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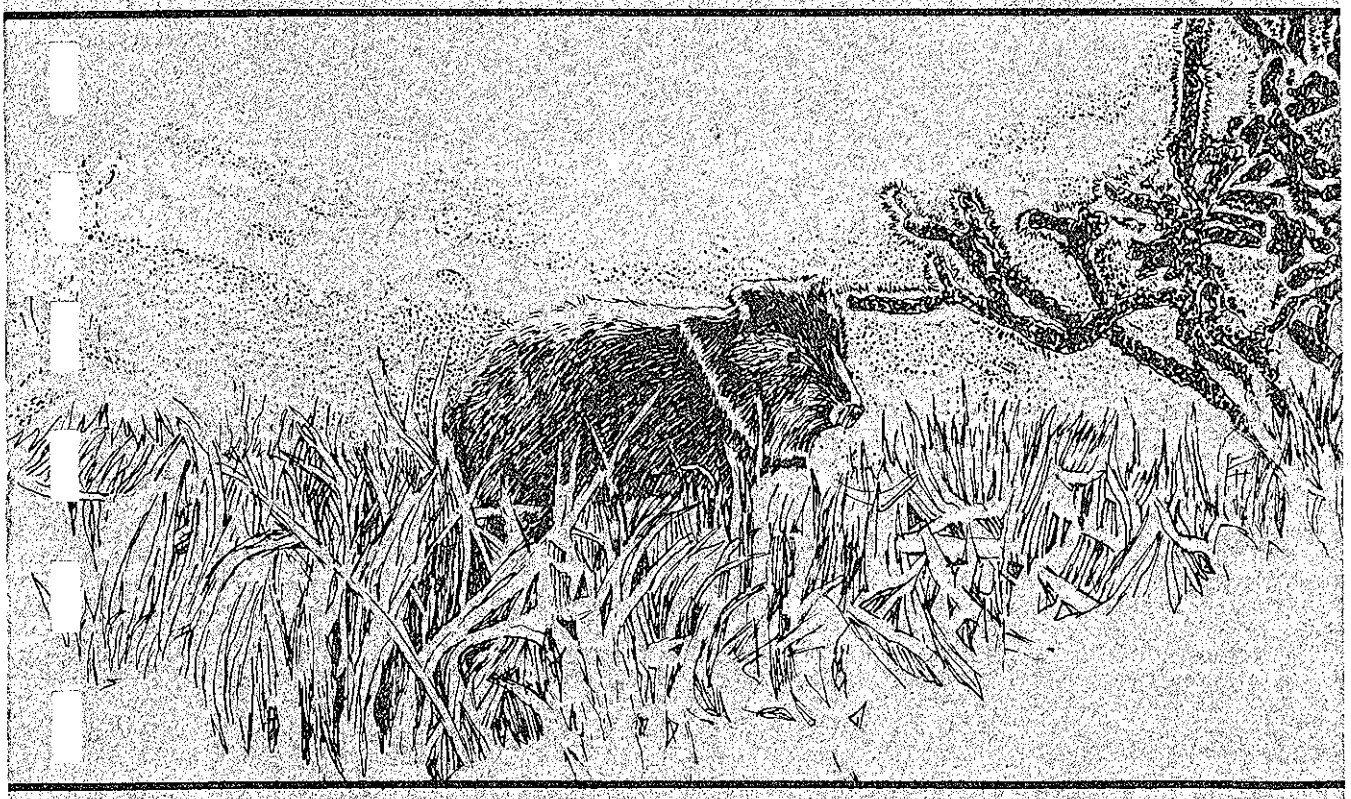
Ecology and Social Behavior of the Collared Peccary in Big Bend National Park

John A. Bissonette



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Ecology and Social Behavior of the Collared Peccary in Big Bend National Park, Texas

John A. Bissonette

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As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering the wisest use of our land and water resources, protecting our fish and wildlife, preserving the environmental and cultural values of our national parks and historical places, and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to assure that their development is in the best interests of all our people. The Department also has a major responsibility for American Indian reservation communities and for people who live in Island Territories under United States administration.

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Summary

A behavioral and ecological study was conducted on collared peccaries for 23 months in Big Bend National Park, Texas. The behavior results were based on 380 hours of direct observation. Five groups were studied intensively.

Activity patterns consisted primarily of feeding and resting. Onset and cessation of active periods was correlated strongly with temperature. Minimum daily temperature accounted for 61.8% of the variation in termination of feeding, and a running minimum daily mean for the previous 6 days accounted for an additional 9%. Maximum daily temperatures and a running mean maximum temperature for the previous 6 days accounted for 39.7% and 14.0% of the variation, respectively, in onset of feeding.

Time budgets were investigated by dividing behavior patterns of active peccaries into feeding activities (feeding, walking and searching, and stopped and searching for food items) and other categories. Feeding activities accounted for most of the active time of peccaries. Adult males, adult females, and juveniles spent 78.6%, 77.9%, and 86.7% of their active time, respectively, in activities associated with feeding. Statistically significant differences existed between certain sex and age classes for time allocated for some activities. The results suggested that the time spent feeding was related to the different reproductive roles of males and females.

Behavior was quantified during the study by sex and age class; 1,166 interactions were recorded from a total of 1,927 peccary observation units. A peccary observation unit is equal to one animal observed during any observation period.

Vocalizations were (1) aggressive; (2) submissive; and (3) alert. Calls have three fundamental characteristics: (1) pitch; (2) intensity; and (3) continuity. Submissive and alert calls were intermediate in intensity compared to aggressive calls. Continuity ranking indicated that submissive calls were not highly broken, but that alert calls were intermittent.

Submissive calls were the highest in pitch of all vocalizations whereas alarm calls ranked from intermediate to low.

Five alert-alarm patterns were recorded: (1) cautious approach; (2) stationary alert; (3) slow departure; (4) cautious departure; and (5) fast departure. In 56% of the cases the peccaries could be observed following alert, and in 87% of these they regrouped. Of the remaining 13%, peccaries did not disperse but stayed tightly grouped. On only one occasion did they scatter and not regroup.

Behavioral patterns used in social interactions were grouped into (1) nonagonistic; (2) sexual; (3) agonistic (dominant animal); (4) agonistic (subordinate animal); and (5) agonistic patterns used in dominance disputes. Twenty-eight distinct or linked patterns were recorded. Contact interactions were found to comprise over 66% of all interactions. However, less than 44% of all interactions were aggressive and, of these, less than 18% were contact interactions. Interaction rates varied from 0.125 to 0.598 interactions per active animal per hour, with a mean of 0.312.

Peccaries were found to hold group territories with little or no overlap by adjacent groups. They marked vegetation and rocks with scent gland excretions, and scat piles were observed scattered along boundary lines. Active defense with dominance reversals at a boundary line was seen on two different occasions.

Groups of peccaries were stable throughout the year, although feeding subgroups were formed regularly by all groups studied. From 1971 to 1974 two new territorial herd formations were recorded. The nuclei for the new groups were the feeding subgroups.

Peccaries have a linear dominance hierarchy including both sexes. Dominant animals were always male, with males or females in lower positions in an order determined largely by size. Young less than 3 months were not included in the hierarchy but were defended by their mothers, while older, nondefended young ranked low.

Alpha males did not allow subordinate males to approach an estrous female. However, subordinate males did not leave the group during the breeding season and did not form separate bachelor groups. Breeding success in males was influenced by hierarchical position. The dominant male in a group did virtually all of the breeding. Subordinate males had a greater probability of being successful if more than one female came into estrous at a time since short tending bonds were formed.

Parturition was seasonal and correlated with the period of onset of heavy rainfall. The mean litter size per adult female was 1.3 young.

Mortality was high in every group studied, ranging between territorial groups observed from 50 to 100% per year of all young produced. The highest mortality occurred on the poorest ranges. Recruitment was relatively low in all groups studied although there was some variation between herds. Sex ratios of 11 herds in Big Bend did not deviate significantly from 1:1.

Peccaries in Big Bend showed a seasonal preference for habitat. Habitats with dense vegetation were used significantly more during the summer months, whereas the more open areas were used during the winter.

Peccaries partitioned their activities differently over four habitat types due in part to ambient temperatures. Foraging activities were concentrated on the bajada during winter and in dense vegetation during summer. Periods of bedding showed a similar pattern.

Territorial group size was stable throughout the year but sub-groups did occur. Significantly smaller subgroups occurred during the summer, whereas during the breeding season in December and January, territorial groups tended to remain together. Habitat type also influenced group size. Significantly larger groups were observed in open, less dense areas, whereas smaller subgroups tended to use denser, more shaded habitats.

Range quality varied between group territories and with elevation. Ranges with higher proportions of the preferred forage species were found at higher elevations. Territorial group size was found to be positively correlated ($r^2 = 0.980$) with percent vegetative cover and percent composition of prickly pear, lechuguilla, and forbs ($r^2=0.927$) but was negatively correlated with percent woody cover ($r^2 = 0.868$). Prediction of carrying capacity can be made accurately by assessment of range cover and percent composition of preferred forage species.

Lechuguilla was the most abundant preferred food item; prickly pear ranked second. Although these two items were the major food sources of peccaries, use in relation to their availability was low. Use of prickly pear varied from 1.7 to 5.4% of that available, while one range sampled for lechuguilla indicated 2.6% use. These figures probably are underestimates because of preference of peccaries for certain plants. Marked prickly pear plants were selected randomly but may not have represented a random sample of those plants actually preferred.

Peccaries showed a preference for certain vegetative parts of lechuguilla. Generally, only the core leaves and basal parts of the modified leaves and the root were eaten.

Food habit studies indicated a strong preference for prickly pear throughout the year, and especially when the fruits were ripe. Lechuguilla was used most heavily during the spring and fall. Seeds of woody plants, fruits, and forbs were preferred and taken when available.

1
Introduction

Collared peccaries *(Dicotyles tajacu)* are social animals and interesting biologically for many reasons. They are the only Tayassuid found in North America (Texas, New Mexico, Arizona, and Mexico). Their unique form and food habits suggested an interesting evolutionary history.

Little behavioral work (Schweinsburg 1969; Sowls 1974) has been done on collared peccaries. Most published papers deal with one of the following: techniques (Bigler 1966; Day 1972c, 1974c; Neal 1959a; Sowls 1961; Kirkpatrick 1957; Kirkpatrick and Sowls 1962); population determinations (Day 1962, 1964, 1965, 1966, 1967a, b, 1968; Householder 1958; Knipe 1942); reproductive biology (Low 1970; McCulloch 1955; Sowls 1960, 1964, 1966; Smith and Sowls 1975); feeding habits (Eddy 1961); studies such as scent gland morphology (Epling 1956) and milk composition (Sowls et al. 1961; Brown et al. 1963), taxonomy (Woodburne 1968, 1969); general natural history (Day 1971b, 1972b, 1974b; Knipe 1957; Neal 1959b; Mauermann 1943; Jennings and Harris 1953); home range determinations (Ellisor and Harwell 1969; Schweinsburg 1971); activity patterns (Bigler 1974; Day 1970, 1971a, 1972a, 1974a); or management (Day 1971c, 1972d, 1974d).

Zervanos (1972) and Zervanos and Hadley (1973) reported on biological adaptation and energy relationships, and Schilling and Stone (1969) completed a cardiovascular study. Phelps (1971) detailed some thermoregulatory relationships for peccaries.

The purpose of this study was to elucidate some of the relationships of resource structure, quality, and availability to social behavior and organization of peccaries. Alexander (1974) stated that predation, highly localized and limited resources, and facilitated food gathering are the only three selective forces necessary to explain the evolution of group living in animals. Predation probably is responsible for group formation in peccaries when resources are not localized or limiting, and since individual peccaries are able to feed without help from conspecifics. Once social groups have been established, selection should maintain a minimum size

large enough to withstand predation. No active group defense has been reported for peccaries and the advantage of numbers may help individuals to escape predation. Individuals may use the group as cover (Alexander 1974) or may cause other group members to be more susceptible to predation (Alexander 1974; Hamilton 1971). Group sizes larger than the minimum necessary to withstand predation should be influenced less by predation pressures and more by available resources. In other words, maximum group size in peccaries is density dependent and influenced by the availability of preferred resources.

McNab (1963) suggested some interesting relationships between social organization and resource use, and stated that for animals to live socially, resources must be abundant enough to allow group living. Increasing the group-range size may compensate in part for a lower resource quality on a given range; however, there should be an upper limit to range size if the area is defended as Schweinsburg (1969) and Sowls (1974) have suggested. As territories approach their maximum defendable size, group size of peccaries should increase to the carrying capacity of that range. However, group size should not affect directly the size of the territory that could be defended. Increased range size entails a higher caloric expenditure by foraging animals. Additionally, if food resources are less abundant per unit area, intragroup competition for these resources increases. The benefits from increased group-range size may involve: (1) Establishment of an area large enough to sustain the minimum group size necessary to withstand predation. Increased range size implies increased resource abundance. (2) Inclusion within the range of an area rich in required resources, at least temporally.

If grouping is the response to predation and if the benefits to individuals of group living are a result of increased numbers of closely associated conspecifics and not group defense, then selection should increase group size of peccaries to the maximum possible for any range. However, the maximum group size possible on any range should be mostly a function of available food resources, although establishment of minimum group sizes must be the result of predation pressures. The carrying capacity in peccaries, however, will be determined by availability of preferred resources.

I have designed the study to test the null hypothesis that group size at carrying capacity in peccaries is not affected by availability of preferred resources. During the field work and in subsequent analyses I attempted to: (1) Establish a quantitative basis for peccary behavior. (2) Determine the pattern of resource use by peccaries. (3) Assess the effect of habitat type on subgroup composition and stability. (4) Determine the precise relationship between range quality, measured by the relative abundance of preferred forage species, and territorial group size and home-range (group-range) size.

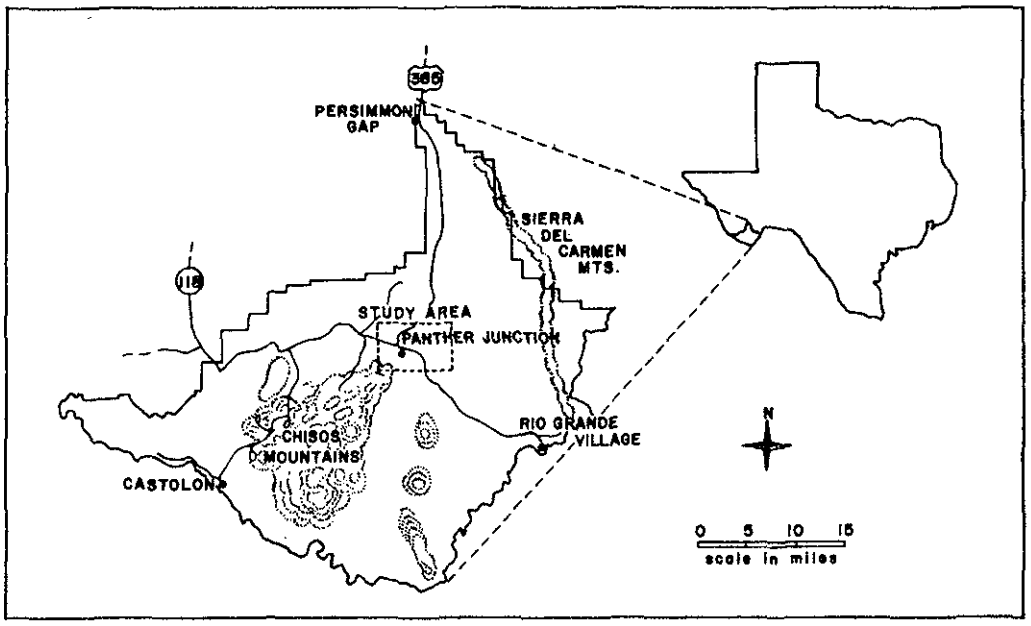

Fig. 1. Map of Big Bend National Park showing study area.

The Study Area

This study was conducted in Big Bend National Park (Fig. 1), which is located in southwestern Texas on the U.S.-Mexican border. Big Bend is situated in the northeastern portion of the Chihuahuan Desert and is comprised of the forested Chisos Mountains, low desert, and riparian vegetation along the Rio Grande, the southern boundary of the Park. The Chisos Mountains are isolated in approximately the center of the Park and are surrounded by desert.

The study site encompassed an area of desert and foothills adjacent to the northeastern portion of the Chisos, with associated canyons and arroyos (Fig. 1). Although peccaries were found throughout the park, field work was restricted to two main vegetation types: (1) Lechuguilla-Creosote-Cactus Association, and (2) Sotol-Grassland Association. Characteristics of Big Bend vegetation have been described by Muller (1937), Taylor et al. (1944), Denyes (1956), and Gelbach (1966). More recently, Wauer (1971) described six vegetation associations for Big Bend.

The study site consisted of five peccary group ranges of approximately 220 ha (550 acres) each (Fig. 2). The entire study area was about 1,100 ha (2,750 acres). The area was selected to allow an assessment of the effects of varying resource characteristics on groups of peccaries. Elevation varied from 1,000 to 1,370m (3,280 to 4,500 ft.). In addition, the five ranges varied greatly in relief. The Panther Canyon and West Hill territories are located in the Sotol-Grassland Association and are characterized by rugged topography (1,200-1,370m or 3,940-4,500 ft. elevation), with canyons and arroyos comprising the greater part of the ranges. The Lower Mouse

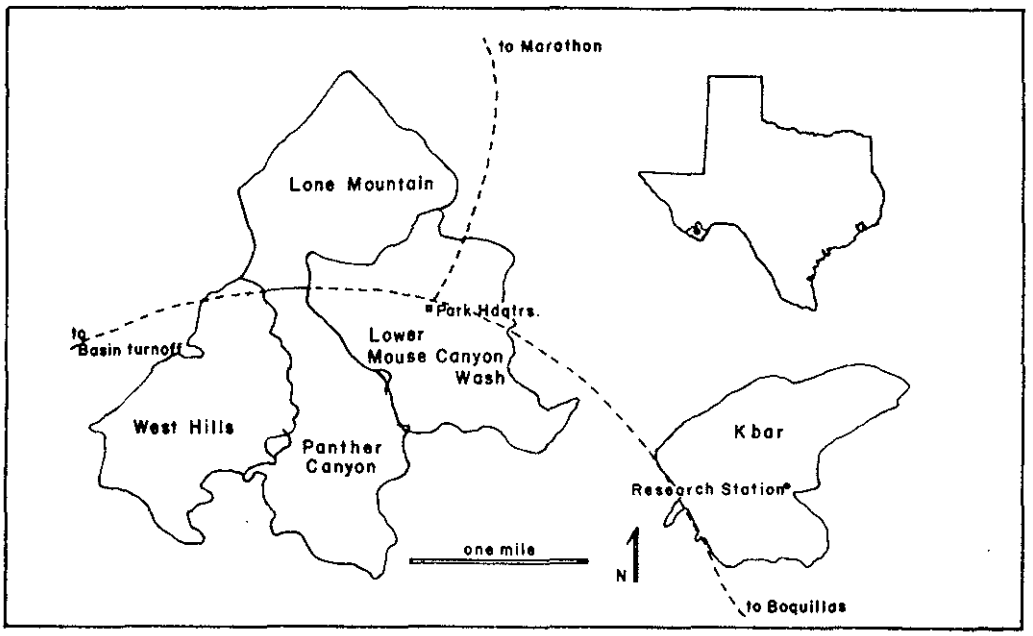

Fig. 2. Study area of five territorial group ranges of peccaries.

Canyon range is intermediate in elevation and represents a transition zone between the high ranges and the two lower elevation ranges. The Lone Mountain and KBar territories range from 1,000 to 1,160m (3,280 to 3,810 ft.) in elevation. They are characteristic of the Lechuguilla-Creosote-Cactus Association.

In terms of species abundance and percent cover, vegetation characteristics varied considerably between the five ranges, with highest quality found in the high elevation ranges. Additionally, the number of bedding sites varied in quality and quantity. The best sites were found in the canyon ranges. Free water was found on the West Hills, KBar, and Lower Mouse Canyon ranges.

Climate

Precipitation patterns in Big Bend are characterized by a summer and fall rainy season, with little or no rain during the rest of the year. Characteristically, rains begin in May and last through October although precipitation may occur unpredictably in other months (Fig. 3). From 1958 to 1973, rainfall ranged from a yearly low of 21.6 cm (8.5 inches) in 1969 to a high of 48.0 cm (18.9 inches) in 1970. The mean for the 16 year period was 33.5 cm (13.2 inches). During the study, precipitation was slightly below average, with values of 32.0 cm (12.6 inches) and 30.2 cm (11.9 inches) recorded for 1972 and 1973, respectively, giving a mean rainfall of 31.2 cm (12.3 inches). Rainstorms tend to be localized rather than general in extent.

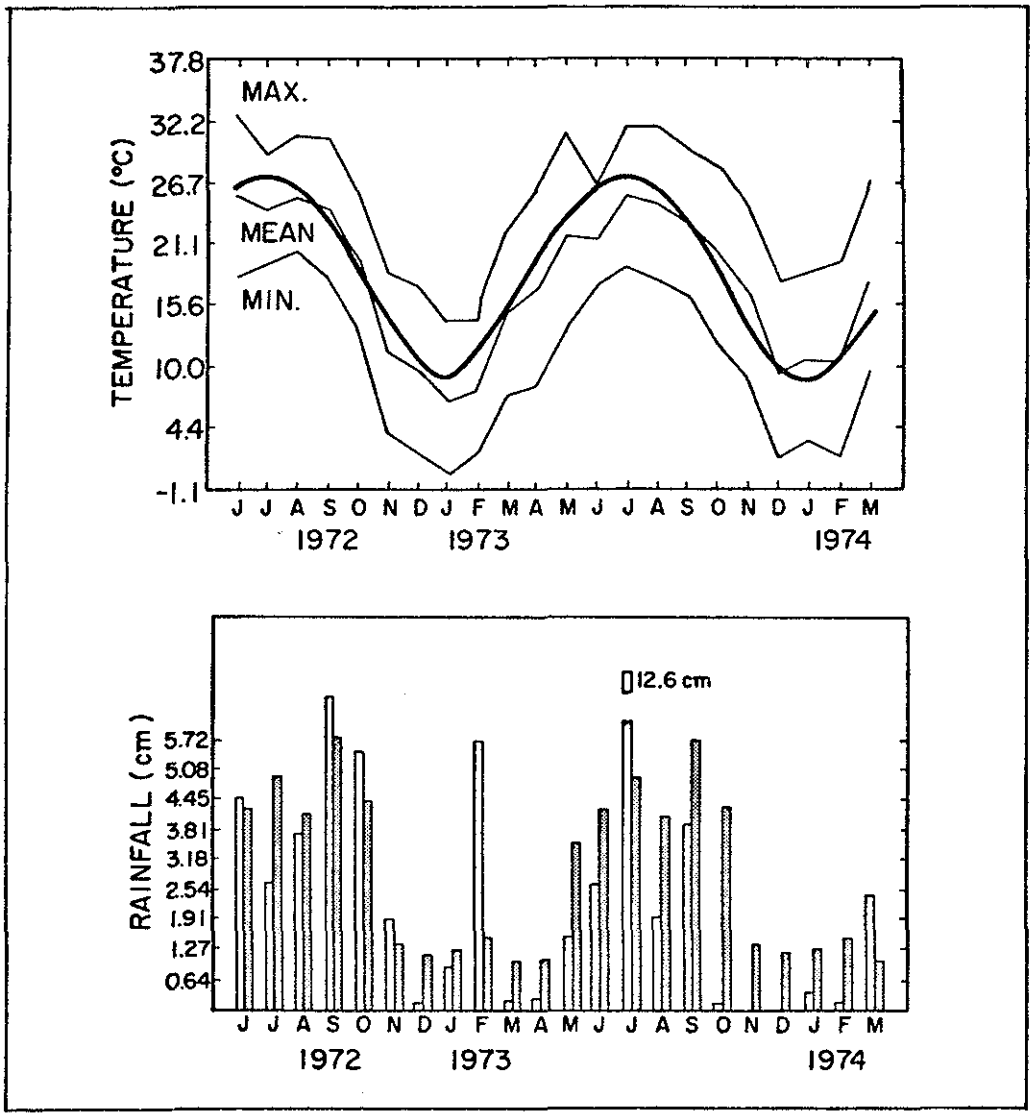

Fig. 3. Climate data for the study area. *Top.* For temperature, the dark, heavy line is the long-term mean. The light curves are data recorded during the study. *Bottom.* For rainfall, the dark bars are the long-term means. The open bars are from the study.

Rainfall varied with elevation, mountains receiving the most and foothills and desert receiving progressively less.

Seasonal temperatures vary greatly, with the hottest monthly temperatures recorded from May through August (Fig. 3). For the period 1958-73, mean maximum temperatures from May to August varied from 36.5° C (98° F) in July 1968 to 26.4° C (80° F) in June 1973. Mean maximum temperatures for the months of November through February ranged from 10.5° C (51° F) in December 1965 to 0.3° C (33° F) in January 1973. The highest temperature recorded during the 16-year period was 41° C (106° F) in July 1958. Extreme temperatures of over 38° C (100° F) were recorded in

every year since 1958 except 1971. The highest temperature that year was 37.2°C (99°F) in June and again in July. The lowest temperature for the period was −15.6°C (4°F) in January 1972.

The highest mean temperature recorded during the study period was 33.2°C (92°F) in June 1972. The lowest mean temperature was 0.3°C (32°F) recorded in January 1973. Extreme temperatures recorded during 1972-73 were 40°C (104°F) in June 1972 and −12°C (10°F) in February 1973.

Mountain temperatures average about 3°C (5°F) cooler than temperatures recorded in the foothills at park headquarters. Temperatures at the lowest elevations along the Rio Grande are 3 to 5 degrees hotter than those recorded in the foothills.

Methods

Direct Observations

Peccaries were located in their natural environment and observed with least disturbance, usually downwind and at distances of 10 to 245 m (30 to 800 feet). Movement of the observer was slow and relaxed and kept to a minimum.

Behavioral interactions were recorded on prepared data sheets whenever two or more peccaries were seen or heard reacting to each other or to any other peccary. In addition to these overt behavioral interactions, the following data were taken at 10-minute intervals: (1) number of animals; (2) habitat type occupied; (3) activity category; and (4) location by map coordinates. The activities were grouped into general, easily recognized categories of: (1) feeding; (2) feeding and walking; (3) walking; (4) standing at alert; (5) resting; and (6) resting and feeding. The habitat was classed into four types: (1) dense wash; (2) open wash; (3) bajada; and (4) drainage. With aerial photographs of the area, it was possible to locate groups of peccaries to within 18 m (60 feet) of their true position.

To assess time budgets by season, activities of individual peccaries were recorded second-by-second for a given sex and age category for two periods: spring-summer (March-July), and fall (October-November) 1975. A total of 31,484 seconds or 8.75 hours was accumulated. A portable tape recorder was used in the field and tapes were subsequently transcribed. Adult males, adult females, and juveniles were observed individually for varying lengths of time. Behavior was classed into the following categories: (1) feeding; (2) walking in search of food; (3) stopped and searching for food items; (4) standing at alert; (5) walking but not looking for food items; (6) lying down; (7) self-grooming; (8) interactions (which were recorded in their entirety) and (9) miscellaneous (a category allowing for the recording of unusual or infrequent behavior). Total elapsed time of each individual observation was recorded. Individual observations were

terminated if any one class of behavior persisted for more than 5 minutes. These data allow for testing variation of activity (1) by season; (2) by influence of habitat on behavior; (3) between territorial groups; (4) by number of animals present; (5) by sex and age class; and (6) by category of behavior.

Identification of Individuals

To facilitate recognition of individuals, an entire group of 23 peccaries (Lower Mouse Canyon herd) was ear-tagged. Two different types of tags were used to allow identification in the event of loss of any one tag. The animals were drawn into a small enclosure with bait, forced into a corner, and captured with a wire net. In addition, distinctive natural marks on individual peccaries from four other groups were recorded for future identification. It was possible to distinguish approximately half of all untagged animals by natural marks.

Range Relationships

After the extent of the range of each peccary group was determined, it was mapped on an aerial photo. Vegetation was stratified from aerial photos and verified on the ground. Each stratum was then sampled by a plotless toe-point method. Starting points and transect line direction were selected randomly. As boundaries were approached, transect directions were reselected. The sampling procedure involved walking the transect lines with a measured step and, at every second step, recording as a "hit" the item in contact with a point on the toe of my right boot. Plants were recorded by genus and species. Hits on nonvegetated areas were classed as: (1) silt; (2) sand; (3) gravel; (4) cobble (over 50 mm or 2 inches diameter); (5) solid rock; (6) litter; or (7) feces. Each vegetative type was sampled until the relative proportions of the four major species ceased to vary more than 2% with each increase in sample size of 100 hits. By this method each stratum of five different ranges was sampled for species composition, relative abundance, and percent ground cover. The Shannon Index (Lloyd and Ghelardi 1964) was used to calculate diversity indexes.

Plant phenologies were recorded for all species found in the study area. Data were taken on the times of (1) greening; (2) flowering; (3) fruiting; (4) seed drop; and (5) decay. Specimens were collected, mounted, and identified.

Food Habits

Five freshly dropped scats were collected per week for a period of 1 year. They were washed through a 1.0-mm mesh screen, frozen, and analyzed with a 10-point sampling frame for frequency of occurrence and percent composition of components. Food items in the scats were identified to genus and species where possible and to major plant group (succulents, grasses, forbs, woody, and other) when not. They were also recorded by

plant part: (1) root; (2) stem; (3) leaf; (4) bark-dermis; (5) fruit; (6) seed; (7) seed pod; (8) flower; (9) fiber, (10) glochid; (11) spine; or (12) other.

Availability and Use of Succulents

To assess production of prickly pear cactus and its use by peccaries, 350 plants, located over the five ranges of peccary groups, were selected randomly. Random points were located on the range map and transect lines selected randomly. Distances were chosen randomly but were always less than 100 paces. Only plants within 3 m (10 ft) of the line were selected. On each plant 20 cladophylls were marked. The cladophylls were measured for length and width and recorded for: (1) height from ground; (2) age; (3) terminal or nonterminal position; (4) number of fruits; (5) accessibility; (6) number of bites removed; (7) size class of bites; (8) presence of insect damage; and (9) presence of storm damage. The plants were reassessed a year later and the following measurements recorded: (1) presence or absence of cladophyll; (2) percent utilization; (3) number of new fruits; and (4) number of new pads on each marked cladophyll.

Lechuguilla *(Agave lechuguilla)* was also sampled to assess use by peccaries. Random transect lines were selected and all plants within 1 m (3 ft) on each side were sampled for: (1) total number of lechuguilla plants; (2) number of plants dead; (3) number alive; and (4) subjective estimate of the degree of usage. In addition, an area 20 x 10m (66 x 33 ft), located in the study area and selected subjectively for its heavy use by peccaries, was sampled completely to test for preference of plant part. Data recorded included: (1) total number of lechuguilla on the plot; (2) number of plants used; (3) number of leaves used; (4) extent of use; and (5) whether the chewed leaves were core, intermediate, or lateral in position on the plant.

Calculation of Interaction Rate

The small size of peccaries and the nature of the habitats in which they are found made direct observation of interactions difficult and sometimes impossible. However, it was possible to record interactions that were seen partially and interactions that were not seen but were heard.

During any observation period there were vocal and nonvocal interactions. Because interactions were brief and the vegetation dense, hearing interactions did not make the animals more visible. However, vocalization may have brought my attention to an interaction I would have missed otherwise. I have no way of assessing this effect.

In order to arrive at an estimation of the total number of interactions and to represent more exactly the interactive frequency of peccaries, I grouped interactions into: (1) interactions seen and heard *(ISH);* (2) interactions seen but not heard *(ISNH)*; (3) interactions heard but not seen *(IHNS).* Interactions not heard and not seen *(INHNS)* were calculated as follows:

There is a ratio of *ISH* to *ISNH* during any period of activity. Hence, both vocal and nonvocal interactions were recorded for every observation period. Because of this, the following relationship is possible. *IHNS* bear the same relationship to *INHNS* as *ISH* bear to *ISNH*.

$$\frac{ISH:ISNH}{IHNS:INHNS} \tag{1}$$

$$INHNS = (ISNH \bullet IHNS)/ISH \tag{2}$$

Equation (2) was used to calculate the total number of interactions per animal per unit time.

2
Activity Patterns

In desert habitats, peccaries show seasonal variation in their movement and feeding patterns (Eddy 1961; Ellisor and Harwell 1969; Schweinsburg 1969; Bigler 1974). In Big Bend during the summer months when daily temperatures were highest, peccaries were inactive and remained in shaded beds during the day. Foraging was initiated in the early evening and continued through the night. The animals retired to dense vegetation in drainages and arroyos early the next morning. During September, October, and November, cooler daytime temperatures prevailed. The animals fed progressively longer in the morning and started activity earlier in the afternoon. During the winter months, when daily temperatures were much lower, peccaries spent more time feeding in the morning and afternoon. As a result, less time was spent in the beds during the day. As nightly temperatures approached freezing, peccaries ceased nocturnal activity and huddled together for warmth, at least during part of the night, as previously reported (Zervanos and Hadley 1973). With the approach of spring, mean temperatures increased and peccaries again began feeding through the night. Feeding in the late morning and early afternoon decreased only with the advent of high daily temperatures in late April and early May.

Analyses of the seasonal activity pattern data (Fig. 4) indicated that cessation of feeding activity in the morning was correlated mainly with minimum daily temperature ($r = -0.736$). In Big Bend the daily minimum temperatures generally occurred about 05:00 to 06:00. Stepwise regression analyses of the times when feeding activity stopped against (1) minimum temperature, and (2) a running mean minimum daily temperature for the previous 6 days gave a correlation coefficient of 0.841 ($r^2 = 0.708$). Minimum temperature accounted for 61.8% of the variation ($r^2 = 0.618$), while the running mean accounted for an additional 9.0% ($r^2 = 0.0899$).

Onset of feeding activity in the afternoon was correlated with maximum daily temperature ($r = 0.644$). A stepwise regression analysis of the time of onset of activity against (1) maximum daily temperature, and

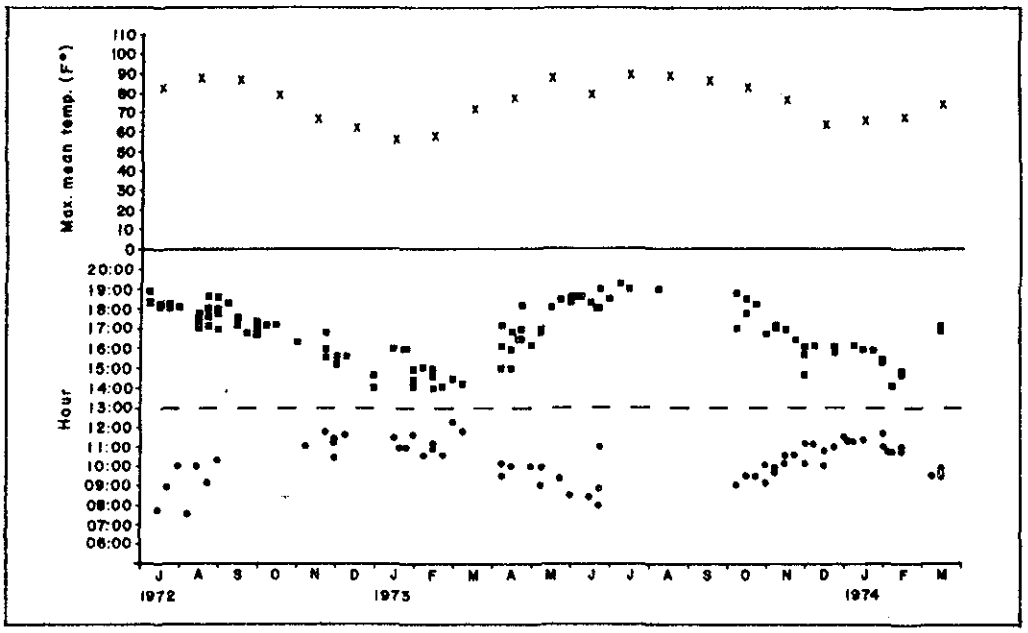

Fig. 4. Time of beginning of peccary activity in the afternoon *(squares)* and end in the morning *(circles)* in relation to temperature *(X)*.

(2) a running maximum daily mean temperature for the previous 6 days gave a correlation coefficient of 0.733 (r^2 = 0.537). Maximum daily temperature and the running mean accounted for 39.7% and 14.0% of the variation (r^2 = 0.397, 0.140), respectively.

These data suggest that temperature alone accounts for a large part of the variation in the onset and cessation of feeding activity in peccaries. The minimum and maximum temperatures on any particular day explained most of the variation. However, mean temperatures from the previous week also are important in predicting activity periods of peccaries because they indicate what the expected ambient temperature might be. These results indicate that peccaries depart from their beds in response to ambient temperatures.

Time Budget of Peccaries

Time budgets of peccaries were divided into two categories: active and bedded. As shown above, bedding periods were influenced by temperature. During periods of bedding, activity was slight and largely concentrated at the start and end of the period. This was due to variation in activity of individual peccaries. Data taken during periods of bedding are not included in the following analyses.

Behavior patterns of active peccaries were quantified easily (Table 1). Feeding activities, including feeding, walking and searching, and stopping and searching for food items accounted for most of the activity. A total of 78.6% of the active time of adult males, 77.9% of adult females, and 86.7%

TABLE 1. Time partitioning of activities for collared peccaries for the periods March-July, October-November.

Activity	AM %	AF %	Juvenile %	Level of significance AM-AF	AF-JY
Feeding	29.3	45.3	34.1	•	†
Walk-Search	34.0	22.7	33.6	•	§
Stop-Search	15.3	9.9	19.0	§	•
Interaction	6.7	4.8	2.8		
Alert	9.3	6.4	3.2		
Walking	1.5	5.4	2.1		
Lie down	1.3	4.9	0.8		
Self groom	1.3	0.5	0.3		
Other	1.3	0.2	4.1		

Excludes time spent bedded.
† = $P \geqslant 0.10$; § = $P \geqslant 0.05$; • = $P \geqslant 0.01$; AM = adult male; AF = adult female; JY = juvenile-young.

of juveniles and young was spent locating and consuming food. Another 16.0% of the active time of adult males, 11.2% of adult females, and 6.0% of juveniles and young was spent in intraspecific behavioral interactions and standing at alert. The remainder of the active time was spent walking, lying down, self-grooming, and other activities.

Statistical differences exist between the percent of time allocated for some activities by certain sex and age classes. When data collected during the spring-summer and fall periods were summed, significant differences became apparent between adult males and females, and also between adult females, and juveniles and young for (1) feeding; (2) walking and searching for food items; and (3) stopping and searching for food (Table 1). For instance, active adult males fed 29.3% of the time, whereas active adult females spent 45.3% of the time feeding. Additionally, adult males spent proportionately greater time walking and searching for food than did adult females (34.0% vs. 22.7%). Adult males spent 15.3% of their time stopping and searching for food items, whereas adult females spent 9.9%. Juveniles most resembled adult males in their foraging time and were most unlike adult females (Table 1).

When activities were analyzed between spring-summer and fall seasons, there were inter- and intra-sex differences in time given to certain activities. In the intra-sex comparisons, both adult males and adult females show significant differences between the percent of time spent foraging during the periods March-July and October-November (Table 2). Adult males spent a significantly greater percent of time feeding in the spring-summer period (36.2% vs. 13.6%). Significantly less time was spent stopped and searching for food items (11.2% vs. 33.6%). Adult females also showed differences in the means when time allocations were compared between time periods (Table 2). In the early period, adult females spent more time

TABLE 2. Time partitioning of activities: Comparisons of percent time allocated within and between sex for two time periods.

	March-July	October-November	Level *t*	Significance F	BPP		Adult male	Adult female	Level of significance *t*	F	BPP
Adult male											
Feeding	36.2	13.6	†	§	0.99		36.2	41.7			0.79
Walk-Search	31.3	35.3					31.3	24.6		§	0.91
Stop-Search	11.2	33.6	•	•	0.97	March-					
Interaction	0.1	0.2		•	0.80	July					
Other	16.3	15.2									
Adult female											
Feeding	41.7	35.3			0.78	October-	13.6	35.3	*	§	0.98
Walk-Search	24.6	33.3	*	§	0.90	November					
Stop-Search	11.2	17.1	*	§	0.90		33.6	17.1	†	*	0.92
Interaction	0.1	0.1									
Other	17.1	10.6									

* = P ⩾ 0.15; † = P ⩾ 0.10; § = P ⩾ 0.05; • = P ⩾ 0.01; BPP = Bayesian posterior probability.

feeding (41.7% vs. 35.3%) but less time walking and searching (24.6% vs. 33.3%) and stopped and searching for food (11.2% vs. 17.1%).

Comparisons between sexes (Table 2) demonstrated differences in the times allocated for a particular activity for both phenological periods. Adult females fed more than adult males (41.7% vs 36.2%) during the spring-summer period, a time that coincided with the last months of pregnancy and the onset of lactation. During the late fall, males fed 13.6% of their active time as compared to 35.3% for females. In both seasons, the means for adult males were less than those for adult females.

The differences between sexes suggest that the time spent feeding is related to the different roles of males and females. Female peccaries have a larger reproductive burden than do males. Carrying the fetus, parturition, lactation, and parental care involve high energy costs, while the male role is confined largely to courtship, copulation and perhaps defense. The high energy costs incurred by the female appear to be met by higher energy intake, as suggested by the additional time spent feeding.

3
Behavior

The following analyses are based on 380 hours of observation; 1,335 hours were spent in the field walking to the ranges and locating the animals. One thousand nine-hundred and twenty-seven animals were observed, representing 159 groups, and 1,166 interactions were recorded. During the study, the peccary population ranged from 89 to 118 animals.

Senses

Vision: Peccaries are not visually oriented and apparently cannot easily detect and distinguish objects by vision alone except at the closest distances (0-3 m or 0-10 ft). A person standing downwind is undetected until approached to within 3 m (10 ft) (Schweinsburg 1969). When presence was detected, the animal lifted its head and sniffed, and often exhibited alarm. Usually the peccary circled downwind to gain the scent.

Olfaction: This sense is well developed in peccaries. Scent alone causes alarm and fright, and scent-marking (Sowls 1974) is important in their social behavior. The well-developed scent gland has been described by Epling (1956) and Werner et al. (1952). Knipe (1957), Neal (1959b), and Werner et al. (1952) have suggested that its function is maintenance of herd integrity and group member recognition. Probably peccaries can recognize conspecifics by scent alone. Seton (1929) thought the scent gland served to keep bothersome insects away, but there has been no verification of this hypothesis. Ewer (1956), Sowls (1969, 1974), and Schweinsburg and Sowls (1972) have indicated that its function is associated with scent-marking within the territory. Schweinsburg (1969) stated that many of the behavioral patterns that serve to establish and reinforce the social order have evolved around use of the scent gland. In Big Bend, 43% (308 of 808) of all interactions recorded involved rubbing the scent gland of one peccary by another group member, indicating that scent is important in the social behavior of peccaries. These and other data also indicate that recognition of group members and their hierarchical rank within the group is accomplished primarily by olfaction associated with reciprocal grooming.

However, territorial marking with the scent gland was observed only seven times in 23 months of field work, indicating that scats may be as important in marking a territory as the scent gland.

Hearing: Schweinsburg (1969) indirectly indicated the importance of hearing in his evaluation of vocalizations of peccaries. He suggested that the soft grunting sound made by feeding peccaries may be a mechanism to maintain group cohesion during feeding. Indeed, the rather extensive vocal repertoire of distinct calls with intergradation indicates that sound communication is important in peccary behavior.

Recognition of Individuals: It became evident that peccaries recognize other group members as individuals. For instance, in the Panther Canyon group, the number two male in the dominance hierarchy never attempted to initiate an aggressive interaction with the alpha male during the breeding season. If the alpha male walked toward him, the beta male turned and walked away.

Conspecifics from neighboring groups were approached immediately by several group members if they happened to cross the territorial boundary. Single, nongroup conspecifics were dominated but not treated in the same manner as an encroaching group. In the latter situation, strong, aggressive chasing occurred, with dominance reversals at the boundary lines. Schweinsburg (1969) reported several instances where supposed non-group conspecifics were seen to join an established group. However, my data indicate that this phenomenon may be a case of seasonal splitting of territorial groups into smaller units.

Auditory Communication

Knipe (1957), Neal (1959b), Schweinsburg (1969), and Sowls (1974) have reported that peccaries make indistinguishable pig-like sounds in conjunction with the readily recognizable "repetitive grunt" and "tooth clack." Actually, peccaries have a rich repertoire of sounds that can be classified as: (1) aggressive; (2) submissive; and (3) alarm. In some instances a vocalization may be used in more than one context.

Aggressive Vocalizations

Bark: Sowls (1974) described the "bark" as closely resembling that of a dog. My observations indicated that the peccary's bark was somewhat more resonant than the bark of a dog and was associated with a growl sound. It was seldom given in repetition. A bark was accompanied usually by piloerection and given in agonistic encounters between adults and in alert-alarm interactions.

Repetitive grunt, alternating pitch continuous grunt, and feeding growl: These three calls are a graded series of calls that varied according to the context in which they were elicited. The "repetitive grunt" was characterized by a series of low sounds that may be represented by the mnemonic, uh-uh-uh-uh. The vocalization was confined exclusively to

feeding interactions. The repetitive grunt was given initially at low intensity but increased in volume and was accompanied by aggressive postures as conspecifics approached one another. With decreasing distance between the two feeding animals, the repetitive grunt may change into an alternating pitch continuous grunt or to a feeding growl. Schweinsburg (1969) has indicated that the repetitive grunt functions in group cohesion. My observations suggest that it is aggressive and used to warn of encroachment on individual space. However, the repetitive grunt sometimes was heard when no conspecifics were close to the vocalizing animal. Under this condition the sound became softer and has been described as a "contentment" sound by Schweinsburg (1969).

The alternating pitch continuous grunt is second in this graded series and closely resembles the repetitive grunt except that the pitch rises and falls rhythmically in a continuous, repetitive sequence. This is a distinct sound, associated only with feeding interactions and heard only when peccaries are foraging close to each other. I have never heard the sound given in any other context. Both approaching animals may give the alternating pitch continuous grunt simultaneously. If the feeding interaction is aggressive this vocalization may terminate with a "feeding growl."

The feeding growl also was given only in feeding interactions. It often was preceded by the repetitive grunt or the alternating pitch continuous grunt or both. If a feeding animal approached to within about 2m (6.6 ft) of another, the peccary approached often made a short but intense growl accompanied by a head turn-mouth open posture. Depending upon the situation, the recipient turned to face the aggressive animal or walked off. The feeding growl was of short duration and high intensity.

Tooth clicking, tooth clack, huff clack, and whoof clack: Schweinsburg (1969) and Sowls (1974) have described a tooth pop or clatter in peccaries. Actually, peccaries exhibited a graded series of calls that ranged from tooth clicking to tooth clacking to huff clacks to whoof clacks. Tooth clicking was the least intense variation of this aggressive pattern. The teeth of the upper and lower jaws were brought together lightly and rapidly to produce a clicking sound. The tooth clack was much more intense and was characterized by an explosive sound made by bringing the teeth together hard. The tooth clack appeared to be a less intense version of the huff clack. In this latter sound, the peccary exhaled without vocalization, followed by one or a series of clacks. As intensity of the interaction increased the huff clacks graded into what I termed whoof clacks. The essential difference was that a vocalization accompanied the rapid exhalation of breath and clacks. All vocalizations in the series were accompanied by aggressive stares and varying levels of aggressive posturing.

Growl: The growl was given by peccaries during aggressive encounters. It differed substantially from the feeding growl in that it was not associated with feeding interactions and was never accompanied or

preceded by other aggressive feeding sounds. Additionally, the growl usually was lower in pitch than the feeding growl. It was of substantially longer duration than the feeding growl and seldom was as abrupt or loud. Often the growl was followed by a tooth clack or huff clack and was always accompanied by aggressive postures. It was often associated with the pattern run-whirl-lunge at. In most cases aggressive physical contact accompanied the growl.

Submissive Vocalizations

Submissive peccaries seldom vocalized while being dominated. When they did, two submissive sounds were recognized easily.

Yip-yip: The yip-yip resembled whimpering and often was repeated several times. It was given usually by a submissive animal to a strong threat and physical contact by a dominant. Any of the subordinate postures described below may have accompanied the vocalization, but the submissive "crouch" and "lie down" postures were used most frequently.

Repetitive yip-ow, yelp: The repetitive yip-ow consisted of a series of submissive sounds given when the subordinate animal was being vigorously and continuously dominated. In many cases the submissive animal was a juvenile. Seldom were two occurrences exactly the same, although all included elements of yip-ow and often yelp and other variable and high-pitched, submissive sounds. The yelp appeared to be a variation of yip-ow and the second in a graded series of calls. It usually was given a single time and occurred when the subordinate animal was rushing to escape a clash with a dominant conspecific.

Alarm Vocalizations

Alarm vocalizations of peccaries contained elements similar to aggressive sounds but were accompanied by distinct alarm postures. There were four calls given in alarm situations.

Alarm grunt: The alarm grunt was a typical alarm sound, repeated at infrequent and unequal intervals and characterized by the mnemonic "uh." Although the sound may have been repeated, it did not form a continuous series. The alarm grunt was made only when a peccary was alerted. It was accompanied by foot-stamping and sniffing the air or other alarm patterns described below.

Repetitive huff, whoof: The repetitive huff was a series of rapid, short, breath exhalations. The animal was usually in motion and searching for the source of the disturbance. The peccary approached and circled me while lifting its nose and sniffing the air. Often, the animal walked hesitantly, holding one foot suspended for 3-10 seconds, then stamping it and quickly lifting and holding the diagonal foot for a similar duration. The huffs were given in synchrony with the stamping of the feet. As the pace quickened, the vocalizations remained in synchrony with each step. If the animal bounded away, huffs were emitted with every leap. The repetitive huff was

accompanied by piloerection. The whoof was similar to the repetitive huff but was louder and often accompanied by a tooth clack.

The previously described aggressive sounds (bark, tooth clack, huff clack, and growl) also were used in alert-alarm interactions in conjunction with alarm sounds. One or more may have been used, with the more aggressive being used in the more intense alert situations. Aggressive sounds used in this context seldom occurred separately but were associated with alarm sounds.

Integration of Peccary Vocalizations

Peccary vocalizations vary in at least three fundamental characteristics: (1) intensity; (2) continuity or degree of intermittence of calls; and (3) pitch. When calls were ranked subjectively on a continuum of each of these characteristics, several patterns emerged (Table 3).

Intensity for 15 vocalizations showed that submissive and alert calls were intermediate to aggressive calls, and the latter occurred at both extremes. Continuity ranking indicated that submissive calls were intermediate in rank but that alert calls tended to be intermittent and the least continuous. Submissive calls were the highest in pitch of all vocalizations, and alarm calls, since they were often aggressive, ranked intermediate to low.

TABLE 3. Ranking of 15 peccary calls for three sound characteristics.

Characteristic					
Intensity		Continuity		Pitch	
Rank and call		Rank and call		Rank and call	
Low	1 Repetitive grunt	Unbroken	1 Growl	Low	1 Growl
	2 APC grunt		2 Repetitive grunt		2 Repetitive grunt
	3 Tooth clicking		3 Tooth clicking		3 Tooth clicking
	3 Yip-yip		4 APC grunt		4 Alarm grunt
	4 Alarm grunt		5 Yip-yip		5 APC grunt
	5 Yip-ow		6 Yip-ow		6 Repetitive huff
	6 Repetitive huff		7 Alarm grunt		7 Repetitive whoof
	7 Repetitive whoof		8 Bark		8 Tooth clack
	8 Yelp		8 Yelp		8 Huff clack
	9 Feeding growl		8 Feeding growl		8 Whoof clack
	10 Tooth clack		9 Tooth clack		9 Feeding growl
	10 Growl		9 Huff clack		10 Bark
	11 Bark		9 Whoof clack		11 Yip-yip
	12 Huff clack		10 Repetitive huff		11 Yip-ow
High	13 Whoof clack	Broken	10 Repetitive whoof	High	11 Yelp

Brackets indicate calls with the same rank; boxes indicate submissive calls; alarm calls are underlined.

APC = alternating pitch continuous.

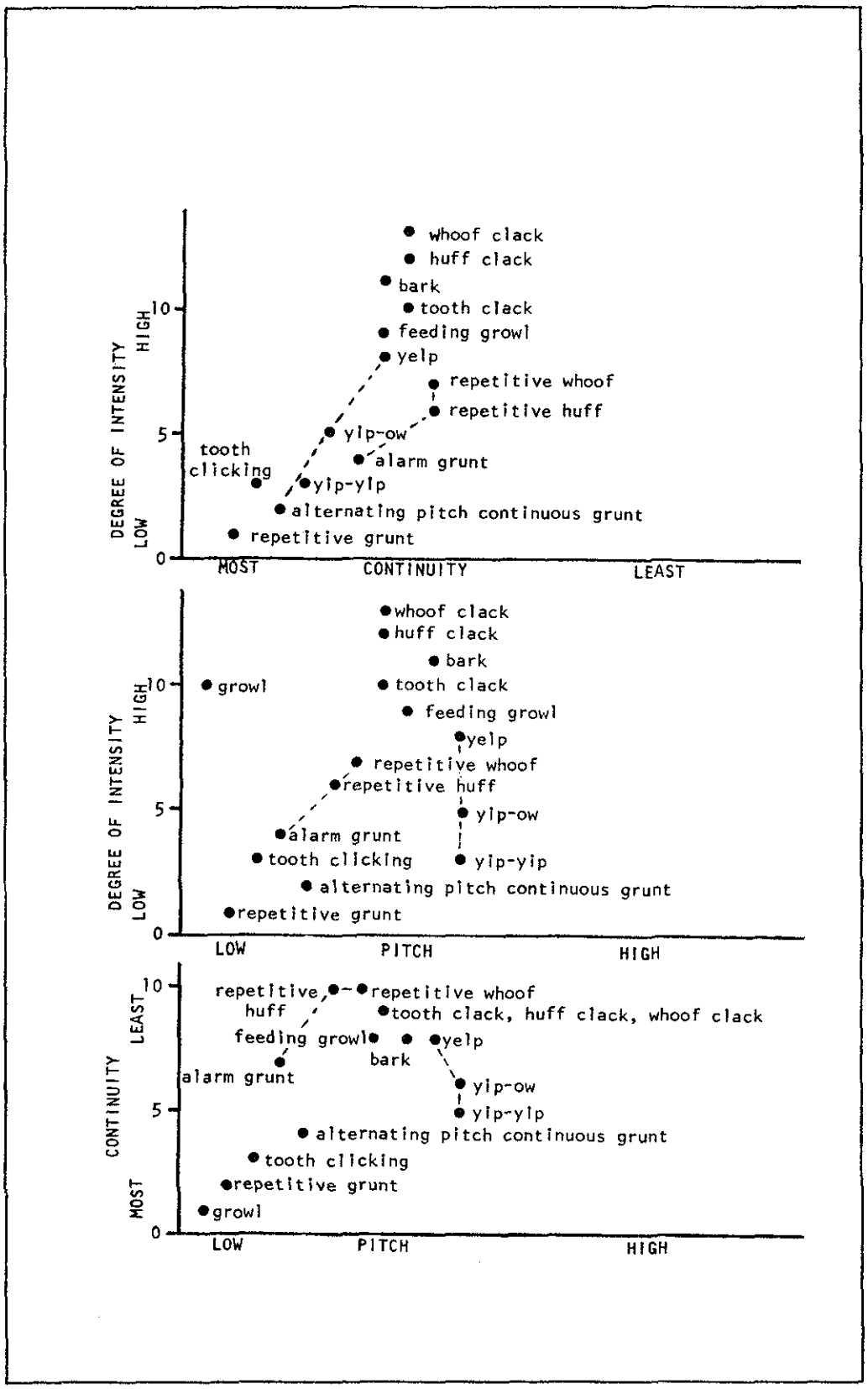

Fig. 5. Relationship of three call characteristics for 15 peccary calls.

To discern the distribution pattern of peccary calls and their relationship to three fundamental characteristics, each characteristic was plotted against each of the other two (Fig. 5). The intensity of calls varied inversely with call continuity for all calls (Fig. 5), including submissive and alert vocalizations. For most calls, intensity varied directly with pitch, while the continuity of calls varied inversely. However, for submissive calls the vocalization became more intense and more intermittent as the animal became more submissive although pitch did not change. Thus, the characteristics of these calls were the reverse of those for most others.

Suiformes have been described as forest dwellers (Bryden 1900; Fradich 1974), and Young (1950) has suggested that their morphology has changed little since the Eocene. The closely related tayassuids originated in South America (Woodburne 1968) and presently occupy many habitats ranging from forests to scrub desert. In these habitats, they are associated predominantly with dense vegetation (Sowls pers. comm.).

Varying ecological conditions, and especially habitat characteristics, can influence the selective forces which mould intraspecific communication. For small, group-living, forest-dwelling ungulates, visual displays may be of limited value due to the nature of the dense vegetation. I suggest that the rich repertoire of sounds used by tayassuids evolved as the most appropriate method of communication, given the dense nature of the habitats these animals are known to inhabit and probably evolved in. The use of the most obvious sound characteristics of intensity, continuity, and pitch and their discrimination by peccaries would appear to have high selective value. Discrimination and use of at least 15 different calls in aggressive, submissive, alert-alarm, and other contexts appears to support this interpretation.

Alert-Alarm Patterns

Peccaries exhibited five classes of response from mild alert to strong alarm when disturbed: (1) cautious approach; (2) stationary alert; (3) slow departure; (4) a very cautious departure with constant sensing of the environment accompanied by vocalization and associated foot stamping and (5) precipitous running with vocalization.

Cautious Approach: The cautious approach has been described under the repetitive huff vocalization. During extreme caution, the animal approached one step at a time, with exaggerated foot lifts and stamps (Fig. 6, left). As a peccary approached, it usually circled downwind. No approaches occurred if I was upwind of the alarmed animal. If it approached, the animal continually tested the air by lifting its head and nose and sniffing. Often the peccary advanced to within 2 m (6.6 ft) before becoming aware of the source of the alarm. A rapid retreat followed and circling continued. As the scent was identified, the animal responded by

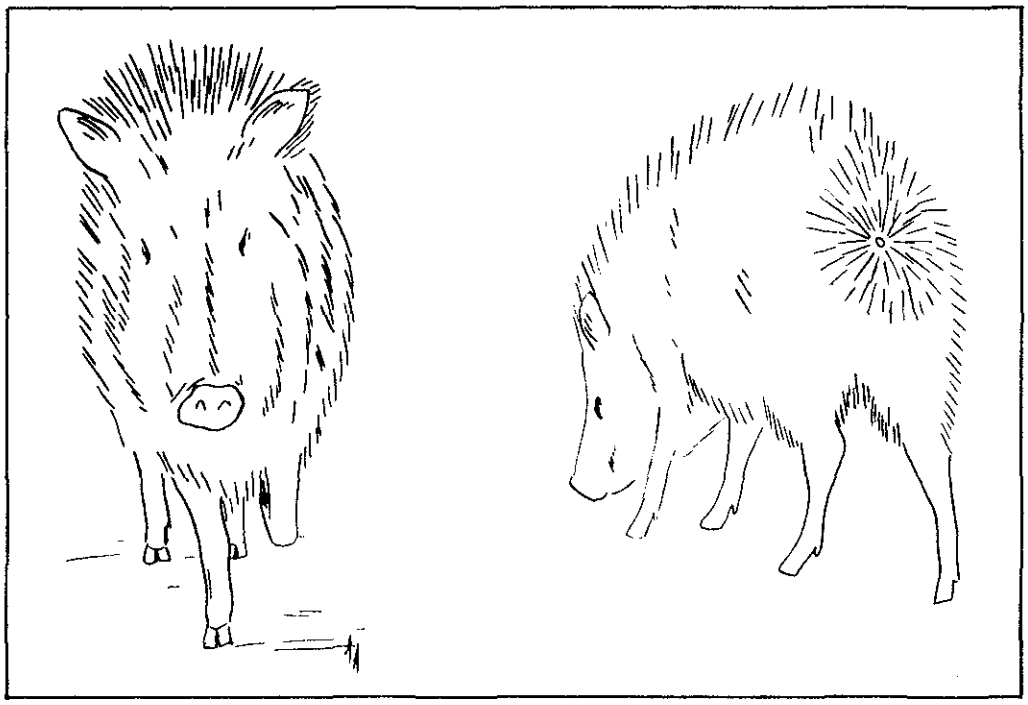

Fig. 6. Postures associated with alert-alarm interactions. *Left*. Cautious approach. *Right*. Stationary alert.

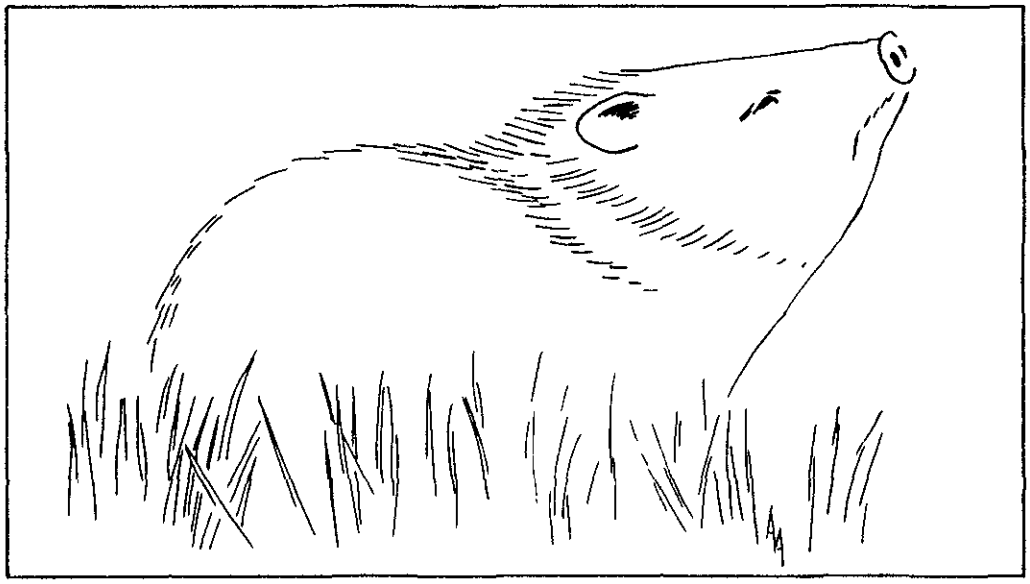

Fig. 7. Nose up-sniff pattern. Note piloerection of head and mane bristles.

either relaxing the alert or by walking or running out of sight. The cautious approach occurred 18% of the time in alert-alarm interactions. I was the cause of alert 96% of the time (Table 4). The cautious approach never occurred alone; one of the remaining four patterns was always given in conjunction with it.

TABLE 4. Patterns associated with alert-alarm interactions.

	Cautious approach	Stationary alert	Slow departure	Cautious departure	Fast departure	Total number	Total %
Source of alarm							
Observer	17	23	34	25	8	90	96
Other	0	0	0	2	2	4	4
Regroup after alarm							
Yes	5	7	11	19	9	46	49
No	0	3	2	1	1	7	7
Unknown	12	13	21	7	0	41	44
Reciprocal groom							
Yes	2	2	3	1	3	9	10
No	9	9	15	5	1	30	32
Unknown	6	12	16	21	6	55	58
Vocalization							
No sound	1	4	3	0	0	7	7
Sniff	2	6	4	1	0	11	13
Repetitive huff	8	6	12	3	1	22	23
Tooth and huff clacks	6	7	12	23	9	51	54
Unknown	0	0	3	0	0	3	3
Cautious approach							
Yes		1	12	3	1	17	18
No		22	22	24	9	77	82
Subcolumn total	17	23	34	27	10	94	
Subcolumn percent	18	24	36	29	11	100	100

The cautious approach is not included in the row total since it always occurred with one of the other four patterns.
Each subcolumn of each row sums to the subcolumn total for that column.

Stationary Alert: When alerted, peccaries often stood motionless except for raising the nose, apparently to test the air (Fig. 7.). The bristles on the dorsal ridge were erected, exposing both the scent gland (Fig. 6, right) and a white line caused by the coordination of the color bands of the dorsal hair (Schweinsburg 1969). The pattern occurred in 24% of alarm interactions, usually in response to mild alarms (Table 4).

Slow Departure: During a slow departure the animal stood with its nose up and turned to locate the source much in the manner described for the cautious approach. The departure was a slow, unwary walk. Resumption of previous activity followed. A slow departure occurred 36% of the time (Table 4).

Cautious Departure: As with other alert patterns, the animal stood and sniffed with nose up and turned as if to locate the source of the alarm. Approach seldom occurred. The animal retreated in a stiff-legged gait, much like that described for the cautious approach. The steps were usually 5-10 seconds apart; the environment was sensed between each step. Each step was accompanied by a synchronized huff or grunt. When the animal was 6-10m (20-30 ft) distant, it often bounded away, vocalizing at each leap. When peccaries were unsure of the nature or source of the stimuli, as evidenced by their actions, the departure was cautious (29%) (Table 4). In most cases the stimulus was a noise made by the observer.

Fast Departure: During a fast departure, peccaries bounded with leaps in excess of 3m (10 ft) in length. Piloerection occurred and explosive huffs were sounded with each leap. This pattern was used in response to a strong stimulus such as an unfamiliar sound. If the direction of the source could not be detected, the peccaries ran in all directions for 5-8m (16-26 ft) and stopped. They then remained perfectly still for periods of up to 20 minutes. If no further alarm followed, regrouping occurred as they returned to feeding. If the animals determined the location of the stimulus, their flight was directed away, with one animal following the other single-file (Schweinsburg 1969). During the flight, no organization of the group relative to sex and age could be detected. Following single-file seemed to be the only organization during alarm flight. During flight of this nature, peccaries stopped and sensed the environment several times, apparently in an attempt to reaffirm the direction, closeness, and nature of the disturbance. Eleven percent of all alerts involved a fast departure (Table 4).

Following alert, the animals regrouped 49% of the time (Table 4). No determination of regrouping could be made in 44% of the interactions because the animals were out of sight. In six of the seven remaining interactions following alert, there was no need to regroup because the herd did not break up. On three occasions, the animals involved were standing together; twice they were walking off together, and once a precipitous run of 3m (10 ft.) occurred. The animals ran together and then stopped and ate. On only one occasion did the peccaries run and scatter and not regroup.

Peccaries ran with mane and dorsal bristles fully erected, exposing the

scent gland. I have never seen liquid emitted from the gland during alarm but Mohr (1961), Neal (1959b), Schweinsburg (1969), and Sowls (1974) have reported that it occurs. On several occasions I noticed a strong musk odor after peccaries had been alarmed and had left the area.

Peccaries reciprocal groomed (see below) in 10% of alert-alarm interactions (Table 4). In 58% of alert interactions I could not determine if reciprocal grooming occurred because of visual obstruction by dense vegetation.

Vocalizations accompanied most (93%) of the alert-alarm interactions (Table 4). Thirteen percent were accompanied by lifting the head and sniffing. Repetitive huffs were recorded in 23% of the interactions and 54% were of such intensity as to be accompanied by huff clacks or tooth clacks. In virtually every case where a clack was given, every member of the group came to alert. The number of conspecifics alerted in a herd and their response appeared to be related directly to the kind and intensity of the vocalization. Ninety percent of all fast departures, 85% of all cautious departures, and 35% of all slow departures were preceded by tooth or huff clacks (Table 4). Fourteen percent of all clack vocalizations were followed by a cautious approach.

Behavior Patterns Used in Social Interactions

Non-Agonistic Patterns

Nose Up-Sniff: In the nose up-sniff, the animal stood with nose raised and wriggled its rhinal disc as if to gain the scent and the direction of its source (Fig. 7). Its head turned from side to side and its body remained in an alert position. Usually a leg was raised and the bristles were erected. This pattern also was used in conjunction with alert-alarm behavior (13%, 11 of 94). If the source of interest was a conspecific, it was approached. If the source was not another peccary, it usually was approached and circled (18%, 17 of 94).

Walk Towards: This approach consisted of one conspecific approaching another. The ears were held in any position and the bristles were seldom erected. The pattern was used in both aggressive and nonaggressive interactions. The approach was the primary pattern used to approach conspecifics.

Nose-Nose Sniff, Body Sniff, and Nose Rub: In the nose-nose sniff two conspecifics approached one another and sniffed noses. The body was tense and the weight was shifted to the hind legs. The ears were forward. Peccaries touched their rhinal discs or sniffed with their noses close together.

The body sniff was very similar except that it involved sniffing of the body. Nose rubbing was a pattern in which a peccary rubbed the head and body of a conspecific with its nose. It sometimes was accompanied by

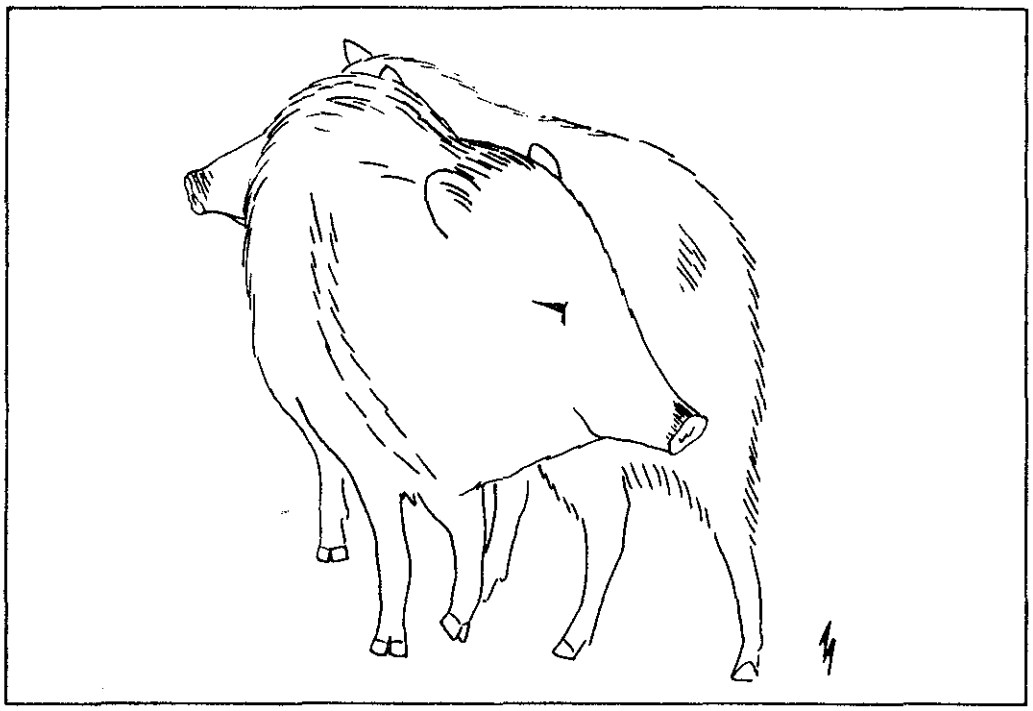

Fig. 8. Reciprocal grooming. Note the position of the head near the scent gland of the conspecific.

nibbling and may be equivalent to grooming. The recipient seldom offered resistance. These three patterns often were associated with reciprocal grooming.

Head Rub, Reciprocal Groom: In head rubbing two animals faced each other and rubbed the sides of their heads together. The body posture was relaxed. It was a nonaggressive pattern and often associated with nose-nose sniffing, sniffing the body, and rubbing the body with the nose.

In reciprocal grooming, an important pattern of behavior in peccaries, the animals approached and stood alongside one another, head to tail. Preliminary sniffing or body rubbing often occurred. Each peccary rubbed its head against the hind leg, rump, and the scent gland of the other (Fig. 8). Enough force was used so that the animals pushed each other around in circles while grooming. During the interaction, the animals leaned against one another, putting the entire length of the body in contact. Although the feet moved to maintain balance, usually the head alone was moved up and down against the conspecific. Reciprocal grooming has been described by Knipe (1957), Neal (1959b), Schweinsburg (1969), Sowls (1974), and by Schweinsburg and Sowls (1972).

In Big Bend, 43% (350 of 808) of all observed interactions involved grooming. Thirty-four percent involved reciprocal grooming, 9% involved grooming by one animal with no reciprocation, and 1% involved head rubbing. In 31% of the interactions (358 of 1,166), I could not determine if grooming occurred. Seventy-two percent of all reciprocal grooming was

TABLE 5. Reciprocal grooming by sex and age class.

	Recipient					
Initiator	AM	AF	J	UA	Total	% of total
Adult male	11 (15.1)	47 (64.4)	7 (9.6)	8 (10.9)	73	26.9
Adult female	25 (30.5)	41 (50.0)	14 (17.1)	2 (2.4)	82	30.3
Juvenile	9 (25.0)	8 (22.2)	7 (19.5)	12 (33.3)	36	13.3
Unidentified adult	2 (2.5)	4 (5.0)	2 (2.5)	72 (90.0)	80	29.5
Total	47	100	30	94	271	100.0
% of total	17.3	36.9	11.1	34.7	100.0	

Figures in parentheses are percent of row totals.
AM = adult male; AF = adult female; J = juvenile; UA = unidentified adult.

associated with mounting (Table 7). In general if mounting occurred during the interaction, preliminary patterns such as nuzzling and grooming were involved more frequently.

Males and females initiated reciprocal grooming with approximately the same frequency (Table 5). Juveniles and young groomed significantly less frequently. Adult males and adult females groomed females significantly more than they groomed males (64.4% vs. 15.1% and 50.0% vs. 30.5%, respectively). Adult females initiated more reciprocal grooms with males than did adult males with males (30% vs. 15.1%). Correspondingly, females groomed juveniles and young about twice as much as males did (17.1% vs. 9.6%). Juveniles and young were relatively unselective and groomed all sex and age classes with approximately the same frequency (Table 5). The initiator stopped grooming first as often as did the recipient.

Occasionally, grooming was not reciprocated. Schweinsburg (1969) indicated that it was usually the dominant animal that groomed and the submissive that did not reciprocate. Sixty-nine nonreciprocated grooms were observed. Males were seen to initiate grooming in 39% of these interactions, females in 29%, juveniles and young in 23%, and unidentified in 9% (Table 6). Adult males groomed adult females in 78% of the interactions they initiated. Seventy-six percent (16 of 21) of these involved an estrous female or occurred during other reproductive activity. On only five occasions did adult males groom adult females (24%, N=21) when no apparent reproductive activity could be detected on that same day. In four of these, however, reproductive activity occurred within 7 days or less of the grooming, indicating the strong relationship between this pattern in males and reproduction. In no case could it be determined that the females were dominant to the male who groomed them. In 48% (10 of 21) of the male-female encounters, the alpha male of the group was involved. In six

TABLE 6. Nonreciprocated grooming by sex and age class.

	Recipient					
Initiator	AM	AF	J	UA	Total	% of total
Adult male	4 (14.8)	21 (77.8)	1 (3.7)	1	27	39.1
Adult female	7 (35.0)	7 (35.0)	5 (25.0)	1 (5.0)	20	29.0
Juvenile	7 (43.8)	6 (37.5)	0	3 (18.7)	16	23.2
Unidentified adult	0	0	0	6 (100.0)	6	8.7
Total	18	34	6	11	69	100.0
% of total	21.6	49.3	8.7	15.9	100.0	

Figures in parentheses are percent of row totals.
AM = adult male; AF = adult female; J = juvenile; UA = unidentified adult.

TABLE 8. Aggressive patterns associated with feeding interactions.

	Pattern associated with feeding				
Aggressive patterns	Yes	No	Unknown	Total	% of total
Head turn-mouth open	16 (64)	1 (4)	18 (32)	25	49
Run-whirl-lunge at	18 69	8 (31)	0	26	51
Total	34	9	8	51	100
% of total	67	17	16	100	

Values in parentheses are row totals.

cases (29%, N=21) I could not determine the status of the male involved. The data indicated that, at least for interactions initiated by adult males with adult females, nonreciprocated grooms are sexual in nature and the initiator is dominant. Female-male and female-female encounters were not associated with breeding behavior and no pattern of dominance related to the initiator of the interaction could be determined.

Sexual Patterns

Courtship in peccaries was limited to a few patterns and was unlike the elaborate behavior described for pronghorn (Kitchen 1972, 1974; Bromley and Kitchen 1974) or for Uganda kob (Buechner 1961). Sniff rump, nuzzle, and mount were patterns exclusively associated with courtship encounters. Other patterns, such as grooming and nose rubbing, were also used. Of 64 courtship encounters, 81% involved patterns not exclusively sexual. In only one instance did no other pattern precede or occur with mounting.

TABLE 7. Preliminary patterns by males associated with sexual encounters.

Type of action	No. of interactions	No. mounts and attempted mounts	Sniff rump	Nuzzle	Reciprocal groom	Non-reciprocal groom	Other nonsexual patterns	Total	% of total
Sexual interactions without mounting	26 (41)		19 (53)	3 (20)	3 (12)	3 (23)	10 (53)	38	35
Sexual interactions with mounting attempted	7 (11)	13 (19)	4 (11)	2 (13)	4 (16)	1 (8)	3 (16)	14	13
Sexual interactions with mounting	31 (48)	56 (81)	13 (36)	10 (67)	18 (72)	9 (69)	6 (31)	56	52
Total	64	69	36	15	25	13	19	108	100
% of total	100	100	33	14	23	12	18		

Figures in parentheses are percent of column totals.

TABLE 9. Reaction of the recipient animal to the dominant pattern "Force up."

	Recipient				Type of contact			Reciprocal groom		Reaction	
	AM	AF	J	UA	Mouth-mouth	Nudge	No contact	Yes	No	Walk off	Lie down
Adult male	1	2	0	1	0	4	0	1	3	3	1
Adult female	0	1	1	1	1	1	1	0	3	1	2
Unidentified adult	0	1	2	1	0	1	3	1	3	1	3
Total	1	4	3	3	1	6	4	2	9	5	6
% of total	9.1	36.3	27.3	27.3	9.1	54.5	36.4	18.2	81.8	45.5	54.5

AM = adult male; AF = adult female; J = juvenile; UA = unidentified adult.

Grooming occurred 38 times, sometimes more than once in an encounter, and was seen in 30% of all sexual encounters (19 of 64).

Sniff rump, nuzzle, and mount: Sniff rump was a pattern used exclusively in courtship. It varied and involved the male sniffing the female's rump or sniffing her groin area from the side. This pattern was noted only in males, although Sowls (1974) reported penis-licking by female peccaries during courtship. If the female was receptive, she stood for mounting. A nonreceptive female walked away or lay down in response to rump sniffing and attempted mounting. Sniff rump occurred in 56% of all sexual interactions. An interaction often included more than one mount or attempted mount (Table 7). Sniff rump is a preliminary pattern and occurred most frequently in sexual interactions not involving mounting (53%).

Males nuzzled before mounting and also while astride the female. Nuzzling involved nibbling, rubbing the nose on the female's body, and

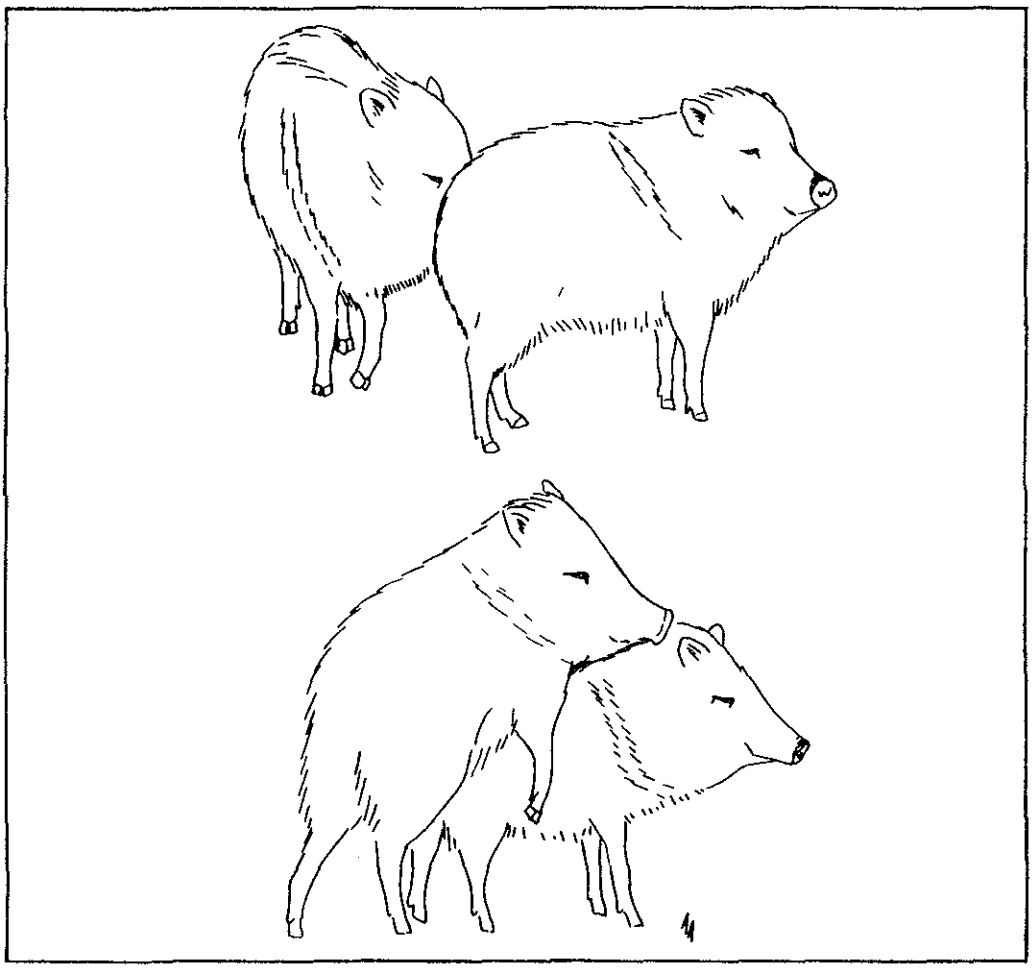

Fig. 9. Reproductive behavior. *Top.* The male is sniffing and nuzzling the perineum of the female. *Bottom.* The male has put his chin on the female's back after mounting.

gently biting her. Twenty percent of all nuzzling patterns occurred during sexual interactions not involving mounting. Thirteen percent and 67% occurred during attempted mounting and mounting, respectively (Table 7). In most instances, nuzzling was directed toward the neck of the female (93%, 14 of 15). A female nuzzling a male during courtship was observed only once. In most cases (97%, 61 of 63) the female was relatively passive and her response was limited to accepting or rejecting the male and to reciprocated grooming (66%, 25 of 38).

Just prior to mounting, the male approached the female from the rear or side (Fig. 9, top). After sniffing the perineum, nuzzling, and grooming, the male mounted (Fig. 9, bottom). While astride, he often nuzzled the female's neck. His chin often rested on her back and his ears were neutral or directed backward.

During the course of the study, 56 mountings and 13 attempted mountings were observed. On four occasions, females mounted males. Sowls (1974) also has observed mounting by females. If a female was receptive, the male mounted once or several times during the period of estrous. On four occasions a female was mounted twice, and on one occasion each, females were mounted four, six, seven, and eight times by the same male during a single bout. On 22 occasions, females were mounted only once although four of these same females were mounted again during later encounters. The maximum number of mountings observed on an estrous female was 19. The same male was involved and the matings occurred over a 3-hour period.

Mountings lasted from 3 to 237 seconds, with a mean of 39 seconds. The mode, or most frequently occurring value, was 20 seconds. The distribution of mountings was skewed, with 62% of the observations being less than 30 seconds in duration.

Agonistic Patterns: Dominant Animal

Stare: The stare was given by a dominant animal to a subordinate. The ears of the dominant were held forward against the head, but seldom neutral. The body was held tense and piloerection was associated increasingly with the pattern as the duration of the stare became longer and thereby more aggressive. If the animal who gave the stare was not facing the recipient, it turned toward the second animal. The relative small size of peccaries (18-27 kg or 40-60 lbs., 50 cm or 20 inches at the shoulder), the dense character of the habitat, and the peccary's rather small eyes made a stare difficult to recognize. Whenever an animal turned its head to or was oriented toward another peccary, and that second animal gave a response, I recorded the pattern of the initiator as a stare.

Head turn—mouth open: This was an aggressive pattern in which a peccary turned its head with mouth open toward an approaching animal. Often a feeding growl accompanied the threat. The ears were laid back, the canines were apparent, and the bristles on the mane and back were erected.

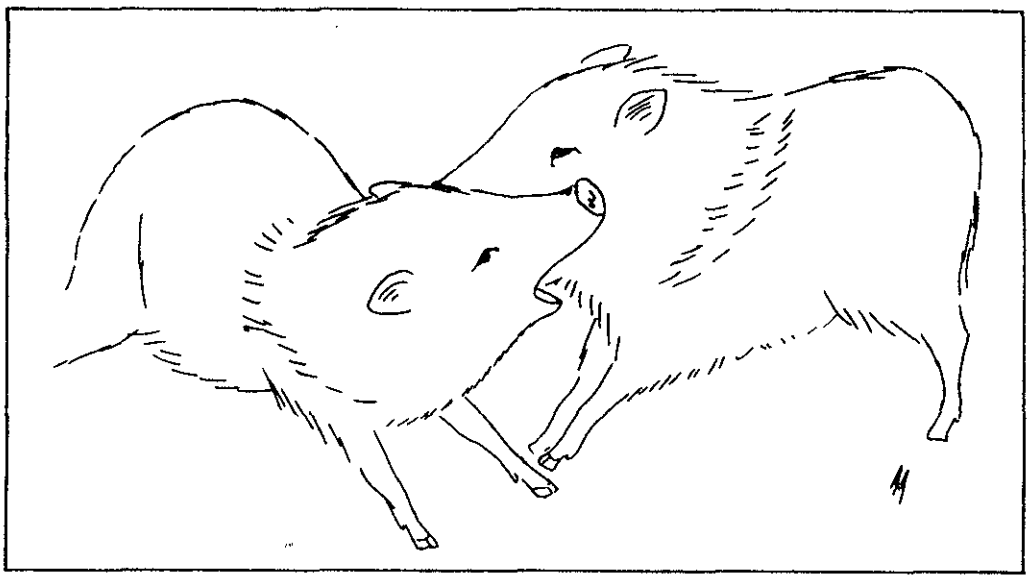

Fig. 10. The dominant peccary *(right)* has lunged at and bitten a conspecific who responded with a yip yip and a sink-back submissive posture. Note the absence of piloerection in the submissive peccary.

The head was outstretched toward the recipient and contact sometimes occurred. If the initiator of the pattern was feeding, a repetitive grunt always preceded the pattern. In 64% of the encounters, feeding close together elicited the head turn-mouth open pattern (Table 8).

Run-whirl-lunge at: This was an aggressive pattern during which the peccary who gave the response ran at, or whirled and lunged at, a conspecific that had approached to within a meter (3.3 ft.) (Fig. 10). The position of the dominant animal was similar to that described above for the head turn-mouth open pattern. Run-whirl-lunge at was most often used (69%) in conjunction with feeding encounters (Table 8). As peccaries fed, they moved with their heads lowered, searching for food items. Any close approach usually led to an aggressive interaction by one of the feeding animals. An approach closer than 1m (3.3 ft.) elicited a repetitive grunt or an alternating pitch continuous grunt and was likely to lead to an encounter in which the resident animal ran or whirled and lunged at the approaching animal. If a fight erupted, the resident usually won (74%, 14 of 19). Possession of food items seemed to confer an advantage unless there was a great disparity in size between the interacting animals. Subordinates won half of the encounters with a more dominant animal if they were in possession of the disputed food item. Sixty percent (9 of 15) of the animals who lost an encounter while in possession of a food item were noticeably smaller than the victor.

Force up: A force up was characterized by a bedded animal being nudged or otherwise coerced into standing and losing its bedding site. In each case the bedded animal was approached by the initiator who then lay

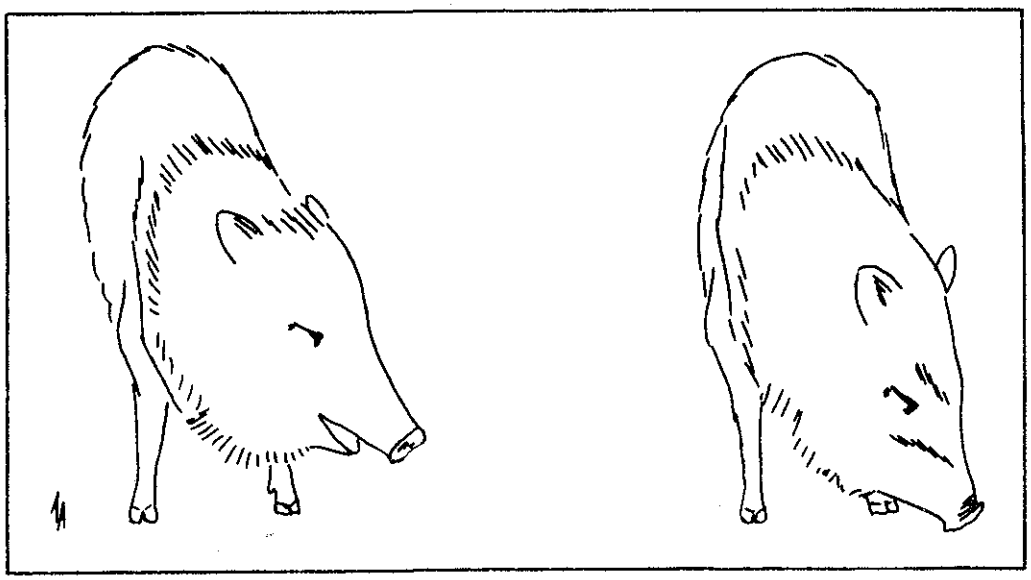

Fig. 11. The submissive animal *(right)* has exhibited a nose down-head low-turn away pattern in response to an aggressive stare by the dominant peccary.

down in the vacated spot. Usually, little apparent aggression occurred. In 6 of 11 encounters observed, the bedded animal was nudged, while in 4 the stare of the approaching animal was sufficient to move the bedded subordinate (Table 9).

Cut off: In a cut off, a walking peccary was intercepted by a second animal, forcing the first to stop. The ears of both animals were neutral, no piloerection occurred, and the animals showed no overt aggression. In two instances a reciprocal groom followed. This pattern was observed three times. Males were involved in each case.

Agonistic Patterns-Submissive Animal

Nose down, head low, turn away: In this linked pattern, the nose and head were lowered, while at the same time the nose was turned away from the aggressive animal (Fig. 11). Piloerection seldom occurred, and the ears were in a neutral position or slightly back. The nose down, head low, turn away pattern was the response given in almost all submissive encounters.

Back up: An animal sometimes retreated from a threat by taking a few steps backwards. During a back up, the submissive animal was always oriented toward the dominant animal. Piloerection frequently occurred. The position appeared to be mainly defensive. Back up was observed five times.

Sink back, crouch, lie down: These patterns were a linked sequence and represented increasing levels of submission to increased domination. In the sink back, the submissive animal rocked back while keeping all four feet firmly on the ground (Fig. 10). If no contact occurred, the nose was

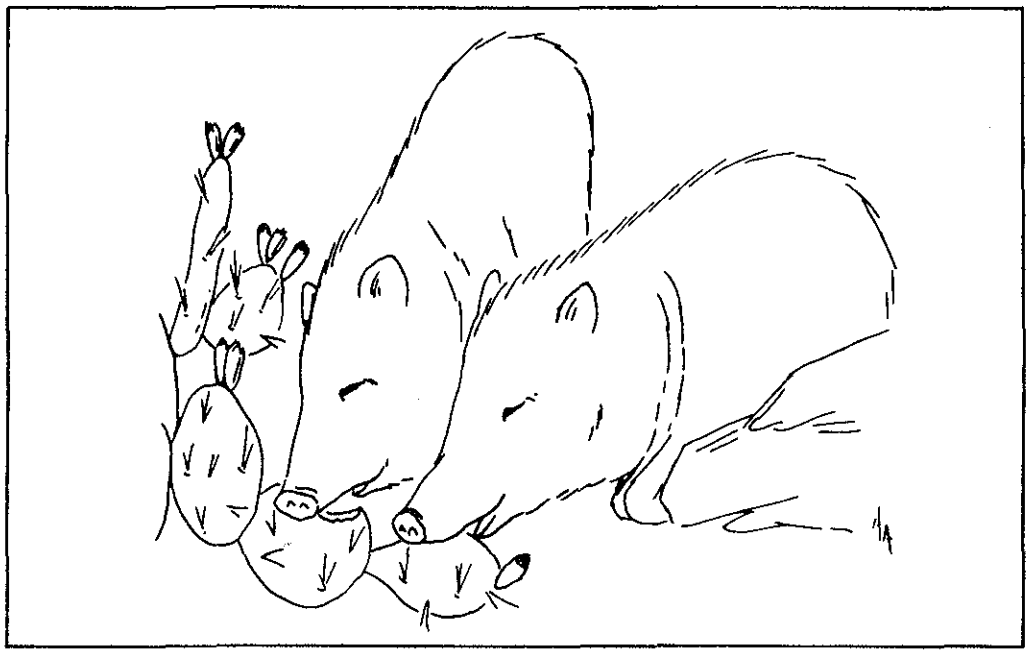

Fig. 12. Two peccaries feeding together with no apparent aggression. The animal on the *left* is dominant. The submissive peccary *(right)* approached the feeding dominant by walking forward on its knees.

lowered and the head turned away from the dominant animal. If the submissive response was stronger, the sink back became a crouch. The animal continued to rock back until the rump was on the ground. The shoulders were lowered and the front feet were folded under the body or extended in front. The front feet were often used to prop the anterior part of the body into a sitting position. The nose was lowered further, the head turned away, and the gaze averted. Lying was the culmination of the sequence and was the response given to a very strong threat. The submissive peccary lay prostrate on its stomach. The chin was stretched out and the head was on the ground. Alternately, the head was turned to the side but the chin was kept on the ground. The animal appeared to be trying to flatten itself to the ground. During submission, vocalizations such as yip-yip, repetitive yip-ow, and yelp occurred. If the three patterns were given in response to a threat, they were given in the linked series. If a crouch was given, it was preceded by a sink back.

Run off: This pattern was the primary response to an intermediate or serious threat given at a distance of more than 2m (6.6 ft). The mane and bristles of the fleeing animal were seldom erected. The ears were held in any position. The linked patterns sink back, crouch, lie down and nose down, head low, turn away and the pattern run off were given in response to serious threats; the posture given depended upon the distance between the interacting animals. For instance, if the aggressor ran at or whirled and lunged at a second animal and was within about 1m (3.3 ft), the response

usually given was the linked pattern nose down, head low, turn away associated with one of three degrees of intensity in the linked pattern sink back, crouch, lie down. If the distance was greater, the usual response was to run off.

Kneel: Kneeling was noted when peccaries approached other feeding animals or when they fed close to other conspecifics (Fig. 12). They also knelt when feeding alone but this action was related to the nature of the food resources, its structure and position. When an animal was kneeling close to a conspecific while feeding, the ears were neutral or laid back and the head was held low. Kneeling in this context was a pattern given prior to overt aggression. It appeared to be an appeasement gesture. Additionally, the tendency for agonistic encounters was less during kneeling. When animals were kneeling, the interactions were decidedly low key.

Agonistic Patterns Used in Dominance Disputes

Mouth-to mouth wrangle: During this pattern, two conspecifics faced one another with noses raised and mouths open, often in contact. The heads were side by side and some pushing, shoving, and wrestling occurred as each peccary bit at its opponent's mouth. The biting was either ritualized or serious. The ears were flat against the head and the bristles were erected. Chest pushing occurred often. It the interaction was mild, the animals raised their heads to contact one another and then gradually lowered their noses together. The animal lowering its head first lost the encounter. If there was clearly a subordinate, it showed submissive postures. As the interactions became serious, the animals engaged in a fight of great variability. The mouth-to-mouth wrangle and fight were patterns in which the recipient countered the aggressive actions of a conspecific. These patterns seemed to result from undecided or incomplete dominance and were defensive as well as aggressive in nature.

Bite: A bite often occurred in response to a similar action or in response to a mouth-to-mouth wrangle. Similarly, it was given with or in response to the patterns 'run-whirl-lunge at' or 'head turn-mouth open' (Fig. 10). The intensity of a bite varied from barely making contact to inflicting serious damage. Biting varied in intensity depending upon the response of the recipient. If reciprocated mildly, the pattern was mild; if reciprocated strongly, a serious fight usually resulted.

Fight: Fights were characterized by the interacting animals earnestly trying to bite each other on the neck and body while, at the same time, taking defensive maneuvers to avoid being bitten. The bristles were fully erected, the ears were flattened to the head, and much growling and tooth clacking occurred. Fights usually occurred when two peccaries were matched closely in size. Fights between males were observed only during times when a female was in estrous. These led to a clear winner and loser. Physical injury, such as torn noses and ears, was inflicted during these fights. Ten fights were observed.

Schweinsburg (1969) and Sowls (1974) describe a "whirl around," in which two peccaries circled one another with jaws locked. This was followed by a "throw down," in which the animals fell to their sides while maintaining jaw contact. I saw neither of these patterns. Schweinsburg and Sowls (1972) indicated that these patterns were observed in penned animals. They have not been reported for free ranging peccaries.

Walk off: Walk off was the pattern used to end an interaction. When given in response to a dominant pattern, it represented submission. It was also used to end nonaggressive encounters. In this context, walk off was the last pattern of the interaction and was followed by a resumption of feeding or of previous activity.

Contact Versus Noncontact Interaction

Sowls (1974) has described peccaries as contact animals. Indeed, 66.8% of interactions observed in Big Bend involved contact (Fig. 13). However, in highly social animals with strong dominance hierarchies, one should not expect a large proportion of the aggressive interactions to involve contact. As expected, in peccaries, 73.1% of all aggressive interactions involved no physical contact (Fig. 13). Similarly, of 474 contact interactions, 82.5% were not aggressive. Only 17.5% of all contact encounters were aggressive and of these only 11 interactions involved a serious fight or other type of strong domination. The remaining 72 were mild contact interactions involving ritualized and mild versions of patterns such as the mouth-to-mouth wrangle (Fig. 13).

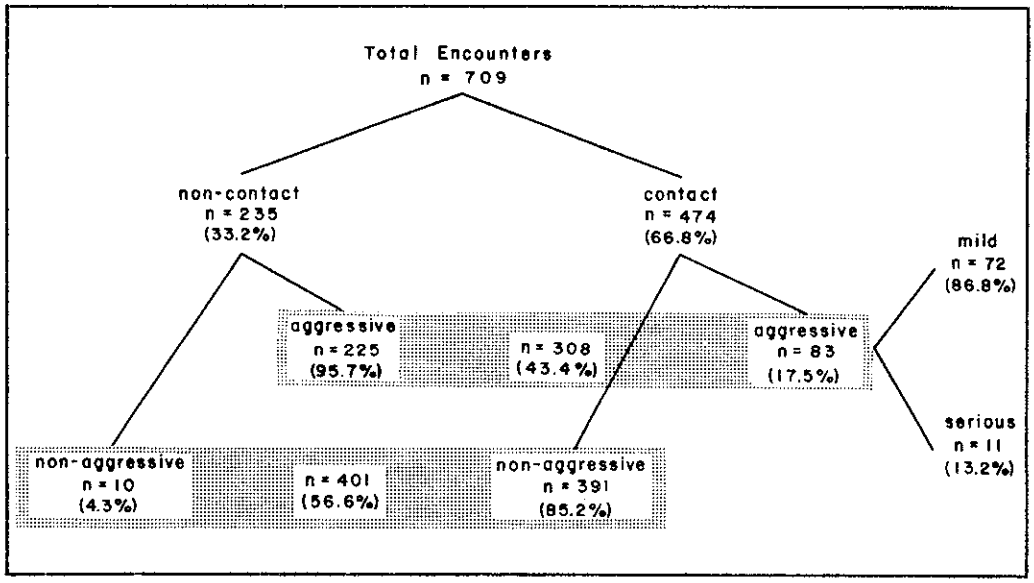

Fig. 13. Nature of intragroup encounters between peccaries.

Interaction Rates

Most interactions between peccaries were associated with foraging activities and varied in number from month to month. In Big Bend, the interaction rates varied from 0.125 to 0.598 interactions per animal per hour, with a mean of 0.312. No patterns emerged although there was a tendency for more interactions to occur just before and during parturition in early summer, and during the breeding season in late fall and early winter. Parturition coincided closely with the onset of the rainy season and production of high quality forage. Probably this was responsible in part for the increased interaction rates during this time, because most squabbles were associated with dominance interactions over choice items of food.

4

Social Organization and Population Characteristics

Group Territories

Description

Peccaries are territorial. Ellisor and Harwell (1969) and Schweinsburg (1969) have stated that herd boundaries were discrete and showed little overlap, but they presented no data to document territoriality. Of the five territorial groups studied extensively, four occupied contiguous ranges, while the fifth was located 0.8 km (0.5 mile) to the east (Fig. 14). All territories were approximately the same size, with Lower Mouse Canyon slightly larger at 245 ha (605 acres) (Fig. 14). The location of park headquarters and a housing development of approximately 19 ha (47 acres) within Lower Mouse Canyon influenced peccary use of this area. Therefore, developed areas were not included in the range size calculation. The Panther Canyon and West Hills territories were characterized by rugged terrain with deep canyons and ranged from 1,220 to 1,370m (4,000 to 4,500 ft) in elevation. Lower Mouse Canyon territory sloped gently to the northeast and was cut by a large wash with steep sides and a wide floor. It was intermediate in elevation at 1,100-1,190m (3,610-3,910 ft). The Lone Mountain territory also sloped northeast and surrounded a large rocky outcrop 1,260m (4,130 ft) in elevation. The major part of the range was at 1,070-1,130m (3,510-3,710 ft) elevation. KBar was the lowest territory at 1,000-1,070m (3,280-3,510 ft) and was essentially flat but with a long, low ridge traversing the range north to south.

Water was available in West Hills, Lower Mouse Canyon, and KBar throughout the year although only the West Hills source was natural. Panther Canyon and Lone Mountain had water available during the rainy season due to natural stone basins (tinajas) in Panther Canyon and a man-made dirt depression (tank) in the Lone Mountain territory. All territories were located next to or overlapped a blacktop road (Fig. 14). All areas had rocky outcrops and very dense vegetation although these were more numerous in the higher ranges.

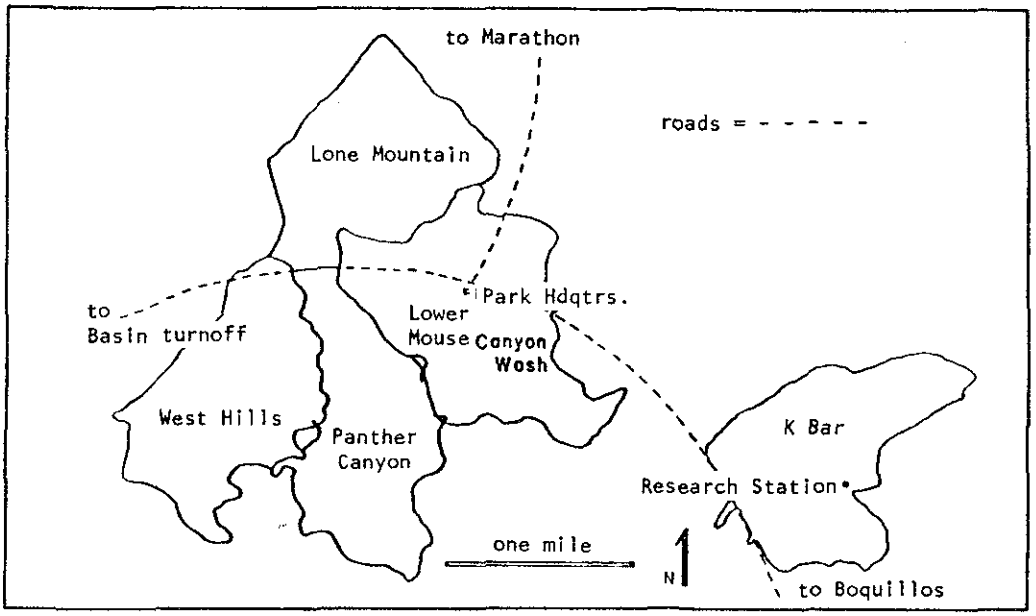

Fig. 14. Nonoverlapping territories of five peccary groups.

Territorial Marking

Peccaries possess a scent gland located on the dorsal ridge line about 24cm (10 inches) above the tail. Epling (1956) and Werner et al. (1952) have described its anatomy and histology. Neal (1959b) believed that the scent gland functioned in group cohesiveness. Schweinsburg (1969) and Sowls (1974) have described its use in marking territories. Peccaries marked one another during mutual grooming. In addition, rocks and shrubs and other objects in the habitat sometimes were marked.

I observed eight cases of marking with the gland. On six occasions males were involved. Sex was undetermined on two occasions. In all cases the marking animals were adults. Vegetation was marked on six occasions and a rock once. On one occasion both a shrub and a rock were marked. Five markings were in the middle of the range near the bedding areas and three were on boundary lines. On all three occasions when boundary lines were marked, sexual activity was associated. I was unable to determine if the alpha male did the marking.

Sowls (1974) reported that peccaries used scat stations when defecating. My observations confirmed this. Scat piles were located near bedding areas and near boundary lines. Although peccaries defecated throughout the range, I found scat piles only in bedding areas and boundary perimeters. Peccaries defecated at the start of activity in the afternoon after rising from their beds. Although the incidental effect of scat piles around bedding areas may have been to identify these places as belonging to one group, it seemed likely that no territorial function was involved. Scat piles near bedding areas may have been the result of necessary physiological processes. The fact that scats were deposited in

piles probably was a carryover from the territorial markings that occurred on boundary lines. I observed the Panther Canyon herd feeding over a ridge and defecating on the ridge top in an area that was later determined to be a boundary line. Boundary lines were not marked with scat in a continuous line but rather by localized scat piles.

Group Stability

Within a territory groups of peccaries were social and remained together through the year. Subordinate males did not leave the group during the breeding season nor were all-male groups formed at any time. Each of the five territorial groups that I observed extensively during the study (Fig. 14) separated into feeding subgroups. The subgroups were usually consistent over time. Some of these subgroups remained separate for as long as 2 weeks. Schweinsburg (1969) indicated that he saw considerable group exchange. Perhaps he saw exchanges between feeding groups that were part of one territorial herd. In the Panther Canyon and Lone Mountain herds, feeding groups consistently fed in the same areas, although the subgroups of the Lower Mouse Canyon, West Hills and KBar herds did not.

In 1972 the KBar herd, consisting of 13 peccaries, had two feeding subgroups of eight and five animals. This was not apparent in 1971 when the group consisted of 12 animals.

The West Hills herd was large, with a maximum size of 28 animals just after the peak of the farrowing season in July 1973. By December mortality had reduced the group to 23. The territorial herd had split into feeding subgroups of 17 and 6 although the number in each group varied.

In 1971 the Lower Mouse Canyon herd consisted of approximately 15 peccaries, with feeding subgroups of approximately 6 and 9 animals. By 1972 the herd had increased to 19 animals and by December 1973, 23 animals had divided into subgroups of 11 and 12 peccaries. There was, however, some variation in the size of the feeding groups.

In 1972, the Lone Mountain group numbered seven animals which split into subgroups of five and two members. By late 1974 the herd size had increased to eight animals, with feeding subgroup sizes of five and three. Although recruitment increased the number in one feeding subgroup, it remained consistent in composition and part of the territory occupied (Fig. 15). The smallest subgroup expanded its range in 1973, as did the larger subgroup in 1974 (Fig. 15, right).

The Panther Canyon herd varied somewhat in the size of its subgroups, but they were the most consistent in composition. In addition, the two feeding groups used different parts of the range and seldom were seen outside their chosen range (Fig. 16). Interactions between the two feeding subgroups were marked by increased hostility, and some interactions approached the intensity and substance of territorial fights and chases. The feeding subgroups numbered approximately 6 and 12 animals in 1972 but

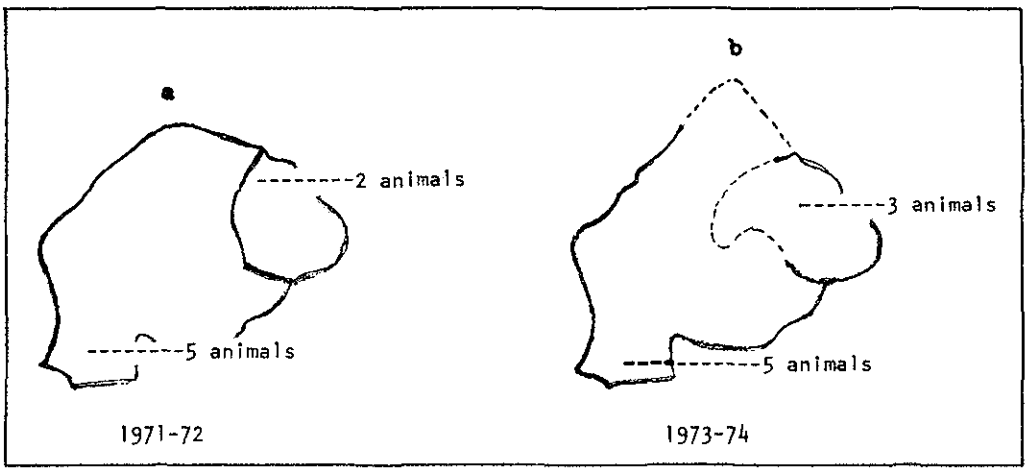

Fig. 15. Feeding subgroup preferences for territory occupied by the Lone Mountain herd. The dotted lines *(right)* represent range extensions.

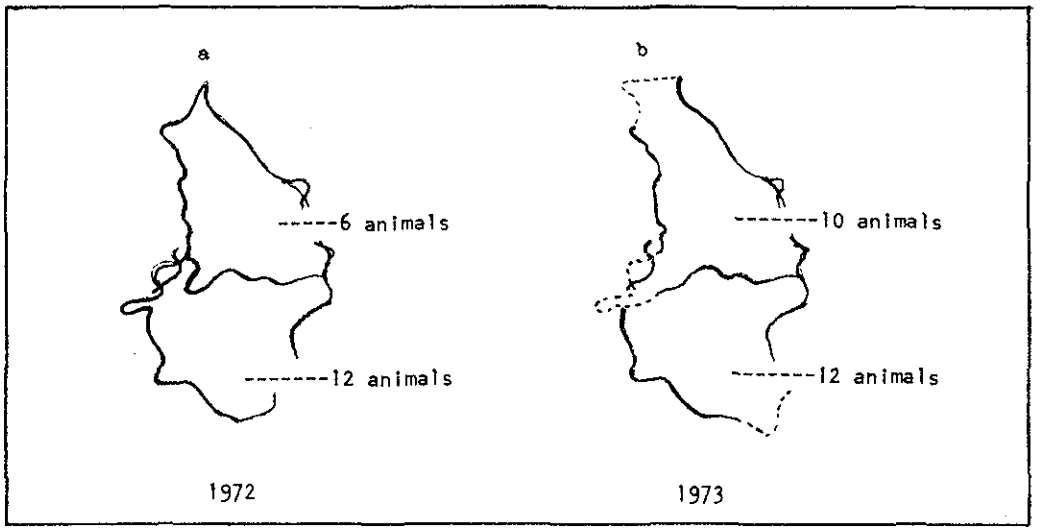

Fig. 16. Feeding subgroup preferences for territory occupied by the Panther Canyon herd. The dotted lines *(right)* represent range extensions, the crossed solid lines *(left* and *right),* territory overlap.

had increased to 10 and 12 animals by late 1973. Both subgroups increased their territory (Fig. 16, right) and by 1974 were considered distinct territorial groups for the reasons discussed below.

I have never seen a strange peccary successfully enter an established group although perhaps this happens occasionally. An attempt was observed on 7 January 1974, when a strange male peccary was sighted in the Lower Mouse Canyon group territory. The animal had not been seen previously in this area. On 14 January this strange peccary (subsequently called Lone Star) was dominated by the beta male (#29) of the Lower Mouse Canyon group. He was also attacked by a female, a juvenile, and a second female. I forced Lone Star to move by walking toward him. As he

walked off, he was followed and continually dominated by #29. As he was approached, Lone Star lay down and tooth clacked, all the while turning so as to face #29. As I approached, he arose and trotted away, and #29 followed and repeated the domination. The sequence was repeated 12 times until Lone Star reached the territorial boundary of the Lower Mouse Canyon and Panther Canyon herds. After Lone Star had crossed a wash into the Panther Canyon territory, #29 turned and walked back to the Lower Mouse Canyon herd 400m (1,310 ft) distant. Lone Star returned to the Lower Mouse Canyon area for several nights in succession until 4 February, after which time he was no longer seen in the area. He was observed on 4 March in the Panther Canyon group territory, which is contiguous to the western part of Lower Mouse Canyon (Fig. 14). The animal was not seen thereafter.

Defense of Territory

Perhaps the strongest evidence for territoriality are dominance reversals along a boundary. I observed dominance reversals twice. Chases were observed four times on two separate occasions. Without exception these territorial interactions occurred during the breeding season when reproductive stakes were highest.

On 21 November, 1974, four peccaries, including a red-colored juvenile female and a black male, crossed from the Panther Canyon territory into the Lower Mouse Canyon territory. The juvenile approached an adult female of the Lower Mouse Canyon herd. As the female stared at her, the juvenile turned and ran. The female immediately gave chase for about 8 to 10 meters (26 to 33 ft). Within seconds, she turned and chased the black male and a third peccary in the same manner. The fourth Panther Canyon peccary had retreated across the wash into his territory. After a few bounds the black male stopped, whirled around, and faced the Lower Mouse Canyon female, who had been huff clacking repeatedly. She vocalized again. The black male turned and walked across the boundary line, followed by the remaining two peccaries. The female began feeding and was bred an hour later by the Lower Mouse Canyon alpha male.

Territories are defended by more than one group member. On 16 January, 1973, I observed the Lower Mouse Canyon and Lone Mountain herds feeding toward one another. Two adult males from the Lone Mountain group approached the Lower Mouse Canyon group. As the first male walked into the midst of the Lower Mouse Canyon herd he was met by an adult male from that group. Both males stared and then rushed at one another, just missing each other. They turned and faced one another and wrestled with mouths open and heads raised. The Lone Mountain male immediately turned and ran away from the Lower Mouse Canyon male, who chased him hard with mouth open. After having run for about 100 meters (330 ft.), the animals whirled abruptly and ran in the opposite direction, with the Lone Mountain male chasing the Lower Mouse Canyon

male. Again, after the boundary line was crossed, the animals changed direction and the Lone Mountain male was chased. The Lower Mouse Canyon male slowed and stopped at the boundary. The Lone Mountain male then stopped and turned, both animals looked at one another, then each turned and walked away. At the same time, a second male from the Lone Mountain group walked into the Lower Mouse Canyon group and was met by an adult peccary (sex undetermined). The intruder was chased out of the area at a full run. He did not stop. The Lower Mouse Canyon peccary stopped at the boundary and then returned to the herd. No dominance reversal occurred. The previous reversals indicated that a piece of land, and not the herd, was being defended.

Establishment of New Territories

Feeding groups seemed to be the nucleus for new territorial group formation. Establishment of a new group can occur successfully if there is a portion of land that can be appropriated from other groups or that is unoccupied. Groups must be large enough to gain protection from predation. Since all sexually mature females breed, reproductive success is most variable in the polygynous males, where hierarchical position determines breeding success. Therefore, it would seem more advantageous for subordinate males to initiate new group formation.

I suggest that the mechanisms for new group formation operate in the following manner. The parent group must be large initially, at least in relation to resource availability. Gradually, the feeding subgroups should spend more and more time apart, with occasional regrouping. Up to a certain herd size, the alpha male of the parent group should discourage breakdown of the group; the subordinates should encourage it. The splinter group with the subordinate male and lacking the alpha male should enlarge its feeding range to a size sufficient for subsistence. The feeding subgroups should become more aggressive toward one another with time. The groups can be said to have made the decisive steps when, during the breeding season, they remain apart and a new alpha male is established in the splinter group.

The Panther Canyon herd exhibited this pattern over a period of 3 years. This herd was composed of 18 peccaries in 1971. During July of that year, the herd split into two feeding subgroups of 6 (group A) and 12 (group B). Occasionally, the feeding groups varied by one or two animals. By the end of the summer of 1973, group A contained 10 peccaries and group B, 12. The groups were seen together only once after 28 November 1972. This was on 16 October 1973 when there were 16 peccaries together in one group.

As the feeding subgroups spent more time apart, they became more independent and the subsequent interactions between members of the two groups were characterized by higher levels of aggressiveness. For instance, on 14 July 1972, an adult (sex undetermined) from Group B walked into

the midst of group A. The peccaries exhibited unusually aggressive behavior and there was much snorting and tooth clacking. The strange animal entered the herd very cautiously with its weight on its haunches as if ready to run instantly. The animal from group B approached two group A peccaries who lay under vegetation. After reciprocal grooming, the first group A animal left and a few seconds later the second animal walked away, leaving the intruder lying alone. When I left the area at 21:05, the strange animal was still separated from the group. Again, on 27 November 1972, a nongroup conspecific tried to enter Group A. He was rebuffed three times by a male and was not allowed to stay in the group. If he remained at least 8-10m (26-33 ft.) distant, he was left undisturbed. After rebuffing the strange peccary, the group A male defecated. Six other group members walked over and, in turn, stood over the defecation. Each sniffed at the scat and then followed the male down the slope into Panther Canyon. The remaining group A members followed. The rebuffed animal remained on the ridge and did not follow the group into the canyon.

In May 1973 a male tried to enter the beds of five peccaries from group A. All the bedded animals arose and lunged at the male who immediately departed and did not return. On 6 April 1973, a male from group A was chased by a male and female from group B. The chase took 1 hour and 40 minutes and was characterized by stopping and starting on the part of the group A male. The group B peccaries, following the scent, also would stop and wait. During the encounter, the female urinated and the male licked the spot. As the group A male entered his herd, he was approached and dominated by the alpha male. The group B peccaries immediately turned when they sighted the group A herd. They returned over the ridge to their herd. These observations indicate strongly that the Panther Canyon herd was splitting permanently into two territorial groups. During the breeding season in December 1973, group B did not join group A and there were 11 animals in group A when several breeding bouts were observed.

Territorial Group Hierarchy

Within a territorial group, peccaries exhibited a linear hierarchy. However, unlike pronghorn (Kitchen 1972, 1974), elk (McCullough 1969), kob (Buechner 1961) and many other group-living ungulates, peccaries have not evolved a male hierarchy distinct from a female hierarchy. Males vs. females dominance depended largely on size. This was probably due to the fact that peccaries lived in cohesive territorial groups the year around. There was always a dominant male in each group. Ranking beneath him, the hierarchical positions were occupied by male or female. Table 10 gives the rankings for individuals from the Lower Mouse Canyon herd. This herd was ear-tagged to facilitate the assignment of position. The four other groups were not tagged, but it was possible to distinguish the alpha male

TABLE 10. Male-female linear hierarchy for collared peccaries of the Lower Mouse Canyon herd.

Rank	Sex	Eartag#	M 15	M 29	F 18	F 28	M 22	M 30	M 19	F 21	F 26	F 24	F 14	M 12	F 3	F 27	F 1	F 20	F 23	F 4	F 13	M 2	UJ	Total wins
1	M	15	—	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	4
2	M	29		—	0	0	1	2	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	6
3	F	18			—	1	1	0	2	0	0	0	0	0	0	0	1	0	0	1	0	2	0	8
4	F	28				—	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	3
5	M	22					—	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	2
6	M	30						—	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2
7	M	19							—	0	0	0	0	0	0	0	1	1	0	0	0	0	0	2
8	F	21								—	2	0	0	0	0	3	0	0	1	0	0	0	0	6
9	F	26									—	1	0	0	0	0	0	0	3	0	0	0	0	4
10	F	24										—	1	0	1	0	2	3	0	0	2	1	0	10
11	F	14											—	2	1	1	0	1	0	0	1	0	1	7
12	M	12										1	1	—	0	0	0	0	0	0	1	0	0	3
13	F	3													—	2	0	0	0	1	0	0	1	4
14	F	27														—	1	0	1	0	0	0	0	2
15	F	1								1							—	0	0	0	0	0	1	2
16	F	20																—	0	0	0	0	0	0
17	F	23																	—	0	0	0	0	0
18	F	4																		—	0	0	0	0
19	F	13																			—	0	0	0
20	M	2																				—	0	0
21	?	UJ																					—	0
Total losses					2	1	3	2	2	1	3	2	2	3	3	6	8	5	6	3	5	4	4	

M = male; F = female; UJ = unidentified juvenile, sex undetermined.

and several naturally marked subordinate animals in each group. Observations from these unmarked herds corroborate the data from the marked group.

In the Lower Mouse Canyon herd, positions 1 and 2 were occupied by males (Table 10). Positions 3, 4, 8-11, and 13-19 were occupied by females. A juvenile male ranked 20th in the hierarchy. High female rank did not confer similar rank on her older offspring. For instance, marked juveniles #1 and #13 occupied positions 15 and 19 in the hierarchy although their mothers occupied positions 8 and 11, respectively. Similarly, UJ (untagged juvenile) and #20 ranked 21 and 16 in the dominance hierarchy, respectively, while their mother ranked in position 10. Female #18, ranking third, had a 2-month-old offspring with no apparent individual rank, while female #28, ranking fourth, had no offspring when marked in late 1973.

When young peccaries reached 2-3 months, they were not protected as closely by their mothers and were more often dominated by older, larger animals. Peccaries younger than 2 months remained close to the female and other peccaries seldom attempted to dominate them. If such incidences occurred, often due to the young pestering older animals, the mother usually defended her young. Very young peccaries, then, assumed the rank of their mothers, although they had not attained positions individually.

Breeding Behavior

Description

Groups of peccaries were stable during all months of the year. Although a territorial group generally segregated into feeding subgroups, they were composed of both sexes. Males did not form separate groups. During periods of reproductive activity, the subordinate males remained with the group although they were not allowed within 7 to 10m (23 to 33 ft) of an estrous female, nor were subordinate males allowed to bed with estrous females. The alpha male formed a tending bond during the period the female was in estrous and usually remained within 7 to 10m (23 to 33 ft) of her although distances varied with individual males.

On 25 April 1973, a subordinate male was chased out of a bedding area by the alpha male at 17:10 hours. The alpha male returned within 5 minutes and at 18:50, bred an estrous female. On 25 June 1973, a dark male was chased out of the Lower Mouse Canyon herd by another male of undetermined rank. The dark male returned within 20 minutes, after feeding away from the herd. No breeding activity was observed. On 25 January 1973, a female was courted by the alpha male of the Panther Canyon group. He bred her several times, and at 11:15 hours both animals bedded with five other females and juveniles. When two subordinate males approached the bedded group, the alpha male rose and stared. The subordinates detoured, walked off, and bedded in another group of three animals. The dominant male remained close to the female for the remainder of the day.

Breeding Success in Males

Variation in reproductive success is highest in polygynous peccary males. All reproductively mature females are bred. However, only the most

TABLE 11. Breeding success of males by hierarchical rank.

Rank	Successful intromission	Mounting only	No mounting	Total	% of total
Alpha	5	13	11	29	45.3
	(83.3)	(59.1)	(30.6)		
	((7.8))	((20.3))	((17.2))		
Subordinate	1	3	6	10	15.6
	(16.7)	(13.6)	(16.7)		
	((1.6))	((4.7))	((9.4))		
Unknown	0	6	19	25	39.1
		(27.3)	(52.7)		
		((9.4))	((29.6))		
Total	6	22	36	64	100.0
% of total	9.4	34.4	56.2	100.0	

Values in parentheses are percents of column tables, values in double parentheses are percents of grand total (i.e., $n = 64$).

dominant males were successful in copulating with females. Whether or not intromission was achieved was difficult to determine. Only if pelvic thrusts accompanied mounting did I consider intromission to have occurred. Six interactions (9.4%) were accompanied by intromission (Table 11). Five encounters involved the alpha male. Only one breeding with intromission involved a subordinate male. In 22 mountings I was unable to determine if intromission occurred. However, 13 of these involved the alpha male while subordinates accounted for only three mountings. I was unable to determine hierarchical position in six of these males. Thirty-six breeding interactions did not include mounting (Table 11).

Alpha males were observed to court females in 45.3% of all sexual interactions, while subordinates were involved in only 15.6% (Table 11). Hierarchical position was unknown in 39.1% of the observations. Nine interactions (13%, n=69) involved more than one male and one estrous female. In two cases, both males mounted the same female. In four of seven encounters (57%) when more than one estrous female was present in the herd, subordinate males were involved in sexual activity. Only once (14%, n=7) was the female mounted by a subordinate. Intromission did not occur.

Timing of Parturition

Peccaries are of South American origin (Woodburne 1968). They probably evolved in environments that were relatively predictable. It is reasonable to expect that breeding occurred during all months and was not restricted by harsh climate. Evidence of year-round breeding in seasonal environments suggests that ancestral habitats were less seasonal, more moderate, and hence more stable in terms of the vital resources needed for parturition and raising of young.

In the seasonal and relatively unpredictable environments of the southwest, peccaries bred in virtually all months of the year but showed strong seasonal peaks of farrowing (Neal 1959b; Low 1970; Schweinsburg 1969; Sowls 1974). Low (1970) suggested that this was due primarily to seasonal variation in rainfall. Jennings and Harris (1953) and Knipe (1957) also recognized a seasonal trend in the peaks of farrowing in Texas and Arizona peccaries.

By observing young in the field and estimating their age, I obtained results similar to those of Low (1970) for west Texas peccaries. Back-dating gave conception dates which correlated quite well with observed breeding activity (Fig. 17). Parturition in Big Bend peccaries related closely to periods of heaviest rainfall (Fig. 18). Sixty-four percent of all young were born during the first 3 months of the rainy season which lasted from May to October. Eighty-six percent of all young were born between May and October. The peak of farrowing occurred with the first rainfall (Fig. 18), and strongly suggests the importance of rainfall as a primary selection pressure in the timing of parturition. Its effect is expressed through variation in quality and quantity of vegetation. The close synchrony of

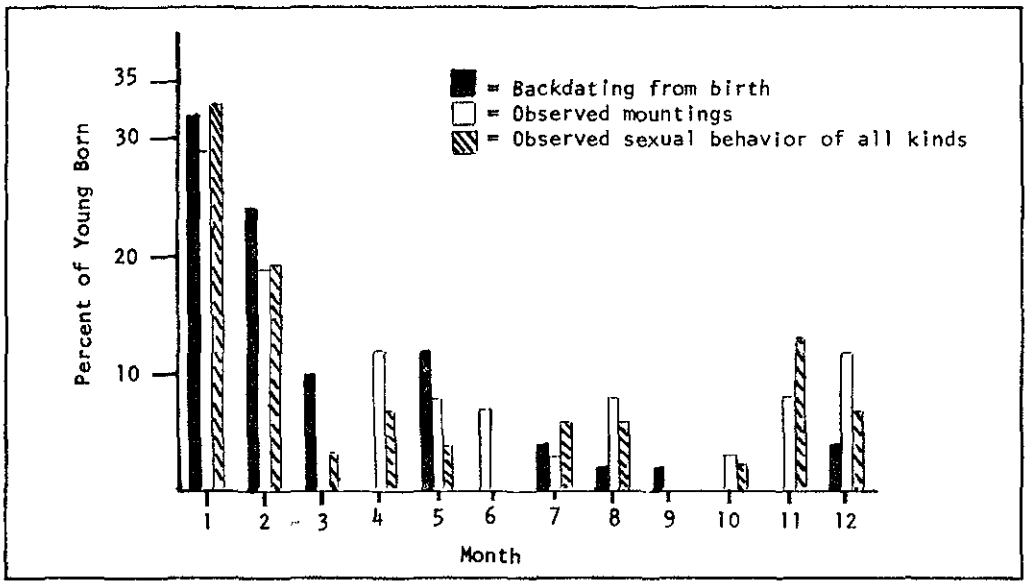

Fig. 17. Comparison of three methods of estimating the conception dates for the periods June-August, 1971 and June-May 1972-74.

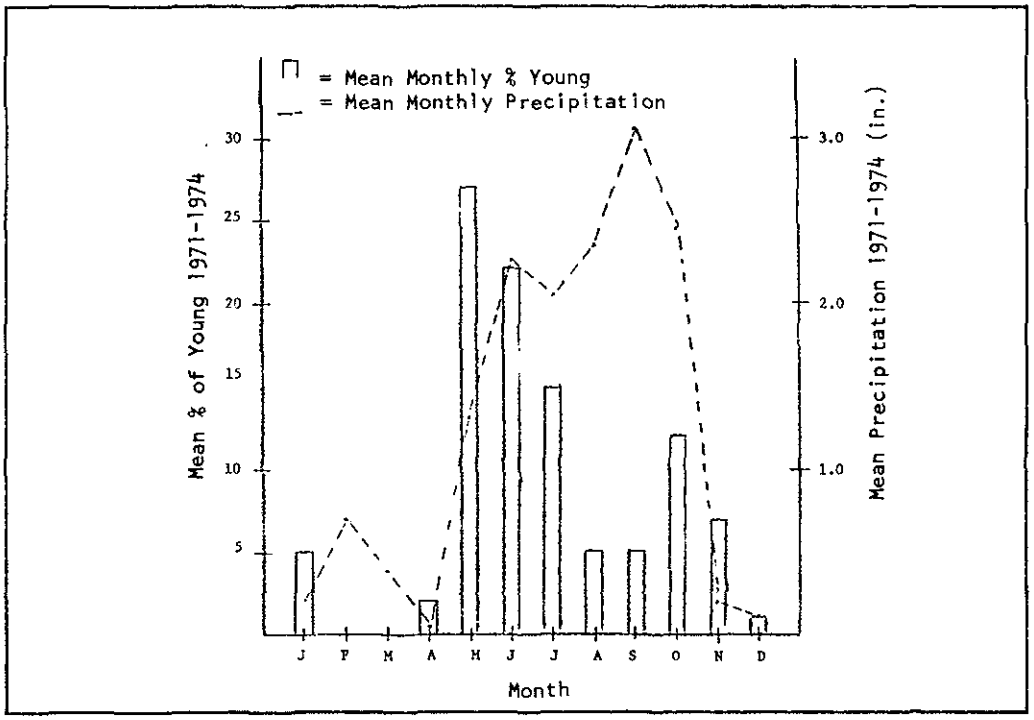

Fig. 18. Percent of young born per month relative to rainfall pattern. *Solid lines* are mean monthly percent young. *Broken line* is mean monthly precipitation.

birth and rainfall tends to support Low's (1970) hypothesis that reproduction of peccaries is associated closely with forage quality which, in arid lands, depends on rainfall. Flowering and fruiting are initiated by the onset of the rainy season, and highest protein levels in the forage are associated closely with the periods of fastest vegetative growth.

Population Dynamics

Birth Rate and Litter Size

Knipe (1957), Neal (1959b), Sowls (1966, 1974), and Smith and Sowls (1975) have reported a mean litter size of two young per adult female peccary. For Texas peccaries, Low (1970) reported a mean litter size of 1.8. It is probable that, in Big Bend, mature female peccaries on adequate diets conceived on the average at least two young per year. However, within a few days after parturition the mean litter size would be expected to decrease due to mortality. I have no record of any female producing more than one litter a year, or more than two young per litter, although this occasionally occurs, as reported by Smith and Sowls (1975) and Low (1970).

Observations during this study included a total of 82 young that ranged from less than 1 day to 8 weeks old when first seen. Of these, 62 (72%) were seen in pairs, were of a similar size, were following a single adult female, and hence were classified as twins. Twenty (24%) young were single piglets. It was not possible to determine how many of the single piglets were single births and not siblings because live births were not observed in the field. The mean number of young per adult female for all subgroups observed was 1.3 (n=47).

Mortality Rates

Mortality rates of 50% per year or greater occurred in every group studied (Table 12). For instance, during the summer of 1973 10 young were born in the West Hills herd. By 5 December five had died, a mortality rate of 50.0% for that year. No doubt mortality reduced the herd further by the time of parturition in 1974.

By 21 August 1972, 12 peccaries had been born that summer in the Lower Mouse Canyon herd, increasing the group to 31 animals including 17 adults and 2 juveniles. Before parturition one year later, 11 of these young peccaries had died, giving a mortality rate of 91.7% for 1972-73. During this time the herd increased by one animal, to a total of 21 peccaries. In 1973, nine young were born. By 1974, the entire group had not exceeded 22 animals entering the farrowing season in late April, indicating a mortality rate of 77.8% for 1973-74. At least 18 young-of-the-year animals had died between 21 August 1972 and April 1974. Recruitment rates were 8.3 and 22.2% for 1972-73 and 1973-74, respectively.

TABLE 12. Summary of the population dynamics for five peccary herds.

	Summer 1971		1971-74	Winter 1973-74		% mortality		
Range	No. adults	No. juveniles	No. young born	No. adults	No. juveniles	1971-72	1972-73	1973-74
PC	15	3	18	19	3	85.7	62.5	100.0
LMC	13	2	24	21	1	NA	91.7	77.8
WH	15	1	12	16	7	NA	NA	50.0
K-	11	1	2	9	3	NA	NA	NA
LM	4	3	5	6	1	NA	100.0	NA

PC = Panther Canyon; LMC = Lower Mouse Canyon; WH = West Hills; K- = KBar; LM = Lone Mountain; NA = not available.

In 1971, the Panther Canyon herd consisted of 18 peccaries. By 1974, the group had split permanently into two distinct territorial herds of 10 and 12 animals each. Prior to separating, the group had increased by only four animals in two breeding seasons, although seven and eight young had been born to the herd in 1971 and 1972, respectively. Before parturition in 1972, the herd had increased by one animal, indicating a mortality rate of young peccaries of 85.7%. Of eight young born in 1972, three were recruited into the herd by early 1973, increasing its number to 22 peccaries. The 1972-1973 mortality rate was 62.5%. At least two young were born in 1973, but no further permanent herd increases were noted by early 1974. Recruitment rates for this herd for 1971-72 and 1972-73 were 24.3 and 37.5%, respectively. There was no recruitment in 1973-74.

The Lone Mountain herd consisted of seven peccaries early in the summer of 1972. No permanent increases had occurred by March 1974, although some recruitment could have occurred as a result of yearling and adult mortality. However, the sex and age ratios remained similar, indicating this was not the case. At least four young were born in 1972 and one young was observed in the herd in 1973.

Similarly, the KBar herd did not increase in number during the study period although the age structure did change slightly (Table 12) indicating that mortality losses had been compensated for by recruitment of young for the period.

A comparison of mortality rates indicated relatively low recruitment in four of the five herds (Table 12). Recruitment rate is equal to 100% minus the mortality rate of young-of-the-year because no young or juvenile dispersal occurs in peccaries. The highest piglet mortality rates tended to occur in the poorest ranges with the smallest group size (KBar and Lone Mountain), although all ranges appeared to be fluctuating around the carrying capacity because mortality rates were generally high. The West Hills group, with a mortality rate of 50%, appeared to be growing the fastest. The data are insufficient to explain this phenomenon. Adult mortality was difficult to document in most cases and caused some

difficulty in interpretation. For instance, a population may be stable with no adult mortality and zero recruitment. Age ratios can provide a clue to what has happened but the existence of feeding subgroups and the variation within them further compound the difficulties in interpretation.

It is reasonable to assume that the mortality of young is dependent upon the relationship of herd size to forage quality both in time and space. Recruitment of young into the breeding population is low in dense populations where the ratio of high quality edible food items per individual is low. Conversely, where the ratio is high and there are more than adequate resources for growth, maintenance, and reproduction, survivorship is higher and the herd size increases as a function of successful recruitment. Poor nutritional condition predisposes animals, especially the young, to higher mortality by predation and other factors as the limits of support of the range are reached. There is no evidence of mortality due to starvation of peccaries in Big Ben.

All groups of peccaries studied in Big Bend were considered to be approaching the carrying capacity of their ranges because these populations had not been hunted since at least 1944. In Big Bend, 1970–73 were years of good rainfall and as a consequence the forage quality was higher than in previous years, increasing slightly the carrying capacity of the area. It was due to these factors that herds of peccaries appeared to be increasing slightly from 1971 to 1974. However, high mortality occurred in nearly every group. Predation on young animals was almost certainly underestimated since the hard as well as soft tissues are often consumed completely when young peccaries are eaten by predators. Additionally, it is probable that all adult mortalities were not recorded due to the nature of the habitat and the size of the ranges as well as the habits of the predators. For these reasons the mortality rates reported above are probably underestimations.

TABLE 13. Sex ratios of 11 herds of peccaries in Big Bend National Park.

Group	Male	Female	Unidentified
Lower Mouse Canyon	7	13	2
Panther Canyon	9	9	5
West Hills	7	9	11
KBar	4	3	3
Lone Mountain	3	4	5
Paint Gap	3	3	4
Rough Spring	3	3	7
Upper Rough Spring	2	3	3
Avery Canyon	3	3	?
North Flat	3	1	1
Estufa East	6	6	2
Total	50	57	
Ratio	87.7	100.0	

Sex Ratios

Sex ratios in 11 herds of collared peccaries in Big Bend were not significantly different from 1:1 (Table 13). The Lower Mouse Canyon herd showed the most unbalanced sex ratio, which resulted from exceptionally high mortality of males (Table 13). In 1972, the male:female ratio for this group was 8:9, in 1973, 7:10 and in 1974, 7:13.

5
Range Quality and Patterns of Utilization

To simplify assessments of use by peccaries, Big Bend vegetation was classed into four easily recognized and distinct habitat types: (1) deep wash; (2) open wash; (3) drainage; and (4) bajada. Deep washes were characterized by dense vegetation, with a good proportion of the larger woody species present: persimmon *(Diospyros texana), Acacia* sp., ash *(Fraxinus* sp.), buckeye *Ungnadia speciosa),* mesquite *(Prosopis* sp.), mescalbean *(Sophora secundiflora),* and others. There was shade in the deep washes throughout the day. Open washes were canyons and arroyos with a predominance of grasses and low shrubs. *Bouteloua* sp., *Aristida* sp., and *Muhlenbergia* sp. tended to be the predominant grasses, while *Parthenium incanum,* shrub acacias *(Acacia* sp.), Mimosa *(Mimosa* sp.), anisacanthus *(Anisacanthus* sp.), broomweed, snakeweed *(Xanthocephalum* sp.), Apacheplume *(Fallugia paradoxa),* and others were the predominant shrubs. Drainages were shallow ditches which funneled runoff and were characterized by denser vegetation of the woody variety than were the surrounding bajada, or open flatland. Bajada vegetation was variable and ranged from creosotebush *(Larrea divaricata)* flats to mixed shrub and succulents to mostly grassland. The following analyses were based on data taken at 10-minute intervals during observation.

Seasonal Preference for Habitat by Peccaries

The proportion of time active groups of peccaries spent in each habitat type over three phenological periods was varied (Fig. 19). During the winter breeding season from November to February, 69.5% of the active time was spent in the bajada, while only 12.1% was allocated to the deep wash. During the period from March to June, peccaries used the deep wash 37.6% and the bajada 40.6% of the time. Use of these two habitats contrasted markedly during the period from July to October. As ambient temperatures increased during the summer, peccaries spent 58.0% of their

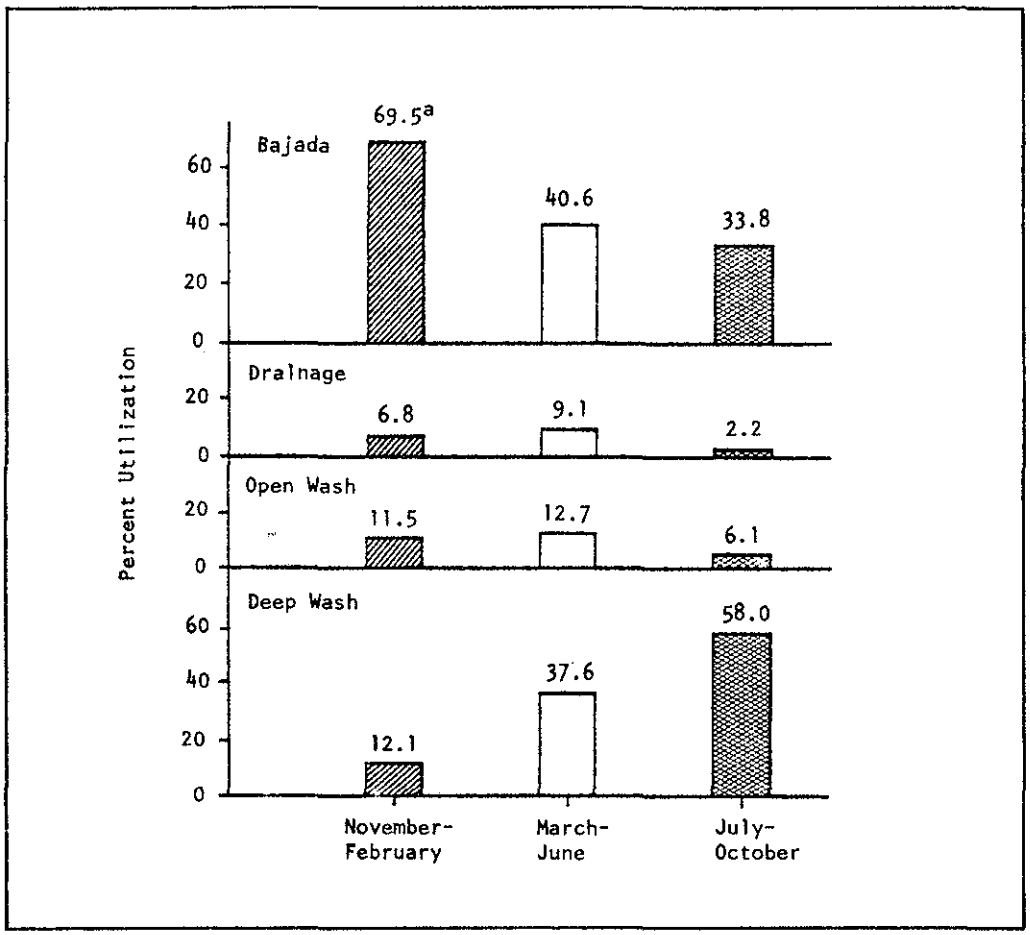

Fig. 19. Seasonal preference for habitat. *(a)* is percent of active time spent in the specific vegetation type during that season.

time foraging in denser, more shaded areas as compared to 33.8% in the bajada (Fig. 19). Relatively little time was spent in either the open wash or drainage at any time during the year although less time was spent in these areas during the summer. Chi-square comparisons between each season were significant at P=0.0005.

A comparison and analysis of habitat preference, by activity, for three phenological seasons (Table 14) indicated that: (1) peccaries partitioned their activities differently over four habitat types; and (2) this allocation was due largely to temperature. Each phenological season represented an increasingly warmer period of the year. The mean maximum temperature for winter (November-February) was 18.8°C (66°F) while spring-fall (March-April, September-October) equaled 26.2°C (79°F) and summer (May-August), 32.0°C (90°F). During winter, the coolest season, foraging occurred almost exclusively in the early morning, the late afternoon, and during the night when temperatures were much cooler. As expected, as daily temperatures increased, peccaries rested less frequently in the open wash and bajada. Increasing use was made of the deep wash and dense

TABLE 14. Habitat preference, by activity, for three seasonal periods.

Activity	Habitat				
	Drainage	Deep wash	Open wash	Bajada	n
Feeding					
Winter	7.1	8.3	5.1	79.4	350
Spring-fall	9.0	18.7	14.9	57.5	134
Summer	11.1	15.9	15.9	57.1	63
Feeding/walking					
Winter	2.5	9.9	12.2	75.3	393
Spring-fall	2.9	21.3	16.2	59.6	272
Summer	6.7	20.1	15.7	57.5	134
Walking					
Winter	8.1	6.5	6.5	79.0	62
Spring-fall	2.0	52.0	12.0	34.0	50
Summer	0.0	26.3	10.5	63.2	19
Standing					
Winter					
Spring-fall	0.0	100.0	0.0	0.0	2
Summer					
Resting					
Winter	2.7	25.8	20.3	51.1	93
Spring-fall	4.4	84.3	0.4	10.9	182
Summer	1.1	94.6	0.0	4.3	248
Resting/feeding					
Winter	15.7	12.2	14.2	57.9	254
Spring-fall	16.0	62.8	4.3	17.0	94
Summer	1.7	86.7	1.7	10.0	60

Each value is a percent of its row total.

vegetation. For example, the time spent resting in the deep wash versus all other areas for winter, spring-fall, and summer increased from 25.8% to 84.3% to 94.6%, respectively, indicating a high preference for shaded areas as ambient temperatures increased. All activities occurred less frequently on the bajada during spring-fall and summer than during winter, whereas all activities in the deep wash occurred less frequently during winter than during the spring-fall and summer periods.

Group Size Variation Over Time and Space

Territorial groups of peccaries were stable throughout the year but smaller subgroups did occur. Smaller subgroups occurred during the summer (Fig. 20) and they reassembled for longer periods during the breeding season. For instance, in Big Bend, from November to February, the mean subgroup size for five herds was 14.2 animals, whereas from

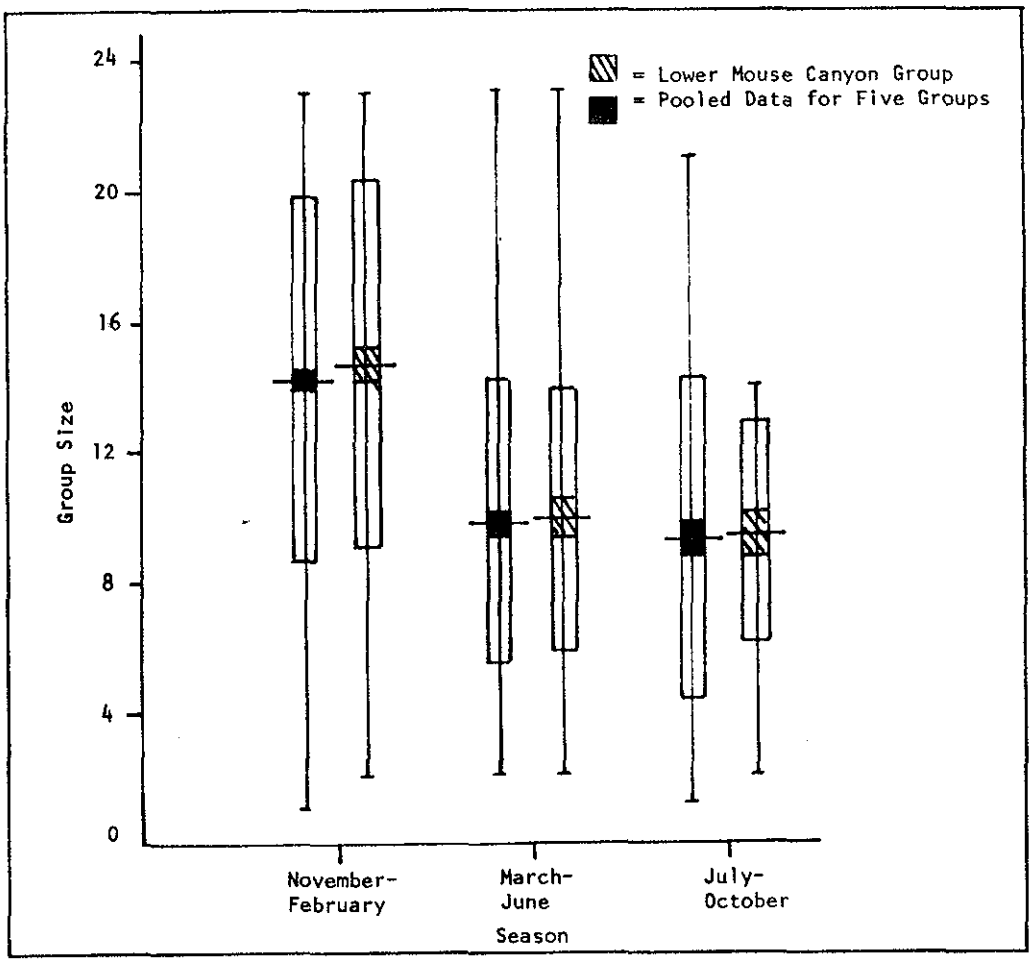

Fig. 20. Influence of season on subgroup size.

March to June and from July to October, mean subgroup size decreased to 9.8 and 9.3 animals, respectively. Data from the Lower Mouse Canyon herd which was studied intensively, corresponded closely to the pooled results (Fig. 20). Mean subgroup size for this group was 14.7 animals from November to February, whereas subgroup size averaged 9.9 for March-June and 9.4 for July-October. The relationship of subgroup size between phenological periods was identical for both the pooled data and the Lower Mouse Canyon herd although the values for the latter were somewhat higher.

Proportionately higher costs may be paid for group living during the summer when very little breeding occurs. At this time, the greatest benefit to individuals living in groups is decreased probability of being eaten. However, for animals living in groups larger than necessary to avoid predation, additional costs are entailed by increased competition, especially for food. There is a number beyond which the benefits gained by increasing the size of the subgroup, even by one animal, will be outweighed by increased costs of competition.

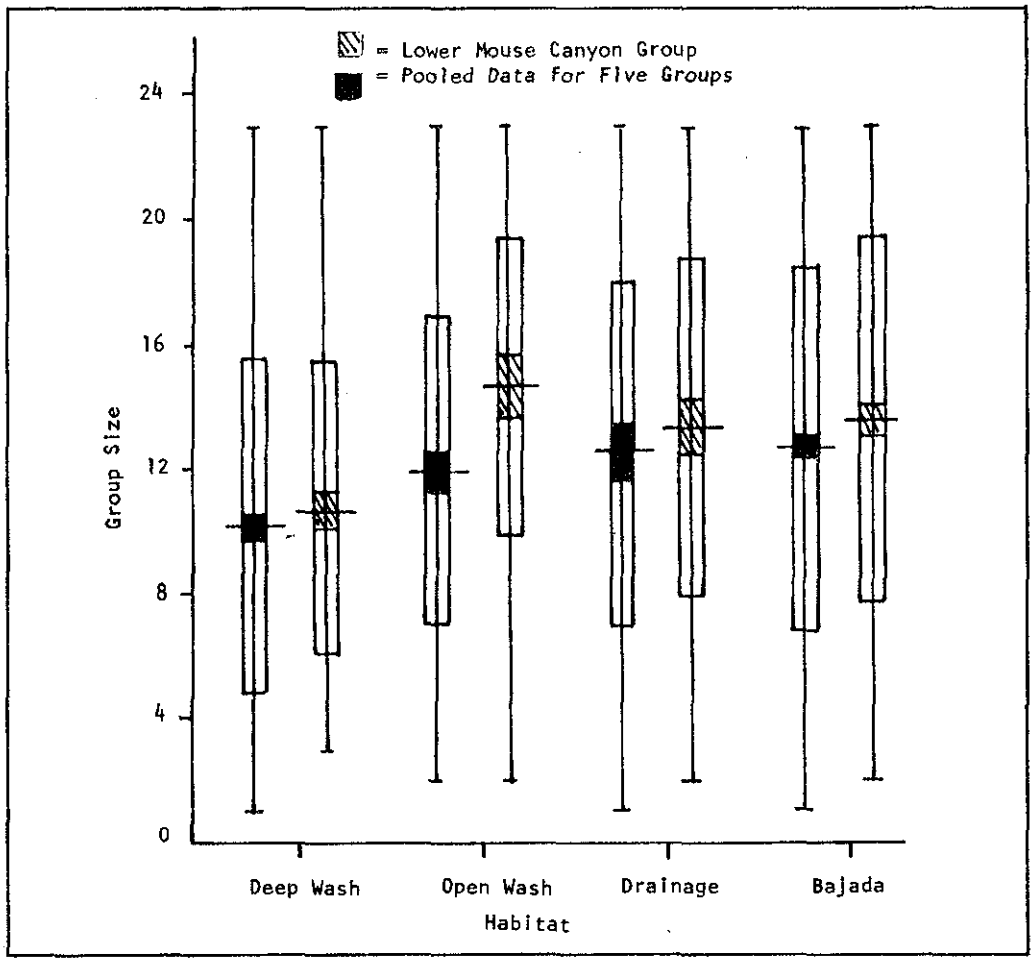

Fig. 21. Influence of habitat type on subgroup size.

Once a secure group size is achieved, proportionately fewer benefits accrue to the average individual by increasing the size of that subgroup, especially during periods of little or no breeding. During the winter breeding season, significantly larger groups form. Increased group size is a clear advantage to the dominant male at this time, because his chances of inseminating a larger number of females are increased. Presumably, if the alpha male is a superior genotype, there is also a benefit to females. If smaller subgroups persisted, some females would be bred by subordinate males of lesser fitness. Subordinate males would realize the greatest probability of reproductive success if small subgroups persisted but would have much less probability of breeding as larger groups formed. Subordinates are likely to breed only if more than one female is in estrous at any time.

When comparisons were made between subgroup size and habitat type, the following patterns became evident. Substantially smaller subgroups (10.3) were found in dense vegetation (Fig. 21), whereas larger subgroups (12.8) were found in the more open areas of the bajada. These

results represented pooled data for all five groups studied. The Lower Mouse Canyon herd (Fig. 21) showed similar trends with a mean of 10.8 for the deep wash and 13.6 for the bajada. Only the group size values for the open wash were different from the pooled data. This was due to the especially wide nature of these washes, coupled with the close proximity of one of the heavily used bedding sites for this group. When this bedding site was used during the summer, the group spent considerable time in the open wash in the early evening after leaving the beds.

Collared peccaries differed in their use of distinct habitat types over time. Habitat selection seemed to be due to two main factors: (1) temperature, and (2) patchiness of the resource base, in both time and space. Concurrent with temperature changes, differences in food quality and quantity influenced the use of the range by peccaries. During the winter season, peccaries relied heavily on lechuguilla and prickly pear. In late spring and early summer the first rains of the year made a profusion of preferred new growth of fruit and protein-rich forbs available. Concomitant changes in group size occurred with habitat preference and use. As peccaries selected different habitats over time, group size varied in response to predation pressures.

It is likely that predation alone may have accounted for most of the difference in subgroup size between habitats. Groups using more open bajada areas may have been subject to higher predation losses because the animals fled rather than mount an active defense by the group. Peccaries captured by predators in the open may have been less able to defend themselves adequately. Peccaries found in denser vegetation seldom ran far when alerted. They hid in the dense vegetation where they were perhaps better able to defend themselves with their canines as they backed into dense vegetation and thereby protected their sides and rear.

As predation acts to increase group size, intraspecific interference competition (Miller 1967) tends to promote smaller groups. The combination of these two main selection factors, coupled with habitat selection as a result of resource availability and preference, results in the formation of different subgroup sizes over time.

Range Quality

Of particular interest in this study was the relationship of group size and group-range size to resource quality and use (Table 15), and in particular, those vegetation classes most heavily used by peccaries.

Tramer (1969) suggested that the evenness (J′) with which species are distributed rather than species richness (H′pop) of community might be expected to vary most in rigorous environments (See Appendix for the calculation of J′ and H′pop). If this is correct, one might expect that differences in the sizes of groups of peccaries would be most highly correlated with the relative abundance of the preferred plant species on any

TABLE 15. Relation of group size and group-range size to number of species and percent relative abundance of four vegetation categories for five peccary ranges.

	Location of peccary group				
	Panther Canyon	West Hills	Lower Mouse Canyon	K-Bar	Lone Mountain
No. animals	22	23	22	12	7
Range size (ha)	201	217	245	210	208
Succulents					
No. species	9	10	14	9	7
% Relative abundance	16	14	24	31	17
Grasses					
No. species	13	16	12	8	11
% Relative abundance	33	37	36	21	34
Forbs					
No. species	55	44	44	27	32
% Relative abundance	18	19	7	7	8
Woody					
No. species	53	39	43	36	35
% Relative abundance	33	30	33	41	41
% Bare ground	36	35	38	44	50

TABLE 16. Components of average diversity for five peccary ranges.

Range	PC	WH	LMC	K-	LM
Group size	22	23	22	12	7
Range size (ha)	201	217	245	210	208
% vegetative cover	66	65	62	56	50
Range values (all vegetation)					
H′pop	4.91	4.63	4.83	4.25	4.80
J′	0.69	0.67	0.71	0.67	0.75
Stratum values (within a vegetation class)					
Succulents					
H′pop	0.70	0.64	0.87	0.86	0.77
J′	0.22	0.19	0.25	0.27	0.27
Grasses					
H′pop	1.34	1.30	1.35	0.76	1.44
J′	0.33	0.32	0.38	0.25	0.42
Forbs					
H′pop	1.07	1.02	0.59	0.51	0.57
J′	0.18	0.18	0.11	0.11	0.11
Woody					
H′pop	1.80	1.67	2.02	2.12	2.02
J′	0.31	0.31	0.37	0.41	0.39

H′pop = number of species weighted by relative abundance; J′ = evenness component; PC = Panther Canyon; WH = West Hills; LMC = Lower Mouse Canyon; K- = KBar; LM = Lone Mountain.

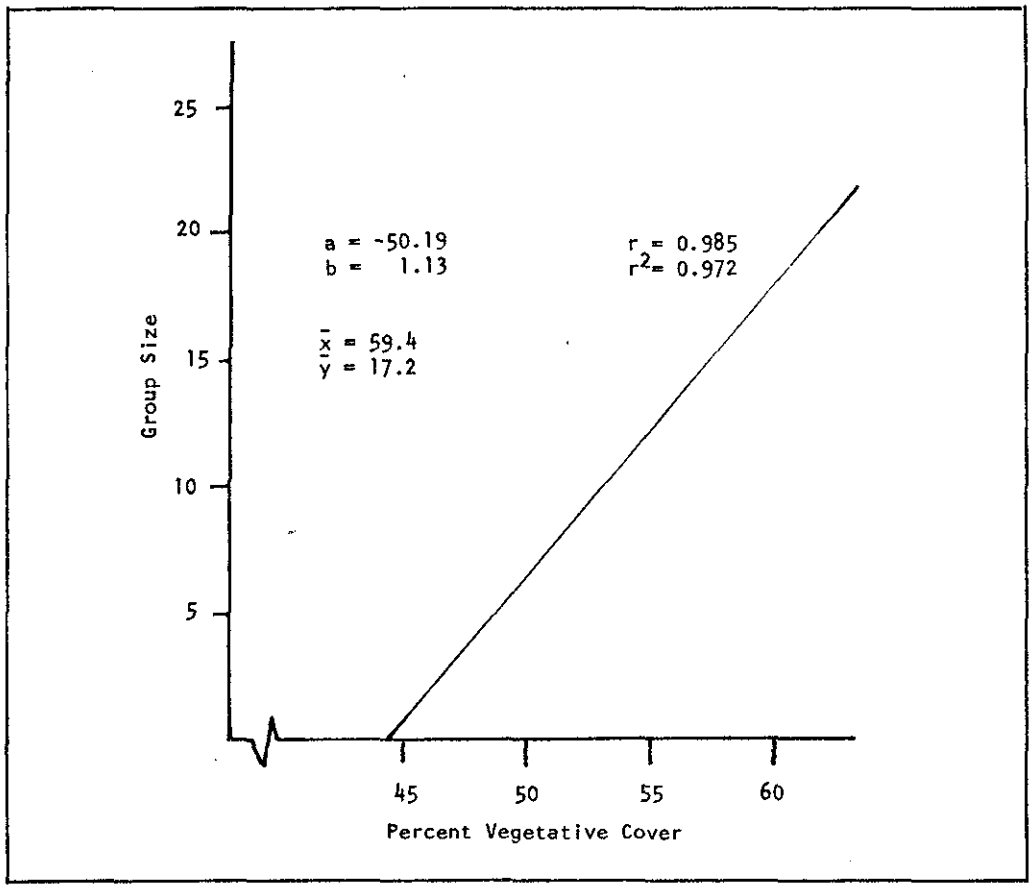

Fig. 22. Regression of peccary group size (number of animals per 10 ha.) on percent total vegetative cover.

range rather than by the total number of species. This seems probable when it is recognized that a low evenness component implies high variation in species abundance. On-the-ground observations confirm that certain species, especially prickly pear, lechuguilla, and some forbs, are very common and that utilization by peccaries is heavy. Mean diversity values, as well as the evenness component, were calculated for the five ranges sampled (Table 16). No significant trends were apparent, and correlations of group size on each class of H′pop and J′ values were not high. However, these diversity values were mean values and they probably mask food preferences. Peccaries eat prickly pear, lechuguilla, and actively select forbs but seldom take grasses and woody vegetation except for the fruits. Range carrying capacity of peccaries was most highly correlated with percent total vegetative cover (Fig. 22). The r^2 value was 0.980 for a sample size of 5, indicating an extremely close fit of the dependent variable to the least squares line of best fit. This means that 98% of the variation in group size at carrying capacity can be explained by measuring vegetative cover only. However, a significant regression against an independent variable, such as

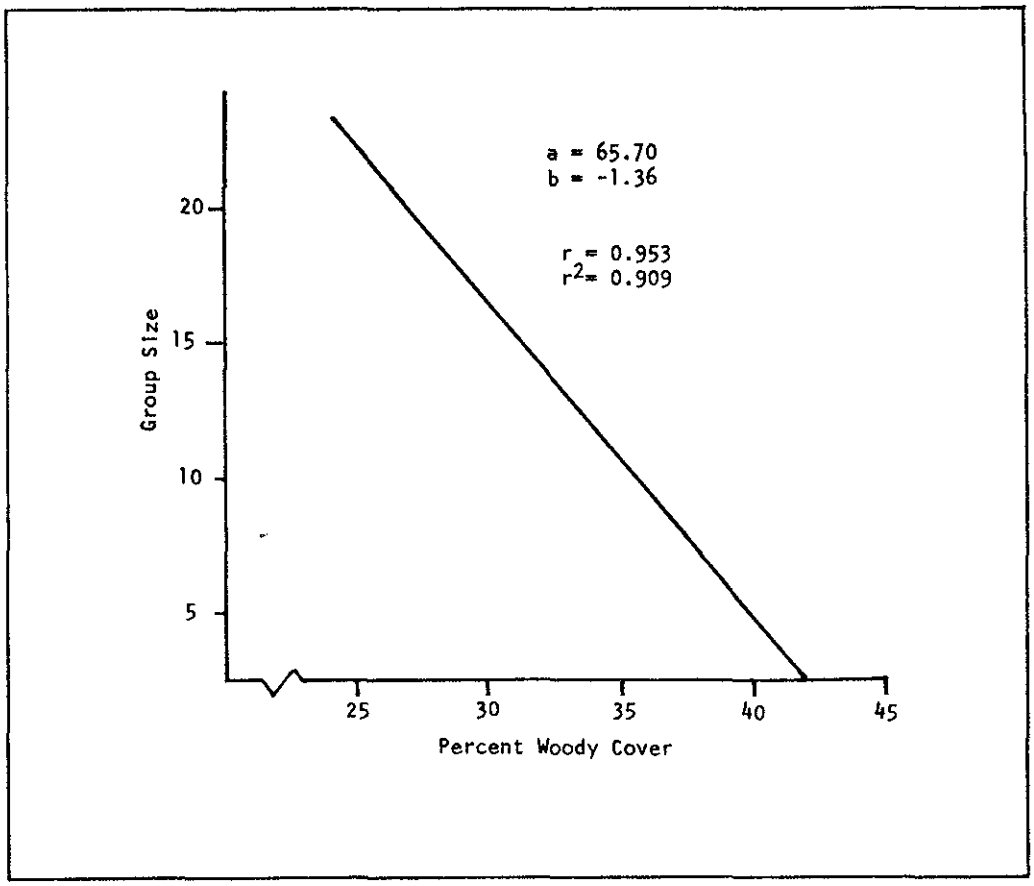

Fig. 23. Regression of peccary group size (number of animals per 10 ha.) on percent woody cover.

percent total cover, tends to obscure an understanding of much of the biology of the system because it implies either that all vegetation is equally important or that percent total cover is itself correlated to other aspects of the range which are important to peccaries. A strong negative correlation ($r = 0.930$, $r^2 = 0.965$) of percent total vegetation cover against percent woody cover indicated that as percent composition of woody vegetation increased, total vegetation cover decreased, most probably as a function of decreasing abundance of succulents, grasses, and forbs. A regression of peccary density against percent woody cover gave an $r^2 = 0.868$ with a negative slope of -1.36 (Fig. 23) and indicated that group size was inversely related to percent woody cover, especially creosotebush, and that peccaries were cueing in on edible, nonwoody vegetation.

Observations, as well as scat analyses (next section), demonstrated that peccaries have a preference for succulents and forbs. Regression analyses of peccary density against prickly pear, lechuguilla, and all forbs, summed as one dependent variable, gave an r^2 value of 0.946 (Fig. 24). This means that knowing the % composition of preferred forage species allows

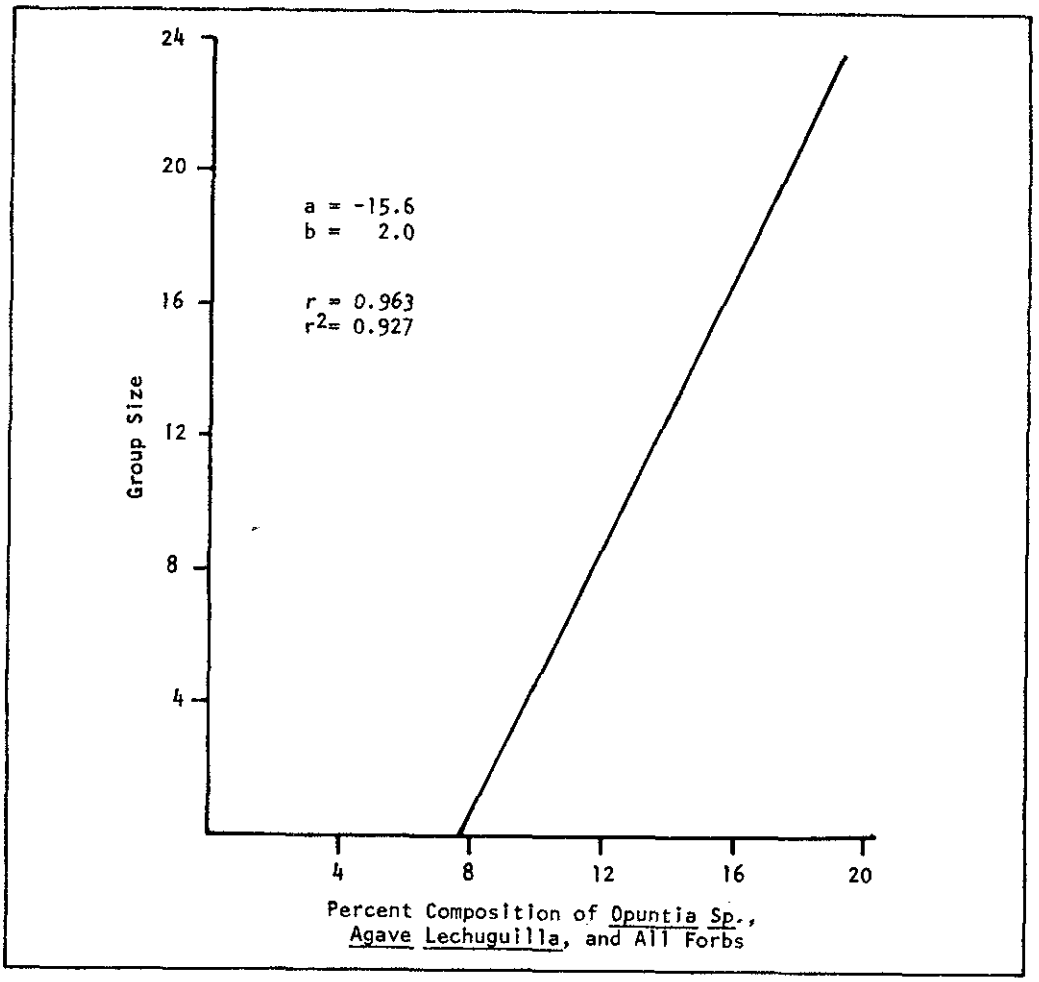

Fig. 24. Regression of peccary group size (number of animals per 10 ha.) on percent composition of *Opuntia* sp., *Agave lechuguilla,* and all forbs for five peccary groups.

one to predict the number of animals at carrying capacity a territory can support. None of the three components were sufficiently independently correlated with group size to obtain significant values in a stepwise multiple regression procedure. These regressions corroborated observations that group size in peccaries was a function of range quality, as defined by those species that comprised a major portion of their diet.

Stands dominated by creosotebush and tarbush *(Flourensia cernua)* are common at lower elevations in Big Bend and may inhibit growth of other plant species and in particular those preferred by peccaries. Group ranges with a high proportion of these two species had small group sizes (Lone Mountain, 7; KBar, 12 peccaries). In addition, these two ranges were characterized by lower elevation, less relief, and fewer washes in which to bed.

Availability and Utilization of Succulents

Lechuguilla was the most abundant succulent, varying from 4.8 to 10.6% composition (Table 17) between the five ranges sampled. Panther Canyon and West Hills, the highest of the five ranges in elevation, had 6.5 and 5.8% composition of lechuguilla, respectively. The Lower Mouse Canyon range, which was intermediate in elevation, had 10.6% while KBar had 9.9% lechuguilla.

Distribution of prickly pear between the five ranges was somewhat different from lechuguilla (Table 17). Percent cover values were substantially lower and ranged from 1.2 to 1.9%. Panther Canyon and West Hills had the lowest percent cover with 1.2 and 1.3, respectively. KBar had 1.4% cover of prickly pear, while Lower Mouse Canyon and Lone Mountain each had 1.9%. It is interesting to note that KBar and Lone Mountain had the highest relative abundance of nonpreferred woody species, as well as the greatest proportion of bare ground (Table 16).

TABLE 17. Availability of prickly pear, lechuguilla, and forbs on five peccary ranges.

	% cover			
	Prickly pear	Lechuguilla	Forbs	Total
Panther Canyon	1.2	6.5	10.6	18.3
West Hills	1.3	5.8	12.9	20.0
Lower Mouse Canyon	1.9	10.6	4.7	17.2
KBar	1.4	9.9	3.4	14.7
Lone Mountain	1.9	4.8	4.5	11.2

Use

Use of available lechuguilla for the Lower Mouse Canyon group was 2.6%. The other ranges were not sampled. Prickly pear utilization varied from 1.7 to 5.4% over the five ranges (Table 18). No patterns are evident relative to group size, range size, or range elevation. However, browsing pressure was similar over the ranges. A majority of the marked prickly pear in every range were either not browsed or browsed very lightly (Table 18). In every range less than 4% of the marked plants were heavily or very heavily browsed.

Peccaries were selective in their use of prickly pear and medium to heavy browsing was concentrated on relatively few plants. This could imply a high variation in the quality of individual cladophylls. Future analyses may show high variability in the chemical composition of components of individual cladophylls and between individual plants.

Preference for Plant Part: Peccaries exhibited a preference for the tender inner core leaves and root as well as for the most basal portions of the outer leaves of lechuguilla. In a subjectively selected, heavily browsed area, 24.4% of all lechuguilla plants were browsed. The core leaves were

TABLE 18. Comparison of use of *Opuntia* sp. by five peccary groups.

		Number of marked plants in each browse category					
Location	% use	None	Light	Medium	Heavy	Very Heavy	Total
Panther Canyon	1.7	9 (32.1)	11 (39.3)	7 (25.0)	1 (3.6)	0 (0.0)	28
West Hills	5.4	6 (23.1)	15 (57.7)	4 (15.4)	1 (3.8)	0 (0.0)	26
Lower Mouse Canyon	4.5	44 (45.3)	36 (37.1)	13 (13.4)	2 (2.1)	2 (2.1)	97
KBar	1.8	47 (47.5)	37 (37.4)	10 (10.1)	3 (3.0)	2 (2.0)	99
Lone Mountain	4.5	44 (47.3)	25 (26.9)	18 (19.4)	3 (3.2)	3 (3.2)	93

Values in parentheses are percent of plants in each browse category for each range.

TABLE 19. Preference of peccaries for plant part and position of leaf of lechuguilla.

Chlorophyll pattern	Leaf position	Part eaten	No. of leaves	% of total
Upper parts green, middle and basal portion white	core	entire plant except spine	166	33.7
Upper parts green, middle; white to light green, and basal portion white	intermediate	basal and middle parts	105	20.5
Upper and middle parts green, basal portion white	lateral	basal	97	19.7
		or not eaten	129	26.1
Total			493	100.0

removed and the root eaten in 5.6% of these plants, while in 18.9% only the core leaves were removed. Of 493 lechuguilla leaves scattered on the ground in the sample area, 20.5% had the basal and middle part of the leaf eaten, while in 19.7% only the basal portion was chewed (Table 19). Twenty-six percent of the leaves were not eaten. Core leaves made up 33.7% of the total. They were heavily browsed.

Peccaries preferred the tender, chlorophyll-absent parts of lechuguilla. Center core and roots were browsed more heavily and in some instances outer leaves were removed to get at the preferred parts. Often the basal-most parts of the outer leaves were eaten. Peccaries chose the light green and white parts of the plant and seldom ate the dark green parts which may have contained high concentrations of secondary compounds.

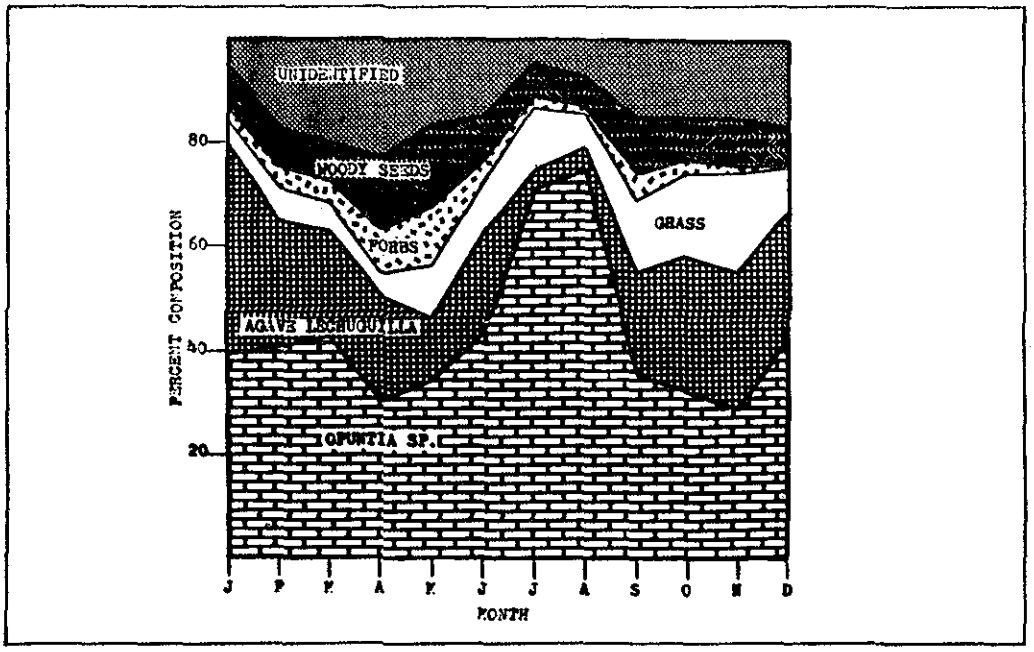

Fig. 25. Percent composition of the major food items of peccaries in 201 scats.

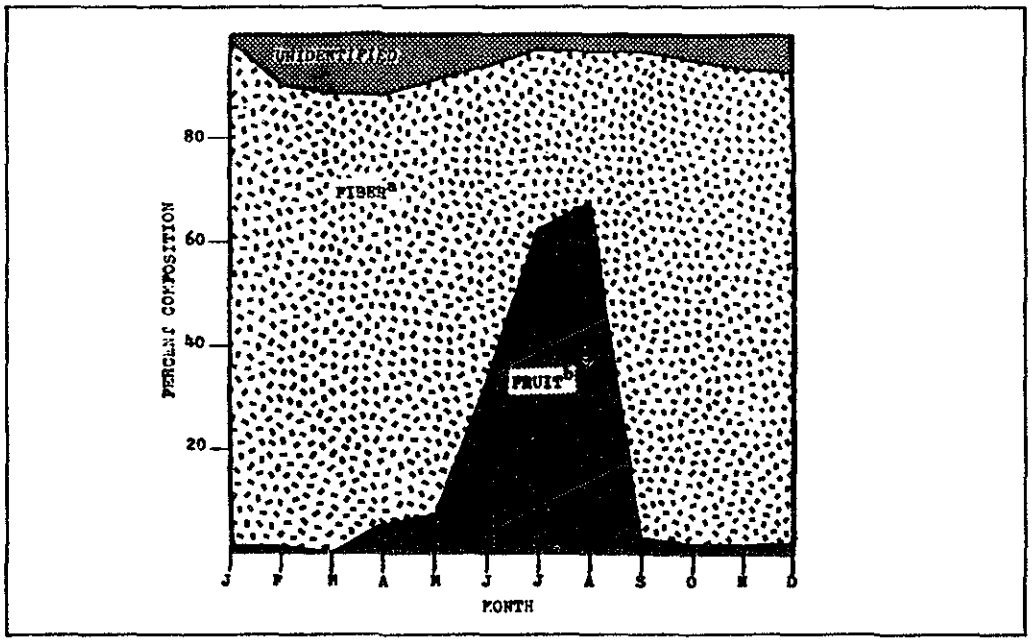

Fig. 26. Percent composition of the major plant components in 201 peccary scats: *(a)* includes root, stem, leaf, dermis, fiber, glochid, and spine; *(b)* includes fruit, seeds, seed pods, and flowers.

Food Habits: Scats were collected weekly and analyzed for percent composition of components and frequency of occurrence. Peccaries ate prickly pear throughout the year and percent composition ranged from 29 to 45% from September to June to a high of 71 to 75% in July and August

(Fig. 25). Correspondingly, lechuguilla ranged from approximately 11 to 41% of the diet from September to June to a low of 3 to 5% in July and August. Increased preference for forbs and woody seeds in April and May was accompanied by a decrease in the use of lechuguilla and prickly pear. After forbs and woody seeds had decreased in abundance and in the diet, lechuguilla was eaten more often in June as was prickly pear, whose fruits were ripening in increasing numbers.

During July and August, prickly pear fruit was selected over other plant parts (Fig. 26). Forbs and woody seeds decreased in quality and quantity during this period. For example, forbs decreased from about 12% in May to 4% in June (Fig. 25) and remained low for the rest of the year. In September, when most prickly pear fruit had decreased dramatically in abundance, lechuguilla leaves were eaten with increasing frequency. Fallen woody seeds were in abundance and were eaten somewhat more frequently than in August (Fig. 25).

Prickly pear occurred in every sample whereas lechuguilla occurred in 95.5% of all scats. Only nine scats did not contain lechuguilla and of these eight were collected in July and August, the months of very heavy prickly pear fruit use. The other scat was collected in May when prickly pear fruits were first used heavily (Fig. 26).

Scat analyses corroborated observations that peccaries ate prickly pear cladophylls and lechuguilla leaves and roots throughout the year but selected fruits, seed pods, and forbs as they became available. Although prickly pear cladophylls always comprised a large proportion of peccary diets, their use declined when the carbohydrate-rich fruits were available.

6
Discussion

The Evolution of Group Living in Peccaries

Alexander (1971) has suggested that predation, facilitated food gathering, and limiting resources may explain the evolution of group living in animals. He further suggested that in some animals group living may have been the result of more than one of these selective factors. Most probably, predation alone accounts for territorial group formation by peccaries although other factors influence group size. This study showed that in Big Bend preferred resources (prickly pear, lechuguilla, forbs) are abundant, not highly clumped, and are eaten easily by individual peccaries. Although summer bedding sites are restricted to dense vegetation in washes and may be somewhat scarce in poorer ranges, their size usually is adequate to accommodate many more individuals than are ever observed in a single herd. Regardless of the size of the herd relative to the size of the bedding area, resting peccaries seldom bedded together as one group, but rather bedded as subgroups of varying size and composition. It is unlikely, therefore, that facilitated food gathering or limiting resources (i.e., bedding sites) are important in group formation and maintenance by peccaries.

In Big Bend the natural complement of predators exists, with the exception of wolves, which were extirpated in the early part of the century. It appears, therefore, that predation as a selective factor is still operating on herds of peccaries in Big Bend. Indeed, Krausman (1976) found that lion scats from Big Bend averaged 13% adult peccary remains by volume, and coyote and bobcat scats averaged 7 and 1%, respectively, of primarily young peccaries. In much of the remaining range in the United States, however, predators have been reduced in number and in some areas, extirpated. Texas, New Mexico, and Arizona have hunting seasons on peccaries and the major cause of mortality in these areas is man.

Group living is possible only if the resources are sufficiently abundant and can be effectively used by groups large enough to withstand predation (McNab 1963). Thus, if grouping in response to predators is achieved at the

expense of efficient use of the resource, removal of predation should result in rather rapid loss of group cohesion over time. Such does not seem to be the case.

The selection pressures most likely to have a negative effect on group size and cohesiveness would seem to stem from the composition, structure, and spatial distribution of the resource base. This should affect both males and females since living socially entails a cost regardless of sex. However, the subsequent effects on the sexes would be different and sexual competition for mates would be modified. Females are bred as they come into estrous and show much less variation in reproductive success than males. Therefore, male cohesiveness should have little effect on whether females live singly or in groups. In contrast, the costs of group living for subordinate males, especially reduced breeding success, would become greater as the benefits of group living decreased. As females began to fragment from the group, the probability of copulation for subordinate males remaining in the group would decrease until solitary living became a better strategy for males.

It is assumed that predation is not such a pervasive force in group formation and maintenance in peccaries as to mask the role of resource availability and distribution in the regulation of group size.

Feeding Subgroup Variation in Time and Space

Although territorial groups are stable, the size of subgroups of peccaries varies in time and space. This study suggests that these changes are the result of two principal factors: intraspecific competition and vegetative cover. Subgroups are smaller during the spring and summer when little breeding occurs. Competition for food may explain why larger groups break apart during this time. In addition to reproductive costs for male subordinates, there are energy costs for all members of the group. Individuals of larger groups have a statistically greater probability of interacting and thus a larger energy cost than do members of smaller groups. Additionally, the mean amount of locally available, high quality, preferred forage on any range decreases as the mean subgroup size increases. Selection should favor the formation of groups just large enough to allow individuals to gain the statistical advantage of increased numbers against predation. Since subgroup sizes during the summer are significantly smaller than during the winter, I assume that these smaller groups are relatively secure from predation. If they were not, larger groups would prevail. Predation pressures, as evidenced by analyses of predator scats (Krausman 1976), appear to be relatively constant through the year.

The existence of larger groups during the winter can be accounted for by vegetative cover preference. During this period, feeding subgroups are fewer in number. At the peak of the breeding season, virtually no fragmentation occurs. However, during the summer, peccaries are forced

by high ambient temperatures to occupy predominantly dense vegetation. As a result, group sizes are significantly smaller. As temperatures decrease in the fall and winter, peccaries spend most of their active and bedded time in more open areas. In addition, during the late fall and winter, fruits, forbs, and seeds of woody plants are no longer available and, as a consequence, peccaries seldom forage through dense, woody vegetation during this time. Groups increase in size significantly when foraging over bajada vegetation (see below for explanation). I suggest that habitat preference is largely responsible for the increase of subgroup size to territorial size during the breeding season. The benefits to alpha males and detriments to subordinates are fortuitous.

Subordinate males should behave so as to fragment the group but appear to have limited success in doing so. Thus the advantage in group living for subordinate male peccaries would be realized only if two or more females were in estrous synchronously. Since only a short tending bond is formed between male and female during estrous, the probabilities of a subordinate male breeding are increased. However, in actual observations, this occurred only once, suggesting that for subordinate males to be successful, the peak of estrous, i.e., ovulation, must be synchronous. I have recorded that the alpha male of the West Hills group followed an estrous female for at least 2 days but abruptly ceased tending her as a second female came into estrous. The first female had been bred several times by the alpha male. As subordinate males began tending the second female, the alpha male assumed dominance over them and tended her. Therefore, it appears that subordinate success is a function of synchronous ovulation by females. Although other factors may operate, competition and habitat preference should be sufficient to explain the largest part of the variation in subgroup size over time.

It appears that predation largely accounts for subgroup variation in space. Defense is more difficult in open areas because no group defense seems to occur. Defense from lion attacks would tend to be more successful in dense vegetation where at least marginal cover is available for retreat. By backing against thick vegetation, a peccary could restrict the predator to a frontal attack, and by doing so increase its probability of survival. The canines of peccaries are formidable weapons.

Peccaries are myopic and visual cues seem unimportant in predator detection. Because of this, predation from heavy cover probably carries little advantage to the predator. It is possible that the actual killing of the prey may be more difficult in dense vegetation than in open areas for the reasons mentioned above.

Determinants of Territorial Group Size

Regardless of the variation of subgroup size over time and space, territorial group size is determined by the quantity and quality of preferred

forage species. Caraco and Wolf (1975) have suggested that group size in any social species may be predicted by hierarchically ranking the most important ecological parameters. Since different group sizes of peccaries exhibit similar territorial range sizes in Big Bend, group size must be a function of resource quality as defined by preferred forage species, because other resources, such as bedding sites, etc., are not limiting. Regressions of group size against percent total vegetative cover and against percent composition of prickly pear, lechuguilla, and forbs gave very high r^2 values. The regressions indicate that population size in peccaries is food limited. The variability in total rainfall in Big Bend and its seasonal aspect directly affect primary production, especially of annual forbs. Although annual and perennial forbs comprised only a relatively small proportion of the total vegetation on any range, they were used heavily when available. The highest primary production of forbs occurred with the onset of spring and early summer rains and coincided with the farrowing peak in peccaries. The high protein content of forbs, and their palatability when growing, made them an ideal resource for lactating females. The health of suckling young and their subsequent survival is related to the diet of the female during pregnancy and lactation and almost certainly to the condition of the female in the fall of the previous year (Low 1970) since fat reserves allow an animal to more easily survive periods of low food quality. Forbs are not widely available and abundant in early spring and summer and certainly are most heavily used during parturition and lactation of peccaries. However, survival and recruitment of young also is related to carrying capacity. For herds at carrying capacity, almost no recruitment occurs, and that which does usually balances the mortality of older animals during that year. However, in herds reduced below carrying capacity by hunting or by unusual circumstances, successful recruitment of young animals may be dependent upon the primary production of protein-rich annual and perennial forbs, as well as prickly pear fruit and late summer seed crops.

Appendix

Calculation equations for the Shannon diversity index.

Mean diversity ($\hat{H}'pop$) was calculated as:

$$\hat{H}'pop = -\sum_{i=1}^{s} \hat{p}i \log_2 \hat{p}i \qquad (1)$$

where pi is the proportion of the ith species in the sample.

The maximum diversity possible for the collection on any range is given by the equation:

$$\hat{H}'max = -\Sigma\ 1/s \log_2 1/s = \log_2 s \qquad (2)$$

where s is the number of species in the collection.

The evenness component ($\hat{J}'$) is given by:

$$\hat{J}' = \hat{H}'pop/\hat{H}'max = \hat{H}'pop/\log_2 s \qquad (3)$$

Measures of mean diversity (H'pop) and the evenness (J') with which those species are distributed are unit free and allow a direct comparison between different vegetation types.

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