair become difficult to measure, includes areas that are not utilized by breeding birds, and promotes a false representation of nesting habitat. In order to avoid problems of duplication, all nests on the same cliff were treated as a single sample unit. Nests along ridgelines with broken cliffs were placed into separate groups when the distance between nests was greater than 100 m. This sample unit is constituted the "nest area" for statistical purposes.

When only one nest was found in a nest area, it was used as the point from which all measurements were taken. When a primary nest could be identified, it was point of measurement. Finally, when no nest nsidered as a primary nest, measurements were a point central to all the nests of the) evidence of nests were found in the majority ned areas. It was therefore assumed that the ation identified by egg collectors was the pri- te at each abandoned area, and all measurements aken from this point.

. for Nest Area and
gle Pair Locations

Nest areas and pair locations have been coded in text for conciseness and to keep the specific loca- ons confidential. Nest areas are numbered from 1 to 4; active pairs (= A) are coded from A1 to A39, and abandoned areas (= H) are coded from H1 to H16. A key of nest area and pair locations is available on request from the author or from the Western Foundation of Vertebrate Zoology, Suite 1400, 100 Glendon Ave., Los Angeles, CA 90024.

Classification and Defini-
tion of Sample Groups

Nest areas located during field studies were classified into two groups: active and abandoned. Areas not reasonably classified into either group were not used in the analyses. Active nest areas met one of two criteria: (1) the area had been the site of a breeding attempt during the field study period (1977 to 1981), or (2) the area contained a nest built up or maintained during the study period.

Nest areas placed in the abandoned group had historical records of use, but were unoccupied and unattended during the study period. Most of these areas had been unoccupied for varying periods prior to the study. Nest areas were not placed in the abandoned group if they contained at least one active nest site, regardless of the number of abandoned nest sites.

The active group was used to represent current (1978) conditions of Golden Eagle nesting areas. The abandoned group was used to represent the current conditions at abandoned nest areas. These two groups are referred to as the "active 1978" sample and the "abandoned 1978" sample, respectively. Historical records were used to reconstruct conditions around nest areas prior to 1928. These records showed that nearly all active and abandoned nest areas were active in 1928. These records were used to create two additional sample groups: one represented conditions at abandoned nest areas as they appeared while these areas were active in 1928 and the other represented conditions at active nest areas as they appeared in 1928. These two groups are referred to as the "abandoned 1928" sample and the "active 1928" sample, respectively, and as the "historical" sample collectively.

The four groups allowed a comparison of the conditions of active areas with conditions at areas that have been abandoned (active 1978 versus abandoned 1978). The historical groups allowed comparison of the magnitude of change at abandoned areas with the magnitude of change of active areas, as well as a comparison of the initial conditions at areas that became abandoned with those that remained active.

Measures of Habitat Change

Habitat variables were measured in concentric circles centered on the primary nest. The geometric shapes of areas that influence eagle nesting are undoubtedly variable and difficult to determine, but a circle centered on the nest location has the lowest *a priori* probability of error in describing this unknown area. Radii were chosen to delimit areas that ranged from about one fifth to about equal to the typical home range of Golden Eagles in the study area (Dixon 1937), 2.5 km, 3.75 km, and 5.0 km around primary nests. Vegetation and land use within these circles were mapped from aerial photographs taken in 1928 and 1978. Because of the poor quality of the 1928 aerial photographs, standard vegetation types (Thorne 1976) could not be mapped. Vegetation types were grouped into categories representing different types of foraging areas for Golden Eagles: (1) grasslands, including overgrazed or highly disturbed shrublands; (2) open shrublands, including inland and coastal sage scrub, creosote bush scrub, and sparse chamise chaparral; (3) dense shrublands, such as mixed chaparral and dense chamise chaparral; (4) woodlands, including oak, riparian, and coniferous woodlands and forests; (5) row crops; (6) orchards; (7) rural housing, including farm structures and housing at densities of one or fewer structures per acre; (8) suburban housing, with more than one house per acre, and commercial and/or industrial areas; (9) bodies of water, including lakes, bays, marshes and estuaries. Measures were made with a polar planimeter on line drawings made on USGS topographic maps. Drawings were made using an overhead projection of aerial photographs cast onto the topographic maps.

Fire History at Nest Areas

Fire frequency within 0.8 km of nest areas was measured for the period of 1920 to 1980. The raw data on fires in San Diego were massed into ten-year blocks and the number of decades when a fire occurred within 0.8 km of each nest area was determined. The distribution of active nests among these fire-frequency categories was then compared to the distribution of the abandoned nests. The distribution of active nests was also compared to an expected frequency based on the proportions of the fire-frequency types within the study area.

Habitat Change Near Nest Areas

Two variables were used to measure habitat alteration at nest areas: alteration above nest areas and alteration below nest areas. Alteration was defined as any area that had been converted from existing vegetation (native or disturbed) into any stage of development: brushing, grading, farming, mining, landscaping, roads, and structures. Included in this definition were areas that had been permanently disturbed by grading or by the complete and permanent removal of vegetation with subsequent construction. Measurements of these variables were made within 0.8 and 1.6 km radii of nest areas.

Aerial photographs showed that alteration of vegetation and topography was practically nonexistent around nest areas in 1928. As a result, the alteration variables were measured for 1978 conditions, but not for the historical conditions. In addition, there was insufficient alteration within 0.8 km of nest areas in either group to justify the use of this smaller radius of measurement.

Measures of Human Activity

Two types of measurements were made of human activity around nest areas: (1) distance to the closest sources of human activity; and (2) the magnitude of human activity within given radii of nest areas. Data for these measurements were taken from aerial photographs (1928 and 1978), topographic maps, and the 1980 census information.

Distance measurements were made to the nearest (1) structure, (2) path, (3) passable road, and (4) major road. A default limit was set on distance in order to avoid biasing the sample groups with cases greater than 3000 m (the average distance between eagle nests); all cases with distances over the default limit were given the value of 3000 m. A structure was defined as any building or habitation occupied by humans. A path was considered as any passage through the vegetation that directed traffic along a specific course and was passable to foot traffic but not by standard two-wheel drive vehicles. A passable road was open to two-wheel drive vehicles but was not a major thoroughfare. Major roads were defined as state highways, interstate freeways, and other major thoroughfares (traffic volume over 2000 vehicles per day, as reported by the California Department of Transportation). These nearest points of human activity were located on aerial photos and plotted onto topographic maps from which distances to nest areas were measured.

The magnitude of human activity around nest areas was measured by determining the number of structures, number of dwelling units, and the human population within given radii of nest areas. Structures were counted within 183, 275, 367, 458 m of nest areas. Separate counts were made for structures at elevations above and below nests. This created a total of eight measurements at each nest area. Dwelling units (the standard name for single-family living units) were counted within 1.6 km of nest areas. Human populations were estimated within 4.8 and 8.0 km radii of nest areas.

Statistical Analyses

Frequency data were analyzed with Chi-square contingency test comparisons or G-test (greater than two by two comparisons). Mensurative data sets with discrete or non-normal distributions were analyzed with a Kolmolgorov-Smirnov test.

Step-wise discriminant analysis and cluster analysis were used to examine the relationship among the four sample groups and among the 139 sample units, as well as to estimate the ability of specific variables to separate the groups given the variance of other variables in the data set. A random number set (with the same mean and variance as the combined groups for each variable) was used to test the strength of the stepwise discriminant function.

Multiple comparisons of the same data set make it unreasonable to choose an alpha level of 0.05, because this probability for a type one error would allow at least one of the 36 statistical tests to reject a hypothesis based on chance rather than real difference between the abandoned and active groups. Therefore, alpha level for all tests was set at 0.025.

Human disturbance variables may have continued to increase at nest areas after abandonment. These changes after abandonment, which cannot be estimated, might have created observed differences between active and abandoned groups not present (or at least significant) when nest abandonments occurred. Differences between active and abandoned areas may therefore be greater than the threshold level of disturbance that causes abandonment.

Estimation of Population Parameters

The number of young fledged per pair per year was recorded for nests visited from 1978 through 1981. Mortalities were recorded only when carcasses were found or reported. Turnover rates of adults at active nest areas were recorded when obvious, but no eagles in the adult population were banded. These data were combined with information taken from the literature to estimate the average fledge among pairs per year and the average fledge per pair over the four years, and to postulate mortality rates. The null hypothesis in this segment of the study was that mortality and natality in the study population were similar to rates in healthy populations of Golden Eagles in other parts of North America.

RESULTS

The Golden Eagle Population

Thirty-eight Golden Eagle pairs occupied home ranges in the study area during the period 1977 through 1981 (Figure 5). One other pair disappeared before the breeding season of 1981, but was still counted in the population estimate for 1980. Two other pairs were occasionally observed in areas where no breeding took place. These birds were not considered breeding pairs, and the quadrats in which they occurred were not used in breeding density measurements.

The nesting of pair A39 escaped detection until 1983 (John Oakley pers. comm.). This pair probably bred in all four years of the study. Three other pairs were considered active because they bred at the beginning of (or less than three years before) the study, even though they ceased breeding by 1981. Pair A29 did not breed during the four years of the study, pair A16 ceased breeding in 1980, but both pairs remained within these areas into 1984. Pair A9 ceased breeding in 1978 and disappeared from the home range by the end of the study.

Only 35 of the 50 sample quadrats had sufficient observations to be used in the 1978 population density estimate. Four pairs and one abandoned home range which occurred outside these quadrats were excluded from the density analysis. The mean density of eagle pairs among the 35 quadrats was 1.00 ± 0.12 s.e. These numbers translate into a density of one pair per 142 to 181 km^2 or 0.55 to 0.70 pairs per 100 km^2.

There are historical records for pairs at or near the locations of 30 of the 39 active pairs. In addition, there are historical records for 16 pairs at locations no longer occupied by breeding pairs. Thus, the documented number of eagle pairs in the study area prior to 1928 was 46. The nine active pairs with no historical records were inaccessible to egg collectors and probably went undetected, suggesting that there may have been as many as 55 pairs in the study area in 1928. The quadrats containing the pairs without records for 1928 were not used. The 32 quadrats with complete historical records had a sample mean of 1.41 ± 0.20 s.e. pairs per quadrat. This produces density of one pair per 88 to 150 km^2 or 0.75 to 1.00 pairs per 100 km^2.

If the three quadrats with undocumented historical pairs are used ($n = 35$), then the mean becomes 1.4 ± 0.17 s.e. pairs per quadrat, approximately the same density. Twenty-three of the quadrats showed no change in number of eagle pairs from 1928 to 1978, seven quadrats lost one pair, and four lost two pair each (one historical pair occurred outside the sample quadrats). This change translates into a loss of one pair per 329 km^2 of the study area.

Population Dispersion and Distribution

The 1978 dispersion of 35 nesting pairs among the quadrats was not significantly different than the distribution predicted by chance alone (G-test for goodness of fit, d.f. = 3; calculated = 2.56, critical = 9.61, $P > 0.05$). There was no evidence of a clustered or regular distribution. If the 15 lost pairs are added to the 1978 population to estimate 1928 population, the dispersion of the latter population also is not significantly different from random (G-test for goodness of fit, d.f. = 3; calculated value = 2.57, critical value = 7.61, $P > 0.05$).

The median distance of active pairs to the Pacific Coast was 29 km, with a range of 3 to 51 km. In 1928 the median distance from the coast was 26 km, with a range of 0.8 to 51 km. There was no significant change from 1928 to 1978 in the distribution of eagle pairs relative to the coast (Kolmogorov-Smirnov contingency test, $n = 30$, $m = 46$, $P > 0.05$).

Breeding Pairs Lost from the Study Area

Sixteen nesting pairs active in 1928 had disappeared by 1978. In eight cases (H2, H4, H5, H6, H7, H9, H14, H16) pairs were absent from both the nest areas and the historical home ranges as defined by Dixon (1937). In two other cases (H15 and H17) pairs disappeared from nest areas and the surrounding areas that probably contained their home ranges. In at least four cases, however, a portion of the historical home range as estimated by Dixon (1937) and nest areas had been incorporated into the home range of adjoining pairs (H1 + A2, H3 + A8, H10 + A10, H13 + A30). Two pairs (H11 and H12) appeared to have been lost from the breeding population, but paired individuals still appeared occasionally near the historical nest areas. Pair H12 may have bred during the study period, but did not use any of their traditional nest areas.

Pair A9 disappeared during 1980 and no pair was present in this home range after that time. It was assumed that this pair was lost from the population.

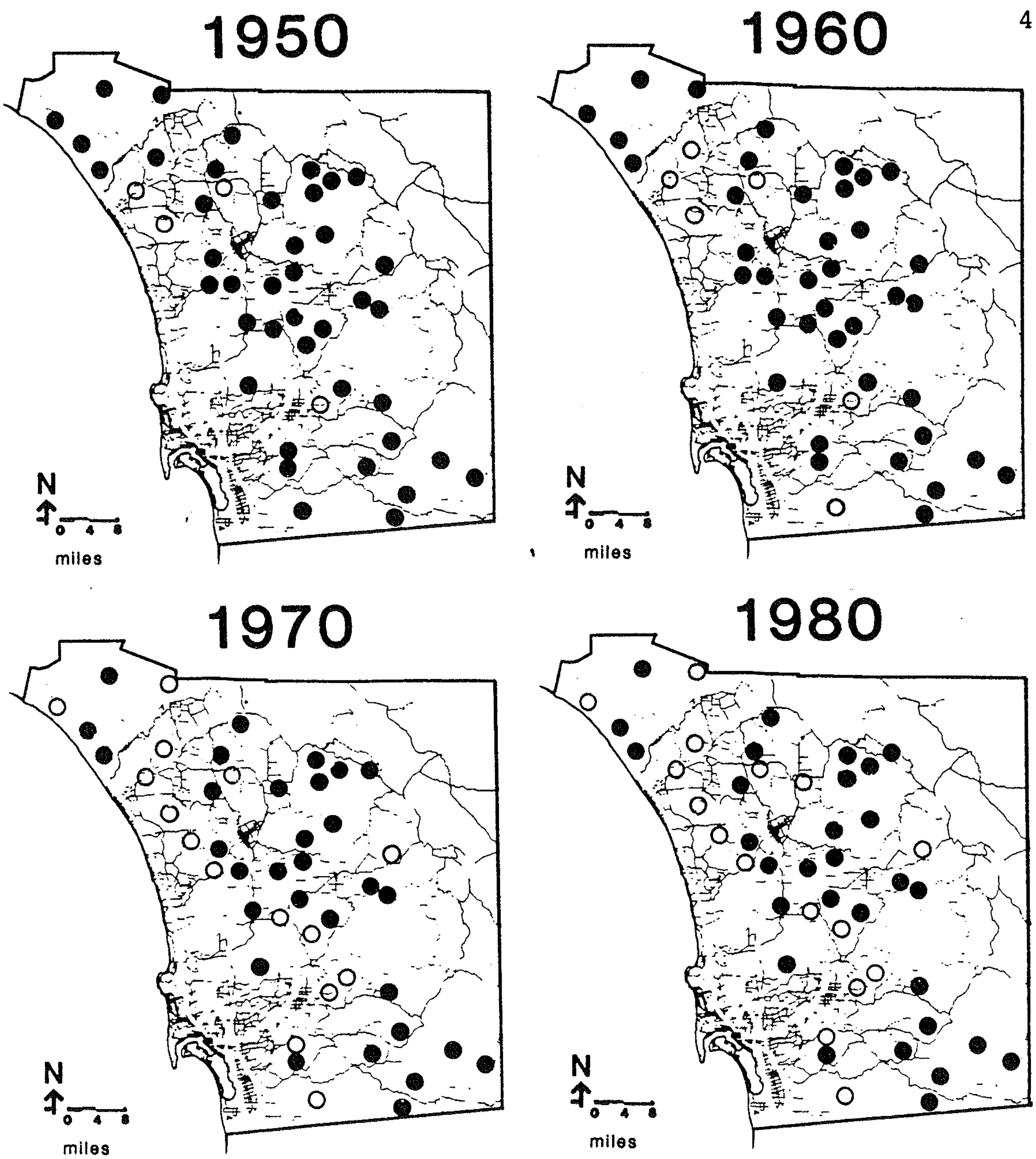
History of Population Change

The notes and recollections of egg collectors suggest that four pairs of Golden Eagles were lost before 1950, two between 1950 and 1960, seven between

1960 and 1970, and one pair between 1970 and 1978 (Figure 6). There was no way to determine the decade during which the two other pairs disappeared. One pair stopped breeding between 1970 and 1978, but remained within their home range throughout the study.

The dates and sequence of abandonment are relatively uncertain for the years 1928 to 1950. By the time of Dixon's (1937) study, development had already begun to encroach upon two pairs on the coast (H4 and H5) and one pair in the foothills (H14). These pairs and a fourth pair north of Escondido (H3), may have been lost prior to 1950. During the 1950's at least two pairs were lost from the foothills: pair H2 in the north and pair H16 in the south. By the end of the 1950's six pairs had been lost from the population: two along the coast, two in the northern foothills and two in the southern foothills.

In 1960 the western edge of the eagle population consisted of twelve pairs: six ringing metropolitan San Diego (H11, H13, H15, A27, A29, and A30), and six along the western edge of the foothills (H1, H6, H10, A1, A2, A16). Gaps in the population had begun to appear around Oceanside, Escondido, and El Cajon (Figure 6). Three pairs were lost from the coast between 1960 and 1970: H1, H6, and H10. Three pairs around San Diego (H11,



● Active areas

○ Abandoned areas

Scale 1:120,000

Fig. 6. Distributional changes in the Golden Eagle population of western San Diego County from 1930 to 1980.

H13, and H15) ceased breeding activity, with pairs H13 and H15 abandoning their territories prior to 1970. Pair A29 lost most of its nesting areas but continued to breed, while pairs A27 and A30 remained undisturbed. Pairs H9 and H17 were lost in the foothills: H9 in the northern agricultural areas and H17 at the eastern edge of a developing valley in Poway. Thus, it appears that seven pairs were lost for the study area from 1960 to 1970.

By 1970 eagle pairs had disappeared from all coastal home ranges except A1 and A2 (both on the military reservation and A16). Most home ranges adjoining developed lands had been abandoned, but A3, A16, and A29 continued to hold territories and breed into the 1970's. Abandonment occurred without pattern in the northern foothills, however, with home range losses scattered throughout the population. Pairs H2, H3, H9, and H17 disappeared, but the adjoining home ranges remained occupied. Pairs H7 and H12 had developed irregular patterns of breeding, even though they were far east of developed areas.

The Distance of Nesting Pairs to Foci of Human Activity

Eight foci of human activity were recognized (Figure 5). The median distance from active pairs

(1980) to these foci was 13.0 km, with a range of 3.5 to 30 km. The median distance between eagle pairs and foci of human activity in 1928 was 12.8 km, with a range of 1.4 to 30 km. A Kolmogorov-Smirnov contingency test showed no significant difference between the distribution of the 1978 and 1928 populations in distance from foci of human activity ($n = 28$, $m = 39$; $P > 0.05$).

Nest Areas Relative to Vegetation Types

From 1977 to 1981 nesting pairs occurred in grassland ($n = 1$); open shrublands ($n = 18$) including sage and desert scrub ($n = 4$), and chamise chaparral ($n = 14$); dense shrublands (mixed chaparral) ($n = 18$); and woodlands ($n = 2$) including riparian woodlands ($n = 1$) and coniferous forest ($n = 1$). The distributions of active pairs among the vegetation types was significantly different from random (G-test for goodness of fit, d.f. = 7; calculated value = 24.0, critical value = 14.1, $P < 0.05$). Inconsistencies occurred in the high number of pairs nesting in mixed chaparral and the paucity of pairs occurring in grassland and agricultural areas.

The distribution of abandoned areas followed a pattern similar to that of the active pairs. Abandoned nest areas occurred in grassland ($n = 1$); open shrublands (n = 21) including sage and desert scrub (n = 5), and chamise chaparral (n = 16); dense shrublands (mixed chaparral) (n = 12); and woodlands (n = 2) including riparian woodlands (n = 1) and oak woodlands (n = 1). There were fewer nests in the grasslands and agricultural areas and more in chamise and mixed chaparrals than would be expected by the proportions of vegetation types (G-test for goodness of fit, d.f. = 7; calculated value = 15.5, critical value = 14.1, $P < 0.05$).

Multivariate analyses showed no relationship between areas of vegetation type and the number of pairs within 15 minute quadrangles (Table 3).

Nest Areas Relative to Fire Frequency

The distribution of pairs among the fire frequency categories was significantly different than would be expected from a random assortment of nests among the proportions of each fire category (G-test for goodness of fit, d.f. = 3; calculated value of 18.30, critical value of 7.61, $P < 0.05$, Table 4). Nest areas with fire frequencies greater than one were more common than expected, while nest areas with fire frequencies of zero were less common than expected.

Table 3. The proportions of vegetation and land-use areas of the Golden Eagle study area in western San Diego County by 15 minute quadrangles.

San Diego County Quadrangle Number	Suburban	Agriculture	Grassland	Open Shrubland	Dense Shrubland	Woodland	Eagles per Quad.
1	0.03	0.06	0.33	0.27	0.26	0.05	3
2	0.04	0.44	0.04	0.18	0.28	0.02	3
3	0.01	0.04	0.06	0.20	0.47	0.22	4
4	0.05	0	0.08	0.69	0.11	0.07	*
8	0.26	0.30	0.08	0.23	0.12	0.01	4
9	0.03	0.08	0.22	0.35	0.16	0.16	3
10	0	0	0.17	0.27	0.24	0.32	*
13	0.47	0.01	0.07	0.43	0.01	0.01	2
14	0.21	0	0.02	0.64	0.10	0.03	3
15	0	0	0.07	0.11	0.65	0.17	3
16	0	0	0.02	0.70	0.21	0.07	*
19†	0.02	0.11	0.06	0.30	0.49	0.02	6
21†	0	0	0.08	0.35	0.55	0.02	1
Total	0.09	0.08	0.11	0.36	0.27	0.09	

*Complete data unavailable for the quadrangle.

†Quandrangle 20 was divided between quadrangles 19 and 21 so that the resulting areas would equal the other 11 quads.

Table 4. The frequency of fires at nest areas in western San Diego County from 1920 to 1980 and over the entire study area. No area burned in more than three of the six decades.

Fire Frequency Categories*	Nest Areas Active	Abandoned	Proportion in Study Area
0	6	12	0.540
1	20	16	0.341
2	7	7	0.108
3	4	0	0.010

*Number of decades in which the area burned between 1920 and 1980 (Krausmann 1981).

Nest Areas Relative to Topographic Heterogeneity

The frequency distribution of sections with nest areas (active and abandoned) varied significantly from the distribution that would be expected from the frequencies of randomly selected sections (Kolmogorov-Smirnov test; $n = 74$, $P < 0.01$). In addition, the frequency distribution of abandoned nest areas ($n = 35$) was significantly different than the frequency distribution of active nest areas (Kolmogorov-Smirnov test, $P < 0.01$, $n = 35$), with the abandoned areas occurring more frequently in the lower values of topographic heterogeneity (Table 5).

Relationship between Nest Areas, Topography and Vegetation

Vegetation type was recorded with the index of topographic heterogeneity in 360 township and range sections (Table 6). The 74 sections with nest areas showed a similar pattern of higher indices in mixed and chamise chaparral, and lower indices in the other vegetation types. The nest area sections, however, had a higher index of topographic heterogeneity than the randomly selected sections when both groups were stratified by vegetation type. Mixed chaparral and chamise chaparral were the only vegetation strata with sufficient sample

Table 5. Frequencies of topographic index* in township and range sections with Golden Eagle nest areas and sections chosen at random in western San Diego County.

Topographic Index Value	Nest Area Frequencies			Random Sample
	Active	Abandoned	Combined	
0	0	1	1	2
1	0	2	2	3
2	0	0	0	5
3	2	1	3	5
4	0	0	0	7
5	0	1	1	8
6	0	5	5	8†
7	1	2	3	7
8	0	3	3	5
9	3	7†	10	6
10	5	4	9†	5
11	9†	4	13	4
12	3	1	4	3
13	4	4	8	2
14	4	0	4	0
15	3	0	3	2
16	0	0	0	1
17	0	0	0	0
18	0	0	0	0
19	0	0	0	0
20	1	0	1	1
21	2	0	2	0
Total	35	39	74	74

*Topographic index was based on the number of contour lines intersecting two perpendicular lines (1.6 km long) drawn through each township and range section.

†Median value of the sample group.

Table 6. Topographic index* relative to vegetation types in western San Diego County.

Topographic Index	Number of Sections per Vegetation Type				
	Grasslands	Agriculture	Inland Sage Scrub	Chamise Chaparral	Mixed Chaparral
0	2	2	0	0	1
1	5	4	3	2	0
2	6	8	5	1	4
3	2	3	2	3	2
4	7†	7	4	6	4
5	4	5†	5	5	7
6	4	5	10†	3	3
7	3	6	4	5†	3†
8	2	2	5	6	3
9	2	1	4	3	4
10	1	1	8	4	3
11	0	0	2	3	2
12	0	1	1	2	1
13	0	1	0	0	1
14	0	0	0	0	1
15	0	0	0	0	2
16	1	0	1	0	0
17	0	0	0	0	0
18	0	0	0	1	0
19	0	0	0	0	0
20	0	0	0	0	1
21	0	0	0	0	0
Total	39	46	54	45	42

*Topographic index was based on the number of contour lines intersecting two perpendicular lines (1.6 km long) drawn through each township and range section.

†Median value of topographic heterogeneity in vegetation types.

sizes to compare the topographic index of sections with nests to the sections selected at random from that vegetation type. The distribution of sections with nests was significantly higher in the topographic index than the distribution of sections chosen at random within the mixed chaparral vegetation type (Kolmolgorov-Smirnov contingency test; $m = 30$, $n = 45$, $P < 0.025$) but not within the chamise chaparral (same test, $m = 30$, $n = 45$, $P > 0.05$).

Nest Areas and Habitat Change

Granite cliffs in the foothills provide most nest sites for Golden Eagles in San Diego County, although some nests occur on the sedimentary cliffs of the coastal terrace and in the trees along the steep canyons of the foothills and mountains. The nest cliffs in the study are typically taller than 15 m but seldom exceed 150 m.

One hundred and eleven nest areas were examined: 39 were classified as native; 35 abandoned; 13 could not be classified into either group; seven areas did not have sufficient historical data to be classified into the abandoned group; and 17 areas could not be used because there were not enough data for an exact location. Nest sites occurred in trees (18.9 percent), sedimentary cliffs (8.0 percent), and granitic cliffs (73.1 percent).

Vegetation

Vegetation was mapped at 9 abandoned areas and 8 active areas, both for 1928 and 1978. The areas of different vegetation types around abandoned nests were not significantly different from those around active nest areas for any of the eight vegetation types (Mann-Whitney U test, $P > 0.05$). Furthermore, only two categories, rural and suburban, showed a significant difference between the 1928 and the 1978 samples around abandoned nest areas (Mann-Whitney U test, $0.025 > P > 0.01$ for the rural comparison, and $0.01 > P > 0.001$ for the suburban comparison.

Habitat Alteration Above and Below Nest Areas

Habitat alteration above abandoned nest areas was not significantly different from that above active areas (Table 7). Thirty-three (85 percent) of the active group and 29 (83 percent) of the abandoned group had less than 41 ha altered above nest areas and within 1.6 km. Only one nest area from each group had more than 202 ha of alteration above nest areas.

Habitat alteration below nest areas was significantly different between active areas and abandoned areas (Table 7). The median score of the active areas was zero m of alteration, while the median of abandoned areas was 31 ha. Twenty-eight (72 percent) of the active areas had less than 31 ha of altered habitat. Only 17 (49 percent) of the abandoned areas had less than 31 ha of alteration below nest areas. The primary difference between the two groups was the high number of active areas with no alteration, although alteration at two active areas exceeded that at nearly all abandoned areas.

Proximity of Disturbance

The distribution of distances from nest area to closest structure in the abandoned group was similar to the distribution of distances in the active group; the difference between the two distributions could be predicted by chance alone. The same situation was true in 1928; the difference could be attributed to chance alone. Both groups, however, showed significant shifts in distribution of distance from 1928 to 1978, with structures closer to nest areas in 1978 than in 1928 (Table 8). Eleven (31 percent) of the abandoned areas and six (15 percent) of the active areas showed no

Table 7. Habitat alteration within 1.6 km of Golden Eagle nest areas in western San Diego County.

	Habitat Alteration in Hectares		
	Active Nest Areas	Abandoned Nest Areas	Statistical Significance*
Above Nests			
Median	0	0	P>0.05
Range	0 to 103	0 to 685	
Below Nests			
Median	0	23	0.05>P>0.025
Range	0 to 213	0 to 460	

*Kolmolgorov-Smirnov contingency test.

Table 8. The distance (m) from Golden Eagle nest areas to sources of disturbance in western San Diego County.

Sample Group	Median	Range	Statistical Significance*
		Structures	
1978 Active	915	5 to >3000	
			0.05>P>0.025
1978 Abandoned	550	90 to >3000	
			P<0.025
1928 Abandoned	1035	240 to >3000	
			0.05>P>0.025
1928 Active	1310	150 to >3000	
		Paths	
1978 Active	245	0 to 790	
			0.05>P>0.025
1978 Abandoned	125	0 to 550	
			P<0.025
1928 Abandoned	365	60 to 820	
			P>0.05
1928 Active	305	60 to 1520	
		Passable Road	
1978 Active	425	0 to 1830	
			0.05>P>0.025
1978 Abandoned	245	0 to 680	
			P<0.025
1928 Abandoned	490	60 to 2750	
			P<0.025
1928 Active	700	60 to 2130	

*Based on Kolmogorov-Smirnov contingency test.

Table 8. Continued.

Sample Group	Median	Range	Statistical Significance
		Major Roads	
1978 Active	1460	30 to >3000	
			$P>0.05$
1978 Abandoned	730	0 to >3000	
			$P<0.025$
1928 Abandoned	>3000	180 to >3000	
			$P<0.025$
1928 Active	>3000	>3000	

change in the distance to nearest structure. Eight (23 percent) of the abandoned areas and three (17 percent) of the active areas had no structures with the default distance (3000 m) in 1928. These figures dropped to one (3 percent) and three (8 percent), respectively, in 1978.

Houses were the most commonly recorded structures (79 percent of all sample units); other types of structures included public facilities such as park and military buildings (11 percent of total); capital facilities (dams, pumping stations, 9 percent of total); and one commercial structure (store, 1 percent). Active and abandoned areas did not differ significantly in the type of nearest structure. Nearly all (91 percent) of the historical areas had a house as the closest structure; capital facilities were the only other type of structures with 9 percent of the total.

Paths were distributed significantly farther from active nest areas than they were from abandoned nest areas. There was a significant shift in the distribution of both the active group and the abandoned group between 1928 and 1978; in both cases, paths were significantly closer to nest areas in 1978 than they had been in 1928. In 1928 the distributions of paths in the active group was not significantly different from the abandoned group.

Twenty-six (67 percent) of the active group and 33 (94 percent) of the abandoned group were within 305 m of paths in 1978. In 1928 these figures were 16 (53 percent) for the active group and 15 (43 percent) for the abandoned group.

Passable roads were distributed significantly farther from the active nests than they were from abandoned areas in 1978. Passable roads were significantly closer to both groups in 1978 than they had been in 1928. In 1928, the distributions of the two groups were not significantly different in their distance to passable roads (Table 8).

Major roads were significantly farther away from active areas than they were from abandoned areas. Major roads were significantly closer to both groups in 1978 than they had been in 1928. No tests were run on the difference in the distribution of the two groups in 1928 because all cases in both groups were beyond the default level of 3000 m (Table 8).

Elevation of Nest Areas Relative to Disturbance

Elevation of nest areas above sources of human disturbance was not significantly different for active and abandoned areas (Table 9). The combination of distance and the angle between nests and disturbance also showed no significant difference for active and abandoned nest areas.

Disturbance Intensity

Only 6 active areas and 11 abandoned areas had any structures within the 455 m. The median number of structures for the 6 active areas was 1; the median for the 11 abandoned areas was 1.5. Only 2 abandoned areas and 1 active area had any structures above them closer than 455 m.

Active areas, as a group, had significantly fewer dwelling units within 1.6 km than abandoned nest areas (Table 10). There were significantly more dwelling units around both active and abandoned areas in 1978 than there had been in 1928. Initially (1928), there was no significant difference between the numbers of dwelling units around members of the two groups.

Human population data were only available for the more densely populated areas of the county. These included only 17 active and 13 abandoned areas in the western half of the study area.

The abandoned group had significantly higher number of persons living within a 4.8 km radius of nest areas

Table 9. Results of Mann-Whitney U-tests comparing distances to disturbance (m) and elevation above disturbance (m) for active and abandoned areas in 1978.*

Source of Disturbance	Distance	Elevation	Distance x Arctangent
Structures	-	-	-
Paths	+	-	-
Passable Roads	+	-	-
Major Roads	+	-	-

*P < 0.05 are marked by "+"; P > 0.05 by "-".

Table 10. Disturbance intensity around Golden Eagle nest areas in western San Diego County.

Disturbance Measure	Nest Areas: Active	Nest Areas: Abandoned	Statistical Significance*
Dwelling Units			
Median	2	16	P<0.025
Range	0 to 425	0 to 1,600	
Human Population within 4.8 km			
Median	2,000	8,000	P<0.025
Range	100 to 32,000	600 to 46,500	
Human Population within 8.0 km			
Median	23,000	41,000	P>0.05
Range	100 to 61,000	15,000 to 12,700	

*Kolmolgorov-Smirnov contingency test.

than the active group. The change (from 1928 to 1978) in the number of persons living within 4.8 km of abandoned areas was also significant, as was the change around the active group (Table 10).

There was no significant difference between the two groups in the number of persons living within a 8.0 km radius of nest areas, although the human population around areas in both groups changed significantly between 1928 and 1978.

Changes in Nest Site Locations within Home Ranges

In 1978 15 pairs used the same primary nest area that their predecessors used in 1928, while 11 pairs showed some change in nest area. For 13 pairs data were insufficient to determine if change had occurred. Eight of the pairs that disappeared between 1928 and 1978 showed change in nest areas prior to leaving the population; for eight areas records were insufficient to determine if change had occurred.

Change in the nest areas was evident in two ways: (1) shift in the location of the primary nest area or (2) nest area abandonment. Seven active pairs abandoned all or part of their nest areas. The most extreme cases involved pairs A16 and A29, which abandoned all nest areas. Pairs A8 and A17 abandoned all except their primary nest area. The remaining three pairs abandoned at least one nest area each, but retained more than one nest area.

Six pairs showed a combination of nest abandonment and a shift in the location of the primary nest location. Pair A10 incorporated the home range of H10, and the primary nest area was relocated on the edge of the two home ranges. Pair A3 moved its primary nest location from the south to the north side of a broad river valley, establishing the new area on a cliff that had been previously used by nesting peregrine falcons (Falco peregrinus). Pair A4 also took over the nest cliff of a pair of Peregrine Falcons; but its former primary-nest area is unknown. The best documented case of movement of the primary nest area occurred with pair A13, which moved twice during the study period as development consumed its nest areas. This pair moved its nest area 1100 m across a wide valley onto the largest mountain in the vicinity. Later, this pair shifted the nest area 153 m upward in elevation and 1120 m in distance. Pair A9 moved approximately 795 m up a canyon, gaining 122 m in elevation, to a new primary nest area.

Four pairs appeared to have shifted their primary nest area prior to the complete abandonment of the home range. The cliff where pair A5 nested was quarried in the 1930's, forcing the pair to shift their primary nest location to adjacent trees. Pair H4 appeared to have moved eastward along the cliffs of a river canyon as the city of Oceanside developed. Pair H6 abandoned its primary nest area on the coast, and either did not reestablish a primary nest area or did so but only for a short period before abandoning the home range. Dixon (1937) described pair H7 as having many nest locations; however, by 1970 the pair resident on this home range had only one nest area. Pair H11 had four documented nest locations, but only nested in one area in the last decade of home range occupancy.

Population Parameters in the Study Area

Natality. Fledging rate and breeding success were recorded for 113 nesting attempts from 1971 to 1981 (Table 11). The majority of records were collected in 1977 (12), 1978 (25), 1979 (23), 1980 (21), and 1981 (19). Fledging rate averaged 1.02 ± 0.07 s.e. young per nesting attempt over all years and all areas. Fledging rate at succcessful areas was 1.40 ± 0.05 s.e.

Nesting attempts with one fledged young accounted for 41 percent (50) of all records, while nesting attempts with two fledged young accounted for 27 percent (33) of all records. Of the nests initiated, 31 percent

Table 11. Mean number of young fledged by Golden Eagle pairs in western San Diego County.

Sample Groups	Mean Number of Young/Pair/Year	95% Confidence Interval
Overall	1.02	± 0.07
By year:		
1970 to 1976	1.47	± 0.16
1977	1.40	± 0.20
1978	1.20	± 0.13
1979	0.86	± 0.16
1980	0.47	± 0.14
1981	1.19	± 0.23
By home range (pair)		
>5 years of data	1.14	± 0.16
4 years of data	0.91	± 0.16
3 years of data	1.00	± 0.12

(30) failed. This estimate of failure rate is undoubtedly low. There were nine cases of pairs not breeding during one of the four years of observation.

The productivity of individual home ranges varied from 0.25 to 1.75 young per year over the four years of the study. The mean productivity per home range was 1.02 ± 0.15 s.e. young per year for nests with 3 or more years of data. It should be noted that 60 percent of these pair records are for consecutive years of data. The remaining records were interrupted by a year with no data. Years with no data were omitted from the analysis.

Mortality. Twelve cases of juvenile mortality were reported in the study area from 1975 to 1981, and one additional bird banded in the study area died in Utah three years after fledging (Peter Bloom pers. comm.). All 12 of these birds were immature, with 11 of them failing to survive one year. Mortality resulted from: shooting at the nest area (3 cases), shooting in other areas (2), collision with an automobile (1), fungal infection (1), starvation (1), and unknown (6).

Mortality of breeding adults was not observed, but a change in breeding females was observed for pair A5. The new A5 female was recognized by her immature plumage. The carcass of an adult eagle was found below A3 in 1982 (John Oakley pers. comm.); this bird may have been a member of the pair. Two adult eagles were present during the subsequent breeding season, so it appears that the dead eagle had been replaced.

James B. Dixon told Hunsicker (1972) that individual female Golden Eagles occupied the same breeding area for 15 to 25 years. Dixon (1937) collected the eggs of one female for over 28 years. He derived these estimates by his extraordinary ability to differentiate females by the patterns of their egg coloration.

DISCUSSION

The Golden Eagle Population

The nesting Golden Eagle population in the study area decreased by approximately one third from 1928 to 1978. Quadrats with only one pair in 1928 tended to retain a pair in 1978; quadrats with two or more pairs tended to lose a pair over the same period.

There were no correlations between the number of nesting pairs and the acreage of suitable forage habitat or the number of pairs lost and the acreage of developed land. This lack of correlation refutes neither the fact that foraging area has been reduced, nor the hypothesis that pairs may have been lost because their foraging areas were consumed by development. It does, however, show that pairs may disappear from a region even when there appears to be enough foraging habitat to support them. Quadrangle 14 is a strong example of this point; three of the original six pairs have disappeared, but native vegetation has been replaced on only about one fifth of the quadrangle. Over 65 percent of the remaining area appears to be suitable foraging habitat (Table 3).

The distribution of pairs among quadrats remained random in 1978 as it had in 1928; it appears that the population is neither clustered nor evenly distributed across the study area. Nest locations were more closely associated with topographic heterogeneity than with particular vegetation types, which correlates with the high frequency of nest location on granite cliffs, a common feature of the rugged San Diego foothills. Dixon (1937) suggested that eagles used ridge updrafts for soaring flight, so that freedom from disturbance may not be the only benefit of high topographic relief. However, since vegetation of steep slopes is often too dense to permit foraging by eagles there should be a limit to the degree of topographic heterogeneity in the home range of Golden Eagles. Approximately 85 percent of all nest areas overlooked (or were on the opposite side of the ridge from) large valleys or areas of relatively low topographic heterogeneity and open vegetation.

Disappearance of Breeding Pairs

Evidence of the breeding population of Golden Eagles in 1928 suggests that pairs were scattered throughout the study area and were absent only from the areas of San Diego, Escondido, El Cajon, and Oceanside. Most home range areas in the interior of the eagle population have remained in use with no discernible pattern of abandonment. Home ranges adjoining developed sections of the study area were abandoned more often than interior areas. However, there was no distinct relationship between the proximity of nests to development and their probability or year of abandonment.

The population does not adjust its overall dispersion in compensation for disturbance suffered by specific pairs (i.e., pairs unaffected by disturbance do not shift their home ranges unless neighboring, disturbed pairs actually disappear from disturbed areas). Pairs that lose some of their nest areas have little opportunity to replace them by moving into the home ranges of adjoining pairs. Pairs whose home ranges are compressed by development eventually stop nesting or leave the home range areas, but adjoining pairs typically did not change their nesting patterns unless they were also under some form of disturbance. Eagle pairs appear to make adjustments within their home ranges to compensate for human disturbances and land development whenever possible.

A difference in the amount of developed land around nest areas was observed between the active and abandoned groups. Nevertheless, it was not possible to equate this conversion of habitat with changes in vegetation significant with respect to foraging. In most cases the portion of a home range area lost to development had initially been a disturbed or rural area. These areas may have lost their value as foraging habitat before the nest areas were abandoned.

The actual increase in suburban acreage from 1928 to 1978 was significantly greater around abandoned areas than around active areas. However, the accompanying decrease in vegetation was evenly distributed through all types. Thus, the loss of a nesting area could not be attributed to the loss of a specified amount of any vegetation type within 2.5 km of nests. Furthermore, the loss of suitable forage area around active areas was equal to, or in some cases greater than, the loss around abandoned areas.

The concentric circle technique used in analyses of vegetation does not accurately reproduce the shape of the home range. Concurrent with this vegetation analysis problem, there is no way to measure variation in the intensity of use across a historical home range. A circle might be the best naive predictor of home range, but it is obviously insufficient to estimate area of use, intensity of use, or the change in these two variables over time. Concentric circle analyses appear to be best at showing the increase and proximity disturbance around nest areas, rather than the loss of foraging area.

Human Disturbance Variables at Nest Areas

Many potentially significant measurements can be taken around abandoned nest areas. The selection of specific variables is typically based on prior observation or hypotheses (Nelson 1979). The majority of the variables considered in this analysis were postulated indicators of disturbance, rather than actual disturbance causes. That many of these variables did not prove significant showed only that they were not good indicators, and does not dismiss their associated disturbances as possible causes of home range or nest area abandonment. Two recurring sources of variation confounded the analyses of these variables: (1) the variable relationship between the actual (although undefined) causal factor and the measured indicator, such as the distance to roads versus the actual amount of disturbance created by the road, and (2) the variation in the tolerance of different pairs to human disturbance.

The variables listed below are in rank from best to worst in discrimination of active and abandoned areas, based on: (1) their ability to separate the two groups, showing significant change at abandoned areas, but no change at active areas, and (2) the number of areas in the active groups that were beyond the median score of the abandoned group in the severity of the disturbance variable. The first criterion measured the ability of the variable to define abandoned areas, the second the ability of the variable to correctly classify nest areas.

Dwelling Units Near Nest Areas

Dwelling unit count was the only variable that showed a significant difference between the active and abandoned groups and a significant change at abandoned areas from 1928 to 1978, yet remained relatively unchanged at active areas over the same period. Nevertheless, eight active areas had larger numbers of dwelling units than the median score of the abandoned areas. The major differences between these two groups was the larger number of active areas with no dwelling units within a radius of 1.6 km, and the opposingly large number of abandoned areas with 50 or more dwelling units within the same radius. Distributions of the two groups between these extremes were similar.

It is impossible to define the direct effect of dwelling units on abandonment of nest areas. It is, however, possible to conclude that the proximity of dwelling units did not cause abandonment; the median number of dwelling units within 455 m of nest areas in both abandoned and active groups was zero. It could be suggested that dwelling units are a measure of habitat alteration; however, the median number of units within 1.6 km of abandoned nest areas was 42; most dwelling units clustered together, and covered only a small portion of the area.

Although Golden Eagles might be disturbed by the sights or sounds from these dwelling units, the number of dwelling units probably indicates extent of human activity and interference near nest areas. There are at least four alternative hypotheses of how increased numbers of dwelling units could be detrimental to nesting pairs: (1) increased probability that the nest location will be found and disturbed, (2) increase in the proximity and the source of persons that might travel near nest sites, increasing the potential for interference, (3) increased number of person-hours in the home range and vicinity of the nest areas, disrupting home range activities, including foraging, and (4) increase in associated annoyances, such as noise and reflected light. The primary assumption of these hypotheses is that nest abandonment and pair loss could result from human disturbance without the necessity of other changes in home range area. Work on Cape Vultures (J. Dobbs pers. comm.) supports this assumption, although it is obvious Golden Eagles show more tenacity in remaining at nest areas.

Human Populations within 4.8 and 8.0 Kilometer Radii

Human population density is another estimate of the potential for human activity near nests. The variable measuring number of persons within 4.8 km had results similar to the dwelling units variable; it separated abandoned areas from active areas, showed a change at abandoned areas from 1928 to 1978, yet remaining constant at active areas over the same period. The sample number of nest areas was restricted to nests in the southwestern third of the study area and did not examine nest areas where the difference between active and abandoned groups might have been more subtle. Given this constraint, the variable at a 4.8 km radius strongly separates the abandoned from the active areas, while the human population within the 8.0 km radius showed no separation of the two groups. In some cases the human population within 4.8 km translated directly into a loss of native areas or vegetation. More often, however, the population around an abandoned nest area could not be equated with vegetation or forage area loss, suggesting that the variable is a measure of the potential for human activity, operating as a source of human disturbance, rather than an actual cause of nest abandonment.

Distance Variables

All four of the distance variables showed a significant change at abandoned areas from 1928 to 1978, but none showed a significant difference between the abandoned group and the active group. Structure and path variables remained relatively constant at active areas while changing at abandoned areas; passable road and major road variables changed as much at active areas as they had at abandoned areas.

The interrelated pattern of development and major road construction makes it nearly impossible to separate the importance of access by the major roads from factors such as land development and human population growth in the regions around abandoned nest areas.

The proximity of structures changed significantly at abandoned areas from 1928 to 1978. The most significant change occurred in the number of structures built closer than 610 m but further than 305 m away from nests which were abandoned. If the proximity of structures causes nest area abandonment, the effect occurs before the distance between structures and nests closes to less than 305 m. Nevertheless, 17 of the abandoned areas had no structures within 610 m, and 13 of the active areas had structures within 610 m. Proximity of structures is not a strong predictor of nest abandonment.

Paths occurred near all abandoned and active areas. They may contribute in a passive way to nest disturbance, but cannot be used to gauge intensity or effect of the disturbance.

Alteration Below Nest Areas

The altered acreage below nest areas (within 1.6 km) was significantly different between the active and abandoned groups. The active group had a higher frequency of areas with no alteration than the abandoned groups. This statistical difference may not, however, have much biological importance. Abandoned areas had a median value of 41 ha of altered area below nests, which translates into about 5 percent of the area surveyed. These disturbed areas typically did not occur within 0.8 km of the abandoned areas. These figures suggest that the difference between the groups, while statistically significant, was biologically insignificant. The alteration of areas around abandoned nests is probably indicative of area-wide development, but does not appear to be a causal factor operating on nest pairs.

Other Variables

Neither alteration above nest areas nor the number of structures within 455 m of the nest areas showed any significant difference between the active group and the abandoned group. The proximity of disturbances around abandoned nest areas was typically farther than 305 m away, and in many cases disturbance was closer to active areas than abandoned areas. These facts strongly suggest that nest abandonment may occur as a function of relatively distant change long before the actual nest area is encroached upon. Nest abandonment can occur as the result of disturbance above nest areas, but the pattern suggests that the nest abandonment typically occurs before development is undertaken on the steep slopes and hilltops of nest areas.

General Conclusions for Disturbance Factors

Two conclusions can be drawn from the human disturbance variables examined in this analysis. First, all factors show a great deal of variability in their relation to eagle nesting activity. Second, no specific factor stood out in separating active and abandoned areas, suggesting a multicolinearity among the variable and, possibly, some unidentified synergistic effects.

The data suggest several trends in nest abandonment which were not anticipated by study design. First, nest areas appear to be abandoned before structures come within 455 m or roads within 305 m. Second, regional increases in human disturbance seem to affect abandonment to a greater extent than changes near nest areas. These regional effects appear to be a function of human presence, rather than habitat destruction. The most reasonable speculation, then, is that nest abandonment is not a function of physical factors but appears to lie in something less easily quantified, presumably patterns of human activity.

Habituation of Nesting Golden Eagles to Human Disturbance

Variance in the human disturbance variables resulted from a number of factors. Nevertheless, the wide range of response to human disturbance shown by the eagles, particularly the degree of overlap in conditions at active and abandoned areas, suggests that there are differential levels of tolerance towards disturbance in the study population. On the average approximately 30 percent of the active areas were beyond the median level of abandoned group on any disturbance variable. Over half of the active areas were beyond the median of the abandoned group in at least two of the variables (it should be noted that half of the active areas that exceeded the medians of the abandoned group in five or more variables were abandoned before the study was completed). Furthermore, nearly all active areas showed an increase in the level of all disturbance variables from 1928 to 1978.

Two alternative (but not necessarily mutually exclusive) hypotheses can be given as an explanation of differences in tolerance levels. First, eagles may possess local traditions (Newton 1979), which form early in life and cause adults to seek breeding areas similar to their natal areas (philopatry). Young reared in areas with higher levels of disturbance might be less adverse to disturbance when selecting nesting areas as adults. Alternatively, individual eagles could be exposed to disturbance in a manner that eventually lowers their sensitivities to conditions that would normally alter nesting behavior. Although the concept has not been rigorously tested, there are numerous anecdotal examples of habituation by predatory birds to disturbances (Edwards 1969; Lish 1975; Steenhof 1976). A common pattern in these accounts lies in the regularity of the specific disturbance.

Population Dynamics

Natality. The fledging success of the study population occurs at the high end of the range of values recorded for other Golden Eagle populations (Table 12). Variation in the fledging success among the pairs of the population was relatively small, with the greatest deviations occurring in pairs whose breeding was disrupted by human activities. One pair (A9) abandoned the home range after three unsuccessful breeding years; however, the lack of breeding success did not cause pairs A16 or A29 to abandon their home range.

It appears that the current population was not depressed as a result of poor fledging success from 1977 to 1981. Haller (1982) observed that fledging success increased in populations where persecution lowered the number of nonbreeding individuals, reducing the level of interference these individuals caused breeding pairs. Thus, the small size of the nonbreeding population in my study area may have favored the high fecundity of breeding pairs.

Mortality rates. The scant mortality data prohibits any empirical estimate of the fledgling survival, adult survival, or turnover rates in nesting areas. The speculation that juvenile mortality occurs more

Table 12. Observed breeding success (per pair per year) of Golden Eagle populations in Europe and North America.

Location	Young per Pair per Year	Source
Scotland	0.4	Sanderman (1957)
Scotland	0.8	Watson (1957)
Scotland	0.6	Everett (1971)
Scotland	0.4	Wier (in Brown 1976)
Scotland	0.5	Wier (in Brown 1976)
Utah	0.7	Murphy (1975)
Idaho	0.67	U.S. Dept. Inter. (1979)
Switzerland	0.4 to 0.6	Haller (1982)

frequently than adult mortality in the study area is a reasonable extension of the limited mortality data and the conclusions of Olendorff (1976) and Steenhof et al. (1985). The relative importance of these two types of mortality in the population dynamics of Golden Eagles in the study area remains uncertain.

A comparison of natality rates and postulated mortality rates suggests that a population with a stable number of breeding pairs probably does not have a recruitment probability below 0.20 (from fledge to first breeding year), unless fledging success is very high or longevity unusual (Table 13). Conversely, a recruitment probability over 0.55 would require extremely low fledging success or unreasonably high adult mortality rates. In actuality, this recruitment probability would have to be expressed as the chance of a fledgling joining the breeding population or being replaced by an immigrating individual in order to account for movement of eagles in and out of the study area.

If the number of breeding pairs remains constant, probability of fledgling recruitment ranges from 0.2 to 0.55, and fledging success ranges from 0.3 to 0.4, then the average life expectancy at the onset of breeding age in the study population should lie between 4 to 16

Table 13. Hypothesized number of breeding years in Golden Eagles relative to fledging rates and the probability of becoming a breeding adult in a stable population.

Probability of Becoming a Breeding Adult	Potential Fledging Rates (young per pair per year)					
	0.40	0.60	0.70	0.80	0.90	1.00
0.20	24.5*	16.2	13.8	12.0	10.6	9.5
0.25	19.4	12.8	11.0	9.5	8.4	7.4
0.30	16.2	10.6	9.0	7.8	6.9	6.2
0.35	13.8	9.0	7.7	6.6	5.6	5.2
0.40	12.0	7.8	6.6	5.7	5.0	4.5
0.45	10.6	6.9	5.6	5.0	4.5	3.9
0.50	9.5	6.1	5.2	4.5	3.9	3.5
0.55	8.6	5.5	4.7	4.0	3.5	3.1
0.60	7.8	5.0	4.2	3.6	3.2	2.8
0.65	7.2	4.6	3.8	3.3	2.9	2.5
0.70	6.6	4.2	3.6	3.0	2.6	2.3
0.75	6.2	3.9	3.3	2.8	2.4	2.1
0.80	5.7	3.6	3.0	2.6	2.2	2.0

*Values are in average number of breeding years.

years, with an average turnover rate of approximately 3 to 11 years within specific home ranges.

Population Dynamics and the Loss of Breeding Pairs

Many authors have shown that Golden Eagles maintain a relatively constant number of breeding pairs per unit area for long periods of time (Brown and Watson 1963, U.S. Dept. Inter. 1979, Haller 1982). If this stability is coupled with relatively constant rates of fecundity and mortality in the adult population, then rate of survival in the nonbreeding population has the greatest potential of any population parameter to absorb environmental fluctuation. The nonbreeding portion of the population may therefore be the compensation factor for environmental change when the population lies below saturation, and becomes the primary cause of density-dependent fecundity rates when population rises above the saturation point.

The studies of Haller (1982) and Steenhof et al. (1983) has shown that this system can be perturbed in at least two ways. First, the size of the nonbreeding population can be depressed through persecution, which can increase fledging success but may lower recruitment rates (Haller 1982). Second, immatures can prematurely join the breeding population if territories are left unoccupied because of human disturbance (Steenhof et al. 1983). In the first case, there may be insufficient eagles in the population to fill vacant territories; in the second case, there may be an insufficient number of breeding adults with a tolerance to human disturbance to fill all the territories of a given area, allowing immature eagles the opportunity to nest prematurely.

The study population has a fledge rate near that of Haller's (1982) persecuted population, and 16 unoccupied territories. There was only one case of an immature eagle breeding within the study area, well below the 3 percent level reported by Steenhof et al (1983). These observations would suggest that the nonbreeding population is below the saturation point and cannot fill all the territories that are vacated by breeding eagles.

Hypotheses on Territory Maintenance and Abandonment

A substantial Golden Eagle population has existed in San Diego County throughout the past 80-year period of development and human population growth. However, as disturbance has increased, pairs have adjusted their nesting locations. Breeding ceased and nests were abandoned as regional conditions exceeded a threshold level, typically before proximal factors, such as roads, are present. Pairs have remained in home range areas without breeding or have disappeared as disturbance increases. Nest areas are typically the focal points of eagle home ranges, and once a breeding pair has disappeared their home range tends to remain unoccupied or is reoccupied only for short periods.

Because eagles maintain stable numbers of breeding pairs and do not necessarily breed every year, it may be advantageous for pairs experiencing habitat disturbance to remain within their home range, even if their breeding becomes irregular, rather than face the uncertainty of establishing a new home range. In fact, some pairs have remained in the study area and have even nested, although disturbance in their home range exceeded that at some abandoned areas. However, nonbreeding eagles may not fill vacancies within these disturbed home ranges because they lack the tolerance that the original occupants gradually developed as disturbance increased. Finally, if the number of nonbreeding eagles is low as a result of direct persecution, then there may not be enough eagles to fill all the vacancies and areas of moderate disturbance may go completely unoccupied as nonbreeders select undisturbed home ranges.

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