MEMORIAS

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MUSEO DE HISTORIA NATURAL "JAVIER PRADO"

No. 9

OLIVER P. PEARSON: Biology of the subterranean rodents, Ctenomys, in Peru.

LIMA

UNIVERSIDAD NACIONAL MAYOR DE SAN MARCOS

1959

BIOLOGY OF THE SUBTERRANEAN RODENTS, CTENOMYS, IN PERU

por

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Sumario

BIOLOGIA DE LOS ROEDORES SUBTERRANEOS, CTENOMYS, EN EL PERU

En el Perú, límite septentrional de su extensa distribución, el género *Ctenomys* está representado por tres especies, todas ellas restringidas a elevaciones de más de 3700 metros.

Ctenomys opimus se encuentra en varios ambientes tales como aquellos dominados por la tola, por el *Nototriche*, y por la gramínea *Festuca orthophylla*. Sobre la superficie la alimentación (sobre vegetación) y la excavación se llevan a cabo de día, casi siempre a una distancia de menos de un metro de una madriguera abierta. Los sistemas de galerías subterráneas se componen de túneles de poca profundidad con ramas laterales cortas. La crianza ocurre de agosto hasta fines de febrero, y el parto entre octubre y marzo. La cría numera de uno a tres individuales. Estos, a su vez, crían antes de tener un año de edad, y probablemente tienen lechigada cada año durante el cual sobrevivan. Ambos sexos son solitarios y silenciosos. La populación puede ser tan densa como 42 por hectárea, pero la densidad de 2.5 por hectárea es más común en ambiente favorable.

Ctenomys peruanus tiende a limitarse a pampas planas y muy apacentadas. Difiere de *opimus* en expresar una llamada burbujeante muy conspicua y en ser colonial. Varias hembras adultas suelen vivir en la misma galería subterránea, aunque los ma-

chos tienden ser solitarios. La mayoría de la cría nace en marzo y abril, en un acondición muy precoz. Les es posible dejar el nido, nutrirse de vegetación verde, y dar la llamada adulta casi inmediatamente. Crían antes de cumplir un año de edad. Las hembras probablemente tienen sólo una cría anualmente. El tamaño de cría fué de uno a cinco individuales. La densidad de la población en una colonia fué 42 por hectárea. La proporción sexual de los ejemplares adquiridos por la cazería fué predominantemente femenina, probablemente porque los machos eran actualmente más escasos como resultado de espaciarse.

Poco se sabe de la tercera especie, *Ctenomys leucodon*.

Las tres especies viven en asociación cercana, en algunos sitios, con una especie de cobayo (*Galea musteloides*). Con *Ctenomys peruanus* fué demostrado que los cobayos se apropian las madrigueras inmediatamente de que los tuco-tucos sean apartados de ellas.

Herbívoros subterráneos sin parentesco alguno através del mundo son admirablemente similares en tamaño y estructura, y no obstante diferentes métodos de excavación, construyen sistemas de galerías que son casi siempre parecidos. Además, muchos géneros roedores subterráneos del mundo han producido un número extraordinariamente grande de especies y subespecies. Pocas de estas especies habitan la misma área. Consequentemente, parece que através del mundo hay solamente un nicho básico ecológico explotable por mamíferos herbívoros subterráneos.

INTRODUCTION

Pocket gophers (*Geomyidae*) are widely distributed in North and Central America and reach their southern limit in rain forest near the Panama-Colombia border. The northern half of South America lacks an anatomical or ecological equivalent of the gopher, but the southern half is the home of many species of *Ctenomys*, hystricomorph rodents of separate evolutionary origin but with gopher-like habits and with a remarkable physical resemblance (fig. 1) to pocket gophers such as *Geomys* and *Thomomys*. This report, based upon collections and observations made by me during 1½ years of field work in the Andes, will describe the biology of *Ctenomys* in southern Peru and will compare it with the biology of other subterranean mammals, especially gophers.

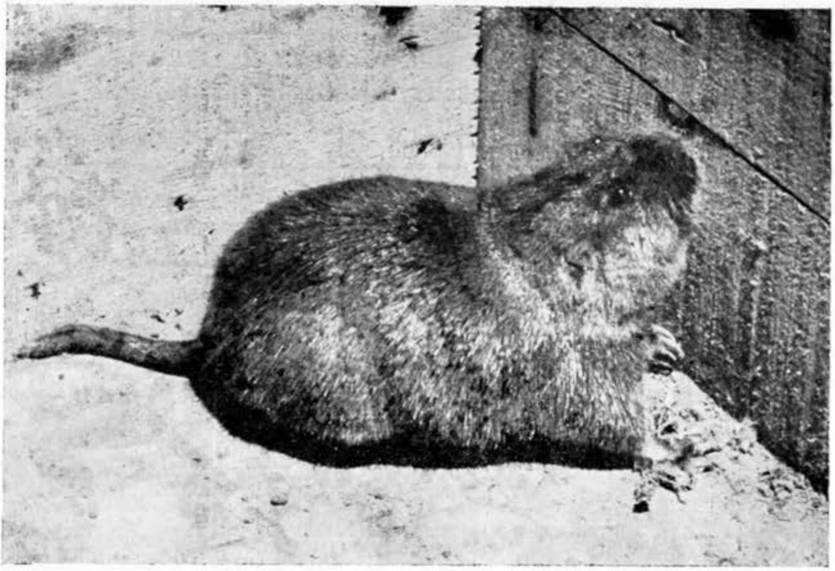

Fig. 1. Captive female **Ctenomys opimus nigriceps.** (Hembra cautiva **Ctenomys opimus nigriceps**).

Representatives of *Ctenomys* range from Tierra del Fuego northward along the Andes to the Department of Puno in southern Peru where three distinct species *(opimus, peruanus,* and *leucodon)* reach the northern limit of the range of the genus. These three species have been taken within 35 kilometers of eachother. The shortest distance known between populations of any two of the species is near Huacullani where *peruanus* and *leucodon* live within 8 kilometers of eachother. Although there are some species differences in altitudinal distribution, the highest known altitudes recorded for *peruanus* and *leucodon* are only 100 and 400 feet lower, respectively, than the lowest altitude known for *opimus* in this region. Consequently, additional collecting may reveal actual contact or overlap between some of these species.

Two of the three Peruvian species *(peruanus* and *leucodon)* have small ranges of only about a thousand square kilometers, although it is possible that additional collecting in Bolivia and northern Chile might reveal a connection between one or both of these and some of the dozens of species described from farther south. *Ctenomys opimus nigriceps* in southern Peru is the northern-most representative of a species that ranges at least as far south as northern Argentina. In view of the large geographic range and morphologic diversity of the whole genus, and the abundance of individuals, one cannot help but wonder why the genus stops where it does in southern Peru. To the north of Lake Titicàca lie pampas that would seem to be well suited to *Ctenomys peruanus*, and in the mountains of the Department of Arequipa north of the Tambo Valley lie miles of *Festuca*-covered slopes and many *Notriche* deserts that would probably support *Ctenomys opimus*. None of them is occupied either by *Ctenomys* or by an ecologic equivalent that might be considered a competitor. The Tambo Valley, cutting in from the Pacific toward Lake Titicaca, is a deep one and for most of its length might be an effective barrier, but between its head and Lake Titicaca lies a high divide along which *opimus* should be able to pass to the north. Possibly tuco-tucos are today dispersing northward along this route but because of their weak dispersal powers may be progressing only slowly. In view of the fact, however, that the northern spread of some other widely distributed species with much better dispersal powers, such as rheas, stops at the same latitude in southern Peru, it seems more probable that some definite but unknown botanic, geologic, or climatic barrier exists.

At elevations between 12,600 and 16,000 feet, where the three species of *Ctenomys* live in southern Peru, the vegetation is sparse and the climate frequently cold and windy. Moderate amounts of snow, hail, or rain fall in the summer months from November to March, but the winters are dry. Mornings are usually sunny with shade temperatures up to 15° C. and afternoons cloudy and windy. Night temperatures frequently fall below freezing and at the higher elevations are sometimes as cold as -15° (Bowman, 1916; Pearson, 1951). Above-freezing temperatures during the day, however, and intense insolation prevent the ground from becoming frozen. By being diurnal and largely subterranean, *Ctenomys* avoids exposure to the colder temperatures, and its microclimate could be more accurately described in terms of conditions within its burrows. The temperature within a *Ctenomys opimus* tunnel 20 centimeters below the surface varied only 6° C. during a day when the shade temperature 30 centimeters above the ground varied 21° (fig. 2).

Ctenomys makes its presence obvious by ejecting mounds of fresh earth, yet some of the people living in southern Peru were not

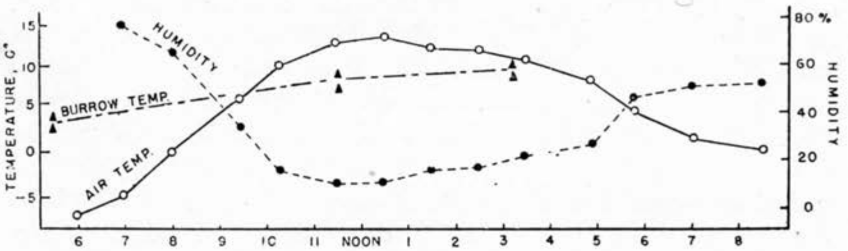

Fig. 2. Temperature and relative humidity in shade, and temperature in burrow of **Ctenomys opimus;** April 18, 1952; 5 km. east of Lago Suche, 14,600 feet, Department of Moquegua, Peru. The pairs of triangles represent temperatures in two different burrows. (Temperatura y húmedad relativa en la sombra, y temperatura en una madriguera de **Ctenomys opimus.** Los pares de triángulos representan temperaturas en dos madrigueras diferentes).

familiar with these animals and others confused them with guinea pigs *(Galea musteloides).* Few distinguished between the three species of *Ctenomys*. *Ctenomys* is called by the following names: tocorro, tocohoro, tojo, tarahuanca, certenejo, and conejo del cerro. The most widespread name in scientific publications, tuco-tuco, is not used in Peru.

In a sparsely populated region where grazing and mining are the only important commerce, the economic importance of *Ctenomys* rests chiefly on its destruction of plants eaten also by sheep, llamas, alpacas, and vicuñas, and on its soil-moving activities. I never heard of any use being made of the skin or meat.

During this study all tuco-tucos collected were measured, the reproductive tracts examined, and selected gonads preserved for sectioning. Skins and skulls of many specimens were prepared and deposited in the Museum of Comparative Zoology and the Museum of Vertebrate Zoology. Specimens of plants were identified by H. Sharsmith and J. Reeder. Tapeworms were identified by M. Voge, staphylinid beetles by C. H. Seevers, fleas by P. T. Johnson and R. Traub, and lice by F. L. Werneck. To all of these people I am grateful for assistance.

Humeri from most of the specimens were saved to use in estimating age. Three *Ctenomys peruanus* humeri showing different degrees of closure of the proximal epiphysis were selected to form a reference series. One with a conspicuous and continuous epiphysis was designated type for age class 2, one with a narrow inconspicuous suture type for age class 4, and one with a faint, partly-obliterated suture type for age class 6. Humeri of both *opimus* and *peruanus* were then compared with this type series and assigned to one of these age classes or to one of the adjacent or intermediate classes. Unfortunately, adequate year-round collections were not available to permit calculation of the absolute chronological age of the various classes, so one must deal only with relative ages.

CTENOMYS OPIMUS

Ctenomys opimus, the most widespread of the Peruvian tuco-tucos, is found in Peru between 13,300 and 16,000 feet. Collections are available from thirteen localities in southern Peru, and the species has been seen at numerous other places. Most specimens are clearly *Ct. opimus nigriceps* Thomas, but a population living at 15,300 feet near the pass at Nevado Livine, Department of Tacna, differs markedly in color and resembles *Ct. opimus opimus* and *Ct. fulvus*. Additional study of this taxonomically difficult genus will be necessary to enable the Livine population to be identified with certainty. It probably will prove to be a subspecies of *opimus*, but there is enough doubt so that I have not included Livine specimens in the following discussions and calculation without mentioning them specifically.

Ctenomys opimus lives in open country in well-drained sandy, gravelly, or cindery soils, usually on slopes but occasionally on pampas. Vegetation is usually so sparse that most of the ground surface is bare. The common *opimus* habitats, referred to by the name of the dominant vegetation, are:

Festuca.— Most *opimus* are found on hillsides among the bunchgrass *Festuca orthophylla*, the needle-pointed culms of which serve as food and nesting material. Tuco-tucos can be detected from miles away by the presence of irregularly shaped bare patches on slopes otherwise dotted with *Festuca* (fig. 3). The tuco-tucos may remove all *Festuca* from areas of ten or twenty square meters up to several acres, and in this bared area one or more *opimus* may live, feeding on the peripheral *Festuca* and on smaller plants within the bared areas. As much as one-quarter of the area of some *Festuca*-covered slopes may be denuded (Pearson, 1951).

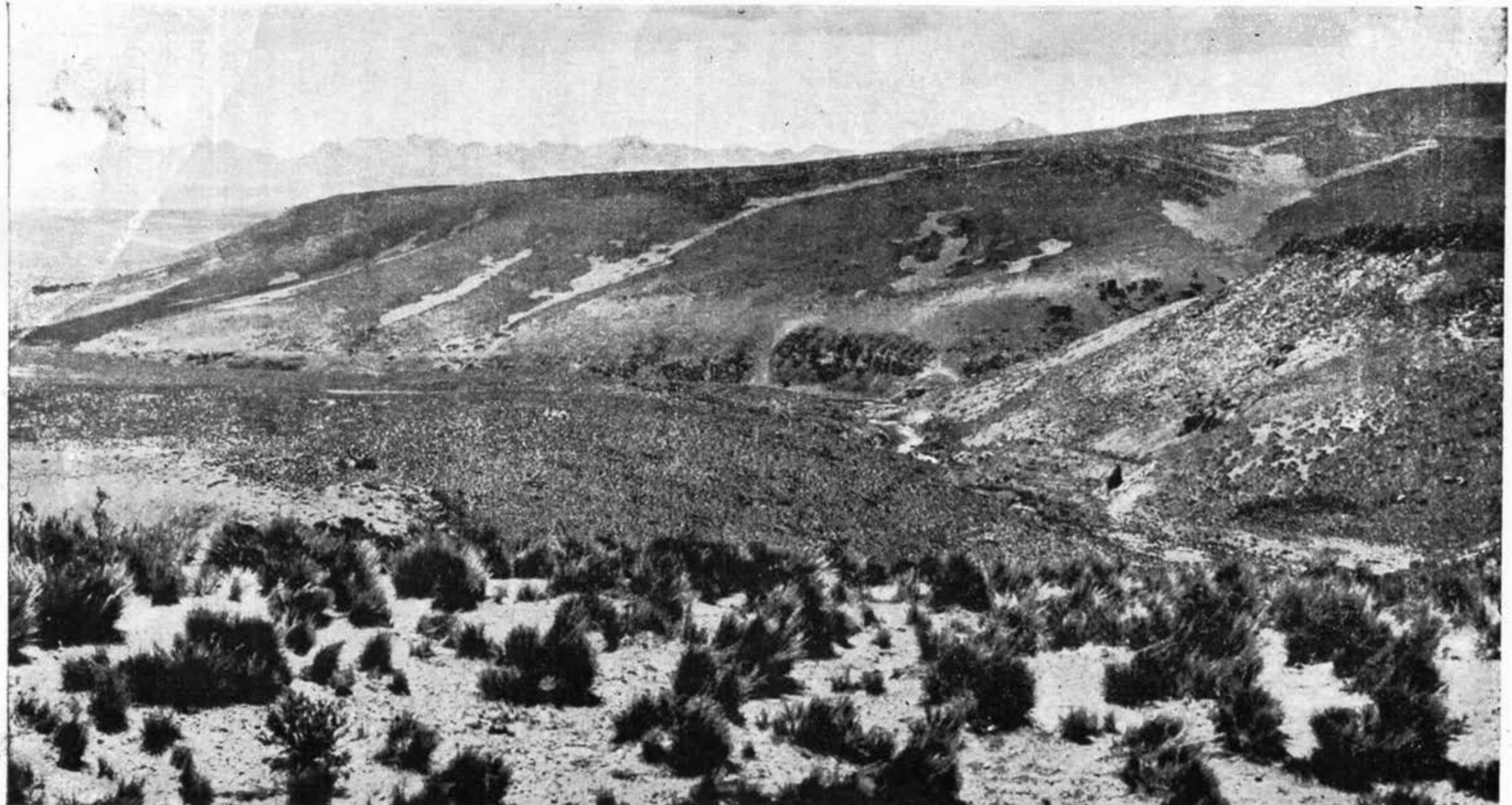

Fig. 3. Hills near Volcan Tutupaca, 15,000 feet., covered with **Festuca orthophylla;** April 22, 1952. Many of the bare patches on the facing slope were made by **Ctenomys opimus.** (Cerros cerca del volcán Tutupaca, de 4500 metros, cubiertos de **Festuca orthophylla.** Muchos de los espacios desnudos de la loma opuesta fueron causados por **Ctenomys opimus**).

Ctenomys opimus is always found at higher elevations than the widespread ichu bunchgrass (*Stipa ichu*).

Tola.— Tola is the Andean equivalent of sage brush. The plants are .3 to 1.3 meters tall, spaced several meters apart, and frequently intermixed with *Festuca*. The commonest tola species in the range of *opimus* in Peru are *Lepidophyllum rigidum* and *L. quadrangulare*. On a few occasions *opimus* was found among scattered *Margyricarpus strictus*, a spiny, almost leafless shrub about one foot tall.

Although tuco-tucos cut tola for food, I have not seen any place where it was certain that they had completely cleared areas of tola, as they clear patches of *Festuca*. There is evidence, however, that they prefer such cleared areas. At one locality *opimus* was living in moderate numbers in a rather rich expanse of tola, *Lepidophyllum rigidum*. Men had cleared about an acre in the center of this expanse to make a football field. The field was growing to a mat-like *Pycnophyllum* and a 5-cm.-high *Calamagrostis*. At least five tuco-tucos were living on this acre, a high population.

Nototriche.— This habitat is one that supports large numbers of *Ctenomys opimus* and other vertebrates, yet despite its unusual nature has received little attention from ecologists. It appears at first glance to be utterly barren sandy desert, but closer inspection reveals several kinds of small plants whose dull leaves lie flush with the surface of the ground. Brushing away the sand reveals a surprisingly large crop of fleshy, tap roots (figs. 4 and 5). Most abundant of these are *Nototriche foetida* (*Malvaceae*) and *N.* sp., but also important are *Geranium sessiliflorum, Astragalus peruvianus, A. Reichei, A. cryptobotrys, Descurainia depressa, Arenaria digyna, Werneria pygmophylla*, and *Draba* sp. A few 5-cm.-high mats of grass, *Calamagrostis curvula*, are scattered at wide intervals. Many square miles of *Nototriche* desert are distributed through the volcanic mountain region of southern Peru, but it is not as widespread a habitat as that dominated by *Festuca* or tola.

Impressed by the hidden productivity of this desert habitat, I made a plant census in one of these deserts at 14,600 feet, 5 km. east of Lago Suche, Department of Moquegua. The plot was not chosen at random but was selected because it appeared to contain

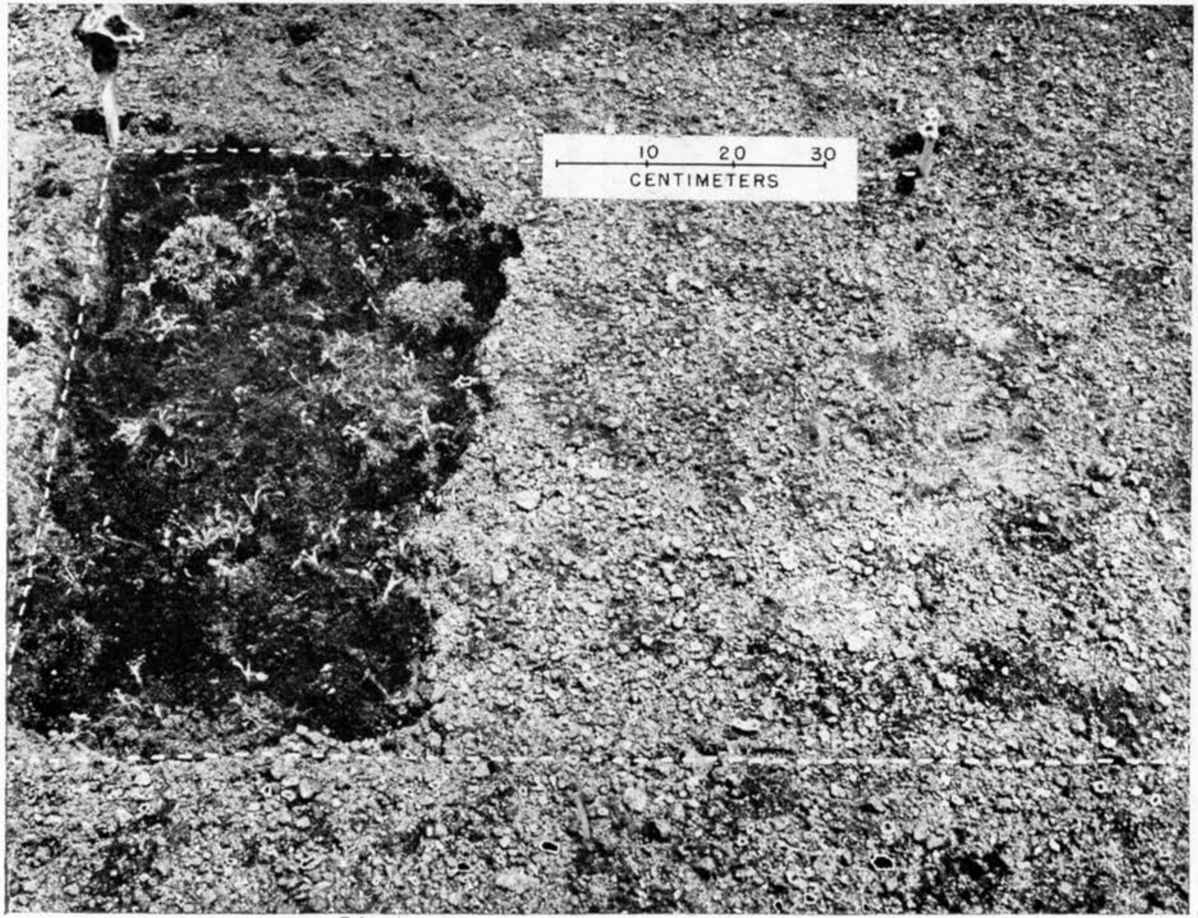

Fig. 4. A 3-foot-square plot of **Nototriche** desert, part of it undisturbed and part excavated to disclose hidden plants such as **Nototriche, Geranium,** and **Astragalus.** January 18, 1952; 5 km. east of Lago Suche, 14,600 feet. (Un terreno de un metro cuadrado de desierto de **Nototriche,** parte intacto y parte cavado para revelar plantas escondidas tales como **Nototriche, Geranium,** y **Astragalus.**

Fig. 5. Plants weighing 477 grams removed from a 3-foot-square (0.84 m^2) plot on the **Ctenomys opimus** census area shown in figure 11. (Plantas pesando 477 gramos quitados de un terreno de un metro cuadrado en el sitio de censo de **Ctenomys opimus** demostrado en la figura 11).

neither maximal nor minimal numbers of plants. It probably contained somewhat more than average. It will be seen from Table 1 that this apparently sterile *Nototriche* desert supported nearly one-fifth as much plant material as good California range land well covered with plants such as filaree, soft chess, and foxtail fescue.

A *Nototriche* desert is usually bordered by *Festuca* and may contain a few widely isolated clumps of *Festuca*. *Ctenomys* seems to prefer those parts of the *Nototriche* habitat that are within about 70 meters of at least a small quantity of *Festuca*.

Other vertebrates living or feeding in the *Nototriche* desert are lizards *(Liolaemus multiformis)*, which take shelter under stones and in *Ctenomys* burrows and which eat both insects and the leaves and blossoms of *Nototriche*, rheas *(Pterocnemia pennata)*, tinamous *(Tinamotis pentlandi)*, Bolivian geese *(Chloephaga melanoptera)*, doves *(Metriopelia aymara,)* hawks *(Buteo)*, Puna miners *(Geositta cunicularia,)* earth creepers *(Asthenes modesta)*, mice *(Phyllotis boliviensis)*, foxes *(Dusicyon culpaeus)*, and vicuñas *(Vicugna vicugna)*.

Digging activity.— Visible feeding and digging activities usually occur between 6:30 and 11 a.m., hours when the sun is usually shining. During many nights of hunting with a flashlight

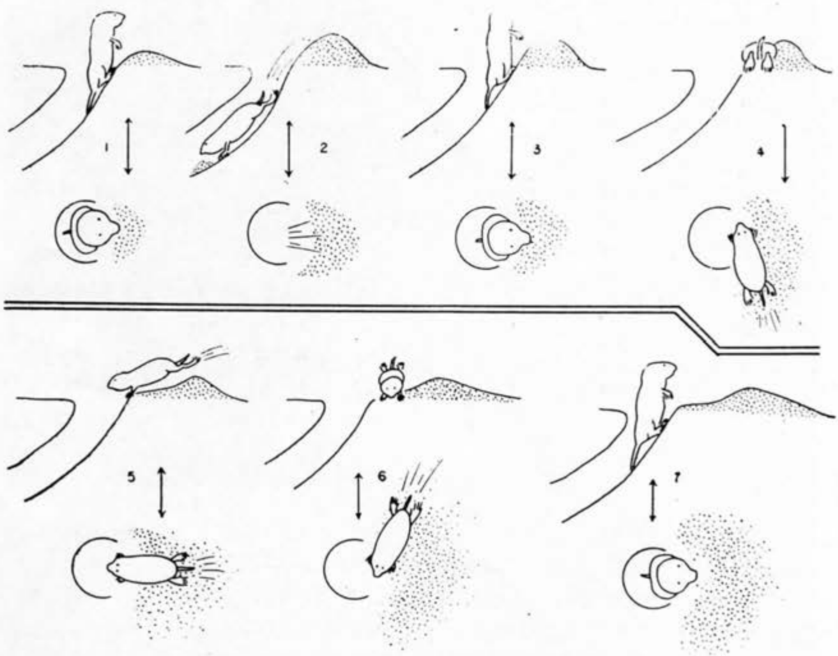

Fig. 6. Seven pairs of diagrams (side and top views) of the excavation procedure of **Ctenomys opimus.** (Siete pares de diagramas (vistas laterales y superiores) del proceso excavacional de **Ctenomys opimus**).

I never saw any tuco-tucos, and fresh earth mounds were seldom formed at night.

Ctenomys opimus burrows by loosening the earth with the front feet and sweeping it out of the tunnels with the hind feet. The procedure, illustrated in figure 6, may continue steadily for more than an hour. The tuco-tuco raises its head out of the burrow opening to look around, then disappears from sight, usually head first. A few seconds later loose dirt begins to spurt out of the hole. After about half a minute the tuco-tuco reappears head first, looks around, emerges from the hole and turns around so that it is facing into the burrow, then by simultaneous flips of the hind feet sweeps the newly dug earth farther away from the entrance, thus making room for more earth to be thrown up from below. During the sweeps by the hind feet, the body at times is supported by the stubby tail. Between the sweeps by the hind feet, the animal swings its hindquarters part way around an arc so that the pile of earth assumes the form of a crescent. After the sweeping is completed the animal may disappear down the hole head first or may turn around and look about with just its head protruding from the hole. When not actually in use, the mouth of the tunnel is frequently plugged with earth.

When Macabee gopher traps are placed in the entrances of burrows, all tuco-tucos caught are caught by the tail, hind leg, or skin of the lower abdomen. The size relationship between animal and trap is such that the animal must have been moving backwards through the tunnel to be caught by the hindquarters. Anthony (1930) noticed this in a different species in Chile. Tuco-tucos probably do not habitually run through their tunnels backward, but when they detect a strange object in the tunnel they probably turn around and attempt to sweep it out with their hind feet.

The feet are specialized for fossorial life (fig. 7). A fringe of stiff hairs on the margins increases the effectiveness of the hind feet as brooms. Combs of bristles are present on the toes of most hystricomorph rodents, and in *Ctenomys* (greek, comb-mouse) *opimus* are used for cleaning the fur, especially the fur of the belly, which becomes caked with dirt. While digging, the animal occasionally pauses and, standing on three legs, scratches the belly with one hind foot. The front feet are equipped with long claws and two large, fleshy, carpal pads (fig. 7) that amount almost to extra digits. The center claws on the front feet are ordinarily about 10 mm. long. A young male whose humerus was probably broken by a rifle bullet on December 11 was captured 36 days later. The leg was partly healed but could not have been of much use, and the center claws had grown during this time to 17 mm., or about 0.2 mm. per day. The claw on the fifth toe grew at a slower rate, 0.12 mm. per day.

Burrow systems in *Nototriche* habitat were extended about 2.6 meters each day. The tuco-tuco responsible for the mounds in figure 8 usually made one new mound each day, occasionally

Fig. 7. Front feet (above) and hind feet (below) of **Ctenomys opimus.** Note the fringe of hairs visible along one side of the hind foot in plantar view, and, in the dorsal view, the combs of bristles arising near the bases of the claws. A slip of black paper has been slipped under the carpal pads. Photograph of a fresh specimen. (Patas delanteras (arriba) y patas traseras (abajo) de **Ctenomys opimus.** Nótese la franja de pelo visible de un lado de la pata trasera en la vista plantar, y en la vista dorsal, los peines de seta creciendo cerca de las bases de las garras. Un pedazo de papel negro ha sido puesto debajo de la parte anterior del pie).

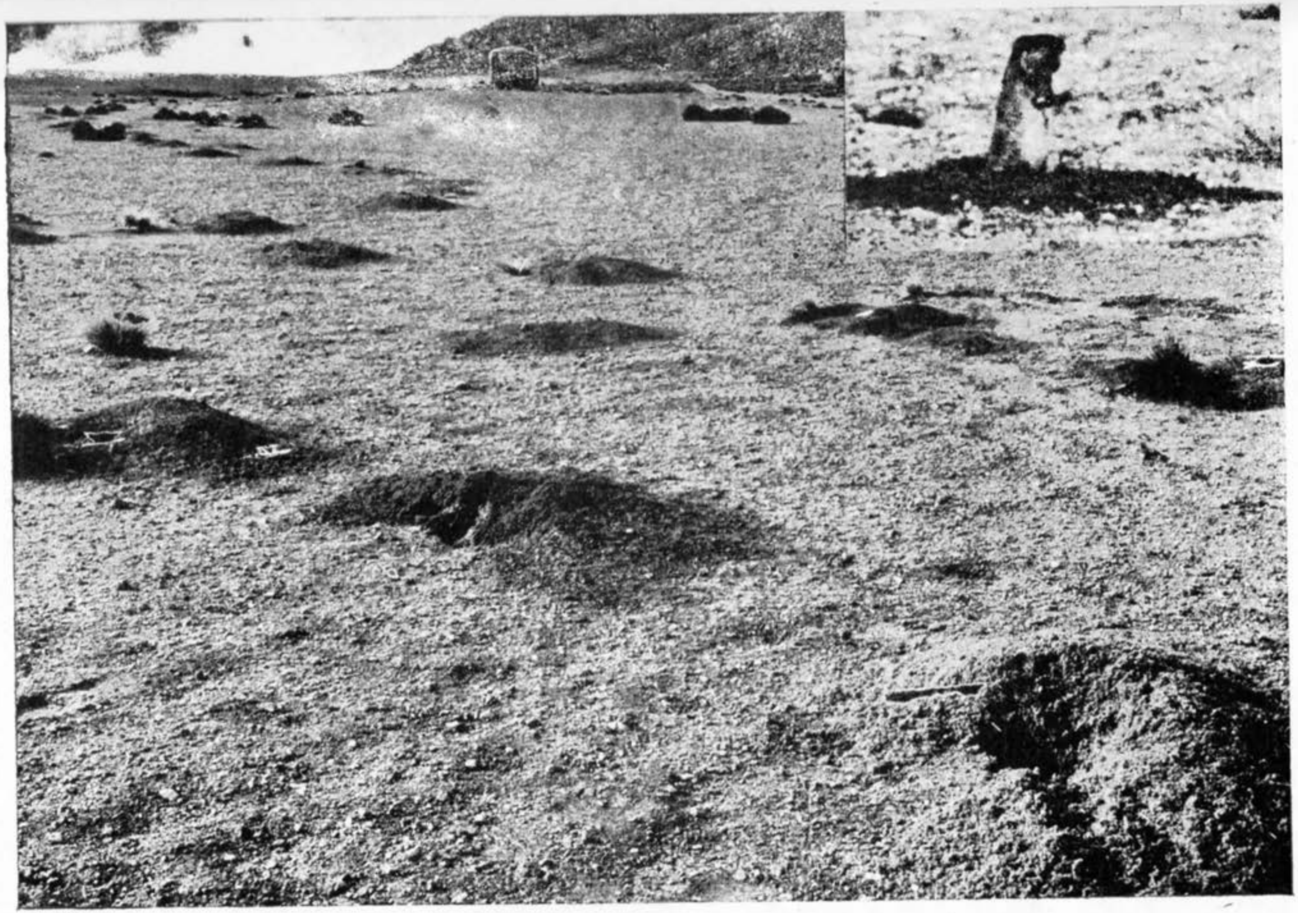

Fig. 8. A series of **Ctenomys opimus** mounds in **Nototriche** desert; January 17, 1952. The mound at lower right marked by the 6-inch ruler is only about one hour old. Those receding in the distance are progressively older. Insert: A **Ctenomys** opimus standing alertly in a burrow opening. (Una serie de montoncitos de tierra hechos por **Ctenomys opimus** en desierto de **Nototriche;** el montoncito abajo a la derecha, marcado por una regla de quince centímetros, tiene apenas una hora. Aquellos a la distancia son progresivamente más viejos. Inserto: Un **Ctenomys opimus** alertamente de pie en una apertura de un sistema de galerías.

two. The distance between 20 successive mounds varied between 1.3 and 3.3 meters. The average mound in this series contained about 10 liters of earth. Since the diameter of the tunnels was 9½ centimeters and the average distance between piles 1.9 meters, it would appear that about three-fourths of the earth loosened in tunneling is brought to the surface rather than packed into unused parts of the tunnel system.

In regions where plant life is more abundant than in *Nototriche* desert, *opimus* does less excavating. Days may elapse without the appearance of new dirt mounds, sometimes without even the addition of fresh earth to old mounds.

Burrow systems of *Ctenomys opimus* usually consist of a single main tunnel from which short lateral branches diverge every few meters. The laterals are usually less than 1½ meters long. The tunnels are rarely more than 30 centimeters below the surface, although we excavated one that went as deep as 75 centimeters. The main burrow may be tortuous or may be, as in figures 8 and 9, rather straight. Burrow systems include one or more chambers

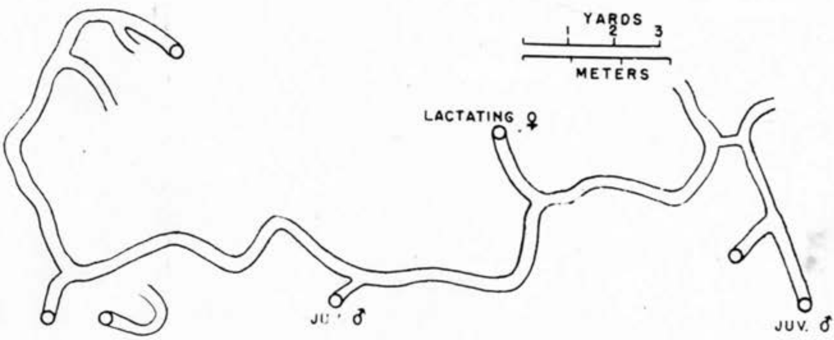

Fig. 9. Diagram of the burrow system of a lactating female **Ctenomys opimus** living on the census area; January 14, 1952. The burrow openings where the female and her two young were collected are shown. (Diagrama del sistema de galerías de una hembra lactante **Ctenomus opimus** viviendo en el área de censo. Se ven las aperturas de la madriguera de la cual la hembra y su cría fueron recogidos).

that may contain considerable quantities of vegetation. One chamber contained a hatful of dry grass cut into lengths of a few centimeters; another contained several cupfuls of old moldy droppings and old pieces of grass, and another a mass of dry papery bark from *Geranium cucullatum*. Freshly cut leaves and stems of plants are sometimes scattered along the tunnels. The various chambers probably are used for nests and food storage. Droppings were found in most of them, and no sealed-off chambers of droppings were found.

Two adults of *Ctenomys opimus* were never seen making use of the same burrow system, and in almost all instances when an adult was collected at the mouth of a burrow, no fresh earth or other sign of activity appeared subsequently in the immediate vicinity. Figure 12 also demonstrates a tendency for adults to be widely spaced. Consequently, it is assumed that the adults are usually solitary.

Feeding.— *Ctenomys opimus* eats roots, stems, or leaves of most of the plants in its habitat, stems of *Festuca orthophylla* probably being the most important food. It eats the tap roots of *Nototriche* and the other plants that it encounters while tunneling, as well as the leaves of these plants on the surface. After a new opening in a burrow system has been made, the tuco-tuco uses it for several days for feeding, first utilizing the closest plants, later venturing as much as two or three body lengths from the hole. The usual procedure when feeding on dwarfed prostrate vegetation is as follows: the animal emerges part of the way or all of the way from one of its holes, scratches with the front feet and nips at the desired leaves and stems and, when they are separated, backs into the burrow carrying the food in its mouth. After being underground for about half a minute, the animal reappears and repeats the procedure. When feeding on the bunchgrass, *Festuca orthophylla, opimus* burrows to the base of the clump, tears or nips off a few blades, then pulls them underground to eat or to use in the nest chamber. When the food is thornbush or tola, the burrows open at the base of the bush and the animal nips woody branches as thick as a pencil and drags them down into the burrow. Some feeding is done from inconspicuous burrow openings that have no earth mounds.

Parasites and associates.— Parasites or associates collected on *Ctenomys opimus* included lice (*Phtheiropoios* sp.), fleas (*Tetrapsyllus bleptus* and *T.* sp.), and staphylinid beetles *(Edrabius pearsoni)*. Two other species of staphylinids were found in the burrows *(Megamblyopinus mniszechi* and *Amblyopinus monticolus)*. The larval tapeworms so abundant in *Ctenomys peruanus* were not found in *opimus*.

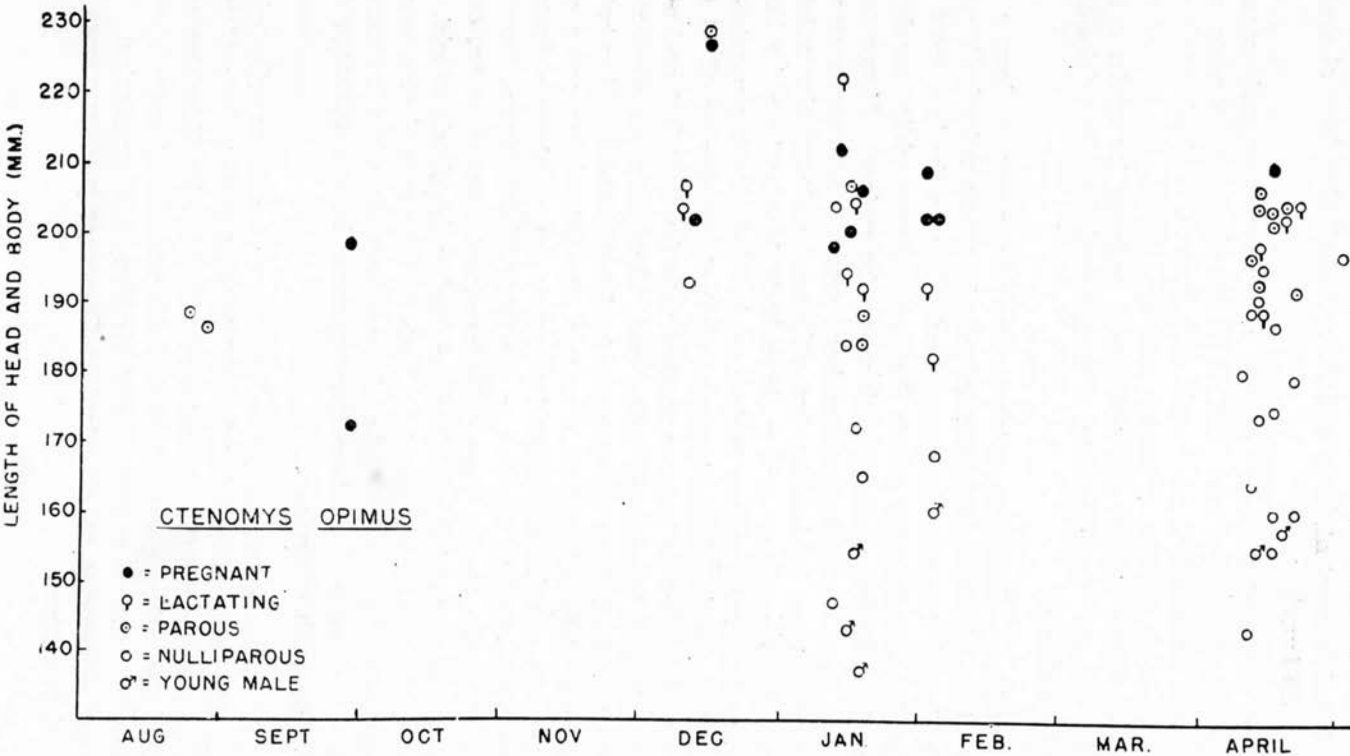

Fig. 10. Reproductive condition of females of **Ctenomys opimus.** Juvenile males have been included to increase the representation of young individuals when estimating the extent of the breeding season. (Condición reproductiva de hembras **Ctenomys opimus.** Machos juveniles han sido incluídos para aumentar la representación de individuales jóvenes cuando se calcula la duración de la temporada de crianza).

Guinea pigs were found living with *Ctenomys opimus* at only one place, 25 kilometers southwest of Pisacoma, 14,000 feet. Since this is near the upper altitudinal limit of guinea pigs and near the lower limit of *opimus* in this region, there are not many opportunities to observe between these two species the close association that occurs between guinea pigs and the other two species of Peruvian tuco-tucos.

Reproduction.— Reproductive performance of the females of *Ctenomys opimus* is summarized in figure 10. Six juvenile males have been included in the figure to give a larger representation of young individuals. Because their reproductive condition seemed to be the same as that of other specimens of *Ct. opimus, twelve* April and early May females from the population near Nevado Livine have been included. It may be seen that pregnant females were taken in September, December, January, February, and April. The April pregnancy was near term and, in the absence of other pregnant females in the April sample, probably marks the end of the reproductive season. From the distribution of pregnant and lactating females in figure 10, and from the fact that pregnancy in the guinea pig, a hystricomorph of similar size, is about 2 months, it is assumed that gestation lasts at least 2 months. Using this assumption, the breeding date of each pregnant female was estimated, and the date of conception of each of the juvenile males was also estimated. It was concluded that copulations occurred in each month from August through February. If gestation is more than 2 months, then the dates of copulation would be advanced accordingly. The April sample gave no indication of successful copulations in March or April. In the absence of adequate collections after April it is impossible to say how long the presumed non-breeding season lasts, but since no juveniles of either sex were taken in the August, September, or December samples, it seems probable that there were few births between August and November and therefore few copulations between June and August. When the direct and indirect data are combined, they suggest that most copulations occur between August and January and most parturitions between October and March.

The smallest, presumably youngest, pregnant female was one with tiny embryos taken September 29; her head and body length was 172 mm. Her weight was not taken, but others of this body size weighed about 160 grams. Many that had reached this size or larger in April were nulliparous and probably had reached breeding size too late in the breeding season to mature sexually. They do breed, however, before they are one year old and, since most large females taken in the middle of the breeding season are either pregnant or lactating, they probably bear young every year in which they survive. Gross and microscopic examination of ovaries of lactating females revealed no new corpora lutea, so there is no post-partum ovulation. The breeding season is long enough, however, so that if gestation is only 2 months and lactation brief there is time for a female to bear a second litter after weaning a first, but it is not known whether any females do this.

Eleven pregnant females carried 20 embryos (average 1.8, range 1 to 3), but one embryo was being resorbed in each of four females. If these embryos are discounted, 10 pregnant females were carrying 16 embryos (average 1.6, range 1 to 2). Four of the healthy embryos were in the left uterine horn and 12 in the right. Only one female was carrying a fetus in each uterine horn, although four of them had ovulated from both ovaries. In 13 parous, non-pregnant females there were 26 placental scars equally distributed between the two horns. Despite the equal distribution of placental scars, which may persist from resorbed fetuses, the evidence suggests a tendency toward unilateral pregnancies as in certain other hystricomorph rodents (Pearson, 1949). Twenty-four ovulations resulted in 16 healthy embryos.

Ninety per cent of the females had closed vaginas, including nulliparous, parous, pregnant, and lactating individuals. I find none of the large, accessory corpora lutea common in some other hystricomorphs, although there is a striking tendency towards luteinization of small ovarian follicles. So numerous are these in ovaries of some pregnant and some lactating females that they dominate the ovary, giving it in sections a quite different appearance than the ovary of *Ctenomys peruanus*.

The two innominate bones of a large, parous female were firmly in contact at the pubic symphysis but, as in males, not fused. The suture is clearly visible in both males and females.

There are three pairs of nipples, the anterior two pairs situated quite laterally. Young as small as 77 grams were captured above ground with green vegetable matter in their stomachs and no recognizable milk. Two juveniles were seen in the same burrow system as a lactating female that had two placental scars in her uterus. One of these juveniles was collected (87 grams) and had vegetable pulp in its stomach. Since the presumed mother was still lactating, it is probable that the young were still nursing but that milk was, as in other hystricomorphs, a secondary part of the diet and had been suplemented by plant material soon after birth.

The smallest young *Ctenomys opimus* seen at the entrance of a burrow was a male that measured: total length, 196 mm.; tail, 59; hind foot, 30; weight, 77 grams; last molar not erupted. Unlike the adults, which are mostly brown, this young was covered with silky black fur, only the hairs of the rump, lower sides, and belly being tipped with brown. The hairs of the dorsal and ventral surface of the tail were swept into a mane or crest both above and below, making the tail seem laterally compressed. Specimens as large as 121 grams were still primarily in juvenile pelage, and specimens as large as 109 grams were collected in the same burrow system as parous females, presumably their mothers.

For males of *Ctenomys opimus* reproductive information is available only from January, February, and April, at which times all of the large males were in breeding condition. Presumably they were in breeding condition also from August to January during the first part of the female's breeding season. Mature spermatozoa are produced when the growing testis becomes about 8 mm. long. All males with head and body less than 200 mm. had small seminal vesicles and testes less than 8 mm. long, and all males larger than 200 mm. had testes between 9 and 13 mm. A 7 mm. testis in a 192 mm. male on April 23 showed active spermatogenesis but still lacked mature spermatozoa. The seminal vesicles had not yet reached adult size.

Males are considerably larger than females. Fourteen sexually mature male *Ctenomys opimus nigriceps* from southern Peru, with testes 10 mm. or longer, had the following average measurements: total length, 314 mm. (range 288-330); tail, 91 (78-103); hind foot, 44.3 (42-47); weight, 439 grams (370-530). Measurements of 32 pregnant or parous females from the same region were: total length, 286 (252-320); tail, 84 (68-95); hind foot, 40.1 (35-44); weight, 284 (233-370). Although it is possible that the individuals in the sample of females were younger than those in the sample of males, hence smaller, this seems unlikely in view of the fact that the epiphyses of the humeri of the females were, on the average, more nearly closed than in the males. Upper incisor teeth of males also average wider than do those of females.

The sex ratio of all *opimus*, most of them collected by shooting but some by trapping, was 35 males to 59 females. Behavioral differences probably account for the bias (see under *peruanus*), but the behavioral basis may be different than in *peruanus* because the females of *opimus* are not as gregarious. Among fetuses old enough to be clearly differentiated there were 5 males and 2 females.

Census.— A 12.4-acre area was set aside near Lago Suche, 14,600 feet, for censusing. The area, an island of *Nototriche* desert surrounded by bunchgrass *(Festuca orthophylla)* and tola *(Lepidophyllum rigidum)*, is shown in figure 11. From the number of fresh diggings, the population density of tuco-tucos was estimated to be slightly higher than average for the other areas of *Nototriche* desert nearby. Except around the margin of the "island", the bunchgrass was not occupied by tuco-tucos, and as a result the census area was isolated from the nearest other tuco-tucos by about 50 meters of unoccupied terrain.

Between dawn and 10 a.m. on January 11, the resident tuco-tucos made 16 fresh earth mounds that, from their spacing, seemed to represent 11 different burrow systems and presumably the work of 11 different adult tuco-tucos. On the next morning at 10 a.m. there were 20 piles of fresh earth. Most of these were either additions to piles formed the day before, or were new piles less than a meter away, but 2 piles were 20 meters or more away from any of the previously marked piles and presumably were made by different individuals, indicating a total population of 13 animals. At 11.30 a.m. on January 13 there were 14 fresh mounds that fell into nine groups. Collecting was begun at this time by shooting and by trapping with Macabee gopher traps, and on January 16 the population shown in figure 12 had been disclosed.

On January 17, 18, and 19 no more animals were captured, although tuco-tucos were still digging in two places, so it is probable that two adults escaped capture. It appears, therefore, that the area supported 13 tuco-tucos: 4 adult females (at sites 2, 5, 6, 14), 3 adult males (at 1, 7, 12), 3 adults of unknown sex (one injured

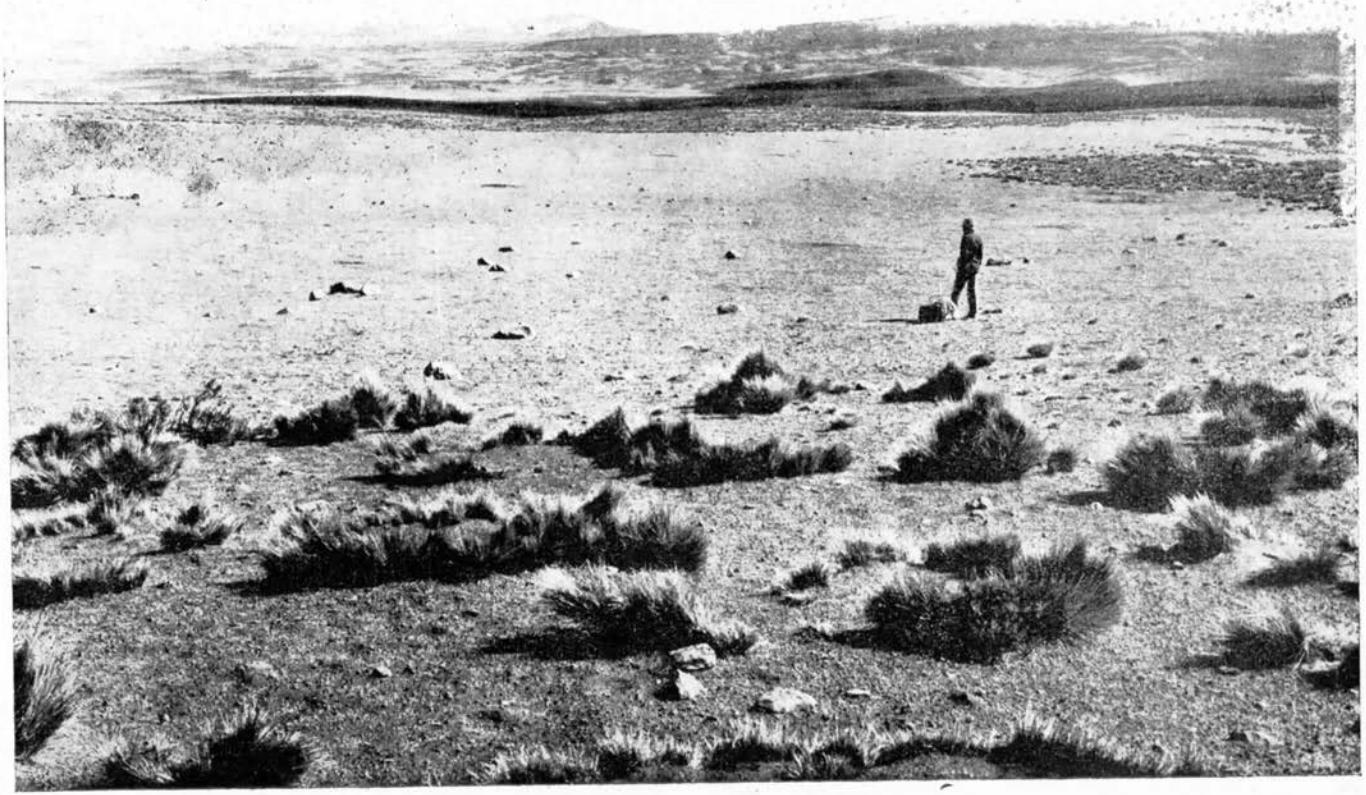

Fig. 11. Part of the 12.4-acre census area for **Ctenomys opimus;** 5 km. east of Lago Suche, 14,600 feet, Department of Moquegua, Peru; January 17, 1952. The bare area of **Nototriche** desert inhabited by **Ctenomys** (one per acre) is surrounded by bunchgrass **(Festuca orthophylla).** For closeup view see figue 4. (Parte del área de censo de 5 hectáreas de **Ctenomys opimus.** El sitio desnudo de desierto de **Nototriche** habitado por **Ctenomys** (2.5 por hectárea) está rodeado de gramíneas **(Festuca orthophylla).** Para la misma vista de cerca, vea la figura 4).

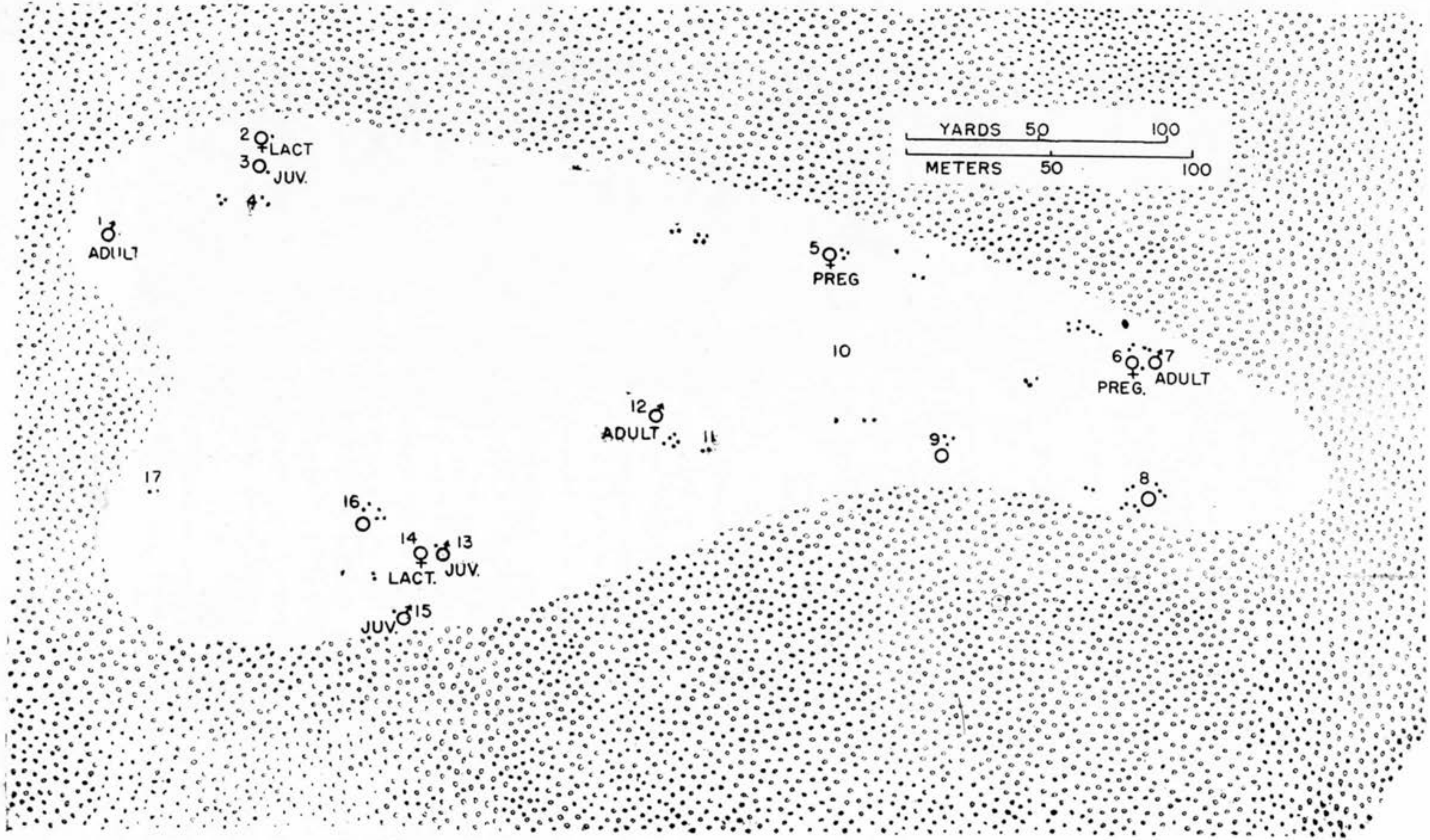

Fig. 12. Location of tuco-tucos (open symbols) and of fresh burrow openings (dots) on the 12.4-acre census area at the time of the first census. (Sitio de tuco-tucos (símbolos abiertos) y de aperturas nuevas de madrigueras (puntitos) en el área de censo en la ocasión del primer censo).

by trap but escaped at 16, 2 still digging at sites 8 and 9), and 3 juveniles (captured at 13 and 15, seen at 3). This gives a population density of approximately one tuco-tuco per acre, or 290 grams of tuco-tuco per acre, and shows that a count of fresh earth mounds can give a good indication of the number of tuco-tucos living in this kind of habitat. If the count is made late in the morning, each set of fresh mounds indicates the presence of one tuco-tuco.

The area was visited again on april 17, when four tuco-tucos were removed and three others were caught in traps but succeeded in tearing loose. No more were captured in the next two days of hunting and trapping, and no fresh mounds of earth had appeared by April 22, when we left the area. These results indicate that on the area where three tuco-tucos remained in January (at sites 4, 8, 9), seven were probably present in April. Of these seven, two, judging by their location, were probably untrapped survivors from January (a juvenile female at 4 and a parous female at 9), leaving five as the number of tuco-tucos that had invaded and remained on the area in three months. One of these presumed invaders was a young adult male (at site 10), and one a young nulliparous female (site 11).

In another desert nearby where tuco-tucos were unusually abundant, six fresh sets of diggings were watched for several days in mid-January, 1952. If each set were to be connected with the adjacent by a line, a polygon would be formed with sides 27, 20, 41, 23, 16, and 32 meters long. These distances are a measure of the spacing of individual *opimus* in the densest population that we encountered. If, over a large area, each tuco-tuco was separated by 27 meters from its neighbors, the population density would be 17 per acre.

CTENOMYS PERUANUS

Ctenomys peruanus is on the average 10 to 15 per cent longer, depending on the sex, and 30 to 60 per cent heavier than *opimus*. It can be recognized by its pale color and by the fact that the hind feet are much darker than the back, sides, and rump. In the field it distinguishes itself by its bubbling call. I have encountered *peruanus* in two places: the broad flat valley of the Rio Callacame about 8 kilometers northwest of Huacullani, 12,600 feet, and on the

Pampa de Queullacota, 13,200 feet, 65 kilometers SSW of Ilave. Both places are level, heavily grazed plains with little vegetation more than an inch high (fig. 13), but nevertheless because of the lower altitude better clothed with small grasses and forbs than the habitat of *opimus*. Scattered clumps of taller bunch grass dot the pampa near Huacullani, but few tuco-tucos live in the places where these clumps are numerous. On the Pampa de Queullacota a few clumps of *Stipa* and a few 20-cm. thorn bushes *(Margyricarpus)* remain despite heavy grazing by alpacas and llamas. The soil on this pampa is gravelly, whereas that on the pampa near Huacullani is gray and somewhat clayey.

Digging.— *Ctenomys peruanus* does much less digging than *opimus*. The number of *peruanus* holes per unit area may be greater, but this reflects not more digging activity but a greater concentration of individuals and burrows that are more permanent. *Ct. peruanus* is colonial. Once a set of tunnels with a couple of dozen openings has been made, several adults may live in it for many days or weeks with little more digging. *Ct. peruanus* will leave its burrow a meter or more while feeding, whereas *opimus* would extend its tunnel rather than expose itself to this extent.

The burrows of *peruanus* are similar to those of *opimus* in that they course close to the surface of the ground, seldom deeper than a third of a meter, but differ by having many more branches than do *opimus* tunnels and smaller earth mounds at the openings. One *peruanus* tunnel that we excavated branched nearly three times for each meter of length. Two chambers were found in this tunnel, one almost filled with droppings, the other containing what appeared to be a nest. The nest chamber was about 30 centimeters in diameter, 15 centimeters high, and 15 centimeters below the surface. The floor was covered with about 6 centimeters of grass tufts among which were a few droppings and numerous staphylinid beetles.

Feeding.— Unlike *Ctenomys opimus*, *peruanus* does not emerge until the sun is well up. Digging, at least above-ground indication of digging, occupies only a small part of the day. Almost all of the surface hours are devoted either to feeding or to peering quietly out of the burrow. *Ct. peruanus* creeps a meter or more from its burrow to scratch and nibble at dwarf vegetation such as *Muhlen-*

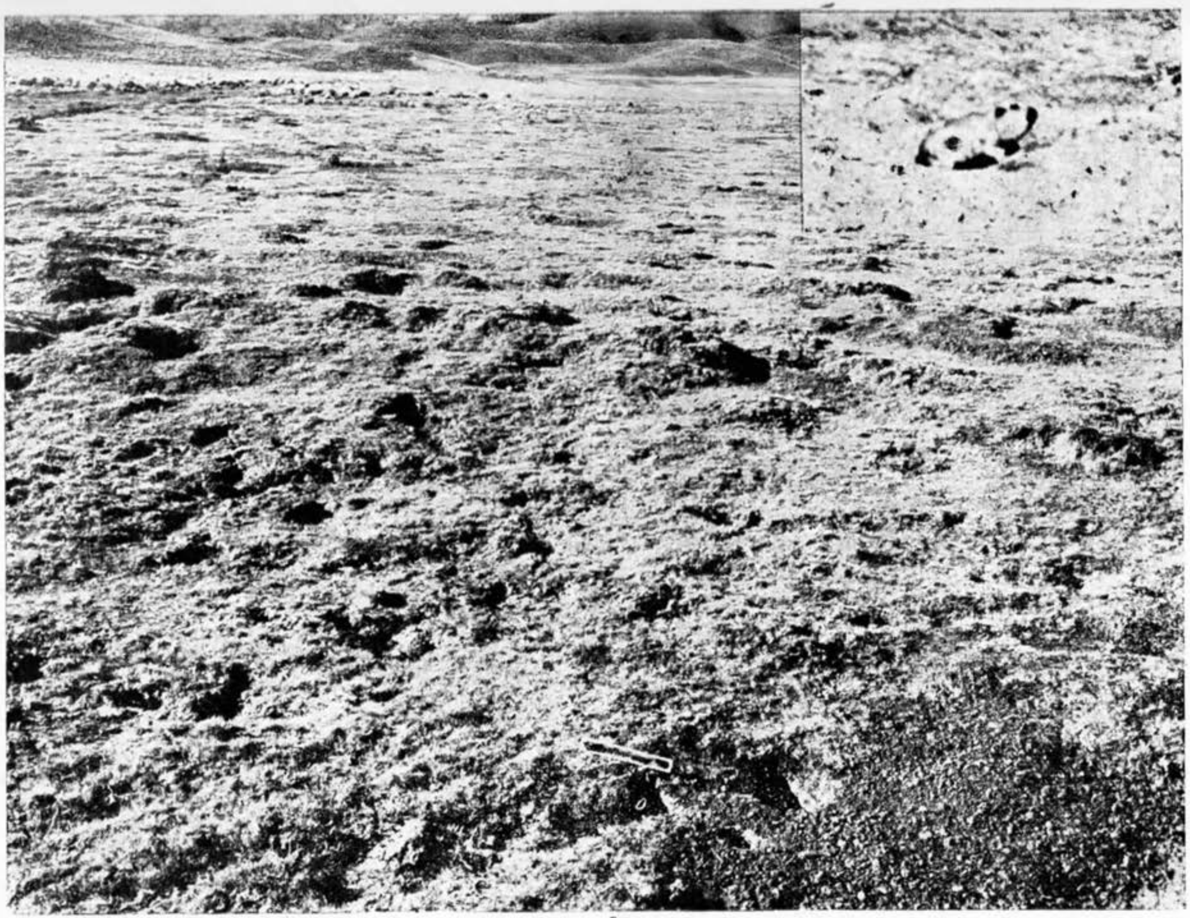

Fig. 13. Census area riddled with burrows of **Cteno mys peruanus** and supporting a population of 17 per acre; April 10, 1952; Hacienda Pichupichuni, 12,600 feet, Department of Puno, Peru. Six-inch ruler and fresh burrow in foreground. Insert: **Ctenomys peruanus** feeding. (Area de censo agujereado de madrigueras de **Ctenomys peruanus** y manteniendo una populación de 42 por hectárea. Regla de quince centímetros y apertura recién-hecha a la delantera. Inserto: **Ctenomys peruanus** comiendo.

bergia fastigiata, Calamagrostis vicunarum, Geranium cucullatum, Oreomyrris andicola, and *Naussauvia*. Unlike *opimus* it does much actual chewing and swallowing out on the surface. When it retreats it usually does so by scuttling backwards into its burrow.

As a result of its different feeding habits, *peruanus* spends more time above ground than *opimus* does. On an area occupied by 29 *peruanus* as many as 16 were sometimes visible at one time, whereas I never saw more than 3 *opimus* at one time on the census area that contained 13 individuals.

Vision.— On one occasion a *Ctenomys peruanus* fled down a burrow when a large hawk flew overhead. On another occasion, a *peruanus* did not react when a large gull flew overhead. These incidents suggest that vision is acute enough to distinguish between hawks and gulls.

Voice.— *Ctenomys peruanus* is the only one of the Peruvian tuco-tucos that vocalizes conspicuously. While *opimus* may grunt or snort when it is being pulled out of a hole in a trap, and sometimes makes a soft fluttering sound at the instant that it pops down a hole when frightened, it cannot equal the musical bubbling sound used by *peruanus* as a warning call. This sound, which probably gave rise to the name tuco-tuco, is made by an animal at an entrance to its burow while it nervously watches a person intruding nearby, and it is made also by the animals underground while a person walks above them. It is made by young only a few days old as well as by adults. The tuco-tuco frightened by the hawk made the bubbling sound while retreating. The sound is reminiscent of that made by liquid poured from a bottle. Hudson (1892), writing of another species, describes it as sounding "like a succession of blows from a hammer; as if a compay of gnomes were toiling far down underfoot, beating on their anvils, first with strong measured strokes, then with lighter and faster...".

Reproduction.— Despite the fact that specimens of females are available only from September through April, certain conclusions about the annual cycle of reproduction can be drawn. None of three females of mature size captured in September was pregnant or lactating (fig. 14). Of three adult females captured in December, all were early pregnant. One of them contained a 2-celled ovum in the oviduct and in the other two, large implantation swellings

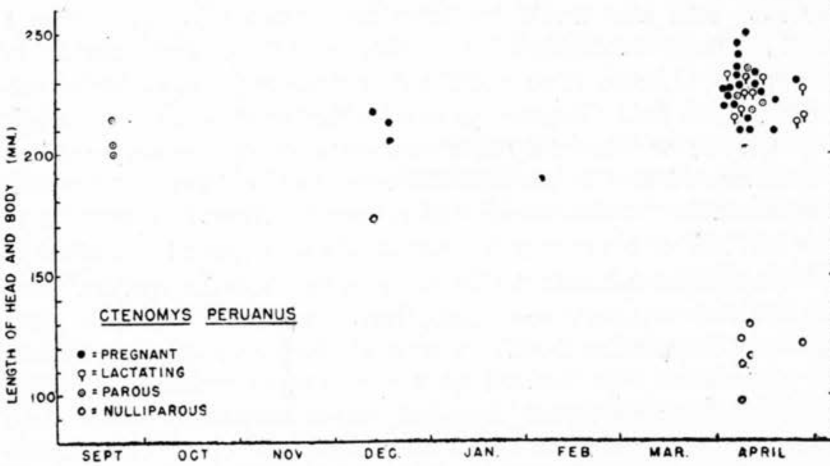

Fig. 14. Reproductive condition of females of **Ctenomys peruanus.** (Condición reproductiva de hembras **Ctenomys peruanus**).

were visible in the uterus, but the embryos in them were not yet detectable macroscopically. The breeding season, therefore, had probably commenced only a short time before, probably late in November. Most of the adults taken in April were either late pregnant or recently parturient, and the juveniles captured in April had been born in March or early April. Since no young two or three months old were captured in the April sample (fig. 14), it is unlikely that females mating late in November had given birth to one litter and become pregnant again in time to be represented as pregnant or lactating in the April sample. Consequently, it appears that gestation lasts almost 4 months. If a larger September sample confirms that no juveniles are present in the population at this time, then it may be further concluded that there is only one litter produced by each female per year. Recently parturient and lactating females collected in April had only old corpora lutea, so there is no post-partum ovulation at this season. Since all of the grown females in the April sample were pregnant, lactating, or, judging by the appearance of the nipples and uterus, parous, it is clear that young become pregnant in their first year, give birth at about the same season as older individuals, and continue to reproduce in each subsequent year.

Females have three pairs of nipples. Nineteen pregnant females carried from 1 to 5 fetuses (average 3.5). Twelve per cent of these embryos, however, were being resorbed, so that the average litter size would not have been more than 3.1 (range 1 to 5). Thirty-six implantations were in the left horn and 27 in the right. Corpora lutea could not be counted reliably by examination in the field. Among the ovaries that were serially sectioned, 31 embryos or placental scars resulted from 35 ovulations, giving an apparent loss of 11 per cent of the ova (but making no allowance for resorption or abortion of entire litters). Several specimens in the first half of pregnancy had an excess of corpora lutea, some of which appeared histologically to be older than the corpora lutea of the current pregnancy, and these less active corpora lutea were not included in the above counts. Such corpora were present in a specimen with 2-celled tubal ova, and so probably represent corpora lutea surviving from an earlier ovulation rather than accessory corpora lutea of the kind found in certain other hystricomorph rodents such as the mountain viscacha and the porcupine.

The vaginal opening is sealed in many but not all specimens in early, middle, and late pregnancy and during lactation. It recloses in many indivduals during lactation and probably remains closed until the next estrus.

The pubic symphysis was not open in nulliparous, pregnant, or parous females. The pubic contact is not solid bone in either males or females and possibly relaxes to some extent in females at the time of parturition, but the two innominate bones are never widely separated as in parous females of gophers and many other rodents.

The following male *peruanus* are available for analysis of reproduction: 1 in September, 5 in December, 3 in February, and 15 in April. The September specimen was the smallest male collected (head and body 207 mm.) and had 12-mm. testes which, unfortunately, were not examined for presence of spermatozoa. All of the other specimens had testes between 15 and 22 mm. in length. Since several indivduals with testes 15 and 16 mm. long were producing spermatozoa and had moderately large seminal vesicles, it is probable that all of the December, February, and April specimens were fertile. This included individuals of age classes 2 through 6. I conclude that males born in March and April are sexually mature before the breeding season in the following December and that they, as well as older males, remain fertile through April at least.

Testes of *Ctenomys peruanus* are surprisingly larger than those of *opimus*, which never reached a length greater than 12½ mm. The bacula and seminal vesicles of *peruanus* are also considerably larger than those of *opimus*.

Judging by degree of closure of the epiphyses of the humeri, there are at least two age classes in the population during April, in addition to newborn young. It is likely, therefore, that many individuals live at least two years.

The young of *Ctenomys peruanus* are well-developed at birth. In three late-pregnant females, the fetuses were well-furred and the largest in each of them measured: total length, 132, 128, 126; tail, 40, 37, 37; hind foot, 21, 22, 22; weight in grams, 35, 36, 33. The two smallest young captured above ground measured: total length, 138, 143; tail, 41, 38; foot, 22, 23½; weight, 35, 37. These active young were scarcely larger than the fetuses, yet they were able to give the bubbling sound of the adults and had considerable amounts of green vegetation in their stomachs. Obviously, lactation plays a minor role. Their pelage, unlike that of young *opimus*, was the same color as that of adults.

Adult males are usually larger than adult females. The following measurements are the average, smallest, and largest of specimens of age class 3 or older. Ten males: total length, 326 mm. (295-346); tail, 84 (81-88); hind foot, 40.0 (38-42); weight, 562 grams (418-663). Twenty-two females of age class 3 or older: total length, 308 (280-333); tail, 78 (67-88); hind foot, 38.5 (37-41); weight, 462 (340-663). The skin of the males is thicker and tougher in the neck region, especially over the throat, the skulls more massive, and the incisors broader.

Associates and parasites.— Several vertebrates use the burrows of *Ctenomys peruanus*, including toads *(Bufo spinulosus)*, lizards *(Liolaemus multiformis)*, mice *(Akodon jelskii, Galenomys garleppi, Phyllotis boliviensis)*, and a sparrow-sized bird, the puna miner *(Geositta cunicularia)*. On one occasion I wounded one of these birds in the middle of a colony of *Ctenomys peruanus*. It promptly ran into a *Ctenomys* burrow. As I approached, a lizard *(Liolaemus)* also ran into the same opening. I marked the burrow and went to get a shovel. When I returned and started to dig, the bird emerged from another hole about two meters away. These birds not only seek shelter but nest underground. Possibly they use *Ctenomys* burrows for nesting, although they are said to be able to dig their own burrows and are certainly able to live in areas where there are no tuco-tucos.

The most important associate is a guinea pig, *Galea musteloides*, which lives in close association with *Ctenomys peruanus* but probably not in the same burrows at the same time. Guinea pigs are not powerful diggers and therefore make use of burrows dug and abandoned by *Ctenomys*. Where tuco-tucos are numerous, the guinea pigs seem to live primarily on the periphery of the tuco-tuco colony, but neverthless they graze frequently only a few feet from grazing tuco-tucos. Only once have I seen a conflict between the two species. A tuco-tuco ran toward a guinea pig that was feeding a meter away, and the quinea pig retreated. Since both species are diurnal and of the same size they probably have the same predators. Guinea pigs, however, are less shy, spend more time on the surface, and venture farther from their burrows, so they are more vulnerable to predation. They probably pay rental on their *Ctenomys-dug* burrows by satisfying the appetites of foxes *(Dusicyon culpaeus)*, dogs, cats, and hawks *(Buteo)* that hunt over these pampas.

Numerous specimens of *Ctenomys peruanus* contained clusters of larval tapeworms free in the abdominal cavity. These larvae were accomplishing an unusual, asexual, exogenous multiplication (Voge, 1954). Other parasites collected from *peruanus* were fleas *(Dysmicus* n. sp. Johnson, *Tetrapsyllus* n. sp. Johnson), chiggers, and staphylinid beetles *(Edrabius peruanus* and *Megamblyopinus germaini)*. The last species was found in what was either a nest or a food storage chamber.

Census.— A study area 82 meters square (1.68 acres) was marked off on the pampa near Huacullani (fig. 13). It was in the center of about 50 acres of similar terrain that supported the densest population of tuco-tucos that we encountered anywhere in Peru. The ground surface was well covered by two kinds of short grasses *(Muhlenbergia fastigiata* and *Calamagrostis vicunarum)* and mats of a prickly-leafed forb tentatively identified from sterile material as a *Naussauvia*. Less abundant were *Oreomyrris andicola* and *Geranium cucullatum*, two rosette-shaped species that scarcely protrude above the ground. A typical 3 x 3-foot area (.84 m^2.) was excavated and all the plant material including roots washed free of dirt and dried. After allowing for loss of some rootlets and leaves during the washing, an estimate was made of the amount of dry plant material present (Table 1).

On April 7, 1952, I counted 245 "very fresh" burrow openings and 319 "fresh" openings on the census area. Very fresh openings showed by the presence of fresh earth or of fresh feeding scratches that they had been used that day, although they may have been opened much earlier; fresh openings appeared to have been used within the last two or three days. Old, apparently unused holes were not counted. Shortly after making the hole-count, I examined the area with binoculars and saw 16 *Ctenomys peruanus* above ground, no guinea pigs. A sweep with the binoculars covering about 90 degrees of the pampa, including the census area, disclosed more than 90 tuco-tucos and about half as many guinea pigs. The following tuco-tucos were then collected from the census area by shooting: 7 on April 7, 14 on April 8, 4 on April 9, and 3 on April 10, a total of 28 weighing 10,952 grms. One adult was known to remain and, judging from the 8 lactating females that were collected, some young may have been overlooked. A few tuco-tucos were shot outside of the census area but within a few yards of its boundary. These are not included in the census. No tuco-tucos seemed to move in from the heavily populated terrain surrounding the census area, although a few guinea pigs were seen on the area during the last two days of collecting.

This almost complete sample removed from a large population contained 5 young females less than a month old, 17 females from age class 2 to 6 (almost all of them pregnant or lactating), and 6 breeding males of age classes 2 to 6. The points of capture of females were scattered throughout the area in what appears to be a random manner (fig. 15) with no tendency toward the even spacing that would result from territorial defense. In fact, four young lactating females were taken within eight meters of a central point. The males were more widely spaced, the closest two being 15 meters apart.

Counting the number of holes showing fresh digging activity was obviously unsatisfactory for censusing this species.

The area was revisited 18 days later. It was immediately apparent that the census plot had been repopulated, not by tuco-tucos but by guinea pigs. A dozen or more guinea pigs were visible on the plot at one time and were using the burrows. Only

TABLE 1. COMPARISONS OF POPULATION DENSITY AND BIOMASS OF TUCO-TUCOS AND GOPHERS. VEGETATION SAMPLES ARE FROM 3 X 3-FOOT PLOTS (0.84 m^2.) AND INCLUDE ROOTS.

Species	Fresh wt. of plants	Dried wt. of plants	No. of animals per acre	Wt. of animals per acre	Gms. of animal per kg. dry plant matter
Ctenomys opimus, Lago Suche, Peru; Jan. 19, 1952.	477 g. [1]	131 g.	1	290 g.	0.46
Ctenomys peruanus, Huacullani, Peru; April 10, 1952.	——	606 [2]	17	6,760	2.30
Thomomys bottae, San Joaquin Exp. Range, Calif., April, 1953.	——	723 [3]	19 [4]	6,570 [5]	1.88

1) Weight of 234 plants washed and air-dried only enough to remove surface moisture. Principal genera **Nototriche, Geranium, Astragalus.**
2) Principal genera **Calamagrostis, Muhlenbergia, Naussauvia, Oreomyrris, Geranium.**
3) Principal genera **Erodium, Bromus, Festuca.**
4) Estimated by Mr. H. E. Childs, Jr.
5) Estimated from preceding column and from data in Howard and Childs, MS.

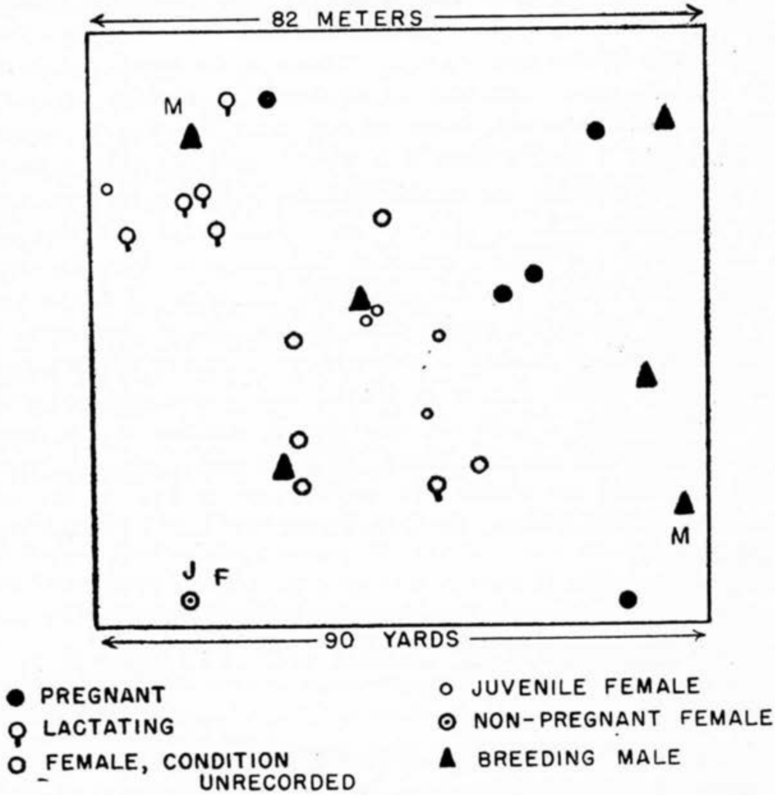

Fig. 15. Sites of capture of **Ctenomys peruanus** on the 1.68-acre census area. Letters represent animals taken on the second census: M represents adult male; F, female; and J, juvenile. (Sitios de captura de **Ctenomys peruanus** en el área de censo de 0.68 hectáreas. Las letras representan animales tomados durante el segundo censo; M representa macho adulto; F, hembra; y J, juvenil).

4 tuco-tucos were on the area: a lactating female and her single young, both taken near where one tuco-tuco was known to remain at the end of the first census, and 2 old males taken elsewhere on the plot. It appears, therefore, that in 18 days the area had been invaded by two male *Ctenomys* and by a dozen or more guinea pigs. This indicates not only that *Ctenomys peruanus* does not disperse rapidly at this season, but that under normal conditions its presence in a burrow system hinders guinea pigs from using that system.

Sex ratio.— Females outnumber males. Our sample from southern Peru, collected entirely by shooting, consists of 22 males and 49 females. On the census area, where all of the resident population was collected, 6 males and 23 females were living. Since among fetuses that were old enough to be sexed accurately there were 20 males and only 10 females, it is obvious that some post-natal environmental factor causes more females to appear in the sample. Possibly there is a much higher mortality of males after birth, or possibly the unbalanced sex ratio can be accounted for by sex differences in territorial behavior. Figure 15 shows that the females do not defend territories and suggests, from the even spacing of the males, that the males *are* territorial. If this is true, in a densely populated region such as the census area some of the males would be pushed to submarginal terrain at the periphery of the colony where danger is greater and where less collecting was done, leaving a high concentration of females at the center of the colony. The sex ratio should be more nearly equal in areas where tuco-tucos are scarce. In confirmation of this, on the less densely populated Pampa de Queullacota we shot 10 males and 10 females.

COMPARISON OF *OPIMUS* AND *PERUANUS*

Although the two species are similar in most respects, there are some interesting differences. *Ctenomys peruanus* has been taken only on flat pampas; *opimus* both on pampas and hillsides and, in southern Peru, always at higher altitudes than *peruanus*. *Ct. opimus* in most places does more tunneling, probably correlated with more sparsely distributed food plants and with the fact that it will not travel on the surface as far from its burrow as will *peruanus*. It also does not stay as long above ground while feeding as does *peruanus*, and thereby would seem to be less vulnerable to predation. The burrows of *peruanus* seem to be more permanent structures with many more short branches and with more openings to the surface. *Ct. peruanus* does not emerge until later in the day than *opimus*.

Important social differences arise from the fact that females of *peruanus* are non-territorial, which permits the development of populous colonies with several adults using the same burrow. Probably correlated with this is the warning sound made by *peruanus; opimus* is solitary and silent. There is some evidence that the *males of peruanus* are territorial and that this coupled with the non-territorial nature of the females permits the building up of a population in which females far outnumber males.

The young of both species are born during or toward the end of the rainy season, with the breeding season of *peruanus* tending to be shorter than that of *opimus*. This tendency for all of the females to give birth in a relatively brief season is perhaps an example of the predator-saturation effect described by Darling (1938), for it is possible that the colonial *peruanus* could "saturate" the local predators and thereby achieve survival of more young, whereas the more widely scattered *opimus* population would gain less by attempting to saturate the predators. The guinea pig associates of *peruanus* are reproducing at the same season and thereby contributing to the saturation effect.

The litter size of *peruanus* is about double that of *opimus*. This would tend to compensate for the fact that *peruanus* spends more time above ground exposed to predators. It does not, however, agree with the fact that the average age of the *peruanus* population, judging by epiphyseal closure, is greater than that of *opimus* (see below). One cannot resist speculating that a sparing effect resulting from the presence of guinea pigs allows a higher percentage of *peruanus* to reach older ages.

Males of *peruanus* are about 1.3 times as heavy as males of *opimus*, yet their testes when mature are more than 5 times as heavy. Ovarian histology is also quite different. An additional difference between the two species is in the juvenile pelage of

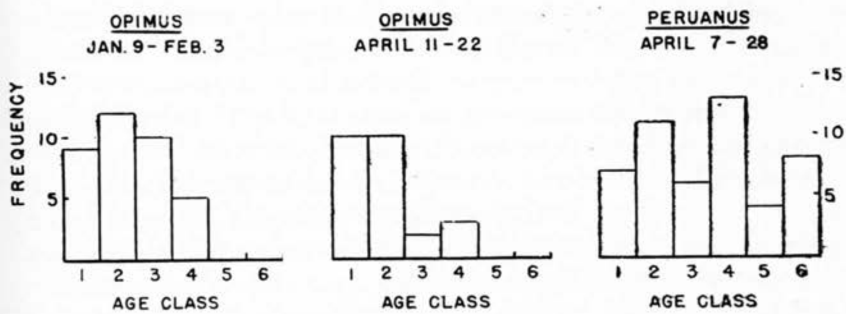

Fig. 16. Distribution of age classes in populations of **Ctenomys opimus** and **peruanus.** (Distribución según las edades en populaciones de **Ctenomys opimus y peruanus**).

the young. In *peruanus* this pelage is quite similar to that of the adults, but in *opimus* it is black and silky.

It may be seen in figure 16 that age structure based on epiphyseal closure is quite different in populations of the two species. Most *opimus* humeri fall into the youngest three classes and none into classes 5 and 6 whereas half of the *peruanus* humeri were class 4 or older. Either there is a species difference in the rate of closure of the epiphyses or a great difference in the age structure of the populations at comparable times of year. I think it less likely that growth and skeletal maturation should be so different in two related species of similar size than that the population structure should differ, so am inclined to interpret figure 16 to mean that few *opimus* reach the older age groups whereas many *peruanus* do. This is somewhat surprising because the presumably shorter-lived *opimus* also has a smaller litter size and lower reproductive potential.

CTENOMYS LEUCODON

Ctenomys leucodon is known only from two localities in Peru about 15 kilometers apart and from nearby in Bolivia. It can be distinguished from the other two Peruvian species by its paler, more procumbent incisors. I have encountered it only once, on April 29, 1952, 10 kilometers southwest of Huacullani, 12,900 feet, where a dozen or more indivduals were living on a few acres of gently sloping grassland. The individuals were non-vocal and made large earth mounds, thereby differing from the *peruanus* that lived only 12 kilometers away, and they were at a lower altitude than *opimus* in this area. *Ctenomys opimus* was living, however, at 14,000 feet only 45 kilometers to the southwest and at 13,000 feet 45 kilometers to the west. One *Ct. leucodon* was trapped and two shot from this population. All three were parous, non-pregnant females and measured: total length, 285, 262, 264; tail, 79, 68, 67; hind foot, 36, 35, 34; weight, 268, 248, 258. The pelvis of one of these was examined; the two public bones were in contact but not fused together. The three other known Peruvian specimens are also females and came from a colony about 15 kilometers away where they were associated with guinea pigs (Sanborn and Pearson, 1947).

DISCUSSION

If one were assigned the task of designing a rodent capable of filling as completely as possible a subterranean niche, one would have to consider many fascinationg engineering and behavioral problems such as optimum body size, locomotory devices and techniques, food sources, information receiving and sending equipment, self-preservation mechanisms and habits, waste disposal, methods of reproduction, the assuring of sexual contact or else modification of the sexual cycle so that infrequent meetings are sufficient, and safe methods of dispersal. When more is known of the biology of the various successful underground species we shall be able to compare and contrast the ways in which all of them have responded to the peculiar demands that their environment has made on them. I shall compare primarily the Peruvian tuco-tucos and the North American gophers (especially *Thomomys*), both of which have adopted a subterranean-herbivorous way of life that results in many behavioral and anatomical similarities and a few interesting differences. Comparison of the two forms gives some insight into which characteristics are truly adaptations for underground life and which are relatively non-critical familial legacies.

Underground movement and digging.— Most subterranean mammals, no matter what their diet or ancestry, are in the comparatively small size range of 50 to 1000 grams. This leads one to suspect that there is a rather strictly determined optimum size and that animals much smaller or much larger than this find tunneling bioenergetically too expensive. It would not be unexpected, of course, to have a slightly different optimum in sand than in clay, or in cold than in warm soils. The size range of adults of the various species of *Ctenomys* is almost the same as among the species of gophers. The Peruvian tuco-tucos are among the larger *Ctenomys* and are of a size comparable to some of the larger *Geomys*. Several authors mention a tendency for gophers in shallow or stoney ground to be small, and for gophers at high altitude to be smaller than representatives of the same species at lower altitudes (see especially Davis, 1939). The altitudinal range of *Ctenomys peruanus* is not great enough to permit such analysis, and no tendency can be shown with available specimens of male *opimus*, but females of *opimus* ranging from 13,300 to 15,400 feet in Peru show a slight tendency toward decreased size at the higher elevations. It is clear, however, that the tuco-tucos living at highest elevations, such as *Ct. fulvus* and *opimus*, are not dwarf forms. They are some of the largest members of the genus. However, despite the altitude they usually live in deep soils.

In addition to the mechanical problems and other influences that act together to determine the optimum body size is sex. In tuco-tucos as well as in gophers the males are larger than the females. Presumably one of the two sexes is closer to the optimum size for tunneling, and the other sex has become larger or smaller for reasons associated with its sex. If we assume that females are of optimum size for digging, and if courtship and copulation occur in the female's burrow system, as claimed for *Thomomys* by Wight (1930), an upper limit is imposed on size of males by the diameter of the tunnels dug by the females. If we assume that males are of optimum size for digging and that females find some special advantage in being smaller, perhaps to allow for increased girth during pregnancy, then a lower limit is imposed on female size by the diameter of tunnel into which the male can follow her. Unfortunately we know far too little about where and how the sexes encounter eachother to allow us to speculate profitably on this subject, for Howard and Childs (ms) disagree with Wight and say that female gophers probably enter the burrows of males for mating.

The burrow systems of the various subterranean rodents such as *Thomomys* (Storer, 1942), *Geomys* (Smith, 1948), *Ctenomys* (Eisentraut, 1933; Escariz de Peverelli, 1952), *Heterocephalus* (Hill, Porter, Bloom, Seago, and Southwick, 1957), *Spalax* (Ognev, 1947), and *Myospalax* (Grassé and Dekeyser, 1955) are quite similar despite differences in digging techniques. Perhaps the most unusual tunnel system is that made by *Spalax* in some regions. By packing the excavated earth into the walls with powerful thrusts of the horny padded nose, this animal can complete a burrow without disposing of any earth on the surface (Montagu, 1924). In other regions *Spalax* makes conspicuous piles of earth (Reed, 1958).

The general similarity of the burrow systems is especially surprising in view of the fact that a long, meandering, branched tunnel is by no means the only efficient method of finding plant food. Some populations of subterranean rodents live almost entirely on underground roots and tubers. If a mining engineer wished to recover, without exposing himself above ground, a great number of ore pockets that were close to the surface, more or less evenly dispersed, and not detectable from a distance, he might, if the ore pockets were closely spaced, make one or more large underground chambers at the depth at which experience taught him to expect to encounter the most ore. Even if the ore pockets were widely spaced there would be little gained by constructing a long meandering tunnel in the fashion of subterranean rodents. The fact that the rodents tunnel as they do suggests that they may be able to detect and localize their food items from a distance (either from below ground or from the exits), that they have not been able to solve the mechanical problem of supporting the roof of a large chamber and would be at a disadvantage if it collapsed, or that the shape of subterranean rodent burrows is influenced largely by needs other than food gathering. Possible advantages of the tunnels of rodents over the block excavation of the engineer would be more-certain encountering of the sexes, more rapid dispersal of the species into new terrain, and less serious impact on the flora. Food collection from meandering tunnels can, however, have a drastic effect on the flora, as shown by the total removal of Festuca by *Ctenomys opimus* (fig. 3), although in this example the animal probably locates plants partly by visión.

The burrow systems of gophers and tuco-tucos are in general quite similar in plan, extent, and depth. Both animals make similar earth mounds, frequently plug the exits with earth, and sometimes have inconspicuous feeding holes unmarked by excavated earth. Although the amount of earth excavated varies with different species and with different habitats, in general it seems that gophers and tuco-tucos do about the same amount of digging each day. It would be difficult to say which was the better digger.

Gophers, tuco-tucos, and others construct along their tunnel systems various small chambers that are sometimes called nest chambers, storage chambers, and latrines. The Peruvian tuco-tucos construct nest chambers and food storage chambers, but I have found no latrines. Droppings seem to be deposited in the other chambers and are not sealed off in special side chambers. Also, the Peruvian tuco-tucos do not seem to store such large amounts of food as do some of the other subterranean rodents such as *Myospalax*. This lack of emphasis on food storage may be correlated with the fact that winters are not long and severe in Peru.

Above-ground movements.— Gophers and tuco-tucos are so short-legged and heavy-bodied that they cannot move rapidly or easily on the surface of the ground. Nevertheless, the gopher *Thomomys* frequently moves on top of the ground, especially during the season when the young are dispersing. Apparently the gain to the species of a relatively rapid and widespread dispersal more than compensates for what must be a heavy loss to predators. At other seasons, dispersal of *Thomomys* is slight (Ingles, Clothier, and Crawford, 1949). *Myospalax* apparently disperses above ground also, but I do not know to what extent tuco-tucos do so. Judging from the frequent occurrence of *Thomomys* bones in owl pellets, gophers come above ground at night more frequently than do tuco-tucos.

Anatomy.— Anatomical similarities between gophers and tuco-tucos are impressive. Many features, such as small, dorsally placed eyes, small ear pinnae, short limbs, short stubby tail, and long claws on the front digits clearly are adaptations to subterranean life. Other similarities such as the skin of the body being very loose and the tail vertebrae being difficult to pull out of the tail sheath when skinning the animal are possibly associated with underground life, but less obviously so.

Despite the great number of species, the pelage colors of gophers and tuco-tucos are seldom gray and tend to be brown or blackish, presumably matching the dark color of the fresh earth ejected at the burrow openings. This matching coloration in tuco-tucos as well as gophers suggests that an important amount of predation on both species occurs at the mouth of the burrows.

Gophers, tuco-tucos, and most other subterranean rodents have broad, robust skulls with heavy incisors. Among gophers this is probably associated with digging, for they use their incisors for loosening dirt and for gnawing through underground obstructions. I do not know whether tuco-tucos use their teeth for digging. Gophers and tuco-tucos are both able to close the lips behind the incisors to keep dirt out of the mouth. The most obvious external difference between the two kinds of animals is the absence of cheek pouches in *Ctenomys*. Many non-fossorial heteromyids have cheek pouches homologous to those of gophers, so the pouches of gophers are not necessarily adaptations for subterranean life.

Almost all digging mammals including gophers and tuco-tucos have long claws on the front digits, but in some diggers such as moles the claws are blunt, broad, and flattened in the plane of the palm whereas in gophers and tuco-tucos the sides of the claws are bent down and meet ventrally in a long sharp ridge to give the claw the appearance of a curved knife. Mole claws seem adapted to scraping or scooping, gopher and tuco-tuco claws to scratching or cutting. The claw on the first digit of tuco-tucos and many gophers is not knife-like, but more like a nail. The front claws of *Ctenomys opimus* seem to grow at about the same rapid rate as those of *Thomomys* (Howard, 1953).

The front feet of gophers are better equipped with fringes of hair than those of tuco-tucos, but tuco-tucos have more luxurious fringes on the hind feet than do gophers. This reflects the different digging techniques of the two. Tuco-tucos sweep dirt out of the tunnels with the hind feet, whereas after a few preliminary sweeps with the hind feet, gophers, using the head, chest, and front feet, push it out in the manner of a bulldozer. The above-ground dirt-disposal process, accomplished by *Ctenomys opimus* with the hind feet (fig. 6), is accomplished bulldozer fashion by *Thomomys* (Sagal, 1942) and presumably by other species of gophers also.

Gophers also lack the toe bristles that tuco-tucos use to clean dirt out of their fur, but since many non-fossorial hystricomorphs have them, these bristles need not be considered an adaptation for underground life.

The plush-like fur of moles is thought to be a subterranean adaptation that permits an animal to move backward or forward in a tunnel without mussing the coat. Neither gophers nor Peruvian tuco-tucos possess such fur. In fact, the fur of many species of tuco-tucos is quite long and lax.

Food.— All subterranean mammals seem to be either highly carnivorous, like moles, or herbivorous; few take full advantage of both the plant and animal food that they may uncover during their tunneling. Presumably their digestive systems have become too highly specialized to take advantage of what would seem to be an obvious way to ease the burden of food gathering. Tuco-tucos and gophers are both highly herbivorous and utilize roots, stems, leaves, blossoms, and fruits of a wide variety of plants. They encounter food during their tunneling and gather it also on the surface near the burrow openings. *Ct. peruanus* does some of its eating while exposed on the surface, but *opimus*, like *Thomomys*, almost always cuts the food items and retreats with them into the burrow to eat them. Lacking cheek pouches, tuco-tucos would seem to be at a disadvantage when transporting food. Both gophers and tuco-tucos store small amounts of food.

Many tuco-tucos and gophers survive in places where there is no standing or running water and no rainfall for several months of the year. Their water needs must be supplied by their diet of vegetation, possibly supplemented with dew, and they must lose water relatively slowly in their humid, subterranean niche.

Bioenergetics.— The energy problem faced by subterranean mammals is essentially that of balancing food intake with the energy used in activities such as basal metabolism, physical activity, lactation, and temperature regulation under thermal stress. Since tuco-tucos and gophers are about the same size and are not known to hibernate, their basal metabolic rates are presumably about the same. They are both well-furred and therefore probably able to withstand cold temperatures without a serious rise in metabolism, although, actually, because of their subterranean habits they are seldom exposed to very cold temperatures and almost never to temperatures warm enough to cause them to expend energy to keep cool. The existence of *Heterocephalus*, a small, completely hairless subterranean mammal unable to adjust to cool or even moderate temperatures (Hill *et al.*, 1957) demonstrates how slight the thermal stress of subterranean life can be. Because Peruvian tuco-tucos live in tropical latitudes, they meet a more equable temperature in the ground than do most gophers, and by being diurnal they avoid the below-freezing temperatures common above ground at night at the high altitudes at which they live.

In the matter of activity, subterranean mammals have special problems. Most non-fossorial small rodents live an easy life surprisingly free of physical exertion, but gophers and tuco-tucos pay for the relative safety of subterranean life with the physical labor of tunnel construction, and this costs additional food. The more they eat the more they must tunnel, and the more they tunnel the more they must eat. The metabolic expense of tunneling can be estimated as follows. The basal metabolic rate of *Ctenomys opimus* is probably about 33 Calories per day, or 1.38 Calories per hour. If the net energy derived from a gram of dry food were 2.3 Calories (Brody, 1945:34), *opimus* would require 14.4 grams of dry food to support its basal metabolism each day. This would amount to the standing crop on about 900 square centimeters of the *opimus* census area in *Nototriche* desert. If a tuco-tuco should dig for one hour each day at a metabolic rate five times the basal rate, this would use 4 x 1.38 = 5.5 Calories that would not otherwise be expended and which could be supplied by about 2.4 grams of food. All of the plants from approximately 150 square centimeters of additional land would be needed to supply this extra energy for burrowing. This would not make a serious impact on the total plant resources. Even if the total daily metabolism averaged three times as much as the basal metabolism (3 x 33 = 99 Calories per day), and even if half of the plants were inedible or were wasted (2 x 99 = 198 Calories), this much food could be supplied for a month by the standing crop on 16 square meters, an area amounting to only 1/250 th of that available to each tuco-tuco on the census plot. It seems, therefore, that the safety of subterranean life is achieved by tuco-tucos at relatively little metabolic cost.

Tuco-tucos living at high altitudes meet the problem not only of supplying calories for strenuous activity, but oxygen. They probably have circulatory and respiratory adaptations for labor at high altitude, but these have never been investigated.

Senses.— Because certain sense organs of successful and highly specialized subterranean mammals are atrophied, one is tempted to believe that it is an advantage for subterranean animals to lose, for example, their vision. Actually, a blind mole is a handicapped mole and has been able to survive only because it seldom emerges. If it could be equipped with acute, trouble-free vision, its probability of survival would be increased. An airplane with radar and radio equipment is a better airplane with a greater life expectancy —if the engineers can install these electric sense organs without impairing the plane's flying ability. A blind or even half-blind subterranean mammal is an example of incompetent design. Vision in both *Ctenomys opimus* and *peruanus* is good enough so that they can see a moving human as much as 50 meters away. From the safety of their burrow entrance they will watch someone stalking them. If vision were inadequate they would not dare to expose themselves in this fashion. Gophers probably do not see this well. The warning system ot the semi-colonial *Ct. peruanus* involving the bubbling warning call is probably set off by visual perception of approaching danger by one of the peripheral members of the colony.

Subterranean mammals must not only orient themselves underground but, since they are in most instances solitary, they should be able to locate eachother easily, especially during the breeding season. What would seem to be the easiest method of locating and identifying the sex of a possible mate is by listening for appropriate calls, but calling does not seem to be used for this purpose by any of the subterranean mammals. Perhaps the sense of hearing is dull. The ear pinnae are slightly larger in vocal *Ctenomys peruanus* than in the non-vocal forms *Ct. opimus*, *Ct. leucodon*, and gophers.

Another possible method of communication is by scent. Above-ground scent dissemination is probably not used by any of the subterranean mammals, but it is quite probable that they leave characteristic odors in their tunnels by which another animal intersecting that tunnel could indentify the sex of the occupant. Moles have well-developed skin glands that may be used for this purpose, but gophers and tuco-tucos do not have conspicuous skin glands. *Ctenomys* does, however, have fairly large anal glands (Pocock, 1922) but these do not produce an odor strong enough to have caused comment by scientists.

Reproduction.— One would expect the reproductive cycle of a solitary, seasonal breeding, subterranean mammal such as a gopher or a tuco-tuco to be adapted to the uncertainty of encountering a mate at the proper time. Of the various kinds of estrous cycles known in other mammals, the most suitable would seem to be that in which the female comes into heat and remains receptive until the stimulus of copulation causes her to ovulate (induced ovulation). With this kind of a cycle she would be ready to take advantage of any chance encounter with a breeding male. Should the females of the species be spontaneous ovulators, they should at least have a series of ovulatory cycles in the event that they do not meet a fertile male at the time of the first estrus. Unfortunately, nothing is known about this aspect of the reproductive cycle of any of the subterranean mammals.

Additional reproductive problems are imposed by the narrowness of the tunnels. The girth of late-pregnant females presumably does not increase beyond the bore of the tunnels that they can dig economically. I find no evidence that this limitation is a serious one, however, for none of the burrowing mammals has taken radical steps, such as oviparity, to avoid the problem, and gophers and tuco-tucos, compared with non-subterranean relatives of comparable size, do not seem to have reduced the size or number of fetuses to facilitate passage through the tunnels. Gestation is thought to be about one month in gophers and more than two months in tuco-tucos. A long pregnancy is apparently a non-adaptive characteristic of hystricomorph rodents, unrelated to subterranean habits. It is surprising to find it retained in *Ctenomys* because the long gestation produces relatively enormous, well-developed fetuses, and passage of large fetuses through the birth canal is especially awkward for fossorial species that must keep the hips narrow enough to allow the brawny shoulders to pass them when the mother is turning around in the tunnels. Gophers bear small, helpless young, and birth is facilitated by such extensive resorption of the pubic symphysis that the innominate bones are widely separated. Tuco-tucos bear large, fully furred young that are able to leave the nest almost at birth, and these are born through a relatively rigid pelvic arch.

Since *Ctenomys* young are so precocious, lactation is less important in *Ctenomys* and survival of the young is probably greater than among gophers.

The vaginal opening of both *Ctenomys* and *Thomomys* is closed throughout most of the year, including during pregnancy. This may be an adaptation to prevent entrance of earth during digging.

The gopher *Thomomys bottae* living under natural conditions in the lowlands of California comes into breeding condition after the winter rains have initiated growth of fresh vegetation, and gives birth and raises its young in the spring when green growth is most abundant (Howard and Childs, MS). In the mountains of California, breeding and parturition are delayed until later in the season (Ingles, 1952), presumably to coincide with the later growing season. Southern Peru lies in the Southern Hemisphere, but despite this the tuco-tucos there give birth in about the same months as gophers in lowland California. This coincidence probably arises from the fact that in southern Peru the winter is dry, rather than wet. Accordingly, young tuco-tucos, like young gophers, are born near the end of the rainy season when vegetation is relatively abundant.

The reproductive rate of gophers is low. Under natural conditions *Thomomys bottae* has a single litter averaging 4.6 each year, the young not usually reproducing until they are a year old (Howard and Childs, MS). The reproductive rate of the Peruvian tuco-tucos is prabably even lower. Even if females of *Ct. opimus* bear two litters per year, sexual maturity is reached slowly and litter size is so small that it is doubtful that their reproductive potential could exceed that of most gophers.

Survival.— For the extra metabolic expense of constructing extensive tunnels, a subterranean mammal receives a more equable climate and greater safety from predators. Many gophers such as individuals of *Thomomys*, survive for two or three years (Ingles, 1952; Howard and Childs, MS), and it appears that once adults have established themselves in burrow systems, mortality is low. Approximations of the age of *Ctenomys* arrived at by examination of the epiphyses of the humeri indicate that the population at all times is composed predominàntly of adults that are at least a year old. It is reasonable to assume, therefore, that many individuals live two or more years. This conclusion is reinforced by the fact that the low reproductive rate could not maintain the population if the individuals were short-lived.

Mortality of tuco-tucos is probably caused primarily by predation, particularly by the coyotelike *Dusicyon culpaeus*, wildcats (*Felis pajeros*), skunks (*Conepatus rex*), and hawks (*Buteo*). Gophers must survive predation by North American equivalents of these in addtion to predation by owls, snakes, weasels, and badgers. The Peruvian tuco-tucos are spared predation by these last forms because there are no badgers; weasels and snakes are almost unheard of, and owls are scarce and being nocturnal would have few opportunities to capture tuco-tucos.

Sex ratio.— The two sexes of a solitary animal such as a gopher, in which both males and females reveal their presence by conspicuous earth mounds, are probably represented in collections in about the same proportion as they exist in the wild, although a possibility of bias in trapped samples is introduced by the larger size of the males, which might enable them to pull out of traps more easily than females. Most trapped samples of gophers show a preponderance of females. Females were most numerous in my samples of *Ctenomys peruanus* obtained by shooting and of *opimus* obtained by shooting and trapping. It was suggested earlier that the preponderance of females could be explained in the case of *peruanus* by the non-territorial nature of the females combined with the territorial nature of the males, but this does not apply to *opimus* or to gophers, in which both males and females seem to be territorial. Among gophers the males apparently live more dangerously. Howard and Childs (MS) have shown that male *Thomonys* are shorter-lived than females. Judging by epiphyseal closure of the humerus, the male samples of both *Ct. opimus* and *peruanus* were younger than the female samples (mean age and SE of *opimus* males 2.0 ± 0.2, females 2.4 ± 0.2; of *peruanus* males 3.4 ± 0.4, females 3.8 ± 0.2).

Male tuco-tucos and gophers are larger than females, and this is true in several other genera of subterranean rodents. The bathyergid mole-rats of the genus *Georychus* are apparently an exception (Roberts, 1951).

Territory.— The individuals of most subterranean species live soiltary lives, even among such unrelated groups as moles, marsupial moles, gophers, tuco-tucos, and *Spalax*. In the case of the gopher *Thomomys bottae*, the area occupied by each individual is probably a genuine defended territory (Howard and Childs, MS), and this may be true also for most of the other species and genera. In view of the presumed difficulty of mate-finding during the breeding season, there must be compensating benefits conferred by being solitary. Enforced dispersal of individuals and the consequent reduction of inbreeding may be one of the benefits.

Ctenomys peruanus provides a partial exception to the generally solitary habits of subterranean species. Several adult females of *peruanus* may occupy the same burrow system, although the males seem to be territorial. This arrangement places the burden of pioneering on the males and provides less relief from inbreeding. *Heterocephalus*, the naked rat, is likewise not solitary (Hill *et al.*, 1957).

Population density.— Because population densities of both gophers and tuco-tucos would be expected to vary greatly with both season and habitat, it is fruitless to make more than rough comparisons. In Table 1 the numbers and weights of *Ctenomys peruanus* and *Thomomys bottae* per acre, the amounts of vegetation available to them, and the ratios of animal matter to plant matter are compared and found to be quite similar. The agreement is due primarily to chance selection of the two study areas, but since the study areas were selected because they contained abundant animals we are probably comparing near-maximun population densities of these species under natural conditions. If such is the case it is interesting that the population limit is about the same in the solitary gopher as in the partly-colonial *Ctenomys peruanus* where territorial defense is not very effective in spacing individuals.

A density of one per acre for the territorial *Ctenomys opimus* (Table 1) is probably higher than average for the terrain occupied by this species, just as 19 per acre is higher than average for all terrain occupied by *Thomomys bottae*. It was mentioned earlier in this report that at one place where *Ctenomys opimus* was unusually abundant they were living at a density that, if continued over a wide area, would amount to 17 individuals per acre. I conclude that the upper limit of population density under natural conditions is approximately equal in both of these species of tuco-tucos and in *Thomomys bottae*. No figures are available for *Ct. leucodon*, and I am not familiar with any comparable censuses for the Eurasian and African genera of subterranean rodents.

Speciation.— All of the major subdivisions of the order Rodentia have produced anatomically similar subterranean genera with similar habits. The sciuromorph representatives are restricted to North and Central America, the hystricomorph representatives to South America, the bathyergid representatives to Africa, and the myomorph representatives to Eurasia and eastern Africa (Ellerman, 1956). Non-fossorial representatives of the sciuromorphs, myomorphs, and hystricomorphs are intermixed on the major continents, but, with the exception of *Tachyoryctes* (a myomorph that enters the range of the bathyergids in Africa), no subterranean representative of one of these taxonomic subdivisions meets any subterranean member of one of the other subdivisions. This geographic separation is due in part to the interposition of humid tropics, a life-zone that the subterranean rodents rarely utilize. However, even within any one of these major taxonomic subdivisions there is relatively little overlap of the ranges of the different subterranean genera. In North America, for example, the ranges of *Thomomys* and *Geomys* are for the most part distinct, and in South America the rare, subterranean *Spalacopus* is not known, on the basis of existing specimens, to occupy the same region as *Ctenomys*.

As a further development of the geographic restriction of families and genera, speciation has flourished to an unusual degree among the subterranean rodents. For example, Ellerman (1941) lists 14 species (21 subspecies) of *Tachyoryctes*, more than 21 species of *Cryptomys*, 13 species (19 subspecies) of *Myospalax*, 8 species (27 subspecies) of *spalax*, 53 species (192 subspecies) of *Thomomys*, 10 species (19 subspecies) of *Geomys*, 7 species (24 subspecies) of *Cratogeomys*, and 51 *species* (61 subspecies) of *Ctenomys*. No doubt the number of species acknowledged will decrease as the taxonomy of the various genera is studied more thoroughly, but even in regions from which large collections have been studied carefully, the number of forms remains impressive. Goldman (1947), for example, recognized 44 named kinds of *Thomomys* in Arizona. Undoubtedly the weak dispersal powers of these animals encourages the evolution of morphologically distinct, isolated or partly isolated populations, but other influences must also be at work because moles, with equally poor powers of dispersal, have not speciated nearly as profusely.

Although among genera of mice such as *Peromyscus*, *Perognathus*, and *Phyllotis* five or even six species of the same genus sometimes live within a few yards of eachother, seldom do the ranges of two species of gophers overlap and even more rarely are two species strictly sympatric (see for example, Hall, 1946). Similarly, species of tuco-tucos, *Spalax* (Méhely, 1913; Ognev, 1947), and *Myospalax* (Ognev, 1947) are rarely sympatric. Presumably the above-ground environment of mice is divisible into a number of microniches so that forms adapted to each are spared prohibitive competition with their congeners. The scarcity of sympatry among subterranean rodents and the striking anatomical and ecological similarity of unrelated forms suggest that no matter what the latitiude, longitude, or altitude there is essentially only one niche exploitable by subterranean, herbivorous mammals.

Summary

The wide-ranging genus *Ctenomys* is represented in Peru at the northern limit of its range by three species, all of them restricted to elevations above 12,500 feet.

Ctenomys opimus lives in several habitats such as those dominated by tola, by *Nototriche*, and by the bunchgrass *Festuca orthophylla*. Above-ground feeding (on vegetation) and digging are carried out in the daytime, almost always within one meter of an open burrow. Burrow systems are shallow tunnels with short lateral branches; loosened earth is swept out of them by simultaneous flips of the hind feet. Breeding occurs from August through February and parturition between October and March. Litter size is from one to three. Young breed before they are one year old and probably bear young every year in which they survive. Both sexes are solitary and silent. Population densities as high as 17 per acre are possible but one per acre is a more usual density in favorable habitat.

Ctenomys peruanus tends to be restricted to flat, closely grazed pampas. It differs from *opimus* by making a conspicuous bubbling call and by being colonial. Several adult females will live in the same burrow system, although males tend to be solitary. *Ctenomys peruanus* spends more time above ground than does *opimus* and ventures farther from the burrows. Most young are born in March and April in a very precocious condition. They are able to leave the nest, feed on green vegetation, and give the adult call almost immediately. They breed before one year of age. Females probably have only one litter each year. Litter size was from one to five. Population density in one colony was 17 per acre. The sex ratio collected by shooting was predominantly female, probably because the males were actually more scarce as a result of spacing themselves.

Little is known of the third species, *Ctenomys leucodon*.

All three species live in close association, at some places, with a species of guinea pig *(Galea musteloides)*. With *Ctenomys*

peruanus it was shown that guinea pigs move into the burrows promptly when the tuco-tucos are removed.

Unrelated subterranean herbivores throughout the world are remarkably similar in size and structure, and, in spite of different methods of digging, they construct burrows that are usually similar. Furthermore, many of the world's genera of subterranean rodents have given rise to an unusually large number of species and subspecies. Few of these species are sympatric. Consequently, it seems that throughout the world there is basically only one niche exploitable by subterranean, herbivorous mammals.

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