

CALIFORNIA FISH AND GAME

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Photo by David Jesse McChesney

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Notes from the Editor

In this issue of the *Fish and Game* Journal there are two papers that will benefit field biologists by offering methodological improvements. These types of papers are valued because they help us do our job in a more effective, credible, and consistent way. I encourage those of you out there working on surveys or captures or restoration, or whatever, where there is something you've found that improves on the protocol or methods, integrates new technology, or analytical techniques, to write up a note for publication. Your shared perspective could be valuable to others who may be struggling with similar issues. The third paper in this issue is on the Mexican barracuda, which occurs in the Gulf of Mexico. We have been fortunate to be receiving many manuscripts from researchers and universities in Mexico. Before boundaries, borders, and walls, fish and wildlife moved freely across the landscape and through the seas, migrating and dispersing, in search of better conditions. More recently, we have seen species typically occurring in more tropical settings moving north, many in response to El Nino and warmer ocean temperatures. The more knowledge we can exchange, the better we may be prepared for the future.

We are honored to have contributions from two renowned photographers gracing our covers. This issue, David Mc Chesney, photographer, author, and conservationist, gave us permission to print his photographs on the front and back covers. As you can see, David is an extraordinary photographer, but he also spends a lot of his time campaigning for the conservation of desert ecosystems, which inspired the topic of his new book, *The Mojave Desert: Miles of Wonder*. Last issue, 103-4, Peter Hemming, an accomplished photojournalist, provided a mesmerizing underwater image of Sockeye Salmon. Each issue we try to select cover images that have some connection to the articles inside. If you would like to share your high-resolution photograph for future possible publication, you can send it to publications@wildlife.ca.gov.

The *Fish and Game* Journal has a commitment to quality science and shares this goal with the Department's Science Institute. After many years of effort to further the capacity of the Institute, I am pleased to announce the hiring of Dr. Christina Sloop, as Science Advisor to lead the Science Institute. Christina has worked in ecology and natural resource conservation across California, and North America's Central and Pacific flyways. She holds a doctorate in Ecology and Evolutionary Biology from UC Davis, a Master of Arts in Conservation Biology from San Francisco State University, and Bachelor of Arts in Biology and Environmental Studies from Sonoma State University. Since 2016, she has led the development of the 30-year Delta Conservation, a multi-agency/multi-stakeholder planning framework to inform the conservation of Sacramento-San Joaquin Delta ecosystems, and the Delta Plan restoration chapter amendment to help direct future state policy. Christina has served as science advisor on state and federal agency technical committees and has led or contributed to the development of a number of conservation planning documents in California including the 2015 State Wildlife Action Plan, 2015 Baylands Ecosystem Habitat Goals Science Update for Climate Change, and 2012 SFBJV San Francisco Bay Monitoring and Evaluation Plan. Welcome Christina.

Armand Gonzales
Editor-in-Chief
California Fish and Game

Reproductive aspects of *Sphyraena ensis* (Perciformes: Sphyraenidae) inhabiting the coast of San Blas Nayarit, southeast Gulf of California

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The Mexican barracuda (*Sphyraena ensis*) represents one of the most important fishing resources on the coast of Nayarit, Mexico. Because of its catch volumes and market prices, this fishery is one of the main economic activities in the region. Despite its relevance, knowledge on reproductive biology of this species in the area is scarce. The purpose of this research is to determine some basic aspects of reproductive biology of the Mexican barracuda. Monthly samplings from February, 2014 to January, 2015 were conducted. Sex ratio and weight-length relationship were determined. The degree of gonadal development was established through qualitative (morpho-chromatic maturity scale) and quantitative (morphophysiological indexes such as GSI, HSI and K) methods. The total sex ratio (1M:1.87F) was different from 1:1 and specimens presented negative allometric growth. The Mexican barracuda population presented constant reproductive activity throughout the year. According to morphophysiological indexes such as GSI and HSI, the period of maximum reproductive activity was observed from April to June.

Key words: length-weight relationships, Mexican barracuda, reproduction, sexual proportion, southeast Gulf of California, *Sphyraena ensis*

Barracudas (*Sphyraenidae*) are neritic pelagic species inhabiting coastal areas in tropical and temperate-warm waters (Nelson et al. 2016). Adults of small species and juveniles of all species of barracuda are gregarious and form schools, while adults of large species are solitary or less gregarious (Sommer 1995). The Mexican barracuda (*Sphyraena ensis* Jordan and Gilbert, 1882) is the most abundant species in the Gulf of California and presents the largest distribution range in the eastern tropical Pacific, from the Gulf of California, Mexico, to the northern portion of Chile (Chirichigno and Cornejo 2001). In the water column, the Mexican barracuda can be found from the surface to 25 m depths

(Robertson and Allen 2008). It is a carnivore species that mainly consumes fish (Blaskovic et al. 2008) and reaches a maximum total length of 137 cm (Robertson and Allen 2008).

The Mexican barracuda represents one of the most important fishery resources on the coast of Nayarit, Mexico (Ulloa-Ramírez et al. 2008). Fishing this resource constitutes one of the main economic activities because of its great volume of capture and sales for human consumption, besides being a species of interest for sport fishing activities. It is also a subsistence fishery that satisfies local need for fish protein, since its meat is considered of good quality, especially in the region. However, despite its importance as a fishery resource in the local economy, there is little information on the biological and ecological aspects of this species.

The biological studies of barracudas worldwide have mostly been focused on feeding habits, these include the trophic aspects of *S. viridensis* in the North-eastern Atlantic (Barreiros et al. 2002), *S. barracuda* in Colombia (Hooker et al. 2007), *S. putnamae* in the Persian Gulf (Mohammadzadeh et al. 2010), among others. In Mexico, the length-weight relationship, feeding habits, and gonadal maturation have been estimated for *S. guachancho* in Veracruz (Bedia et al. 2011). While in the Mexican Pacific, a similar study was conducted for the pelican barracuda, *S. idiaestes* in which the length-weight relationship, condition factor and trophic level were determined (González-Acosta et al. 2015). Regarding the Mexican barracuda, there are only a few incidental reports of this species in some studies (Bianchi 1991, Madrid et al. 1997, Abitia-Cardenas et al. 2002, Aceves-Medina et al. 2008). Despite the fishing and ecological importance of *S. ensis* in the area, there is a gap of knowledge on its reproductive biology. Therefore, the purpose of this research was to determine some basic aspects of reproductive biology of the Mexican barracuda in order to provide information that supports the regulation of its fishery in the region.

MATERIALS AND METHODS

Monthly samplings were conducted from February, 2014 to January, 2015 in the coast of San Blas, Nayarit (21° 24' N, 105° 15' W and 21° 33' N, 105° 24' W). Organisms were obtained from coastal commercial fishing, which were captured with line and hook. For each organism, the total length (TL) and weight (W) were recorded. Subsequently, gonads and liver were removed and weighed individually. Sex was determined through direct observation of the gonad. The annual and monthly sex ratio was estimated. To establish whether the sex ratio differed from 1:1, a chi-square test (χ^2) was performed (Zar 2010). Length was compared between sexes by non-parametric Kruskal-Wallis test (Zar 2010). The length-weight relationship was determined for the whole sample and separated by sex respectively. Parameters a and b were estimated using the linear regression model ($\log Wt = \log a + b \times \log TL$) on log-transformed data. A log-log plot (Log TL vs Log TW) was used to remove outliers (Froese 2006). To determine the growth rate of barracuda, the obtained slope was compared with the hypothetical value of 3 (isometry) by Student's t-test (Zar 2010).

To establish the degree of gonadal development, qualitative and quantitative methods were used. The qualitative method consisted on establishing a morpho-chromatic scale for females and males of *S. ensis*, based on the morpho-chromatic scale proposed by Agger et al. (1974) and adapted for this species. Subsequently, the reproductive cycle was described considering the monthly frequencies of each stage of gonadal development. The quantitative method consisted of calculating the gonadosomatic index ($GSI = \text{weight of the gonad} / \text{weight of the fish without gonad} \times 100$), hepatosomatic index ($HSI = \text{liver}$

weight / weight of fish without liver * 100) and the relative condition factor ($K = W_{(fish\ weight)} / aL_{T(fish\ length)^b}$) according to Le Cren (1951). Monthly variations of GSI, HSI and K by sex and month were analyzed with non-parametric Kruskal-Wallis analysis of variance. Spearman correlations were estimated between indexes and stages of gonadal development.

RESULTS

A total of 319 barracudas were sampled, 208 of which were females and 111 males. The overall sex ratio (1M:1.87F) was different from 1:1 ($X^2=29.50$, $df = 1$, $P=0.000$). Although in most months the sex ratio was higher for females, only in March, September, November, December and January the sexual proportion was significantly different from 1:1. May was the only sampled month in which male ratio (1M:0.24F) was statistically higher than female ratio (Table 1). Size distribution ranged from 32.7 cm to 58.7 cm TL (mean=45.24 cm TL) and weight ranged from 141 g to 836 g (mean=426.73 g) in females, while males presented from 30.6 cm to 53.5 cm TL (Mean=40.76 cm TL) and from 119 g to 638 g (mean=336 g). Comparisons of female/male size indicated that females were larger in total length ($H=7.426$, $df = 1$, $P=0.005$) and weight ($H=7.419$, $df = 1$, $P=0.006$).

TABLE 1.— Sexual proportion of the Mexican barracuda, *Sphyraena ensis* from southeast Gulf of California.

Month	Male	Female	Proportion M:F	X^2	P
February	12	23	1:1.9	3.46	0.062
March	4	20	1:5	10.67	0.001*
April	15	7	1:0.47	2.91	0.088
May	17	4	1:0.24	8.05	0.004*
June	7	8	1:1.14	0.07	0.791
July	19	10	1:0.53	2.79	0.094
August	12	17	1:1.42	0.86	0.353
September	5	23	1:4.6	11.57	0.000*
October	12	19	1:1.58	1.58	0.208
November	5	25	1:5	13.33	0.000*
December	2	25	1:12.5	19.59	0.000*
January	1	27	1:27	24.14	0.000*
Total	111	208	1:1.87	29.50	0.000*

* Significant difference ($P < 0.05$).

The length-weight relationship in the Mexican barracuda, *S. ensis* showed that growth is negatively allometric for the overall sample, presenting a slope value ($b=2.796$) lower than the hypothetical isometric value ($t=1.96$, $P=0.000$). Similarly, negative allometric growth was observed in males ($b=2.829$, $t=1.98$, $P=0.000$) and females ($b=2.814$, $t=1.97$, $P=0.000$) (Table 2).

TABLE 2. — Length-weight relationship parameters for the Mexican barracuda from the southeast Gulf of California, Mexico. N= sample size, Range= minimum and maximum, a = proportionality coefficients (intercept), $aCI95\%$ = confidence limits for a , b = allometry coefficient (slope), $bCI95\%$ = confidence limits for b , and r^2 = coefficient of determination.

		Total length (cm)	Total weight [g]	Relation parameters					
	N	Range	Range	a	$IC_{95\%} a$	b	$IC_{95\%} b$		r^2
Females	208	32.7–58.7	141–836	0.0061	0.0042 0.0079	2.9178	2.8397 2.9959		0.9824
Males	111	30.6–53.5	119–638	0.0091	0.0048 0.0135	2.8160	2.6897 2.9422		0.9738
Both sexes	319	30.6–58.7	119–836	0.0073	0.0056 0.0090	2.8732	2.8131 2.9332		0.9829

Gonadal development was characterized at the macroscopic level. For females, five stages of development were established: resting, early developing, late developing, mature and spent (Table 3). In males, four stages of development were established: resting, developing, mature and spent (Table 4). Regarding the reproductive cycle, it was observed that *S. ensis* presents constant reproductive activity throughout the year (Figure 1). Females were found in mature stage in all months, except for November and December. However, in these same months females were found in early and advanced stages of development. Likewise, females were observed in the resting phase throughout the year, except from May to July (Figure 1a). In males, mature organisms were found throughout the year without exception. The resting stage in males was observed during most of the sampling period, except from April to July and in January (Figure 1b). However, in the latter only one male corresponding to the mature stage was found (Table 1 and 2).

Gonadosomatic (GSI) and hepatosomatic (HSI) indexes showed a seasonal variation in both males and females following the same pattern of behavior (Figures 2 and 3). The mean GSI and HSI values were highest from April to June, the highest mean GSI value was observed in May, which was 1.83 and 2.08 for males and females, respectively (Figure 2). The HSI mean value was highest in April and June for females (3.56 and 3.61, respectively) and in April (3.04) for males (Figure 3). The analysis of variance indicated that GSI values were higher in females than males ($F=3.752_{df=1}$, $P=0.0489$), while HSI did not present significant differences between sexes ($F=1.475_{df=1}$, $P=0.2244$). The relative condition factor did not show a defined pattern in either sex. In females, the maximum monthly average value was 0.91 and minimum 0.81 (mean=0.88), while males presented a maximum value of 0.96 and minimum 0.87 (mean=0.90).

TABLE 3.— Stages of gonadal development in the ovary of *Sphyraena ensis* according to the morpho-cromatic scale.

Stage	Description
Resting	Thin and elongated ovaries, with translucent red color.
Early developing	Enlarged and flaccid ovaries, with light brown color.
Late developing	Larger and turgid ovaries, with yellowish color. Small oocytes can be observed. Evident external vascularization.
Ripe	Large, turgid and fully filled ovaries, intense yellow. Large oocytes can be easily observed. Very vascularized internally but less evident externally.
Spent	Flaccid and empty ovaries, with reddish brown color.

TABLE 4.— Stages of gonadal development in the testis of *Sphyraena ensis* according to the morpho-cromatic scale.

Stage	Description
Resting	Thin and compact testis, with cream color. May present light red tones.
Developing	Large testis, compact and firm to the touch, with pale cream color and light shades. Vascularization can be easily observed externally.
Ripe	Testicle robust and firm to the touch, with whitish color. The collecting tubule is whiter in the inner part of the lobes, it easily ejects semen when exposed to slight pressure.
Spent	Flaccid and empty testicle, with brown cream color.

The GSI and HSI showed to be good indicators of gonadal development in the Mexican barracuda. According to the correlation analysis, females presented a positive correlation between GSI ($R=0.887$, $P=0.0001$) and HSI ($R=0.852$, $P=0.0004$) with regard to the late developing stage, whereas these same indexes showed a negative correlation at the resting stage (GSI, $R=-0.963$, $P=0.0000$; HSI, $R=-0.828$, $P=0.0008$). Males exhibited a positive correlation between GSI and the mature stage ($R=0.687$, $P=0.0112$) and negative correlation between GSI and the resting stage ($R=0.707$, $P=0.0019$).

DISCUSSION

The lengths found in this study ranged 30.6 cm to 58.7 cm TL. The maximum length found was lower than that reported as record length (137 cm) for *S. ensis* (Robertson and Allen 2008). This could be attributed to the sampling area, since the organisms used for this study were collected near the coast and according to Whitehead et al. (1986), small barracudas are found close to coastal areas, while the largest individuals are found in the open sea. With regard to length by sex, it was observed that females were larger than males. Nikolsky (1963) suggests that females reach greater lengths as a reproductive strategy, for this allows them to produce more eggs. The sex ratio of the Mexican barracuda was 1:1.87 (M:F). Higher proportions of females have been detected in other species of barracuda from different regions: *S. chrysotaenia* (Rizkalla 1985, Allam et al. 2004), *S. barracuda* (De Sylva

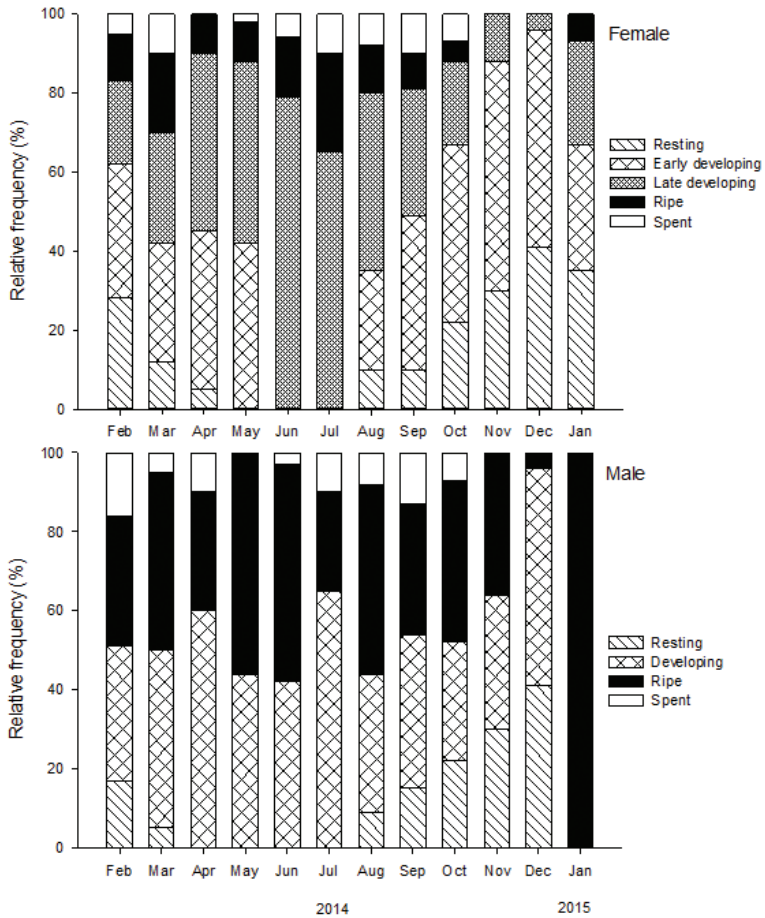


FIGURE 1.— Monthly frequencies of the gonadal developmental stages for females and males of *Sphyraena ensis*.

1963, Kadison et al. 2010), *S. sphyraena* (Allam et al. 2004), *S. guachancho* (Bedia et al. 2011), and *S. idiaestes* (González-Acosta et al. 2015). However, in species such as *S. obtusata*, *S. chrysotaenia*, *S. jello* (Okera 1982), *S. flavicauda* (Allam et al. 2004) the highest ratio has been reported for males. According to Nikolsky (1963), the sex ratio can show variations among populations and may vary during their life cycle due to changes in environmental factors, food availability, mortality, and others, acting differently for each sex. According to length-weight relationship, it was observed that *S. ensis* presents negative allometric growth, which means that individuals grow more in length than weight. Within the family Sphyraenidae, the type of growth is variable among species, for instance, isometric growth has been reported for *S. putnamae* (Mohammadizadeh et al. 2010) and *S. idiaestes* (González-

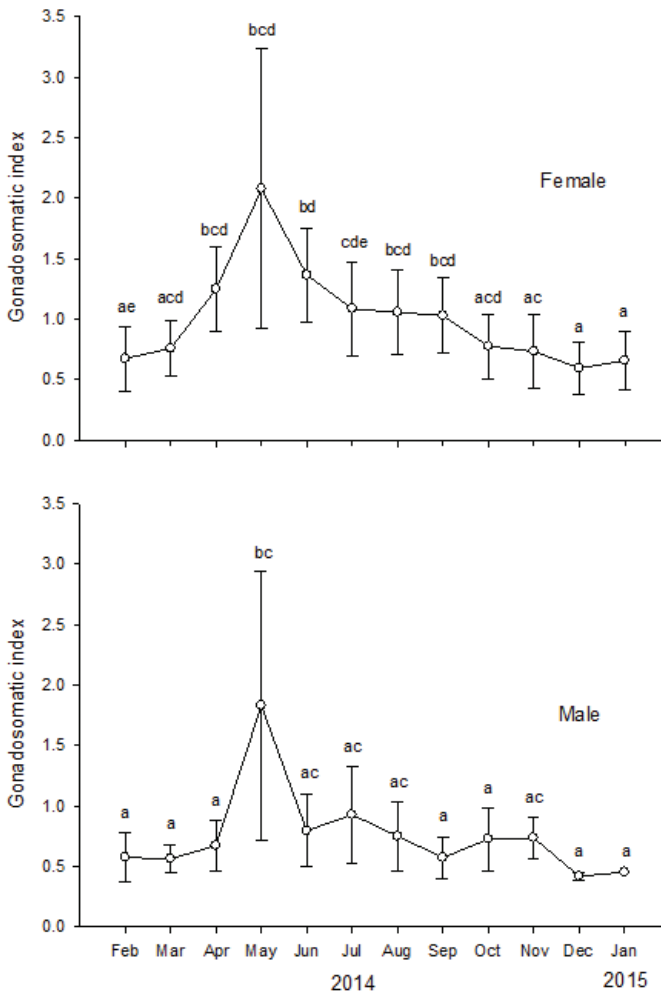


FIGURE 2.— Monthly variation of mean values of the gonadosomatic index for females and males of *S. ensis*. Means that do not share the same superscript are significantly different ($P < 0.05$). Bars correspond to standard error.

Acosta et al. 2015). In the Mediterranean Sea, Kalogirou et al. (2012) analyzed the growth rate of *S. viridensis* ($b=2.76$), *S. sphyraena* ($b=2.97$), and *S. chrysotaenia* ($b=2.85$) and found different types of growth even in species of the same region. For *S. guachancho*, different types of growth have been detected according to the sampling season (isometric growth in the rainy season and allometric in windy and dry seasons) (Bedia et al. 2011). Begenal and Tesch (1978) point out that differences in the length-weight relationship can be found with

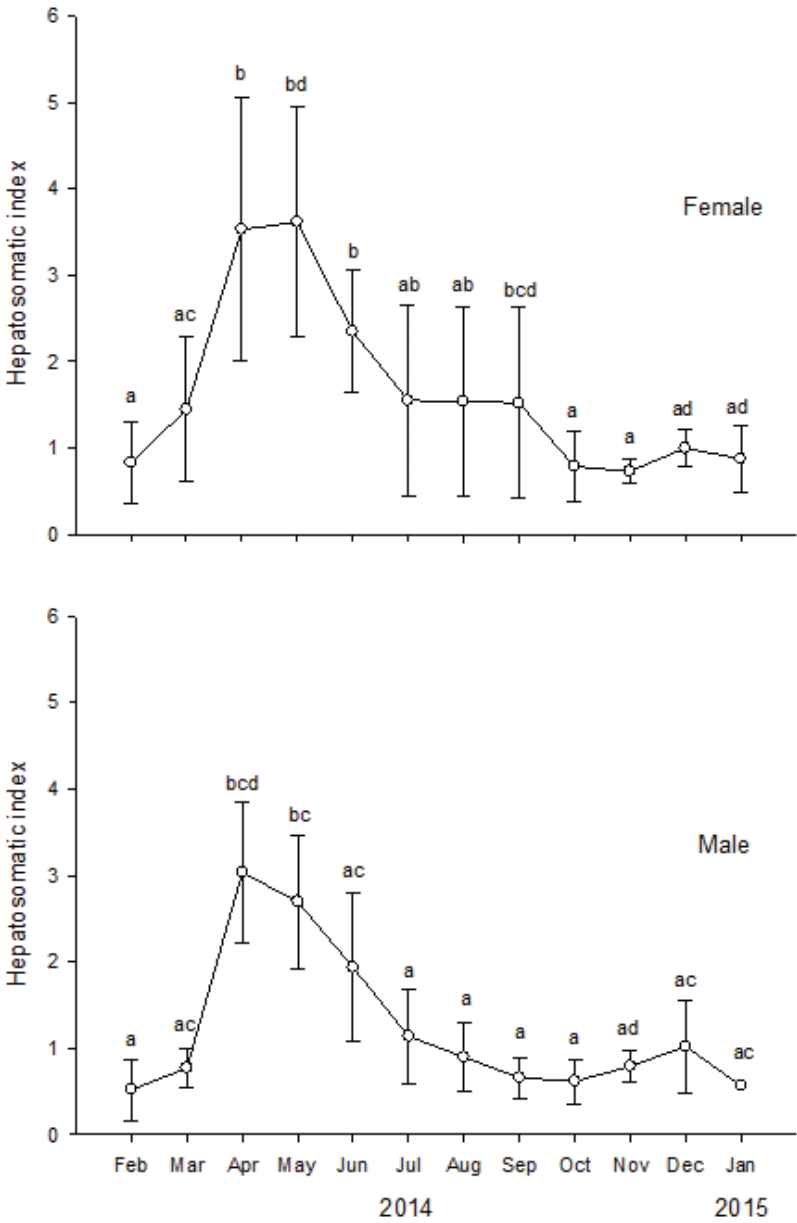


FIGURE 3.— Monthly variation of mean values of the hepatosomatic index for females and males of *S. ensis*. Means that do not share the same superscript are significantly different ($P < 0.05$). Bars correspond to standard error.

regard to sex, sexual maturity, season and even time of the day as a result of stomach filling; therefore, changes in *b* value can be found in different developmental stages, first sexual maturity and when important environmental changes occur. The reproductive activity of *S. ensis* in the study area remained constant throughout the year. Females in mature stage were observed in all of the sampling months except for November and December; however, the proportion of females at that stage was low and rarely reached 20%. Similarly, mature males were observed during all sampling months. According to the morphophysiological indexes such as GSI and HSI, the period of maximum reproductive activity was observed from April to June. The highest reproductive activity is associated with the highest GSI values, while minimum values are related to resting periods (Htun-Han 1978). In this regard, during April, May, and June there was a high proportion of organisms at developing stages (males), early developing and late developing stages (females), and a low or null proportion of organisms at resting stage. This explains the fact that despite mature organisms being detected throughout the year, the GSI value from April to June was high because it is based on the relationship between gonad weight and total weight of the organisms (Bolger and Connolly 1989). In other barracuda species, a single spawning peak has also been reported: *S. barracuda* from May to November (De Sylva 1963), *S. obtusata* from November to December (Okera 1982), *S. sphyraena* from June to November (George et al. 1998); however, in some cases it is very extended, as occurs with *S. guachancho*, where the highest reproductive activity is from June to February (Bedia et al. 2011). In *S. barracuda* a reproductive period (maturity and spawning) was observed from March to November with different peaks in GSI (Kadison et al. 2010).

The GSI and HSI are good indicators of reproductive period. In females, a positive correlation was observed between these indexes and the late developing stage, while a negative correlation was found when compared to the resting stage. Several studies have addressed these indexes together with *K* value in order to evaluate the reproductive capacity, since vitellogenesis and gametogenesis mobilize energy and body fat (Abascal et al. 2004, Kanak and Tachihara 2008). The GSI and HSI increase as the gonadal development progresses because the liver is the main organ responsible for vitellogenin production, which will furtherly be distributed to the gonads (Henderson and Tocher 1987) for oocyte maturation. In this connection, the energy and body fat obtained from food are temporarily stored in the liver and gonads during the processes of vitellogenesis and gamatogenesis. In males, a positive correlation was observed between GSI and the developing stage, while a negative correlation was found between GSI and the resting stage. These relations could be explained by the progression of gonadal development in males, where the gonads increase their size due to cellular differentiation, even when there is no reserve storage of sexual cells, as occurs in females. Regularly, *K* is negatively correlated with GSI or degree of maturity (Maddock and Burton 1999), reflecting the transfer of somatic energy to the gonads for gametogenesis support (González and Oyarzún 2002). This correlation was not found in this study. However, *K* shows a slight tendency to decrease during the month that presented the highest GSI value (May) in both females and males.

In conclusion, the Mexican barracuda population showed the mature stage most of the year in the study area although in a low proportion, the highest reproductive activity according to GSI and HSI was presented from April to June. Therefore, these months of increased reproductive activity can be suggested as a closure period in order to establish a sustainable fishery management plan.

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Comparison of rabbit abundance survey techniques in arid habitats

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We evaluated the strengths, weaknesses, relative effort, and cost of four survey techniques for indexing black-tailed jackrabbit (*Lepus californicus*) and desert cottontail (*Sylvilagus audubonii*) abundance in arid scrub habitats in the San Joaquin Valley of California in April 2004. The four survey techniques were aerial, spotlight, track station, and visual encounters along foot transects. Rabbit abundance indices in areas with and without shrubs were 5.79/km and 0.04/km for aerial surveys, 0.5/km and 2.94/km for spotlight surveys, 1.53/km and 0.27/km for visual encounter surveys, and 52% and 40% visitation rates for track station surveys. Visual encounter, spotlight, and aerial surveys all provided species-specific counts of individuals that can be used to estimate an index of abundance (e.g., number/km) or density using distance methods. Track stations provided a visitation rate but the number of individuals and species could not always be determined. Visual encounter and aerial surveys measured diurnal habitat use, spotlight surveys measured nocturnal habitat use, and track stations measured both. For visual encounter and spotlight surveys, rabbit observability was reduced in areas with shrubs compared to areas without shrubs resulting in a habitat bias. Road availability can limit access for visual encounter, spotlight, and track station surveys but not aerial surveys. For two biologists working two 8-hour days, estimated number of sampling units and costs (labor, materials, travel) for each technique were 24 track stations (\$27.05/station), 40 km of visual encounter transects (\$16.36/km), 140 km of aerial transects (\$16.00/km), and 100 km of spotlight transects (\$6.80/km). Project objectives, study site attributes, and budgets will determine which survey technique might yield the best results and be most cost-effective for a given project.

Key words: Abundance indices, aerial surveys, arid scrub habitat, black-tailed jackrabbits, desert cottontails, spotlight surveys, track station surveys, visual encounter surveys

A variety of techniques have been used to measure the abundance of rabbits. These techniques include track counts (on transects or plots), fecal pellet counts (on

transects or plots), visual counts (on driving routes, walking transects, or spotlight routes), and mark-recapture methods involving live-trapping, among others (Wywiłowski and Stoddart 1988, Murray 2003, Mitchell and Balogh 2007). All techniques have advantages and disadvantages with regards to labor requirements, ease of application, data quality, and costs. Thus, the technique used varies among projects depending on objectives, study site attributes, and staff time or funding limitations.

We assessed the relative merits and costs of four techniques to index the abundance of black-tailed jackrabbits (*Lepus californicus*) and desert cottontails (*Sylvilagus audubonii*) in arid scrub habitat. Rabbit abundance was indexed to assess spatial and temporal patterns in prey availability for endangered San Joaquin kit foxes (*Vulpes macrotis mutica*; Nelson et al. 2007, Cypher et al. 2009). The four techniques were visual encounter surveys along walking transects, spotlight surveys, aerial transects, and track stations. We compared rabbit detection rates, labor and time requirements, and costs among techniques and also summarized biases and limitations associated with each technique and the resulting data.

MATERIALS AND METHODS

Study area.—We indexed rabbit abundance in the Lokern Natural Area (LNA) located approximately 10 km west of the town of Buttonwillow in Kern County, California (Figure 1; 35° 22' N, 119° 34' W). The LNA encompassed approximately 140 km² and comprised a mix of public and privately owned lands. Much of the region was alluvial with flat to gently sloping terrain and elevation was approximately 100 m. The region has a Mediterranean climate characterized by hot, dry summers, and cool, wet winters with frequent fog. Mean maximum and minimum temperatures were 35°C and 18°C in summer, and 17°C and 5°C in winter. Annual precipitation averaged approximately 15 cm and occurred primarily as rain falling between October and April (National Oceanic and Atmospheric Administration 2002).

The vegetation community was characterized as Lower Sonoran Grassland (Twisselman 1967) or Allscale Scrub Alliance (Sawyer et al. 2009). The community consisted of arid shrublands with a sometimes dense herbaceous cover dominated by non-native grasses and forbs. Desert saltbush (*Atriplex polycarpa*) and spiny saltbush (*A. spinifera*) were the dominant shrubs while cheesebush (*Ambrosia salsola*) and bladderpod (*Peritoma arborea*) also were common. Ground cover consisted primarily of annual grasses and forbs, and was dominated by red brome (*Bromus madritensis*) and red-stemmed filaree (*Erodium cicutarium*). Large portions of the area were devoid of shrubs due to repeated wildfires; saltbush is not fire-adapted and fire frequency has increased due to the non-native grasses (Sawyer et al. 2009). The LNA is within a region considered to be important habitat for the conservation of a variety of rare animal and plant species (U.S. Fish and Wildlife Service 1998).

Indices compared.—We indexed rabbit abundance using four survey methods: visual encounter, spotlight, aerial, and track station. All surveys were conducted in April 2004 to control for temporal variation in rabbit abundance. Four field biologists were used to conduct all of the surveys with a pair of biologists conducting each individual survey.

Visual encounter surveys consisted of an observer slowly walking along a 1-km transect and counting all rabbits observed. The surveys were conducted between mid-morning and mid-afternoon when rabbits typically were resting. The transects were triangular in shape (~0.33 km per side such that the observer ended back at the starting point. Starting points were randomly selected and with the restrictions that they needed to be within

1 km of a road (to facilitate access) and separated by at least 1 km. A GPS unit was used to navigate the transect and each required approximately 15-20 minutes to complete. Fifteen transects were in areas with shrubs and 15 were in areas without shrubs (Figure 1).

Spotlight surveys were conducted at night and consisted of two observers (one driving) shining spotlights from a vehicle while slowly driving along a route. All routes were along existing gravel roads and all surveys were conducted from pickup trucks. Routes were driven at approximately 10-15 km/h while two observers shined two-million candle-power spotlights out of opposite sides of the vehicle. When an animal or eye-shine was observed, the vehicle was stopped and binoculars were used to determine whether the animal was a rabbit. Spotlight routes totaled approximately 29.6 km with 11.7 km in areas with shrubs and 17.9 km being in areas without shrubs (Figure 1).

Aerial surveys were conducted during the day from a 4-seat Bell Ranger helicopter with one observer in the front passenger seat and one observer on the opposite side in a back seat. The helicopter was flown at approximately 35 km/h at altitudes of 50-100 m above the ground along transects and flushed rabbits were counted. Eleven transects were flown with 22.8 km in areas with shrubs and 16.0 km in areas without shrubs (Figure 1). Transects varied in length were subjectively chosen to traverse large blocks of habitat.

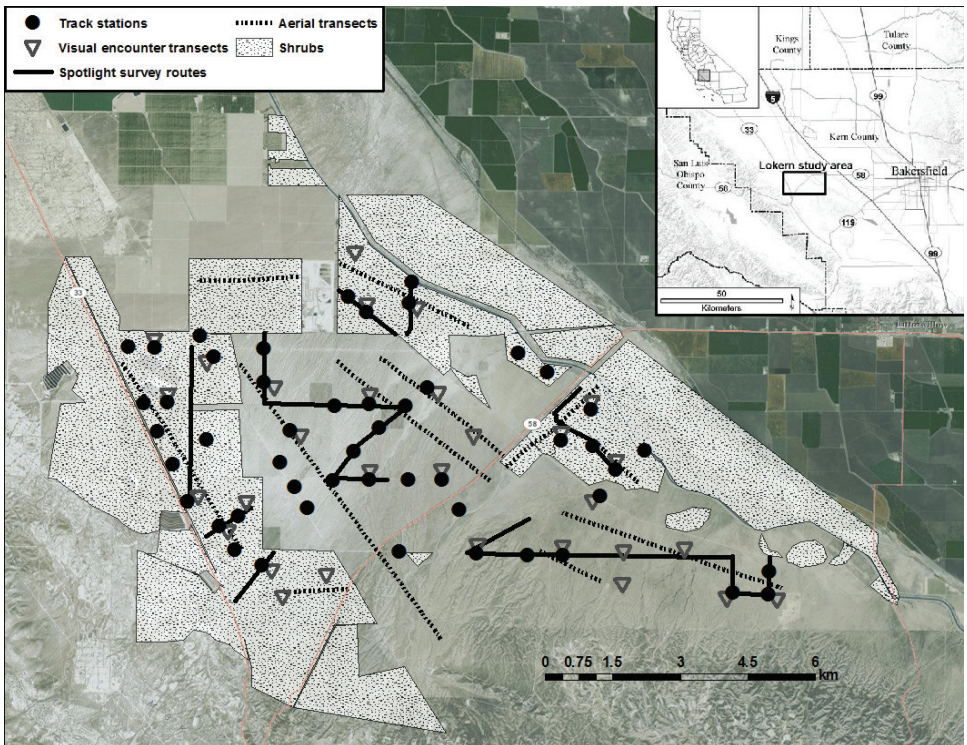


FIGURE 1.—Locations of aerial transects, visual encounter transects, spotlight transects, and track stations for rabbit surveys conducted in April 2004 on the Lokern Natural Area, Kern County, California.

We established track stations throughout the study area and individual stations were separated by a minimum of 0.5 km (Figure 1). This spacing was based on the diameter (~ 0.2 km²) of typical home range sizes for black-tailed jackrabbits (Lechleitner 1958, French et al. 1965) and was used to reduce the likelihood that individual rabbits visited multiple stations in one night. Of 50 stations created, 25 were in areas with shrubs and 25 were in areas without shrubs. The stations were located on the edge of the road to avoid disturbance by vehicles. Each station was created by removing vegetation, rocks, and debris from an approximate 1-m² area. Dry, powdery dirt collected from the study site was sifted over the area to create a smooth layer at least 0.5 cm thick. A handful of commercial alfalfa pellets was placed in the center of each station along with a 2.5-cm² plaster of Paris square infused with carrot oil (J.R. and Sons, Monroeville, Ohio, USA). The stations were created one day and then checked the next day. Visits by rabbits were determined by identifying tracks recorded in the soft dirt of the stations. Generally, we could not identify tracks to species. Also, the actual number of rabbits that visited a station could not be determined from the tracks, and therefore the station was recorded as "visited" if any rabbit tracks were present.

We determined the number of rabbits detected for each technique in areas with and without shrubs. For visual encounter, spotlight, and aerial surveys, we used a 2-way analysis-of-variance to compare mean number of rabbits among techniques and between habitats, and to examine interactions between these two factors. Fisher's least-significant-difference test was used to conduct pair-wise comparisons among technique x habitat combinations. We also used contingency table analysis with a chi-square statistic and a Yate's correction-for-continuity (Zar 1984) to compare proportions of track stations visited by rabbits between habitats. *P*-values < 0.05 were considered significant.

To compare productivity and costs between techniques, we estimated the number of sampling units (e.g., kilometer of transect, track station) that could be comfortably completed by two field biologists working two 8-hour days. We used two days as a standard because that is the minimum number of days required to conduct a track station survey because the stations need to be created one day and then checked the next day. For comparison purposes, we estimated the cost for completing all work using standardized rates of \$20/h for labor and \$0.40/km for vehicle use, and also added any other costs associated with employing each technique.

RESULTS

Among visual encounter, spotlight, and aerial surveys, the mean number of rabbits/km was highest for aerial surveys conducted in areas with shrubs and the lowest was for aerial surveys conducted in areas without shrubs (Table 1). The difference in mean rabbits/km among techniques approached significance ($F_{2,47}=3.141$, $P=0.052$) and was higher in areas with shrubs compared to areas without shrubs ($F_{1,47}=4.766$, $P=0.034$). Interactions between technique and habitat were significant ($F_{2,47}=9.068$, $P\leq 0.001$). In areas with shrubs, mean rabbits/km was highest for aerial surveys and lowest for spotlight surveys (Table 1). However, in areas without shrubs, mean rabbits/km was highest for spotlight surveys and lowest for aerial surveys. The proportions of track stations visited (Table 1) were similar between stations in areas with and without shrubs ($\chi^2_1=0.725$, $P=0.395$).

Among the survey techniques, aerial surveys were the most expensive (\$2,240) due to the cost of chartering a helicopter and pilot (Table 2). The total cost for two days of surveys for the other three techniques was comparable (\$654.40-\$689.20). Track station surveys were the most expensive technique per sampling unit while spotlight surveys were the least expensive (Table 2).

TABLE 1.—Results for four survey techniques used to index rabbit abundance in the Lokern Natural Area, California during April 2004.

	Survey techniques							
	Visual encounter		Spotlight		Aerial		Track station	
	(rabbits/km)		(rabbits/km)		(rabbits/km)		(visitation rate)	
	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range	Visited	Rate
Shrubs present	1.53±0.69	0-10	0.50±0.37	0-2.7	5.79±1.80	2.2-12.9	13	0.52
Shrubs absent	0.27±0.21	0-3	2.94±1.14	0-6.67	0.04±0.04	0-0.19	10	0.40
Sample units	15 1-km transects with shrubs = 15 km		6 transects (1.2-3.5 km) with shrubs = 11.7 km		6 transects (1.5-4.9 km) with shrubs = 22.8 km		25 stations with shrubs	
	15 1-km transects without shrubs = 15 km		6 transects (2.4-4.5 km) without shrubs = 17.9 km		5 transects (1.6-7.7 km) without shrubs = 16.0 km		25 stations without shrubs	

TABLE 2.—Comparison of costs for four survey techniques used to index rabbit abundance in the Lokern Natural Area, California during April 2004. The number of sampling units and costs are based on two 8-hour days by two biologists.

Survey parameter	Survey technique			
	Visual encounter	Spotlight	Aerial	Track station
Sampling units	40 1-km transects	100 km of routes	140 km of transects	24 track stations
Labor	32 h	32 h	32 h	32 h
Labor costs (\$20/h)	\$640	\$640	\$640	\$640
Driving distance ^a	36 km	100 km	0 km	23 km
Driving cost (\$0.40/km)	\$14.40	\$40.00	\$0	\$9.20
Other costs	\$0	\$0 ^b	Helicopter charter: 2 h x 2 d @\$400/h = \$1,600	Alfalfa pellets: \$10 Carrot oil lure: \$30
Total costs	\$654.40	\$680.00	\$2,240.00	\$689.20
Cost per sample unit	\$16.36/km	\$6.80/km	\$16.00/km	\$28.72/station

^a Only includes travel while conducting the work; does not include travel to and from the study site.

^b Assumes that all spotlighting equipment was already available and did not need to be purchased.

DISCUSSION

All of the survey techniques we employed were successful at detecting a sufficient number of rabbits to produce a useful index of abundance. Visual encounter, spotlight, and aerial surveys provided a count of individuals. In track station surveys, it usually was not possible to determine whether a single or multiple rabbits visited a station, and therefore the counts derived are a minimum number. Each technique has further advantages and disadvantages, which we summarize below. The importance of these depends upon study site attributes, project objectives, available funding, and staff and time constraints.

Data biases.—Habitat conditions may reduce the efficacy of some survey techniques and produce inherent biases in the data. In particular, shrubs can substantially reduce visibility. This was particularly evident for spotlight surveys, which was the only technique where indices were lower for areas with shrubs. Rabbits generally are more abundant in areas with shrubs, which provide cover from predators and thermal cover (Brown and Krausman 2003, Flinders and Chapman 2003), and this was reflected in the indices for the other techniques. However, visibility also likely was reduced in shrub areas during visual encounter and aerial surveys. In aerial surveys, the vantage point of observers above the shrubs and the tendency for rabbits to flush from cover due to the noise of the helicopter probably helped to largely overcome visibility issues. In shrub habitats in Utah, higher jackrabbit density estimates from surveys conducted on horseback compared to surveys on foot were attributed to the elevated position of the observer (Wywiałowski and Stoddart 1988). Rugged or undulating terrain also can cause a reduction in visibility. This was not a significant factor on our study site as the terrain was mostly flat except for occasional dry washes. Track stations were the one technique in which visibility was not a factor.

Related to visibility, visual encounter, spotlight, and aerial surveys allow for species identification in areas where multiple species occur and in situations where such data are relevant. Although we did not report species numbers, we were easily able to distinguish between black-tailed jackrabbits and desert cottontails during visual encounter and aerial surveys. Species identification was sometimes difficult during spotlight surveys when animals were on the edge of the range of illumination. For track stations, species identification is possible from tracks, mostly based on size differences, but requires good quality tracks.

Another inherent bias on our study site resulted from the diel timing for each technique. Black-tailed jackrabbits and desert cottontails are primarily nocturnal (Fitch 1947, Lechleitner 1958, Flinders and Hansen 1973, Costa et al. 1976). Consequently, visual encounter and aerial surveys primarily reflect diurnal habitat use when rabbits may largely be in resting cover. Spotlight surveys primarily reflect nocturnal habitat use when rabbits are usually foraging and more active. In heterogeneous landscapes such as the LNA, these techniques would produce biased habitat-specific indices because rabbits tended to be in shrub areas during the day and then were observed venturing out into areas without shrubs at night. Track stations avoid this bias as long as they are operated for 24 hours. If the objective is to produce a site-wide index of abundance and habitat-specific indices are not needed, then a diel-associated bias is avoided as long as habitat types are surveyed in proportion to their representation on the study site. This bias would not be a factor in more homogeneous landscapes.

One final bias is that false-negatives could occur in track station surveys because they require that rabbits come to a specific, relatively small location and leave evidence. Also, a visit to a station may not be recorded if track quality is poor or

tracks are misidentified. Additionally, high visitation by rabbits or other species, especially by rodents, can obliterate tracks and result in rabbit visits being missed.

Data analyses.—Data from some of the techniques lend themselves well to more in-depth analyses. For visual encounter, spotlight, and aerial transects, the effective width of the area being surveyed can be determined by measuring the distance from the transect to each rabbit observed (we did not do this in our study). This information can then be analyzed using distance techniques to calculate a density estimate (Smith and Nydegger 1985, Harris 1986, Wywiałowski and Stoddart 1988), which can then be extrapolated to the entire study site to produce a total population estimate. Determining belt width and calculating densities also standardizes the abundance estimates facilitating comparisons between habitats and study sites. Because of their higher vantage point, aerial surveys likely survey the widest belt. Density and population estimates cannot be derived from track station surveys because the effective area sampled is unknown. Also, as mentioned previously, it may not be possible to determine when multiple rabbits are visiting a station.

Effort and costs.—Track station surveys required the most time to complete. Two days are required to obtain data because stations are created one day and then checked the next. Other logistical challenges for track stations are that sudden changes in weather, such as rain or strong winds, can obfuscate tracks before data are collected. For all of the techniques except aerial surveys, decent road access throughout the study area is required to adequately sample rabbit abundance.

Per sampling unit, spotlight surveys were the least expensive technique and might be the favored option on projects with small budgets. Aerial surveys probably sampled the greatest area per unit time due to the distance covered.

Risks.—Regarding risks, visual encounter, spotlight, and track station surveys all involve operating vehicles to travel around the study site. On our study site, the roads were unpaved and unmaintained, and therefore travel speeds were low, as was the risk. Aerial surveys involve inherent risks associated with flying, but the risk was considered low due to a relative lack of obstacles and slow flying speeds and low altitude. Rattlesnakes (*Crotalus oreganus*) were observed during both visual encounter and track station surveys. Finally, valley fever (also known as coccidioidomycosis) can be a significant concern depending upon the study site location and whether soil from the study site is used as the tracking medium. Our study site was in an area where spores from the *Coccidioides* fungus are extremely prevalent in the soils and valley fever is considered to be “highly endemic” (Center for Disease Control and Prevention, <http://www.cdc.gov/fungal/diseases/coccidioidomycosis/causes.html>). This risk can be reduced through use of protective equipment (e.g., dust masks) or by using another tracking medium (e.g., diatomaceous earth, fire clay).

Other techniques.—Other common techniques used to index rabbit abundance include pellet counts and live-trapping (Murray 2003, Mitchell and Balogh 2007). Pellet counts can be conducted on plots or in belt transects. Counts involving plots might incur labor costs similar to track station surveys, particularly if the plots are visited initially to clear existing pellets. Counts involving belt transects might incur costs similar to our visual encounter surveys. Particularly in arid environments, challenges can include distinguishing between recently deposited versus old pellets if sampling units are not cleared first. Pellet persistence can vary among habitats and microsites (Iborra and Lumaret 1997). Also, pellet deposition rates likely vary with diet, and this could complicate comparisons between habitat types or seasons (Murray 2003). Finally, pellet counts may not be useful if counts of individuals or species identifi-

cation are important. Live-trapping entails setting traps and checking the next day. Obtaining a sufficient sample size to make valid temporal or spatial comparisons could require a number of days of trapping, depending on the number of traps deployed and capture rates. Initial costs for trapping and handling equipment could be high. Also, trapping methods could be restricted in areas such as our study site where listed species are present. Finally, handling animals requires a level of expertise, and live-trapping always involves some risk to the animals.

In summary, the choice of survey technique will depend upon project objectives, available funding, study site attributes (e.g., habitat types, road access), and time and staff constraints. In relatively sparsely vegetated arid habitats such as our study site, we recommend the use of aerial surveys (assuming the availability of sufficient funding) to index rabbit abundance because large quantities of data can be collected in just one day, and these suffer fewer of the biases that affect the other techniques. For more limited budgets, automated field cameras are being used increasingly to survey for a variety of species and may constitute an effective strategy for surveying for rabbits with the development of an appropriate methodology.

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Field method for estimating the weight of tule elk from chest circumference

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Key words: California, *Cervus canadensis nannodes*, field techniques, girth, Tule elk, weight

Wildlife biologists with the California Department of Fish and Wildlife (CDFW) routinely use remotely delivered chemical immobilization agents to capture tule elk (*Cervus canadensis nannodes*). Many of the common immobilization and reversal agents for elk have dosages based on body weight (Kreeger et al. 2002) - but how do you determine the weight of an animal before you have it in hand? Wildlife manuals generally only provide a broad weight range for tule elk, and until now, biologists have been forced to use their best guess based on these unrefined estimates to determine drug dosages. Delivering the correct dosage of agonist is imperative because under dosing may lead to the non-recovery of a darted animal or unsafe handling conditions, while overdosing may lead to unnecessarily long anesthesia times or the death of an animal. In addition, under dosing the antagonist may lead to partial reversal or the animal may succumb to the agonist again, which may lead to injuries, leave animals vulnerable to predators and weather, and death.

However, obtaining the weight of such a large animal in the field is problematic; the required tripod and scale are heavy, cumbersome, and not easily transported into remote capture sites. Therefore, the goal of our study was to provide field personnel with an easy way to estimate tule elk weights in order to quantify, learn, and hone their estimates prior to drug delivery without having to pack cumbersome equipment into the field. We achieved our goal by developing a method of estimating the weight of tule elk from their girth based on approaches first developed by Parker (1987) and Cook et al. (2003) for Rocky Mountain elk (*C. c. nelsoni*). Our method allows biologists to obtain tule elk weights using just a measuring tape and a conversion table so that over time, they are able to refine their weight estimates to more effectively and ethically use chemical immobilization agents to capture tule elk.

We collected morphometric measurements during the capture and handling of tule elk associated with two field projects in Merced County, California from 2013 through 2017. The first project was at San Luis National Wildlife Refuge (37°

6°N, -120° 28'W), and the second project was near San Luis Reservoir (37° 01'N, -121° 01'W). All elk ($n=52$) were captured using helicopter net gunning or chemical immobilization via free-range darting following capture and handling protocols set forth by the CDFW Wildlife Investigations Laboratory (Wildlife Investigations Lab, 2014) and the American Society of Mammologists guidelines (Sikes et al. 2011).

For the free-range darting captures, Pneu-Dart® compression rifles (Pneu-Dart Inc., Williamsport, PA) and 2 ml Pneu-Dart® barbed tri-port darts with 3.8 cm needles were used to immobilize animals not captured with the helicopter and net gun. Laser rangefinders were used to determine the distance to each elk and animals were darted at distances from 20 m - 80 m. Specific individuals were not pre-selected for capture; animals were targeted that presented a safe shot for chemical immobilization within the specified sex and age classes required for each project.

All elk included in the analysis are either adults or subadults (i.e., yearlings); calves were excluded due to the low sample size. The presence or absence of the third molar (M3; Peek 1982), as well as the overall size and body conformation of the animal determined age class. Animals weighing less than 90 kg that had no M3 tooth were classified as calves. Adult males (63%, $n=19$) that were captured in March were in the early stages of antler development and the remainder of adult males (37%, $n=11$) had fully developed antlers. Single cast antlers weighed on average 2.59 kg ($n=17$, $SE=0.18$) and thus added relatively little weight to the overall estimate. Most adult female elk (91%, $n=20$) were captured during March near the end of pregnancy (McCullough 1971); the remaining two females were captured during December and February. All captured elk were weighed using the same Brecknell Model CS2000 digital scale suspended from a 454 kg chain hoist affixed to a 2.4 m collapsible metal tripod (Figure 1). A steel-framed helicopter litter and standard ratchet straps were used to suspend the elk from the scale. The weight of the litter and straps were subtracted from the final weight, which was recorded to the nearest pound and converted to kilograms. The chest circumference of each elk was measured with a flexible vinyl measuring tape positioned around the animal at the apex of the chest just posterior to the front legs (Figure 2). Measurements were recorded to the nearest centimeter.

All data were analyzed using r-programming language (R Core Team 2015). First, data were input into the weight/girth power functions with both sexes combined to assess fit (Cook et al. 2003; Parker 1987). Models were then constructed from the data using *lm* function for linear models and the *nlm* function for the power functions in the Metrics Package (Hamner 2017). Model fit was evaluated using root mean square errors (*RMSE*) in the *pastecs* package (Grosjean and Ibanez 2014); the error is expressed in the same units as the response variable (kg).

A total of 52 tule elk was captured: 22 females, 15 adults and 7 subadults; and 30 males, 16 adults and 14 subadults. The mean weight of adult female tule elk was 150 kg (95% *CI* 15.6, range 70–201 kg, $n=22$) and the mean weight of adult male tule elk was 171 kg (95% *CI* 16.6, range 91–235 kg, $n=30$). The power model fit best for the adult male elk and the linear model fit best for the adult female elk (Table 1).

We were initially concerned that the potential variability in fetal calf sizes might unduly increase the observed variability in mean adult female weights resulting in poor model fit, but this was not the case. Because we found only minor differences in fit between power and linear models for adult females, we suggest using the power model for calculating weight estimates due to the likely allometric relationship between body weight and chest girth (McMahon 1975) (Figures 3 and 4). Our data did not fit the models built for Rocky Mountain elk as well as the models built specifically for tule elk, which would be expected due to the allometric differences between the sub-species (McCullough 1971).

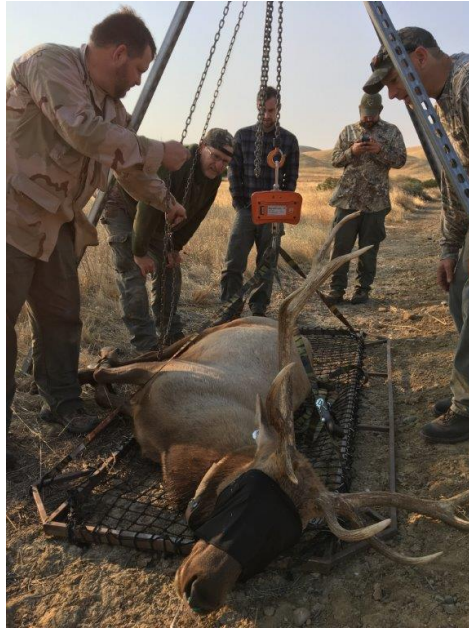


FIGURE 1. —Transportable apparatus for weighing tule elk including collapsible metal tripod, crane-scale, heavy-duty pulley, and metal-framed helicopter transport litter.



FIGURE 2. —Proper location of measuring tape to obtain chest circumference of laterally recumbent tule elk to estimate live weight.

TABLE 1. —Fit of linear and power models to predict live weight of adult tule elk from chest circumference.

Model	<i>n</i>	Equation	<i>RMSE</i>	<i>r</i> – <i>value</i>
Power – Adult Males	30	$y = 0.00001x^{3.321}$	11.7	0.96
Linear – Adult Males	30	$y = 3.74x - 349.35$	12.3	0.96
Power – Adults Combined	52	$y = 0.00003x^{3.171}$	12.9	0.95
Linear – Adult Females	22	$y = 3.37x - 298.41$	13.3	0.92
Power – Adult Females	22	$y = 0.00007x^{2.978}$	14.0	0.91
Linear – Adults Combined	52	$y = 3.60x - 330.53$	16.8	0.95
Parker 1987	8	$y = 0.00036x^{2.635}$	16.8	-
Cook et al. 2003	425	$y = 0.00046x^{2.618}$	22.5	-

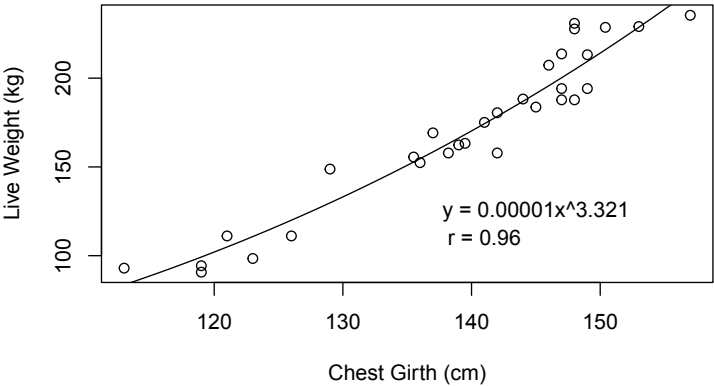


FIGURE 3. —Relationship between adult male tule elk chest girth and live weight (*n* = 30).

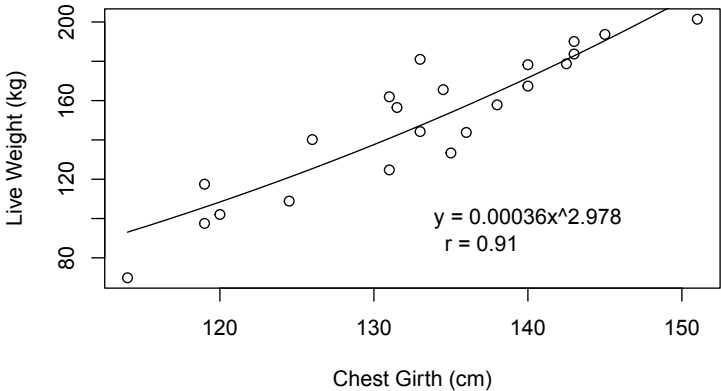


FIGURE 4. —Relationship between adult female tule elk chest girth and live weight (*n* = 22).

Our results provide a useful approach to estimate weights of tule elk in the field with only a measuring tape and a conversion chart (Table 2).

TABLE 2. —Live weight estimates from chest circumference for adult male and adult female tule elk.

Adult Male $y = 0.00001x^{3.321}$		Adult Female $y = 0.00007x^{2.978}$	
Chest Circumference (cm)	Weight (kg)	Chest Circumference (cm)	Weight (kg)
125	92	110	84
130	105	115	96
135	119	120	109
140	134	125	123
145	151	130	138
150	169	135	155
155	188	140	172
160	209	145	191
165	231	150	212

If greater accuracy is needed, the tripod and scale are required. Although these models were developed to aid in immobilizing animals, they are applicable in numerous scenarios where determining field weights of tule elk is desirable and transporting heavy equipment is not practical. It is recommended that CDFW biologists continue to collect both the scale weights and girth measurements of captured tule elk to hone the predictive models and further enhance the ethical chemical capture and handling techniques used in the field (Casady and Allen 2013).

ACKNOWLEDGMENTS

C. Langner and D. Casady contributed equally to the preparation of this paper. The California Department of Fish and Wildlife, the Federal Aid in Wildlife Restoration Grant W-86-R, and the Rocky Mountain Elk Foundation generously provided funding for this study. We would also like to thank the United States Fish and Wildlife Service, the California Department of Water Resources, and the California Department of Parks and Recreation for their support and granting us access to their properties. We would also like to thank S. Langner for the tripod design and construction, D. Fidler, N. Graveline, E. King, and T. Kroeker for their capture expertise, J. Garcia for photo editing, J. Hobbs, the former CDFW elk program coordinator, for all his help and support, and the anonymous reviewers who provided useful comments and greatly improved the manuscript.

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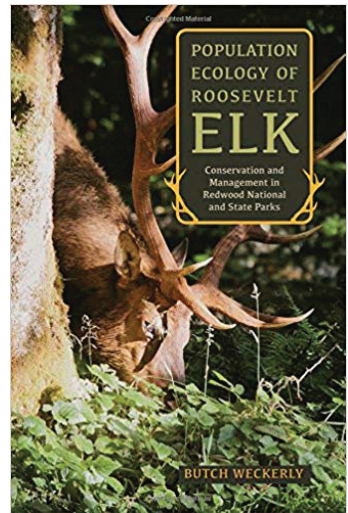
BOOK REVIEW

Population ecology of Roosevelt elk: conservation and management in Redwood National and State Parks

Butch Weckerly. 2017. University of Nevada Press, Reno, USA. 224 pages (hard cover). \$54.95. ISBN: 978-1-9438-5950-4

This book recaps Butch Weckerly's 20-year stream of contributions toward understanding the population ecology and behavior of Roosevelt elk (*Cervus elaphus roosevelti*) in and near Redwood State and National Parks in northwestern California, USA. The book calls heavily upon the current literature and Dr. Weckerly's personal experiences as he sorts through many of the ecological and behavioral questions he has addressed during his career. In a sense, this contribution resembles the efforts of Joel Berger in his book (*Wild horses of the Great Basin*), several of George Schaller's books (*The Serengeti lion*, *Stones of silence*, *Mountain monarchs*), Val Geist's work (*Mountain sheep: a study in behavior and evolution*), a recent work by Alan Rabinowitz (*An indomitable beast*), and James Estes' recently published account of his research career (*Serendipity: an ecologist's quest to understand nature*), wherein each of those authors incorporated many first-hand and personal experiences into the scientific material presented in those books.

Dr. Weckerly's book aims at understanding the population ecology and behavior of a specific population of Roosevelt elk, based on work that was often accomplished on a 'shoe-string' budget as characterized by the author. Its value lies in the fact that it provides in one treatise a summary and synthesis of decades of research on the ecology of those animals along California's northern coast. This book adds to similar efforts that have characterized elk populations from specific sites like that of Douglas Houston (*The Northern Yellowstone elk: ecology and management*), Mark Boyce (*The Jackson elk herd: intensive wildlife management in North America*), and Dale McCullough (*The tule elk, its history, behavior and ecology*). To date, most of the research published on Roosevelt elk in northwestern California has had its origin with students completing M.S. degrees at Humboldt State University. Several of those theses have resulted in important contributions to the literature but have been, out of necessity, the result of investigations that were of short duration. A very positive aspect of Weckerly's work is that it extends across a lengthy period, thereby allowing the author to have made observations and conducted investigations under a multitude of ecological or environmental conditions. During this extended period, Butch was able to document the independent dynamics of several subpopulations (herds) of female elk, follow and experience the extirpation of one of those subpopulations, establish the likelihood of a metapopulation of



elk within the parks, and arrive at some conclusions in the context of population persistence. Few authors have had the luxury of being able to put 20 continuous years of effort into a single species in a single study area, and Butch is to be commended for his persistence in doing so.

Population ecology of Roosevelt elk contains a very fine discussion of redundancy and resiliency that will be helpful to all concerned with populations of large mammals in this changing world. It will also serve as a fine example of what can be done with financial support that ranged from nearly nothing in the worst years to very little—even in the ‘good’ years—when an investigator puts his or her mind to it, and this work is a testament to perseverance. Although not written in layman’s language that is easily understood, members of the public that are interested in the ecology of large mammals, including naturalists, hunters, and individuals with a specific interest in Redwood State and National Parks, will find this work to be of value. I also see this work contributing substantially to the persistence and viability of Roosevelt elk in the Parks and surrounding area. Additionally, I suspect the work will be useful in college courses, and that it will be particularly valuable for use in graduate seminar groups or graduate courses centered on the population ecology and behavior of large mammals—and elk in particular.

I found the manuscript to be well organized, but transitions between chapters could be enhanced by a closing statement at the end of each chapter, and a well-worded statement at the beginning of the subsequent chapter that places the forthcoming information in the context of what had been summarized on the preceding page. Pure and simple, this book is about science. Weckerly is well-known for his attention to detail and for his quest for accuracy, and he has used an extensive list of sources and references that demonstrate his familiarity with the current literature, including references dated as recently as 2016.

This book is, in part, a synthesis of 20 years of publications on Roosevelt elk in the Parks, and relies heavily on the author’s long-term investment in time and on his prior contributions. Although not all the material presented is novel, the author has pulled prior results into the ‘context of conservation’ and, as such, it is extremely valuable. Although the text is technical, it provides a detailed summary of Weckerly’s extensive work on a large, charismatic herbivore inhabiting a relatively pristine area of California. Students of population ecology, natural history, and those with an interest in large herbivores in general will have an appreciation for the author’s efforts. I also suspect this work will provide the grist for graduate-level discussions at Humboldt State University for several years into the future.

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FROM THE ARCHIVES

Ecology of a cottontail rabbit (*Sylvilagus Auduboni*) population in Central California

By HENRY S. FITCH

UNITED STATES FISH AND WILDLIFE SERVICE

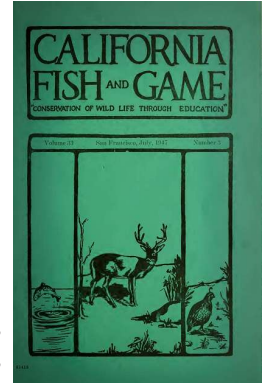
The cottontail rabbit of the western Sierra Nevada foothills (*Sylvilagus auduboni vallicola*) is sufficiently abundant in some areas to figure in the ecology and economy of the region in various ways—as a game animal as a reservoir of disease potentially transmissible to humans; and as a destroyer of vegetation, either cultivated crops or forage on range lands. During the course of wildlife studies at the San Joaquin Experimental Range, data were collected bearing on various phases of cottontail ecology. Especially during 1939, 1940, and 1941, many rabbits were live-trapped incidental to the trapping of ground squirrels, and information was obtained as to their numbers and activities, and various other factors, on an 80-acre area.

The experimental range is situated in, and typical of, a foothill belt used primarily for grazing of beef cattle. Interest in the rabbits in this region centers in their effect on range forage. The species is little hunted in this part of the State partly because other more popular small game species are abundant, partly because it is heavily infested with fleas, and partly because it is considered unsafe to handle since it is a carrier of tularemia. This region is mainly open woodland of oak (*Quereus douglasii* and *Quercus wislizenii*) and pine (*Pinus sabiniana*), occasional patches of chaparral and an annual type forage of broadleaf herbs and grasses; mostly it is rolling land, but there are occasional bluffs and ravines. The soil is generally shallow and rocky; outcrops and loose piles of decomposing granite rock are prominent features of the terrain. The brush patches and rock piles provide shelter for numerous wildlife species including the cottontail. The climate is one of mild winters and hot, rainless summers with temperatures over 100 degrees F. Annual precipitation averages approximately 22 inches.

This study was part of a program of wildlife investigation planned and initiated by Everett E. Horn of the U.S. Fish and Wildlife Service, in collaboration with the California Forest and Range Experiment Station, U.S. Forest Service. Lowell Adams, Freeman Swenson, Frank Hagarty and Bernard Mitchell helped with the live-trapping. Howard Twining, Daniel F. Tillotson and John E. Chattin analyzed scats and pellets in connection with the predation phase of the work. Assistance rendered by WPA Project No. 165-2-08-225 is acknowledged.

METHODS

The rabbit population was intensively studied on an 80-acre area by marking for future identification and releasing all that could be live trapped. At each capture, sex, weight, catalogue number or formula, and exact location of the animal were recorded in the field.



Those taken in 1939 and 1940 were marked with serially numbered aluminum ear tags and colored celluloid disks manufactured for use by commercial rabbit breeders; those trapped in 1941 were marked by toe clipping. Food habits data were obtained on this same area by following rabbits as closely as possible recording the kind and amount of vegetation taken.

SEASONAL BAIT ACCEPTANCE

During 1939, 1940 and 1941, trapping effort was fairly constant year-round; on the 80 acres where population studies were made, approximately 200 traps were kept set for several days each week. Differences in the catch of rabbits reflected both actual changes in their number and changing season acceptance of the grain baits used. Throughout the growing season October through May, while green food was abundantly available, rabbits only rarely entered the traps. It is assumed that natural foods were much preferred to the grain mixture of wheat and milo maize with which the traps were baited. In summer after the main forage crop had dried out, grain was taken freely, and nearly all recorded captures of rabbits were in the dry season—summer and early fall. The total number of captures recorded each month during the three-year period in which live trapping was in progress is shown in Fig. 48. Each year the catch was highest in August at the peak of the dry season. Trends

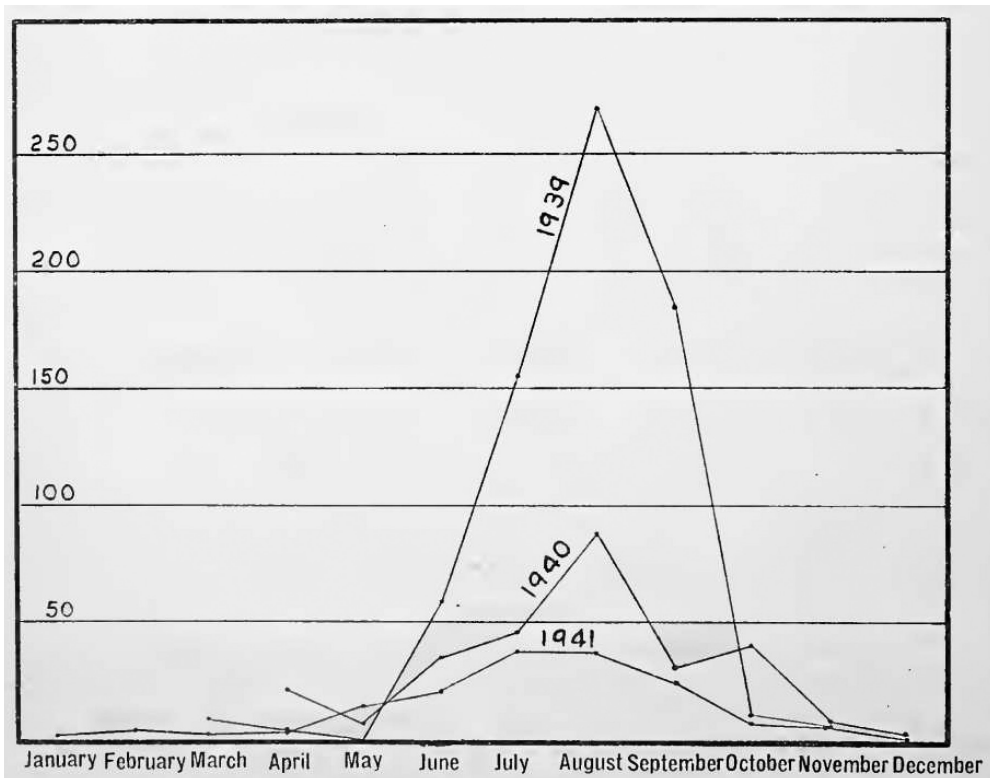


FIGURE 48.—Numbers of captures of cottontails from month to month on 80-acre trapping area in three different years. Trapping effort was fairly constant through the year and the fluctuating catch reflects seasonal variation in bait acceptance.

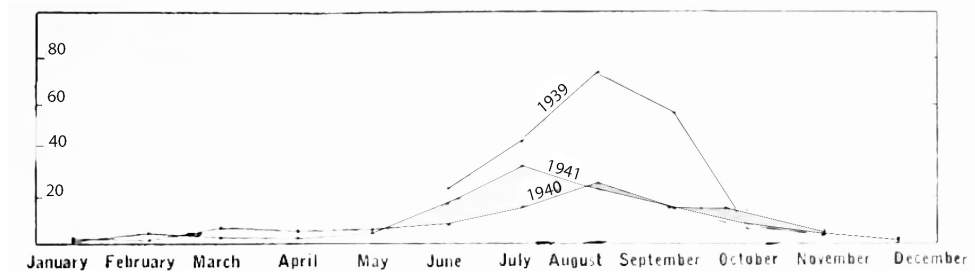


FIGURE 49.—Numbers of cottontails live-trapped on an 80-acre study area each month in 1939, 1940, and 1941. The month-to-month changes in total catch are influenced mainly by changing bait acceptance rather than by actual changes in numbers of rabbits.

were similar for all three years, but in 1939 bait was taken much more readily. During the dry season that year natural food was scarce due to the short forage crop and early drying. In 1941 the forage crop was heavier and succulence longer persisting than in 1940, and the catch of rabbits was correspondingly light. During the course of live trapping, the few rabbits caught in winter and spring were often individuals which had been trapped frequently during the preceding dry season, and had perhaps acquired a special liking for the bait used.

MOVEMENTS

During the three-year period, 228 rabbits were trapped a total of 1,159 times. The different locations of capture for an individual provided information concerning extent of foraging range, homeing propensities, and shifts in centers of activities.

Foraging Range.—Numerous captures of some individuals within a fairly short time revealed the extent of normal foraging activities or “cruising radius.” As the numbers of records on individual rabbits increased, the foraging ranges plotted from them usually tended toward an oval shape. In many instances diameters of foraging ranges may be indicated by the maximum distance recorded between points of captures. When records are few, the distance is apt to be unrepresentatively short. For the 134 individuals each trapped at different locations on the area, maximum distances between points of capture, “foraging diameters,” are presented in Table. 1.

TABLE 1.

	2 captures	3 to 5 captures	6 to 11 captures	11 to 21 captures	21 or more captures
Number of rabbits	27	36	39	27	5
Average of foraging diameters in feet	451	496	723	781	1,044
Extremes of foraging diameters in feet	30-1,450	50-1,200	250-2,100	250-1,700	820-1,300

If the sexes differ in extent of home range, the difference is slight. Females may move about somewhat less than males, but some of the largest home ranges, plotted for individuals having many repeat records, were those of females. The average "foraging diameter" for all females (72) captured at more than one point was 626 feet, as against 632 feet for the entire group of 124, including both sexes. If the distances between captures actually represent the extent of foraging areas, home ranges of, roughly, eight or nine acres for both sexes were indicated, but probably in most instances the areas were somewhat larger. Ingles (1941: 234) wrote of this same species studied at a locality 200 miles northwest: "The home range of a male rabbit may be as much as 15 acres since three were taken at stations 400 yards apart. The home range of a female rabbit is often less than an acre, which may be shared with as many as four other rabbits."

The difference may be due to the spotty distribution of food and of shelter—scattered clumps of blackberry thickets—where Ingles' study was made. His conclusions were based on comparatively few individuals on a small area. The open and uniform terrain on the Experimental Range would promote extensive movement.

Measured distances between points of capture are not entirely satisfactory for showing home ranges. The shorter distances represent individuals for which the records do not reveal the true extent of the areas covered while the longer distances in some instances may represent unusually long foraging trips, and in others possibly reflect shifts of headquarters over periods of time. The median of "foraging diameters" recorded, for all those with more than five captures, was 700 feet. This distance is probably roughly representative of the diameter within which most of the activities of an individual are confined.

Several opportunities arose to watch the extent of movements of unusually tame and easily recognizable individuals frequently encountered in the field. Two in particular were intensively observed and were often followed in attempts to record their feeding. One of these was an old female, the other was a young of the year slightly more than half-grown. Both were somewhat more limited in their observed movements than were other individuals whose ranges were revealed by trapping, but the observations were made principally around dusk. Though activity is pronounced at that time of day, it appears that the rabbits then tend to forage in proximity of cover, ranging more widely after dark. Individuals were often trapped at night in areas of open grassland where they were never seen to venture in the daylight, and droppings were also abundant in such places.

Small young have much smaller foraging areas than have adults. One was usually seen foraging within a few yards of some pile of rock or brush or similar shelter into which it might dash at any alarm. Young less than half-grown were trapped in small numbers; usually a larger size is reached by the time the dry season sets in rendering grain bait more attractive than natural foods. A few young did seem to acquire a taste for the bait early in the season, and these entered traps frequently, each always at about the same place near the edge of some covert. The rabbits moved a good deal more widely than the ground squirrels which were trapped on the same area.

Homing.—Ability to return within a short time to the home range with which it was familiar was demonstrated by each of three rabbits which made homing movements of 4,400 feet, 3,550 feet, and 3,150 feet respectively, after being trapped and removed from the experimental range headquarters where cottontails were often troublesome in taking bait set out to trap quail. Twenty others similarly trapped and removed to the rabbit study area slightly more than three-fourths mile away, all failed to make homing movements, apparently. Ten were never recaptured, and the remaining 10 were recaptured on the study area; several of

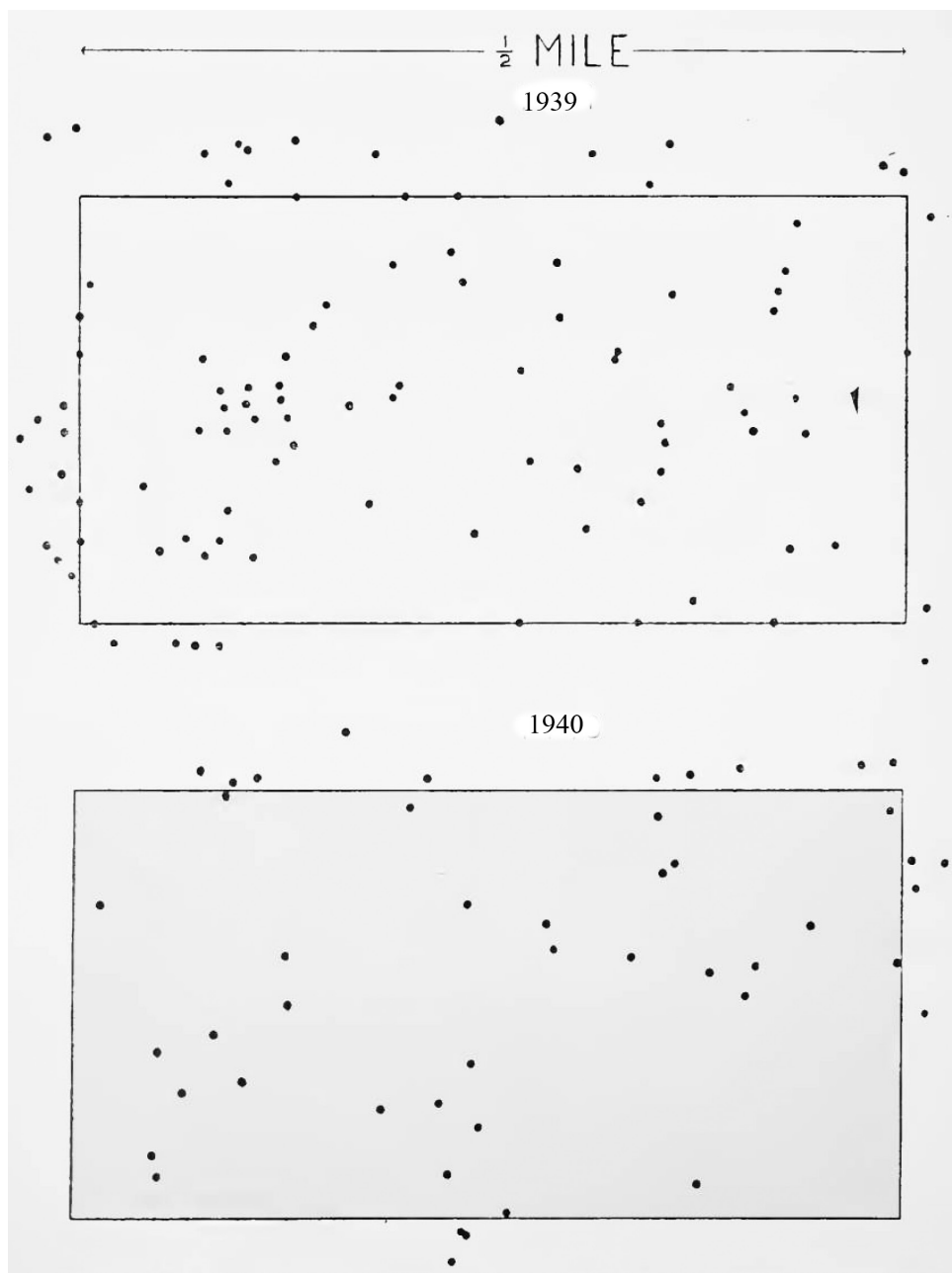


FIGURE 50.—Map showing distribution of individual cottontails live-trapped in 80-acre study area in summers of 1939, 1940. Each dot represents central point of an individual home range. Note relative abundance in 1939, and concentration near left margin of area where water was available.

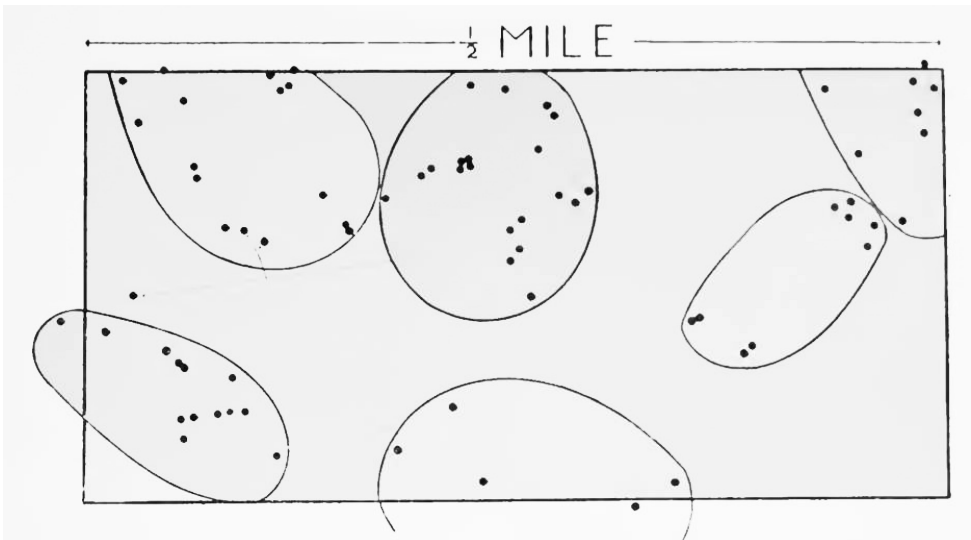


FIGURE 51.—Home ranges of sex different cottontails on 80-acre study area, as plotted for each from points of capture over periods of months. Three outlying points of capture from home range in upper center evidently resulted from trips to water supply outside usual range.

them were taken repeatedly over long period of months indicating that they had settled down in the new location near where they were released. Distances of movement from the point of release recorded for members of this group after recapture varied from zero to 2,200 feet.

Shifts of Range.—Only one clear-cut instance of shift in range, or migration was obtained. This involved a male trapped five times within a two-week period in August, 1940, when it was less than half-grown. All these records were within an area of 450 feet diameter. The remaining record for this animal was obtained on June 2, 1941, when it was killed near the headquarters area, having made a movement of 3,300 feet.

The study area was not well adapted for the recording of long movements since it was only a little wider than the maximum diameter of a foraging area, and but twice as long. Shifts of range in most cases would have taken the rabbits beyond its boundaries where they would not have been recorded except by accident.

However, such shifts may be an important factor in affecting the population turnover which is apparent from the trapping records. Many rabbits were caught frequently over periods of weeks and then disappeared abruptly from the records even during the dry season when bait acceptance was still good. Perhaps most of these were actually eliminated by predators and other causes of natural death, but some possibly transferred their activities elsewhere.

During the dry season of 1939, forage in general, and especially succulence and water, was unusually scarce. Near one end of the study area, seepage in the dry creek bed, and a nearby stock trough, furnished watering places much used by the rabbits. Trapping records that year indicated some clustering in this part of the area, while the 1940 records were more evenly distributed.

Further evidence of shift in foraging range to include critically needed food or succulence was obtained at the headquarters area. Here, two unfenced lawns were watered regularly through the summer. These lawns were within a cleared area adjacent to

roads, buildings and a small orchard, where rabbits were rarely seen during the green season. But in the dry season, especially in 1939, the lawns were exceedingly attractive to the cottontails. Shortly before dusk they would begin to congregate, and later in the evening a person driving up in a car would often see as many as 30 dashing from the lawns to seek cover. It seemed evident that most of the individuals involved had extended or actually transferred their foraging ranges to include areas of the lawns.

POPULATION

On the 80-acre area where live-trapping was carried on, information was obtained regarding the population density of cottontails. In computing the numbers actually present, use was made of the Lincoln Index—the ratio obtained in a given sampling period, of previously marked individuals recaptured to all those caught, including some not previously marked. The census formula used was as follows:

Total population of 80 acres

Number Caught January to July

=

Number caught August to December

Number caught January to July and
recaptured August to December

In choosing the two sampling periods necessary for the computation, most plausible figures were obtained by division into a January to July preliminary period during which part of the population was trapped and recorded, and an August to December post-census sampling to obtain the ratio of the previously marked individuals to the population as a whole. This division of periods was made to include, in each, a part of the July-August season of maximum bait acceptance. Other divisions in which one or both periods fell within a spring or fall season of poor bait acceptance and few captures produced obviously distorted census figures. The number trapped which were used in the census, were as follows:

Year	January to July	August to December	Both Periods
1939	49	78	25
1940	22	31	13
1941	49	35	18

From these figures, census computations were made as follows:

1939 census:	$x/49= 8/25$	$25x=3722$	$x=153$ cottontail
1940 census:	$x/22=31/13$	$13x= 682$	$x= 53$ cottontail
1941 census:	$x/49=35/18$	$18x=1766$	$x= 95$ cottontail

In each instance the figure obtained represents the number present in early summer—a population of adults, and subadults or well-grown young of the year. Aside from the pronounced year-to-year fluctuations suggested by the above figures, the population of course, goes through an annual cycle resulting from the seasonal limitation of breeding, but the pattern of this cycle cannot be shown with present data. The population presumably undergoes rather gradual reduction throughout the dry season, until it is again augmented by the annual

crop of young, perhaps several litters for each female during the course of the breeding season. Most of these small young are rapidly eliminated during the time they are helpless in the nest and for many weeks afterward while they are extremely vulnerable to predation.

The annual Lincoln Index census probably gives a fairly accurate approximation of the numbers present on the area. Checks were obtained by the use of one-month sampling periods. From these censuses the following figures were obtained for July and August for each of the three years.

	1939	1940	1941
July	153	39	760
August	152	36	38

These are considered less accurate than the figures from the six-month sampling periods, mainly because of the smaller numbers involved. The August 1941 figures are considered particularly unreliable since they were dependent upon the small and inadequate sampling in September of that year when bait acceptance was poor.

Even assuming that the actual census figures obtained are an accurate representation of the numbers on the area, they do not indicate correctly the population density, for many of the animals trapped on the area ranged outside it in varying degrees, some perhaps merely overlapping its boundaries in the course of their wanderings. By plotting the range of each individual rabbit, on the basis of distribution of its sites of capture, attempt was made to determine what percentage of its range lay outside the study area. Those having numerous records all well inside the boundaries were assumed to forage entirely within the area. Those whose records of capture clustered along one edge were assumed to range mainly outside, the estimated percentage depending on the pattern of the location records and the known extent of typical foraging ranges in other individuals. Those for which only a single record was available near an edge, were assumed to range almost entirely outside the area. In a few instances where only one or two location records were available, the estimate was merely a guess but usually the range was roughly evident. In several samplings by live-trapping of a peripheral strip, many of the marked rabbits were recaptured and the extent and direction of their activities outside the main study area were indicated. Attempt was made to estimate to the nearest 10 percent the portion of each range falling within the trapping area, but at best these estimates are merely approximations.

For 103 rabbits trapped on the area in 1939, the sum of percentages of ranges on the area totaled 6,575; dividing by 100, there were the equivalent of nearly 66 complete "rabbit ranges" within the 80-acres area. This indicates a population density of one cottontail to 1.2 acres. For the 47 trapped in 1940 percentages of ranges totaled 3,000, representing 30 "rabbit ranges" or a population density of one per 2.6 acres. Using the data in a different manner, it appears that of the 103 present in 1939, 55 had ranges centering inside the area, 35 centered outside, and 13 centered in the immediate vicinity of the boundary, or yielded such meager data that it could not be determined on which side they centered. In 1940 comparable handling of data indicated that 32 centered inside and 15 outside the area.

It is evident that, in the vicinity of the trapping area at least, the 1939 summer population had undergone sharp reduction by the summer of 1940, but with no apparent cause. In a preliminary paper on ecology of wildlife species of the San Joaquin Experimental Range (Horn and Fitch, 1942;115) it was stated concerning the cottontail population: "****during 1939 and early 1940 their numbers remained fairly stable except for seasonal fluctuations.

During the summer of 1940 the numbers dropped to less than half of the 1939 summer populations, most of this reduction occurring over a six-weeks' period." Further study of the data suggests another interpretation. No dead or diseased rabbits were seen during the time of the supposed reduction which was based mainly on impression. But it does appear that the reduction must have involved unusually heavy mortality of adults rather than mere variation in the success of the annual crop of young. Thus of the 103 rabbits caught on the area in 1939, only 9, or 8.7 percent were recaptured in 1940. But of the 47 total caught there in 1940, 18, or 38 percent were recaptured in the 1941 season. Survival expectancy of adults was more than four times as high in the summer of 1940—other things being equal. Possibly during the critically dry conditions of 1939, the animals moved about so much more extensively that this, rather than actual mortality, was an important cause of population turnover on the 80 acres.

In the early summer of 1940 an attempt was made to determine the population density of the rabbits over the range as a whole. Road counts were made, driving in a car at 10 miles per hour after dark in the early part of the night at times apparently favorable for rabbit activity. The roads followed passed through 12 different experimental pastures totaling 1,754 acres in area. For each road count made on these various pastures a comparable road count was made on the 80-acre study area where the population was evident through live trapped data. Thus the relative abundance could be judged from the numbers seen per unit of time on any area as compared with the trapping area.

On the 80-acre trapping area, in 739 minutes of driving, there were seen 41 rabbits, or an average of one in 19.8 minutes. In 1,023 minutes of driving on roads of the other pastures, 88 were recorded—an average of one in 11.7 minutes. Thus rabbits were apparently 1.7 times as abundant on the larger area. The population of the trapping area was computed at one to 2.6 acres, or .384 per acre. Thus the population density of the 1,754 acres would amount to $1.7 \times .384$, or .654 rabbits per acre. This is the only available computation of the cottontail population over the experimental range as a whole, but it represents a low point in both the year-to-year fluctuations and the annual cycle. Thus, at times it may amount to several per acre, especially in areas that are unusually favorable as cottontail habitat.

The 80-acre study area appeared to be one of the less favorable places on the Experimental Range more rugged terrain with abundant granite rock piles, patches of chaparral, and fallen live-oaks with their dense protective screen of twigs, provided optimum cottontail habitat.

FEEDING

The feeding of cottontails on the Experimental Range is determined by the changing seasonal availability of food plants. In this region the food consists almost entirely of annual grasses and broadleaf herbs. In late fall, winter, and early spring (the growing season) many species were suitable for food, providing succulence and high protein and mineral content. In the summer dry season feeding conditions were much less favorable; protein and mineral content of the forage crop in general had dwindled, crude fiber had increased, and only a few species retained succulence. This remaining succulence was concentrated in the larger swales, and creek beds, but in years that are more than ordinarily dry it may be largely lacking. Presence of water then becomes a critical factor.

Seasonal trends in the feeding habits are best illustrated by extracts from field notes concerning feeding behavior recorded on different dates.

In late March feeding rabbits were observed to take tips of grass blades, foxtail fescue (*Festuca megalura*) and soft chess (*Bromus mollis*), stems of popcorn flower (*Plagiobothrys nothofulvus*), and fruits of filaree (*Erodium botrys*). Throughout April the flowering heads of an abundant small composite, gold fields (*Baeria chrysostoma*) were an important food. Popcorn flower stems and soft chess heads and once a plant of everlasting (*Filago gallica*) were also observed eaten in April. A rabbit eating heads of soft chess was seen to reject those of red brome (*Bromus rubens*) after reaching up to sniff them.

In June dry heads of soft chess were an important food perhaps because of ready availability. One rabbit watched for 58 minutes took 244 heads of soft chess and nothing else. Slender-leaf rush (*Juncus oxymetris*), heads of foxtail fescue, plants of Spanish clover (*Lotus americanus*), stalks of tarweed (*Hemizonia vergata*), leaves and seed heads of Australian chess (*Bromus arenarius*), and head of clover (*Trifolium* sp.) were taken in quantity; oat (*Avena barbata*) and leaves and bark of button-willow (*Cephalanthus occidentalis*) were also seen eaten on one or more occasions.

In July several observations indicated that stalks and heads of soft chess continued to be the principal foods. Stalks and heads of fescue, lupine (*Lupinus formosus*), tarweed, turkey mullein leaves (*Eremocarpus setigerus*), dock (*Rumex* sp.) and, on one occasion, dry oak leaves were seen taken. The turkey mullein, dock, and tarweed were apparently used because of their succulence at this season when most other vegetation was dry.

In August tarweed was increasingly used. In one rabbit followed throughout a foraging period, tarweed was estimated to comprise 90 percent of the meal. In feeding on tarweed the animal usually cut the stalk and ate outward from its base, discarding the terminal parts. Soft chess heads and straws continued to be important foods. Several times rabbits were observed grazing on the surface mat of cast seeds of foxtail fescue. Rushes (*Eleocharis* and *Juncus*) already too closely cropped to be accessible to stock, continue to provide an important source of food and succulence to the rabbits. Spanish clover, turkey mullein, dock and thistle (*Cirsium* sp.) also were recorded as being eaten in August.

In September rabbit grazing on cast fescue seeds was recorded several times; also use of soft chess, toad rush, flowers of tarweed, and dry navaretia (*Navaretia* sp.)

The only October feeding record obtained was of a cottontail taking a dry turkey mullein plant.

The quantities of forage required to maintain a cottontail are not well known. In a summer feeding experiment, a 340-gram young fed for 25 days on dry wheat, with water available, ate on the average 14.5 grams daily—only 4.1 percent of its body weight. A 950-gram adult in 11 days of feeding ate an average of 23.7 grams daily—only 2.5 percent of its body weight. However, both rabbits lost some weight during the experiment, and this concentrated food is unrepresentative of their diet in the wild. Ingles (1941:239) records that two adults which he fed a mixture of green forage for a 15-hour period ate 209 grams and 171 grams, respectively. In estimating rabbit damage on the range, allowance must be made for the fact that plants cut and destroyed are often only partly eaten, that vegetation is adversely affected by trampling, on the runways and elsewhere, and that plants eaten back in the early stages of growth are stunted. The total damage therefore greatly exceeds the loss of vegetation actually consumed by the rabbits.

WEIGHTS

Weight was recorded at each capture, and was found to fluctuate widely. Adults usually weighted between 750 and 1,300 grams; those in good condition frequently weighed more than 1,000 grams. Day to day fluctuations of 40 grams or more were often recorded, apparently due mainly to differences in extent of feeding before capture. Individuals caught frequently over periods of weeks often tended to lose weight, possibly as a result of facial bruises sustained in their attempts to escape, which perhaps made eating difficult and painful. Seasonal trends in weights are somewhat obscured by this tendency to weight loss in consistent repeaters.

In late summer of 1939 there was a general downward trend in weights evidently resulting from the short forage crop with lack of early disappearance of swale succulence during the dry season. No such tendency at this time of year was apparent in 1940. Maximum weights were recorded in April and May, but few were caught at that season, as bait acceptance was poor.

For an adult female caught 21 times in nine different months over an 18-month period, average monthly weights were as follows: August, 1930—1,052 grams; September, 1939—1,012 grams; January, 1940—1,055 grams; April, 1940—1,225 grams; July, 1940—1,180 grams; August, 1940—1,110 grams; May, 1941—1,300 grams; August, 1941—1,055 grams; February, 1942—(dead in trap)—825 grams.

Unusually complete weight records were obtained for one female rabbit first trapped as a small juvenile soon after leaving its nest, and recaptured frequently during the ensuing 17 months, even during the winter season when bait acceptance was low. The weight records for this individual are shown in Figure 52.

REPRODUCTION

Breeding is ordinarily limited to the late fall, winter, and spring months—the growing season when green forage is abundant. In rabbits trapped during the dry season, the genitalia had retrogressed so that sex was not readily determined, and it was evident that breeding activity had ceased. The reproductive physiology may be controlled by the seasonal change in diet. As an exceptional instance, a one-third grown young was seen in November, 1946, in the headquarters area. It must have been born during the dry season, but the watered lawns and gardens around the headquarters buildings may have provided green feed necessary to stimulate reproduction at a season when it does not normally occur. Orr (1940:143) stated that “The breeding season of the Audubon cottontail in California extends from December to June.” On the experimental range observations suggest that it may begin and end somewhat earlier. Concerning the rate of reproduction, Orr (*loc. cit.*) stated: “Sufficient data are lacking to definitely state the number of litters born annually, but considering the length of the breeding season it is not improbable that in many instances this number may exceed two. The average number of young per litter based on records of 19 pregnant females, is 3.6 with extremes of two and six.”

On November 9, 1940, an adult female was seen gathering dry grass for nesting material and carrying it to a burrow beneath an oak bush. After pulling up each mouthful, she would deposit it in the freshly dug burrow. Many mouthfuls of grass were gathered, all within three or four feet of the bush. This was probably near the beginning of the breeding season and the nest evidently was being prepared for a litter of young.

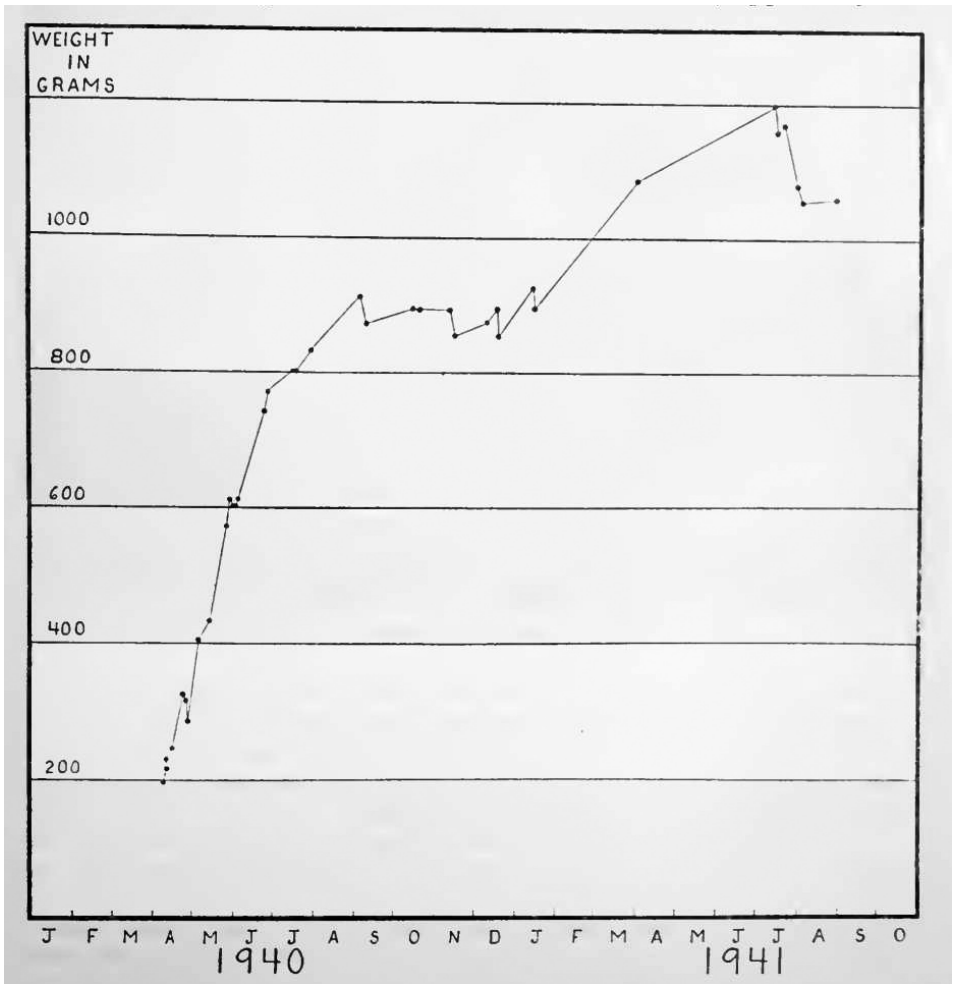


FIGURE 52.—Weights of a female cottontail on dates of capture beginning soon after leaving nest, showing rapid gain for first three months with more gradual and less regular subsequent growth.

On January 18, 1939, a nest was found on the surface of the ground in a rounded depression, well concealed by a dense covering of high grass. This was in a swale of an ungrazed area. The one young in the nest weighed 60 grams.

On the following day a destroyed nest was found where it had been dug out, in an exposed situation in sandy soil near a creek bed. The nest chamber was three inches below the soil surface, and the cavity was about eight inches long by five inches deep with a bed of dry digger pine needles, a softer interior of dry fescue and rush, and lining of rabbit fur. A fresh ground squirrel digging and feces were found about a foot from the nest suggesting the possibility that one of these rodents had robbed it.

On January 25, 1939, a nest with two small young rabbits was discovered. The nest cavity was just beneath the ground surface, and was lined with rabbit fur but had no plant material. The entrance and the cavity itself were so small that it would seem impossible for an adult cottontail to enter. The young still had their eyes closed, and had a sparse covering of hair.

On January 28, 1941, at about 10 a.m., another adult was seen making its nest. It was under a live-oak and was moving in a brisk, jerky fashion examining the ground litter minutely, and from time to time picking up dry oak leaves in its mouth. Having obtained a small mouthful of leaves, with a few straws and other debris mixed in, it entered a freshly dug hole with a mound of still moist earth in a more exposed situation on the other side of the tree. After a few seconds it backed out having deposited its load, and resumed the search. In a period of about five minutes it made 15 trips into the hole with nesting material—mostly dry oak leaves and some dry grass (probably soft chess). At 4:30 p.m. the site was located with difficulty and it was observed that the hole was plugged with loose earth and the burrow mound leveled and completely covered with a layer of dry oak leaves. Four weeks later this hole was dug out. The entrance was covered with dry oak leaves. The litter of young presumably had been destroyed early by heavy rains. The nest cavity about a foot from the entrance, contained evidence of dead young rabbits.

Ordinarily the nests are so well concealed that they are rarely found while in use, but remains of those dug out and destroyed by predators were found frequently during the winter and spring months. Usually it was not possible to identify the predator involved. Only a few of those seen destroyed were recorded. On March 21, 1939, three such destroyed nests were recorded, and in the first week of May, 1938, several were noticed.

On April 10, 1939, a small young cottontail was seen in tall grass a few inches from the entrance of its nest burrow, into which it ran when disturbed. The burrow was dug out and was found to have a tunnel about eight inches long leading to a nest chamber five inches beneath the ground surface, which seemed barely large enough to contain an adult rabbit. It was lined with grass and a small amount of fur. Only the one young was found in it.

The nest recorded latest in the season was one discovered on May 24, 1938, when attention was attracted to it by a rattlesnake which was swallowing a very young rabbit and had three others already inside it. An adult cottontail was about 15 feet distant, and remained in the vicinity, allowing close approach. The nest was not dug out at the time of discovery but was investigated later in the day. At this time a second rattlesnake was found partly inside the nest, and it had eaten three more young cottontails evidently of the same litter. The entrance to the burrow was barely large enough to admit the snake's body, but it was partly plugged with loose dirt. The entrance led into a rounded chamber about 7 x 4 x 4 inches, with a nest of dry grass (soft chess and foxtail fescue) lined with rabbit fur.

From the foregoing accounts it is obvious that the habits of the cottontail in this locality are variable, as regards site selected for birth of litter, type of breeding burrow or lack of it, and composition of nest. Ingles (1941 :24) has shown that the female cottontail may not even enter the breeding burrow but returns to it infrequently to allow the young to suckle as she stands over the entrance. In some of the nest burrows discovered this arrangement seemed unlikely because the nest chamber was several inches from the entrance. But other nests were so small that it was difficult to see how the adult could have squeezed inside. It is probable that squirrel burrows are sometimes used as breeding places by the cottontail. Extensive squirrel burrow systems may have as many as 100 open holes, many of which are not connected underground, and only a few of the entrances are regularly used by the squirrels in going to and from their nests. One winter morning freshly dug mounds of earth heavily tracked by cottontail were often found beside such burrows, showing that the rabbits had enlarged underground portions during the night.

Several times remains of cottontail too young to have left the nest were found partly eaten on ground squirrel burrow mounds, presumably victims of the squirrels. On one oc-

casion a squirrel was seen carrying a live young cottontail in its mouth. Once a cottontail was seen chasing a squirrel around the edge of a bush, possibly in defense of its nest.

NATURAL ENEMIES

Several kinds of mammalian predators, at least four species of raptorial birds, and two of the larger species of snakes, all numerous on the experimental range and elsewhere in the general region, prey regularly upon cottontail. Many records of predation were gathered, and an attempt was made to compute the population density of each species which might be important as a rabbit predator. These data are not sufficiently complete to afford a clear picture of the role of predation in limiting the cottontail population, especially since the reproductive potential of the rabbits in this region is not well known. Some predator species take only the small young before these have left the nest. Other kinds take heavy toll from the adult populations, but it is evident that the inexperienced young are especially susceptible to predation by many natural enemies. The combined toll of the several predators comprises an impressive total, which must be a major factor if not the decisive one in limiting cottontail distribution and abundance.

Coyote.—Control of coyotes by trapping was begun on the experimental range in the winter of 1935-36. The recorded numbers eliminated each year from the 4,600-acre area were as follow: 1935-36, 35; 1936-37, no record; 1937-38, "about 30"; 1938-39, "about 30"; 1939-40, 13; 1940-41, 13; 1942, 7; 1943, 5; 1944, 8; 1945, 1. Each year an unknown number was also eliminated from adjoining ranches. It is evident that in recent years the population has been held far below its former level. In 1939 and 1940, at the time the rabbit population was studied the coyote population averaged perhaps one to 300 acres between the breeding season and the time of control operations the following winter.

In a year-round collection of 1,173 coyote seats, mostly from regular defecating places on roads and trails of the experimental range, in 1939 and 1940, 1,924 vertebrate prey items were identified. These made up most of the food, though supplemented by a few occurrences of grasses, berries, insects and some carrion. Of the 1924 items, "rabbit" (presumably cottontail but possibly pertaining to the relatively rare jack rabbit in a few instances) made up 19.6 percent (21.1 percent in 1939, 17.0 percent in 1940). A truer interpretation of the relative importance of rabbit in the coyotes' diet here may be gained by computing its percentage weight of the total. The total live-weight of recorded items was estimated by obtaining the average weight for each species, multiplying this by the number of its occurrences, then adding up these totals. Cottontail, with an average of 800 grams, was the heaviest kind of prey recorded taken by coyotes in this locality. The weight used as standard for the cottontail, and those for other prey species represent in each case that of a small adult. Many or perhaps most of the prey animals taken by coyotes may have been immature. The ratio of juveniles in various states to adult animals was perhaps roughly similar for each, but the usual adult weight affords the best standard of comparison.

Another variable is introduced by the inexact correspondence between number of scat occurrences and number of individual prey items eaten. But for squirrel- and rabbit-sized prey animals fairly close correspondence might be expected (Murie, 1946 : 275). For mouse-sized rodents, and more minute items less accurate figures on the number eaten could be obtained, but this inaccuracy would not affect the proportions of the larger and more important items to any great extent. In general, the assumption of one prey animal of the average weight of the species for each scat occurrence, is thought

to afford a rough approximation of the percentage by weight of the coyote's diet. The same assumption has been made for the other carnivores and raptors discussed below. In Table 2 prey weights by percentage were obtained from computations on this basis.

TABLE 2.—Composition of Coyote Food (Based on 1,173 scats)

Species	Prey		Occurrence in coyote food	
	Average weight in grams	Number of occurrences	Computed percentage by weight of total recorded prey	
Cottontail	800	377	45.4	
Ground squirrel	500	414	31.2	
Gopher snake	500	79	6.0	
Woodrat	200	162	4.9	
Pocket gopher	100	234	3.5	
Kangaroo rat	60	361	3.3	
Other (29 kinds)	variable	297	5.7	
Totals		1,924	100.0	

It is indicated that by weight cottontail made up a greater percentage of the diet than did any other kind of prey, and amounted to nearly half of the total.

Gray Fox.—At the time of the study, gray fox were probably somewhat more abundant than coyotes on the area, judging from trappings' estimates and the greater frequency with which they were seen. However, no basis for estimating their actual numbers is available. In June, 1938, a den was located with seven half-grown pups. Scattered remnants of prey in the vicinity included parts of several cottontail.

A small collection of 887 fox scats made on the experimental range contained 102 vertebrate prey items, besides a few insects, berries, and other plant material, and one occurrence of carrion. The scats were collected at different times of year but mainly represented the fall months.

The number of occurrences and computed percentages of the total prey weight for the principal prey species of the gray fox are presented in Table 3.

TABLE 3.—Composition of Gray Fox Food (Based on 87 scats)

Species	Prey		Occurrence in gray fox food	
	Average weight in grams	Number of occurrences	Computed percentage by weight of total recorded prey	
Cottontail	800	11	35.7	
Ground squirrel	500	12	24.4	
Woodrat	200	17	13.8	
Bird (4 kinds)	variable	10	10.2	
Pocket gopher	100	14	5.7	
Kangaroo rat	60	17	4.1	
Other	variable	21	6.1	
Totals		102	100.0	

Though this sample is too small to be relied upon, its trend seems to indicate that rabbit was the most important single prey species of the fox, and made up more than a third of the total.

Badger.—Digging of badgers was frequently seen on the study area, but no basis for estimating the population of badgers was discovered. It is unlikely that these predators are able to catch adult cottontail except under unusual circumstances, but they may be responsible for much of the predation on small young in the nest. On many occasions cottontail nests dug out and destroyed by mammalian predators were found. Though the predator involved was never definitely identified, it is probable that badgers figured in at least some instances.

A badger kept in captivity throughout one summer consumed daily one small adult cottontail or its equivalent.

Bobcat.—Judging from the occurrence of their tracks, bobcats are fairly common in the more brushy and rocky parts of the Experimental Range, but nothing was learned concerning their actual numbers, or the food taken by them. As they are known to prey extensively upon rabbits elsewhere, (Grinnell, Dixon, and Linsdate, 1937: 615, 618, 620) it is probable that they take large numbers of cottontail locally.

Red-tailed Hawk.—This large raptor was determined to occur in a permanent population of about one to 160 acres, with an additional unstable population of fledged young and migratory adults, (Fitch, Swenson and Tillotson, 1946). Many instances of predation on cottontail were recorded. On one occasion the head of an ear-tagged adult male rabbit from the study area was found beneath the perch of a hawk about a quarter mile from where the rabbit had been trapped. On January 30, 1941, a hawk was seen to catch an adult cottontail by a sudden steep swoop from its perch on a 15-foot oak snag. The rabbit must have emerged from brush at the foot of the tree to cross an open space, completely unaware of the danger. It took the hawk about two minutes to kill the rabbit.

Among 625 prey items of the hawks recorded as brought to the young in the nests, cottontail were third in abundance with 62 records (all of young ones), and on the basis of weight were computed to comprise 26.5 percent of the total. Among 4,036 prey occurrences from 2,094 red-tailed hawk pellets, the more important kinds both in numbers and percentages of total weight are presented in Table 4.

Table 4.—Composition of Red-tailed Hawk Food (Based on 2,094 pellets)

Species	Prey	Occurrence in red-tailed hawk food	
	Average weight in grams	Number of occurrences	Computed percentage by weight of total recorded prey
Ground squirrel	500	1,049	49.5
Cottontail	800	322	24.2
Gopher snake	500	190	8.9
Pocket gopher	10	794	7.4
Rattlesnake	300	70	2.1
Other	variable	1,611	7.9
Totals		4,036	100.0

Cottontail was third in abundance among all prey taken by the hawks, and comprised about one-fourth of the total prey weight taken.

Cooper Hawk.—A few pair of these hawks nest on the experimental range, and in winter the population is considerably increased by migrants, but no definite figures on their numbers were obtained. In 1939, two nests were observed, and a total of 41 prey items were recorded, two of which were young cottontail (Fitch, Glading, and House, 1946 :153). The other prey items were all of smaller kinds, mainly birds and lizards, and the cottontail were estimated to comprise approximately 16 percent by weight of the recorded food.

In one instance an adult cottontail found freshly killed and partly eaten under the edge of a bush was thought to have been the victim of a Cooper hawk. These hawks are considered of secondary importance as cottontail predators because of their relatively low numbers, small size and preference for other kinds of prey.

Horned Owl.—These large and common owls feed much more extensively on rabbits than on any other kind of food. Seven times, in the fall of 1938, spring and fall of 1939, and 1940, and late winter of 1941 and 1947, counts were made of horned owls heard at different points on a 1,920-acre section of the range. These counts representing the minimum number of owls present, varied from 5 to 25. Roughly, a population of one owl to a hundred acres is indicated. A sample of 654 pellets representing approximately 1,471 individual prey items was analyzed in 1939, 1940 and 1946. For the principal prey species, number of occurrences and computed percentages of total weights were as presented in Table 5.

TABLE 5.—Composition of Horned Owl Food (Based on 654 pellets)

Prey Species	Average weight in grams	Occurrence in horned owl food	
		Number of occurrences	Computed percentage by weight of total recorded prey
Cottontail	800	205	61.1
Woodrat	200	240	17.9
Kangaroo rat	60	201	4.5
Pocket gopher	100	115	4.3
Ground squirrel	500	13	2.4
Reptile (at least 8 kinds)	variable	44	5.0
Bird (at least 12 kinds)	variable	45	2.3
Other (including many insects)	variable	608	2.5
Totals		1,471	100.0

It is indicated that cottontail made up more than half the food by weight, though taken in slightly smaller numbers than woodrats.

Barn owl.—These are much less common than horned owls on the Range, and were seen at only a few places. In a collection of 240 pellets there were 517 prey items of which 415 were pocket gopher and pocket mouse. Only four were cottontail (all young) which were computed to make up around 3 percent of the total prey weight represented by the sample.

Rattlesnake.—This reptile is probably the most common of all rodent and rabbit predators on the Range. Over a three-year period 679 were marked and released, and

the ratio of these recaptured to others seemed to indicate a population of two or three per acre, but accurate census is impracticable as the figures might be distorted by many unknown variables. Of the rattlesnakes recorded, nearly half were adults. A total of 271 prey items were identified from stomachs and droppings of the snakes. For the principal prey species, number of occurrences and computed percentages of total weights see Table 6.

TABLE 6.—Composition of Rattlesnake Food (Based on 271 food items)

Kind of prey	Average weight in grams	Number of occurrences	Percentage of total prey weight
Ground squirrel	206	111	70.5
Cottontail	206	24	15.2
Kangaroo rat	60	32	5.9
Gopher	67	2	2.5
Other	variable	92	5.9
Totals		271	100.0

Though this food sample is small, as compared with those obtained for carnivores and raptors, prey weights were determined with a precision not practicable for the predatory mammals and birds. Food items were palpated from snake stomachs, and were actually weighed, except those in which digestion had reached an advanced stage.

From these figures it appears that cottontail make up nearly one-sixth of the snakes' food. As a result of the winter and early spring breeding season most of the young were already too large for the snakes to eat when the latter emerged from hibernation. The peak of rattlesnake activity occurs during April, May and early June and all the records of rabbits occurred during that time, involved late litters of young rabbits in the nest and large adult snakes in every instance. Squirrels and kangaroo rats were often found dead, showing evidence of rattlesnake bite, but some of the snakes involved were known to have been too small to eat the animals they had killed. Some rabbit mortality may occur also. On June 28th, an adult rattlesnake was seen to strike a cottontail in the field. Rabbits are probably less liable to be killed in this way than are burrowing rodents which often encounter the snakes underground.

Gopher Snake.—This species is much less common than the rattlesnake locally—perhaps only one-fourth as numerous. A total of 70 food items were palpated from gopher snake stomachs; and an analysis of these is presented in Table 7.

Table 7.—Composition of Gopher Snake Food (Based on 70 food items)

Kind of prey	Average weight in grams	Number of occurrences	Percentage of total prey weight
Cottontail	400	3	37.1
Ground squirrel	180	5	27.9
Woodrat	200	3	18.6
Bird egg	8.5	20	5.3
Gopher	130	2	4.0
Other	variable	37	7.1
Totals		70	100.0

The high percentage of cottontail in this small sample may be unrepresentative. One giant gopher snake, nearly seven feet long, had eaten an adult cottontail which weighed as much as most of the smaller food items combined. Such incidents as this must be rare, and comparatively few gopher snakes are big enough to swallow any but nesting cottontail.

Discussion.—The data set forth above suggest that the cottontail bears the brunt of predation pressure from most of the larger species of mammal, bird, and snake predators. The breeding season is long, and adult females may soon replace lost litters, or may normally rear two or more litters in a year, thus offsetting the heavy losses to natural enemies.

The summer population of adults and well-grown young after the breeding season amounting in 1939 to one per 1.2 acres, represents a rabbit-weight of about 670 grams per acre, a figure to be born in mind in connection with measured predation factors.

Computation of the rabbit-weight per acre eliminated by predation has been attempted on the basis of the known or estimated population of each predator species, the normal daily food requirement, and the percentage of the food weight which rabbits comprise. The population of coyotes was computed at one to more than 300 acres; the fox population at possibly the same figure (or probably somewhat more), the red-tailed hawk at one to 160 acres; horned owl at one to 100 acres; rattlesnake 2.5 per acre; gopher snake, 6 per acre. Reducing these figures to population density per acre and multiplying by the food requirement, and the percentage comprised by rabbit, we obtain the data presented in Table 8.

TABLE 8.—Cottontail Weights Consumed by Predators

Kind of predator	Population per acre	Food requirement per day in grams	Food weight per acre per day	Food per acre per year	Percentage of prey weight of cottontail	Weight of cottontail per acre eliminated annually by predators
Coyote	.0033 x	600 =	1.98 x 365 =	722 x	45.4 =	328.0
Rattlesnake	2.5 x	2 =	5.00 x 365 =	1825 x	15.2 =	277.4
Horned owl	.010 x	120 =	1.20 x 365 =	437 x	61.1 =	267.0
Gopher snake	.6 x	2 =	1.2 x 365 =	438 x	37.1 =	162.5
Fox	.0033 x	300 =	.99 x 365 =	361 x	35.6 =	129.0
Red-tailed hawk	.0062 x	120 =	.74 x 365 =	270 x	24.2 =	65.0
Total						1228.9 grams

This summation does not include the rabbits eliminated by bobcats and badgers, but both are among the more important cottontail predators.

Thus it appears that predation annually might eliminate a rabbit-weight of about double the nonbreeding population of adults and well grown young present in summer. Admittedly, at each stage of the computation a substantial margin of error is probable so that the figures obtained cannot be considered more than a rough indication of the magnitude of losses to each kind of predator. If, in the food composition of a predator, the proportion of young were higher among cottontail than among other kinds of prey, the percentage of cottontail computed would be too high. However, it is probably that the proportion of young among

the ground squirrel, woodrat, and gopher snake, in prey samples was fully as large as among cottontail. Each of these species has, like the cottontail, a high reproductive potential and a rapid population turnover with even greater differentials between young and adult weights and they were the only ones other than cottontail comprising substantial percentages of the diet in any of the predators. The populations of predator species are variable according to time and place, and all of them are computed on a somewhat doubtful basis for application to the experimental range as a whole; for the red-tailed hawk and horned owl, however, the figures used represent the absolute minimum. For rattlesnakes, gopher snakes, coyotes, and especially foxes, the population figures are less definite. The average daily individual food consumption under natural conditions is somewhat speculative. This is especially so in the case of the snakes, and the figure used is based on the average individual weight, assuming that each snake consumes twice its body weight during the growing season as suggested by data obtained from several kept in confinement. For the rattlesnake most feeding records were obtained in April and May when small cottontail are available—but from June through October rabbits are not breeding and their young have grown too large to be swallowed. Few feeding records were obtained for snakes during this latter two-thirds of their active season, as they are then secretive or nocturnal. But it may be surmised that kangaroo rats and gophers are then substituted for the young rabbits and squirrels taken in spring.

For the horned owl there is a probability that the numbers of cottontail assumed to have been eaten was too high, for, unlike the other prey species, the cottontail is large enough to furnish several owl meals. Thus one might be counted several times from its limb bones and vertebrae appearing in several pellets, whereas the other prey species were generally identified from skulls revealing accurately the actual numbers eaten.

The predation calculated is not necessarily too high; it seems entirely possible that the rabbits are adopted to withstand such pressure by virtue of high reproductive potential. Ingles (1941 :243-6) records an instance of a female marked soon after birth, which had matured and produced a litter of its own at the age of six months. Many of the young born early in the breeding season in fall, may mature in time to produce litters before the breeding season is ended by the drought conditions of the summer. Females that are mature in the fall at the beginning of the breeding season might be expected to produce nine young apiece during the seven or eight months of green growth if the average of 3.6 young per litter and two or three litters annually mentioned by Orr (*loc. cit.*) is representative. Females which lose their litters early might produce an even greater number. The young at birth probably weigh around 30 grams, and upon leaving the nest from 11 to 14 days later, they have increased to several times this weight. Growth during subsequent weeks is extremely rapid (Fig. 52).

In recent years ecologists have tended to minimize the importance of predation factors in controlling vertebrate populations. Errington (1946) has summed up the literature of predation, and presents a fairly convincing case to show that “intraspecific self-limiting mechanisms basically determine the population levels maintained by the prey. ***the patterns revealed may look remarkably little influenced by variations in kinds and numbers of predators.”

Concerning rabbits, Errington (*op. cit.* 154-155) states that though more tolerant of crowding without intraspecific strife, “they are by no means free from automatic mechanisms [determining their upper and lower population limits in a given habitat.] ***again and again lagomorphs recovering from depressed levels show rapid population gains from one year to the next, the attentions of wild flesh eaters notwithstanding.”

The matter is not merely one of lagomorphs being prolific or of making their gains when enemies are either numerically or proportionally scarce, as there are too many instances of lagomorphs populations apparently conforming to patterns, even despite pronounced differences in numbers of such able hunters as horned owls and foxes."

On the San Joaquin Range there is no direct evidence that predation actually holds the cottontail population to any given level. The situation is complex, however, because several common predators take large numbers of cottontail without being entirely dependent on them; all could probably adjust themselves to absence of cottontail by taking larger numbers of the abundant ground squirrels, woodrats, and other rodents. The predators also prey to some extent upon each other, at least hawks, owls, coyotes and foxes all prey upon both rattlesnake and gopher snake. Individual predators are long-lived as compared with their rabbit or rodent prey, and survive fluctuations in the populations of the latter. Even on areas of a few acres, the cottontail, or rodents, are not uniformly abundant but are concentrated where conditions of food and cover favor them; they are sensitive to changing weather conditions which result in expansion or contraction of their preferred ecologic niches, and their numbers change in response. Each species is, however, favored by a different set of conditions, so that increase in one kind is apt to be accompanied by a more or less compensatory decrease in another. The kangaroo rat, for instance, is favored by arid conditions with sparse vegetation and its peak in numbers on the Experimental Range followed a series of dry years. The ground squirrel is also favored by a sparse forage crop, whereas the cottontail prefers a habitat with thickets providing surface cover. Response to such conditions can be seen in the varying abundance of rabbits and rodents on different parts of the Range; on the ungrazed headquarters area, having chaparral thickets and rank growth of swale vegetation, cottontails are more numerous than elsewhere, squirrels and kangaroo rats less so.

While changes in abundance of both cottontails and predators are known to have occurred since 1935, records are too fragmentary to show either clear cut correlation or lack of it. Coyotes were first controlled in the winter of 1935-36, and 35 were trapped during a few weeks period. Nearly as many were caught in each of several succeeding years, but by 1939 the population was much reduced. In August, 1936, at the time they were still numerous, Kenneth A. Wagnon recorded in his field notes that cottontail were extremely abundant around the Experimental Range headquarters, where as many as 50 congregated on the lawns in the evening, and he speculated that this high rabbit population might be the attraction for the coyotes. The reduction of coyotes to a fraction of their former numbers did not result in any noticeable increase in rabbits. The hawk and owl populations have been stable, but rattlesnakes over the Experimental Range as a whole, have doubtless been somewhat reduced by the continual drain on their population imposed by human activity.

Intraspecific, self-limiting mechanisms in the cottontail population of the Experimental Range were not evident, either. It is doubtful whether any mortality results from intraspecific strife—no fighting or other evidence of intolerance was observed even when many rabbits were concentrated on a small area. Their food supply is subject to even heavier use by other herbivores, particularly domestic stock, so that the amount remaining at the end of the dry season is not determined primarily by the number of cottontail. Conditions of critical severity with respect to availability of moisture may occur late in the dry season, for at this time cottontail congregate at water, and avidly seek any remaining succulent vegetation. Rabbits in situations where no water is available may compete severely with each other for preferred foods such as rushes, already so closely

cropped as to be unavailable to grazing stock. For young in the nest, weather conditions may be critical and heavy rains may result in their death by chilling or even drowning.

So far as observed, however, actual mortality in nearly all instances involved predation, upon individuals which were not obviously handicapped or diseased and which were well provided with food and shelter. That is, they were not part of a surplus population crowded out into a precarious marginal existence in critical periods, as in cases cited by Errington (op. cit.).

"Vulnerability" of the cottontail population may depend not so much on the conditions of food and shelter available to the rabbits as on the numbers of predators present and the relative availability to them of ground squirrels, woodrats, pocket gophers and kangaroo rats. At least it seems fairly certain that the medium to high populations of these several rodents make possible the existence of the predators which account for most of the rabbit mortality.

Disease.—Evidence of disease was rarely noticed among the rabbits trapped, through nearly all of them were heavily infested with large fleas. On one occasion a cottontail died suddenly for no apparent reason when it was being removed from a trap, suggesting the possible existence of shock disease in the population but no autopsies or laboratory tests were carried out to verify this hypothesis.

On February 17, 1941, a cottontail evidencing sluggish behavior was noticed, and it allowed an observer to approach within eight feet, then crawled into a rock crevice. It made no effort to escape when picked up and died two hours later. There was a swelling about the size of a walnut on the lower jaw, containing a yellowish white mass of cheesy consistency, and a slightly smaller inguinal swelling. The liver was somewhat darkened with well-separated yellowish spots on its surface. This rabbit had an unusually heavy infestation of fleas; it was estimated that there were at least 100 on its head alone. Other rabbits seen at this location on the same day and during subsequent weeks appeared to be normally healthy.

Herman and Jankiewicz (1943) examined 43 cottontails from the experimental range, and found coccidian infections prevalent; six different types were described. The infections did not appear to be acute and their effect on the rabbits is not known. Cottontail experimentally infected with *Eimeria stiedae*, a coccidial liver pathogen of domestic rabbits did not develop severe infections, as do domestic rabbits, suggesting partial immunity. The only ectoparasite recorded by these authors was a flea (*Ctenocephaloides felis*). The animals were shipped to these authors in Los Angeles and the ectoparasites were probably lost during handling prior to shipment. Internal parasites found by them included two intestinal protozoans (*Trichomonas*, *Chilomastix*), two nematodes (*Obeliscoides cuniculi* and *Nematodirus leporis*), and several cestodes (*Taenia pisiformis*, *Citotaeia variabilis* and other species of the same genus and *Raillietia retractilis*).

SUMMARY

The cottontail is abundant in open woodlands of the Sierra Nevada foothill belt in central California. At the San Joaquin Experimental Range it competes heavily with livestock in use of the vegetation. During the summer dry season, the rabbits took grain baits freely, but during the growing season they preferred succulent natural foods.

Knowledge of the changing seasonal bait acceptance is of practical value in connection with management operations. At times, locally, it may be desirable to remove, by poisoning, cottontail populations which are known to be diseased, or which are causing obvious damage to cultivated crops or range forage. More often it may be de-

sirable to retain the cottontail population while removing certain harmful rodent species. Ground squirrels, for instance, are controlled by annual poisoning on many of the foothill ranges. Squirrel poisoning operations during the winter or spring months would result in relatively light losses to the cottontail population since grain bait is not especially attractive to the rabbits at that season; but summer or early fall squirrel poisoning might at the same time reduce the rabbit population even more drastically.

Live trapping and marking of rabbits through a three-year period resulted in 1,159 captures of 228 individuals, and indicated that these animals are attached to definite small areas. Diameters of "foraging areas" within which individual rabbits usually stayed were roughly perhaps 700 feet, but were variable and occasionally long foraging trips were made. Immature animals appear to range less widely than adults. Of 23 rabbits released at a distance from the point of capture, three made homing movements of 4,400, 3,550 and 3,150 feet respectively; 10 were recaptured near the place of release, and the others were not again recorded.

One rabbit was recorded to have shifted its range a distance of 3,300 feet. Such movements may be fairly common and important in the population turnover of small areas. Water and succulence in the dry season attract unusual concentrations of cottontails.

In censusing the population by the ratio of marked ones to others during the dry season of each year on the 80-acre study area, the following numbers were recorded: 1939, 153; 1940, 53; 1941, 95. Allowing for movements outside the 80 acres, the population density was calculated as one per 1.2 acres in 1939 and one per 2.6 acres in 1940. In its cottontail population, the 80-acres study area was below the average of the experimental range as a whole. Road counts over 1,754 acres of the experimental range compared with similar counts on the trapping area, indicated a population density for these pastures 1.7 times that of the study area.

Observations on the feeding habits indicated that in spring the common forage plants most used by cattle, soft chess, foxtail fescue, broadleaf filaree, popcorn flower, and gold fields, make up the bulk of the cottontail diet. Through the summer heavy use of soft chess continues, but as the forage crop in general dies out, there is a distinct tendency to concentrate on swale vegetation where succulence remains. Clovers, rush, and dock are swale plants especially sought at this time. Leaves, seeds, and stems of tarweed, and leaves and stems of turkey mullein are often taken in summer. These along with dock, constitute plants rather unpalatable to livestock, so that competition is somewhat reduced during the dry season. Cast seeds of foxtail fescue constitute an important food source during the dry season.

Numerous wildlife species predatory on cottontails occur in the region of the experimental range. In order of their importance, predators included the coyote, rattlesnake, horned owl, gopher snake, gray fox, and red-tailed hawk. From the proportion of rabbit found for each species in the course of numerous scat, pellet, and stomach examinations, the population density of these predators, and the individual food requirement of each kind, it was estimated that predation factors annually might consume a cottontail weight of 1,229 grams per acre. This greatly exceeds the weight of the cottontail population actually present in late summer, before the breeding season begins. Nevertheless, the cottontail may be able to withstand this severe predation pressure by virtue of this long breeding season with possibly several litters of young annually for each adult female.

One diseased and dying rabbit was found, but no evidence was obtained that disease causes extensive mortality or affects population trends in this locality.

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LITERATURE CITED

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Front.—The Black-tailed Jackrabbit grows to 24" long and can run at speeds of 35 miles per hour to elude prey. Known as the “Desert Hare,” it is born open-eyed and fully-furred and must fend for itself at a very early age.

Rear.—The Desert Cottontail shares territory with the Black-tailed Jackrabbit and commonly “plays” with other members of its species by leaping straight up into the air when startled or eluding a charge.



Photo by David Jesse McChesney



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