

PROXIMAL CAUSES OF DISPERSAL IN YELLOW-BELLIED MARMOTS.

by

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ABSTRACT

The relative importance of adult-yearling interaction, and individual behavioral phenotypes, on dispersal of yearling yellow-bellied marmots was investigated. Two marmot colonies near Gothic, Colorado were studied; one was treated as an experimental colony from which all adults were removed, the second as a control was left undisturbed. Analysis of dispersal patterns and behavioral observations indicated that agonistic behavior between adults and yearlings is not necessary for dispersal to occur. Dispersal of male yearlings appears to be independent of adult-yearling interactions, although dispersal of female yearlings probably is mediated by social interactions. Individual behavioral phenotypes could not be used to predict which animals dispersed, nor the relative timing of their departure. Dispersal can be viewed as an important mating strategy; for yearling males it is likely to be the only

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Introduction

Dispersal of a particular age-class occurs in most social ground-dwelling sciurids (Armitage, 1974; Downhower and Armitage, 1981; Garrett et al., 1982; Mclean, 1982; Pfeifer, 1982; Svendsen, 1974), but the proximate cause or mechanism that determines which individuals disperse remains unclear.

Yellow-bellied marmots (Marmota flaviventris) live in social groups comprised of one or more matriline with an associating territorial male (Armitage, 1984). Yearlings, animals one year old, may be present; juveniles emerge in mid to late July and remain in the colony throughout their first summer. Virtually all male yearlings and approximately sixty percent of female yearlings disperse. The timing of departure varies; 57% of males, and 30% of females disperse by mid-July, while 81% of males, and 61% of females, disperse by the first week of August (Downhower and Armitage, 1981).

Behavioral interactions among individuals were cited as a cause of dispersal in a variety of small mammals (see Gaines and McClenaghan, 1980 for review). Agonistic interactions between adults and young, or between dominant and subordinate individuals, may cause dispersal (Armitage, 1974; Carl, 1971; Downhower and Armitage, 1981; Fairbairn, 1978). However, such a relationship has not been supported by other studies (Armitage, 1973; Pfeifer,

1982). The ontogeny of social interactions, rather than aggression just prior to dispersal, may predict which animals leave the natal group and the relative timing of their departure (Bekoff, 1977). Individuals that are asocial do not initiate interactions, or avoid interactions, with other colony members and will disperse first, whereas those who interact more will most likely delay dispersal (Bekoff, 1977).

The timing of dispersal in yearling yellow-bellied marmots indirectly supports the predictions made by Bekoff's social cohesion hypothesis outlined above. High levels of amicable behavior between adults and yearlings were associated with a delay in dispersal. Male dispersal was not related to levels of aggression; however, agonism was associated with earlier dispersal of females (Downhower and Armitage, 1981).

The purpose of this study was to test whether absence of adults would delay or prevent dispersal by yearlings, and to relate individual behavioral phenotypes to the timing of dispersal. Higher than expected rates of agonistic interactions occur between adults and yearlings (Downhower and Armitage, 1981). If the hypothesis that dispersal is proximally mediated by agonistic interactions between adults and yearlings is correct, the removal of adults should significantly delay or prevent dispersal. In addition, if dispersal did occur, removal of adults (and consequent removal of adult-yearling interactions)

allows examination of the relationship between the behavior of individual yearlings and the timing of dispersal.

Materials and Methods

Marmots were studied from 15 June through 15 August in 1982, and 17 June through 12 August in 1983. Data were collected from two localities during 1982; North Picnic Colony was the experimental colony and Picnic Colony was the control. In 1983, only data from North Picnic were gathered. The characteristics of the two localities are described elsewhere (Armitage, 1974). The colonies are located approximately 3.4 and 3.8 kilometers north-west of the Rocky Mountain Biological Laboratory, Gothic, Colorado.

Each year, all animals were trapped. Upon capture, animals were transferred to a handling bag, weighed, sexed, permanently tagged with fingerling ear tags (if not done previously), and given distinct marks using Nyazol fur dye to facilitate subsequent recognition during field observations. Age was determined from previous years' trapping data, and weight (Armitage et al. 1976); extent of nipple development indicated if a female was pregnant and minimal age could be estimated accordingly.

During 1982, all adult animals at North Picnic colony were removed at first capture; when immigrants appeared in

the study site, trapping was resumed until they were caught and removed.

Marmots were observed between 06:45 and 11:00 h (MDT) each morning except in inclement weather. In 1982 and 1983, observations were conducted at North Picnic colony from 17 June through 15 August, and from 19 June through 8 August respectively. Picnic colony was observed intensively only from 14 June through 15 July in 1982. Later observations at Picnic colony were sufficient to determine presence or absence of particular individuals, but not extensive enough to include in the analysis of behavior among colony members. Observations totaled 130 hours at North Picnic and 85 hours at Picnic in 1982, and 100 hours at North Picnic in 1983.

Each colony was scanned continuously with a field model telescope or binoculars; the location of each individual was determined with a clear, numbered grid overlying a photograph of the area. Animals' positions were recorded at 10-minute intervals. All behavioral interactions were noted with a detailed description of the interaction including the location, identity of initiator and recipient, and the duration of the interaction. Interactions were later classified as cohesive or agonistic and grouped accordingly. Greeting, allogrooming, and play were classified as cohesive behaviors; avoidance, chase and flight as agonistic.

For analysis, the period of study was divided into 1-week periods and all calculations made per week. Each 10-minute interval of observation was treated as a separate survey. Individuals rarely were observed during each 10-minute survey throughout a particular morning. Therefore, in order to estimate the amount of time an animal spends in social activity in relation to other activities, the availability of the animal for interaction was incorporated into the calculations (methods in Michener, 1980).

The average frequency of observation for each animal was calculated by summing the number of surveys in which the individual was seen and dividing by the total number of surveys for that week. Interaction rates were similarly calculated; the total number of interactions observed over a one week period for each animal was divided by the number of surveys in which the animal was observed (Table 1). The interaction rates at Picnic colony include only those interactions involving yearlings as one or both participants. Adult-adult interactions were not germane to the study and were excluded.

Independence among the frequency of interactions, the frequency of observations, and weekly number of surveys, were tested by correlation and regression analyses after establishing that the data were normally distributed.

The average proportion of time spent interacting over the study season was calculated by dividing the total

number of interactions per individual over the summer by the total number of surveys in which the animal was observed. The interactions were then separated into amicable and agonistic, and an average proportion of time spent interacting that was agonistic was calculated for each animal. The data were compared using Fischer's exact probability test (Siegel, 1956) to determine if the proportion of time spent interacting, or spent interacting agonistically, differed between the two colonies or between years.

The date of dispersal was considered to be the last day on which an individual was observed. The total number of dispersers and number of female dispersers were compared between the two colonies by a Chi-square analysis. The number of male dispersers was not compared because there was only one male yearling at Picnic colony. To test the relationship between agonistic behavior and dispersal, the dates of dispersal and the average proportion of time spent interacting agonistically were compared by Kendall's rank correlation.

Rates of social behavior and the amount of aggression among marmots are related to the animals' use of space (Armitage, 1977; Frase, 1982). Surface II, a computer graphics program (Sampson, 1975), was used to plot the census data for each animal. The result is a 3-dimensional block diagram in which peak height represents

frequency of observation for each grid-square. The diagrams provide a visual representation of the use of space by each individual.

Results

Yearling disappearance, dispersal, and recruitment

Ten yearlings, 6 female and 4 male, were resident at North Picnic colony at the onset of the study in 1982. Two resident adult females were removed before observations began. Following removal of the adult females, two 3-year old females, who were born at North Picnic but had dispersed as yearlings, returned to the colony. Six adult males immigrated to the colony one at a time. Three of the males were 2-year olds that were tagged as young from three different colonies; none was born at North Picnic. All immigrants were captured and removed within three days of first sighting, except an animal (not one of the above) that arrived late in the season and could not be caught. All six female and one male yearling remained at North Picnic at the end of the season in 1982. Three male yearlings dispersed; one was last seen on 10 July, the second on 20 July, and the third on 22 July. The male that had not dispersed by mid-August in 1982 dispersed after the study had ended, or before it began in 1983, since he was the territorial male at Picnic colony in 1983. The six females were present as 2-year olds in June 1983; two of them subsequently disappeared.

An immigrant female was present and remained in the colony throughout the 1983 season. The resident male was a 3-year old that was caught and removed early in 1982; he probably was the immigrant that appeared late in 1982.

Five yearlings, 4 female and 1 male, were resident at Picnic colony in June of 1982. Picnic colony usually supports 2 harems, Upper and Lower (Armitage, 1974). In 1982, five adult females, 1 adult male, and 4 yearlings (3 females and 1 male) resided at Upper Picnic; three adult females, 1 adult male, and one yearling female resided at Lower Picnic. All four yearlings from Upper Picnic dispersed; the yearling female at Lower Picnic was present when the study ended in 1982 but was not present in 1983.

The number of yearling dispersers vs. non-dispersers differed significantly between the two colonies (G-statistic, $P < 0.05$), however, the timing of dispersal did not differ significantly.

The most striking result of this study is the large number of recruits at North Picnic colony in 1982. An individual is classified as a recruit if it remains in its natal colony at the end of its yearling year. Six yearling females in 1982 remained at North Picnic when the study ended in mid-August and were present as 2-year-olds in 1983. From 1964 through 1981, only three of 20 female yearlings born at North Picnic remained as 2-year-olds.

Observations and Interactions

For 14 of 15 yearlings from both colonies, the

frequency of observation was not significantly correlated with the number of surveys. For two adult animals the frequency of observation was significantly correlated with the number of surveys. However, three significant correlations is only slightly greater than the number expected by chance. The frequency of observation also was independent of the number of surveys at both colonies. The amount of variation explained by regressing the observation frequency on the number of surveys ranged from 4.0 to 68.7 percent ($X = 24.44$, $SD = 20.93$; 1 significant F value) at North Picnic and from 0.0 to 74.7 percent ($X = 31.91$, $SD = 32.55$; 1 F value significant) at Picnic colony in 1982.

Although the frequency of observation varied among individuals and among weeks there was no significant seasonal trend at either colony. The frequency of sighting individuals between the two colonies did not differ in 1982; overall, each individual was sighted during 16-29% ($X = 0.22$, $SD = 0.15$) of all surveys at North Picnic and during 17-26% ($X = 0.22$, $SD = 0.14$) of all surveys at Picnic colony. However, individuals were sighted significantly less during 1983 at North Picnic than at North Picnic or Picnic in 1982 ($P = 0.01$, $P = 0.02$, respectively).

The frequency of interaction for each individual was neither correlated nor dependent upon the frequency of

observation or the number of surveys at either colony. The frequency of interaction and the frequency of observation was significantly correlated in only 4 of 33 cases at both colonies in the two years of study; the interaction frequency was significantly correlated with the number of surveys for only 4 of 33 animals at both colonies during the two years. In 1982 the variance explained by regression of the interaction frequency on the frequency of observation ranged from 0.10 to 65.8 percent at North Picnic ($X = 16.63\%$, $SD = 22.49\%$; 1 F value significant) and from 0.10 to 97.00 percent ($X = 29.24$, $SD = 29.90$; 1 F significant) at Picnic. Regression of the frequency of interaction on the number of surveys explained 1.6 to 76.9 percent of the variation ($X = 31.82$, $SD = 26.51$; 1 significant F value) at North Picnic and 0.30 to 98.80 percent of the variation ($X = 37.92$, $SD = 34.72$; 2 significant F values) at Picnic. Interaction rates calculated over all animals declined significantly over the season at North Picnic colony ($F = 175.75$, $P < 0.0001$) but not at Picnic colony. Such a result may be due, in part, to the difference in the number of weeks analyzed for the two colonies. The interaction frequencies for yearlings ranged from 0.00 to 0.67 ($X = 0.22$, $SD = 0.17$; Table 1) at North Picnic, and from 0.00 to 0.50 ($X = 0.16$, $SD = 0.16$; Table 1) at Picnic. The individuals of the two colonies differed in their frequencies of interaction; Picnic colony animals

interacted less than North Picnic marmots (Fischer's exact probability, $P = 0.002$). Furthermore, if only data among yearlings is considered, yearlings at Picnic colony interacted less than yearlings at North Picnic ($P = 0.01$; Table 1), and a significantly greater proportion of the time they spent interacting was agonistic ($P = 0.01$; Table 1).

Behavior and Dispersal

Although the yearlings from Picnic colony were involved in more agonistic interactions than those from North Picnic, and 80% of them dispersed, the timing of dispersal was not significantly correlated with agonism at either of the two colonies. There also was no significant difference between yearling dispersers and non-dispersers at North Picnic in the frequency of interaction or proportion of time spent interacting agonistically. Neither of the 2-year olds that dispersed in 1983 was observed to interact agonistically prior to their departure. Analysis of the number of interactions initiated by yearlings at North Picnic revealed no significant difference (Fischer's exact test, $P = .50$) between dispersers and non-dispersers in the tendency to initiate interactions.

Play behavior may substitute for aggression and provide the means by which dominance-subordinance relationships are established (Armitage and Johns, 1982).

The frequency of play, and the percentage of interactions that were play, were significantly greater for North Picnic yearlings than for those at Picnic (Wilcoxon two-sample test, $P < .05$; Table 1). Dispersers played significantly more than non-dispersers ($P < 0.025$) and the percentage of interactions that were play was significantly greater for dispersers ($P < 0.025$) at North Picnic colony. However, male yearlings play more than females (Armitage, 1974 and this study), and it is the male yearlings who dispersed. Therefore, the significance difference in play behavior could be interpreted as a sex difference, rather than difference between dispersers and non-dispersers.

Space Use and Interaction Rates

In 1982, the home ranges of all individuals at Lower Picnic overlapped (Brody, 1984). However, animals whose home ranges overlapped most were related and had the greatest number of interactions. Animal 573, the 2-year old daughter of female 310, had an almost identical home range to that of her mother. Both females acted agonistically towards the yearling female (animal 672) at Lower Picnic and towards the yearlings at Upper Picnic. The home range of 672 was almost identical to that of her 3-year old full sister, 632. Two-thirds of the interactions 672 was involved in were with 632, and all were amicable. Half of the interactions between yearling

672 and other colony members were agonistic. The adult male at Lower Picnic had an extensive home range that included within it the home ranges of all other colony members.

At Upper Picnic, all individuals' home ranges overlapped. The four yearlings at Upper Picnic were siblings and their space-use patterns were almost identical. The interactions among yearlings were amicable; the interactions between yearlings and other colony members were wholly agonistic. The home range of the adult male overlapped, but did not encompass, all other animals' at Upper Picnic.

In 1982, all yearlings at North Picnic had overlapping home ranges (Brody, 1984). Like Picnic colony, those individuals with the greatest amount of overlap also exhibited the highest number of interactions. Two sets of two yearlings, 880 and 884, and 876 and 891, shared home burrow systems and had almost identical home ranges. Each of these pairs were probable sibs and most interactions occurred between the two animals of each pair.

In 1982, by mid-July, eight of ten yearlings had expanded their home-ranges to include a ledge of cliffs at the upper edge of the study area. By the end of the season in 1982, all but two individuals were using this area almost exclusively.

The adult male who immigrated to the area and was not

captured, was first seen on 20 July. However, he was not observed to interact with any of the yearling males still present, and did not overlap with their use of space.

The space-use patterns of individuals at North Picnic colony were similar in 1983 to 1982. Females 880 and 884 again shared the same burrow system and had similar home ranges. Female 876, who in the previous year had shared a burrow with her brother 891, had a constricted home range and disappeared in early July. She probably was displaced by female 640, who frequently was observed in her previous home range and produced a litter nearby. The adult male present in 1983 ranged widely over the entire area.

There were two apparent differences in use of space in the two years; the home ranges of animals in 1983 were generally smaller, and there was little use of the cliff area.

Discussion

The results of this study indicate that the proximal causes of dispersal are not the same for males and females. Four main hypothesis regarding the cause of dispersal may be applied to marmots: (1) there is a genetic basis for dispersal; (2) individuals disperse as a means to avoid inbreeding; (3) dispersal is based upon behavioral phenotypes, either of the dispersing animal or of the other members of the colony who in effect, "force"

individuals to emigrate, and (4) dispersal is a result of an individuals' assessment of its' mating potential in the colony which it inhabits.

The four hypotheses are not mutually exclusive, and it is important to distinguish between the cause of dispersal and the effect. Hypotheses (1) can be viewed as an ultimate reasons for dispersal, while hypotheses (3) and (4) as proximate causes; hypothesis (2) falls in both catagories. The avoidance of inbreeding can be acted upon by selection and therefore be an ultimate reason why individuals disperse. Animals' "assessment" of the probability of mating with relatives however, may be proximate cause for dispersal.

Although few studies have addressed the issue, there is no empirical evidence to suggest that dispersal is controlled by a genetic polymorphism in ground squirrels (Michener and Michener, 1977).

Individuals may disperse to avoid inbreeding; there is evidence of such occurrences in black-tailed prairie dogs (Hoogland, 1982). Sex differences in dispersal patterns of most ground squirrels probably functions to promote outcrossing (Dobson, 1979). In marmots, the demographic probability of incest is very low (Armitage, 1974). Thus, incest avoidance is likely a consequence of male dispersal rather than a cause.

Past studies suggested that the nature of

interactions between yearlings and adults determines whether yearlings are recruited or disperse (Armitage, 1975; Armitage, 1984; Armitage and Downhower, 1974). While probably true for females, yearling male dispersal appears to be independent of adult-yearling interactions.

Individuals may be "forced" to emigrate because of aggressive conflicts with the colony residents, or simply to avoid such agonistic encounters. The amount of aggression among marmots may be related to their use of space, proximity thus becoming an important determinant of which animals coexist in a colony (Frase, 1983). At North Picnic, those individuals who frequented the same areas most often had higher rates of interaction than those whose home ranges and space-use patterns were dissimilar. The levels of aggression could not be interpreted strictly by proximity because yearlings at Upper Picnic had little home range overlap with adults from Lower Picnic and yet were subject to agonistic behavior from Lower Picnic adults. At North Picnic, few interactions were agonistic despite a high degree of home range and space-use overlap. Marmots may aggressively chase intruders even before such animals come close to their home range (Armitage, unpublished data). The levels of agonism observed depend largely on the relatedness of the individuals involved (Armitage and Johns, 1982). In other ground squirrels, aggression serves not to maintain boundaries of established neighbors, but to ward off immigrants (Dobson,

1979; Dunford 1977; Getty, 1981).

Aggression does not adequately explain male marmot dispersal. In this study, yearling males dispersed despite the absence of adults and a lack of agonistic interactions; and although yearling males may disperse in order to avoid the resident territorial male (Armitage, 1974), the timing of dispersal is not related to aggression. Although we cannot conclude, with absolute certainty, that the immigration of the adult male in 1982 did not cause the dispersal of yearlings, it is unlikely that his presence was the cause for several reasons: at least one yearling male dispersed prior to the immigrants appearance, there was no apparent antagonism between the immigrant and the remaining yearlings, other individuals had moved in previously and not caused dispersal of those present, and the new animal used an area not currently frequented by the eventual dispersers.

The social cohesion hypothesis, or dispersal based on individual behavioral phenotypes, hypothesis is not directly contradicted by the interactions and dispersal of marmots; however, it is not sufficient to explain the patterns of dispersal observed. Bekoff (1977) predicted that those individuals most likely to delay dispersal would engage in frequent social interactions and form strong social bonds.

Play, a common form of social interaction among

yearling marmots, probably is important in the social development of individuals which may ultimately determine who disperses and when (Bekoff, 1977). Although individuals at North Picnic engaged in frequent play bouts, and did not differ in their overall frequency of interactions from non-dispersers, dispersal occurred despite the apparent social bonds that were established. Thus, dispersal in marmots cannot be predicted solely by the behavioral phenotypes of individuals. In order to attempt to interpret the dispersal patterns, one must look at the structure of the mating system.

Females are philopatric and males associate themselves with a colony of females (Armitage, 1984). Adult males are territorial and exclude all other males from their home range. The chance of a yearling male obtaining residency and ultimately breeding in its natal colony is so low that they have no choice but to disperse to find mates.

Uinta ground squirrels aggregate on favorable habitat but all animals live individually (Armitage, 1982). Dispersal in Uinta ground squirrels is density-dependent. In populations where densities are low, fewer juveniles disperse and a higher percentage of yearlings breed. At high densities emigration offers Uinta ground squirrels their only chance for reproduction (Slade and Balph, 1974). In marmots, dispersal of males is density-independent (Armitage and Downhower, 1974). An adult male

is almost always present. Dispersal is therefore the only option for reproductive success available to yearling male marmots.

Individuals may opt to delay dispersal, however. There are both cost and benefits to doing so. Sufficient weight and adequate hibernacula are two important determinants of overwinter survival (Anderson et al., 1976). Dispersers move through forested areas where forage is limited (Shirer and Downhower, 1969). Weight gain, and fat storage in particular, may be crucial for dispersal (Downhower and Armitage, 1981). Thus, yearling dispersers face a trade-off of staying in their natal colony to fatten versus leaving in time to find an adequate place to overwinter.

Yearling males from North Picnic colony did not show a delay in dispersal that was statistically different from times reported previously (Downhower and Armitage, 1981). However they did disperse late in the season relative to the dispersal dates of male yearlings from previous years (Downhower and Armitage, 1981).

Explorations and movement to peripheral areas of the colony often precede dispersal (Armitage, 1974 and this study). By exploring, yearlings may become familiar with surrounding areas and locate hibernacula. I originally believed that yearlings moved to the cliff area in response to the increased height of vegetation in 1982.

Rocky outcrops provide lookouts and sunning spots. The vegetation may hinder animals' ability to spot predators or bask in the sun. However, this conclusion was not supported by the space-use patterns of animals in 1983. The vegetation became extremely dense by early July, and yet individuals were rarely observed in the cliff area. I thus conclude that the movement patterns observed in 1982 were a precursor of dispersal.

A number of lines of evidence suggest that agonistic behavior and a lack of cohesive behavior are the primary cause of dispersal in female marmots. Female yearlings disperse early when rates of agonistic behavior are high (Downhower and Armitage, 1981) and yet females may be recruited despite high rates of agonism if one or more adult female is sociable (Armitage, 1977). Yearling dispersers at Picnic colony received only agonistic behavior from adults; cohesive behaviors occurred only among themselves. The female who remained at Picnic colony throughout 1982 also experienced agonistic behavior but had frequent cohesive interactions with her sister. Thus it may be the ratio of amicable to agonistic interactions that is important in determining which yearling females will be recruited. The non-dispersers at North Picnic colony (all female) engaged only in amicable, cohesive interactions with siblings and other yearlings.

Females are most reproductively successful if they can exclude other matrilineages from the colony in which

they live (Armitage, 1984). Therefore, females should act aggressively towards other, unrelated individuals in an attempt to garner the available resources for their own direct descendants. Cohesive interactions prevail among closely related animals, while dispersive interactions predominate among distant relatives (Armitage and Johns, 1982). At North Picnic, failure of matriline to persist, and dispersal of introduced animals was associated with the residency or immigration of highly aggressive females (Armitage, 1984). Although in this study the colony was not followed long enough to determine if matriline will persist, the large number of females recruited suggest that a lack of agonism allowed the females to remain.

Female dispersal is coincident with aggression in other ground squirrels as well. Spermophilus elegans females are philopatric and competition for quality breeding sites probably causes females to interact aggressively. Female dispersal was related to levels of aggression (Pfeifer, 1982).

Ultimately, the outcome of dispersal is the structure, both social and genetic, of the population. Dispersal may serve to regulate numbers and provide the means for gene flow in small mammal populations (Dobson, 1979; Krebs, 1978; Michener and Michener, 1977; Schwartz and Armitage, 1980; Slade and Balph, 1974; Yeaton, 1972). Dispersal can also be viewed as a mating strategy

(Armitage, 1984), particularly in species such as marmots that breed polygynously and where males, and some females, do not reproduce in their natal colonies.

Reproductive success or failure of offspring determines the fitness of parents. Dispersal should be timed so as to maximize the individual fitness of the disperser or the inclusive fitness of the disperser and its parents (Armitage, 1981). Although the risk to dispersers is probably high (Dunford, 1977; Gaines and McClenaghan, 1980; Quanstrom, 1971), dispersal is not necessarily maladaptive for the individual (Slade and Balph, 1974). Obviously, dispersal is not maladaptive in marmots because all males who eventually become breeding adults were at one time dispersers. Many females are also successful dispersers who enter colonies or live peripherally and reproduce (Armitage, 1984; Armitage and Downhower, 1974). The large number of immigrants to North Picnic colony after the residents were removed in 1982 is strong evidence that marmots are present in habitats surrounding colonies. It appears that, at least in many cases, animals are aware of vacancies in colonies nearby and take advantage of such by moving into unoccupied space. Immigrant females often established residency and produced offspring at North Picnic colony (Armitage, 1984).

While broad generalizations regarding dispersal are difficult to make (Gaines and McClenaghan, 1980), one

theme appears to underlie dispersal in social ground squirrels; dispersal is male-biased and the proximal causes are different for males than for females. The patterns of dispersal that we see must ultimately be interpreted in light of the mating structure of the population and reproductive strategies available to individuals. Female marmots may, depending on the social composition of their natal colony, remain in the colony where they were born and reproduce successfully. Males, on the other hand, must emigrate in order to have a chance at reproductive success.

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Table 1. Interaction rates for yearling marmots at North Picnic and Picnic colonies during the first four weeks of study in 1982. A = total interaction rate; B = rate of play; C = agonistic interaction rate. Numbers below play and agonistic interaction rates denote percentage of interactions that were classified accordingly.

Animal	Week											
	1			2			3			4		
	A	B	C	A	B	C	A	B	C	A	B	C
North Picnic												
891	0.21	0.19 0.90	0.00	0.35	0.22 0.62	0.02 0.06	0.31	0.18 0.56	0.02 0.06	0.20	0.12 0.60	0.02 0.10
876	0.29	0.24 0.82	0.00	0.30	0.23 0.78	0.00	0.26	0.14 0.53	0.00	0.14	0.11 0.75	0.00
894	0.56	0.67 0.78	0.00	0.25	0.19 0.75	0.00	0.23	0.15 0.67	0.00	0.11	0.11 0.75	0.00
896	0.67	0.56 0.78	0.05 0.07	0.50	0.45 0.91	0.00	0.42	0.26 0.62	0.00	0.07	0.00	0.00
878	0.19	0.19 1.00	0.00	0.19	0.06 0.33	0.00	0.31	0.28 0.91	0.00	0.50	0.50 1.00	0.00
882	0.38	0.31 0.83	0.00	0.39	0.39 1.00	0.00	0.12	0.12 1.00	0.00	0.20	0.20 1.00	0.00
798	0.32	0.24 0.75	0.00	0.37	0.21 0.57	0.05 0.14	0.28	0.12 0.43	0.08 0.28	0.50	0.00	0.00
640	--	--	--	0.36	0.28 0.80	0.00	0.29	0.19 0.67	0.00	0.50	0.25 0.50	0.00
880	0.56	0.12 0.22	0.06	0.18	0.09 0.50	0.00	0.18	0.12 0.67	0.00	0.14	0.00	0.00
884	0.25	0.00	0.00	0.14	0.07 0.50	0.00	0.19	0.12 0.67	0.00	0.07	0.00	0.07 1.00
Picnic												
672 F	0.16	0.00	0.00	0.13	0.06 0.44	0.00	0.12	0.00	0.04 0.30	0.16	0.02 0.10	0.05 0.30
741 FD	0.47	0.07 0.14	0.27 0.58	0.14	0.00	0.10 0.68	0.13	0.03 0.25	0.03 0.25	0.15	0.00	0.15 1.00
661 FD	0.27	0.09 0.34	0.09 0.34	0.28	0.07 0.25	0.14 0.51	0.18	0.18 1.00	0.00	0.00	0.00	0.00
646 MD	0.00	0.00	0.00	0.00	0.00	0.00	0.57	0.14 0.25	0.43 0.75	0.00	0.00	0.00
751 FD	0.50	0.25	0.25	0.15	0.08	0.08	0.45	0.18 0.40	0.18 0.40	0.00	0.00	0.00

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APPENDIX I.

Table 1. Average frequency of observation of each yearling marmot at North Picnic Colony, 1982 and 1983.

Animal	Week							
	1	2	3	4	5	6	7	8
	1982							
891	.44	.42	.51	.52	.49	.29	.04	.09
876	.35	.40	.59	.58	.51	.23	.10	.24
894	.29	.28	.16	.32	.22	.01	--	--
896	.19	.18	.18	.14	.04	--	--	--
878	.28	.12	.33	.05	.02	.07	.18	.10
882	.15	.21	.39	.15	--	--	--	--
798	.24	.16	.24	.02	.02	.08	.24	.12
640	--	.11	.20	.04	.05	.10	.32	.23
880	.14	.20	.16	.14	.04	.20	.33	.30
884	.07	.22	.15	.14	--	.30	.47	.34
	1983							
876	.11	.24	.04	--	--	--	--	--
828	.13	.25	.24	.37	.06	.04	.04	--
878	.14	.15	--	--	--	--	--	--
880	.11	.13	.04	.07	.21	.24	.37	--
884	.00	.09	.14	.20	.38	.35	.44	--
798	.22	.18	.26	.13	.08	.04	.03	--
640	.10	.22	.09	.12	.11	.03	.03	--
260	.09	.24	.10	.13	.16	.27	.00	--

Table 2. Average frequency of observation of each marmot at Picnic Colony, 1982.

Animal	Week			
	1	2	3	4
666	.12	.28	.32	.01
174	.05	--	.03	.21
553	.20	.23	.29	.26
556	.21	.29	.39	.14
483	.24	.36	.15	.16
571	.07	.20	.37	.18
464	.34	.39	.34	.34
632	.33	.51	.49	.56
631	.09	.21	.20	.33
573	.19	.30	.27	.26
672	.32	.47	.49	.43
741	.15	.14	.26	.19
661	.12	.11	.14	.06
646	.08	.01	.07	.07
751	.05	.09	.09	.01
435	.06	--	.04	--
Unmarked	.24	.26	.29	.16

Table 3. Average frequency of interaction per marmot over four one-week intervals, Picnic Colony, 1982.

Animal	Week			
	1	2	3	4
666	.33	.42	.26	.00
474	.00	--	.25	.07
553	.05	.09	.06	.14
556	.15	.26	.32	.11
483	.26	.19	.17	.09
571	.28	.11	.20	.12
464	.15	.16	.17	.08
632	.19	.10	.14	.12
631	.00	.10	.12	.08
573	.05	.04	.16	.03
672	.16	.03	.12	.16
741	.47	.14	.13	.15
661	.27	.28	.18	.00
646	.00	.00	.43	.00
751	.50	.15	.27	.00
435	.00	--	.00	--
unmarked	.33	.06	.11	.14

Table 4. Average frequency of interactions per marmot over one-week intervals at North Picnic Colony, 1982 and 1983.

Animal	Week							
	1	2	3	4	5	6	7	8
	1982							
891	.21	.35	.31	.20	.09	.15	.33	0.0
876	.29	.30	.26	.14	.10	.20	0.0	0.0
894	.56	.25	.23	.11	0.0	0.0	--	--
896	.67	.50	.42	.07	.33	--	--	--
878	.19	.19	.31	.50	.50	0.0	.40	0.0
882	.38	.39	.125	.20	--	--	--	--
798	.32	.37	.28	.50	.50	0.0	.29	0.0
640	--	.36	.29	.50	0.0	.11	.26	.05
880	.56	.18	.18	.14	0.0	.06	.17	.08
884	.25	.14	.19	.07	--	.04	.13	.125
	1983							
876	.00	.00	.00	--	--	--	--	--
828	.30	.17	.22	.23	.00	.25	.00	--
878	.20	.28	.00	--	--	--	--	--
880	.17	.00	.50	.25	.18	.07	.14	--
884	.00	.50	.28	.12	.12	.04	.18	--
798	.21	.40	.30	.31	.00	.00	.00	--
260	.00	.31	.33	.21	.20	.09	.00	--

Table 5. Correlation analysis of average frequency of interaction-average frequency of observation, average frequency of interaction-number of surveys, and average frequency of observation-number of surveys over one-week intervals at North Picnic Colony, 1982 and 1983.

Correlation Coefficients			
Animal	Freq. Int. - Freq. Obs.	Freq. Int. - No. Surveys	Freq. Obs.- No. Surveys
1982			
891	0.172	0.365	0.515
876	0.457	0.823*	0.406
894	0.626	0.702	0.618
896	0.811*	0.674	0.829*
878	-0.097	-0.269	0.317
882	0.561	0.877*	0.683
798	0.183	0.128	0.217
640	0.122	0.302	-0.419
880	-0.033	0.458	-0.200
884	-0.030	0.515	-0.339
1983			
876	---	---	-0.396
828	0.438	0.342	0.079
878	0.988*	-0.291	-0.270
880	-0.514	-0.290	0.177
884	-0.218	-0.505	0.223
798	0.787	-0.190	-0.499
640	0.500	-0.024	-0.499
260	0.394	-0.433	0.168

Table 6. Correlation analysis of average frequency of interaction - average frequency of observation, average frequency of interaction - number of surveys, average frequency of observation - number of surveys, over four one-week intervals at Picnic colony, 1982.

Correlation Coefficients			
Animal	Freq. Int. - Freq. Obs.	Freq. Int. - No. Surveys	Freq. Obs. - No. Surveys
666	0.719	-0.180	0.017
174	-0.030	-0.145	0.220
553	0.256	0.764	0.283
556	0.985*	0.053	-0.114
483	0.450	-0.678	0.342
571	-0.283	-0.994*	0.218
464	0.327	-0.351	0.646
632	-0.900*	-0.974*	0.873
631	0.591	0.646	0.774
573	0.130	-0.357	0.864
672	-0.575	-0.601	0.661
741	-0.454	-0.795	-0.161
661	0.749	-0.331	-0.547
646	0.260	-0.257	-0.733
751	0.313	-0.902	-0.020
435	--	--	-0.988*
Unmarked	-0.147	-0.844	-0.307

*P < 0.05

Table 7. Simple linear regression of average frequencies of interaction on average frequencies of observation and number of surveys over eight one-week intervals. (adj. = adj. for degrees of freedom; F = MS regression/MS residual) North Picnic colony, 1982.

Animal	Avg. Freq. of Int. on Avg. Freq. of Obs.			Avg. Freq. of Int. on No. of Surveys		
	r ²	r ² adj.	F	r ²	r ² adj.	F
891	3.0	-13.2	0.18	13.4	-1.10	0.92
876	20.9	7.7	1.59	67.7	62.3	12.59*
894	39.2	29.0	3.86	49.2	40.8	5.82
896	65.8	60.1	11.54*	45.5	36.4	5.00
878	0.9	-15.6	0.06	7.2	-8.2	0.47
882	31.5	20.1	2.76	76.9	73.0	19.95*
798	3.3	-12.8	0.21	1.6	-14.70	0.10
640	1.5	-14.9	0.09	9.1	-6.00	0.60
880	0.1	-16.5	0.01	21.0	7.8	1.59
884	0.1	-16.6	0.01	26.6	14.3	2.17
1983						
880	26.4	11.7	1.79	8.4	-9.9	0.46
884	4.8	-14.3	0.25	25.5	10.6	1.71
828	19.2	3.0	1.18	11.7	-5.9	0.66
798	62.0	54.4	8.15	3.6	-15.6	0.19
260	15.6	-1.3	0.92	18.8	2.5	1.17
876	--	--	--	--	--	--

Table 8. Simple linear regression of average frequencies of interaction on average frequencies of observation and on number of surveys over four one-week intervals. (adj. = adjusted for degrees of freedom; F = MS regression/MS residual) Picnic colony, 1982.

Animal	Avg. Freq. of Int. on Avg. Freq. of Obs.			Avg. Freq. of Int. on No. of Surveys		
	r ²	r ² adj.	F	r ²	r ² adj.	F
666	51.8	27.6	2.14	3.2	-45.1	0.07
174	0.1	-49.9	0.002	2.1	-46.8	0.04
553	6.5	-40.2	0.14	58.4	37.6	2.81
556	97.0	95.5	65.98*	0.3	-49.6	0.01
483	20.3	-19.6	0.51	46.0	19.0	1.70
571	8.0	-38.0	0.17	98.8	98.2	165.06*
464	10.7	-34.0	0.24	12.3	-31.6	2.80
632	81.1	71.6	8.56	94.9	92.3	36.91*
631	34.9	2.4	1.07	41.8	12.7	1.43
573	1.7	-47.5	0.03	12.8	-30.0	0.29
672	33.1	-0.4	0.99	36.1	4.2	1.13
741	20.6	-19.1	0.52	63.2	44.8	3.34
661	56.2	34.2	2.56	11.0	-33.5	0.25
646	6.8	-39.8	0.14	6.6	-40.1	0.14
751	9.8	-35.3	0.22	81.3	72.0	8.71
435	--	--	--	--	--	--

*P < 0.05

Table 9. Simple linear regression of average frequency of observation on number of surveys over eight one-week intervals. (adj. = adjusted for degrees of freedom; F = MS regression/MS residual) North Picnic colony, 1982 and 1983.

Animal	r ²	r ² adj.	F
891	26.5	14.3	2.17
876	16.5	2.5	1.18
894	38.2	27.9	3.71
896	68.7	63.5	13.18*
878	10.0	-5.0	0.67
882	46.7	37.8	5.25
798	4.7	-11.1	0.30
640	17.6	3.8	1.28
880	4.0	-12.0	0.25
884	11.5	-3.2	0.78
1983			
876	15.7	-1.1	0.93
828	0.6	-19.2	0.03
878	7.3	-11.3	0.39
880	3.1	-16.2	0.16
798	24.9	9.9	1.66
884	5.0	-14.0	0.26
260	2.8	-16.6	0.14

*P < 0.05

Table 10. Simple linear regression of average frequency of observation on number of surveys over four one-week intervals. (adj. = adjusted for degrees of freedom; F = MS regression/MS residual) Picnic colony, 1982.

Animal	r ²	r ² adj.	F
666	0.0	-50.0	0.001
174	4.8	-42.7	0.102
553	8.0	-38.0	1.80
556	1.3	-48.1	0.03
483	11.7	-32.5	0.26
571	4.7	-42.9	0.10
464	41.7	12.5	1.43
632	76.1	64.2	6.38
631	60.0	39.9	2.99
573	74.7	62.0	0.59
672	43.7	15.5	1.55
741	2.6	-46.1	0.05
661	30.0	-5.0	0.86
646	53.7	30.5	2.32
751	0.0	-49.9	0.001
435	97.6	96.4	82.37*

*P<0.05

Table 11. Comparison of time spent interacting, and interacting agonistically, between North picnic and Picnic yearlings, 1982.

Animal #	Avg. Proportion of Time Inter.	Proportion of Time Inter. Agonistically

North Picnic		

891	0.23	0.05
876	0.21	0.00
894	0.27	0.12
896	0.44	0.00
878	0.25	0.00
882	0.24	0.00
798	0.27	0.10
640	0.22	0.05
880	0.21	0.08
884	0.12	0.12
Picnic		

672	0.14	0.16
741	0.19	0.62
661	0.20	0.29
646	0.12	1.00
751	0.11	0.60

Differences between the colonies in both measurements, using Fisher's exact probability; $p = .01$.

APPENDIX II.

Appendix II. Patterns of space-use by yellow-bellied marmots at North Picnic Colony, 1982 and 1983.

LIST OF FIGURES:

1. Yearling 896, male, 1982.
2. Yearling 894, male, 1982.
3. Yearling 882, male, 1982.
4. Yearling 891, male, 1982.
5. Yearling 884, female, 1982.
6. Yearling 880, female, 1982.
7. Yearling 640, female, 1982.
8. Yearling 876, female, 1982.
9. Yearling 878, female, 1982.
10. Yearling 798, female, 1982.
11. Adult 260, male, 1983.
12. Adult 884, female, 1983.
13. Adult 880, female, 1983.
14. Adult 828, female, 1983.
15. Adult 640, female, 1983.
16. Adult 876, female, 1983.
17. Adult 878, female, 1983.
18. Adult 798, female, 1983.

FIG. 1

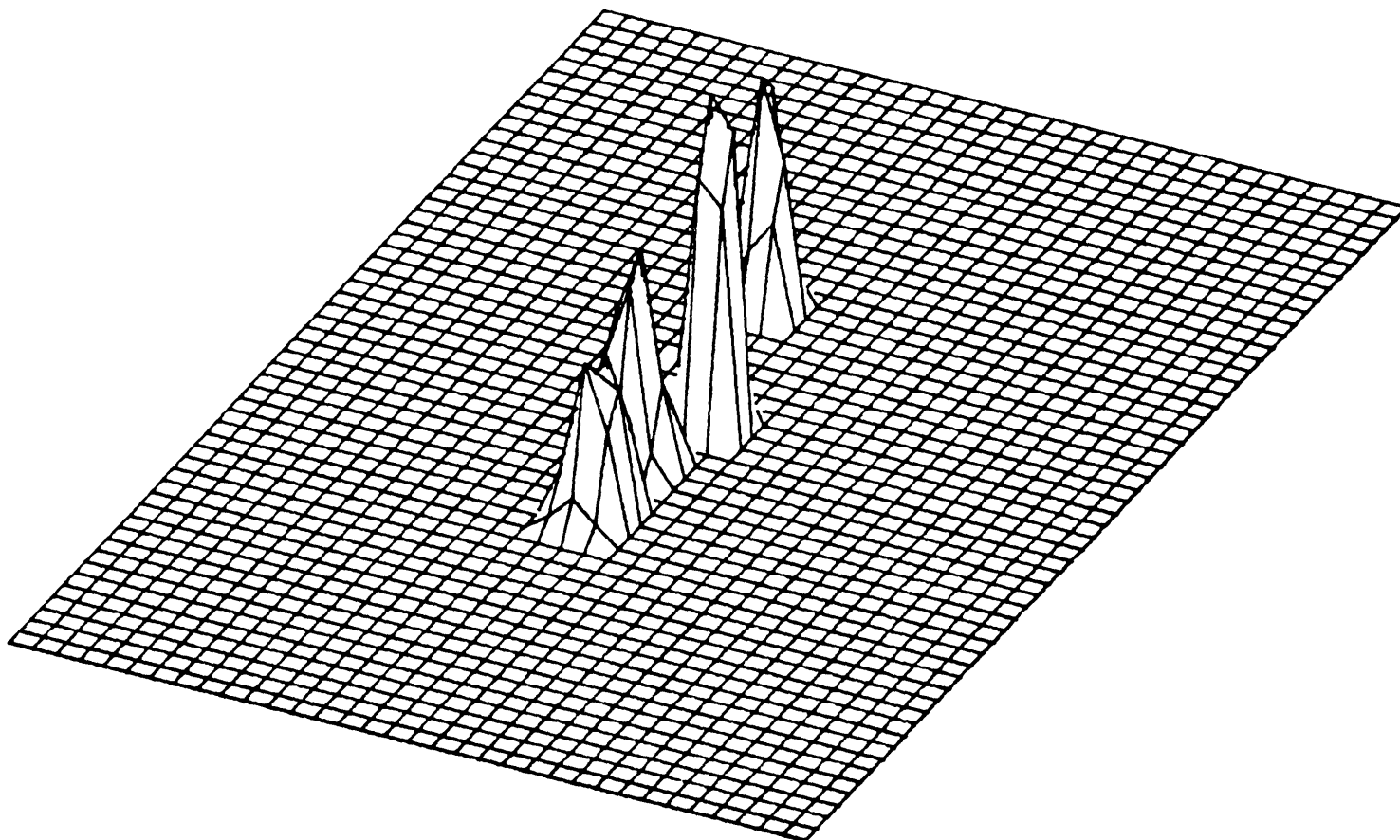


FIG. 2

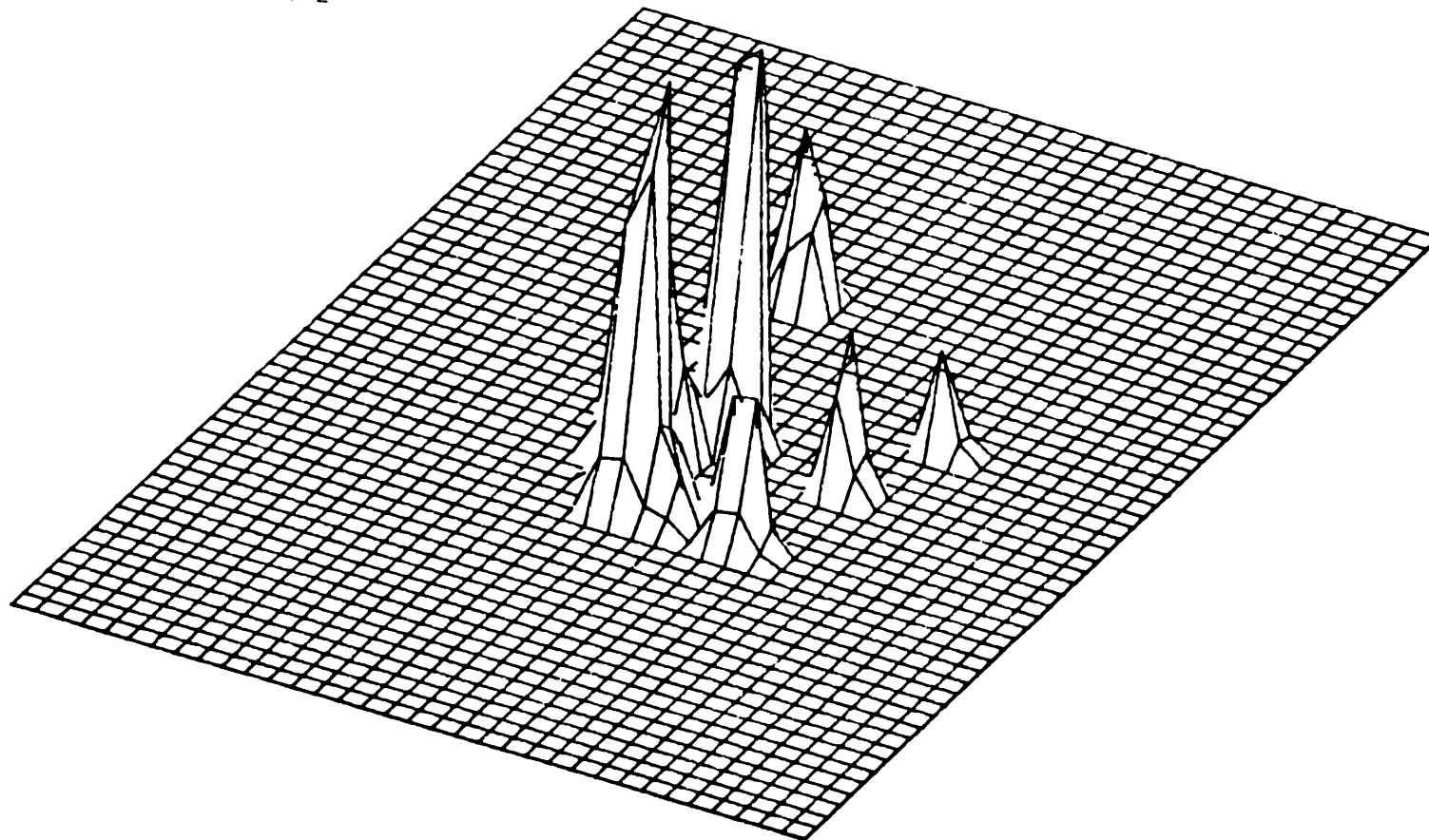


FIG 3.

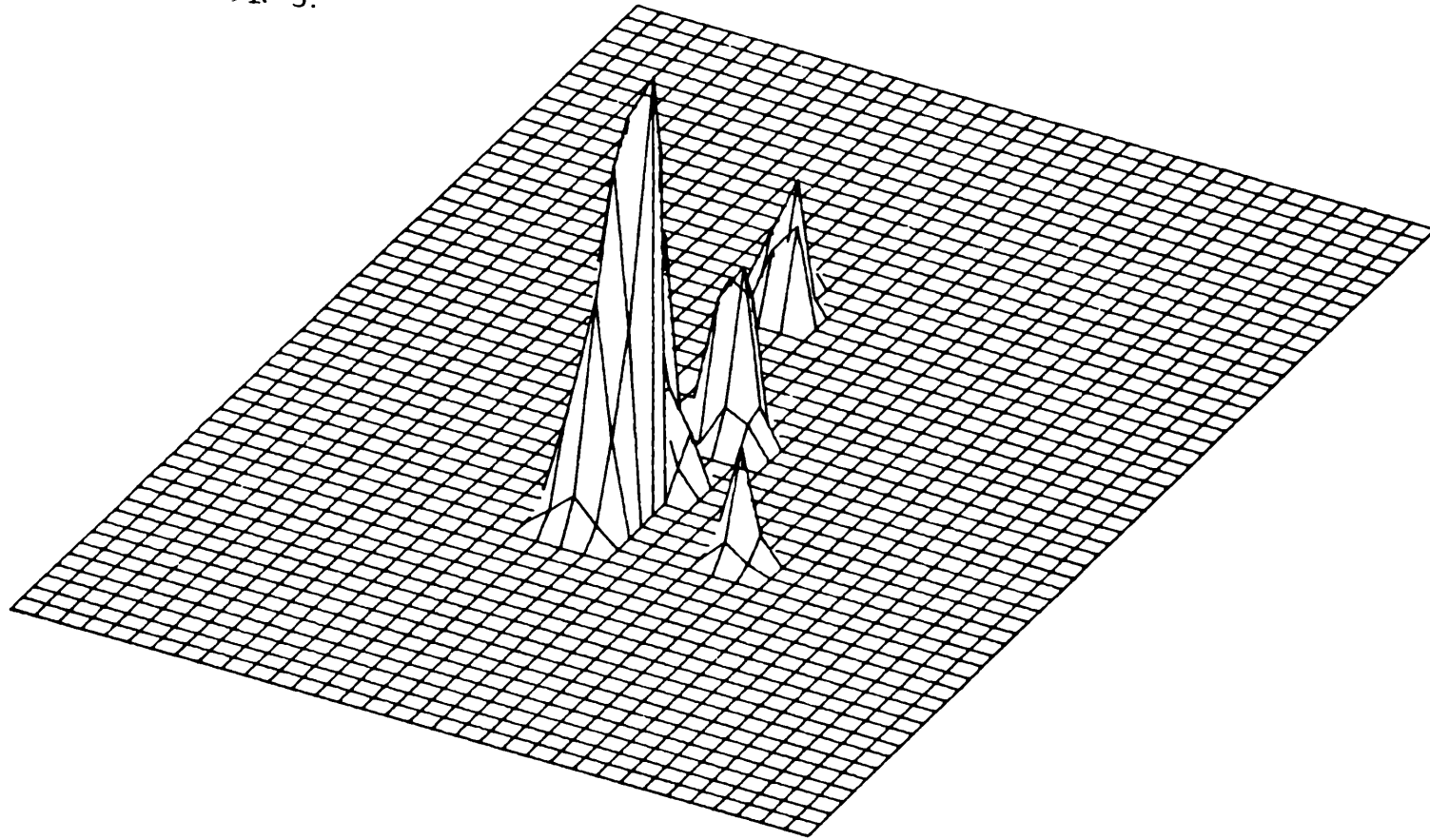


FIG. 4

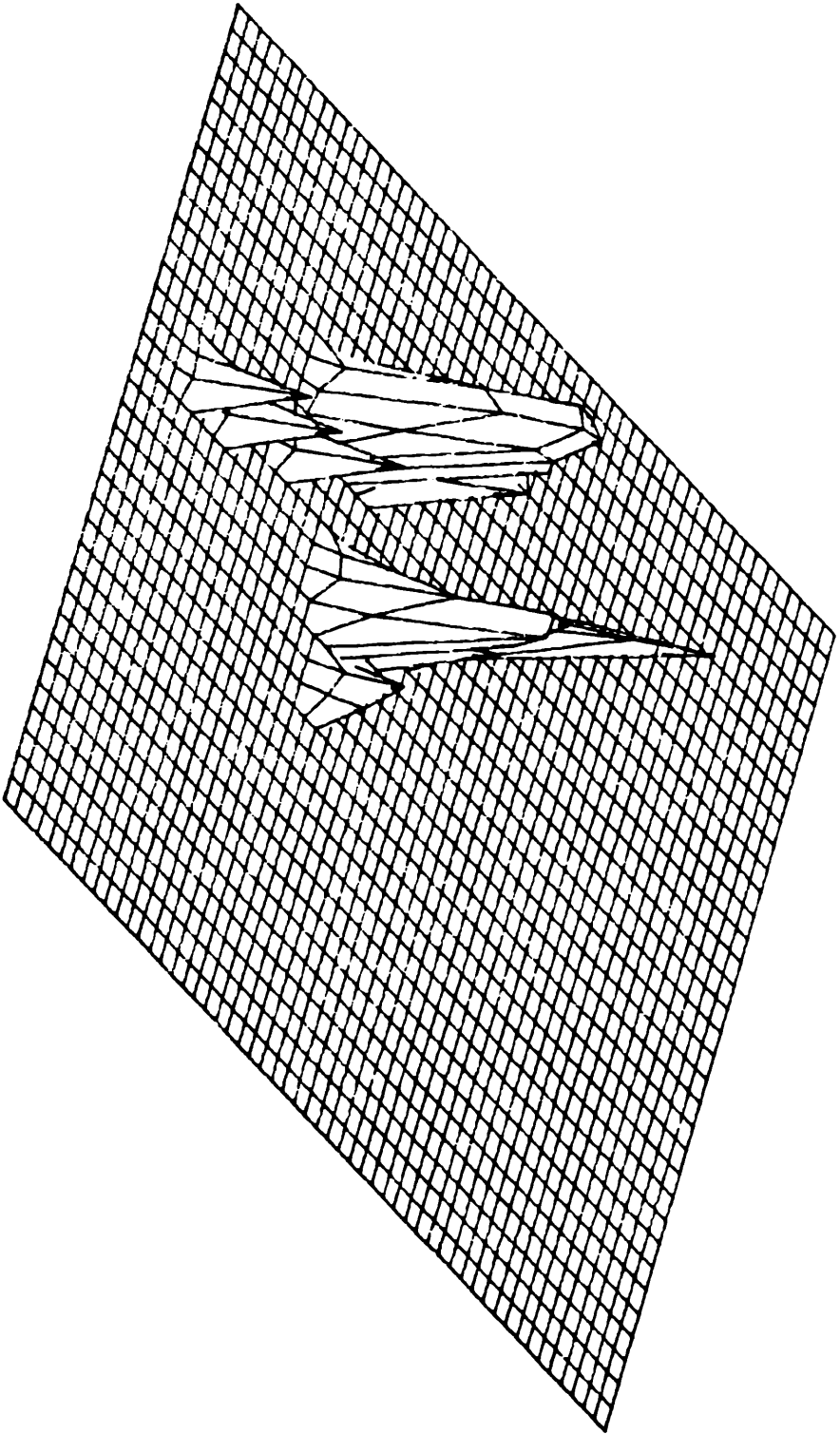


FIG. 5

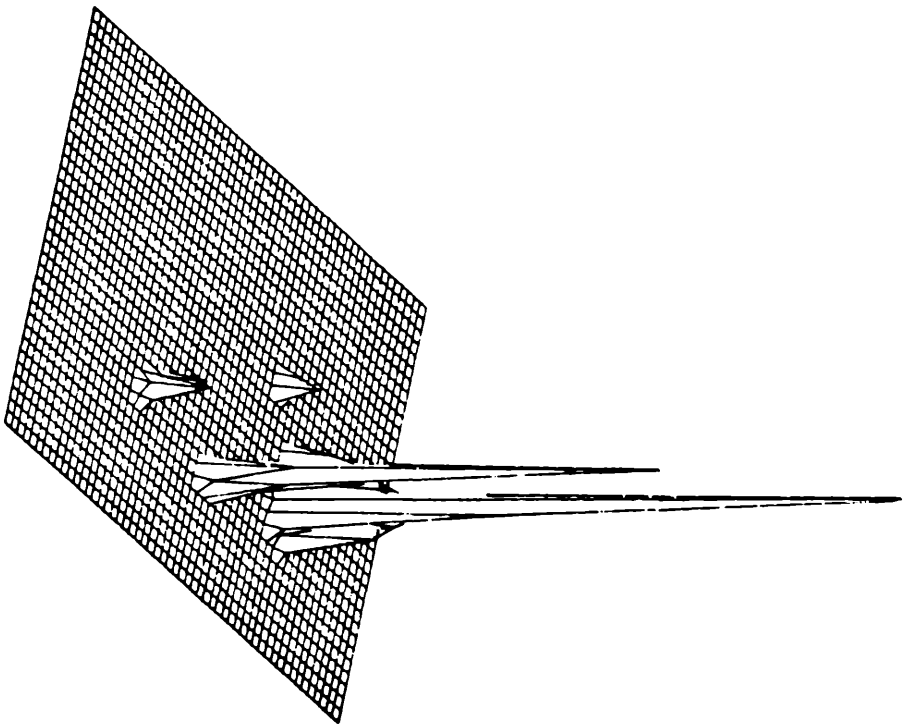
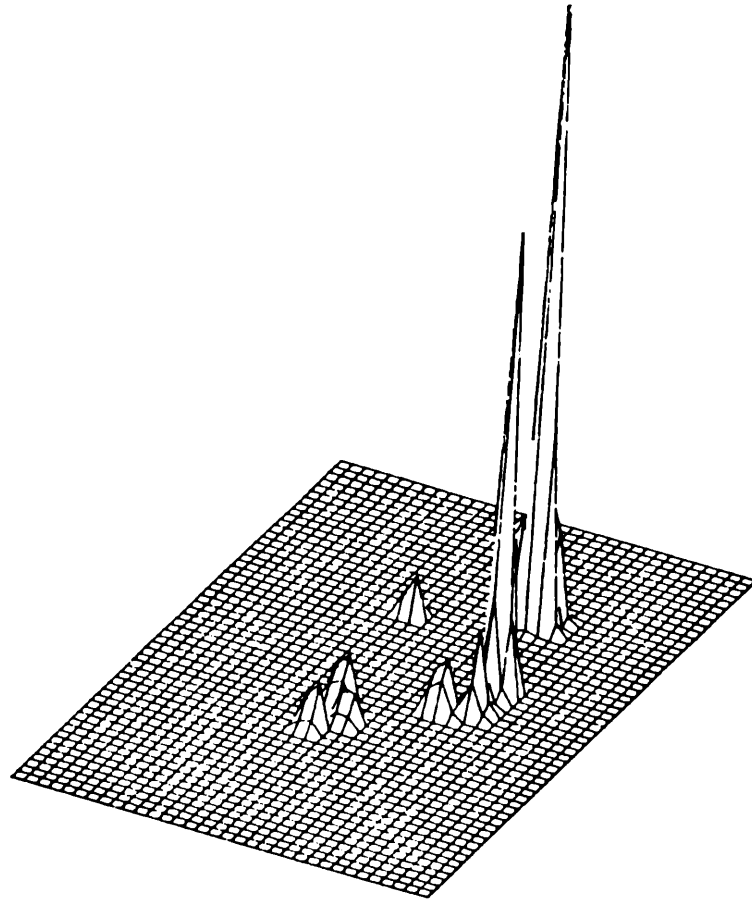


FIG. 6



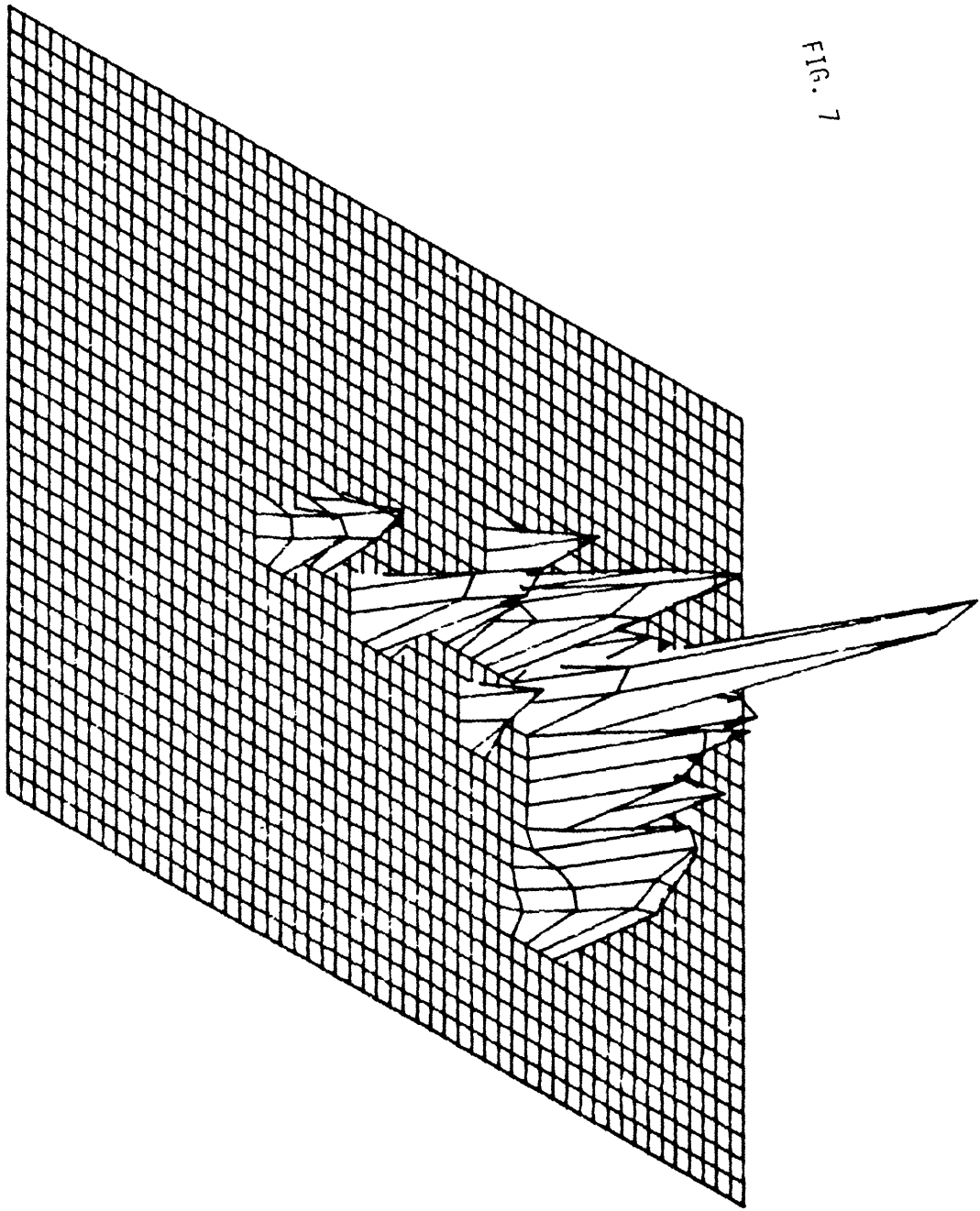


FIG. 7

FIG. 8

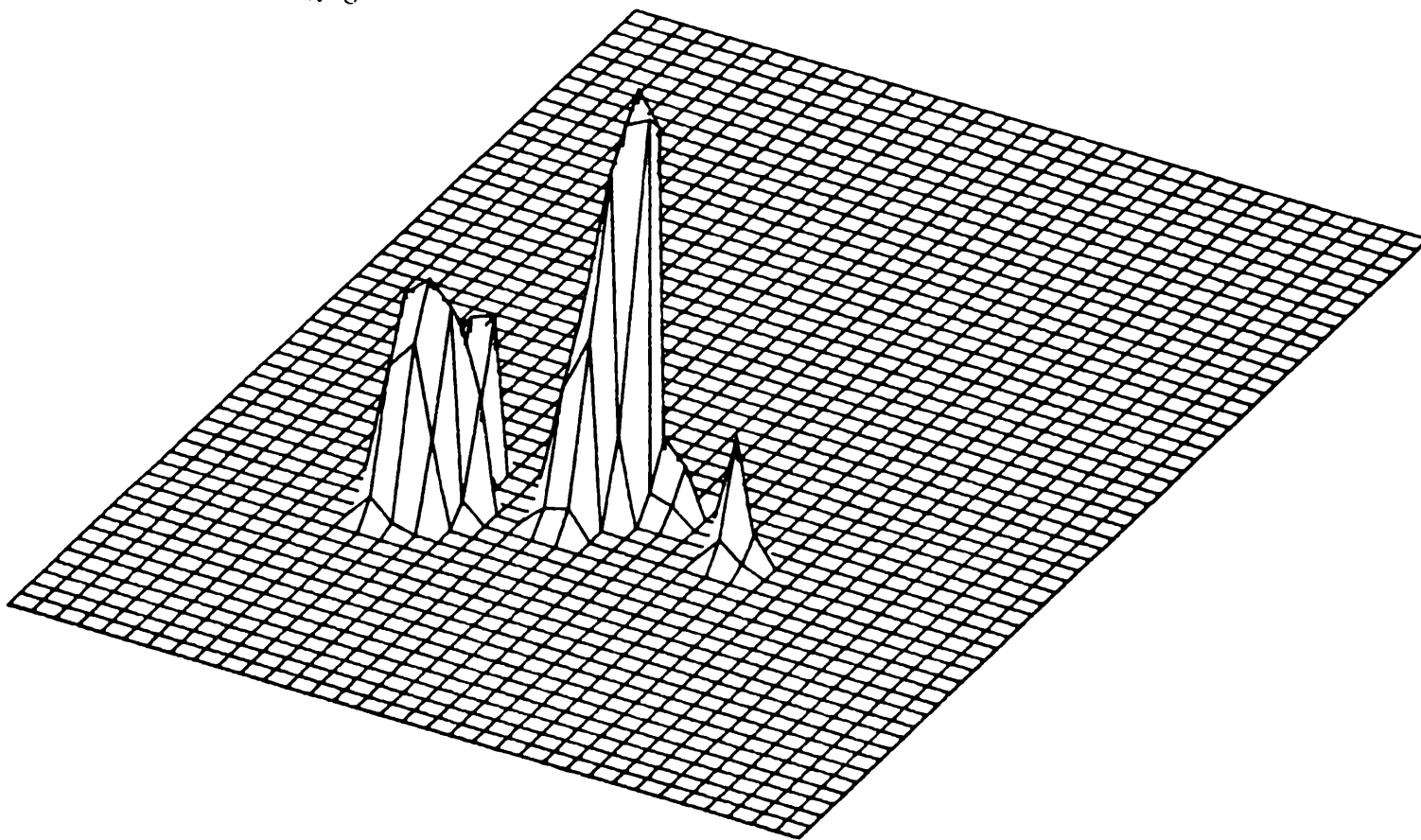
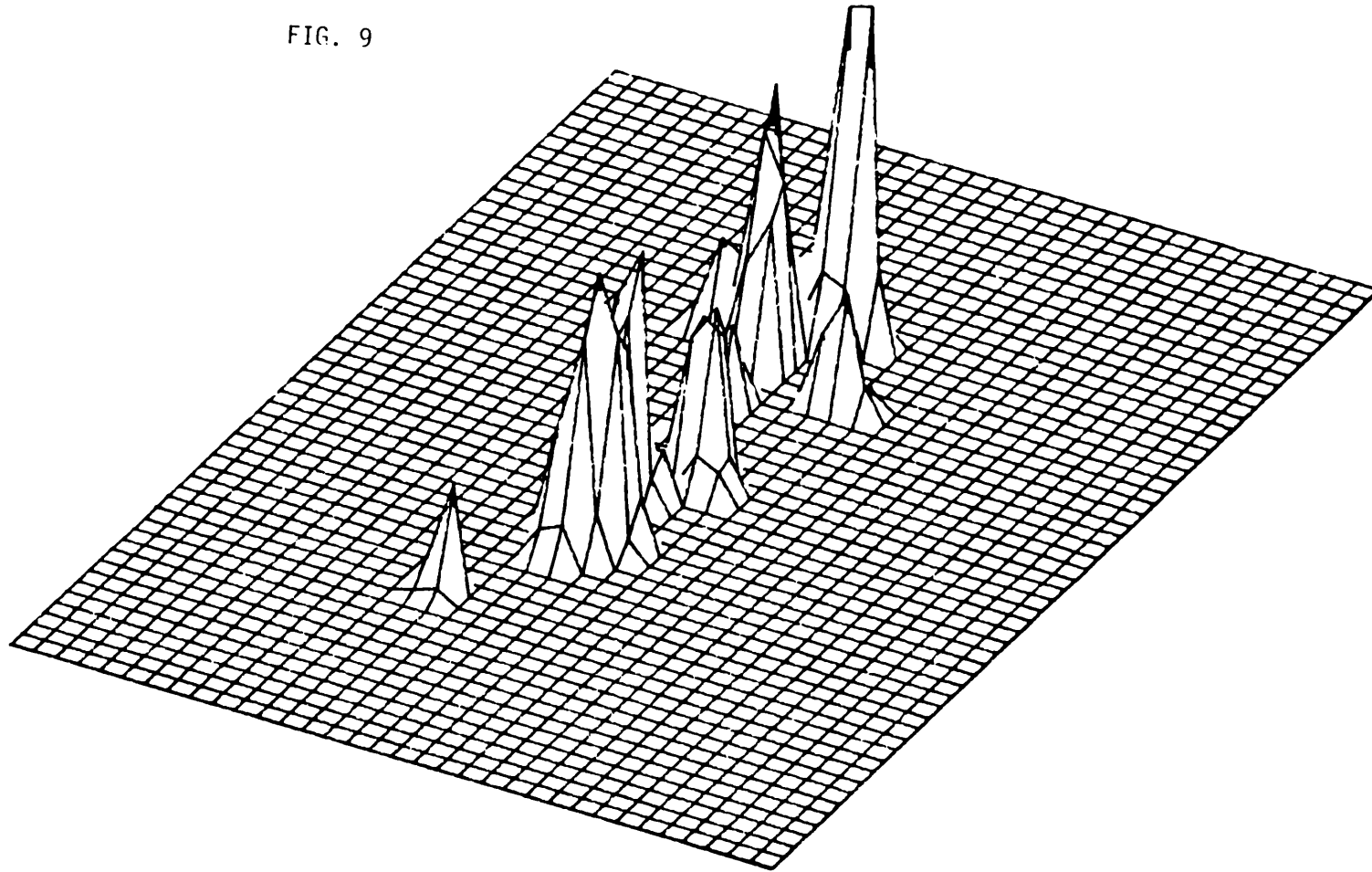


FIG. 9



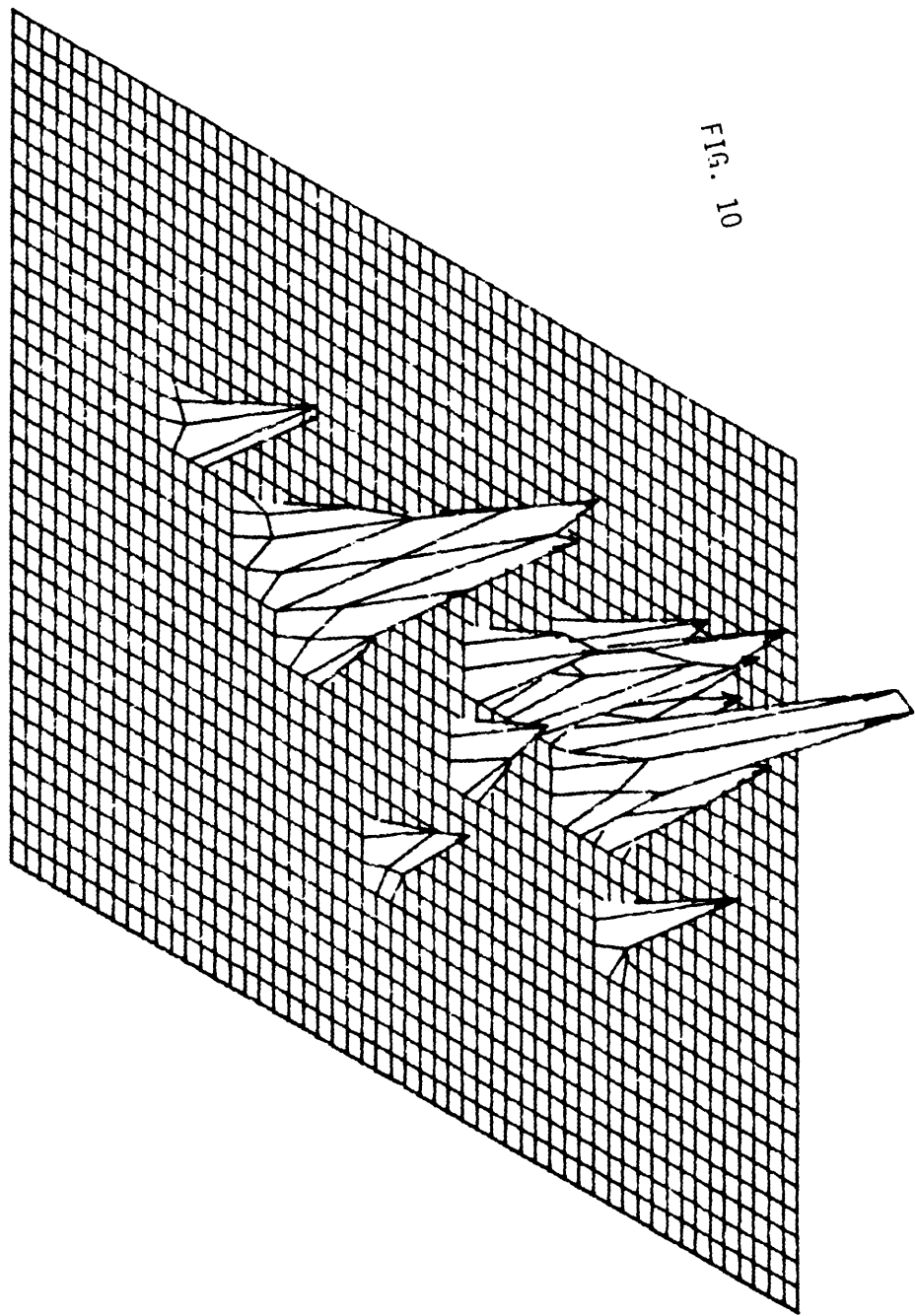


FIG. 11

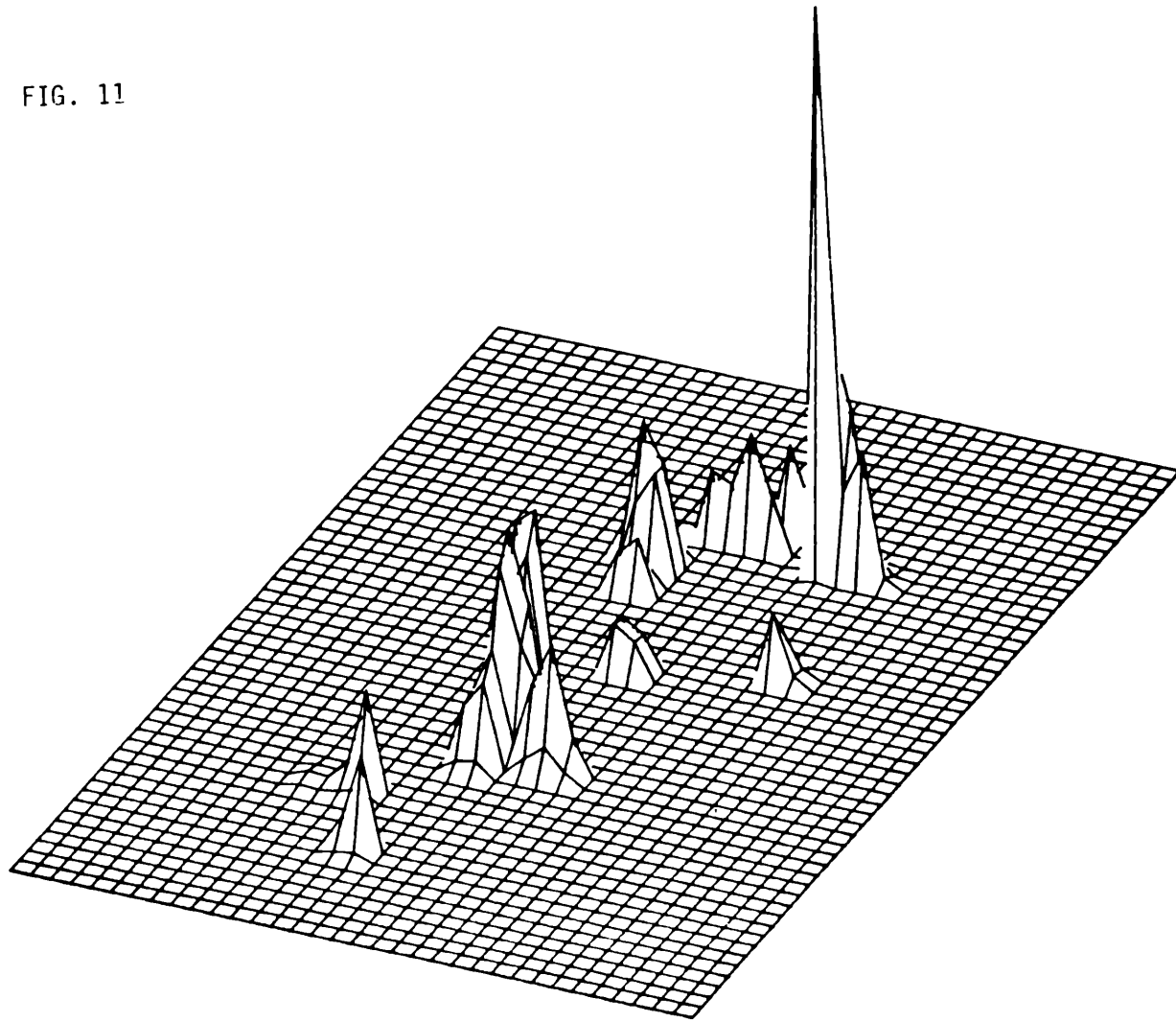


FIG. 12

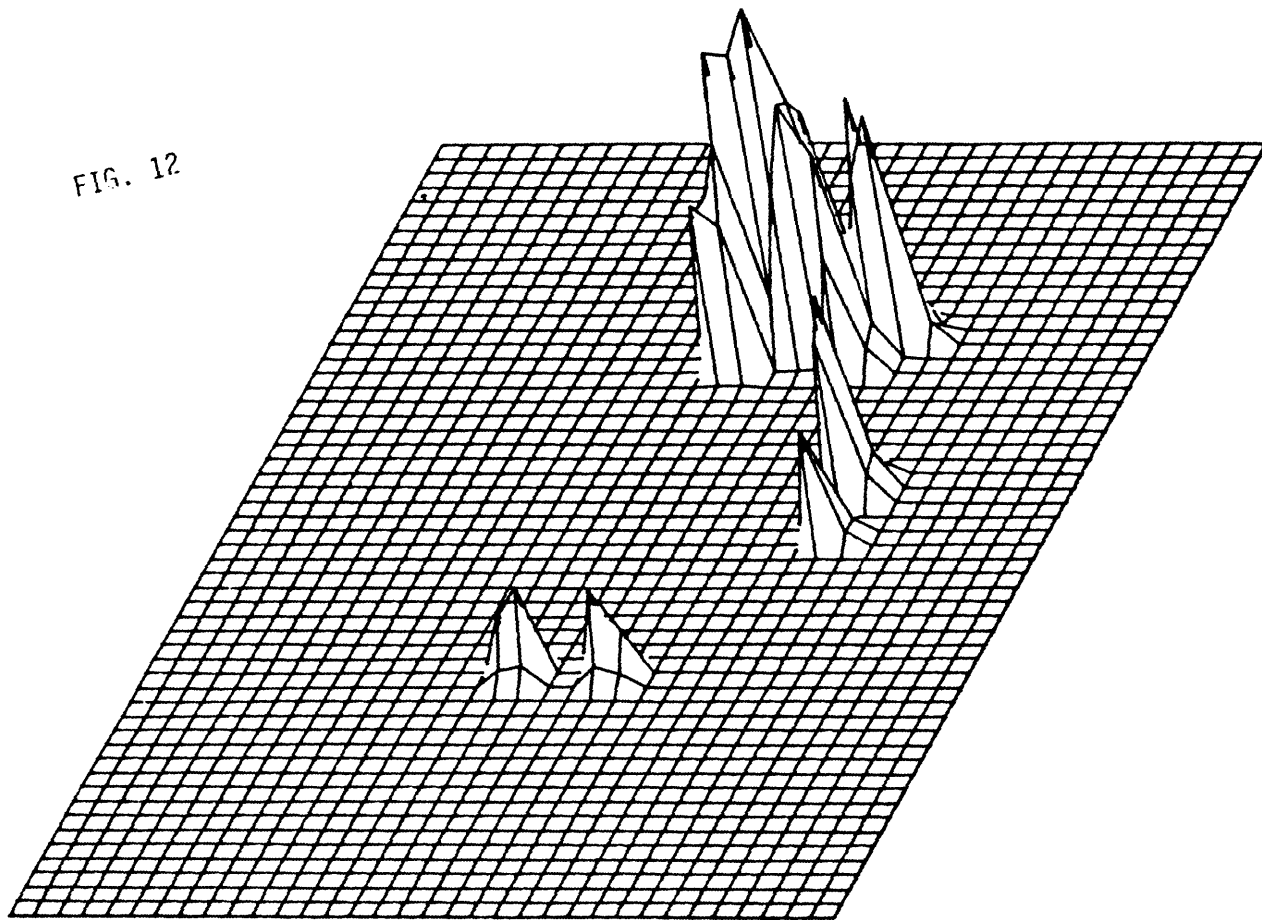


FIG. 13

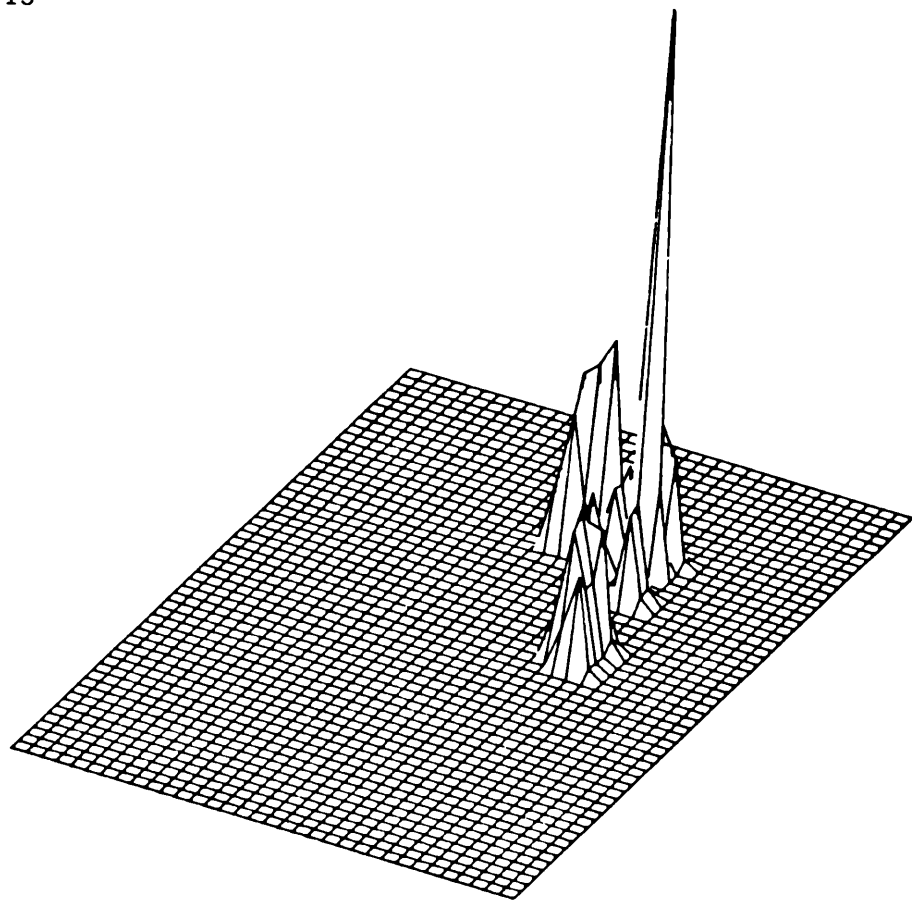


FIG. 14

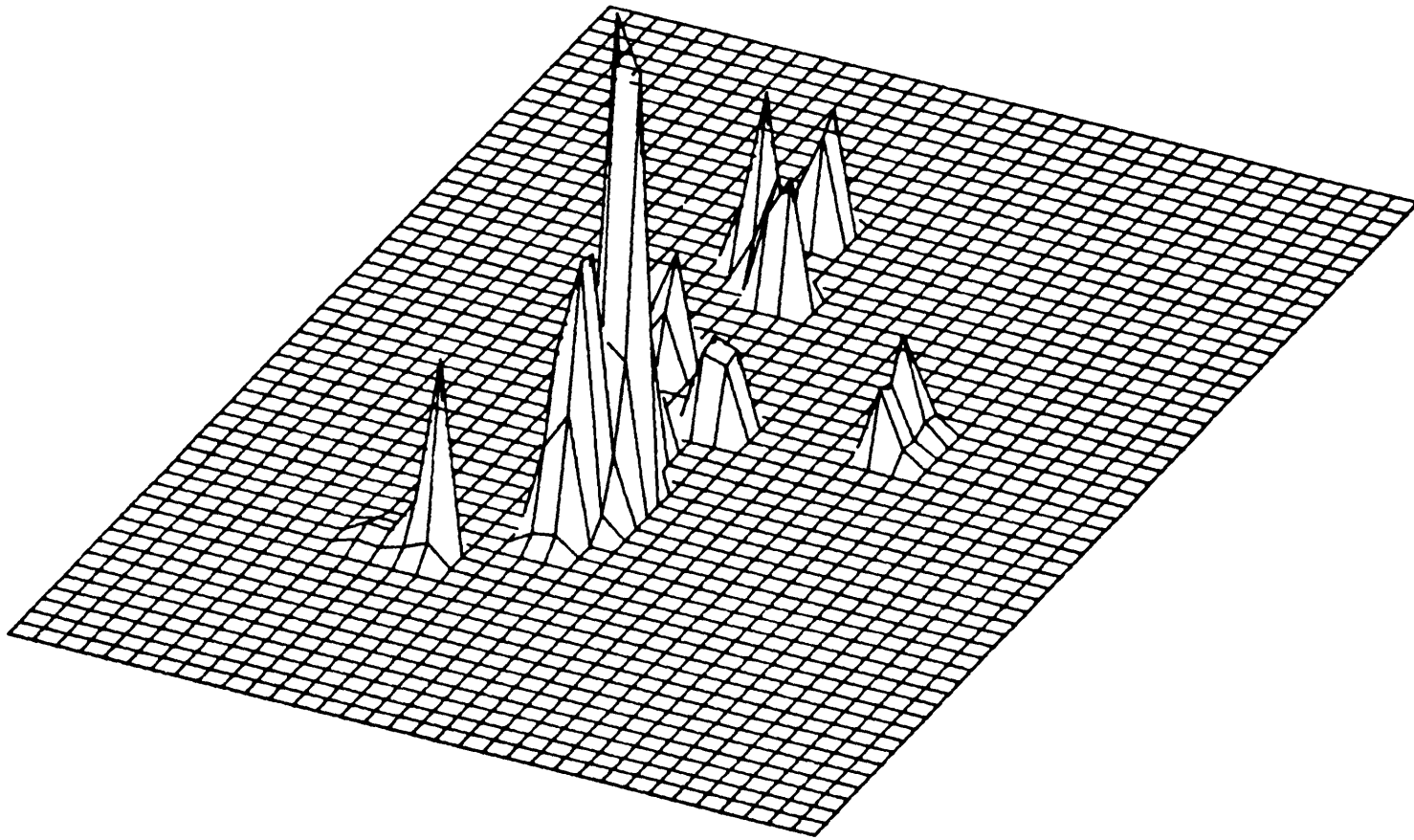


FIG. 15

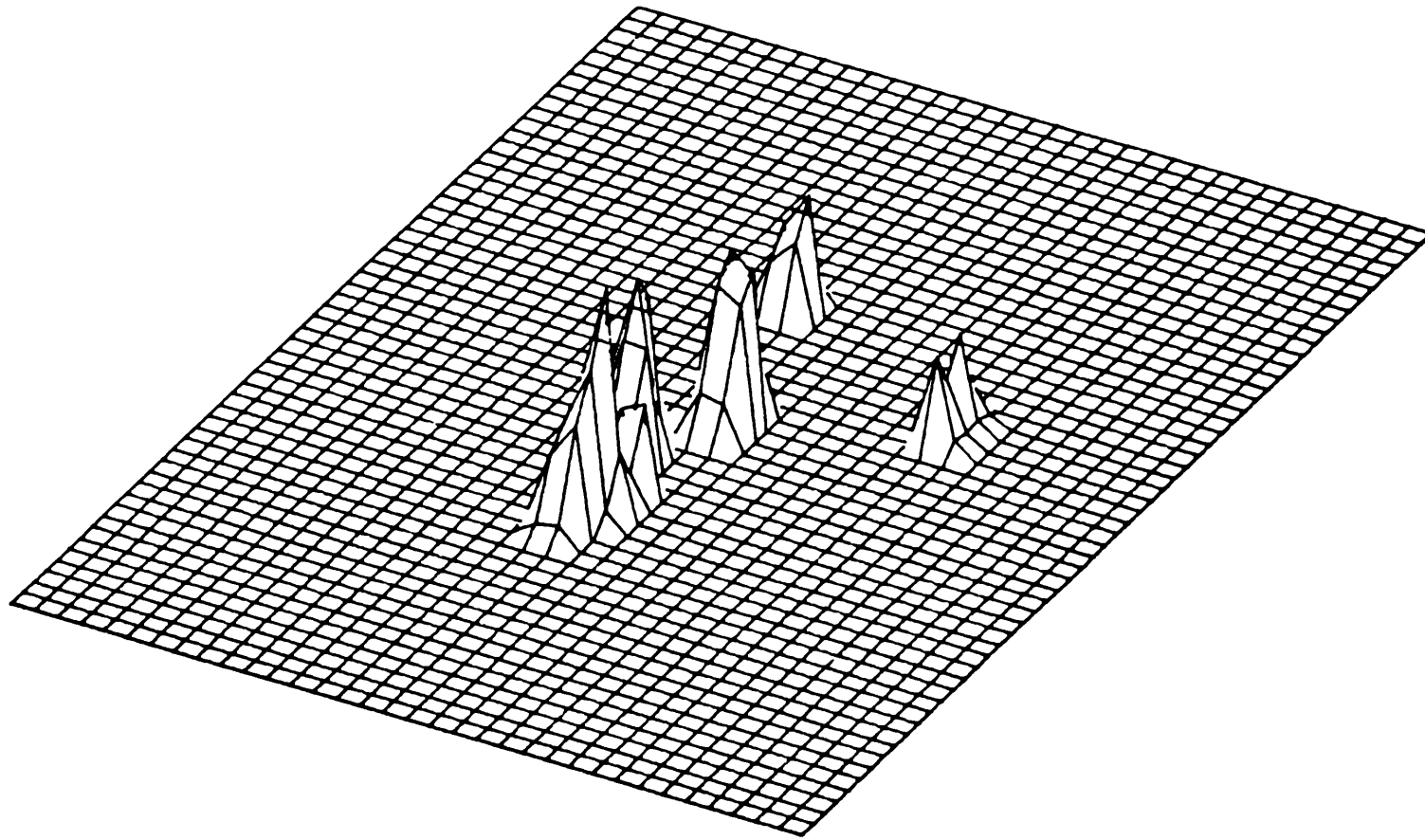


FIG 16.

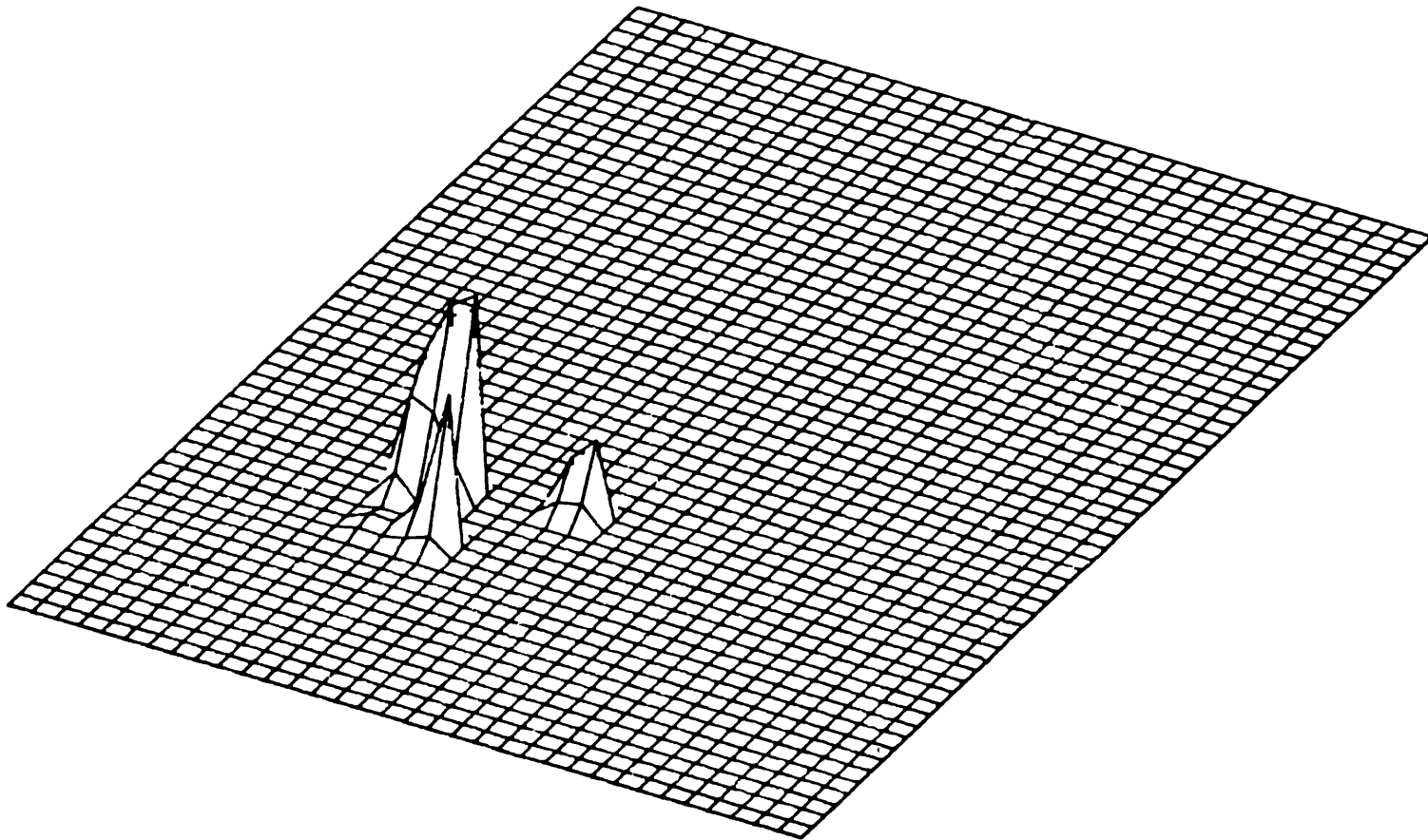


FIG. 17.

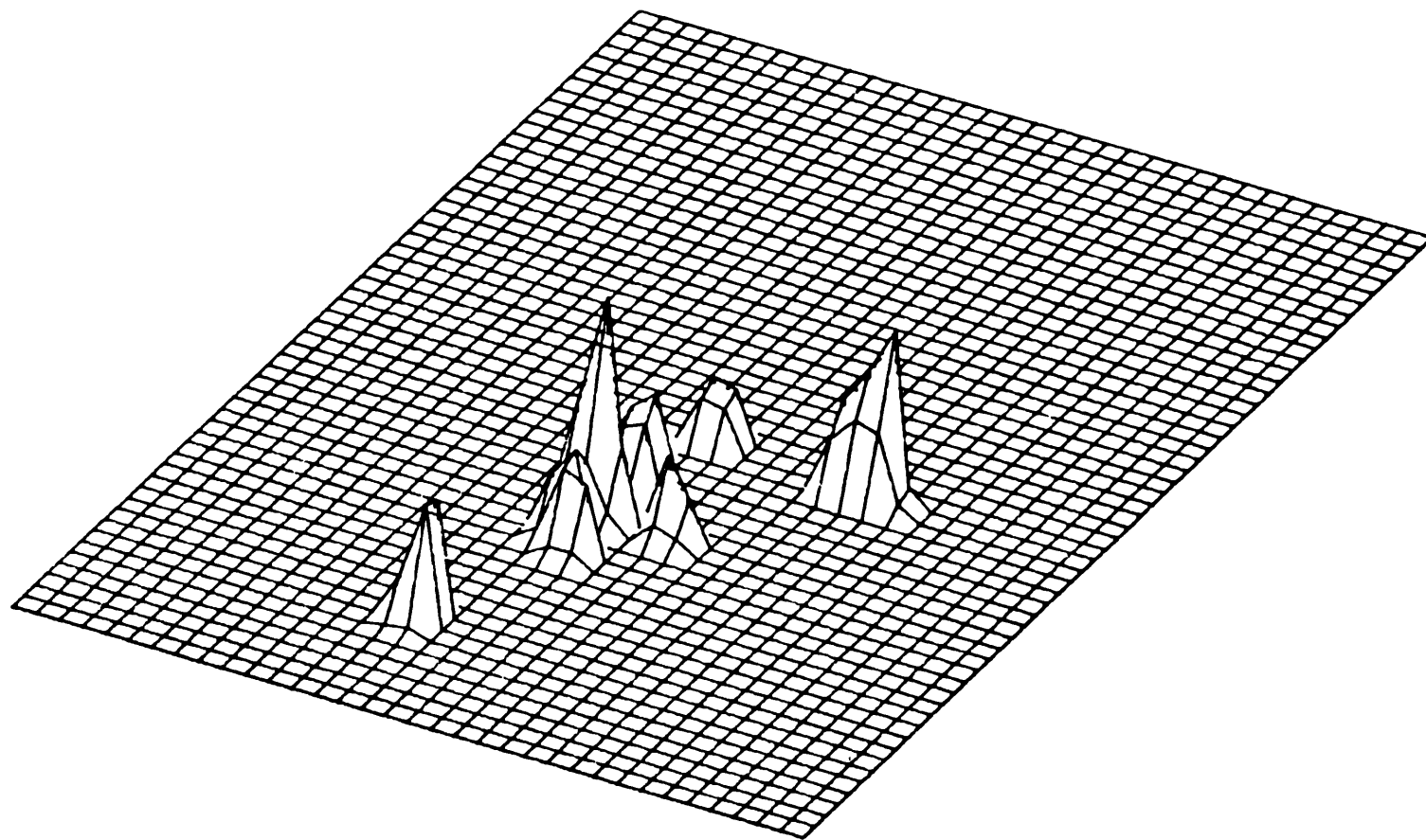
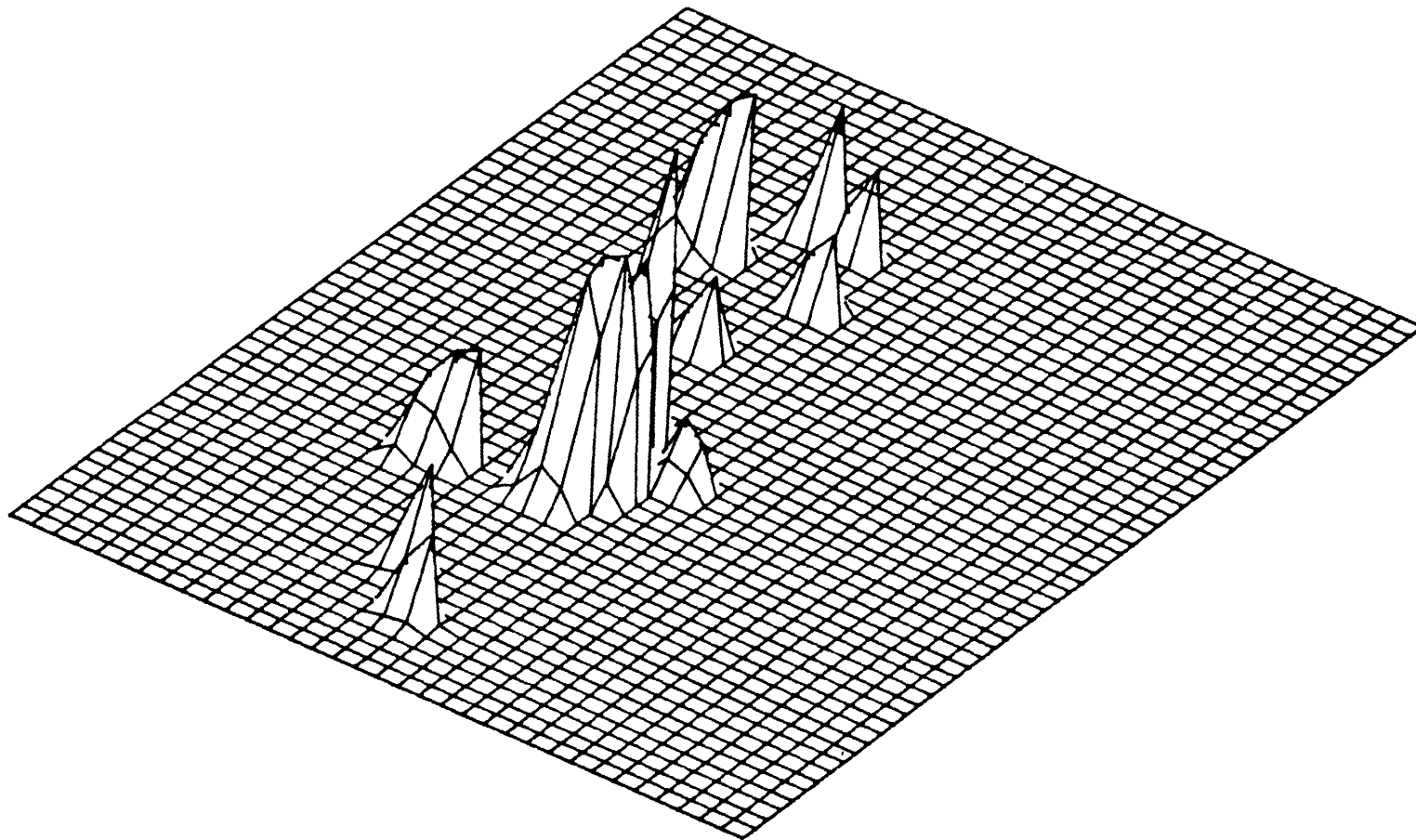


FIG. 18



APPENDIX III.

Appendix III.

During the summers of 1982 and 1983 females were trapped and brought into the laboratory. The data contained in this appendix are from 3 litters born to females in the laboratory. The first three tables are weights of young in individual litters. The final table summarizes the growth and development data for the three litters.

Table 1. Weights of young born to female 143-144; young
were born on 18 June 1982. All measurements are
reported in gms.

26 June	68.65	79.99	90.00
29 June	97.50	108.00	107.40
02 July	132.82	151.97	156.86
06 July	190.0	205.0	225.0
09 July	235.1	258.5	278.7
12 July	300.0	317.5	354.0
14 July	370.7	388.8	438.8
17 July	401.5	410.3	474.9
20 July	412.5	417.8	482.0

 Table 2. Weights of young born to female 539-540; young were born on 13 June 1983. All measurements are reported in gms. Young were individually marked on 19 July; columns preceding and including this date are individual animals.

21 June	50.85	56.28	62.88	64.00	64.52	67.40
25 June	67.40	75.20	85.89	93.97	94.94	
28 June	88.10	98.80	113.80	115.60	126.80	127.00
01 July	110.6	127.6	158.8	159.8	160.9	
05 July	148.0	170.9	216.1	219.4	219.5	220.6
07 July	167.8	193.2	226.3	245.9	250.8	252.9
09 July	191.5	216.6	253.6	277.2	279.6	284.2
11 July	214.6	239.6	287.3	313.7	315.0	320.8
13 July	236.7	259.5	316.4	341.5	346.5	354.0
15 July	266.3	293.8	357.7	383.5	389.9	398.5
17 July	289.8	317.3	391.5	419.1	432.6	434.4
19 July	313.9	346.8	424.1	455.4	463.2	471.4
21 July	350.0	350.0	450.0	500.0	500.0	550.0
24 July	350.0	350.0	500.0	550.0	500.0	550.0
26 July	350.0	375.0	550.0	600.0	800.00	600.0
28 July	375.0	375.0	575.0	1075.0	1075.0	625.0
30 July	405.0	415.0	580.0	645.0	655.0	580.0
01 Aug.	500.0	500.0	750.0	775.0	800.0	900.0
03 Aug.	600.0	600.0	900.0	900.0	975.0	1000.0
05 Aug.	600.0	550.0	950.0	950.0	1005.0	1005.0
07 Aug.	700.0	700.0	1100.0	1100.0	1200.0	1300.0
10 Aug.	850.0	850.0	1200.0	1025.0	1250.0	1250.0

 Table 3. Weights of young born to female 545-955; young were born on 11 June 1983. All measurements are in gms. Young were marked on 13 July; columns proceeding, and including, that day are individual animals.

21 June	073.62	079.46
25 June	99.08	117.28
28 June	113.8	149.8
01 July	168.5	204.9
05 July	225.9	274.0
07 July	260.1	321.3
09 July	297.2	362.2
11 July	337.4	441.4
13 July	375.5	448.5
15 July	432.9	512.6
17 July	479.0	576.5
19 July	511.9	607.8
21 July	650.0	750.0
24 July	550.0	700.0
26 July	650.0	750.0
28 July	800.0	1075.0
30 July	750.0	875.0
01 July	850.0	950.0
03 August	1000.0	1200.0
05 August	1050.0	1250.0
08 August	1200.0	1400.0
10 August	1200.0	1450.0

Table 4. Summary of growth and development of young from three litters, born to females in the laboratory during the summers of 1982 and 1983.

	Litter		
	1	2	3
Adult female weight	2.4 kg	2.6 kg	1.9 kg
Number of young	6	3	2
<u>Weight/young</u> (day 7 for litters 1 and 2; day 10 for litter 3)			
X	60.99 gm	79.55 gm	76.54 gm
SD	6.18	10.68	4.13
Range	50.85-67.40	68.65-90.00	73.62-79.46
<u>Wean Weight/young</u>			
X	281.83 gm	428.90 gm	329.70 gm
SD	44.65	40.08	45.96
Range	214.6-320.8	401.5-474.9	297.2-362.2

Overall Litters

Weight/young (7 days)
(excluding litter 3)

X	=	67.17 gm
SD	=	11.17
Range	=	50.85-90.00

Wean Weight/young

X	=	330.64 gm
SD	=	76.52
Range	=	214.60-474.90

The following other developments were noted:

- (1) Eyes were closed at birth but in all individuals opened between 26 and 28 days.
- (2) Young were born with very fine hair, by two weeks the skin no longer showed and there was enough hair to mark the young with fur dye.
- (3) I do not know precisely when the young began to eat solid food as they were never active in my presence. I would estimate that young began to take solids at about three weeks of age, they were certainly eating solid food by 4 weeks of age.

The litter of 2 young (litter no. 3) are excluded from the overall measures at 1 week since the first weights of those young were taken at 10 days. Weaning is assumed to occur at approximately 4 weeks of age.