POPULATION ENERGY RELATIONSHIPS OF THE AGRIMI (CAPRA AEGAGRUS CRETICA) ON THEODOROU ISLAND, GREECE

Thesis for the Degree of Ph. D.

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NICOLAOS PAPAGEORGIOU

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ABSTRACT

POPULATION ENERGY RELATIONSHIPS OF THE AGRIMI (*CAPRA AEGAGRUS CRETICA*) ON THEODOROU ISLAND, GREECE

By

Nicolaos Papageorgiou

A study was conducted on Theodorou island (68 hectares) during 1973 to determine the population energy relationships of the Cretan wild goat or agrimi. The density, sex and age ratios, individual weights and other pertinent data of the agrimi on Theodorou island were obtained by direct measurement of the total population. In 1973 the population density was 1.4 individuals/hectare. The sex ratio was 1:1 among both kids and adults. The kid:adult ratio was 14:100, while the kid:female ratio was 36:100. From weight data a body growth curve was constructed.

Survivorship data were obtained from the analysis of 55 skulls of animals dying of natural mortality before 1973. Combining survivorship data and body growth data the productivity of the population was estimated to be 0.86 kilocalories per square meter per year.

The living biomass of the agrimi population was measured to be 5.4 kilocalories per square meter. In kilocalories per square meter per year the available food, food consumed, feces and maintenance metabolism were calculated to be 173.3, 110.3, 44.1 and 65.3, respectively. Using these values, efficiency ratios were calculated for the agrimi. The efficiency of secondary production in relation to food consumption was 0.78%, which is comparable to the near 1% value calculated for other large wild herbivores.

The following agrimi population parameters were also calculated: life expectancy, 5.9 years; net reproductive rate, 1.14; annual turnover, 14.9%; annual mortality rate, 15.7%; innate rate of increase, 2.09/100/year; and generation time, 6.8 years.

The present agrimi population was found to be causing serious range deterioration. To insure the permanent preservation of the agrimi population and its range a calculated 33% reduction of the population is recommended.

POPULATION ENERGY RELATIONSHIPS OF THE AGRIMI

(*CAPRA AEGAGRUS CRETICA*) ON

THEODOROU ISLAND, GREECE

By

Nicolaos Papageorgiou

A THESIS

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DEDICATION

To Constantinon and Vaian Papageorgiou

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INTRODUCTION

Most ecological studies of populations have been oriented toward description of structure and the analysis of demography. Rarely have these studies considered the functions of populations within ecosystems. It was not until the classic concept of community dynamics, developed by Lindemann (1942), that population ecologists became interested in biological energetics.

Energy flow information enables a comparison of ecosystems as well as the relative evaluation of productivity in populations which are diverse in size and rate of metabolism (Odum, 1971).

This knowledge is urgently needed today in a man-dominated world in which communities of wild herbivores are major consumers of primary production, and therefore, the most important converters of forage to human food. Based on energy flow data, man can intelligently manipulate ecosystems and make full use of his limited natural resources.

The complexity of terrestrial ecosystems and the lack of suitable techniques for energy flow studies have limited information concerning terrestrial ecosystem energetics, in contrast to progress made in aquatic or "laboratory" ecosystems (Engelmann, 1966; Petrusewicz and McFayden, 1970).

A *Microtus* food chain analysis (Golley, 1960) was the first major work in terrestrial energetics. Over the past few years, investigators have attempted to examine the energy flow of large wild herbivores (Petrides and Swank, 1966; Buechner and Golley, 1967; DuPlessis, 1972;

Bobek, et al., 1973). Although these studies have measured both the primary productivity of the habitat and the secondary productivity of a herbivore population, none has examined the dynamic interaction between both components.

To assist in correcting this deficiency, a semi-tropical ecosystem was studied on the island Theodorou, offshore Crete, Greece. Undertaken between March to November 1973, specific objectives were: (1) to appraise primary productivity and the pattern of vegetational changes associated with ungulate grazing; (2) to obtain information concerning the agrimi standing crop, energy assimilation, and other aspects of secondary productivity; and (3) to provide sound recommendations for the permanent management of this endangered species.

History and Description of Area

The study was conducted on the uninhabited island of Agii Theodori. The island, commonly known as Theodorou, was officially designated in 1963 as the Theodorou Wildlife Reserve and was set aside as a sanctuary for the preservation of the agrimi or Cretan wild goat (*Capra aegagrus cretica* Schinz, 1838). The Reserve's stock originated from successful introductions in 1928 (1 pair), 1937 (1 pair), and 1945 (1 pair) (Schultze-Westrum, 1963). These were captured from the endemic agrimi population in the White Mountains of western Crete. The Theodorou reserve now supports a relatively high agrimi population which is limited from exponential increase only by natural forces.

Historically, the island has never been cultivated and was utilized only as a winter grazing range for domestic sheep from a nearby village on Crete. The island's vegetation, therefore, was open to unrestricted grazing by domestic stock until the introduction of the agrimi population.

Theodorou island is an isolated mass of limestone rock lying eight kilometers northwest of Chania, the captial of Crete (Figure 1). It's nearest point lies 850 meters from the coast of Crete. Approximately triangular in shape, the island is 1550 meters long and 750 meters wide with an area of approximately 68 hectares (Figure 2). At its highest point, Theodorou rises 156 meters above sea level. Its' north, east, and west shores terminate in near-perpendicular limestone cliffs, and at its' south shore by a gradual slope to the sea.

The climate of Theodorou is maritime and semi-tropical, with year-round high temperatures. Available data for the last decade (National Meteorological Service, Chania) indicate a mean annual temperature of +18.8 degrees C with mean annual maxima and minima of +22.6 degrees C and +15.1 degrees C, respectively. Extremes have been recorded, however, as low as +1.8 degrees C (January, 1968) and as high as +41.4 degrees C (July, 1960).

Rainfall is low and unevenly distributed over the year. Maximum rainfall tends to coincide with minimum temperature (Figure 3), and about two-thirds of the average 691 millimeters annual rainfall occurs during winter. Monthly precipitation is usually highest in January, averaging nearly 130 millimeters in that month. Rainless periods of two to three months duration are common during summer months. Neither frost nor snow has been recorded in this area.

Soils on Theodorou island are reddish in color, well drained, and poorly developed. Derived almost entirely from metamorphosed limestone and lacking decaying organic matter on the surface, they are limited to B and C horizons (Table 1).

Temperature and rainfall are generally conducive to plant growth from late winter to early spring. Additional moisture in autumn results

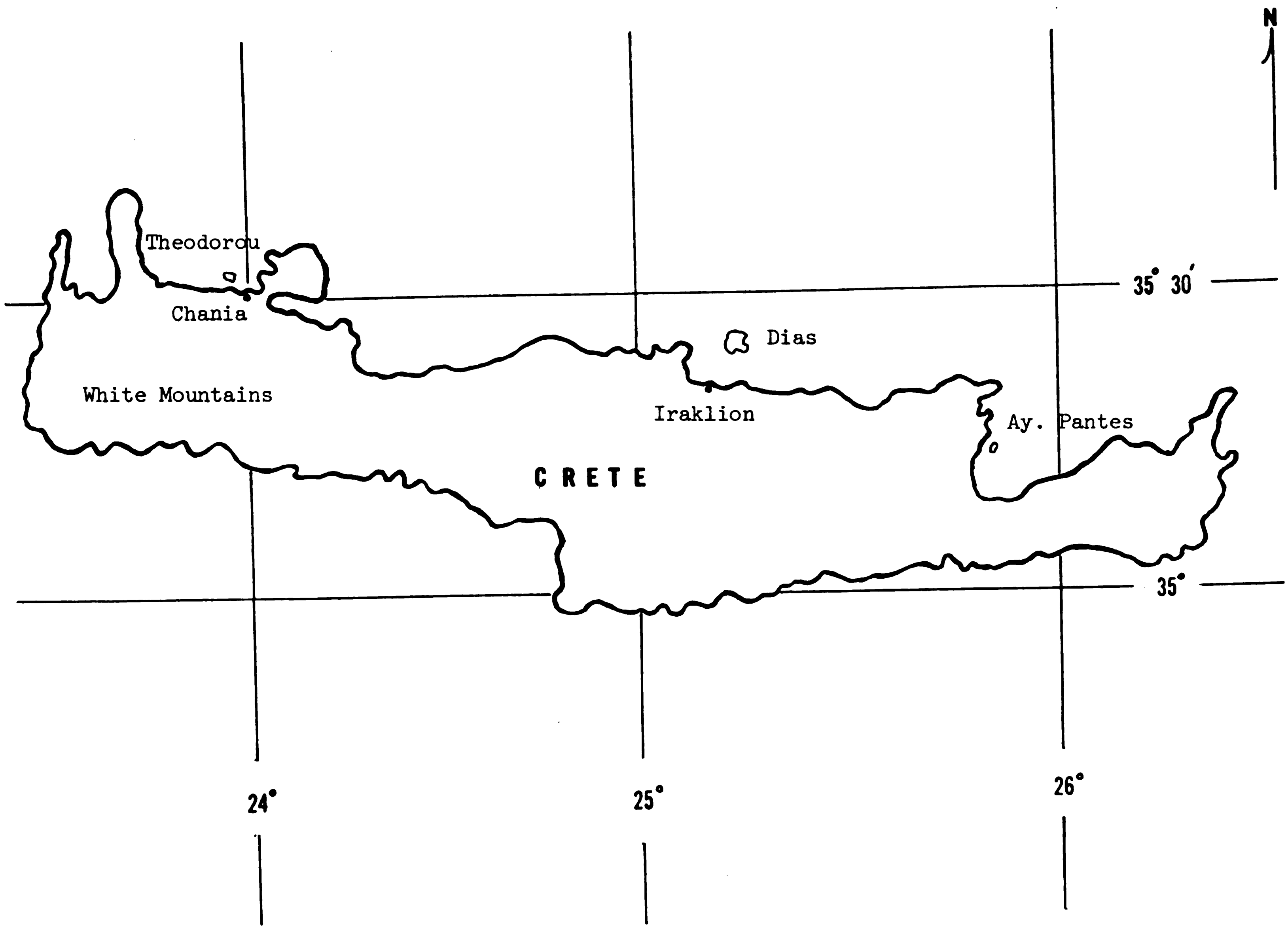

Figure 1. Map of Crete, Greece.

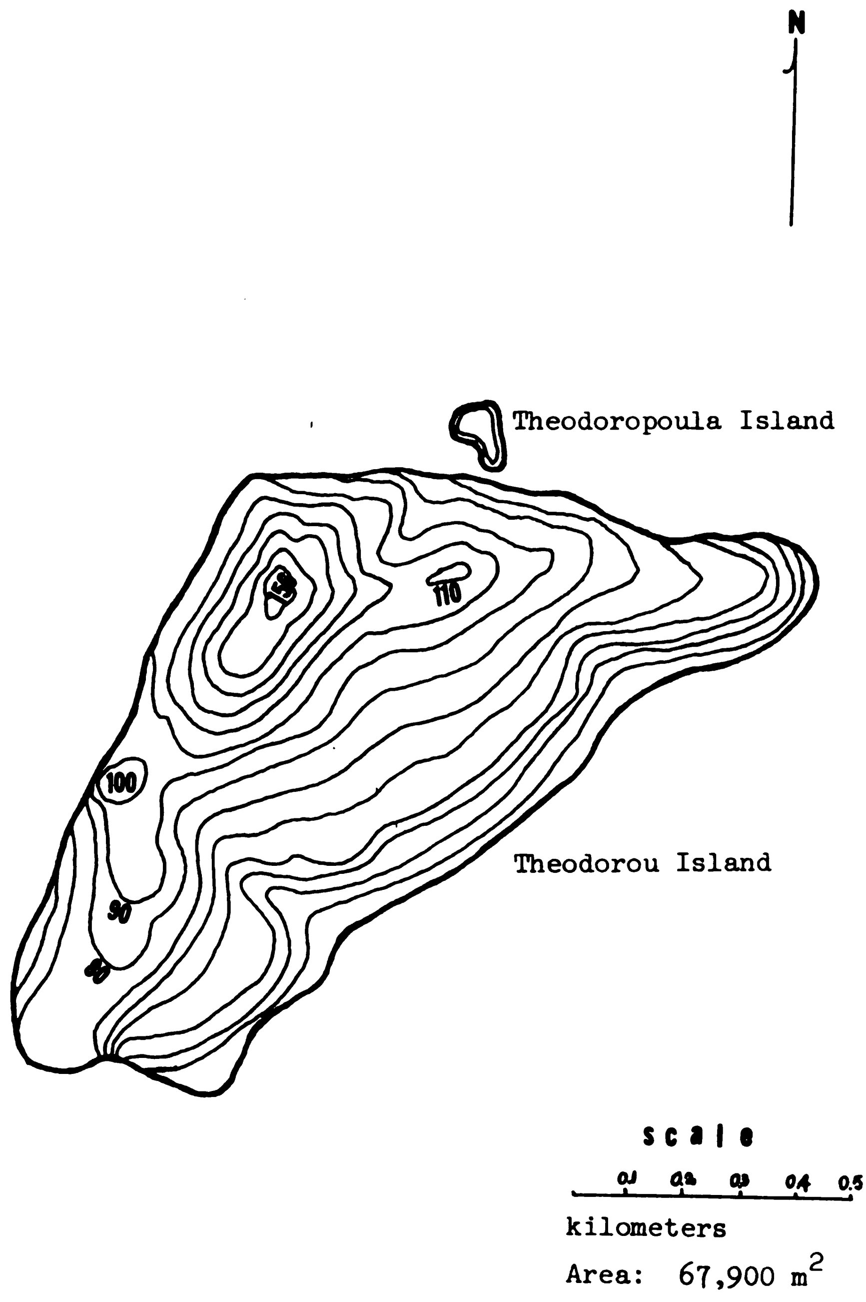

Figure 2. Topographic map of Theodorou island.

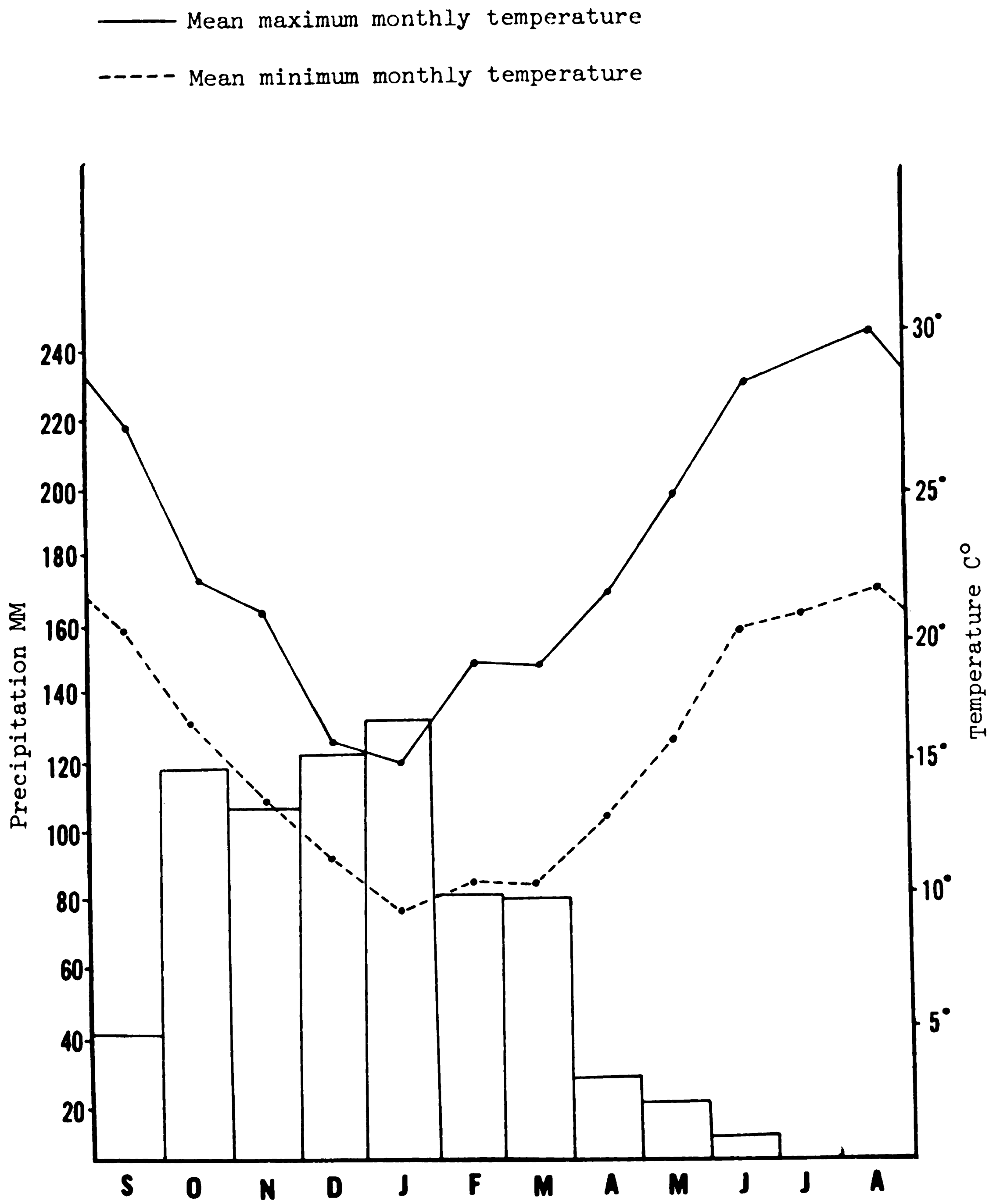

Figure 3. Distribution of precipitation and maximum and minimum air temperatures during the year. Based on 1960-70 climatic data of National Meteorologic Service, Chania, Crete, Greece.

Table 1. Analysis of soil samples from widely separated sites on Theodorou and Theodoropoula islands, Crete, Greece, July, 1973.

			Percentage			Horizon Depths (in cm)	
	Sample	pH	Silt	Sand	Clay	A	B
Theodorou							
	1	7.5	27.4	27.4	45.2	--	7.0
	2	7.1	20.6	23.6	55.8	--	12.0
	3	7.3	26.2	25.7	48.1	--	17.0
Theodoropoula							
	1	7.3	28.0	39.3	32.7	11.0	15.0
	2	7.4	26.8	42.2	31.0	12.5	18.0

in some vegetative regrowth. The amount of forage produced then, however, is usually of little significance to grazing.

Basically, the island supports a Pistacia-Poterium-Thybra plant association with other vegetation present in degraded form. Associated plant species are listed in Table 2.

Relatively few animal species are present. Common faunal species inhabiting the island or utilizing it during migratory transition are: Eleonora falcon (Falco eleonorae), blackbird (Turdus menula), Greek partridge (Petrix graeca), raven (Corvus corax), rock martin (Hirundo rupensis), cormorant (Phalacrocorax sp.), and the introduced Norway rat (Rattus norvegicus) and European hare (Lepus europeus).

Special attention was given to the herbivorous hare and rat population densities to detect any possible effect they might have on the agrimi population. Two pairs of hares were released by the local hunting club in 1965. Though now not scarce, the hare population did not appear to increase during the study period. In 1973, a relatively high rat population density was evidenced by numerous tracks, feces and burrows which were in contrast to their low density found in 1971 (Papageorgiou, 1972).

Running streams and freshwater springs are non-existent. To meet the water requirements of the agrimi herd, therefore, a system was constructed by the Forest Service to collect runoff water in two fenced reservoirs of about 100 cubic meters each. The main responsibility of the appointed wildlife guard is to retrieve water from those reservoirs for the agrimi population. Six containers on the center of the island are filled daily during the summer and constitute the only source of fresh water. This is not required during other seasons due to collection

Table 2. Food preferences and relative plant cover, frequency and density on Theodorou and Theodoropoula islands, Greece, Spring, 1973.

	Overgrazed Theodorou island				Ungrazed Theodoropoula island			
Species[+]	A Relative Cover[a] %	B Relative Frequency[b] %	C Relative Density[c] %	D D=A+B+C Importance Index Value	A Relative Cover %	B Relative Frequency[b] %	C Relative Density[c] %	D D=A+B+C Importance Index Value
Shrubs:								
*Phlomis fruticosa	9.43	4.27	2.53	11.90				
Poterium spinosum	23.34	8.49	7.88	29.00				
Thybra capitata	14.17	4.39	3.42	15.48				
**Olea oleaster	0.32	.30	.09	.56				
**Colycotome villosa	9.39	3.31	1.22	9.61				
**Cistus incanus	0.20	.42	.33	.86				
Euphorbia paralias	8.94	1.93	.94	7.71				
*Capparis spinosa					4.36	3.53	.29	6.42
**Ephedra campylopoda					3.27	3.53	.29	5.82
*Pistacia lentiscus	22.43	5.42	2.44	20.02	14.80	4.70	.39	14.09
TOTAL SHRUBS	88.24				22.34			
Forbs:								
*Scilla maritima	2.49	4.64	3.80	9.79				
*Asphodelus microcarpus	1.53	2.16	1.27	4.26				
Sedum sp.		.12	.71	.83				
Vicio tenuifolia		.18	.23	.41				
Vaillantia sp.	.02	1.14	2.11	3.26				
Psoralea bituminosa	.12	.96	1.03	2.06				
Ruta angustifolia	.22	.12	.09	.33				
Mercurialis annua		.48	.61	1.09				
*Teucrium polium	.64	2.35	1.74	4.44				
Helichryium italicum	3.12	2.10	1.27	5.06				

Table 2 (cont'd.)

Species	Overgrazed Theodorou island				Ungrazed Theodoropoula island			
	A Relative Cover %	B Relative Frequency %	C Relative Density %	D D=A+B+C Importance Index Value	A Relative Cover %	B Relative Frequency %	C Relative Density %	D D=A+B+C Importance Index Value
Atractylis cancellata	.05	1.32	2.16	3.51				
Cirsium sp.	.16	1.02	.75	1.57				
Althae officinalis		.12	.05	.17				
Anagylis arvensis		.18	.61	.79				
Nigella damascina		.12	.14	.26				
Hymenocarpus circinatus	.06	1.63	1.03	2.69				
Plantago lagopus	.52	2.05	8.49	10.82				
Ornitholagum sp.		.18	.05	.23				
Medigago sp.	.02	.72	.47	1.20				
*Rheichardia picroides	.04	1.93	3.23	5.18				
Centranthus calcitropa	.02	2.04	2.95	5.01				
Scorpiurus subvillosa		.42	.28	.70				
Serapias vomeracea								
Trifolium aruense		.36	1.36	1.72				
Trifolium pollenscens		.48	1.27	1.75				
Knautia arvensis	.29	3.61	4.69	5.46				
Anagila arvensis	.05	2.77	2.02	4.82				
Malva micaensis	.30	4.82	4.07	9.38				
Orospermum picroides	.04	1.99	.50	3.51				
Anthyllis tetraphylla		.54	.37	.91				
Trifolium argarium	.16	4.33	4.64	9.06				
Ornithogalum pyrenaicum		.72	2.53	3.25				
Crucianella sp.	.05	1.50	1.59	3.11				
Helianthemum sp.	.07	3.31	4.03	7.38				
Linaria pellisseriana		.12	.04	.16				

Table 2 (cont'd.)

Species	Overgrazed Theodorou island				Ungrazed Theodoropoula island			
	A Relative Cover %	B Relative Frequency %	C Relative Density %	D D=A+B+C Importance Index Value	A Relative Cover %	B Relative Frequency %	C Relative Density %	D D=A+B+C Importance Index Value
Calamintha sp.	.06	1.93	2.06	4.02				
Trifolium aureum		.42	.61	1.03				
Trifolium stellatum	.31	3.85	4.64	8.66				
Aster tripolium		.24	.19	.43				
Lotus corniculatus	.02	1.99	1.27	3.27				
Melilotus officinalis								
Scandix pectenveneris	.04	.54	.61	1.15				
Tordylium apulum	.04	1.38	.95	2.38				
Graphalium neglectum	.04	.42	.05	.49				
Asparagus sp.	.08	.66	.33	1.03				
Malcolmia sp.					3.00	9.41	14.27	25.51
*Obione portucaloides					42.78	15.29	4.31	45.77
Trifolium scrabrum					0.55	3.52	2.20	6.05
Parietaria sp.					0.55	4.71	3.16	8.20
Crepis sp.						4.71	1.15	5.86
**Lotus creticus					6.81	10.59	2.63	17.44
**Raphanus raphanistrum					9.26	8.23	3.74	17.64
*Crithmum maritimum					5.45	2.35	.23	5.97
**Allium sp.					3.54	7.06	4.50	13.73
Erythrea centaureum	.02	.66	1.27	1.83	1.91	9.41	8.15	18.72
TOTAL FORBS	10.57				73.84			
Grasses:								
Lolium parene					0.55	2.35	.47	3.16
Koeleria phleoides					3.27	7.06	53.64	63.70

Table 2 (cont'd.)

	Overgrazed Theodorou island				Ungrazed Theodoropoula island			
	A Relative Cover %	B Relative Frequency %	C Relative Density %	D D=A+B+C Importance Index Value	A Relative Cover %	B Relative Frequency %	C Relative Density %	D D=A+B+C Importance Index Value
Pholiurus incurvatus						3.53	.47	4.00
Bromus sterilis	.16	2.77	2.81	5.66				
*Andropogon pubenscens	.95	2.77	1.41	4.69				
Stipa tortilis	.08	1.57	1.41	3.02				
Aegilops sp.		.72	1.30	2.08				
TOTAL GRASSES	1.19				3.69			
TOTAL ALL VEGETATION	100.00	100.00	100.00		100.00	100.00	100.00	

$$a = \frac{\text{Cover of individuals of species x}}{\text{Total cover of individuals of all species}} \text{ X } 100$$

$$b = \frac{\text{Frequency species x}}{\text{Sum of frequency values of all species}} \text{ X } 100$$

$$c = \frac{\text{Number of individuals of species x}}{\text{Total number of individuals of all species}} \text{ X } 100$$

* Preferred forage species

** Highly preferred forage species

\+ Unmarked plants are not forage species of fresh water in natural pools and to the retention of water in forage.

Off the east part of Theodorou lies a small island, Theodoropoula (Figure 2). The strait that separates the two islands is only about 10 meters wide and is guarded on the Theodorou side by an almost perpendicular cliff about 80 meters high. Theodoropoula is very small; about 120 meters by 60 meters and at its highest point rises approximately 15 meters above sea level. It is roughly rectangular in shape, flanked to the north, east and west by perpendicular cliffs and to the south by steeply shelving slopes broken here and there by outcrops of rock. The rocky surface of the island is composed of small limestone flakes and splinters. These may be up to 50 cm in length and most are sharpened into cutting edges, making walking very difficult.

Soil profiles examined at various locations on the island revealed shallow mature soils with an accumulation of decaying organic matter forming the top soils (Table 1). The distinct A and B horizons, basic in reaction, are derived from limestone bedrock.

There is no fresh water available on the island. No signs of any mammalian life, even small rodents, were found on the island. Theodoropoula has never been disturbed by the activities of man, domestic animals or wildlife according to the records of the Greek Forest Service at Chania.

The island basically supports an <u>Obione</u>-<u>Pistacia</u>-<u>Lotus</u> vegetative association (Table 2). It was judged, based on historical records, vegetation composition and soil development, that it is in "virgin" condition and represents the climatic "climax" plant community. The two contrasting islands afforded a unique opportunity for comparative ecological studies.

Composition of plant communities is controlled by many environmental factors. Physiographic, climatic and biotic factors all are considered to be of vital importance in controlling the local distribution of plant species (Nichols, 1917, 1923; Tansley, 1935; Weaver, 1936; Clements, 1936; Ellison, 1960). Since all other factors were equal on the two islands, and the study islands were in close proximity and originated from identical parent-material, the effects of the single variable, grazing, clearly seemed to be determinable.

Certain areas of Theodorou island are not exposed to a salt-spray factor equal to that found on Theodoropoula island. There are, however, many areas on Theodorou which are similar in this respect to Theodoropoula, but still support a different vegetative association. It was concluded that salt-spray, though important in controlling local distributions of species (Oosting and Billings, 1942), was not responsible for the distinct differences between the floras of the two islands. It was concluded that the two islands originally supported similar vegetation and that grazing was mainly responsible for the differences in vegetative patterns on the two islands.

ANALYSIS OF VEGETATION

Where excessive grazing plays a dominant role, dynamic changes are usually evidenced as negative succession, or regression of vegetative associations.

The relic method (Clements, 1934) is commonly used to determine the magnitude of change within an ecosystem and this investigation utilized this procedure. In this study, the ungrazed islet of Theodoropoula evidently represented a relic assemblage of the more mature vegetation once present on the overgrazed Theodorou.

FIELD METHODS

Vegetation Analysis on Theodorou Island

Rectangular plots equal to one square meter seemed best suited to sample the characteristics of the community, and a wooden frame, 2 by 0.5 meters was made. These dimensions were utilized to provide maximum variation within plots and minimum variation among plots (Christidis, 1931). Plots were evenly distributed systematically throughout the island. It was assumed that this procedure provided a representative sample of the island plant community. The species-area curve (Cain, 1938) was used to determine the number of plots needed in order to sample the vegetation adequately. Cain (1938) states that sampling is adequate when a 10 percent increase in the sample area results in an increase of species equaling 10 percent of the total present. Braun-Blanquet (1932) considers the sample adequate when the species-area curve becomes approximately horizontal. On Theodorou, 140 square-meter plots were necessary for an adequate sampling of the vegetation according to Cain and Braun-Blanquet (Figure 4).

To insure an even distribution of the samples and because of additional information also sought by the single sampling, the actual sample size taken was substantially larger than necessary as indicated by the species-area curve.

Vegetation inventory data were gathered from 230 plots spaced at 50-meter intervals along parallel north-south lines, also 50 meters apart. The distances between plots were measured using a metal tape and the lines were kept equidistant using a hand prismatic compass. In each plot, the number of forbs and grasses rooted within the plot, and the number of annual twigs per shrub were tallied by species. Along a line determined by the western border of a plot, any overhanging vegetation was also measured by species to determine the percent of cover (Canfield, 1941).

Net forage production was determined, using only those plant species which contributed to the animal's diet (Papageorgiou, 1972). The browse and herbage net primary production was determined by combining the twig count method (Shafer, 1964) with a modification of the weight measurement procedure developed by Beruldsen and Morgan (1934). Using this combined method, counts of twigs and individual grasses and forbs by species were converted to annual production by estimating the dry-weights of average, ungrazed, full-grown twigs and herbaceous materials. Specimens of unbrowsed annual twigs and ungrazed individual herbaceous plants for use in weight determination were collected from randomly-located plants and sites at the end of their growing season. Since an adequate number of ungrazed plants of some

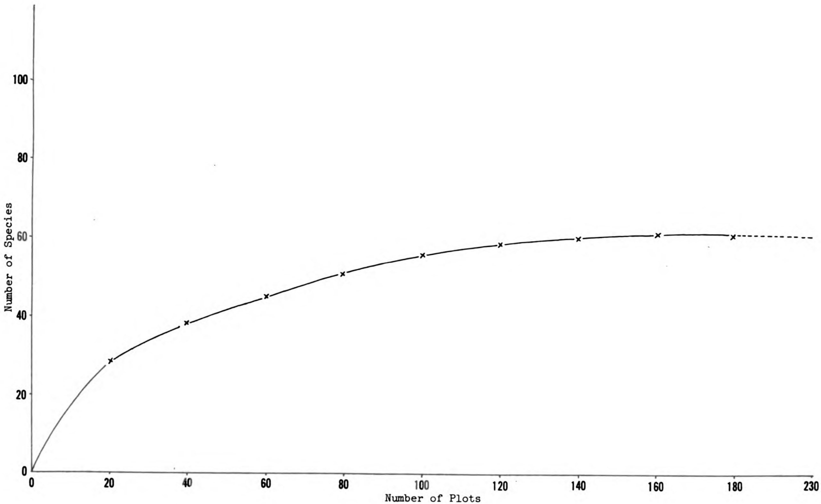

Figure 4. Species-area curve for the vegetation on Theodorou island. 1973.

palatable species could not be found on the open range, it was necessary to collect some specimens from within eight fenced exclosures which had been constructed in 1971. These 6-8 square-meter exclosures had been constructed throughout the island and included the major local plant associations.

The use of cage methods (Ivins, 1959; National Research Council, 1962), which are reported to be more desirable for forage production studies on year-round grazed habitats, were not feasible for use on Theodorou due to their high cost and the large number required for a reliable sample. In addition, the procedure employed in this study avoided additional damage to the already overgrazed range.

Vegetation Analysis on Theodoropoula Island

The vegetation inventory on Theodoropoula was obtained in the same fashion as that on Theodorou. Fifteen plots, each of one square-meter, were evenly distributed throughout the island. Cover and individual species present within the plots were recorded. From these data, frequency and density were calculated. Potential forage production of Theodoropoula island was based on species palatability as exhibited during a feeding experiment (see beyond). Because of the small size of the island, the absence of grazing animals and the lack of shrubs on the range, the "clipping and weighing" method (Brown, 1954; National Research Council, 1962) was used to estimate net forage production.

Clippings of herbaceous plants were made at ground level and placed in referenced plastic bags for subsequent weighing. Weights were converted from wet to dry by applying moisture content coefficients determined experimentally for each species.

The vegetative survey was initiated in early spring when most species were readily identifiable but several unidentified specimens were assigned a reference number until positively identified by the Department of Botany, University of Thessaloniki, Greece.

A two-part feeding experiment was conducted to determine the response of agrimi to "climax" species vegetation collected from Theodoropoula island. To test palatability and order of preference, equal amounts of each species was offered to a caged agrimi. After 2 hours, the remaining portions were weighed and divided by the amount offered to determine relative preference values.

Following this, tests were made of the relative preferences of "climax" forage species of Theodoropoula in comparison with the "disclimax" forage species of Theodorou. For three days a mixed diet of "climax" forage species and "disclimax" forage species was presented to a penned agrimi. The daily weight consumed was determined for each species by subtracting residues found the next day. For each species, the ratio percentage in diet/percentage available indicated their relative degree of preference (Petrides, unpublished).

LABORATORY PROCEDURES

Forage samples of each species were dried at 105 degrees C for 24 hours in a vacuum oven. After cooling to room temperature in a dessicator, the dried samples were weighed to the nearest .001 gram on an analytical balance. The difference in weight was reported as percent moisture. Samples were then stored for further analysis in Whirl-Pak polyethylene bags to prevent the absorption of moisture.

The nutrient characteristics of forage species were determined by the Forest Research Center, Thessaloniki, Greece. Protein, fat and fiber contents were determined by the Kjeldahl, Soxhlet and Henneberg-Stohmann methods, respectively. Gross energy caloric values were determined in the laboratories of the Department of Animal Husbandry, Michigan State University, using a Parradiabatic oxygen bomb calorimeter.

RESULTS AND DISCUSSION

"Climax" Community

The term climax, as used in this paper, refers to the highest type of vegetation which the area evidently was able to develop under prevailing climatic and edaphic conditions on the experimental islands. Theodoropoula island, which has never been grazed or cultivated, was considered to represent climax vegetation in the area.

Vegetation on the island (Table 2) consisted of 16 species: 3 shrubs, 10 forbs, and 3 grasses, comprising 22.34, 73.84, and 3.82 percent of the total cover, respectively. Principally a forb-type association, according to the importance-value index (Table 2), *Pistacia lentiscus*, *Obione portucaloides* and *Koelaria phleoides* were the most important plants among shrub, forb and grass species, respectively. The forb, *Obione portucaloides*, noticeably dominated the climax community covering 42.78 percent of the area where plant life could exist. The Obionetum thus appears to be the climatic "climax" community on the island when the normal course of vegetation succession is not held at an intermediate stage by grazing. Other major plants in the order of their importance in the climax community included: *Pistacia lentiscus*, *Raphanus raphanistrum*, *Lotus creticus*, *Caparis spinosa*, *Crithmum maritimum*, Allium sp., Ephedra campylopoda, Malcomnia sp., and Koelaria phleoides. These species comprised 53.75 percent of the island's vegetative cover. Species of secondary importance included Erythrea centaurium, Trifolium scabrum, Pariefolia sp., Lolium parene and Pholiurus incurvatus. These species contributed only 3.46 percent of the vegetative cover.

Most dominant plants of the climax community were palatable to livestock and wildlife. While these species covered Theodoropoula island, they are completely absent or confined to inaccessible crevices of cliffs on Theodorou and throughout most of the Mediterranean region where grazing occurs.

Disclimax Community

The term disclimax refers to a plant community in equilibrium with the climate and other components of the ecosystem, but somewhat degraded as a result of the persistent adverse effects of a particular factor such as fire, or in this case, heavy grazing. Theodorou island has been subjected to grazing for a prolonged period and displays a typical disclimax community. An intensive survey of the island (Table 2) yielded 58 plant species which included 7 shrubs, 47 forbs and 5 grasses, contributing 88.24, 10.57 and 1.19 percent of the vegetative cover, respectively. The dominant shrub-type association on Theodorou was in contrast to the forb "climax" association on Theodoropoula (Figure 5). Importance values indicated (Table 2) that Poterium spinosum, Scilla maritima, and Andropogon pubenscens were the most significant among shrub, forb, and grass species, respectively.

The shrub Poterium spinosum, comprising 23.34 percent of the island cover, was the major dominant. Other important plants associated with the poterietum community, in descending order of importance, included

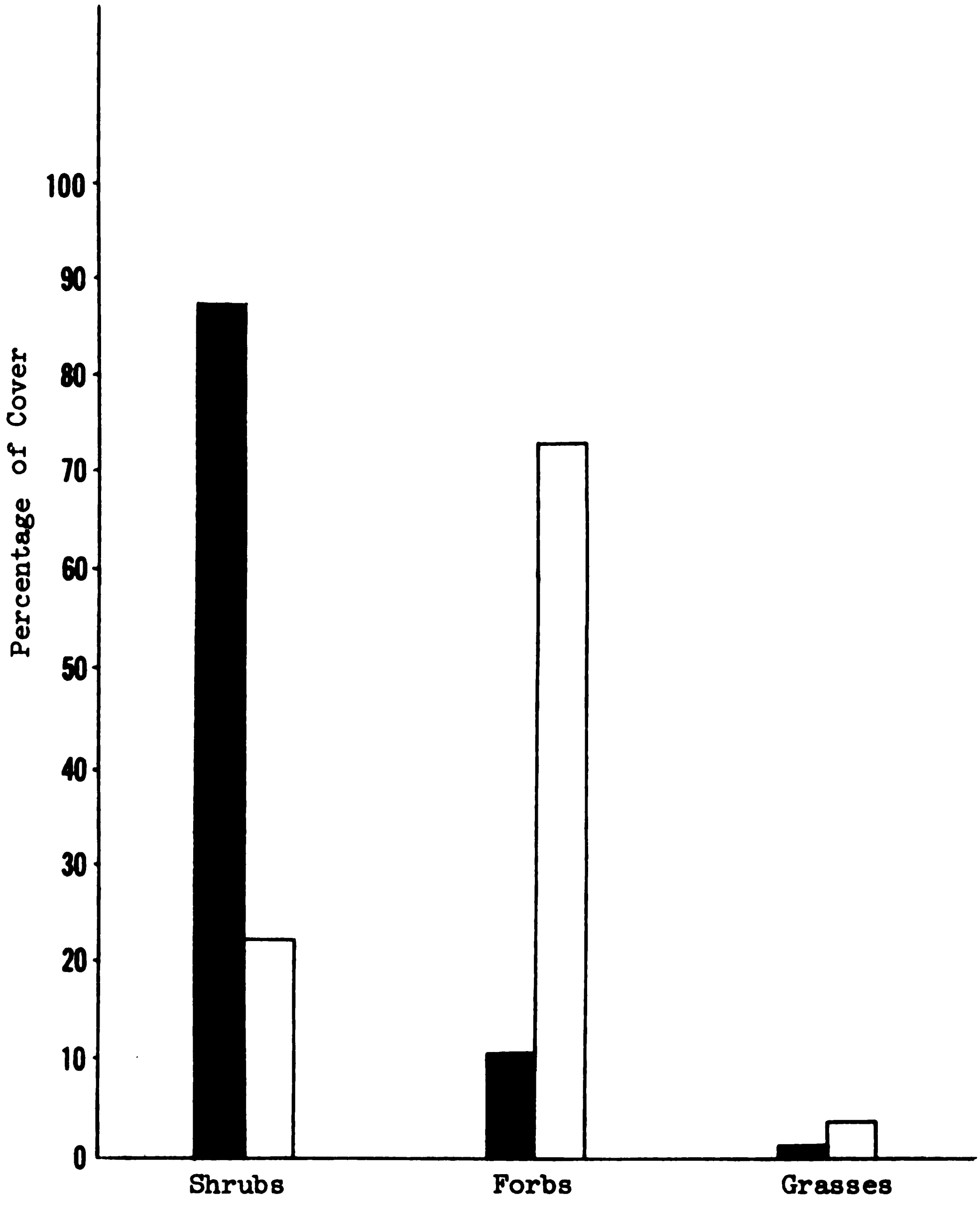

Figure 5. Comparison of vegetation on heavily-grazed Theodorou (solid bars) and totally-ungrazed Theodoropoula (open bars) islands, Spring, 1973.

Pistacia lentiscus, Thybra capitata, Calycotome villosa, Phlomis fruticosa, Euphorbia paralias, Scilla maritima and Asphodellus microcarpus. These species comprised 68.92 percent of the vegetative cover of the island. The remaining 51 plant species were of little significance to the plant community, contributing only 7.74 percent of the cover. The Theodorou island plant community was completely dominated by spiny shrub species of low palatability to goats. This vegetation, unfortunately, is typical of the overgrazed lands in this part of the Mediterranean region.

Distinct differences were evident in the floristic composition of the two islands. Sixteen species were found on the ungrazed island, while 59 were recorded on the overgrazed island. Only three of the species encountered on the ungrazed islet were observed on the overgrazed island. Plants encountered on both islands were Pistacia lentiscus, Caparis spinosa and Erythrea centaurium.

Few individuals of Caparis spinosa were encountered on the overgrazed island and, did not fall within the sample of Table 2. The presence of Pistacia lentiscus on the overgrazed island was probably due to its low palatability to agrimi and to the deep root system of this climax shrub.

Similarity Index

The similarity index "I", proposed by Whittaker (1960) was used to measure the similarity between the two sampled vegetations. The proportionate similarity between two samples, A and B, is given by the formula:

$$I = 1 - 0.5 \left(\sum_{i}^{s} \left| a_i - b_i \right| \right)$$

where a_i is the proportion of the total number of individuals, in sample A belonging to species i, b_i is the proportion in sample B belonging to species i, and s is the total number of species. Complete similarity is indicated by I = 1.0, with complete dissimilarity indicated by I = 0.0.

Where it may be assumed that the two areas had a similarity index of I = 1.0 before the introduction of grazing, on Theodorou island, the similarity index value for the current vegetation on the two islands was found to be I = 0.002. This indicated almost complete dissimilarity of the two vegetative communities. The evident drastic change in the floristic composition of Theodorou island dramatically illustrates the power of grazing as an environmental factor.

Effect of Grazing as an Environmental Factor

The results of the feeding experiment revealed that most of the climax plant species found on Theodoropoula were palatable to the penned agrimi. In descending order of early summer food preference, the animal utilized Lotus creticus, Ephedra campylopoda, Raphanus raphansitrum, Obione portucaloides, Allium sp., Pistacia lentiscus and Caparis spinosa.

The "climax" forage species were also preferred over the "disclimax" species (Table 3), the "climax" species receiving 80 to 100 percent utilization with a free-choice diet.

The preference for "climax" species by the agrimi is probably rooted in evolution. The relic "climax" association is probably representative of the vegetative cover on comparable coastal sites on Crete prior to disturbance by man and domestic animals. The agrimi as it evolved abilities to survive in early habitats had to develop adaptations

Table 3. Comparative forage-preference ratings for forage species from Theodorou and Theodoropoula islands, Summer, 1973.

Species	A Dry weight per species available gr	$B=\frac{A}{\Sigma A}X100$ %	C Dry weight per species in diet gr	$D=\frac{C}{\Sigma C}X100$ %	$E=\frac{D}{B}$ forage-preference ratings	$F=\frac{C}{A}X100$ percentage consumed
Ephedra campylopoda*	235	15.3	235	20.0	1.31	100.00
Lotus creticus*	393	25.6	393	33.5	1.31	100.00
Raphanus raphanistrum*	167	10.9	167	14.2	1.30	100.00
Caparis spinosa*	75	4.9	65	5.5	1.12	86.67
Olea aleaster	40	2.6	30	2.6	1.00	75.00
Obione portucaloides*	118	7.7	66	5.6	0.73	55.93
Scilla maritima	100	6.5	54	4.6	0.71	54.00
Pistacea lentiscus	135	8.8	71	6.1	0.69	52.59
Rheichardia picroides	101	6.6	47	4.0	0.60	46.53
Cistus incanus	88	5.7	29	2.5	0.44	32.95
Asphodelus microcarpus	81	5.4	16	1.4	0.13	19.75
TOTAL	1533		1173			

Feeding trial period - August 22, 1973 - August 25, 1973

* Forage species from Theodoropoula island

to it. Among those adaptations were physiological ones which enabled it best to utilize the dominant plant species.

Selective feeding on preferred climax species probably induced the observed vegetative changes on Theodorou island. Subsequently, selective grazing pressure favored the less preferred "invader species". Climax species which do not now constitute forage for agrimi apparently have disappeared from Theodorou island. This may be the result of overutilization and soil erosion followed by competition from invader species, but utilization of preferred climax species by domestic livestock, prior to the introduction of the agrimi, doubtless also contributed to their replacement.

The effect of overgrazing is further dramatized by a small protected area (20 m^2), lying 10-15 m above sea level on Theodorou island. This area is made inaccessible on all sides by a 90 degree cliff, 50 meters high. This natural barrier completely excluded all herbivorous animals, other than rodents. There the area was exclusively vegetated by the relic climax species _Obione portucaloides_, _Allium_ sp., and _Caparis spinosa_ which otherwise were found only on the ungrazed island. This relic area indicates the character of the community presumably more widely present on Theodorou island, prior to heavy grazing.

Forage Production

The net forage production of the overgrazed island was calculated as 42.95 $\pm$ 2.53 g (dry weight) per square meter (429.5 $\pm$ 25.40 kg per hectare) per year (Table 4). In terms of energy, 173.30 $\pm$ 24.94 kcal of gross energy were produced per square meter (1732.6 $\pm$ 249.4 Mcal per hectare) per year.

Table 4. Basic data for the calculation of annual forage and protein production on Theodorou island, Crete, Greece. April-June, 1973.

Species	Average number of twigs or plants per plot mean ± S.E.	Average dry-weight per twig and/or plant (g) mean ± S.E.	Forage production per square meter (g) mean ± S.E.	Gross dry-weight energy kcal/g	Gross energy production per square meter (kcal) mean ± S.E.	Crude protein %	Average forage protein production per square meter (g) mean ± S.E.
Pistacea lentiscus	19.648 ± 2.035	0.835 ± 0.035	16.406 ± 1.809	4.138	67.888 ± 23.906	4.731	0.776 ± 0.084
Phlomis fruticosa	5.691 ± 0.773	1.595 ± 0.041	9.077 ± 1.253	4.137	37.551 ± 5.183	8.412	0.764 ± 0.105
Calycotome villosa	7.478 ± 1.093	0.838 ± 0.045	6.266 ± 0.974	3.950	24.751 ± 3.845	3.875	0.242 ± 0.037
Scilla maritima	0.813 ± 0.094	5.261 ± 0.238	4.277 ± 0.507	3.673	15.709 ± 1.861	2.781	0.119 ± 0.014
Andropogon pubenscens	0.296 ± 0.043	12.525 ± 0.709	3.707 ± 0.439	4.007	14.853 ± 1.755	3.510	0.130 ± 0.015
Asphodelus macrocarpus	0.239 ± 0.041	9.362 ± 0.430	2.362 ± 0.417	3.775	8.917 ± 1.569	2.331	0.055 ± 0.009
Teucrium pollium	3.030 ± 0.552	0.153 ± 0.007	0.463 ± 0.007	3.868	1.790 ± 0.001	3.887	0.018 ± 0.001
Cictus incanus	0.413 ± 0.161	0.501 ± 0.020	0.207 ± 0.079	4.342	0.898 ± 0.106	4.825	0.010 ± 0.004
Olea oleaster	0.469 ± 0.213	0.324 ± 0.009	0.152 ± 0.071	5.158	0.784 ± 0.133	3.750	0.006 ± 0.009
Cupressus sempervirens	0.065 ± 0.098	0.505 ± 0.017	0.033 ± 0.047	3.610	0.119 ± 0.161	3.855	0.001 ± 0.003
TOTAL			42.95 ± 2.534		173.26 ± 24.943		2.121 ± 0.141

In contrast, net forage productivity of ungrazed Theodoropoula island (Table 5) yielded 147.40 ± 18.33 g of forage (dry weight) per square meter (1470.0 ± 183.30 kg per hectare) per year. In units of gross energy, 497.60 ± 67.35 kcal were produced per square meter (4976.18 ± 673.5 Mcal per hectare) per year.

As shown in Table 2, cover, frequency and density values for forage species on the ungrazed island were all higher than on the heavily-grazed area. They comprised 80.5, 58.8, and 30.2 percent, respectively, of the total vegetation on Theodoropoula, in contrast to the comparable values of 47.4, 27.6 and 21.3 percent, respectively, on Theodorou. A graphic comparison of these values (Figure 6) further demonstrates that the calculated floristic parameters are approximately double in magnitude on the ungrazed island as compared with those on the overgrazed island.

It is evident that overgrazing initiated a destructive set-back in vegetative succession resulting in a change in the vegetative composition and in the establishment of a plant community less preferred by herbivores and ordinarily less productive. These changes induced an approximate four-fold decrease of forage production per unit area of the overgrazed island compared to that of the ungrazed island.

The total protein productivity of forage on Theodorou island, furthermore, was calculated to be about one-fifth that of the climax forage species found on Theodoropoula island, per unit area (Tables 4 and 5). Chemical analyses of respective forage species on Theodorou and Theodoropoula islands indicated a considerable difference in the quality of forage production. The differences in average protein concentrations of Theodoropoula (Table 5) and Theodorou forage species (Table 4) were

Table 5. Basic data for the calculation of annual forage production on Theodoropoula island, Crete, Greece. May-June, 1973.

Species	Dry forage production per square meter (g) mean ± S.E.	Gross energy per dry weight kcal/g	Energy production in kcal/m^2 mean ± S.E.	Crude protein %	Average forage protein production per square meters (g) mean ± S.E.
Obione portucaloides	83.240 ± 11.674	3.056	254.381 ± 35.675	5.775	4.807 ± 0.675
Pistacea lentiscus	22.738 ± 10.6	3.440	78.218 ± 36.46	8.480	1.928 ± 0.898
Raphanus raphanistrum	15.300 ± 5.385	3.729	57.053 ± 20.080	6.300	0.964 ± 0.339
Allium sp.	8.940 ± 3.948	3.994	35.706 ± 5.617	4.810	0.430 ± 0.189
Ephedra cambylopoda	6.635 ± 6.08	4.307	28.576 ± 26.186	8.050	0.534 ± 0.489
Lotus creticus	5.936 ± 1.985	4.145	24.604 ± 8.227	11.812	0.701 ± 0.234
Malcolmia sp.	4.648 ± 1.374	4.105	19.080 ± 5.638	5.950	0.276 ± 0.081
TOTAL	147.437 ± 18.330		497.618 ± 67.350		9.640 ± 1.308

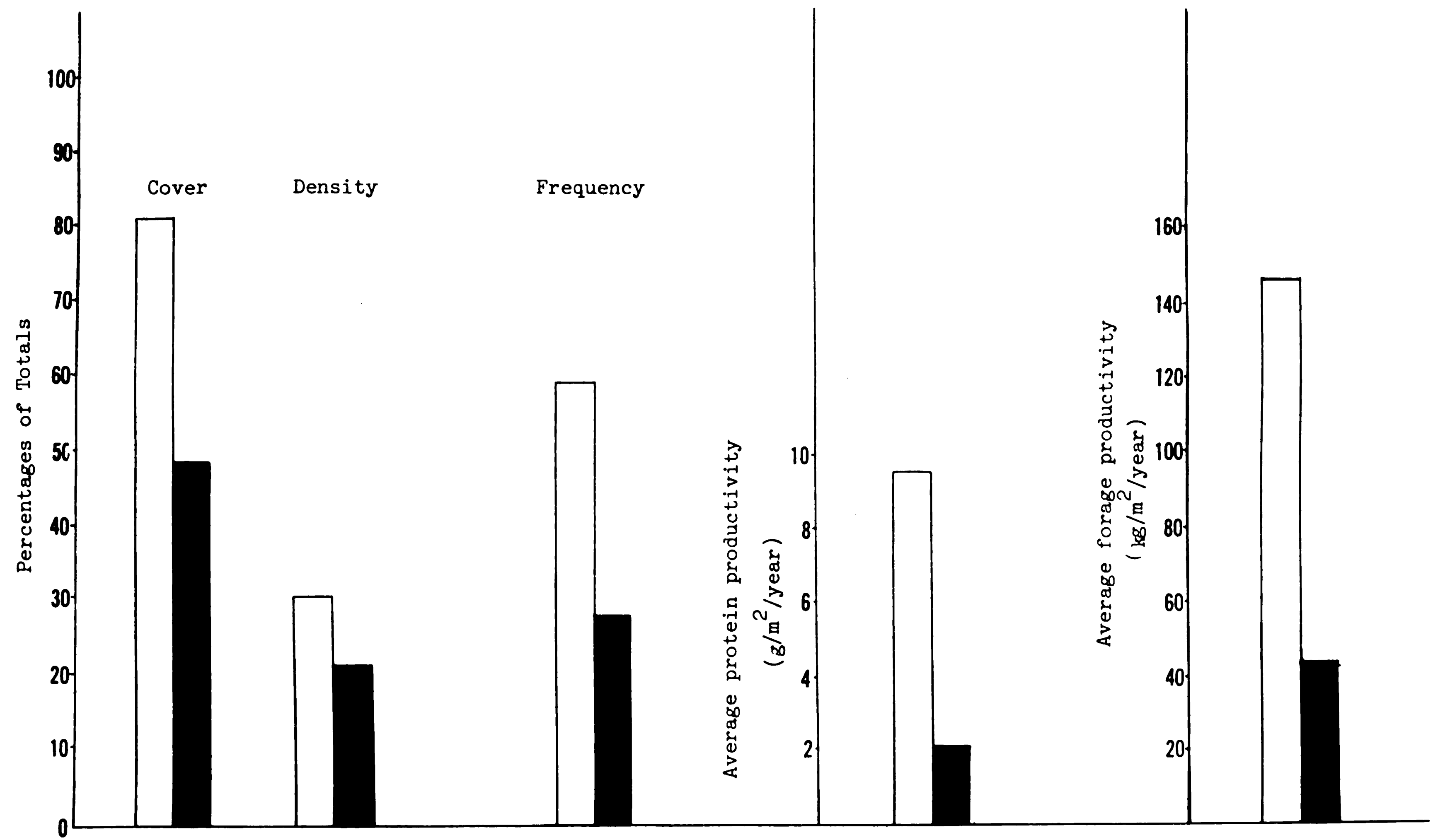

Figure 6. Comparison of cover, density, frequency and productivity of forage species found on Theodorou (solid bars) and Theodoropoula (open bars) islands. Spring, 1973.

remarkable. This change can be attributed chiefly to the differing edaphic conditions on the two islands.

Over-grazing on Theodorou island has been responsible for increased erosion and leaching of nutrients from the soil. The unavailability of nutrients to the plant community on depleted soils is evidenced by Pistacia lentiscus, which on the ungrazed island had a protein content of 8.48 percent compared to 4.73 percent on the overgrazed island. Forage quality, as well as quantity, thus was affected by overgrazing and resulted in reduced range carrying capacity.

Protein resources in turn may limit such population parameters as natality, survival and individual body growth, ultimately affecting secondary productivity.

Species Diversity

Species diversity for the two study areas was measured, using the Shannon-Wiener formula (Wilson and Bossert, 1971):

$$H_s = -\sum_{i=1}^{s} P_i \log_e P_i$$

where H_s = amount of diversity in a group of species s.

s = the number of species in the group.

P_i = the relative abundance of the ith species measured from 0 to 1.0.

$\log_e P_i$ = the natural logarithm of P_i.

Density values were calculated to be, H_{59} = 3.584 and H_{16} = 1.475 for the grazed and ungrazed areas, respectively. These values are significantly different (P .05).

The current study confirms the observations of Paine (1966) and Harper (1969) that, when predation is missing or excluded from a system, the system becomes less diverse and tends to converge toward simplicity.

As shown in Table 2, the climax plant community in the ungrazed area was completely dominated by a single species, *Obione portucaloides*. This species comprised approximately 43 percent of the vegetation and may be labelled a "climax dominant" or "keystone" species (Paine, 1969). This forb monopolizes the habitat due to successful competition under the existing environmental conditions. The dominance by "keystone" species yields relatively low species diversity and results in simplicity for the "climax" community.

Under intensive grazing pressure, the preferred dominant (*Obione portucaloides*) was removed, evidently opening a variety of unoccupied ecological niches to invader species. No simple generalizations can be made regarding the effects of herbivores on plant species' diversity. This study indicates that grazing is a potentially powerful diversifying force. After the grazing factor was introduced to the "climax" community species, diversity became higher.

As grazing intensity increases, less-palatable species are consumed and species tending toward unpalatability remain. Where animal population dispersal is prevented, long continuation of grazing evidently will lead to an ingress of new "disclimax keystone dominant" species in the form of toxic and spiny species. Ultimately, this process will lead to ecosystem simplicity and lower species diversity.

Range Trend

A vegetation analysis was conducted to detect range trend. Plant species were categorized relative to agrimi food preferences, as either high-preference, low-preference, or avoided (Papageorgiou, 1972). Vegetative analysis of Theodorou island revealed a low contribution of highly-preferred forage species ("decreasers") in the total flora. Low-preference ("increaser") plants and avoided ("invader-increaser") species made up most of the island's vegetation. Total vegetative cover (Figure 7) there consisted of 10.6 percent decreasers, 36.8 percent increasers and 52.6 percent invader-increasers. Approximately half of the island's vegetation was occupied by plants of the "agrimi-avoided" category.

The percentages of frequency and density for decreasers, increasers, and invader-increasers were: 6.4 and 3.4; 19.3 and 11.4; and 74.4 and 85.2, respectively. These data indicate a definite downward trend in vegetative quality. Although it seems that range conditions on Theodorou could not be much less conducive to providing a healthful permanent habitat to support an agrimi population, continued uncontrolled grazing there perhaps could result in even more complete range deterioration and in the total dominance of non-forage species.

POPULATION ANALYSIS AND PRODUCTIVITY IN THE AGRIMI

Studying the significance of biological productivity is a concrete rather than an abstract way to integrate the facts of energy flow with those of population dynamics. Knowledge of the size of standing crop associated with maximum level of productivity and the extent to which the crop can be exploited on a sustained yield basis are obviously vital concerns in the management of ecosystems for the improvement of human welfare.

Secondary production is a function of reproduction, body growth and survival of the growing and reproductive age classes in an animal population (Petrides et al., 1969). The data needed for calculating productive values, then, are census figures or the numbers of animals per unit area, information on sex and age structure so that the growing

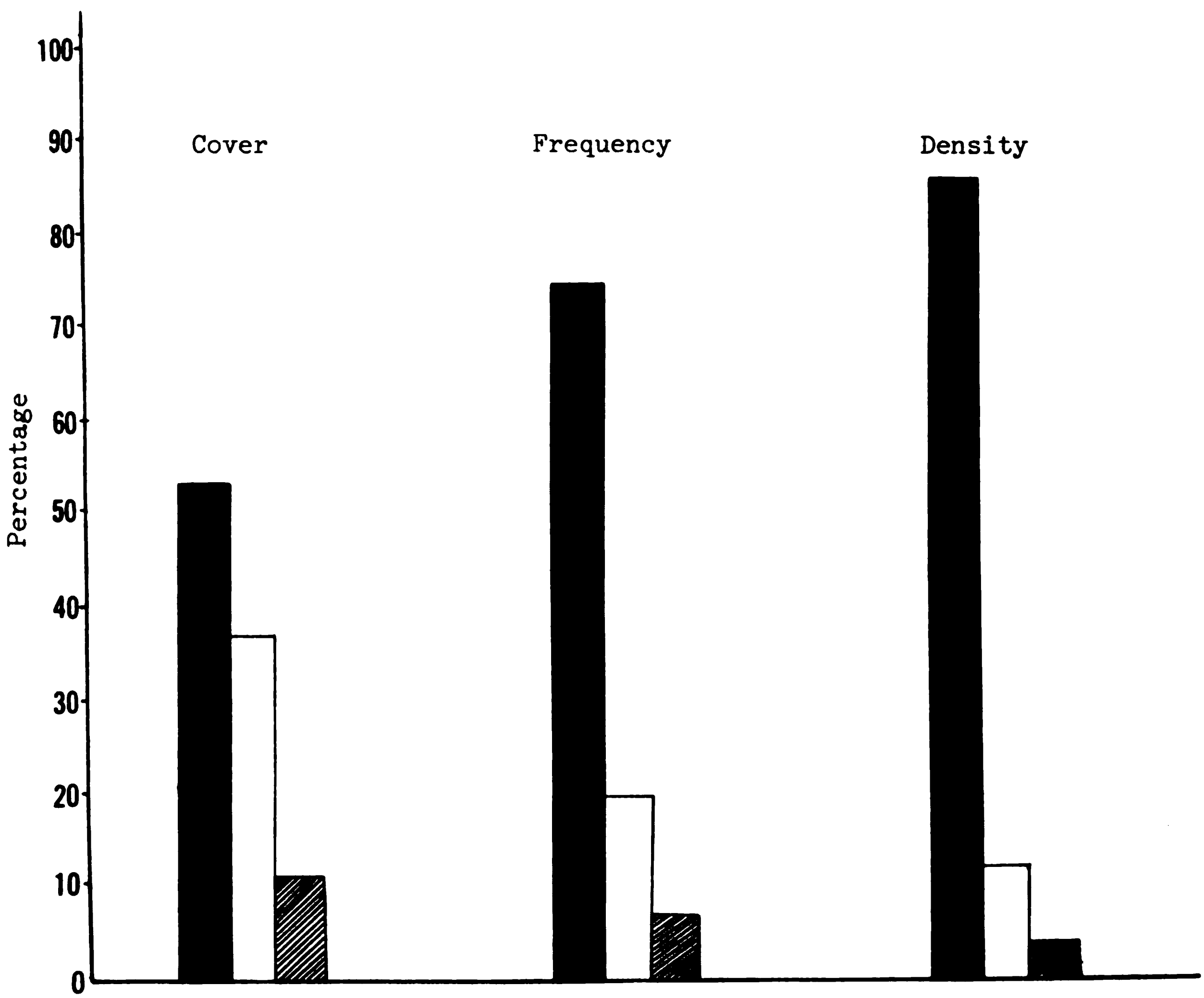

Figure 7. Cover, frequency and density of invader increasers (solid bars), increasers (open bars), and decreasers (cross hatched bars) found in 230 plots on Theodorou island, Spring, 1973.

individuals can be accounted for, knowledge of the birth rate, body-growth curves and knowledge of survival patterns in the growing age classes.

Difficulties in appraising all the above parameters, especially in determining a reliable body-growth curve, may account for the few attempts undertaken to study productivity in free-ranging wild herbivores (Engelmann, 1966; Milner, 1967; DeVos, 1969). The agrimi population in the island of Theodorou being at a high density in a natural ecosystem and available for direct count, accurate sex determination, precise age calculation, and complete capture and weighing offered an unparalled opportunity for the accurate estimation of productivity for a wild large-herbivore population.

FIELD METHODS

Population data were obtained from Greek Forest Service Annual Reports. Supplemental information was obtained by interviews with present and former personnel who had served as guards of the Theodorou Wildlife Reserve.

Current population data were obtained by a complete capture and a direct count of agrimi population. The census commenced in mid-June, 1973, after all the kids were born and extended until mid-September, 1973. The agrimis were trapped at the sole source of fresh water available on the island. The trap used consisted of a corral, about 60 m by 40 m in size, constructed around the small water reservoir. The fence was approximately 2 1/2 meters in height.

Animals were allowed access to the water through one of two doors, each about 1 1/2 meters in width, located on the north and south walls of the corral. The west wall was constructed in the shape of a funnel which narrowed to a wooden cage trap, about 5 m^2 in area. The corral was baited daily with about 40 kg of alfalfa and observed from a distance of about 70 meters. Upon the entrance of an animal to the corral, the doors were closed by pulling nylon cords controlled from the observation point. After the animals were secured, the observers entered the corral funnel and drove the animals into the wooden trap. Once inside the trap the animals were easily held for determination of sex, age, weight and other body measurements.

Trapping was conducted for 3 consecutive days each week during the 3-month capture operation. Trapping was suspended for 4 consecutive days per week to allow shy animals in the population to adjust to the corral and to secure water without fear of human presence. Without this precaution the fearful animals were forced either to suffer serious dehydration or to drink salt water from the ocean as was observed several times during the study period.

The annual growth rings of the agrimi's horns provided a satisfactory method for age determination (Couturier, 1961). Special care was given to the accurate age determination of old animals, especially females, due to the closeness of annual rings produced in the later years of life.

The author's familiarity with the pattern of annual growth rings in domestic goats contributed to the reliability of age determination during the agrimi study. Determination of the animals' sex was readily determined even at distances of 100 meters due to the distinct sexual dimorphisms of body size and horn development (Appendix). In the kids, where sexual dimorphism is not so pronounced, the genital organs were observed in captives to determine sex.

The animals were weighed to the nearest 10 grams using a 500 kg balance. Standard body measurements were recorded to the nearest millimeter. After all data were recorded, each animal was marked with a numbered metal ear tag. In addition to ear tags, the animal's horns were coded with white paint so that each animal was easily identifiable in the field as an individual.

Both horns of males and females with a kid were painted white. Only the left horn was painted white in females without young. This technique was employed to determine possible kid mortality during the study period. It was observed that young animals accompanied their mothers constantly from 1-2 days after birth until 6-8 months of age. Agrimi mothers seen without young during this period after once being observed with one, were assumed to have suffered kid mortality.

After the trapping period, to validate the assumption that the complete population was captured, three weeks of observation was undertaken in the island, and especially at the water source, with the aid of field glasses (5x70). During this period no unmarked animals were observed, suggesting that in all probability all the animals were captured.

Throughout the 9 month period, continuous surveillance was maintained on the island to discern any mortality as revealed by animal carcasses.

The agrimis' confinement to the island eliminated the possibility of unrecorded immigration into or emigration from the study area. An intensive systematic search of the island was undertaken to collect the skulls and horns from which the age and sex could be discerned. The sex of carcasses one year or less in age was impossible to determine due to minimal horn development. Therefore, a 1:1 sex ratio was assumed for mortality in this age class.

RESULTS AND DISCUSSION

Sex and Age Composition

Of the total 97 animals present and captured during the summer of 1973, 50 were males and 47 females (Table 6). The sex ratio of 1:1.06 is not significantly different from unity (P   .05). From birth throughout each age class, mortality was shared equally in males and females.

By age, the population consisted of kids (young of the year), 15 percent; yearlings, 13 percent; and adults, 72 percent. The kid to adult ratio was 14:100; the kid to female ratio was 36:100, while the kid to yearling ratio was 1:1.

The observed percentages reveal some agrimi population characteristics. The low kid and yearling percentages represent a very low reproductive rate. A low kid mortality after the first month, as indicated by the kid:yearling ratio, suggests a high kid mortality shortly during the first month after birth. An intensive systematic survey of the island after the breeding season, however, indicated a first-month mortality of only two kids. Only 16 of the 29 adult (two to nine years) females gave birth. Looked at in one way, this suggests the presence of a self-regulatory mechanism operating within the population to maintain an equilibrium between population density and food resources. From another standpoint, however, it indicates one of the harmful effects of poor forage on agrimi welfare. The impoverished food resources on the island probably act as a density-dependent factor limiting the physiological potential of the population to reproduce. Fecundity in agrimi, as in deer (Cheatum and Severinghaus, 1950; Taber, 1953; Taber and Dasmann, 1958), bighorn sheep (Buechner, 1960; Steeter, 1969), thar (Caughley, 1969), and moose (Markgren, 1973), apparently is closely

Table 6. Agrimi population sex-age structure as determined by complete count. Theodorou island, Crete, Greece, Summer, 1973.

Age (years)	Males	Females	Kids	
			Males	Females
0-1	7	7	--	--
1-2	7	6	--	--
2-3	2	5	1	1
3-4	6	4	2	1
4-5	4	5	1	1
5-6	3	3	1	2
6-7	1	4	1	1
7-8	1	2	--	--
8-9	4	6	1	1
9-10	11	2	--	--
10-11	3	1	--	--
11-12	1	1	--	--
TOTAL	50	47	7	7

regulated by the nutritional requirements of an animal and fulfillment of those requirements by the range, before and during the reproductive season.

From a graphic plot of the population structure (Figure 8), it appears that the majority of the living population consists of old animals, particularly in the 9-11 year age-classes. This unexpected age distribution may be due to an unusually high rate of natality or a high rate of survival of the 1963, 1964, 1965 year-class animals. This phenomenon known as "dominant age class" has not been reported or at least seems not to have been emphasized in reports for large mammals, although it has been observed repeatedly in fish populations (Hjort, 1926; Lawler, 1965).

Life Tables

The life table (Deevey, 1947; Hickey, 1952) is a convenient format for describing the mortality schedule of a population. It is based on the age distribution at death.

In this study, 55 skulls were found of animals which had died prior to 1973 on Theodorou. Due to the small size of the island and the systematic survey undertaken, it is unlikely that any skulls were overlooked. Since the non-acid soil of the island was conducive to specimen preservation, it is estimated that they represented natural mortality of the agrimi over at least the last 4 to 5 years.

Life tables were constructed by sex to enable comparisons of mortality rates in both male and female segments of the population. As is usual in the analysis of life tables, it was assumed that (a) the sample represents the population age frequency at death, and (b) the population was stable during the period that mortality occurred. The

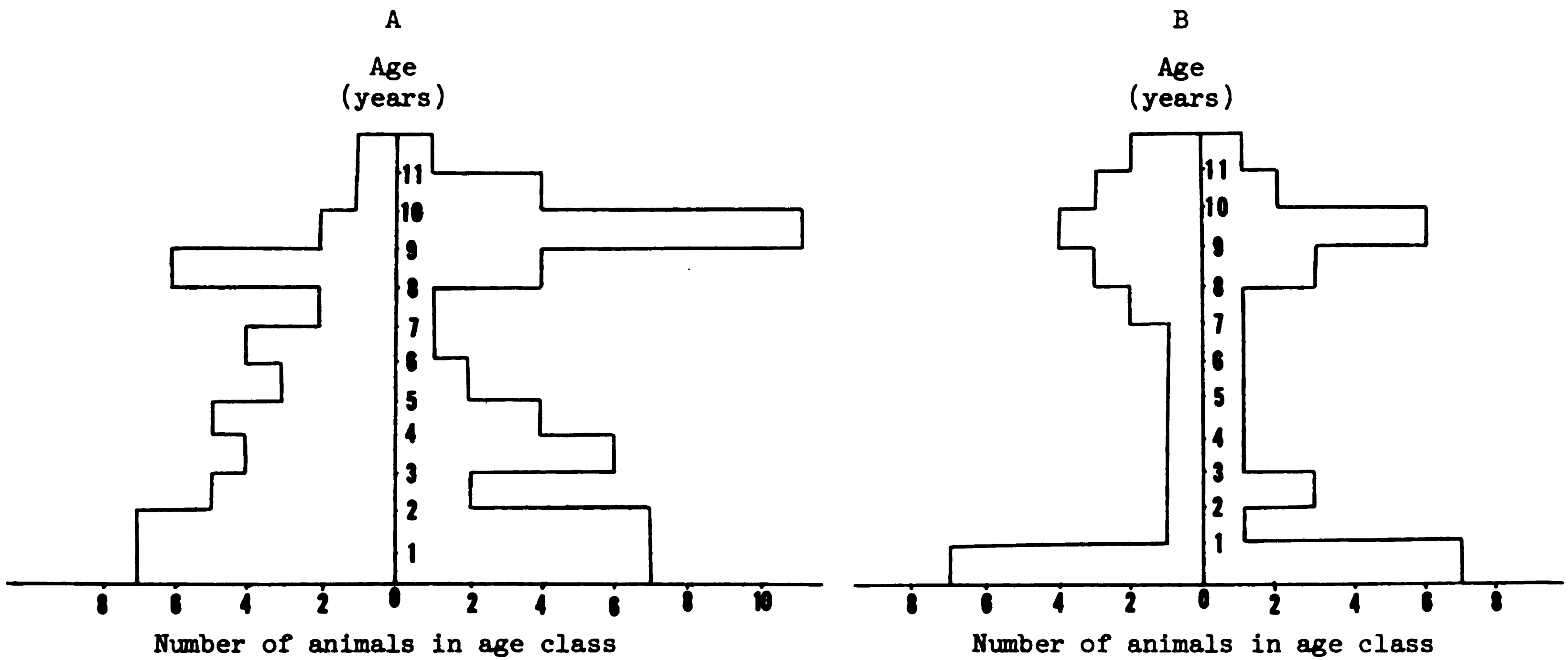

Figure 8. Age pyramids for the agrimi: A. The 1973 age structure of the living population; B. The age structure of animals dying over the past five years. Age classes represent absolute numbers, with males on the right and females on the left of each vertical axis in each pyramid.

Table 7. **Life table for the male agrimi** (Capra aegagrus cretensis) based on the known age at death of 27 animals dying before July 1973 on the island of Theodorou, Crete, Greece.

Age (Years)	Number dying in age interval out of 1000 born	Number surviving at beginning of age interval out of 1000 born	Mortality rate per 1000 animals living between ages x and x + 1	Median number of animals alive between x and x+1	Number animal-years remaining to be lived for each age x	Average length of life remaining for each age x	Age as % deviation from mean length of life
x	d_x	l_x	$q_x = \frac{d_x}{l_x} 1000$	$L_x = \frac{l_x + l_{x+1}}{2}$	$T_x = \Sigma L_x - L_{x-1}$	$e_x = \frac{T_x}{l_x}$	$x' = \frac{x - e_o}{e_o} 100$
0-1	250	1000	250.0	875	5821	5.82*	-100.0
1-2	36	750	48.0	732	4946	6.59	- 82.8
2-3	71	714	99.4	678	4214	5.90	- 65.6
3-4	35	643	54.4	625	3536	5.49	- 48.4
4-5	36	608	59.2	590	2911	4.78	- 31.2
5-6	36	572	62.9	554	2321	4.05	- 14.0
6-7	36	536	67.1	518	1767	3.29	+ 3.0
7-8	36	500	72.0	482	1249	2.49	+ 20.2
8-9	107	464	230.6	410	767	1.65	+ 37.4
9-10	214	357	599.4	250	357	1.00	+ 54.6
10-11	107	143	748.3	89	107	0.74	+ 71.8
11-12	36	36	1000.0	18	18	0.50	+ 89.0
TOTAL	1000	6323		5821			

*average longevity of the population

Table 8. Life table for the female agrimi (<u>Capra aegagrus cretensis</u>) based on the known age at death of 28 animals dying before July, 1973 on the island of Theodorou, Crete, Greece.

Age (Years)	Number dying in age interval out of 1000 born	Number surviving at beginning of age interval out of 1000 born	Mortality rate per 1000 animals living between ages x and x + 1	Median number of animals alive between x and x+1	Number animal-years remaining to be lived for each age x	Average length of life remaining for each age x	Age as % deviation from mean length of life
x	d_x	l_x	$q_x = \frac{d_x}{l_x} 1000$	$L_x = \frac{l_x + l_{x+1}}{2}$	$T_x = \Sigma L_x - L_{x-1}$	$e_x = \frac{T_x}{l_x}$	$x' = \frac{x - e_o}{e_o} 100$
0-1	259	1000	259.0	870	5939	5.93*	-100.00
1-2	37	741	49.9	722	5069	6.84	- 83.13
2-3	37	704	52.6	685	4347	6.17	- 66.27
3-4	37	667	55.5	648	3662	5.49	- 49.40
4-5	38	630	60.3	611	3014	4.78	- 32.54
5-6	37	592	62.5	573	2403	4.05	- 15.68
6-7	37	555	66.7	536	1830	3.29	+ 1.18
7-8	74	518	142.9	481	1294	2.49	+ 18.04
8-9	111	444	250.0	388	813	1.83	+ 34.90
9-10	148	333	444.4	259	425	1.27	+ 51.77
10-11	111	185	600.0	129	166	0.89	+ 68.63
11-12	74	74	1000.0	37	37	0.50	+ 85.49
TOTAL	1000	6443		5939			

*average longevity of the population

Table 9. Life table for the agrimi (*Capra aegagrus cretensis*) based on the known age at death of 55 animals, dying before July 1973 on the island of Theodorou, Crete, Greece. Both sexes combined.

Age (Years)	Number dying in age interval out of 1000 born	Number surviving at beginning of age interval out of 1000 born	Mortality rate per 1000 animals living between ages x and x + 1	Median number of animals alive between x and x+1	Number animal-years remaining to be lived for each age x	Average length of life remaining for each age x	Age as % deviation from mean length of life
x	d_x	l_x	$q_x = \frac{d_x}{l_x} 1000$	$L_x = \frac{l_x + l_{x+1}}{2}$	$T_x = \Sigma L_x - L_{x-1}$	$e_x = \frac{T_x}{l_x}$	$x' = \frac{x - e_o}{e_o} 100$
0-1	255	1000	255.0	872	5870	5.87*	-100.0
1-2	37	745	49.7	726	4998	6.71	- 82.9
2-3	54	708	76.3	681	4272	6.03	- 65.9
3-4	37	654	56.6	635	3591	5.49	- 48.8
4-5	36	617	58.3	599	2956	4.79	- 31.8
5-6	37	581	63.7	562	2357	4.06	- 14.8
6-7	36	544	66.2	526	1795	2.30	+ 2.2
7-8	54	508	106.3	481	1269	2.50	+ 19.2
8-9	109	454	240.1	399	788	1.74	+ 36.2
9-10	182	345	527.5	254	389	1.13	+ 53.3
10-11	109	163	668.7	108	135	0.83	+ 70.3
11-12	54	54	1000.0	27	27	0.50	+ 87.3
TOTAL	1000	6373		5870			

*average longevity of the population

first assumption, however, may not have been met for the 0-1 year-class animals. Carcasses of immature animals, especially those dying soon after birth, tend to decay faster than those of adults, so that they are underrepresented in skeletal surveys. There is evidence to support the second assumption, however, in that the calculated population parameters (a) net reproductive rate, (b) generation time, (c) innate rate of increase, and (d) average mortality rate, are all much as would be expected.

Net Reproductive Rate

The net reproductive rate, or replacement rate (R_o) is the average number of offspring produced by an animal during its lifetime (Lotka, 1945). It is customary and convenient to calculate net reproductive rate using only the female segment of the population (Leslie and Ramson, 1940; Birch, 1948; Evans and Smith, 1952), assuming that the male segment increases at an equal rate. This assumption is well supported for the agrimi (Figure 9). The net reproductive rate (R_o) is the summation of the products of the fraction of female animals surviving to each age (l_x) and the average number of female offspring per female at that age (m_x) (Table 10). Since only one female was present in the 7-8 year-class agrimi population, the m_x of the age group was estimated by averaging the values immediately preceding and following.

The net reproductive rate for the agrimi population, calculated to be $R_o = 1.14$, was based on two independent sources of data; the survivorship (l_x) of the dead animals (Table 8), and the fecundity (m_x) of the live population (Table 6). Assuming that l_x and m_x values will remain reasonably constant, this value indicates that one animal is going to be replaced by 1.14 animals at the end of one generation period. It is

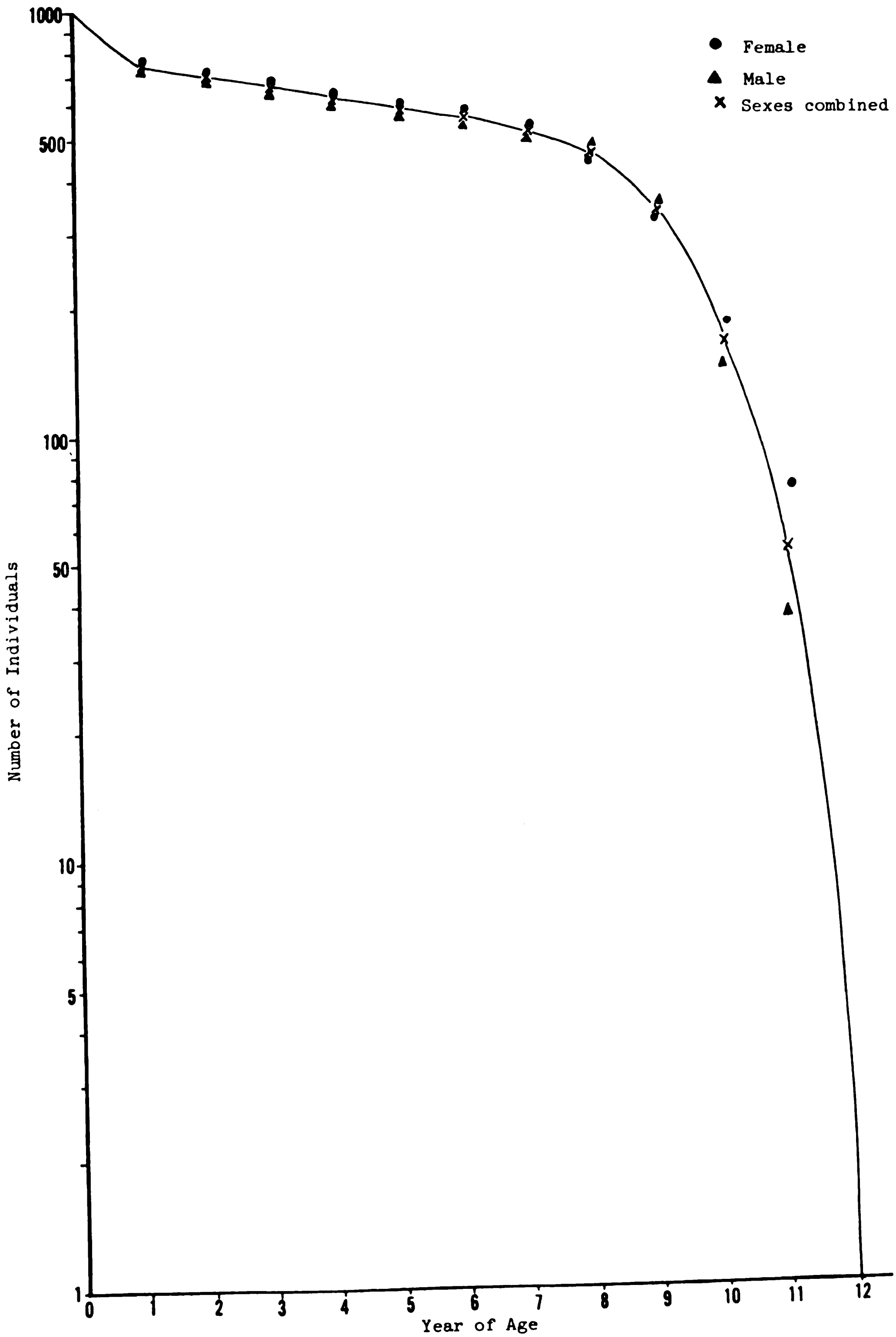

Figure 9. Survivorship curve for the agrimi on Theodorou island, Crete, Greece.

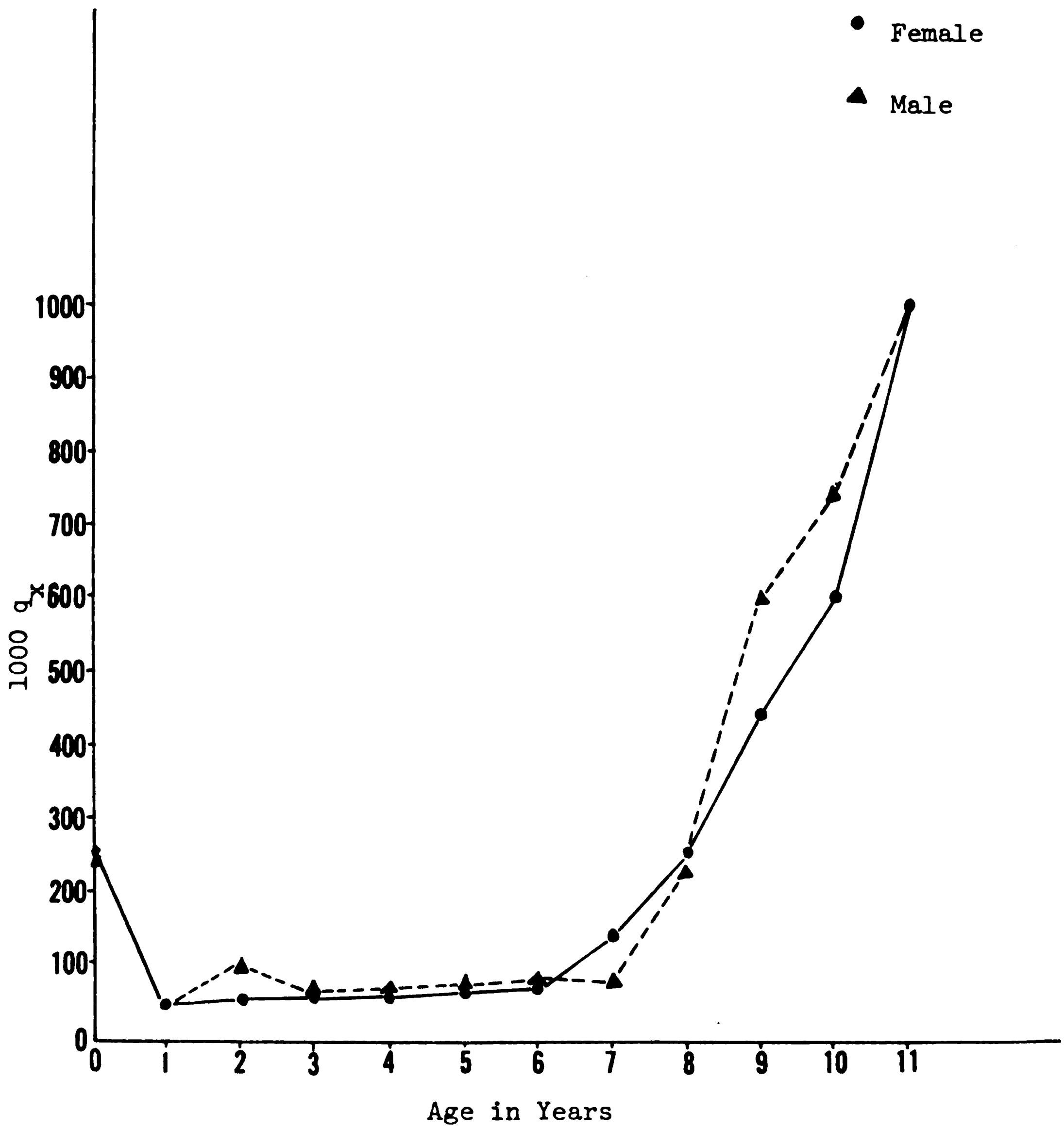

Figure 10. Agrimi mortality rate per 1000 for each age interval of 1 year, plotted against the start of the interval.

Table 10. Survivorship (l_x), fecundity (m_x) and reproductive value (v_x) of the female agrimi population, Theodorou island, Crete, Greece, 1973.

Age (Years)	l_x (1)	m_x (2)	$l_x m_x$	$l_x m_x x$	v_x
0-1	1.000	--	--	--	--
1-2	0.741	--	--	--	--
2-3	0.704	0.200	0.140	0.423	1.400
3-4	0.667	0.250	0.166	0.664	1.500
4-5	0.630	0.200	0.126	0.630	1.000
5-6	0.592	0.666	0.394	2.364	1.333
6-7	0.555	0.250	0.138	0.966	0.500
7-8	0.518	0.200*	0.103	0.824	0.500
8-9	0.444	0.166	0.073	0.584	0.142
9-10	0.333	--	--	--	--
10-11	0.185	--	--	--	--
11-12	0.074	--	--	--	--
TOTAL		1.932	1.140	6.455	

*See text

[1]From Table 8

[2]From Table 6

apparent from this calculated value that as competition intensified, it reduced and finally halted population growth at some level of homeostasis with the habitat's carrying capacity (Slobodkin, 1961; Slobodkin et al., 1967). The sum of the m_x column (Table 10), equal to 1.932, is the gross reproductive rate, or the average number of young animals expected to replace any animal living throughout an entire reproductive period.

Generation Time

The generation time (T) is the mean lapse of time between an animal's birth and the mean data of birth of its offspring. Dublin and Lotka (1925) suggest the following formula to estimate the mean length of a generation:

$$T = \frac{\sum l_x m_x X}{\sum l_x m_x}$$

Solving this formula (Table 10), the mean generation time for the female agrimi is 6.3 years. A comparison of this value based on dead (l_x) and alive (m_x) animals (Table 6) with the 5.9 year calculated mean life expectancy of the female agrimi based on dead animals (Table 8), provides evidence that the agrimi population is stable. That the mean period elapsing between the birth and death of a female almost coincides with the period between the birth of a female and the birth of its first offspring, indicates that one animal is replaced only by one offspring.

Innate Rate of Increase

The innate rate of increase (Southwood, 1966) is a measure of animal population growth under natural conditions. In addition, this population parameter can be used to compare populations under different conditions and/or management programs where generation times may vary considerably.

The calculated net replacement rate for the agrimi population (R_o = 1.14) suggests an approximate but reasonable estimation of the agrimi's innate capacity to increase. From the data of Table 10 and using the formula proposed by Caughley and Birch (1971) where $r_c = \frac{\log_e R_o}{T}$ the agrimi's innate rate of increase (r_c) can be calculated to be 0.0209/head/year, or the population is able to expand at a rate of 2.09/100/year, assuming that the products ($l_x m_x$) remain unchanged.

Mortality Rate

The mean annual mortality rate is a significant figure used in judging the performance of animal populations. The average mortality rate is the sum of the individuals dying in all age groups (Σd_x) divided by the sum of the individual alive in all groups (Σl_x). The mean annual mortality rate ($\Sigma d_x / \Sigma l_x$) was calculated of the dead animals to be 15.7 percent (Table 9) for the agrimi population. Capture data revealed that the agrimi's annual population replacement rate for 1973 was 14.4 percent (Table 6). Comparison of the values indicates a stable agrimi population (Buechner, 1960).

An examination of the four previously calculated population parameters supports the assumption that the agrimi population was in homeostasis with the carrying capacity of the habitat.

The findings of this study indicate the necessity that further research on agrimi population dynamics be undertaken to ascertain if natural population are regulated by internal self-regulatory mechanisms, (Slobodkin et al., 1967; Hairston et al., 1960) or if population control is dictated by external environmental fluctuations (Andrewartha and Birch, 1954; Ehrilich and Birch, 1967) or both.

Data obtained from the Greek Forest Service Annual Reports (1969-1972) by interviews with a Forest Service employee who has guarded the island over the past 20 years, indicated that fluctuations in the agrimi population level have not exceeded 7.5% from the mean (100 animals) for the years 1969 to 1972. Buechner (1960) suggests that fluctuations as small as these indicate a stationary population. Although this evidence is somewhat subjective it does, however, tend to support the data-derived evidence that the population is stationary.

Survivorship

A survivorship curve is a graphical representation of the number of organisms surviving at the start of some age interval (Krebs, 1972). Logarithms of the expanded numbers of agrimi alive at each age (columns l_x, Tables 7 and 8) are plotted against the corresponding time intervals (Figure 9).

As evident by the graphical representation, both sexes are alike in having a very steep initial slope, indicating a high mortality during the first year of life. During the second to seventh years there are only small losses among animals, while the rate of loss tends to become steeper in the later years of life. The animals were not subject to hunting or exposed to predation. In all probability, the principal cause of mortality was starvation, a food limitation in quality or more likely in quantity. The effects of starvation may have been augmented by disease and/or parasitism but this matter was not investigated.

The agrimi population exhibited the usual survival pattern for a large mammal population which is not heavily hunted (Petrides and Swank, 1966; Spinage, 1971) or subject to predation (Murie, 1944; Mech, 1966).

In such a population, the highest mortality is suffered by the very young and the very old. The most favorable survival rate is characteristic of young adults, and changes in survival rates are gradual.

The average life expectancy from birth (e_o) for male and female agrimi was calculated (Tables 7 and 8) to be 5.82 and 5.93 years, respectively, and of either sex 5.87 years. The maximum ecological life span for the agrimi was found to be 12 years for both sexes.

The observed high longevity attained by many breeding adults may be partly due to a low representation of young animals which have characteristically high metabolic rates (Taber and Dasmann, 1957). When young are proportionally low the chances for survival of breeding adults appears to improve due to the reduction in competition for food.

Reproductive Value

The standard measure of the contribution of an individual to the next generation is the reproductive value (V_x) of the individual at each age x (Table 10). This value determines the worth of individuals in each age category in terms of offspring contributed to the next generation. The formula proposed by Fisher (1958) is:

$$V_x = \frac{\text{the number of female offspring produced at this moment by females of age x or older}}{\text{the number of females of age x alive at this moment}}$$

The reproductive value is zero for females 0-2 years of age, peaks at 1.5 at the age of 2-3 years old, and thereafter decreases gradually (Table 10). Females showed a zero reproductive rate in the 9-10 year age class and older.

The mortality rates exhibited by the population when compared to the calculated reproductive values indicated an important feature of a natural regulatory mechanism. As indicated by the survivorship curves (Figure 8), the mortality is high mainly in very young and very old animals, which have practically no reproductive value. Natural regulatory mechanisms take the form of a skillful or "prudent" predator, or other mortality cause, as some ecologists like to say (Slobodkin, 1968). Such mortality, when concentrated on age groups with the lowest reproductive values, does not affect the reproductive growth of the prey population and thus exploits that population with highest efficiency.

An almost identical pattern of mortality was reported for the Dall sheep (Murie, 1944) in Mt. McKinley National Park, Alaska, where the sheep population was constantly under heavy pressure from wolves, which also took mainly lambs and very old animals.

Living Biomass

The total mass of living organisms present in a population or in any arbitrary ecological unit at a given moment in time and space is referred to as the living biomass of one or more species. Since all individuals were captured, the biomass of the agrimi population was measured by simply summing their weights. The total population biomass was calculated to be 2175.8 kilograms on the 68-hectare island (31.99 kilograms per hectare; 3.20 grams per square meter).

Even though considerable information on the caloric values for biological material has been published (Golley, 1961; Slobodkin and Richman, 1961; Gorecki, 1967), no data are available for large mammals. Petrides and Swank (1966) assumed 1.5 kcal gross energy/g live weight for elephants; Du Plessis (1972) used the same figure for the blesbok; while Bobek et al. (1973) estimated the gross energy caloric value of the roe-deer to be 2.161 kcal/g live weight.

Due to the protected status of the agrimi, only one animal could be sacrificed for analysis in this study. One male agrimi, 5 years of age and 27.45 kg in weight, was carefully selected as a representative specimen for carcass analysis and caloric determination. Moisture, fat, protein, and ash were determined according to standard methods of analysis (AOAC, 1970). Protein and fat contents of the sacrificed animal were determined to be 4737.2 g and 2437.8 g, respectively (Table 11). Assigning a gross caloric value of 9.4 kcal per gram for fats and 5.65 kcal per gram for proteins, (Maynard and Loosli, 1969), the caloric content of the entire animal carcass was calculated to be 49,681 kcal. From this, a gross energy value of 1.80 kilocalories per gram live weight was calculated for the live animal. Applying 1.8 kcal/g live weight, the living biomass of the agrimi's was calculated to be 5.44 kcal/square meter.

Individual Growth and Rate of Weight Gain

In productivity studies it is essential to know the weight gains of the organism under study during each age interval. Since the entire population was of known age, and each animal was weighed, the mean weights per age class were easily determined. Males were markedly heavier than females after the first year of age (Figure 11). The males reached their maximum body weight at eight years of age, after which a constant body weight was observed. Females attained maximum body weight at the sixth year of age, after which a slight decrease in body weight was indicated.

Rate of Tissue Production

From survivorship and weight-growth curves, cohort biomass production can be easily calculated.

Table 11. Percentage composition of the carcass of a 5 year old male agrimi's body.[1]

Item	Weight (g)	Water	Protein	Fat	Ash	Total Weights Protein (g)	Total Weights Fat (g)
Skin	1897.0	54.8	38.6	5.5	1.1	732.0	104.3
Soft tissue[2]	1546.0	74.3	19.6	5.0	1.1	303.0	85.0
Horns	402.0	29.0	60.4	2.8	7.8	242.8	11.3
Compound stomach	1900.0	64.3	22.7	12.4	0.6	413.3	235.6
Bones	3300.0	37.1	24.6	10.7	27.6	811.8	353.1
Skeletal muscle	10917.0	63.5	20.3	15.1	1.1	2216.1	1648.5
TOTAL	19962.0					4737.2	2437.8

[1]Analysis made at Veterinary School at Aristotelion University, Thessaloniki, Greece.

[2]Heart, liver, lungs, kidneys, brain, breeding organs, intestines

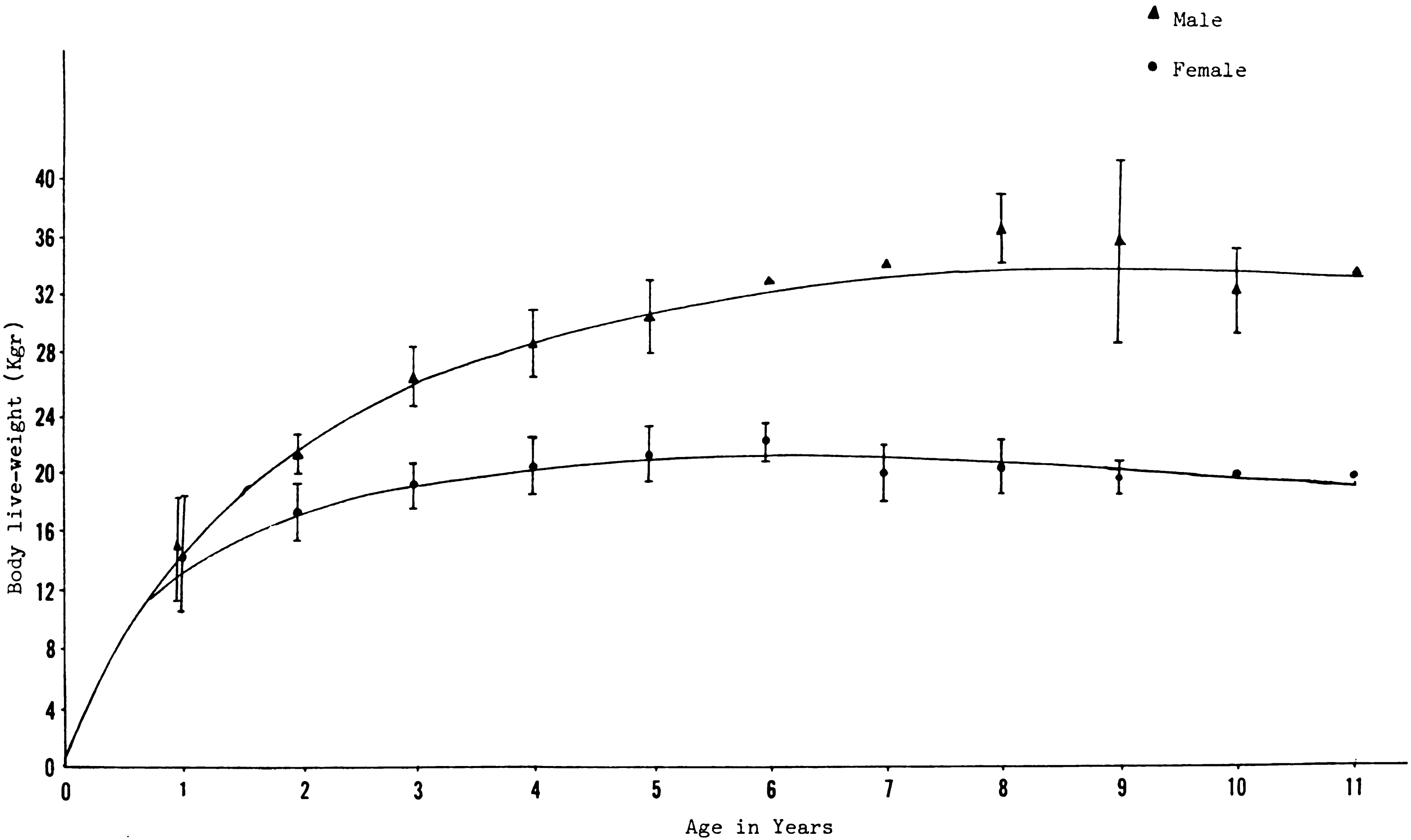

Figure 11. Growth curves for the agrimi from individual weights of the total captured population on Theodorou island, Crete, Greece, Summer, 1973. Vertical lines represent the range in observed weights and averages by each age class.

The protoplasm synthesized by a cohort of 1000 male agrimi during their lifetime totaled 25864.2 kilograms (Table 12). Since the model population lived a total of 6323 years, average growth production per male per year was 4.090 kilograms. Following the same computations as for males, the protoplasm synthesized by an average female agrimi (Table 13) was 2.591 kilograms per year. Since the agrimi population had a sex ratio of approximately 1:1, the average growth production per agrimi was calculated to be 3.345 kilograms per year. At 1.8 kilocalories per gram live weight, an average of 6012.0 kilocalories of gross energy per year was fixed as protoplasm by each individual animal. For 97 agrimi on 68 hectares, or 1.426 agrimi per hectare, the annual production per individual agrimi was 8573.11 kilocalories of gross energy per hectare (0.857 kilocalories of gross energy per square meter per year). The graphical representation of biomass gains and losses in the hypothetical cohort throughout its life span (Figure 12) characterizes the living biomass of agrimis at any given time.

The living biomass is greatest and remains almost stable between the ages of 2 and 8 in the male and 1 and 6 in the female. After age 8 in the males and 6 in the females, a total harvest could be made to avoid a rapid biomass loss due to mortality.

ENERGY REQUIREMENT AND UTILIZATION BY THE AGRIMI

Methods and Procedures

Little scientific information is available on the nutrition and energy requirements of either wild or domestic goats. The total annual energy requirements of a population depends on: (a) the density of the population, (b) the demographic components of the population, (c) the physical conditions actually experienced by individual animals, and

Table 12. Production data for the male agrimi on the island of Theodorou, Crete, Greece, 1973.

A	B	C	D	E	F	G	Population weight changes (kg)		J	K
Age x (years)	Number alive at the beginning of age x	Number dying between age x and x-1	Weight average at beginning of age x (kg)	Weight increment between age x and x-1 (kg)	Average weights between ages x and x-1 (kg)	Weight change from age x to mid-point of interval x (kg)	H=Living population (B) x (E)	I=Mortality (C) x (G)	Total population weight changes (H)+(I) (kg)	Total population weight losses as mortality (C)x(F) (kg)
0	1000		1.080	1.080			1,080.0		1,080.0	
1	750	250	15.237	14.157	8.158	7.078	10,617.8	1769.5	12,387.3	2039.5
2	714	36	20.600	5.363	17.918	2.681	3,829.2	96.5	3,925.7	645.0
3	643	71	26.625	6.025	23.612	3.012	3,874.1	213.9	4,088.0	1676.5
4	608	35	28.762	2.137	27.693	1.068	1,299.3	37.4	1,336.7	969.3
5	572	36	30.666	1.904	29.714	0.952	1,089.1	34.3	1,123.4	1069.7
6	536	36	32.500	1.834	31.583	0.917	983.0	33.0	1,016.0	1136.9
7	500	36	34.100	1.600	33.300	0.800	800.0	28.8	828.8	1198.8
8	464	36	37.350	3.250	35.725	1.625	1,508.0	58.5	1,566.5	1286.1
9	357	107	35.866	-1.484	36.608	-0.742	-529.8	-79.4	-609.2	3917.1
10	143	214	32.350	-3.516	34.108	-1.758	-502.8	-376.2	-879.0	7299.1
11	36	107	32.350		32.350					3461.4
12	0	36	32.350		32.350					1164.6
TOTAL	6323	1000							25,864.2	25864.0

Table 13. Production data of the female agrimi on the island of Theodorou, Crete, Greece, 1973.

A	B	C	D	E	F	G	Population weight changes (kg)		J	K
Age x (years)	Number alive at the beginning of age x	Number dying between age x and x-1	Weight average at beginning of age x (kg)	Weight increment between age x and x-1 (kg)	Average weights between ages x and x-1 (kg)	Weight change from age x to mid-point of interval x (kg)	H=Living population (B) x (E)	I=Mortality (C) x (G)	Total population weight changes (H)+(I) (kg)	Total population weight losses as mortality (C)x(F) (kg)
0	1000		1.080	1.080			1,080.0*		1080.0	
1	741	259	14.183	13.103	7.631	6.551	9,709.3	1696.7	11406.0	1976.4
2	704	37	17.020	2.837	15.601	1.418	1,997.2	52.5	2049.7	577.2
3	667	37	19.100	2.080	18.060	1.040	1,387.4	38.5	1425.9	668.2
4	630	37	20.222	1.122	19.661	0.561	706.9	20.8	727.7	727.5
5	592	38	21.016	.794	20.619	0.397	470.0	45.1	485.1	783.5
6	555	37	22.100	1.084	21.558	0.542	601.6	20.1	621.7	797.6
7	518	37	20.325	-1.775	21.212	-0.887	-919.4	-32.8	-952.2	784.9
8	444	74	20.016	-0.309	20.170	-0.154	-137.2	-11.4	-148.6	1492.6
9	333	111	20.016		20.016					2221.8
10	185	148			20.016					2962.4
11	74	111			20.016					2221.8
12	0	74			20.016					1481.2
TOTAL	6443	1000							16695.3	16695.1

*Reproduction

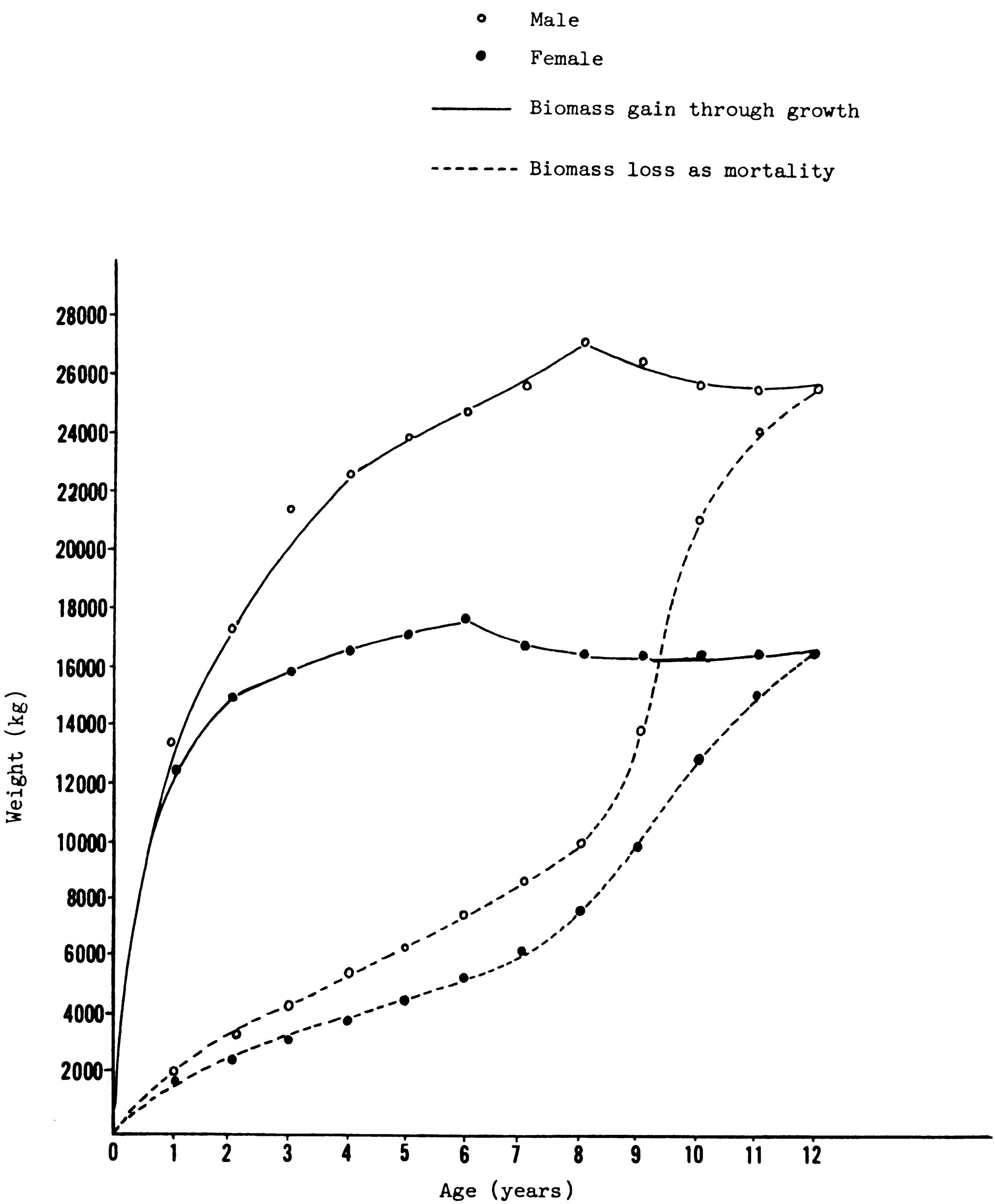

Figure 12. Production-mortality relationships of one cohort of the agrimi.

(d) the composition and quality of available food. Field metabolism studies with free-ranging wild animals are difficult due to the complexity of these parameters. To determine accurately the energy and nutrient requirements of a population, those of each individual must be summed (Robbins, 1973). This is, however, impractical for most free-ranging wild herbivores.

Estimates of population energy requirements in the wild can be approximated by utilizing data from feeding experiments with captive animals. In consequence, a feeding trial was conducted using agrimis of each sex, average in weight and age. These were two 4-year old males and two 3-year old females of average weights for each sex.

Digestion cages were designed to allow reasonable freedom of movement for one agrimi at a time. The cages (2 X 1 meters) were constructed of wood with wire on the floor. The mesh was large enough to allow the passage of feces into a collection device. Separate food and water containers were attached to the sides of each cage. Water was provided ad libitum throughout the experiment. The animals were confined to the cages for a 3-4 week precollection period to adjust to captivity prior to the one week feeding trials.

During the trials, food intake and fecal excretion data were recorded, from which food digestion values were calculated. The 3 species of forage utilized in the feeding trial were proportionally fed to simulate the natural diet. These three species, Pistacia lentiscus, Scilla maritima, and Asphodelus macrocarpus, normally comprise about 55 percent of the island's forage production. The selective feeding exhibited by the agrimi toward highly palatable species results in these species becoming scarce during the summer period when the experiment was conducted.

Animals were fed at 12:00 A.M. each day at which time the uneaten and discarded food from the previous day was collected and subtracted from the initial weights. At the same time feces were collected and weighed. These weight values were converted to dry weight by a previously-established percentage moisture content.

Results and Discussion

Energy Requirements

The average daily food intake required for the maintenance of captive male agrimi was found to be (Table 14) 461.7 g dry-weight or 1.74 percent of the animal's live weight. Of the food ingested, 273.6 g dry-weight was digestible matter, yielding a dry matter digestibility coefficient of 59.3 percent for the males. The average daily food intake of a female agrimi was 294.76 g dry-weight or 1.75 percent of the animal's live weight. Of the food ingested, 177.62 g dry-weight was digestible, yielding a digestibility coefficient of 60.2 percent for the females.

Food requirements of free-ranging animals as compared to caged ones have been investigated by a number of workers. Graham (1964) reported that grazing sheep expend 40% more energy than caged animals for maintenance requirements. Other workers have calculated this value for sheep to be 33% (Lambourne and Reardon, 1963), and 24% (Langlands et al., 1963). Devendra (1967), in his study of Malayan goats, reported that free-ranging animals consumed about 44% more food than in the confinement.

For the agrimi, it was assumed that the daily food intake was equivalent to the maintenance requirements of penned animals, since there was no weight fluctuation during the feeding trial.

Table 14. Average daily food consumption and utilization on dry-weight basis by 4 captive animals on Theodorou island, Crete, Greece, August, 2-9, 1973.

Sex	Live Weight (kgr)	Average feed intake (g)	Average feed intake As % of live weight	Feces (g)	Food Materials digested (g)
Male	26.400	449.28	1.70	180.58	268.71
Male	26.450	272.13	1.79	195.71	278.42
Female	16.600	308.41	1.85	119.14	189.27
Female	16.900	281.11	1.66	115.14	165.97

Based on those values, an increase of about 40% of the maintenance requirements over those of the caged animals was applied as an estimate of the maintenance requirements for free-grazing agrimis.

The daily average food intake required for the maintenance of a free-ranging male agrimi, therefore, was judged to be approximately 646.4 g dry-weight or 2.44 percent of the animal's live weight. These values for the female agrimi were calculated to be 412.7 g dry-weight and 2.46 percent, respectively.

From these data, the agrimi population was calculated to consume an average 51.36 kg dry-weight of forage per 68 hectares (0.755 kg dry-weight per hectare) per day. On an annual basis it was calculated that 275.70 kg dry-weight per hectare (27.57 g per square meter) were consumed by the agrimi population. If it is safe to assume a conversion factor of 4 kcal of gross energy per g of dry forage (Table 4), it may be calculated that the agrimi population consumed 110.28 kcal of gross energy per square meter per year.

The Efficiency of the Agrimi as a Mammalian Herbivore

Energy values for the agrimi population on the island of Theodorou are summarized in Table 15, and compared with similar data on Michigan white-tailed deer, East African elephant, and South African blesbok.

The ratio of growth/standing crop may be used as an index to productivity when comparing populations. Agrimi growth was calculated to be equal to 16% of the standing crop while the respective values for other herbivores were the white-tailed deer 50%, elephant 4.8%, and blesbok 29% (Table 15). These ratios for each population must be considered in the context of its environment. While the rate of productivity was measured for each population in its native habitat, it cannot

Table 15. Summary of energy relations of the agrimi population on the island of Theodorou with other large herbivores. (Data are in kilocalories of gross energy per square meter per year).

Productivity	White-tailed deer[1]	African elephant[2]	S. African blesbok[3]	Cretan agrimi
Living biomass	1.3	7.1	7.41	5.44
Food produced	--	747.0	582.0	173.26
Food consumed	52.6	71.6	218.3	110.28
Feces	12.5	48.3	65.8	44.11
Growth	0.64	0.34	2.12	0.86
Maintenance	39.5	23.0	150.4	65.31[4]
Efficiency Ratios:				
Food Consumed / Living biomass	41.4	10.1	29.5	20.41
Assimilation / Living biomass	33.9	3.3	20.6	15.61
Growth / Food consumed	0.012	0.005	0.0097	0.0078
Growth / Living biomass	0.5	0.048	0.29	0.16
Assimilation / Food consumed	0.76	0.32	0.69	0.61

[1]Data from Davis and Golley (1963).

[2]From Petrides and Swank (1966).

[3]From Du Plessis (1972)

[4]Derived by subtraction.

be assumed that each was on range in optimum condition. In fact (Petrides, personal communication), all species were on ranges overgrazed to varying degrees.

The ratio of food assimilated/food consumed for the agrimi was calculated to be 0.61. (Assimilation equals the gross energy of food consumed minus the gross energy of the feces). This value is lower than that of the white-tailed deer, (0.76), and the blesbok, (0.69). The ratio for the elephant, which is known to digest very little of the food it consumes, was only about 0.33.

The efficiency of meat production in relation to forage consumption (ecological growth efficiency) was calculated to be 0.78% for the agrimi. That is, 0.78% of the consumed food was changed into agrimi biomass. For the white-tailed deer, elephant, and blesbok, the corresponding figure is 1.2 percent, 0.5 percent, and 0.97 percent, respectively. These data indicate that the agrimi's ability to convert primary production to secondary production is similar to that of blesbok (its closest relative in this series) and lower than that of white-tailed deer.

The agrimi's tissue-growth efficiency (growth/assimilation) was calculated to be 1.3 percent. Respective figures for other herbivores are: white-tailed deer, 1.6%; elephant, 1.5%; and blesbok, 1.4%.

In the natural world animals are subjected to variables other than their own physiological characteristics which may affect their ecological efficiency. The low ecological efficiency of the agrimi population may also be attributable to such factors as the quantity and mainly quality of food consumed, and this depends greatly on the quantity and quality of forage available. The ecological efficiency of populations, therefore, cannot be conveniently considered to be 10%

or any other standard ratio, but should be determined for each population in question.

Data from this study in comparison with available data for other natural large herbivores suggest that the magnitude of ecological growth efficiency for these species is about 1% if a rule-of-thumb is needed.

Range Carrying Capacity

The carrying capacity of an area has been defined as the maximum number or mass of organisms which can be sustained by the environment for an indefinite period (Petrides and Swank, 1965).

Carrying capacity is a concept which is delineated by the constantly changing interactions between the animal requirements and the range supply (Robbins, 1973). Carrying capacity can be predicted by calculating the animal requirements, measurement of the biological characteristics of the range, and the division of the range supply by the animal requirements over time. Energy and nitrogen are two major factors in the nutritional interaction between agrimi requirements and the range supply.

The nitrogen supply of the range was estimated only for the spring season. Since the nitrogen content of vegetation is subject to great seasonal variation (French, 1944), the carrying capacity should be based on year-round measurements.

In this study, the determination of range carrying capacity was based on forage caloric production and was compared to the energy requirements of the consumers. The island's average forage productivity was calculated to be 173.26 kcal per square meter per year (Table 4). However, the range's forage production for the agrimi was reduced by the presence of Olea oleaster and Calycotome villosa, which due to the development of spines after mid-summer make these species unpalatalbe. Therefore, a conservative carrying capacity of the island was calculated to be about 147.61 kcal/m^2/year.

As a general rule in temperate-zone range management (Stodart and Smith, 1943), 50 percent of forage is said to be removable annually without harm to the range. On this basis, it may be calculated that the energy which may be safely removed by herbivores on Theodorou on a sustained basis is about 73.80 kcal per square meter (50.186 X 10^6 kcal per total island) per year.

The average daily gross energy requirements of an agrimi in this study were calculated to be 2118 kcal or 773106 kcal per year. Therefore, a population of about 65 animals could be sustained indefinitely on the island's rangeland. Such a herbivore density does not, though, allow for range recovery from serious overgrazing.

The present agrimi population of 97 animals suggests that a 33.0 percent reduction is required. To achieve a sustained balance between herbivore and range, 33 percent of each age class in the population should be removed. Since the rainfall for 1973 was intermediate it is safe to base the carrying capacity on the forage production for this year.

SUMMARY

A study was undertaken during 1973 on Theodorou island (68 hectares) to determine the population energy relationships of the Cretan wild goat (*Capra aegagrus cretica*) or agrimi. A total capture of the population enabled the precise measurement of all population parameters. The population density was 1.4 agrimi per acre or a total population of 97. The sex ratio was 1:1 among both kids and adults. The kid:adult ratio was 14:100, while the kid:female ratio was 36:100. The following population parameters were calculated: net reproductive rate, 1.14; generation time, 6.2 years; average life expectancy, 5.9 years; innate rate of increase, 0.0209/animal/year; population turnover rate, 14.4 percent; and average mortality rate, 15.7 percent. Age-specific survivorship data indicated high mortality in very young and very old animals.

The productivity of the agrimi population was calculated to be 0.86 by combining survivorship data with the body growth curve.

The living biomass of the agrimi population was measured to be 5.4 kilocalories per square meter. In kilocalories per square meter per year the available food, food consumed, feces and maintenance metabolism were calculated to be 173.3, 110.3, 44.1 and 65.3, respectively.

Using these values, efficiency ratios were calculated for the agrimi. The efficiency of secondary production in relation to food consumption was 0.78%. This value is comparable to similar values for the white-tail deer, African elephant, and South African blesbok.

Theodorou island (68 hectares) has been subjected to grazing for a prolonged period by livestock and the agrimi, the Cretan wild goat, resulting in vegetative changes. Nearby Theodoropoula island (1 hectare)

never disturbed by man, domestic animals, or wildlife, supports a true climatic "climax" vegetation. Various parameters of the vegetation were measured to determine by comparison the effects of grazing and its absence.

Sixteen native plant species were found on the ungrazed island, while 58 species were recorded on the overgrazed island. Only three of the "climax" plants encountered on the ungrazed island were observed on the overgrazed island and these were on a small peak protected by steep cliffs.

A similarity index value of the vegetation sampled on the two islands was 0.002, indicating almost complete dissimilarity. The observed vegetative differences are evidently the effect of heavy grazing. The climax community was dominated by palatable forb species, particularly Obione portucaloides, which comprised about 43 percent of the vegetative cover of Theodoropoula island. In contrast, the overgrazed island was characterized by an unpalatable shrub type association in which Poterium spinosum contributed approximately 23 percent of the total vegetative cover. Perennial shrubs comprised 88.2 percent of the floristic cover on the overgrazed island, compared to 22.3 percent on the ungrazed island. These data indicate complete substitution of "climax" palatable forbs by unpalatable shrubs, the result of selective grazing.

The net productivities of the important forage species on the ungrazed and overgrazed islands were calculated to be about 1470 and 430 kilograms dry-weight per hectare per year, respectively. Therefore, the overgrazed island produced only 29.2 percent as much yearly forage per unit area as on the ungrazed island. Percentage of cover, frequency and density of forage species on the overgrazed island also was lower, about half that on the ungrazed island. These changes have been the result of replacement of original palatable species by relatively unpalatable invader plants due to overgrazing.

Chemical analysis revealed that the average protein content of forage species on the ungrazed island was nine percent, rather than the four percent on the overgrazed island.

The low protein content on Theodorou island is probably the result of floristic and edaphic changes induced by overgrazing. The floral diversity of the overgrazed island (3.584) was calculated to be more than twice that of the ungrazed island (1.475). The increase in species diversity is due to overgrazing of the dominant plant species (Obione portucaloides), which comprise about 50 percent of the "climax" flora. Thereby several new ecological niches were made available for the more complex community of invader species.

Preferred food plants of the agrimi on the overgrazed island have been reduced to only 15.6 percent of the island's total edible forage and 10.6 percent of the total vegetative cover of the island. In contrast, preferred food plants on the ungrazed island comprise 80.4 and 68.7 of the average forage production and vegetative cover, respectively.

Free-ranging animals were estimated to consume 648.4 g and 412.7 g dry forage daily for males and females, respectively. Since average body weights were 24.6 kg for males and 16.7 kg for females, these figures represented approximately 2.5 percent of the animal's live body weight for either sex. About 59 percent of the dry matter ingested was apparently digested. The carrying capacity of the island was estimated to be 65 animals, suggesting a needed 33.0 percent reduction in the existing population size.

RECOMMENDATIONS FOR SPECIES MANAGEMENT

The agrimi, or Cretan wild goat, is one of the four subspecies of the species Capra aegagrus (Dolan, 1965) from which the domestic goat was derived (Scheiner, 1898; French, 1970). Today it is in serious danger of extinction. Preservation of the free-ranging animal as a pure strain in the White Mountains of western Crete (where the animal still occurs wild) is difficult due to frequent interbreeding with widespread domestic stock (Danford, 1875). Furthermore, the diseases and parasites of the domestic strain affect the wild population (Zervas, 1961). The small uninhabited coastal islands off the nearby coast of Crete, Theodorou, 68 hectares, Dias, 1350 hectares, and Agii Pantes, 40 hectares, today serve as agrimi reserves. Among the three, only on Theodorou has the wild purebred strain been preserved (Schultze-Westrum, 1963; Dolan, 1965).

The dense agrimi population is imposing a heavy grazing pressure on Theodorou island. This deterioration of the range complex is resulting in a progressive decrease of forage production and in a concurrent reduction in agrimi productivity. If this present trend is left unchecked, a steady decline in the agrimi population seems certain to result.

The following measures should be taken to improve the survival opportunities for the agrimi and its ecosystem on Theodorou island:

1. A herd reduction of about 33% for each age class is required. A capture-transplant program which would place excess animals on other suitable uninhabited islands would both enable the survival of Theodorou environment and assist in expansion of the agrimi population. The White Mountains National Park, the original native

range of the agrimi would be a preferred site for the restoration of this species except for the certain danger of hybridization with domestic goats. Only if the park could be completely fenced and the present feral domestic goats exterminated, could this area be considered as a possible refuge for the species.

2. After the new recommended population density is achieved, assessments of population dynamics should be conducted annually. Based on these data, further adjustments must be made to maintain the population at a level which insures survival for both the agrimi and its habitat.

3. An investigation of the possibilities of chemical and non-chemical control of undesirable plants such as Thybra capitata, Poterium spinosum, and Euphorbia paralia, should be undertaken. Control of these species may hasten the process of succession toward more palatable seral stages. All potential dangers to the agrimi and to other plant and animal life should be appraised elsewhere prior to the use of control measures on Theodorou.

4. A program of fertilization and seeding palatable species inside graze-proof fences should be initiated. Such plants should include: Olea oleaster, Cistus incanus, and Cupressus sempervirens. Such a program cannot be successful until the reduction of agrimi population pressure on the range is achieved.

5. The impact of rats, hares and seed eating birds on the island's forage production should be appraised.

6. The carrying capacity in terms of nitrogen production should be estimated for Theodorou island.

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APPENDIX

APPENDIX 1

Weights (kilograms) and body measurements (centimeters) for each individual in the agrimi population, from Theodorou island, Crete, Greece, 1973.

Ear-tag number	Sex	Age (Years)	Weight (kg)	Total Length	Height at Shoulder	Horns: out-side curve	Horns: circum-ference at base	Tail	Ear	Front Foot: Length	Front Foot: Width	Hind foot: Length	Hind foot: Width
61702	F	5	18.310	85.0	51.0	13.5	6.5	6.3	10.0	4.0	3.0	3.5	2.5
	F	0-1/2											
61703	F	3	14.700	79.0	47.0	11.5	7.0	7.0	9.0	4.2	3.0	3.5	2.2
61704	F	5	22.100	86.0	49.0	17.0	7.0	8.0	10.0	4.0	3.0	3.7	2.5
	M	0-1/2	2.250										
61705	F	4	18.350	82.0	53.0	15.0	7.0	7.2	10.0	4.0	3.0	3.7	2.5
	M	0-1/2	7.900										
61706	F	3	19.150	81.0	47.0	13.0	7.7	7.0	10.0	4.5	3.0	4.0	2.5
61707	M	10	38.350	110.0	59.0	49.0	18.0	10.0	12.0	5.5	3.5	4.5	3.0
61730	M	2	13.800	72.0	48.0	18.0	10.0	8.0	10.0	4.0	3.0	3.5	2.0
61766	M	11	34.100	110.0	64.0	52.0	18.0	11.0	11.5	4.5	3.5	4.5	2.8
61760	F	4	20.350	82.0	55.0	19.5	8.1	7.0	10.0	5.0	3.4	4.1	2.7
	M	0-1/2	3.510										
61749	M	4	26.400	89.0	57.0	30.0	16.0	8.5	10.5	5.0	3.3	4.5	3.0
61790	M	4	26.450	89.0	59.0	28.5	15.5	9.0	10.5	4.6	3.5	4.0	2.8
61729	F	7	21.150	84.0	54.0	16.4	6.0	8.5	9.0	4.5	3.0	3.5	2.5
	M	0-1/2	3.700										
61728	F	2	13.250	75.0	49.0	10.2	5.5	7.0	10.0	4.0	3.0	3.5	2.4
61727	M	2	16.750	79.0	51.0	17.5	10.3	8.0	10.5	4.3	2.7	3.7	2.5
61708	F	2	15.000	77.0	48.0	9.5	5.0	7.0	10.0	4.0	2.7	3.7	2.7
61721	M	9	39.500	102.0	62.0	51.0	15.0	9.5	11.0	5.3	4.5	3.8	3.0

Appendix 1 (cont'd:)

Ear-tag number	Sex	Age (Years)	Weight (kg)	Total Length	Height at Shoulder	Horns: out-side curve	Horns: circum-ference at base	Tail	Ear	Front Foot Length	Front Foot Width	Hind Foot Length	Hind Foot Width
61780	M	10	34.450	104.0	70.0	50.0	18.0	10.5	11.0	5.0	3.2	4.2	2.8
61731	M	10	36.900	105.0	70.0	55.0	17.0	10.0	11.0	4.8	3.1	4.0	2.5
61724	M	10	31.300	105.0	68.0	48.0	16.0	11.0	11.0	5.0	3.2	4.0	2.9
61795	M	10	41.700	115.0	73.0	66.0	19.0	11.0	11.5	5.2	3.7	4.8	2.8
61739	F	4	19.100	90.0	60.0	11.0	6.0	8.0	11.0	4.3	2.7	3.5	2.3
61733	F	5	20.300	86.0	55.0	22.0	7.0	10.0	11.0	4.7	2.9	3.6	2.8
61734	M	4	25.400	99.0	60.0	35.0	18.0	9.0	11.0	5.0	3.0	4.3	2.5
61761	F	10	18.900	98.0	60.0	29.0	9.5	9.0	11.0	4.5	3.0	4.0	2.8
61740	M	4	25.900	94.0	61.0	35.0	17.0	9.0	11.5	4.5	3.2	3.7	2.6
61771	F	4	18.600	86.0	55.0	15.0	9.0	8.0	11.0	4.5	2.6	3.5	2.5
	F	0-1/2	5.850										
61712	M	2	15.400	81.0	54.0	20.0	15.0	9.0	11.0	4.0	2.8	3.5	2.2
61713	F	9	18.500	102.0	59.0	17.0	7.0	9.5	11.0	4.3	2.8	3.7	2.6
61719	M	10	40.700	110.0	70.0	61.0	19.0	11.0	12.0	5.5	3.8	4.5	2.8
61732	M	5	29.200	106.0	66.0	45.0	17.0	9.5	11.0	4.7	3.3	4.0	2.6
61716	F	6	21.700	88.0	60.0	20.0	7.0	8.0	11.5	4.5	3.0	3.8	2.3
	F	0-1/2	6.300										
61711	F	9	18.700	87.0	60.0	19.0	10.0	8.5	10.5	4.5	3.2	3.8	2.5
61752	M	7	32.900	98.0	65.0	40.0	18.0	9.0	11.5	4.7	3.0	4.0	2.5
61755	M	10	40.400	107.0	73.0	58.0	15.5	11.0	12.0	5.5	3.8	4.5	2.8
61754	F	3	19.150	84.0	56.5	12.0	6.5	8.0	10.0	4.2	2.8	3.8	2.3
61756	F	8	17.500	95.0	55.0	12.0	6.3	8.5	10.5	4.7	2.8	3.7	2.6
61751	F	6	19.850	96.0	55.0	17.0	6.5	8.0	9.0	4.0	3.0	3.5	2.5
	F	0-1/2	6.230										
61753	F	8	18.900	98.0	58.0	15.0	6.5	8.0	11.0	4.3	2.9	3.5	2.2

Appendix 1 (cont'd:)

Ear-tag number	Sex	Age (Years)	Weight (kg)	Total Length	Height at Shoulder	Horns out-side curve	Horns circum-ference at base	Tail	Ear	Front Foot Length	Front Foot Width	Hind Foot Length	Hind Foot Width
61735	M	5	26.100	106.0	67.0	32.0	18.0	10.5	11.5	5.0	3.2	4.5	2.7
61720	M	3	20.900	97.0	65.0	31.0	17.0	9.5	11.5	4.4	3.2	3.8	2.4
61714	M	11	33.300	108.0	70.0	55.0	19.0	11.0	11.5	5.3	3.5	4.5	2.9
61722	F	3	16.100	86.0	54.0	12.0	8.0	8.5	11.0	4.4	2.7	3.5	2.1
	M	0-1/2	7.900										
61781	F	6	20.100	92.0	55.0	14.0	9.0	8.0	10.5	3.8	3.0	3.5	2.3
	F	0-1/2	4.850										
61779	M	5	28.200	95.0	67.0	34.0	16.0	9.5	11.5	4.7	3.3	4.0	2.3
61789	M	2	14.600	80.0	55.0	22.0	12.0	8.0	10.5	4.0	2.9	3.6	2.2
61767	M	4	28.050	100.0	63.0	32.0	17.0	8.5	11.0	4.8	4.0	4.0	3.5
61726	M	6	29.300	107.0	59.0	39.0	14.2	8.5	10.5	5.0	3.2	4.3	2.5
61723	F	9	22.100	92.0	54.0	20.0	7.1	8.5	10.5	4.1	2.9	3.5	2.5
	F	0-1/2	4.900										
	F	9	20.400	90.0	58.0	21.0	8.0	8.5	10.5	4.5	3.5	4.0	2.3
61769	M	10	28.400	95.0	65.0	42.0	18.0	9.0	11.0	5.0	3.5	4.3	2.8
61768	M	2	17.900	83.0	54.0	27.0	14.1	9.0	11.0	4.3	3.1	4.0	2.5
61759	F	2	10.100	76.0	40.0	10.5	4.5	6.5	9.0	3.5	2.3	3.0	2.3
61758	F	7	22.450	86.0	55.0	22.0	6.0	8.0	10.0	4.5	3.0	4.0	2.5
61764	M	11	28.500	100.0	65.0	53.0	18.0	10.0	11.5	5.5	3.8	4.0	2.8
61757	M	3	20.300	90.0	55.0	29.0	15.0	7.5	11.0	4.5	3.0	3.5	2.3
61765	M	2	16.500	82.0	49.0	21.0	12.0	8.5	10.0	4.0	2.8	4.0	2.4
61725	F	7	22.400	86.0	53.0	19.0	6.5	9.5	10.5	4.5	3.0	3.9	2.8
	M	0-1/2	5.650										
61791	F	2	18.300	80.0	56.0	13.0	6.5	7.5	10.0	4.5	3.0	3.5	2.5
61762	M	4	27.550	90.0	60.0	32.0	14.0	10.0	11.0	4.6	3.7	4.0	2.7

Appendix 1 (cont'd:)

Ear-tag number	Sex	Age (Years)	Weight (kg)	Total Length	Height at Shoulder	Horns: out-side curve	Horns: circum-ference at base	Tail	Ear	Front Food: Length	Front Food: Width	Hind Foot: Length	Hind Foot: Width
61742	M	5	31.550	100.0	63.0	41.0	15.0	10.0	11.0	5.0	3.6	4.0	2.6
61743	M	6	32.550	105.0	65.0	48.0	15.5	9.0	11.5	5.0	3.6	4.2	2.5
61744	M	10	37.200	110.0	68.0	60.0	18.0	9.5	12.0	5.3	3.6	4.5	3.0
61776	M	6	30.150	105.0	59.0	37.5	14.3	8.5	10.5	5.0	3.2	4.3	2.5
61750	M	8	34.100	107.0	59.5	39.0	15.2	8.7	10.5	5.3	3.6	4.5	2.9
61792	F	9	20.400	95.0	57.0	21.0	9.8	8.2	11.5	4.2	3.0	3.5	2.5
61799	M	2	13.000	80.0	50.0	15.0	10.0	8.5	10.0	4.0	3.0	3.5	2.5
61793	F	12	20.100	92.0	56.0	20.5	7.0	8.5	11.5	4.5	3.5	4.0	2.5
61794	M	10	33.900	105.0	68.0	50.0	18.0	8.5	11.0	5.2	3.7	4.2	2.7
61769	M	11	33.500	110.0	68.0	57.0	18.0	9.5	11.0	5.5	3.5	4.5	2.9
61748	F	7	22.400	95.0	58.0	15.0	7.5	9.0	10.0	4.2	3.0	3.0	2.2
61763	M	9	35.600	107.0	67.0	53.0	14.0	9.0	11.0	5.5	3.5	4.0	2.7
61747	F	2	13.300	77.0	47.0	9.0	6.5	7.5	10.0	3.7	2.7	3.2	2.3
61746	M	2	13.950	80.0	52.0	14.5	10.0	9.5	10.5	4.0	3.0	3.3	2.5
61745	M	9	41.100	115.0	72.0	62.0	17.0	10.5	11.0	5.3	3.6	4.5	3.0
61798	F	9	20.050	83.0	52.0	14.0	7.5	8.0	10.0	4.2	2.5	3.5	2.3
	M	0-1/2	4.850										
61778	M	9	33.200	112.0	70.0	46.0	18.0	10.0	12.0	5.0	3.3	4.5	2.8
61797	F	2	15.150	77.0	55.0	13.0	6.8	8.0	10.0	4.1	2.7	3.7	2.4
61788	F	5	20.100	85.0	56.0	14.0	8.0	8.5	10.5	4.1	3.0	3.6	2.2
61775	F	10	18.500	89.0	60.0	18.0	9.0	8.5	11.0	4.5	3.1	4.0	2.5
61773	M	10	33.600	105.0	70.0	52.0	18.0	10.5	12.0	5.5	3.5	4.7	3.0
61774	M	10	33.500	105.0	70.0	57.0	18.0	9.5	11.5	5.3	3.3	4.5	2.9
61777	F	11	20.100	91.0	60.0	19.0	10.0	8.5	10.0	4.5	3.0	3.8	2.4
61715	F	8	19.500	100.0	60.0	18.0	10.0	8.5	10.0	4.5	2.9	4.0	2.4
	F	5	20.300										
	F	3	17.300										
	F	0-1/2	5.200										

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