

AN ABSTRACT OF THE THESIS OF

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A feral pig population on Santa Catalina Island, California, was studied for 17 months beginning in July 1980. Density was estimated to be 21 to 34 pigs/km² (95% confidence interval) using capture-recapture techniques. Dry season home ranges determined from radio-telemetry data were small and differed significantly between boars and sows. Patterns of habitat use according to vegetative community, topographic position, slope, aspect, elevation, vertical distance to water, and horizontal distance to water were examined. During the dry season, pigs preferred cool moist canyon bottoms, the result of both a physiological need for free water and behavioral responses to high environmental temperatures. Patterns of utilization during the wet season appeared to be primarily a function of food availability. Diets were primarily herbaceous, although small amounts of insects and vetebrate matter were eaten, and varied seasonally. Fruits and forbs were the most preferred foods in the dry season, while fruits, grasses and forbs were most preferred during the wet season. Seasonal differences in diets reflected changes in availability and phenology of plants. Seasonal trends were apparent in acid detergent fiber, cellulose, and crude protein levels in the

diet, but not in acid detergent fiber, phosphorus, gross energy, digestible energy, protein digestibility and cellulose digestibility. Diets were characterized as high in fiber, low in energy and seasonally deficient in protein. Kidney fat and femur marrow fat indices indicated pigs declined in body condition in summer and fall, and improved in winter and spring. Optimal performance of pigs on Catalina appeared to be linked to the quantity of the acorn crop in early fall and the timing and duration of fall-winter rains. A seasonal pattern in breeding was evident, with conception apparently linked to both nutrition and photoperiod. Fertility declined in late spring and summer as photoperiod increased; onset of estrus and breeding in fall or winter were regulated by nutritional status of sows. Litter size as measured by fetal counts was 5.00 ± 0.36 S.E., and sows averaged 0.86 ± 0.17 S.E. litters over a 12 month period. Most sows were older than 1 year when they first conceived, and litter size increased from puberty and peaked at 2-3 years of age. Intrauterine mortality of fetuses averaged 25% and piglet mortality was estimated to be 58% prior to weaning. Mortality rates appeared to be higher for piglets born in summer than in winter or spring.

Ecology of Feral Pigs on Santa Catalina Island

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Ecology of Feral Pigs on Santa Catalina Island

Introduction

Introduced plants and animals generally have a negative effect on some portion of the biota of any non-native environment in which they become established. Islands are particularly susceptible to perturbation resulting from establishment of exotic species. This occurs indirectly as a consequence of the quality that makes island ecosystems so unique - their isolation. Evolution has proceeded in spectacular and often unique paths for those few colonists that successfully dispersed across oceanic barriers to islands. Encountering environments where competitive and predatory pressures were relaxed, these colonists often expanded their niches and exploited new habitats and resources normally exploited by other species in mainland associations. Man's introduction of mainland species, especially those generalists whose superior competitive and predatory abilities have been manipulated and refined over tens of thousands of years, have proved devastating to island biota. In many instances, the outcome is extinction for the more sensitive and often most unique insular species.

Feral pigs (Sus scrofa) are one of numerous exotics introduced by man onto islands that have contributed to the demise of insular plants and animals. Only by drastically reducing or, if possible, eradicating these species will some unique life forms continue to exist. The manuscripts presented in this thesis report basic ecological data for a feral pig population on Santa Catalina Island, California. Such information is imperative for development of management programs aimed at reducing this population to a level where impact is minimized.

I. DIET, NUTRITION, AND CONCEPTION IN FERAL PIGS ON SANTA CATALINA
ISLAND

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Abstract

Dietary preference, nutrition and their effect on animal condition and conception were examined in a feral pig population on Santa Catalina Island, California. Diets were primarily herbaceous, and varied seasonally. Fruits and forbs were the most preferred foods in dry season diets, while fruits, grasses and forbs were most preferred during the wet season. Seasonal differences in diets reflected changes in availability and phenology of plants. Abrupt dietary shifts to annual grasses and forbs in winter were strongly influenced by precipitation patterns. Seasonal trends were apparent in ADF, CEL and CP levels in the diet, but not in ADL, PHOS, GE, DE, protein digestibility and cellulose digestibility. Diets were characterized as high in fiber, low in energy, and seasonally deficient in protein. KFI and FMF indices indicated pigs declined in body condition in summer and fall, and improved in winter and spring. Optimal performance of pigs on Catalina appeared to be linked to the quantity of the acorn crop in early fall and the timing and duration of fall-winter rains. A seasonal pattern in breeding was evident, with conception apparently linked to both nutrition and photoperiod.

Fertility declined in late spring and summer as photoperiod increased; onset of estrus and breeding in fall or winter were regulated by nutritional status of sows.

Wild pigs (*Sus scrofa*) are the most successful exotic big game species in North America, due in part to their ability to exploit a wide variety of habitats and their appeal to hunters. Pigs often pose a management dilemma for land use agencies that attempt to provide populations for recreational hunting because of their tendency to disrupt native biota in sensitive ecological areas (Bratton 1974, 1975; Spatz and Mueller-Dombois 1975, Wood and Barrett 1979, Howe et al. 1981, Diong 1982, Singer et al. 1984) and alter natural patterns of nutrient recycling (Singer et al. 1984). Diets of wild pigs have been described for diverse habitats (e.g. Scott and Pelton 1975, Barrett 1978, Giffin 1978, Wood and Roark 1980, Everett and Alaniz 1980); however, the effect of nutrition on animal condition, reproduction and survival are not well known. A more complete understanding of these interrelationships would permit wildlife biologists to better achieve their specific pig management goals. In this paper, I report dietary preference for a feral pig population on Santa Catalina Island, changes in selected nutritional attributes of these diets, and influences of dietary and nutritional quality on condition and breeding patterns.

Support for this project was provided by the Santa Catalina Island Conservancy, Northwestern Los Angeles Resource Conservation District,

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STUDY AREA

Santa Catalina Island is located 32 km off the coast of southern California at the Palos Verdes Peninsula. Positioned southeast to northwest in orientation, it is approximately 35 km in length and about 13 km at the widest point, encompassing an area of approximately 194 km² (Figure 1). Topography of the island is rugged and precipitous, consisting of deep, steep-walled canyons and sharp ridges, reaching a maximum elevation of 631 m.

The climate of Catalina is Mediterranean, semi-arid in nature and characterized by warm dry summers and mild damp winters. Surface weather is influenced by a shallow coastal marine layer that results from upwelling of cold Pacific Ocean waters. Average temperatures range from 12.7 C in January to 19.2 C in July; annual precipitation averages 31 cm, with most effective rainfall occurring in late fall and winter (Dunkle 1950). During this study (July 1980 through September 1981), 24 cm of rainfall were recorded from December 1980 through April 1981, with most occurring in February and March. Periodic drought is a regularly occurring phenomenon. Permanent and seasonal seeps and small streams occur in the larger canyon systems.

Vegetative communities on Catalina include oak woodlands, chaparral, coastal sage scrub, California grassland and limited riparian zones. Communities are patchy in distribution, influenced by slope, aspect, soils, exposure to coastal winds and grazing by feral animals. Thorne (1967) described these communities and their species associations in detail. Plant communities have been mapped by ground

reconnaissance (Santa Catalina Island Company 1975) and color infrared aerial photography (Minnich 1980).

Field work was concentrated in a 60 km² study area (Figure 1) in which all major plant communities were represented. Feral pigs were introduced into this area from Santa Rosa Island in the mid 1930's (Overholt and Sargent 1971, J. White, pers. comm.). The feral ancestry of the Santa Rosa population dates at least to the late 1800's, and possibly as early as the late 1500's (Mayer 1983). Pig distribution is now island-wide. Feral goats (Capra hircus) occupied about 15 percent of the study area, and California mule deer (Odocoileus hemionus californicus) and bison (Bison bison) were common throughout; all ungulates are nonnative.

METHODS

Eight adult pigs (> 8 months of age) were shot each month, 4 at the end of the first week and 4 at the end of the third week, from July 1980 through September 1981. Pigs were aged by dentition to 26 months following Matschke (1967). A 26-36 month age category was defined based on the partial eruption of molar M^3 . Animals with M^3 fully erupted were classed as > 36 months. Pigs were sexed and a stomach sample, fecal sample, femur and kidney were taken and frozen until analysis. Sows were examined for reproductive activity (pregnancy or lactation). Pregnancy was indicated by the presence of corpora lutea (Schilling 1974) or fetuses. Additional pigs were shot in some months to increase sample sizes for condition and reproductive analyses.

Food habits were determined by microhistological analysis of stomach samples at the Wildlife Food Habits Analytical Laboratory, Texas Tech University. Plant species in the study area were identified following Munz (1974) and a reference collection was established for histological identification. Data were tabulated on a frequency basis, converted to relative density (Sparks and Malechek 1968), and examined by month and season. Plant phenology and rainfall patterns were used to differentiate diet by wet season (January through May 1981) and dry season (July 1980 through December 1980, June 1981 through September 1981). Differences in consumption of forage classes within and between seasons were analyzed using a one-way analysis of variance (ANOVA) or Mann-Whitney U-test.

The relative availability of plant species in the study area was estimated for the 2 seasons. The study area was stratified by plant communities and thirty-two circular plots (28 m²) were distributed and sampled in August 1980, March 1981 and August 1981. Individual plant species and forage classes were assigned an availability rating by ocular estimation of percent cover using the following scale: 1, rare, % cover < 1%; 2, infrequent, 1% < % cover < 5%; 3, frequent, 5% < % cover < 15%; 4, abundant, % cover > 15%. Data were rescaled using a weighted mean (Dixon and Massey 1969) to account for unequal breadth of cover categories, and plant species were assigned availability ranks of 1 to 4. Species in the diet not detected during vegetative sampling were assigned a rating of 1. Dry season results (August 1980 and 1981 sampling) were pooled before analysis. Preference ratings were calculated for the plants in the diets using the formula of Chamrad and Box (1968):

$$\text{Preference rating} = \frac{\% \text{ frequency of occurrence} \times \text{relative density}}{\text{availability rank}}$$

Percent frequency of occurrence was the percentage of stomachs in which a species was recorded for that season. Preference was indicated for those species or forage classes with high preference ratings relative to all other species or forage classes in the diet.

Stomach and fecal samples were dried at 50°C to a constant weight and ground through a 1 mm screen in a Wiley mill. Percent acid detergent fiber (ADF) and percent acid detergent lignin (ADL) were determined following the procedure of Goering and Van Soest (1970) at the Wildlife Habitat Laboratory, Department of Forestry and Range

Management, Washington State University. Percent cellulose (CEL) was expressed as ADF minus ADL; this fraction also included some acid-insoluble ash, mainly silica (Goering and Van Soest 1970). Percent nitrogen (N) was assayed by micro-Kjeldahl digestion (AOAC 1970), and digested samples were analyzed for N and percent phosphorus (PHOS) with an autoanalyzer at the Forage Analyses Laboratory, Department of Soil Science, Oregon State University. N was multiplied by 6.25 and expressed as percent crude protein (CP) in the diet. All results were tabulated on a percent dry matter basis. Gross energy (GE) was measured using a Parr adiabatic bomb calorimeter and reported as kcal/gram dry matter (DM).

Variation in nutritional quality of the diet was examined by month and season for ADF, ADL, CEL, CP, PHOS, and GE using a one-way ANOVA, Kruskal-Wallis one-way ANOVA or Mann-Whitney U-test. When significant differences between months were indicated by ANOVA, significant differences between treatment means were determined by the Student-Newman-Keuls (SNK) multiple range test, or using distribution-free multiple comparison tests (Hollander and Wolfe 1973). An index to apparent digestibility (0 to 100%) of protein and cellulose by pigs was calculated for each month using the equation of Stoddart et al. (1975):

$$\text{Apparent Digestibility} = 100 - 100 \left(\frac{\% \text{ indicator in forage}}{\% \text{ indicator in feces}} \times \frac{\% \text{ nutrient in feces}}{\% \text{ nutrient in forage}} \right)$$

Naturally occurring lignin (ADL) was used as an indigestible indicator to correct for digestibility. Mean monthly values of dietary and fecal ADL, CP, and CEL were considered representative of dietary

nutritional quality and animal performance on the feed and were used in the equation. Some digestibility coefficients for protein were calculated to be negative; these were assigned a value of zero. Metabolic fecal nitrogen (MFN), nitrogen other than that in the undigested feed which is excreted in the feces, can lead to higher fecal protein values than accounted for by diet alone. When digestibility of protein is near zero, MFN results in a negative digestibility coefficient (D.C. Church, pers. comm.). MFN sources include unabsorbed constituents of digestive juices, cellular debris and mucus from the gastric and intestinal tract, microorganisms and nitrogenous compounds excreted into the gut. Digestible energy (DE) of the diet was calculated for each month by subtracting the mean fecal GE corrected for digestibility (mean corrected fecal GE = mean uncorrected fecal GE $\times \frac{\text{mean ADL in forage}}{\text{mean ADL in feces}}$) from the mean dietary GE value for that month. Seasonal differences in protein digestibility, cellulose digestibility, and DE were evaluated from monthly values by oneway ANOVA. Spearman's rank-order nonparametric correlation coefficient was calculated to measure the association of protein and cellulose digestibility with dietary ADF, ADL, CEL, CP, and DE, and the association of DE with dietary ADF, ADL, CEL, CP, protein digestibility and cellulose digestibility.

Change in body weight of adult pigs was examined by sex as an indicator of dry season dietary quality. Pigs livetrapped from June 1981 through September 1981 were weighed to the nearest half kilogram at initial and final capture. Change in body weight for each pig was expressed in kilograms per day and as a percentage of initial body

weight per day; significance changes were implied if 95% confidence intervals for mean values did not include zero. Differences between sexes were examined using a Mann-Whitney U-test.

Condition of animals was investigated using the kidney fat index (KFI) (Riney 1955) and by analysis of the fat content of the femur marrow (FMF) (Coblentz 1979). Differences in fat indices by sex and month were evaluated using a 2-way ANOVA for nonorthogonal designs. When significance was indicated, differences between factor level means were tested using the SNK multiple range test. For adult sows, differences between fat indices and current reproductive state (functional nonreproductive, pregnant or lactating) were examined using a one-way ANOVA and SNK multiple range test.

Fetal litters were counted and crown rump measures were recorded to estimate fetal age (Warwick 1928, Henry 1968a). Piglets captured in the field were aged by dentition (Matschke 1967) and pooled with aged fetuses. Conception dates were computed to examine breeding patterns of pigs on Catalina. A gestation period of 115 days (Henry 1968b, Mount 1968) was used to calculate conception dates.

All data were analyzed using the Statistical Package for the Social Sciences (Nie et al. 1975, Hull and Nie 1981) unless otherwise indicated. ANOVA models were evaluated for normality and homogeneity of variances, and when significant deviations were apparent, appropriate transformations of data were applied. If model aptness after transformation was still unacceptable, nonparametric methods were used. Untransformed means are presented for all results. Significance was accepted at a probability level of $P < 0.05$ unless otherwise noted.

RESULTS AND DISCUSSION

Diet

Foods consumed by feral pigs on Catalina were primarily herbaceous (Table 1) and consumption by forage class varied significantly ($P < 0.0001$) within season. Dry season diets were dominated by fruits and seeds, which were eaten in significantly greater amounts than other forage classes. Fruits of prickly pear cactus (Opuntia spp.) (30.5%) and lemonade berry seeds (Rhus integrifolia) (12.0%) comprised the major items in this forage class. Forbs were also an important dry season component of the diet and were consumed in significantly greater amounts than grass, roots, browse, or insects. Australian saltbush (Atriplex semibacata) (14.8%) a creeping perennial accounted for 80% of all forbs eaten during the dry season. Smaller amounts of grass, roots, browse, insects and vertebrate matter were eaten. Most roots were bulbs of the blue dick (Dichelostemma pulchella). Except for Happlopappus venetus, most browse was consumed incidentally while feeding on other items. Preference ratings (PR) for forage classes identified fruits and seeds (PR = 1907) as most preferred followed by forbs (PR = 733); roots (PR = 140), grass (PR = 101) and browse (PR = 56) were not highly sought by pigs (Table 1). On a species basis, prickly pear fruit (PR = 1477) was the most preferred food in the dry season diet, followed by Australian saltbush (PR = 487) and lemonade berry seeds (PR = 304).

Wet season diets were predominantly grass, forb and fruits and seeds (Table 1), which were consumed in significantly greater amounts

than roots, browse or insects. The major foods in wet season diets were annual brome grasses (Bromus diandrus, B. mollis, and B. rubens) (18.4%), prickly pear cactus fruits (10.8%), Christmas berry seeds (Heteromeles arbutifolia) (10.5%), lemonade berry seeds (7.4%) and bur clover (Medicago polymorpha) (7.0%). Fruits and seeds (PR = 1515) were the most preferred wet season forage followed by grass (PR = 663) and forbs (PR 618); browse (PR = 102) and roots (PR = 16) were not highly preferred (Table 1). Preferred species in the wet season diet included prickly pear cactus fruits (PR = 796), lemonade berry seeds (PR = 448), the bromes (PR = 363), Christmas berry seeds (PR = 290) and bur clover (PR = 194).

Seasonal dietary differences were detected. Dry season diets were significantly higher in seeds and fruits ($P < 0.0001$) and roots ($P < 0.0001$) whereas wet season diets contained significantly larger amounts of grass ($P < 0.0001$) and forb ($P = 0.016$) (Figure 2). Browse and insect consumption did not vary between seasons. Seasonal differences in diets reflected changes in availability and phenology of plants, and some dietary changes were strongly influenced by precipitation patterns on Catalina. Fall and early winter rains trigger abundant growth of annual grasses and forbs that seed, dry out and die as precipitation declines with approaching summer. In 1980, rainfall ended in May, and no rain was recorded until December. Rainfall continued through April 1981. Dietary shifts in January 1981 to utilize annual grasses and annual forbs (Figure 3) and their decline in importance in May and June illustrate shifts that resulted from rainfall-vegetation interactions. Timing of first effective fall

rains and the extent of the rainy season determined the duration of importance of annual forb and grass in the diet. Australian saltbush, a perennial forb that remained green and growing during dry summer months, was consumed in much greater amounts during the dry season when other green forage was uncommon (Figure 3).

A large variety of fruits and seeds were consumed by pigs when seasonally available. Differences in time of flowering and seeding and the size of individual seed crops accounted for their availability over most of the year (Figure 4). Prickly pear cactus, oaks (Quercus spp.), elderberry (Sambucus mexicana) and lemonade berry generally flowered in the spring, and seeds and fruits were available in summer and fall. During this study, prickly pear fruits were extremely abundant and were consumed in large amounts through the fall and early winter until most were gone. The acorn crop in fall of 1980 and 1981 was very poor, and oak mast only appeared in the diet for several months in low quantities. When acorns are abundant, they remain in the diet in large quantities until spring (Scott and Pelton 1975, Barrett 1978, Wood and Roark 1980). Christmas berry flowered in summer, and ripe berries were eaten in winter and spring when they began to drop from trees.

Diets of wild pigs on Catalina and in other habitats (Scott and Pelton 1975, Springer 1977, Barrett 1978, Giffin 1978, Wood and Roark 1980, Everett and Alaniz 1980, Genov 1981a, Coblenz and Baber 1984) indicate that pigs are generalists capable of exploiting a variety of forages successfully. Diets are primarily herbaceous, but small amounts of vertebrate and invertebrate foods are consumed. Forage

utilization appears to be a function of both availability and phenology of vegetation. Overall, fruits and seeds appear to be the most preferred foods and are consumed in large quantities whenever available. Green grass in earlier phenological stages and green forbs appear to be a staple, but are avoided as plants mature.

Some foods such as roots appear to be more important in the diet when predictable foods such as acorns fail (Scott and Pelton 1975) or when above ground vegetation is scarce (Barrett 1978, Genov 1981a, Baron 1982). However, root consumption can be strongly influenced by the type of below ground foods available. In high elevation northern hardwood forests in Great Smoky Mountains National Park, corms of the spring beauty (Claytonia virginica) constituted 1/3 of the spring-summer diets of European wild boar even though above ground herbaceous diversity and cover was high (Howe et al. 1981). In that study, woody roots were not preferred (Howe et al. 1981). In coastal South Carolina and coastal Texas roots of plants from marsh sites were exploited in spring and summer (Springer 1975, Wood and Roark 1980).

Abrupt shifts in diet to utilize seasonally available forages are common, particularly to annual vegetation resulting from rainfall in semi-arid habitats (Barrett 1978, Figure 3) or to oak mast (Pine and Gerdes 1975, Barrett 1978, Springer 1977, Wood and Roark 1980).

Nutrition

Diets of wild pigs on Catalina varied significantly with respect to ADL ($P = 0.002$), CEL ($P = 0.045$), CP ($P < 0.0001$), PHOS ($P = 0.001$) and GE ($P = 0.017$) over the 15 month study period, but not in ADF ($P =$

0.067) (Table 2, Figure 5). Diets were high in fiber throughout the study (mean ADF = 39.7 ± 0.7 S.E.). Lignin reached highest levels during the transition from wet to dry season (May = 21.2 ± 2.4 S.E., June = 15.9 ± 3.2 S.E. 1981), a result of consumption of mature annual grass (May = 25%, June = 18%) and browse and stone containing lemonade berry seeds (May = 25%, June = 19%). Increases in lignin concentrations occur in grasses and forbs with maturation, and browse generally has higher lignin than either (Stoddart et al. 1975). Highest levels of CP (16.0 ± 1.2 S.E.) and PHOS (0.49 ± 0.18 S.E.) occurred during the wet season (February).

Seasonal trends were apparent in CP, but not in PHOS. Dietary CP was significantly ($P < 0.0001$) greater during the wet season (13.8 ± 0.7 S.E.) than dry season (8.1 ± 0.4 S.E.), however PHOS did not vary ($P = 0.16$) between seasons (wet = 0.26 ± 0.05 S.E., dry = 0.18 ± 0.03 S.E.). With the beginning of active plant growth, CP level in herbage increases, but later declines as plants mature (Stoddart et al. 1975). CP levels in diets of Catalina feral pigs followed this trend during the wet season (Table 2). Seasonal trends were also apparent in ADF and CEL concentrations. ADF ($P = 0.024$) and CEL ($P = 0.012$) were higher in wet season (ADF = 41.8 ± 0.8 S.E., CEL = 29.5 ± 0.9 S.E.) than dry (ADF = 38.6 ± 0.9 S.E., CEL = 26.7 ± 0.6 S.E.), probably due to greater consumption of grasses and forbs (Figure 2). ADL (12.1 ± 0.5 S.E., $P = 0.48$) and GE (3917 kcal/kg DM ± 33 S.E., $P = 0.08$) did not vary between seasons.

Digestibility of protein by pigs was variable (Table 3) but did not differ significantly ($P = 0.30$) between wet ($20.5\% \pm 7.1$ S.E.) or

dry ($12.0\% \pm 4.3$ S.E.) seasons. Endogenous nitrogen excreted in the feces elevated fecal nitrogen; therefore, true digestibility of protein was probably higher than determined. Apparent digestible protein (DP) levels indicated pigs obtained little to no usable protein from the diets during some months (Table 3) and experienced a negative nitrogen balance. Presumably protein requirements were met or supplemented through muscle catabolism when diets were deficient. DP was higher during the wet season, reaching 6% in March, but fell to 0% by May, and tracked the seasonal CP levels in the diet. Digestibility of protein, fat, nitrogen-free extract and dry matter is known to be inhibited in pigs by high fiber content in the diet (Cole et al. 1972, Kidder and Manners 1978). Pond et al. (1962) reported a decline in protein digestibility of 10-13% for pigs on high fiber diets (7% crude fiber) compared to low fiber diets (3% crude fiber). Although correlation analysis did not reveal an association between protein digestibility and ADF ($r_s = -0.23$, $P = 0.41$), ADL ($r_s = -0.44$, $P = 0.10$) or CEL ($r_s = 0.19$, $P = 0.49$) in this study, the consistently high fiber content in diets of pigs on Catalina probably acted to depress digestibility of proteins and other nutritional constituents. The extent to which this occurs depends upon the chemical nature of the fiber, its physical association with the constituents of concern, its concentration and the physiological state of the pig (ARC 1981). No relationship was evident between protein digestibility and CP ($r_s = 0.42$, $P = 0.12$) or DE ($r_s = 0.51$, $P = 0.06$) level in the diet.

Some digestion of fiber (cellulose) occurs through microbial fermentation in the large intestine of pigs (reviewed by Cranwell

1968, Barrett 1978). Digestion of cellulose was evident but variable in this study (Table 3), and it did not differ significantly ($P = 0.08$) between wet ($21.1\% \pm 9.0$ S.E.) and dry ($35.7\% \pm 3.3$ S.E.) season (mean = $30.9\% \pm 4.0$ S.E.). Keys and DeBarthe (1974) found cellulose digestion to range from 21 to 48% and Farrell (1973) reported values of 39 to 50% in trials with domestic pigs on diets ranging from 8 to 17% cellulose. Differences in cellulose digestibility result from many factors including the chemical structure of the fiber, physical condition of the material and feeding conditions, thus broad generalizations about fiber digestibility are not possible (ARC 1981).

No significant correlation was found between cellulose digestibility and dietary ADF ($r_s = -0.39$, $P = 0.16$), ADL ($r_s = -0.47$, $P = 0.08$) or CEL ($r_s = 0.12$, $P = 0.68$) levels; however, an inverse relationship probably existed at lower fiber levels. Pond et al. (1962) reported declines of 23-40% in crude fiber digestibility as crude fiber level in the diet was raised from 3 to 7%. Declines in nutrient digestibility with increasing fiber content of the diet may be most pronounced at low fiber levels. At the very high fiber levels recorded in diets of pigs on Catalina, most inhibition of digestibility due to fiber may have already been expressed.

Increases of crude fiber in the diets of pigs lead to a reduction in DE and an increase in dietary feed intake; however, increased intake is usually not sufficient to compensate for reduced DE levels (ARC 1967, Cole et al. 1972). High fiber levels in the diets of feral pigs on Catalina probably accounted for the low DE levels observed (Figure 5). Correlation analysis revealed that DE declined with ADF

($r_s = -0.51$, $P = 0.05$) and ADL ($r_s = -0.58$, $P = 0.024$) level in the diet, and was positively correlated ($r_s = 0.86$, $P = 0.001$) with cellulose digestibility. No association was noted with CP ($r_s = -0.21$, $P = 0.46$), protein digestibility ($r_s = 0.50$, $P = 0.06$) or CEL ($r_s = 0.00$, $P = 0.99$). DE in the diet did not differ significantly ($P = 0.11$) between wet (1192.3 kcal/kg DM \pm 279.6 S.E.) and dry (1580.0 kcal/kg DM \pm 83.3 S.E.) season. Low dietary DE during the early part of the wet season (Figure 5) reflected the abrupt shift to utilization of annual grasses and forbs, a poor energy source for pigs due to the high content of poorly digestible cellulose. Low DE levels in May 1981 occurred when ADF and ADL levels in the diet reached a maximum.

Energy requirements for maintenance (ME_m), that energy required to maintain body functions, body temperature and necessary activity in the absence of tissue gain or loss in a thermoneutral environment, were calculated for Catalina pigs using the formula $ME_m = 171.8 \text{ kcal } W(\text{kg})^{0.63}$ (ARC 1981). Adult sows (mean weight = 27.6 kg \pm 1.0 S.E., $N = 80$) would require approximately 1389 kcal/day and adult boars (mean weight = 32.3 \pm 1.73 S.E., $N = 58$) 1534 kcal/day. Average ad libitum consumption for growing-finishing swine of 20 to 35 kg body weight is about 1.5 kg air-dry feed (NRC 1979). The energy values of the diet of Catalina pigs (Figure 5) indicate that ME_m is probably surpassed in most months however, total energy requirements may not be met. In the natural Catalina environment, energy requirements would have been substantially higher than ME_m due to higher levels of activity,

physiological demands such as pregnancy and lactation and climatic variations.

Pigs generally compensate for low energy levels in the diet by an increase in feed intake (ARC 1967, NRC 1979). The low energy, high fiber diet of feral pigs on Catalina would necessitate increased food intake to meet total energy expenditure. Size of the gut, rate of passage and digestibility of the diet would determine if these levels were met and a negative energy balance avoided.

The estimated levels of CP, PHOS and DE in the diets were usually below nutritional levels required for optimal performance by swine fed a fortified grain-soybean meal diet as reported by the NRC (1979). Optimal nutritional values for bred gilts and sows and young and adult boars were 12.0% CP, 0.60% PHOS and 3400 kcal/kg DE of diet; optimal values for lactating gilts and sows were 13.0% CP, 0.50% PHOS and 3395 kcal/kg DE of diet (NRC 1979). Only during January 1981 through April 1981 of the wet season did protein levels approach or surpass the optimal level for adult swine (Table 2); protein levels remained below 10% in all other months and reached a low of 6.5% and 6.6% in November and July 1980, respectively. PHOS levels approached optimal values only during February 1981 (0.49 ± 0.5 S.E.), (Table 2), and DE remained well below recommended values for optimal performance (Figure 5). These results imply that feral pigs on Catalina subsisted on a suboptimal diet for much of the year.

Direct application and interpretation of NRC optimal values to this population may be unreliable for several reasons resulting in optimal values being either too high or too low. The common domestic

pig of early American settlers in California was the lard (fat-type) pig (Barrett 1978), and the Catalina feral stock appeared to be of this origin. Data indicates the lean-type pig developed for maximum meat production requires a higher level of dietary protein than the fat-type pig (McConnell et al. 1971), and although not stated specifically, the NRC (1979) report appeared to be directed towards optimal performance in lean-type pigs. Thus protein requirements necessary for optimal performance in the Catalina population may be somewhat lower than specified by NRC (1979). Energy requirements were probably greater than NRC (1979) recommendations due to higher energy costs incurred from movements to seek out food and shelter, behavioral interactions and climatic variations. The commercial rations developed for swine and used in the NRC (1979) evaluation are generally concentrated and milled to break plant cell walls and facilitate availability of cell contents, making them easily digestible, as opposed to the coarse structure of wild diets. True digestibility and assimilation efficiency of nutrients should be greater with these commercial feeds than the high fiber, low energy diet characteristic of Catalina pigs that limits digestibility. This was verified by metabolism trials with collared peccaries (Tayassu tajacu) on commercial and natural diets (Gallager et al. 1984). Thus, based on differences in digestibility and assimilation, nutritional levels in diets of Catalina pigs may need to be higher for pigs to derive a level of nutrition necessary to sustain optimal performance as specified by the NRC (1979). Maximum utilization of dietary protein is linked to energy level of the diet. When energy is

limited, dietary protein is diverted from anabolic pathways and oxidized to meet energy demands (ARC 1981). Energy deficiencies were apparent much of the year for pigs on Catalina, complicating evaluation of dietary protein sufficiency.

Although no significant differences in digestion of dry matter, GE or CP were evident between domesticated fat-type and lean-type pigs (McConnell et al. 1971), feral pigs on Catalina may be capable of achieving greater digestibility of high fiber diets. For example, Bohman et al. (1953) reported enlarged stomach and intestines in pigs fed diets higher in fiber; an increase in stomach size relative to body size would allow for increased forage consumption, and increased size of the large intestine would improve digestibility of fiber. Nutritional adequacy of the natural diet of the Catalina population may be assessed most reliably by examining animal performance on this diet.

Animal Condition

Feral pigs on Catalina were in good body condition during the wet season (winter-spring), but declined in condition during the dry summer months and into fall (Figure 6). KFI for adult pigs did not differ significantly ($P = 0.251$) between boars and sows, and the sex X month interaction was insignificant ($P = 0.618$); however, KFI did vary significantly ($P < 0.0001$) between months. KFI remained low (5 to 10%) from July 1980 through February 1981, increased to $32.9\% \pm 3.8$ S.E. in May, and returned to the 5-10% range by September (Figure 6). FMF results were similar, with no significant ($P = 0.181$) sex effect

or sex X month interaction ($P = 0.814$), but a significant ($P < 0.0001$) month effect. FMF generally declined from July 1980 to a low of $30.5\% \pm 4.5$ S.E. in December, and increased during the wet season to a high of $90.7\% \pm 2.3$ S.E. in May 1981 (Figure 6). FMF declined dramatically through the summer months.

Pigs monitored during the summer months of 1981 steadily lost weight, but there was no significant difference in weight loss ($P = 0.48$) or percentage decline ($P = 0.27$) between the sexes. Mean weight loss was 0.07 kg/day ± 0.01 S.E., and mean percentage loss was 0.26% /day ± 0.04 S.E. Weak emaciated animals were not uncommon in the fall.

Condition indices confirmed that pigs subsisted on suboptimal to poor diets for much of the year, and diets were seasonally deficient in protein and energy. During the dry summer months, nutrition was at or below maintenance levels, and animals declined in condition and lost weight. Pigs in this study continued to decline in condition through the fall, probably due to a poor acorn crop. Acorns, although low in protein, provide a high energy food source (Lund and Sandstrom 1943) and are consumed in large quantities when available. Condition improved in winter when an abundance of high protein green herbage was available; however, the inability of pigs to effectively utilize grass and forbs as an energy source (Figure 5) probably delayed recovery of condition. When diet quality declined in late spring, stored energy reserves were utilized until depletion. Thus, optimal performance of pigs on Catalina appeared to be linked to the quantity of the acorn crop in early fall and the timing and duration of fall-winter rains

which stimulated growth of annual grasses and forbs. A similar pattern was reported for the Dye Creek feral pig population in north-central California (Barrett 1978). Optimal nutrition for feral pigs on Catalina would occur when a large acorn crop contributing energy to the diet coincided with early rains that promoted growth of high protein foods. This combination would result in optimum utilization of nutrients and optimum animal performance.

Conception

A seasonal pattern in breeding was evident for pigs over a 2 year period on Catalina (Figure 7). Breeding was continuous through the fall and winter of 1979/1980, with a peak in January. No conceptions were recorded in spring, and a small peak was noted in summer; no further breeding was evident through the fall of 1980. In mid-winter 1981, an abrupt peak in breeding occurred with few conceptions in spring and a small conception peak again in summer.

Nutrition appeared to be one factor regulating time of breeding on Catalina. Failure of important food sources such as oak mast (Matschke 1964, Henry 1966, Graves and Graves 1977, Singer and Ackerman 1981) or green herbage due to extended drought (Nichols 1963) is known to alter normal reproductive patterns. The acorn crop was large in the fall of 1979, and rainfall began early and was abundant (59 cm) during fall and winter. Nutritional patterns discerned in 1980-81 indicated nutrition would have been optimal under the conditions of 1979. Sows probably regained condition rapidly and bred early. Recent reproductive history probably accounted for the

duration of breeding through fall and winter. Sows which had more recently weaned litters would have been in poorer physical condition and would have required longer to regain body condition and breed. The acorn crop was poor in the fall of 1980, and rainfall for the wet season began late and was below normal (24 cm). Nutrition was deficient (Table 2, Figure 5) and animals were in poor physical condition. As a result they did not regain condition until midwinter (Figure 6) and bred late (Figure 7).

Conception in sows on Catalina appeared dependent upon diets of sufficient nutritional quality to attain some threshold of body condition. Poor nutrition is known to both delay puberty (Sadleir 1969, Mitchell 1973, Ozoga and Verme 1982) and to influence time of breeding (Mitchell and Lincoln 1973, Mauget 1982) in wild animals, particularly in semi-arid areas (Sadleir 1969) such as Catalina. Energy reserves appeared to be important for the onset of estrus. Pregnant sows had significantly greater levels of stored fat, as measured by KFI and FMF indices, than lactating or nonreproductive adult sows (Table 4). Similar associations between fat reserves and breeding have been documented for red deer (Cervus elaphus) (Mitchell and Lincoln 1973, Mitchell et al. 1976) and caribou (Rangifer tarandus) (Leader-Williams and Ricketts 1982, Thomas 1982). In humans, a ratio of lean body weight to fat of about 3:1 is necessary for puberty and maintenance of female reproductive ability (Frisch 1984).

Under normal husbandry conditions, estrus in domestic swine is a regular phenomena, occurring approximately every 21 days (Hughes and

Varley 1980). Patterns of conception on Catalina indicated some synchronization in time of breeding, with periods in which physiological or behavioral anestrus were evident (Figure 8). Acute undernutrition will produce irregular estrus and temporary infertility in domestic swine (Duncan and Lodge 1960, Maclean 1968, Wrathall 1975), and will inhibit ovulation in humans (Frisch and McArthur 1974) and other mammals (Hammond 1955). Nutritional levels in diets of Catalina pigs and their performance on these diets revealed undernutrition in this population for a portion of the year. Anestrus was probably influenced by these extended periods of poor nutrition. Matic (1952, cited in Duncan and Lodge 1960) reported that 70% of sows deprived of green forage as a result of drought were infertile, but recovered when green feed was again available.

Photoperiod may also have been a major factor influencing time of breeding of pigs on Catalina. In domestic pigs, the estrus cycle is controlled through hormonal regulation by the hypothalamus and pituitary glands (Hughes and Varley 1980). However, the external environment does appear to exert some regulatory control on reproduction. Declines in fertility and breeding performance of domestic sows are known to occur in summer months (Love 1978, Paterson et al. 1978, Hurtgen et al. 1980), and in a study to differentiate the effects of temperature and season, season of year was implicated as the principle causative factor (Hurtgen et al. 1980).

Declines in fertility in late spring and summer were apparent in this study (Figure 7), and photoperiod may have been the proximate

cause. This decline was also evident for the Mauna Kea feral population in Hawaii (Giffin 1978) and for wild boar x feral pig crosses in Texas (Springer 1977). In South Carolina, pregnancy rate of feral pigs as determined by necropsy was low (22%) in late spring and summer but increased to 97% in fall (Wood and Brenneman 1977). In a 12-year study of reproductive patterns of wild boar in France, wild boar appeared to be photoperiodic with respect to reproduction, with anestrus increasing in late spring as daylight and environmental temperatures increased; anestrus approached 100% of sows in summer (Mauget 1982). Onset of ovarian activity and breeding in fall appeared regulated by annual variation in the mast crop, with wild boar breeding early (October) in good mast years and later (December) in poor mast years (Mauget 1982). A similar but less distinct pattern was evident for European wild boar in Tennessee (Conley et al. 1972, Duncan 1974, Singer and Ackerman 1981); however, conception patterns were somewhat obscured due to the inclusion of large numbers of backdated juveniles and adults pooled over years in these analyses. Adults and juveniles can only be placed in broad age categories using tooth eruption, and individual variation in eruption pattern is great (Sisson and Grossman 1938, Matschke 1967), leading to substantial errors when backdating.

Sweeney et al. (1979) calculated conception and farrowing patterns for feral pigs at the Savannah River Plant, a recent feral population of about 20 years, from backdated juvenile and adult pigs. They concluded that animals bred throughout the year, but most occurred in mid-fall and less in late spring (J. Sweeney, pers. comm., Sweeney et

al. 1979). When only aged fetuses from this population were examined (Sweeney 1970), most breeding appeared to occur in fall and winter, with very little in spring and summer; however, the sample size was small. In mainland California, Pine and Gerdes (1973) reported a peak in breeding from October through January in the Monterey County wild boar X feral pig hybrid population, while Barrett (1978) observed no summer anestrus and relatively constant breeding in the Dye Creek feral population. Diong (1982) reported the Kipahulu Valley, Hawaii, feral population bred continuously, but declines were evident in spring, and again in late summer and early fall. This population had a feral history of about 35 years, as compared to about 1200 years for the Mauna Kea population (Diong 1982).

Late spring and summer declines in fertility appear to be a regular phenomenon in some feral and hybrid wild pig populations and in wild boar populations. Photoperiod is the most probable environmental cue regulating seasonal anestrus. The degree of photoperiodic synchronization in wild pig populations probably depends upon the length of time the population has been feral and the degree of interbreeding with wild boar. Nutrition also appears to exert a regulatory control on reproduction in both feral pigs and wild boar. Fertility declines in late spring with increasing daylight, while nutritional status of the sow regulates the onset of estrus in the fall. The nutritional plane of sows as influenced by diet and or recent reproductive history would influence breeding patterns during periods of higher fertility.

Table I.1. Mean seasonal diets of wild pigs expressed as relative density, and percent frequency of occurrence, availability rank, and preference rating for items in the diets of wild pigs collected on Santa Catalina Island, California. July 1980 through September 1981.

Food Item	Wet Season				Dry Season			
	Relative Density	% Frequency of Occurrence	Availability Rank	Preference Rating	Relative Density	% Frequency of Occurrence	Availability Rank	Preference Rating
GRASS								
<u>Agrostis diegoensis</u>					0.2	2.5	1 ^b	<1
<u>Avena barbata</u>	2.8	34.2	4	24	1.1	13.9	4 ^b	4
<u>Bromus spp.</u>	18.4	78.9	4	363	0.6	19.0	4 ^b	3
<u>Festuca megalura</u>	0.1	2.6	3	<1	0.1	2.5	3 ^b	<1
<u>Hordeum glaucum</u>	3.7	50.0	3	62	1.2	30.4	3 ^b	12
<u>Hordeum leporinum</u>					0.1	1.3	1 ^b	<1
<u>Lamarkia aurea</u>	0.2	5.3	1	1	0.1	2.5	1 ^b	<1
<u>Melica imperfecta</u>					0.1	1.3	1	<1
<u>Muhlenbergia microsperma</u>	0.5	7.9	2 ^a	2	1.8	15.2	2 ^b	14
<u>Poa annua</u>	1.6	21.1	1 ^a	34	0.2	5.1	1 ^b	1
<u>Poa scabrella</u>	0.2	5.3	1	1				
<u>Stipa spp.</u>	0.1	5.3	2	<1	0.1	3.8	3	<1
Unknown Grass	0.3	10.5			0.4	15.2		
Total Grass	28.0	94.7	4	663	6.0	67.1	4	101
OTHER MONOCOTS								
<u>Dichelostemma pulchellum</u>	1.6	23.7	1 ^a	38	0.1	1.3	1 ^b	<1
<u>Typha sp.</u>	0.1	2.6	1 ^a	<1				
Unknown Monocot					0.1	2.5		
FORB								
<u>Atriplex semibaccata</u>	2.8	31.6	1	88	14.8	65.8	2 ^b	487
<u>Bolisia incana</u>	0.6	10.5	3	2.1	0.1	1.3	3 ^b	<1
<u>Capsella bursa-pastoris</u>	0.2	2.6	1 ^a	<1				
<u>Centaurea melitensis</u>	0.3	5.3	1	2				
<u>Claytonia perfoliata</u>	0.5	7.9	2	2				
<u>Erodium spp.</u>	2.0	34.2	2	34	0.1	1.3	2 ^b	<1
<u>Galium aparine</u>	0.6	10.5	2 ^a	3	0.1	1.3	2 ^b	<1
<u>Gila angelensis</u>	2.2	31.6	1 ^a	70	0.4	5.1	1 ^b	2
<u>Lepidum nitidum-nitidum</u>	0.3	7.9	1 ^a	2				
<u>Lotus argophyllus ornithopus</u>					0.1	2.5	1 ^b	<1
<u>Lotus strigosus</u>	1.2	28.9	2	17	0.5	5.1	2 ^b	1
<u>Malva parviflora</u>					0.1	1.3	1 ^a	<1
<u>Marrubium vulgare</u>	2.1	18.4	3	13	0.3	5.1	1 ^b	2
<u>Medicago polymorpha</u>	7.0	55.3	2	194	0.6	8.9	2 ^b	3

Table 1.1. Continued

Food Item	Wet Season				Dry Season			
	Relative Density	% Frequency of Occurrence	Availability Rank	Preference Rating	Relative Density	% Frequency of Occurrence	Availability Rank	Preference Rating
<u>Pholistoma racemosa</u>	3.6	42.1	3	51	0.3	5.1	3 ^b	<1
<u>Plantago erecta</u>	0.1	2.6	2	<1	0.2	3.8	2 ^b	<1
<u>Rorippa nasturtium aquaticum</u>	0.1	2.6	1	<1				
<u>Salsola pestifera</u>	0.3	5.3	1 ^a	2	0.4	7.6	1 ^a	3
<u>Sisymbrium officinale</u>					0.1	1.3	2 ^b	<1
<u>Sonchus asper</u>	0.1	2.6	1	<1				
Total Forb	24.0	97.4	4	618	18.1	79.7	2	733
BROWSE								
<u>Happlopappus venetus furfuraceus</u>	1.3	15.8	1	21	0.3	3.8	2	<1
<u>Heteromeles arbutifolia</u>	4.7	42.1	3	66	1.8	26.6	3	16
<u>Quercus spp.</u>	0.5	10.5	4	1	2.7	31.6	4	21
<u>Rhus integrifolia</u>					0.1	1.3	4	<1
Total Browse	6.5	65.8	4	102	4.9	48.8	4	56
Unknown Forb/Browse	4.5				2.4			
FRUIT/SEED								
<u>Arctostaphylos catalinae</u>	0.2	2.6	1 ^a	<1	0.4	5.1	1 ^a	2
<u>Heteromeles arbutifolia</u>	10.5	55.3	2	290	5.3	38.0	2	101
<u>Opuntia spp.</u>	10.8	73.7	1	796	30.5	94.9	2	1477
<u>Prunus ilicifolia lyonii</u>	0.6	7.9	1 ^a	5	2.6	21.5	1 ^a	56
<u>Quercus spp.</u>	0.6	13.2	1 ^a	8	3.3	26.6	2	44
<u>Rhus integrifolia</u>	7.4	60.5	1	448	12.0	75.9	3	304
<u>Sambucus mexicana</u>	0.3	10.5	1 ^a	3	2.4	35.4	1 ^a	85
Unknown Seed	1.6	23.7			0.7	17.7		
Total Seed	32.0	94.7	2	1515	57.2	100.0	3	1907
ROOTS/BULBS/TUBERS	2.2	28.9	4	16	8.5	65.8	4	140
INSECTS	1.7	23.7			3.2	49.4		
CARRION						8.9		

^a Not sampled in plots; assigned availability rate of 1.

^b Present only as a cured annual during the dry season; spring value assigned.

Table I.2. Relative proportions of acid detergent fiber (ADF), acid detergent lignin (ADL), cellulose (CEL), crude protein (CP), and phosphorus (PHOS) in the diets of wild pigs collected on Santa Catalina Island, California. July 1980 through September 1981.

Month	Sample Size	ADF	ADL	CEL	CP	PHOS
1980						
July	7	35.9 a ¹	9.5 a,b ²	26.4 a,b	6.6 a,	0.15 a,b ²
August	7	40.1 a	12.8 b,c	27.3 a,b	8.3 a,b	0.09 a,b
September	7	37.6 a	10.7 a,b,c	26.8 a,b	9.0 a,b	0.27 a,b,c
October	7	37.1 a	10.8 a,b,c	26.3 a,b	8.1 a,b	0.10 a,b,c
November	7	43.4 a	13.6 a,b,c	29.8 a,b	6.5 a	0.07 a
December	7	36.5 a	12.5 a,b,c	24.0 a,b	8.3 a,b	0.16 a,b,c
1981						
January	7	42.7 a	12.7 a,b,c	30.0 a,b	13.1 b,c,d	0.26 a,b,c
February	7	42.3 a	10.0 a,b	32.2 b	16.0 d	0.49 c
March	7	39.3 a	7.2 a	32.1 a,b	15.8 d	0.17 b,c
April	7	38.9 a	10.6 a,b,c	28.3 a,b	14.3 c,d	0.16 b,c
May	7	46.0 a	21.2 c	24.8 a,b	9.8 a,b,c	0.20 a,b,c
June	7	43.4 a	15.9 b,c	27.5 a,b	8.3 a,b	0.28 a,b,c
July	7	36.3 a	9.9 a,b	26.4 a,b	7.3 a	0.15 a,b,c
August	7	39.3 a	10.6 a,b,c	28.7 a,b	8.8 a,b	0.23 a,b,c
September	7	36.8 a	13.2 a,b,c	23.6 a	9.9 a,b,c	0.31 a,b,c

¹ Common letters indicate treatment means were not significantly different.

² Distribution free multiple comparisons based on ranks were used to test treatment means for ADL and PHOS at an experiment wise P = 0.20.

Table I.3. Crude protein (CP), cellulose (CEL) and their digestibility in the diets of wild pigs collected on Santa Catalina Island, California. July 1980 through September 1981.

Month	Sample Size	CP \pm S.E.	CP Apparent Digestibility Coefficient	Apparent Digestible Protein	CEL \pm S.E.	CEL Apparent Digestibility Coefficient
1980						
July	7	6.6 \pm 1.0	0	0	26.4 \pm 1.6	43.7
August	7	8.3 \pm 0.9	0	0	27.3 \pm 2.8	21.7
September	7	9.0 \pm 1.4	11.2	1.0	26.8 \pm 1.6	45.4
October	7	8.1 \pm 0.8	29.6	2.4	26.3 \pm 1.0	38.9
November	7	6.5 \pm 0.4	0	0	29.8 \pm 1.0	44.3
December	7	8.3 \pm 0.8	0	0	24.0 \pm 2.3	20.1
1981						
January	7	13.1 \pm 2.0	8.0	1.1	30.0 \pm 2.4	4.0
February	7	16.0 \pm 1.2	28.0	4.5	32.2 \pm 1.1	18.0
March	7	15.8 \pm 1.3	38.1	6.0	32.1 \pm 1.3	43.7
April	7	14.3 \pm 1.3	28.6	4.1	28.3 \pm 1.6	40.0
May	7	9.8 \pm 0.7	0	0	24.8 \pm 2.3	0
June	7	8.3 \pm 1.2	2.5	0.2	27.5 \pm 2.0	28.4
July	7	7.3 \pm 0.8	20.6	1.5	26.4 \pm 2.4	44.5
August	7	8.8 \pm 1.4	21.3	1.9	28.7 \pm 2.4	44.7
September	7	9.9 \pm 1.8	35.0	3.5	23.6 \pm 1.7	25.4

Table I.4. Comparison of fat indices (mean \pm S.E.) for different reproductive classes of adult (> 8 mo) sows collected on Santa Catalina Island, California. July 1980 through September 1981.

	Reproduction Class		
	Nonreproductive	Pregnant	Lactating
FMF (%)	45.6 \pm 5.4a ¹	83.9 \pm 4.7b	58.1 \pm 5.7a
KFI (%) ²	7.8 \pm 1.0a	24.3 \pm 2.9b	11.7 \pm 1.4a

¹ Common letters within each condition index indicates treatment means did not vary significantly.

² Distribution-free multiple comparisons based on ranks were used to test treatment means for KFI at an experimentwise $P = 0.10$.

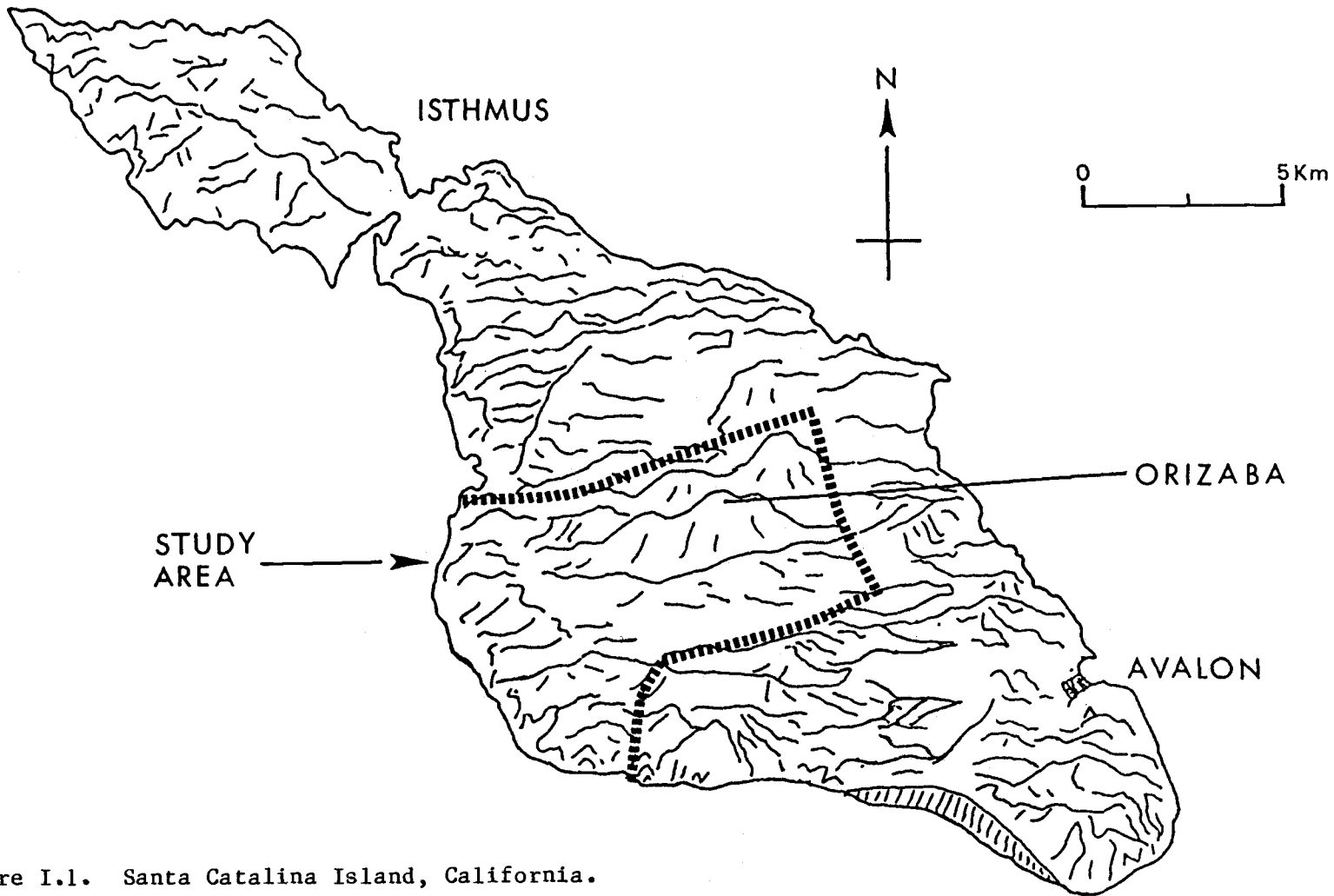


Figure I.1. Santa Catalina Island, California.

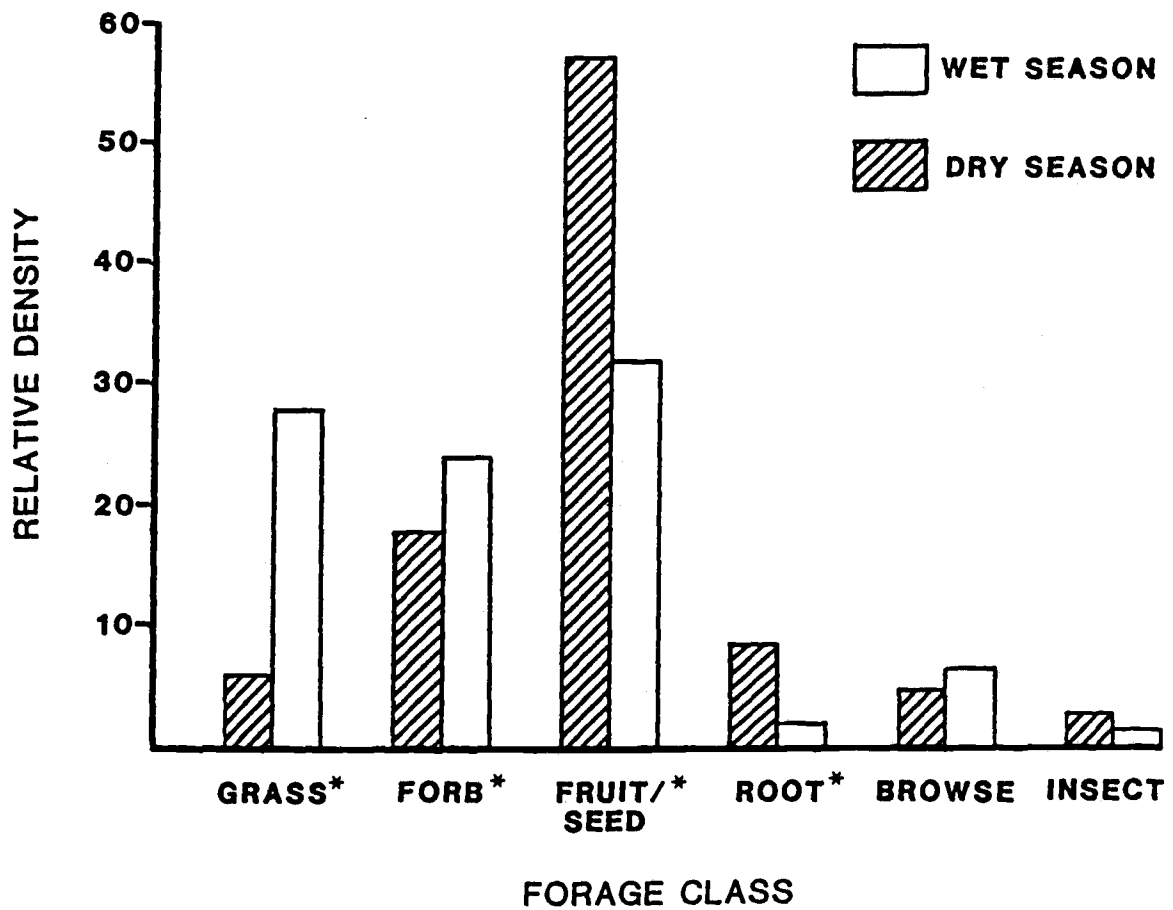


Figure I.2. Seasonal comparisons of forage classes in the diets of feral pigs collected on Santa Catalina Island, California. July 1980 through September 1981. A (*) indicates that forage class varied significantly between wet and dry season.

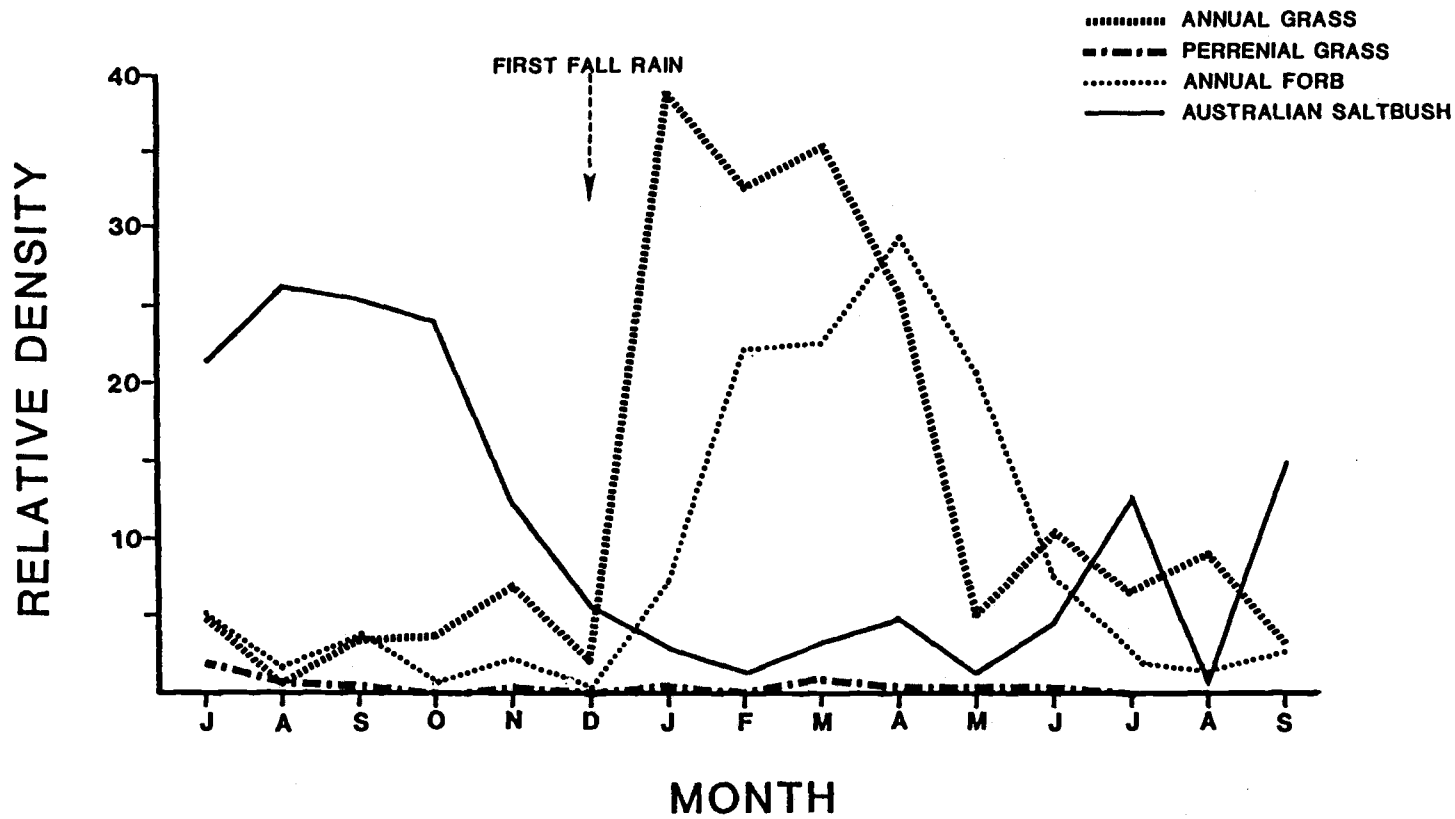


Figure I.3. Relative proportions of annual grass, perennial grass, annual forb and Australian saltbush in the diets of feral pigs collected on Santa Catalina Island, California. July 1980 through September 1981.

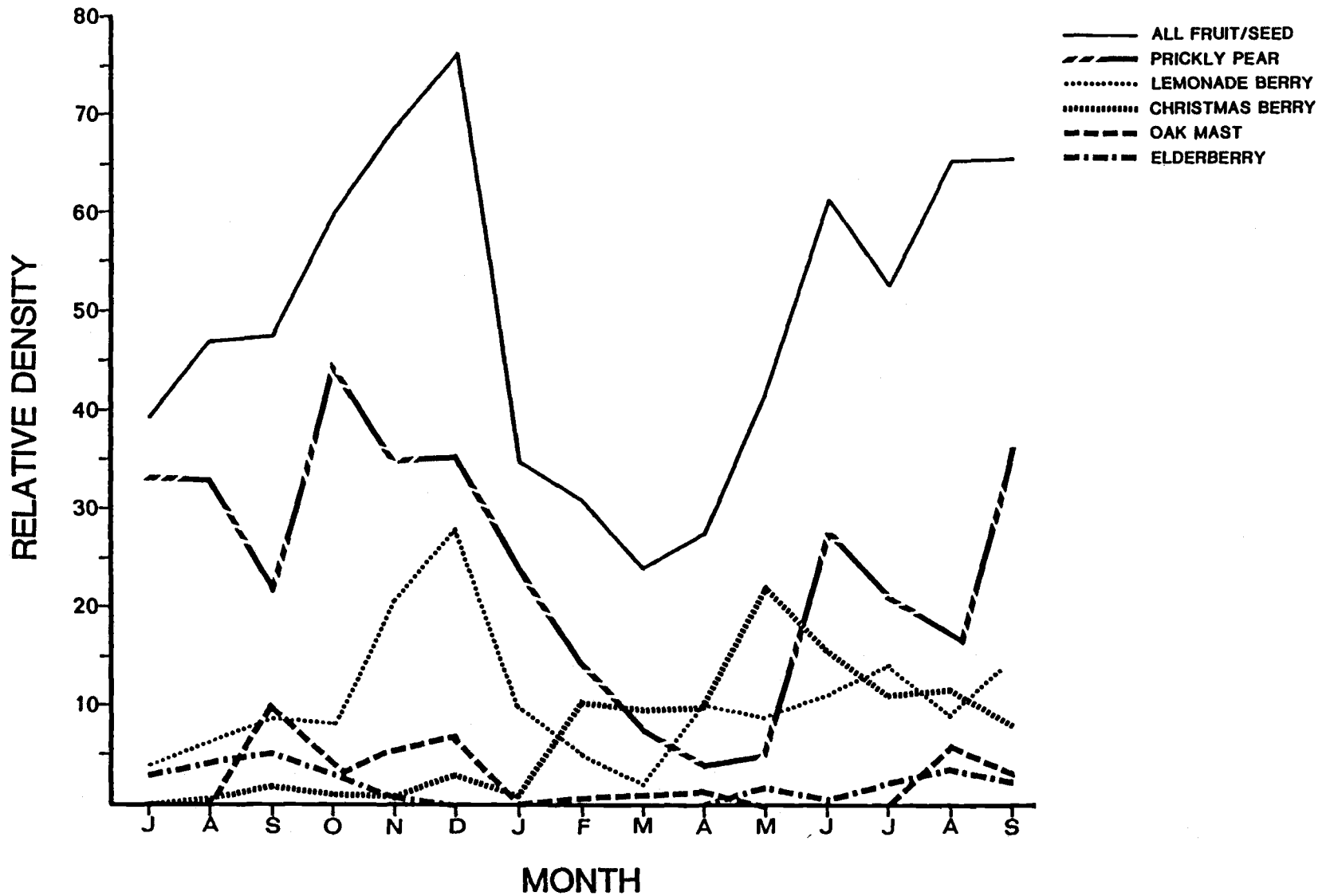


Figure I.4. Relative proportions of different fruits and seeds in the diets of feral pigs collected on Santa Catalina Island, California. July 1980 through September 1981.

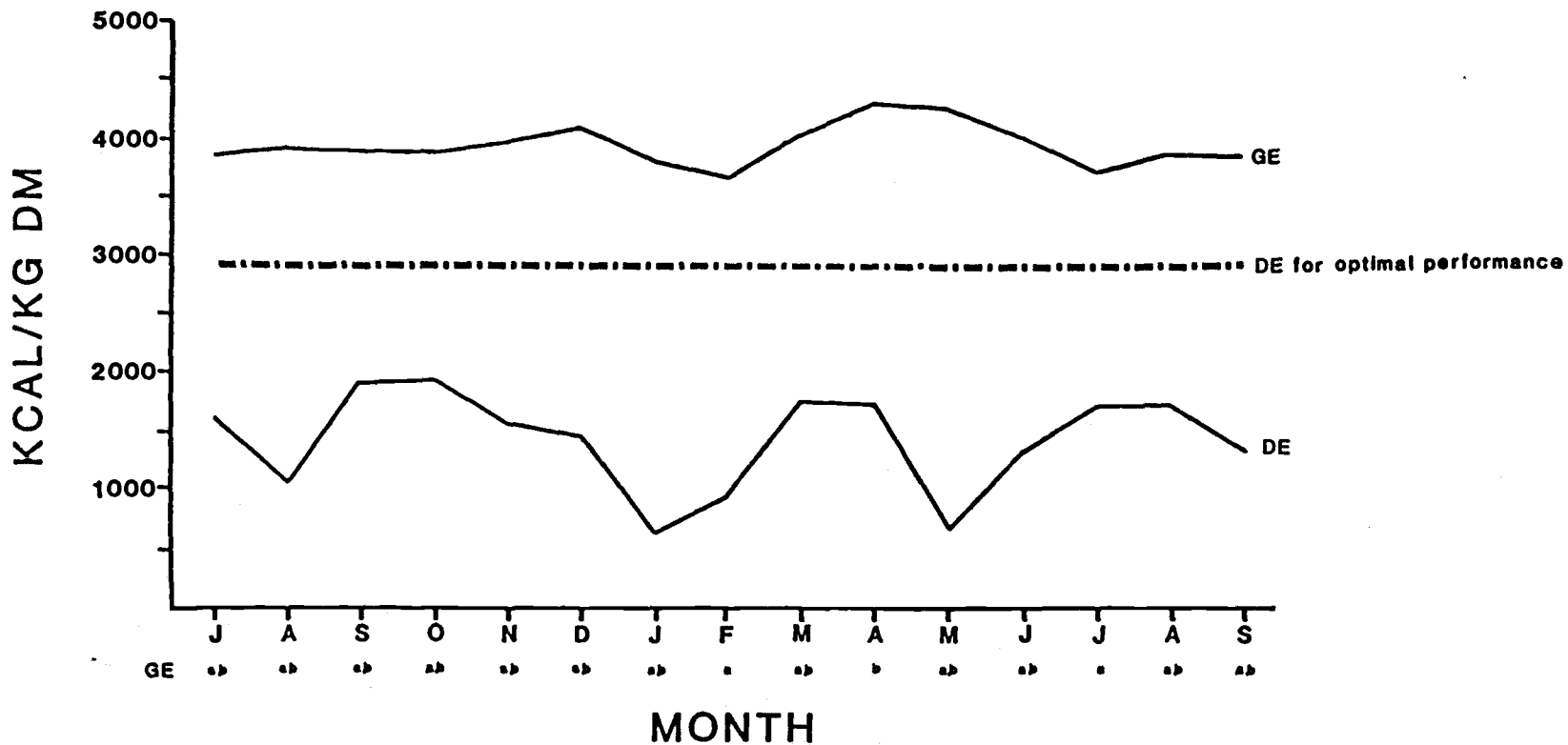


Figure I.5. Gross energy (GE), digestible energy (DE) and level of DE needed for optimal performance (NRC 1979) in the diets of feral pigs collected on Santa Catalina Island, California. July 1980 through September 1981. Common letters for GE indicate treatment means were not significantly different.

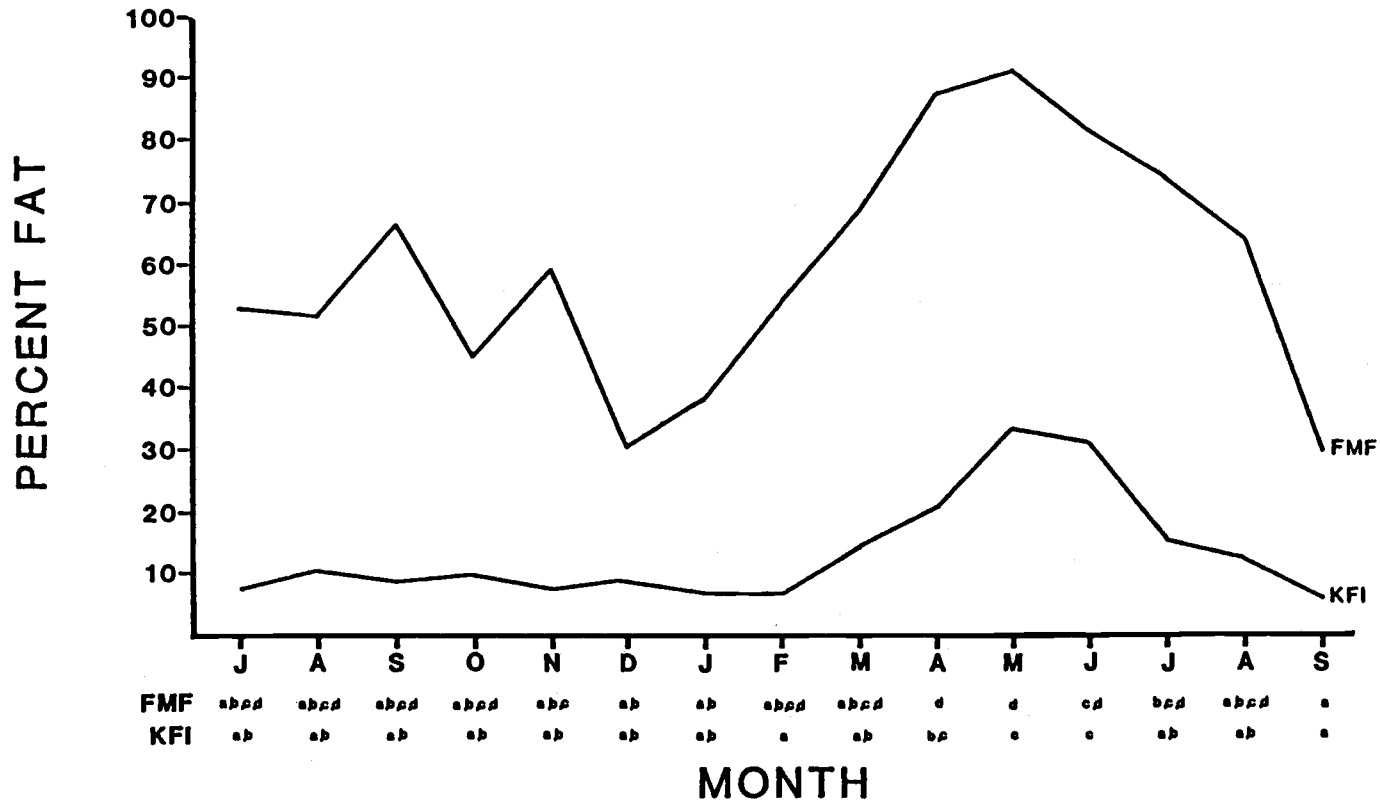


Figure I.6. Kidney fat (KFI) and femur marrow fat (FMF) condition indices for adult feral pigs collected on Santa Catalina Island, California. July 1980 through September 1981. Common letters indicate treatment means were not significantly different.

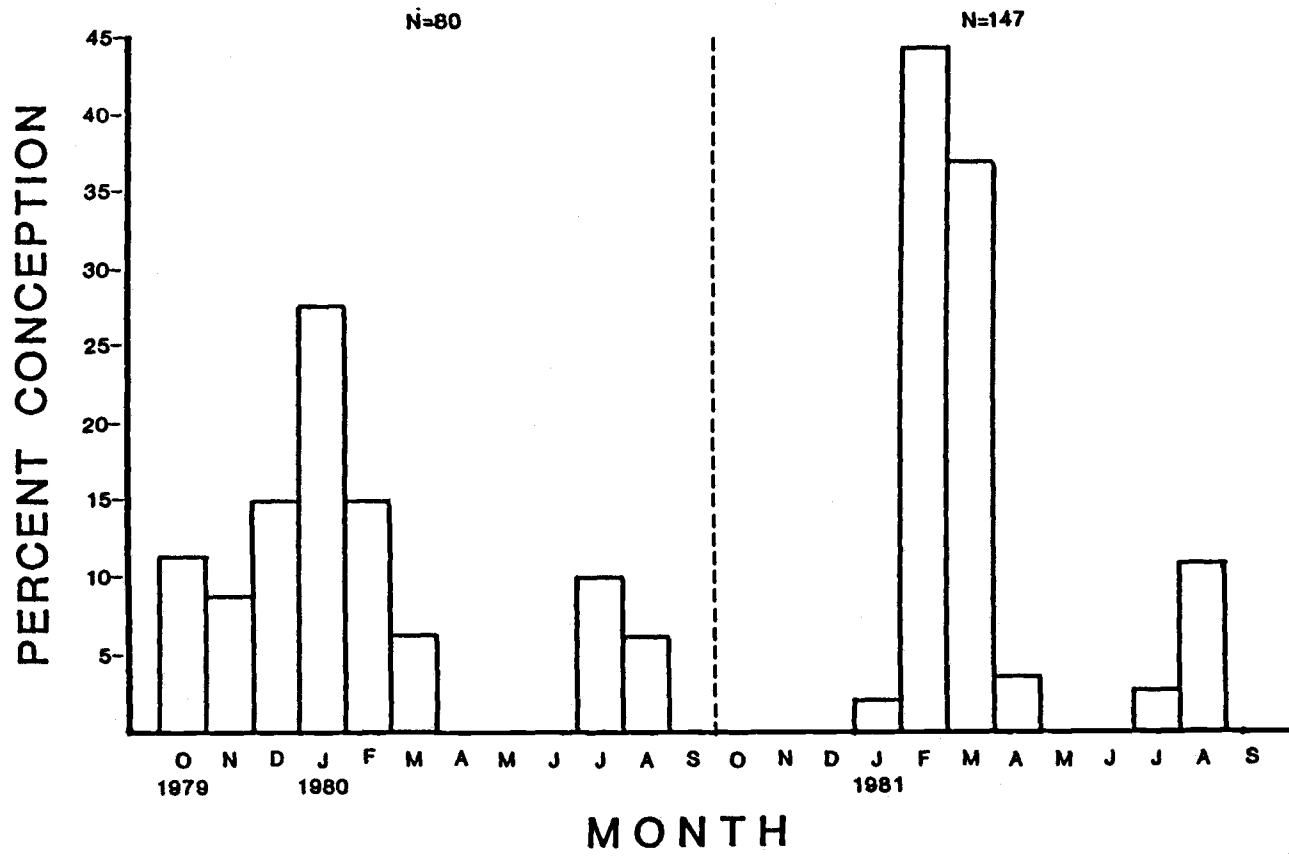


Figure I.7. Distribution of conceptions (%) by month and year for aged fetuses and piglets collected on Santa Catalina Island, California. July 1980 through September 1981.

II. DENSITY, HOME RANGE, HABITAT USE, AND REPRODUCTION
IN FERAL PIGS ON SANTA CATALINA ISLAND

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Abstract

A feral pig population on Santa Catalina Island, California, was studied for 17 months beginning in July 1980. A total of 136 pigs were marked and 188 recaptured during capture-recapture studies at 2 sites. Density was estimated to be 21 to 34 pigs/km² (95% confidence interval) using program CAPTURE. Dry season home ranges determined from radio-telemetry data were small and differed significantly between boars (1.42 km² ± 0.14 S.E. - minimum convex polygon; 2.44 km² ± 0.30 S.E. - harmonic mean method) and sows (0.67 km² ± 0.09 S.E. - minimum convex polygon; 1.46 km² ± 0.14 S.E. - harmonic mean method). Patterns of habitat use according to vegetative community, topographic position, slope, aspect, elevation, vertical distance to water and horizontal distance to water were examined. During the dry season, pigs preferred cool moist canyon bottoms, the result of both a physiological need for free water and behavioral responses to high environmental temperatures. Patterns of utilization during the wet season appeared to be primarily a function of food availability. Seasonality in time of birth was evident, with piglets born in winter and spring (1980) or spring and summer (1981). Litter size as

measured by fetal counts was 5.00 ± 0.36 S.E. and sows averaged 0.86 ± 0.17 S.E. litters over a 12 month period. Most sows were older than 1 year when they first conceived, and litter size increased from puberty and peaked at 2-3 years of age. Intrauterine mortality of fetuses averaged 25% and piglet mortality was estimated to be 58% prior to weaning. Mortality rates appeared to be higher for piglets born in summer than in winter or spring.

Domestic swine (*Sus scrofa*) were introduced into California by the Spanish some time after the 1500's (Barrett 1978, Mayer 1983) and land use practices of early settlers probably soon resulted in the establishment of feral populations. Eurasian wild boar, the conspecific ancestor of domestic breeds, were transported from a game preserve in North Carolina and released in Monterey County in late 1925 or early 1926 (Shaw 1940, Pine and Gerdes 1973, Mayer 1983). State agencies and private landowners dispersed descendants of these pigs to other parts of the state where they interbred freely with existing feral populations. Today, wild pigs (feral pigs or wild boar x feral pig crosses) occur in at least 23 of 58 counties in California (Mayer 1983).

Feral pigs were introduced onto Santa Catalina Island in the mid 1930's, obtained in trade from Santa Rosa Island for Catalina Island California quail (*Lophortyx californicus catalinensis*) (Overholt and Sargent 1971). The purpose of this introduction was to establish a population of pigs to eat rattlesnakes (*Crotalus viridis helleri*), which continue to remain numerous on the island. The origin of the

Santa Rosa population is uncertain. Feral pigs have been present on that island at least since the late 1800's and possibly as early as the late 1500's (Mayer 1983). Although pigs on Catalina are harvested annually through a sport hunting program, they remain abundant, and have contributed significantly to the alteration of native insular communities (Baber and Coblentz - unpublished data).

Despite their popularity as a game animal in California and their propensity towards negative effects on ecosystems in which they are introduced (Bratton 1975, Challies 1975, Spatz and Mueller-Dombois 1975, Wood and Barrett 1979, Diong 1982, Coblentz and Baber 1984, Singer et al. 1984), few studies (Pine and Gerdes 1973, Barrett 1978, 1982; Van Vuren 1984) have been conducted on wild pigs in their present range in California. Wild pigs have been studied extensively in other areas of the United States (e.g. Conley et al. 1972, Bratton 1975, Springer 1977, Sweeney et al. 1979, Wood and Roark 1980, Singer et al. 1981, Diong 1982), however, these habitats differed markedly from the semi-arid Mediterranean communities commonly inhabited by wild pigs west of the Sierra Nevada Mountains.

The objectives of this study were to determine densities, home range size, habitat use patterns, reproduction, and piglet mortality for a feral pig population in semi-arid habitat. Dietary preference, nutrition and conception patterns for this population were reported elsewhere (Part I). The importance of this information for management of wild pig populations in California is two-fold. In sensitive ecological areas, these data are necessary for design of programs to reduce pig numbers. At sites managed for sport hunting, this

information will aid development of regulations for sustained harvest of animals.

Support for this study was provided by the Santa Catalina Island Conservancy, Northwestern Los Angeles Resource Conservation District, Los Angeles County Fish and Game Commission, National Rifle Association, Western Foundation of Vertebrate Zoology, Oregon Agricultural Experiment Station and Oregon State University Computer Center. I am grateful to J. Gross, C. Scafidi, R. Callas, J. Ganey, D. Garcelon and D. Van Vuren for assistance in the field. Helpful comments on this manuscript were provided by Drs. B.E. Coblenz, R.G. Anthony, J.C. Buckhouse and R.M. Storm. This is Oregon Agricultural Experiment Station Technical Paper no. .

STUDY AREA

Santa Catalina Island is the largest of 4 islands in the southern Channel Island group and encompasses an area of approximately 194 km² (Figure II.1). Located 32 km off the coast of southern California at the Palos Verdes Peninsula, it is classified as a fringing island due to its close continental association. The geologic origin of Catalina is volcanic and although its size has varied over the past 30 million years due to tectonic activity and sea level oscillations, no evidence of a link to the mainland or other islands exists (Veder and Howell 1980). The topography is rugged and precipitous, reaching a maximum elevation of 631 m. Steep-walled canyons, sharp ridges and narrow valley basins predominate.

The climate of Catalina is classified as Mediterranean, characterized by warm dry summers and cool damp winters. It is strongly influenced by proximity to the sea. The average temperature is 12.7 C in January and 19.2 C in July; annual precipitation averages 31 cm with most effective rainfall occurring in late fall and winter (Dunkle 1950). During this study (July 1980 through September 1981), only 24 cm of rainfall were recorded from December 1980 through April 1981. Periodic drought is a regularly occurring phenomenon. Permanent and seasonal seeps and small streams are found in the larger canyon systems, however, many are ephemeral during the summer months and in low rainfall years. Several small water catchments and reservoirs have been constructed to provide water for people, livestock and wildlife.

Predominant vegetative communities on Catalina were oak woodlands, chaparral, coastal sage scrub, California grassland and riparian. Community distribution is patchy, influenced by slope, aspect, soils, exposure to coastal winds and grazing by feral animals. Vegetative communities and species assemblages were discussed by Thorne (1967). Plant communities were mapped by ground reconnaissance (Santa Catalina Island Company 1975) and color infrared aerial photography (Minnich 1980).

Field research was intensified in a 60 km² study area (Figure II.1). Feral pigs have been present in this area since the mid 1930's (J. White, pers. comm.), and are now island wide in distribution. Feral goats occupied about 15 percent of the study area, with California mule deer (Odocoileus hemionus californicus) and bison (Bison bison) distributed throughout; all ungulates are nonnative.

METHODS

Population Density

Density of pigs in the study area was estimated at 2 sites using capture-recapture techniques. Pigs were captured in box or corral traps baited with oat hay and dairy feed; traps were baited in late afternoon and checked the following morning. At first capture, animals were immobilized with a combination of ketamine hydrochloride and xylazine hydrochloride (Baber and Coblenz 1982). Pigs were aged by dentition to 26 months following Matschke (1967). Animals with molar M^3 partially erupted were aged at 26-36 months, and at >36 months when M^3 had fully erupted. Pigs were sexed, weighed, measured following Brisben et al. (1977) and tagged in both ears with duplicate numbered, color coded plastic ear tags. Drugged pigs were moved to shaded sites for recovery. Five traps were operated during each trapping night and trap results for 5 consecutive nights were pooled into 1 trap period (25 trap nights) for analysis. If an animal was captured more than once in a given trap period, only the result of first capture was used in data analysis (Otis et al. 1977).

The Middle Canyon site (Figure II.1), located in the central portion of a major inland drainage system, was trapped from August through November 1980. Oak woodland, coastal sage scrub and California grassland were the dominant plant associations here. Traps were positioned in grain fields in a 0.5 km² area of canyon bottom, and were relocated periodically. Fields had been harvested in late spring and were bare except for loose oat seeds and some dry season

greenup that attracted pigs from surrounding areas to feed. A large reservoir was located nearby. The Salta Verde site (Figure II.1), an exposed coastal slope strongly influenced by the Pacific Ocean, was trapped from July through August 1981. Coastal sage scrub and grassland communities predominated with some small stands of oak woodlands. Traps were positioned around a small water catchment that was visited regularly by most pigs in the area during summer.

Capture-recapture data were analyzed by program CAPTURE (Otis et al. 1978) for population closure and an estimate of population size was computed for the model selected as most appropriate. Known mortalities during the trapping program were deleted from data sets before analyses and subsequently added to population results derived from CAPTURE, following the recommendations of Otis et al. (1978). When removal models provided the best fit, any mortalities previously deleted were returned to data sets and new estimates were obtained using that removal model. The area utilized by each population, represented by the smallest convex polygon enclosing relocations of eartagged or radiotagged pigs from that population, was measured using a digitizing planimeter. Density was computed by dividing the estimate of population size by the area of use.

Upon completion of the capture-recapture experiment at Salta Verde, a removal program was implemented to compare with the results obtained from CAPTURE. Pigs were kill trapped for 3 weeks until the water catchment dried up, after which pigs were hunted during the first 2 hours of daylight for the next 9 days. An estimate of

population size was calculated using Chapman's (1951) unbiased version of the Lincoln estimate,

$$\hat{N} = \frac{(\text{marked animals in population} + 1) (\text{all animal killed} + 1)}{(\text{marked animals killed} + 1)}$$

and by tallying together all animals marked, those unmarked animals killed and those unmarked animals identified but not killed.

Home Range

Ten pigs (6 adult boars and 4 adult sows) were trapped and fitted with radiocollars to measure home range size during the dry season. Animals were monitored for 7 months, from May through November 1981. Bearings were taken from established ridgetop relocation stations and locations were plotted by triangulation on U.S. Geological Survey topographic maps (scale 1:24,000). Some radiotagged animals were trapped as part of other related studies; these observations were included in the estimation of home range size. Locations were converted to an X-Y coordinate system using a digitizing planimeter for analyses.

Data were analyzed for outliers and home range size was computed for a 95% utilization contour (harmonic mean method - Dixon and Chapman 1980, as modified by Samuel et al. 1983), 95% ellipse (Jennrich and Turner 1969), 95% weighted ellipse (Samuel and Garton, in press) and minimum convex polygon (Mohr 1947) using computer program HOME RANGE (Samuel et al. 1983). Locations identified statistically as outliers were examined and if technical or biological justifications were evident, these points were excluded from all

analyses except the weighted ellipse. The weighted ellipse model identified potential outliers and reduced their influence by weighting individual points under a bivariate normal distribution (Samuel and Garton in press). Location data were tested for bivariate normality and bivariate uniformity (Samuel et al. 1983) to aid in selection of the most appropriate home range model. Difference in home range size between the sexes was determined by one-way analysis of variance (ANOVA). Home range results for the minimum convex polygon method were compared statistically by one-way ANOVA and multiple contrasts with other studies that reported pig home range estimates by this method using radio-location data.

Habitat Use

From July 1980 through September 1981, observations of pigs were recorded by vegetative community, slope, aspect, elevation, horizontal distance to nearest water, vertical distance to nearest water, distance to cover, and position relative to the surrounding topography (hilltop, canyon bottom, midhill). Observations were located on U.S. Geological Survey topographic maps (scale 1:24,000) to estimate approximate elevation, horizontal distance to nearest water and vertical distance to nearest water. Slope was measured to the nearest degree using a clinometer. Cover, defined as any vegetative structure sufficient to obscure the pig in question, was visually estimated to the nearest meter. Data were grouped by wet (January 1981 through May 1981) and dry seasons (July 1980 through December 1980, June 1981 through September 1981) for analyses. Seasons were differentiated by weather and plant phenological patterns.

Proportions of availability for vegetative communities, aspect, elevation and topographic position were estimated by sampling 300 random coordinates on study area maps. Preferential use of these habitat parameters by season was determined using the method of Marcum and Loftsgaarden (1980). Observed pig use was compared with availability by a chi-square test of homogeneity; when use differed from availability, preference or avoidance was predicted by constructing simultaneous confidence intervals using the Bonferroni approach (Marcum and Loftsgaarden 1980). Seasonal differences in use of slope, horizontal distance to water, vertical distance to water and distance to cover were determined by one-way ANOVA or Mann-Whitney U-Test.

Reproduction

Adult sows were shot monthly and examined for reproductive activity (pregnancy or lactation). Pregnancy was indicated by the presence of corpora lutea (Schilling 1974) or fetuses. Corpora lutea and fetal litters were counted, and fetal crown rump measures recorded to estimate fetal age (Warwick 1928, Henry 1968a). Piglets were captured, aged by dentition (Matschke 1967) and pooled with aged fetuses to determine birth dates. When possible, piglets were observed and group size recorded before capture. A gestation period of 115 days (Henry 1968b, Mount 1968) was used to calculate birth dates. The mean number of litters produced per adult sow per year was computed following Davis and Golley (1963), and variation in litter size by age class was inspected. Prenatal and postnatal mortality

were examined by comparing corpora lutea counts, fetal litter size, and observations of piglet group sizes arranged by age class using one-way ANOVA and the Student-Newman-Keuls (SNK) multiple range test. Intrauterine mortality was defined as the difference in the proportion of corpora lutea represented by fetuses. Postnatal mortality for piglet age classes was estimated relative to fetal litter size.

Statistical significance was accepted at a probability level of $P < 0.05$ unless otherwise indicated.

RESULTS AND DISCUSSION

Population Density

A total of 94 pigs were marked and 130 recaptures recorded in 325 trap nights at the Middle Canyon site (Table II.1). Capture frequencies ranged from 1 to 10, with 52% of animals trapped on more than 1 occasion. Six pigs were known to have died during trapping: 3 roadkills, 2 killed by dogs, and 1 from trap related injuries. No captured pigs were of an age that indicated they were born during the trapping program.

The most appropriate model for estimating population size by CAPTURE was model M_b , a modification of Zippin's (1956, 1958) removal model. This model provides the best fit when probabilities of capture vary as a result of behavioral responses to initial capture. Pigs at this site appeared to become "trap-happy" after first capture; probability of recapture (0.20) was double the probability of first capture (0.10). Population size was estimated to be 121 ± 15 S.E. (95% confidence interval of 94 to 150 pigs). Area of use by this population was measured to be 4.4 km^2 , and density was estimated at 28 pigs/ km^2 (95% confidence interval of 21 to 34 pigs/ km^2).

The assumption of population closure for the Middle Canyon population was not testable because behavioral variations in probability of capture existed. For population estimation using CAPTURE to be applicable, the assumption of population closure must be valid. A biological assessment of this assumption should be made regardless of the results of the statistical test of closure. I was

confident that this assumption was met at the Middle Canyon site. No births were recorded during trapping and few births were evident outside of this area during this period (See Reproduction). Six mortalities (3 adult, 3 juvenile) were recorded and accounted for in estimation procedures. No doubt other natural mortality occurred, however, if natural mortality acts equally on marked and unmarked animals (as was probably the case), estimators generally will not be biased (Seber 1973). Emigration and immigration were considered negligible.

A total of 42 pigs were marked and 58 recaptures documented in 200 trap nights at the Salta Verde site (Table II.1). Capture frequencies of animals ranged from 1 to 8; 57% of marked pigs were trapped more than 1 time. Three pigs died of heat stress during recovery from immobilization and none of the animals marked had been born during the trapping program.

Model M_h , developed by Burnham and Overton (1978, 1979), was selected by CAPTURE as the most appropriate fit to Salta Verde data set. Model M_h assumes each animal has its own constant probability of capture independent of others (heterogeneity of capture probabilities). Average probability of capture for this population was 0.21, and population size was estimated at 63 ± 6 S.E. (95% confidence interval of 51 to 75 pigs). Area of use by the Salta Verde population was 2.3 km²; density was estimated to be 27 pigs/km² (95% confidence interval of 22 to 33 pigs/km²).

The test for population closure was not rejected ($P = 0.13$), which agreed with my biological assessment. No evidence of birth was

detected during trapping at this site, although births were recorded in the study area during this period (see Reproduction). Most sows here may have farrowed in May and June. Litters that were born in July either did not survive, or were not old enough to travel to the trap site. In Poland, piglets did not appear on trap sites until 6 weeks of age (Jeziarski 1977). Mortality was accounted for in 3 cases. Four radiocollared pigs at this site remained within the boundary of the population use area during the experiment, supporting our contention that emigration and immigration were negligible during trapping.

In the removal effort at Salta Verde, a total of 50 pigs were killed over the 1 month period (Table II.2). This total included 4 radiocollared pigs not actually killed, but declared statistically dead when the opportunity arose to kill them. Eleven marked pigs were not killed, however, 3 were observed during the hunt removal, but escaped. Two other unmarked, but identified animals escaped removal. The fate of 81% (34 of 42) of pigs known to be alive during trapping could be accounted for; 1 adult sow, 5 adult boars, and 2 juvenile males were unaccounted for.

Using Chapman's (1951) version of the Lincoln index, population size at Salta Verde was estimated at 71 pigs. By tallying all animals marked, killed or observed, population size was estimated at 63 pigs. Both compare favorably with the results obtained using CAPTURE and fall within computed 95% confidence intervals, strengthening confidence in the estimates.

Density estimates did not differ between the Middle Canyon and Salta Verde sites. Confidence intervals were combined to establish an estimated density (0.95) of 21 to 34 pigs/km² for the study area. Density was much greater than estimates reported for feral pigs and wild boar X feral pig crosses in similar habitat in California, and approached densities reported for tropical communities in Hawaii and the Galapagos Islands (Table II.3).

Quality of habitat for pigs on Catalina was considered marginal during this study; nutrition was inadequate, pigs lost body weight and condition declined over a large portion of the year (Part I). Yet, pigs were able to survive and reproduce successfully at moderate densities. Population size was extrapolated to be 1260 to 2040 pigs over the study area. The estimated density probably represented a maximum for Catalina during the period of study. Many sites outside of the study area were severely impacted by feral goats and probably supported much lower densities of pigs.

Optimum conditions for reproduction and survival in the Catalina feral pig population appeared linked to the quantity of the acorn crop in fall and the duration of fall-winter rains which stimulate growth of nutritious forage (Part I). During this study, rainfall was below normal (24 cm vs 31 cm average) and oak mast crops were poor. In other years when rainfall is more abundant and oak mast crops are large, density may increase and be substantially larger than I estimated. In Great Smoky Mountains National Park, wild boar densities in northern hardwood forest increased 46% when a good oak mast year followed a poor one, and decreased 64% following a mast

failure (Singer and Ackerman 1981). When periods of drought prevail, pig numbers have been reported to decline drastically (Giffin 1978). This response to drought has been observed on Catalina (D. Propst, pers. comm.). At these times, pig densities on Catalina are probably substantially lower than our estimates.

Home Range

Results of analyses on dry season home ranges of feral pigs using program HOME RANGE are presented in Table II.4. Statistical outliers were detected in most data sets, however, few were considered biologically relevant. Four relocations from data sets of 3 boars were excluded before home range estimation; 2 were judged to be technical errors and 2 were deemed legitimate movements out of the normal area of use. Both ellipse models were considered unacceptable because no data set fit a bivariate normal distribution. The minimum convex polygon (MCP) and harmonic mean methods provided a suitable fit to some data sets, but not to all. Because direct comparison between methods is not appropriate (Anderson 1982), results from both methods were reported for all animals. Dry season home range size differed significantly between boars and sows for the MCP method ($P = 0.004$) and the 95% utilization contour ($P = 0.04$). Dry season home range size for boars averaged $1.42 \text{ km}^2 \pm 0.14 \text{ S.E. (MCP)}$ and $2.44 \text{ km}^2 \pm 0.30 \text{ S.E. (95\% utilization contour)}$; range size for sows averaged $0.67 \text{ km}^2 \pm 0.09 \text{ S.E. (MCP)}$ and $1.46 \text{ km}^2 \pm 0.14 \text{ S.E. (95\% utilization contour)}$. Home ranges of both boars and sows overlapped extensively.

Validity of the MCP method was questioned for most data sets; only 2 fit a bivariate uniform distribution, the underlying utilization distribution necessary for finite boundaries to be appropriate (Metzgar 1973, Samuel and Garton in press). In addition, the assumption that home range shape was convex is probably unreasonable, and overestimates range size when untrue. The wide usage of MCP in the literature, however, makes this method appealing as an index to home range size for intraspecific comparisons.

Samuel et al.'s (1983) extension of Dixon and Chapman's (1980) harmonic mean measure of activity was intended as a distribution-free alternative when other models failed. Home range size was estimated using contours chosen as a specified percentage of the animals utilization distribution. Results of this method were suspect in some data sets with outlying points (Table II.4). In those cases, the 95% utilization contour was seriously affected by the outlying points. This resulted in large areas apparently not used by pigs to be included in range size estimates. Smaller percentile contours could be used to minimize the effects of outliers, however, choice becomes arbitrary based on plot appearance rather than biology.

Results obtained by the MCP method were used as an index to home range size for comparison with other wild pig populations for which range sizes were estimated by the MCP method using radio-location data. Home ranges for boars and sows on Catalina were generally smaller (but often not significantly so) than those reported for other populations (Table II.5). Catalina boar home range size did not differ significantly from the Kipahula Valley population ($P = 0.29$),

Hobcaw Barony boars tracked 5-12 months ($P = 0.24$), or Hobcaw Barony boars tracked 17-19 months ($P = 0.30$); however, boar home range size at the Savannah River Plant was significantly ($P = 0.001$) larger. Home range size for sows on Catalina did not vary from Kipahulu Valley sows ($P = 0.21$) or Hobcaw Barony sows tracked 5 to 8 months ($P = 0.29$), but were significantly ($P = 0.019$) smaller than Hobcaw Barony sows tracked 12-27 months. Although not compared statistically, home range size in both summer and winter ranges for wild boar in Great Smoky Mountains National Park were substantially larger than ranges on Catalina.

Home range sizes were remarkably similar for these wild pig populations in divergent habitat ranging from tropical rain forest to arid sage-woodlands (Table II.5). However, these comparisons are not conclusive considering the large differences in average number of relocations between studies, the small sample sizes involved, and the varying tracking intervals between studies. The MCP method exhibits a strong sample size bias, particularly for small sample sizes (Jennrich and Turner 1969). Differences resulting from individual heterogeneity, age class variations, or social status may confound interpretation when sample sizes are small. Longer tracking periods may incorporate seasonal ranges, permanent or temporary range shifts, and increased incidence of movements at the periphery of the range in home range estimates.

Other researchers have estimated wild pig home ranges to be considerably larger, however their methods were unclear. For example, Barrett (1978) estimated home range size of feral boars to be at least

50 km², and 10-25 km² for feral sows in the arid Sierra foothills of California. In New South Wales, Australia, range size was reported to be 10-50 km² for feral boars and 5-20 km² for feral sows (Giles 1978). At these sites, pigs were reported to move large distances in search of food and water during dry seasons. Generally, home range size in wild pigs is believed to vary inversely with resource abundance and density (Singer 1981, Singer et al. 1981, Diong 1982).

Habitat Use

Dry Season - During the hot dry season, use of habitat components by pigs on Catalina indicated a preference for cooler, moist canyon bottoms (Tables II.6 and II.7). The riparian zone was the only preferred vegetative community, used more than in proportion to its availability. These sites were avoided during the wet season. Topographically, use of canyon bottoms exceeded that expected while midslopes and ridgetops were avoided. Flat aspect was preferred, warm dry south slopes were avoided and other aspects were used in proportion to availability. Lower elevations (100-199 m) were preferred to higher elevations (300-399 m). ANOVA indicated slopes used by pigs were gentle and vertical distance to water was less during the dry season; horizontal distance to water did not vary between seasons (Table II.7).

Patterns of habitat use by pigs illustrated both a physiological need for free water and behavioral responses to increased environmental temperatures. Pigs meet their water requirements by drinking free water, from the moisture content of their forage and

from metabolic pathways. These requirements are modified by environmental factors, and increase as levels of protein, sodium, potassium, and fiber in the diet increase (ARC 1981). Free water appeared to be a necessity for pigs on Catalina. In late spring, summer and early fall, little rainfall occurred on Catalina. Ambient temperatures reached a maximum, annual vegetation cured, seeps dried up and most portions of streams went underground. At these times, pigs actively sought remaining water sources to drink, usually approaching water at dusk after leaving mid-day bed sites.

Dry season diets consisted primarily of fruits of the prickly pear cactus (Opuntia spp.), lemonade berry seeds (Rhus integrifolia) and Australian saltbush (Atriplex semibacata) (Part I). The high moisture content of prickly pear fruits and the low protein level of the diet probably aided water balance but the high fiber content may have had a negative effect (Part I). It is doubtful, however, that water requirements could have been met entirely by diet under dry season environmental conditions.

Due to a lack of sweat glands, pigs must rely on behavioral thermoregulation to maintain a favorable heat balance in hot environments (Mount 1968, Signoret et al. 1975). Behavioral thermoregulation was evident in pigs on Catalina during portions of the dry season. Mean maximum temperature per month ranged from 21 to 28 C during summer. Animals were primarily crepuscular and nocturnal at these times, minimizing activity during the hotter portions of the day. Pigs frequented cool, moist sites to wallow and bedded by day in thick vegetation. A dependence on free water and behavioral responses

to high ambient temperatures are commonly reported for wild pigs (Eisenberg and Lockhart 1972, Barrett 1978, Giles 1978, Van Vuren 1984) and domestic swine (Mount 1968, Signoret et al. 1975) in hot, arid climates.

The major foods in dry season diets were abundant in coastal sage communities, the dominant vegetative community on Catalina, and Australian saltbush was common in grassland communities. Distribution of these items probably accounted for use of these communities in proportion to availability (Table II.6). Oak woodland communities were avoided during the dry season, however, this interpretation was probably biased to some degree. This community was the least open of all vegetative communities on Catalina, so visual observations of pigs were restricted and underestimated utilization. Yet use was probably less during this study than in other years due to poor oak mast crops in 1980 and 1981. Oak mast is a major summer-fall food for pigs in California, and these communities are exploited heavily when mast is available (Pine and Gerdes 1972, Barrett 1978, Barrett, 1982, Van Vuren 1984). Alternative foods characteristic of dry season diets in this study were uncommon in oak woodlands except where the canopy was more open. The value of oak woodland communities as dry season foraging sites would have been low. European wild boar in Tennessee were reported to exploit alternative communities when oak mast failed (Singer et al. 1981). In other years when mast crops were larger, usage would be greater than observed during this study.

About 1% of the study area (2 sites) was cultivated for oat hay (Avena sativa) in spring. These sites were exploited heavily and

highly preferred by pigs living in these areas. In late spring, pigs fed on vegetative growth and seeds of oats, using the cover provided by the oats to feed during the day or night. In summer after the hay had been cut and baled, pigs foraged on loose oat seeds in fields, predominately at night. The poor quality of natural forage at these times (Part I) probably accounted for preference of these sites. Use of cultivated areas (cropland and pastures) is commonly reported for wild pigs in different habitats (Mackin 1970, Springer 1977, Andrzejewski and Jezierski 1978, Barrett 1978, Hone et al. 1980, Barrett and Pine 1980, Genov 1981a, 1981b). In Poland, use of these sites by wild boar varied inversely with food requirements and availability of natural foods (Mackin 1970, Andrzejewski and Jezierski 1978, Genov 1981b).

Wet Season -- Winter rains on Catalina recharged streams and seeps, and stimulated an abundant growth of succulent annual grasses and forbs. Diets of pigs shifted to exploit these food resources, but fruits continued to remain an important dietary component (Part I). Preference for grassland communities and use of oak woodlands in proportion to availability (as compared to avoidance in the dry season) (Table II.6) were probably to exploit the abundance of grasses and forbs prevalent in these communities. The dependence on free water observed during the dry season ceased. Riparian areas were frequented less than in proportion to their availability and few pigs were observed drinking from streams, seeps and reservoirs. Succulent forage probably met most water requirements for pigs under these environmental conditions.

Canyon bottoms were used less than in the dry season, but were still preferred, and ridgetops continued to be avoided (Table II.6). Use of midslopes, however, increased from the dry season. Patterns in use of elevations, slope, and vertical distance to water, and a decline in preference for flat aspect (Tables II.6 and II.7) all illustrated increased distributions of pigs at midslope sites. Most grasslands were located at midslope and ridgetops, and oak woodlands were distributed over canyon bottoms and midslopes. Mesic north and east slopes were frequented more than in the dry season, with east aspects used in greater proportion than availability. Use of west slopes declined and southern aspects continued to be avoided. Abundance of annual grasses and forbs was generally greater on north and east slopes, and less on western and southern aspects.

Patterns of utilization of habitat components by pigs during the wet season appeared to be a function of food availability. Relationships between abundance of forage species, plant communities and topography indicated a high degree of association between these variables, which together influenced pig distributions. Use of cool, moist sites in response to high ambient temperatures ceased during the wet season, and behavioral thermoregulatory patterns changed. Activity patterns shifted to crepuscular and diurnal as ambient temperatures declined. On Santa Cruz Island, California, patterns of activity, vegetative community and topographic use (Van Vuren 1984) were similar to those observed in this study.

Ridgetops were frequented less than in proportion to availability in all seasons on Catalina. Avoidance was probably due to steep

slopes associated with these sites and lack of cover. Pigs generally preferred low to moderate slopes, and remained close to cover (5.9 meters \pm 0.3 S.E.) in all seasons (Tables II.6 and II.7). Ridgetops generally were open, and grasslands or coastal sage scrub communities predominated at these sites. The need for cover may have been a major behavioral characteristic regulating use of some sites on Catalina. Very open habitats (extensive grasslands) may have been avoided by day unless topographic relief was present; these sites were often observed to be exploited at night. In the Sierra foothills of California, use of areas by pigs increased with increased density of vegetation (Barrett 1982).

Reproduction

Seasonality in time of birth was exhibited by the Catalina population (Figure II.2). Most piglets were born in winter and spring in 1980, and late spring and summer in 1981. Small peaks in fall were evident during both years. Lactation patterns corresponded with, and lagged estimated farrowing peaks (Figure II.3).

Breeding patterns in pigs on Catalina appeared to be regulated by photoperiod and nutrition (Part I). Fertility declined in late spring and summer, probably due to increasing photoperiod. Most conception occurred in fall or winter, as evidenced by birth peaks shown in Figure II.3), and apparently depended upon the nutritional status and condition of the sow (Part I). In years when oak mast crops were large and winter rains were abundant and early (1979), breeding occurred in fall and winter and resulted in births during winter and

spring (as in 1980). When mast crops failed and winter rains were late (1980), sows bred in winter and spring after regaining condition and farrowed in spring and summer (as in 1981).

A small number of sows on Catalina conceived at 5-7 months of age, however, most were older than 1 year before they bred successfully (Table II.8). Male and female domestic pigs (Anderson 1980, Pond and Maner 1984), feral pigs (Sweeney et al. 1979, Barrett 1978) and wild boar (Conley et al. 1972, Duncan 1974) reach puberty before 1 year of age. In wild boar and wild boar X feral pig crosses, most sows first successfully conceive as yearlings, although small proportions do breed earlier (Springer 1977, Singer 1981, Singer and Ackerman 1981). Mean litter size of Catalina sows as measured by fetal counts was 5.00 piglets \pm 0.36 S.E. (range 1 to 8, n = 27) and was similar to that reported for other wild pig populations (Table II.9). Sex of piglets did not differ ($P > 0.99$) from a 1:1 ratio. Litter size in domestic pigs (9 to 14 - Dziuk 1977, Anderson 1980, Hagen and Kephart 1980) was considerably larger than that reported for Catalina and other wild pigs, apparently a function of higher ovulatory rates rather than lower intrauterine mortality (Hagen and Kephart 1980).

For the 12 month period beginning in July 1980, the number of litters produced annually per adult sow averaged 0.86 litters \pm 0.17 S.E. A small number of animals were believed to have produce 2 litters. Under most conditions, wild pigs produce only 1 litter annually, although small proportions have been documented to produce 2 (Singer and Ackerman 1981, Diong 1982, Mauget 1982). Production of 2 litters annually was estimated to occur in 3% of wild boar in

Tennessee (Singer and Ackerman 1981). In contrast, one feral population in California was reported to average 2 litters per year (Barrett 1978). Frequencies of double production may increase when entire litters are lost soon after birth (Barrett 1978) or when nutritious forage is abundant for most of the year.

Mean litter size in sows increased from puberty and peaked at 2-3 years of age (Figure II.4). Mean litter size declined slightly in older sows. Similarly, mean litter size of wild boar in Tennessee (Singer and Ackerman 1981) and France (Mauget 1982) was smaller for young breeding females than prime aged sows. This is the pattern typically reported for large mammalian species (Caughley 1977). Ovulation rates in domestic swine generally increase through the first 4 or 5 estrous cycles and litter size of sows bred at first estrous are smaller (Anderson 1980, Pond and Maner 1984). Litter size patterns observed with maturity on Catalina were probably a function of this.

Intrauterine mortality averaged 25% in the Catalina population (Table II.10). This was comparable to the 30-40% embryo loss reported for domestic swine (Wrathall 1975, Anderson 1980, Pond and Maner 1984) and the 23-34% losses for wild pigs in the United States (Table II.9). Prenatal mortality in wild boar in France was substantially less. Most prenatal losses in domestic swine occur within the first 25 days (before or just after implantation), and are resorbed; losses occurring after day 40-50 may be aborted, mummified or stillborn (Wrathall 1975, Anderson 1980, Pond and Maner 1984). No mummified or abnormal fetuses

were observed in this study, suggesting most prenatal mortality occurred in the first trimester of pregnancy.

Mortality in piglets on Catalina was estimated at 58% by the 7-19 week age class (Table II.10). High postnatal mortality is reported in most wild pig populations. Natal and post-partum losses were estimated to be 36% for wild boar in Tennessee (Singer and Ackerman 1981) and 48% for feral pigs in Hawaii (Diong 1982) for similar age classes. In Poland, piglet mortality in wild boar for the first 3 months of life was reported as 19% (Jeziarski 1977); for feral pigs in California, mortality was 70-90% by 6 months of age (Barrett 1978).

Differential mortality between piglets born in different seasons may occur on Catalina. Mortality rates were probably higher for summer litters than winter or spring litters. Nutrition in the Catalina population was optimal in winter and spring, but poor in summer and also in fall when mast crops failed and rains were late (Part I). Sows that nursed litters in winter and spring when the plane of nutrition was high appeared to maintained body condition longer and lactated for longer periods. Those piglets were probably weaned later and in better condition, and were probably better able to survive the summer season. Condition of lactating sows declined rapidly in summer when nutrition was poor. Many of these animals appeared unable to sustain lactation for 3 to 4 months. As a result, those piglets were probably weaned earlier and in poorer condition, and likely had higher mortality rates on the nutritionally poor diet. Piglets in poor physical condition were observed frequently, and natural mortalities were not uncommon in late summer.

Table II.1. Summary of trap results for feral pigs on Santa Catalina Island, California.

Trap period	Number captured per period	Number marked per period	Number recaptured per period	Capture frequencies
Middle Canyon Site				
1	11	11	-	45
2	14	11	3	20
3	18	12	6	11
4	16	9	7	5
5	13	9	4	5
6	13	6	7	2
7	18	6	12	3
8	16	7	9	0
9	27	10	17	2
10	16	3	13	1
11	27	6	21	0
12	18	3	15	0
13	17	1	16	0
Totals	224	94	130	
Salta Verde Site				
1	9	9	-	18
2	10	9	1	9
3	11	6	5	7
4	12	6	6	2
5	12	4	8	3
6	20	8	12	2
7	12	0	12	0
8	14	0	14	1
Totals	100	42	58	

Table II.2. Results of pig removal at the Salta Verde capture-recapture site, September 1981.

Removal method	Number killed	
	Marked	Unmarked
Trapping	30	13
Shooting	1	6
Totals	31	19

Table II.3. Some densities of wild pigs reported in the literature.

Location	Pig type	Habitat	Method	Density pigs/km ²	Source
California	feral	coastal sage-oak woodland-grassland	capture-recapture	21-34 ^a	This study
California	feral	dry oak woodland	tagging & aerial survey	5-8	Barrett 1978
California	wild boar X feral cross	chaparral-woodland	Lincoln index	0.5-0.8	Pine & Gerdes 1973
Hawaii	feral	koa rainforest	capture-recapture	22-52 ^a	Diong 1982
Hawaii	feral	ohia rainforest	track counts	0-9	Diong 1982
Hawaii	feral	rainforest	strip census	3-63	Giffin 1978
Hawaii	feral	mountain pasture	strip census	39 ^b	Giffin 1978
Tennessee	wild boar	northern hardwood forest	line transect	3-10	Singer & Ackerman 1981
Tennessee	wild boar	oak-pine-pasture	line transect	2	Shaffer 1979
Galapagos Islands	feral	evergeen steppe forest	removal	78	Coblentz & Baber 1984
Galapagos Islands	feral	herb-grass meadow	removal	39	Coblentz & Baber 1984

^a 95% confidence intervals.

^b Maximum density in best habitat.

Table II.4. Dry season home range size (km²) for 10 adult feral pigs monitored from May through November 1981 on Santa Catalina Island, California.

Animal number	Number of relocations	Number of statistical outliers	95% utilization contour ^a	95% ellipse ^{b,e}	95% weighted ellipse ^{c,e}	Minimum Convex polygon ^d
BOARS						
716	74	0	2.48 ^h	2.84	2.49	1.98
779	68	9	3.70 ^h	2.18	1.45	1.63
780	73	0 ^f	1.74 ^h	1.58	1.08	1.20
781	71	12 ^f	2.80 ^h	1.88	1.67	1.41 ⁱ
782	73	1 ^g	1.76 ^h	2.25	1.92	1.26 ⁱ
783	61	3 ^g	2.17 ^h	1.53	1.30	1.03
Mean	70		2.44	2.04	1.65	1.42
SOWS						
481	58	3	1.57 ^h	0.68	0.53	0.52
482	76	3	1.03	0.60	0.45	0.58 ⁱ
483	41	1	1.60 ^h	1.73	1.50	1.92 ⁱ
484	73	11	1.62 ^h	0.57	0.32	0.64
Mean	62		1.46	0.90	0.70	0.67

- ^a Dixon and Chapman (1980).
^b Jennrich and Turner (1969).
^c Samuel and Garton, in press.
^d Mohr (1947).
^e Data did not fit a bivariate normal distribution.
^f Two outliers deleted before home range estimation.
^g One outlier deleted before home range estimation.
^h Contour seriously affected by outlying relocations.
ⁱ Data fit a bivariate uniform distribution.

Table II.5. Home range size for radiotracked wild pigs estimated using the minimum convex polygon technique.

Location	Type	Time monitored (mo)	Average number of relocations per pigs	Habitat	Home range size (km ² ± SE)		Source
					Boars (N)	Sows (N)	
California (Santa Catalina Island)	feral	7	67	coastal sage-oak woodland-grassland	1.42 ± 0.14 (6)	0.67 ± 0.09 (4)	This study
Hawaii (Kipauhala Valley, Maui)	feral	5-17	not given	koa-ohia rainforest	2.03 ± 0.25 (5)	1.12 ± 0.24 (4)	Diong 1982
South Carolina ^a (Savannah River Plant)	feral	3-10	383	pine-hardwood forest	5.32 ± 1.38 (4)	4.37 (1)	Kurtz and Marchinton 1972
South Carolina (Hobcaw Barony)	feral	12-27	245	pine-hardwood forest-salt marsh	2.26 ± 0.43 (3)	1.78 ± 0.17 (3)	Wood and Brenneman 1980
South Carolina (Hobcaw Barony)	feral	5-12	95	pine-hardwood forest-saltmarsh	1.10 ± 0.38 (6)	1.18 ± 0.57 (3)	Wood and Brenneman 1980
Tennessee (Great Smoky Mountains National Park)	wild boar	summer ^b range	>25 ^d	Northern hardwood forest	3.81 (9)	3.47 (4)	Singer et al. 1981
Tennessee (Great Smoky Mountains National Park)	wild boar	winter ^c range	>25 ^d	pine-hardwood forest	3.89 (9)	2.66 (4)	Singer et al. 1981

^a Home range size remeasured by the minimum convex polygon method using a digitizing planimeter.

^b about 3 months duration.

^c about 7 months duration.

^d Minimum numbers of relocations.

Table II.6. Seasonal use (%) of habitat by feral pigs on Santa Catalina Island, California. July 1980 through September 1981.

Habitat component	Availability (%)	Use (%)	
		Dry season	Wet season
Vegetative Community		382 ^a	214 ^a
Oak woodland	25.6	16.8 ^b	23.8
Chaparral	3.0	3.4	0.5 ^b
Grassland	22.0	24.1	38.3 ^b
Coastal sage	45.6	40.6 ^b	36.9 ^b
Riparian	3.7	15.2 ^b	0.5 ^b
Aspect		382 ^a	214 ^a
North	23.7	18.6 ^b	29.9 ^b
South	29.7	20.2 ^b	16.8 ^b
East	9.3	11.0	18.2 ^b
West	20.0	20.9 ^b	14.5
Flat	17.3	29.3 ^b	20.6
Elevation		380 ^a	214 ^a
0-99 m	5.0	3.4	0.9 ^c
100-199 m	17.3	30.1 ^c	7.9 ^c
200-299 m	25.7	33.0	29.4
300-399 m	37.7	21.7 ^c	40.7
400-499 m	13.0	9.9	16.4
> 500 m	1.3	1.8	4.7
Topographic position		381 ^a	214 ^a
Bottom	30.3	55.1 ^d	46.3 ^d
Middle	44.3	31.0 ^d	36.9 ^d
Top	25.3	13.9 ^d	16.8 ^d

^a Sample size.

^b Differs significantly (simultaneous $P < 0.10$, individual $P < 0.02$) from availability.

^c Differs significantly (simultaneous $P < 0.12$, individual $P < 0.02$) from availability.

^d Differs significantly (simultaneous $P < 0.06$, individual $P < 0.02$) from availability.

Table II.7. ANOVA results of seasonal habitat use by feral pigs on Santa Catalina Island, California. July through September 1981.

Habitat component	Dry season mean \pm S.E.	Wet season mean \pm S.E.	Significance
Slope (degrees)	9.6 \pm 0.5	16.1 \pm 0.9	P < 0.0001
Vertical distance to water (meters)	43.8 \pm 3.3	48.9 \pm 3.4	P = 0.04
Horizontal distance to water (meters)	351.7 \pm 17.1	357.9 \pm 21.8	P = 0.83
Distance to cover (meters)	6.0 \pm 0.4	5.9 \pm 0.6	P = 0.94

Table II.8. Approximate age at conception for 83 pregnant or lactating¹ sows on Santa Catalina Island, California. July 1980 through September 1981.

Age class (months)	N	% of Sows Conceiving
< 7.5	3	3.6
7 - 12	11	13.3
12 - 18.5	18	21.7
18.5 - 26.5	15	18.1
25.5 - 36	15	18.1
> 36	21	25.3

¹ Midpoint of lactation (~ 1.5 months) arbitrarily assigned to lactating animals to estimate age at conception.

Table II.9. Reproductive parameters for some wild pig populations reported in the literature.

Location	Pig type	Corpora lutea	Fetal litter size	Prenatal mortality (%)	Source
California	feral	6.67 ± 0.30 SE	5.00 ± 0.36 SE	25.0	This study
California	feral	8.5	5.6	34	Barrett 1978
Hawaii	feral	7.7	5.9	23.4	Diong 1982
South Carolina	feral	10.8	7.4	31.5	Sweeney et al. 1979
South Carolina	feral		5.3 ± 2.1		Wood & Brenneman 1977
Georgia	feral	7.5	4.9	34.7	Sweeney 1979
Captive herd	feral	8.7 ± 0.3 SE	6.2 ± 0.5 SE	29.1	Hagen & Kephart 1980
Texas	wild boar X feral cross		4.2		Springer 1977
California	wild boar X feral cross		5.0		Pine & Gerdes 1973
Tennessee	wild boar	6.3	4.8	25.9	Conley et al. 1972
Tennessee	wild boar		4.8 ± 0.6		Singer & Ackerman 1981
France	wild boar	5.26 ± 0.25 SE	4.60 ± 0.18 SE	12.5	Mauget 1982

Table II.10. Prenatal and postnatal mortality in feral pigs on Santa Catalina Island, California. July 1980 through September 1981.

Physiological Class	Sample Size	Group Size \pm SE ¹	Estimated % Mortality ²
Prenatal			
Corpora lutea	27	6.67 \pm 0.30	
Fetal	27	5.00 \pm 0.36	25.0
Postnatal			
3-7 week	11	3.09 \pm 0.46a	38.2
7-19 week	11	2.09 \pm 0.28a	58.2

¹ Common letters indicate those treatment means did not vary significantly.

² Prenatal mortality computed relative to corpora lutea; postnatal mortality computed relative to fetal group size.

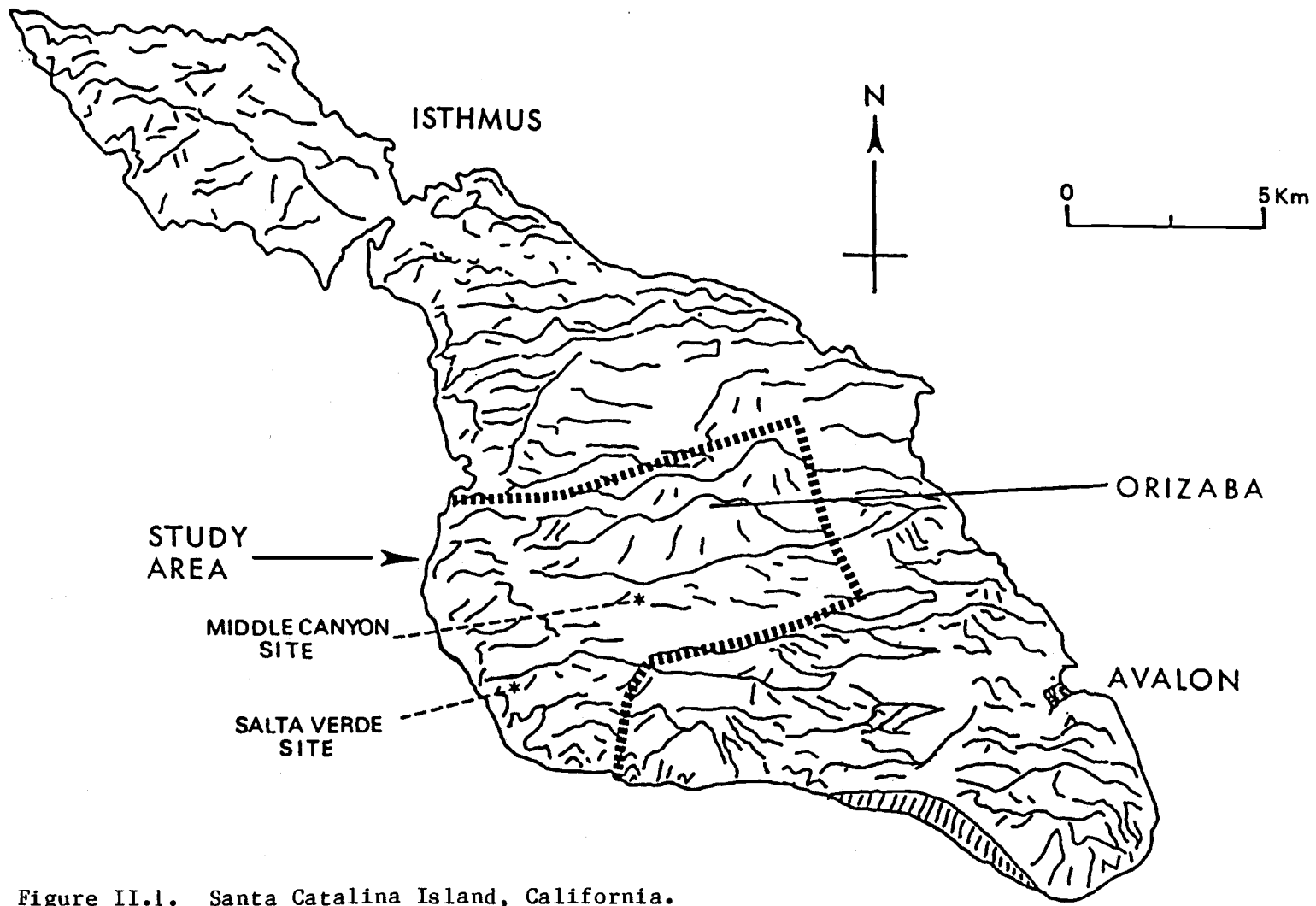


Figure II.1. Santa Catalina Island, California.

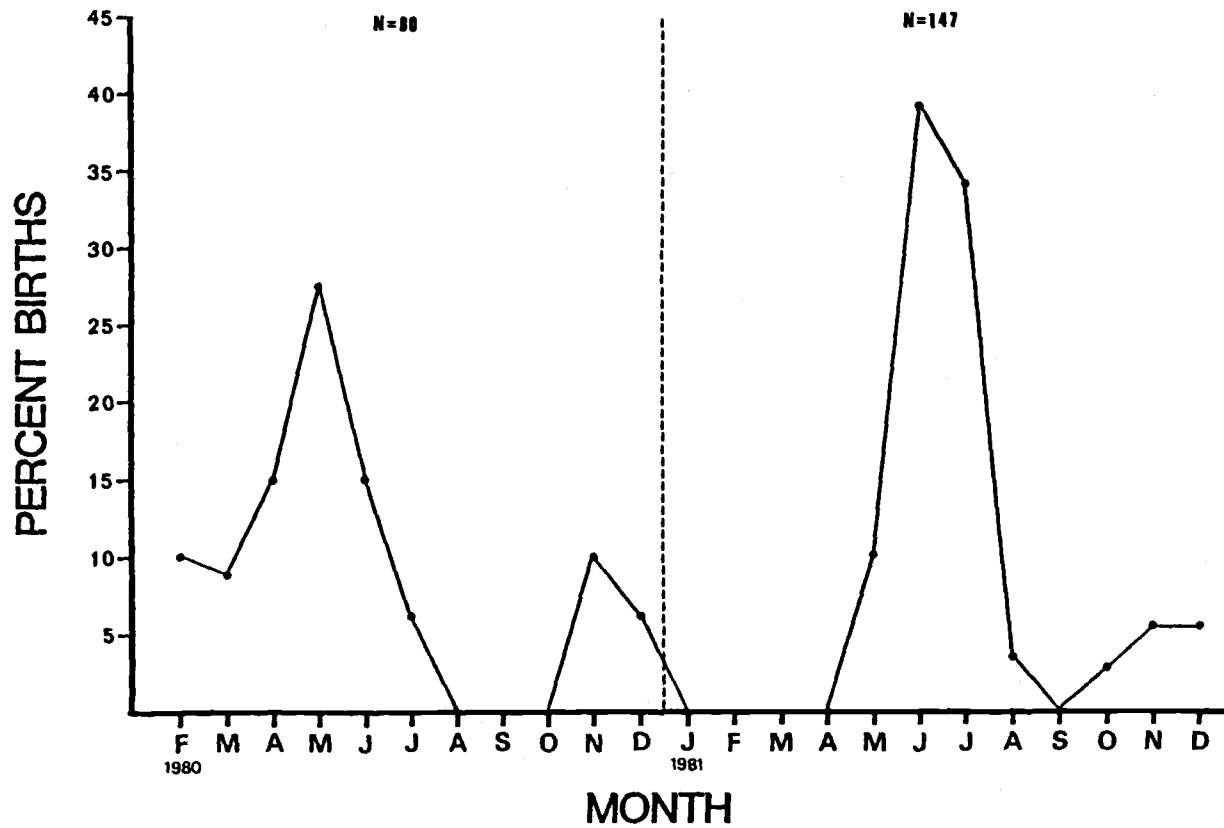


Figure II.2. Distribution of births (%) by month and year for aged fetuses and piglets collected on Santa Catalina Island, California. July 1980 through September 1981.

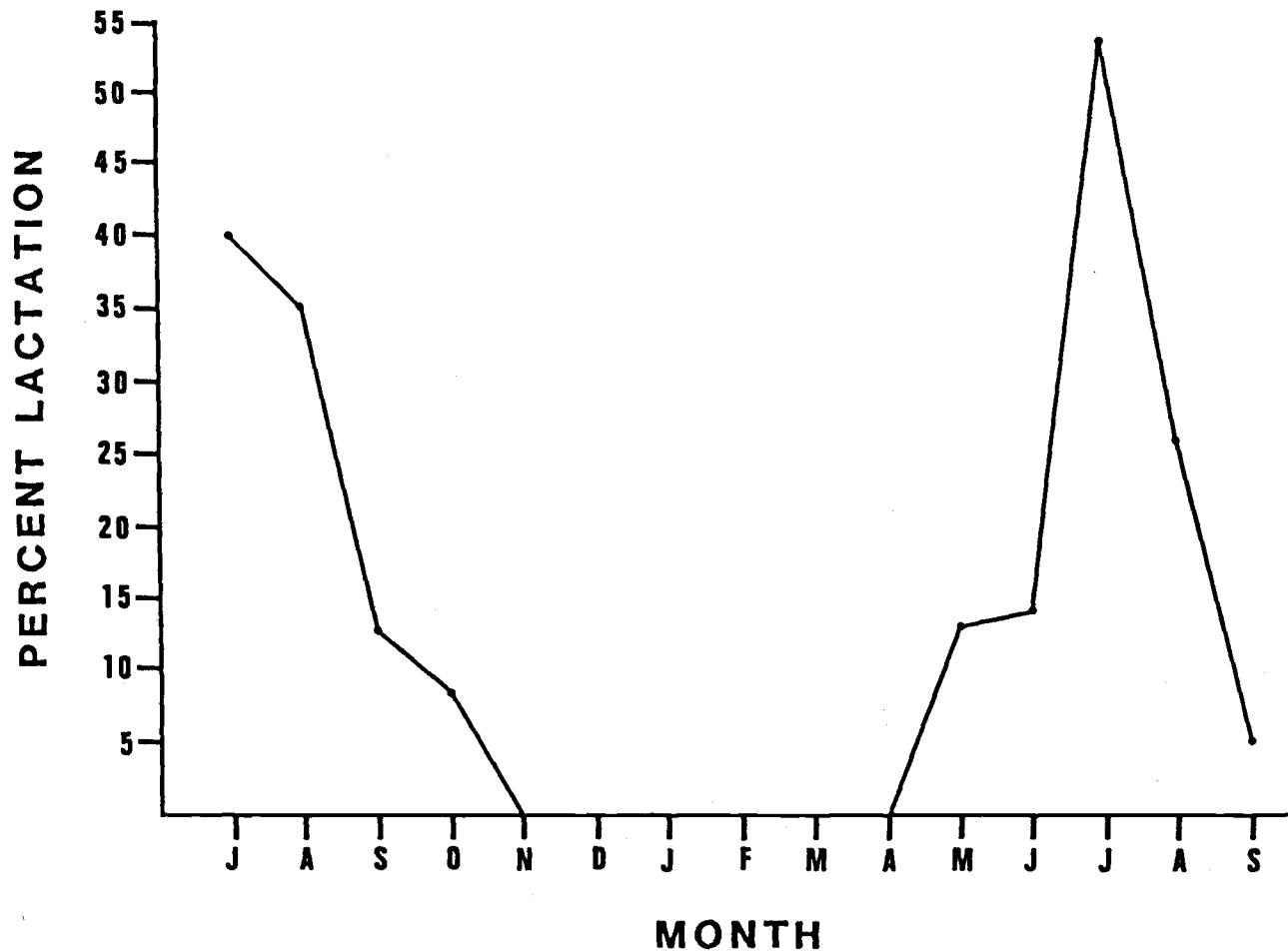


Figure II.3. Lactation rate per month in adult sows (> 7 mo) examined on Santa Catalina Island, California. July 1980 through September 1981.

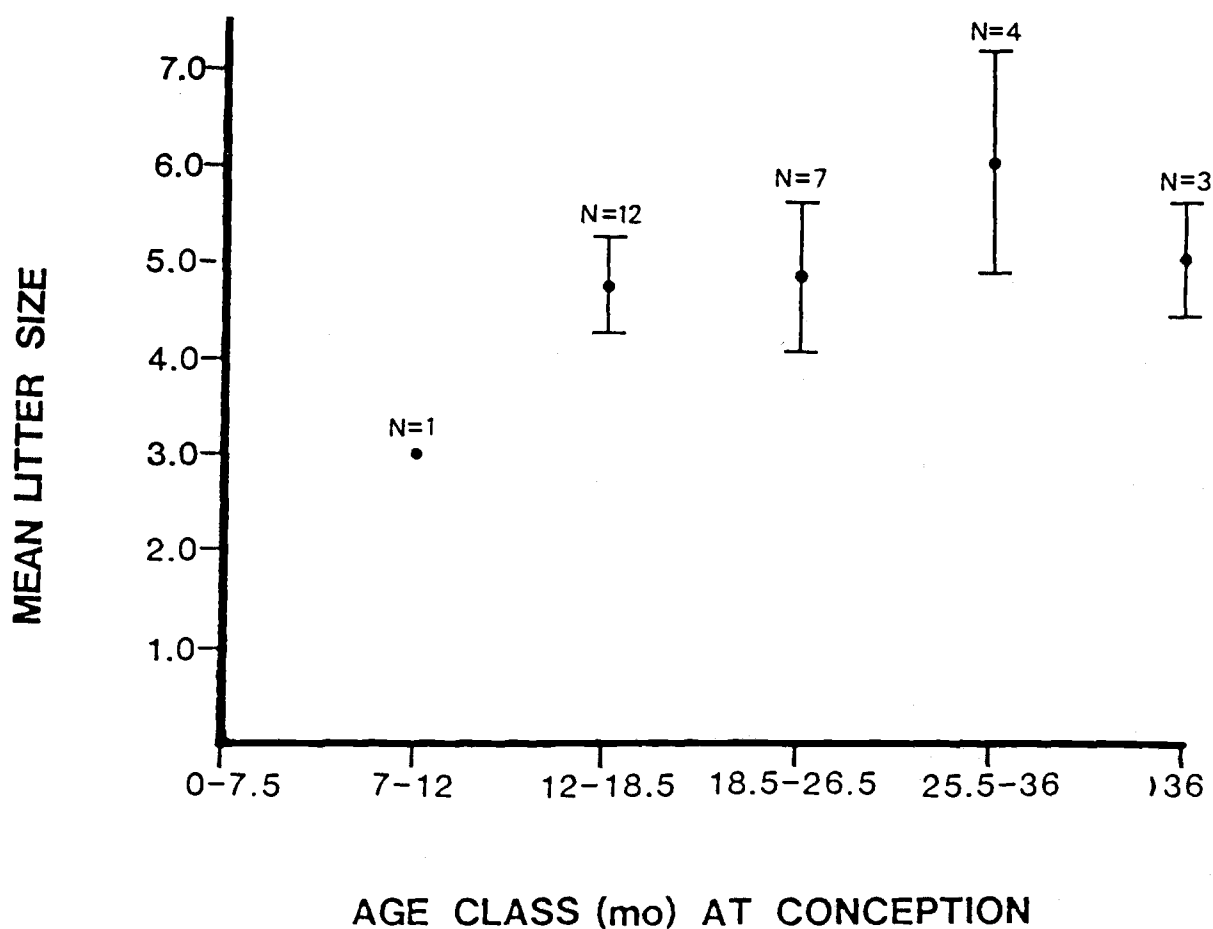


Figure II.4. Mean litter size (\pm S.E.) by age class for 27 pregnant sows examined on Santa Catalina Island, California. July 1980 through September 1981.

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