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Reproductive Behavioral and Physiological Traits in Domestic, Wild, and Hybrid Ovis

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REPRODUCTIVE BEHAVIORAL AND PHYSIOLOGICAL TRAITS IN DOMESTIC, WILD, AND HYBRID *OVIS*

by

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Kara-Lynn Crocker-Bedford

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ABSTRACT

Reproductive Behavioral and Physiological Traits

in Domestic, Wild, and Hybrid *Ovis*

by

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Utah State University, 1982

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Department: Biology

This study was part of a program to develop new genotypes of sheep (*Ovis* spp.) and goats (*Capra* spp.) which are more useful for food and fiber production. The study examined the influence of domestication on behavioral and physiological traits of ewes and lambs, the influence of a single or twin offspring on ewe and lamb behaviors, and general relationships between ewes and lambs during the lambs' first month of life.

Domestication has caused the intensities of observed traits to diverge greatly from the tendencies shown by wild populations. Domestication has produced increases in measurements associated with maternal care, discovery learning, tolerance or inclination for closeness with conspecifics, length of the breeding season, fertility, birth weight, and growth rate. Behaviors associated with imitative learning have decreased with domestication. Domestication has not altered length of estrous cycle nor length of gestation. The partly domestic groups were intermediate to the most domestic and wild groups for three traits: maternal care, birth weight, and growth rate. However, other hybridization factors apparently altered the intermediate position of the partly domestic groups for the remaining traits: learning in the young, proximity of conspecifics, and fertility. The study's findings indicated that the development of new crossbreeds is an advantageous method of improving sheep and goat productivity.

Some behavioral differences between ewes and their single lambs and ewes and their twin lambs resulted from the earlier physical development of singles as compared to twins: Singles played more and spent less time close to their mothers. Mothering capacities, sibling competition, and a sibling bond caused behavioral differences between ewes and their twin young and ewes and their single young: Twins suckled more, gained less weight, spent more time close to their mothers, stood more, and received less sniffing from their mothers than did singles. The ewe-lamb bond did not vary between ewes and their single lambs and ewes and their twin lambs.

The high occurrence of simultaneous behaviors and the maintenance of close contact between ewes and their offspring and between twins contributed to the cohesion and organization of the flock.

(136 pages)

INTRODUCTION

The human population of the world is currently at 4.5 billion, and it is predicted to reach 6 billion by the year 2000. As a consequence present food shortages, already critical in parts of the world, will grow in severity. In addition to the increasing need for food in general, many countries are faced with shortages of food protein.

Although the earth's croplands can yield more food grain through improved agricultural practices, only about 10 percent of the world's land surface is comprised of agricultural land. On the other hand, as much as 40 percent of the earth's land surface is classified as range-land--lands unsuitable for cultivation but suitable for grazing (Hannah 1975). Rangelands can provide food for human populations only through the production of meat by wild and domestic herbivores which use the forage resources of these areas.

On a worldwide basis, domestic sheep and goats are the major converter of rangeland forages to human foods (Spillett et al. 1979). Sheep and goats were among the first animals domesticated by man (Zeuner 1963), and today there are over 900 recognized breeds or strains of domestic sheep (O. aries) and over 250 breeds of domestic goat (C. hircus) (Mason 1969, Terrill 1979). More than half of the domestic ruminants found in the developing nations are sheep (Spillett et al. 1979). In these countries, sheep and goats are especially important in the economies of the many nomadic and pastoral peoples. Sheep and goats provide meat, milk, and wool or hair and are associated with few cultural or religious restrictions throughout most of the world. As well as these advantages, domestic sheep and goats exhibit high fertility, adaptability to many environments, rapid growth rate, efficient conversion of forage into animal tissues (Spillett et al. 1979), and are easily herded.

Wild sheep have been a successful group in terms of attaining a wide geographic distribution and a variety of forms: 36 to 40 races exist today (Geist 1971). Other attributes of wild sheep which are desirable for animal protein production are the high reproductive rates and large size of certain species, efficient conversion of forage into animal tissues, and excellent meat quality (Spillett et al. 1979).

In addition, despite a wide variation in karyotypes, most sheep genotypes (species, subspecies, races, or breeds) are interfertile as are most goat genotypes. The International Sheep and Goat Institute (ISGI) was established primarily to take advantage of this interfertility in order to develop new genotypes of sheep and goats that are even more useful for the production of food and fiber. The present study, as part of the main program of the ISGI, had three objectives.

The first objective was to document differences among the various groups used in the ISGI's program, in several behavioral and physiological traits which are important in ungulate production. These traits are maternal care, learning in the young, proximity of conspecifics, breeding parameters, fertility, birth weight, and growth rate. Two suppositions were formed. First, the groups which have been under domestication longer exhibit the greatest departure from wild populations for the traits. Second, the hybrid offspring of domestic and wild or domestic and semi-domestic parents are intermediate to domestic and wild stock for the characteristics.

The animals belonging to the wild genotypes used in this study had been living under captive conditions for several generations. This situation was a favorable one for the study's purposes, because both the wild and domestic animals that were studied had therefore had similar environments in which to develop their learned behaviors and traditions. Thus, differences between the study's domestic and wild animals were more likely to be genotypically determined than environmentally determined.

The second objective was to compare the behaviors of ewes and their single offspring with the behaviors of ewes and their twin offspring during the lambs' first month of life. Since domestication generally has led to higher fertility, it is worthwhile to study the effects of the higher fertility on the behavior of ewes and their twin lambs. Such study could enhance our understanding of lamb abandonment, lamb survival, and lamb growth rate. Three suppositions were considered. First, ewes and their single young form a stronger bond than do ewes and their twin young. Second, certain behavioral differences between single lambs and twin lambs are caused by physical developmental differences between singles and twins. Third, mothering capacities, sibling competition, and a sibling bond cause behavioral differences between ewes and their single young and ewes and their twin young.

The third objective was to estimate the general relationships between ewes and their lambs during the lambs' first month of life. It is important to consider aspects of the ewe-lamb relationship which indicate tendencies common to different species and breeds of sheep. Two suppositions were formulated. First, the ewe-lamb bond undergoes changes as the lamb grows older. Second, the ewe-lamb bond contributes to the cohesion of the flock.

REVIEW OF LITERATURE

The Influence of Domestication on Ewe and Lamb Traits

Quantitative comparisons of the behavioral patterns of wild and domestic sheep have not been attempted in previous studies. Observations of wild sheep indicate that they exhibit considerable aggressiveness, and that the social transmission of acquired patterns of behavior is an important mode of adaptation in wild sheep societies (Geist 1971). It has been suggested that domestication has induced changes in these behavioral traits, so that domestic sheep show an increased docility and a reduced ability for certain kinds of learning (Spillett et al. 1979, Torres-Hernandez and Hohenboken 1979, Gluesing et al. 1980). Several workers have considered behavioral differences between breeds of domestic sheep. Park's (1979) review indicated breed differences have been found for mating activity of rams, periods of grazing, individual space requirements while grazing, and social dominance behavior.

Studies comparing specific behaviors of a domestic species with those of the related wild species have generally used canids, rodents, and gallinaceous birds as subjects. Fox's (1976) study of prey-catching and killing behavior in beagles and coyotes showed that the complete temporal pattern of catching, killing, and ingesting the prey was shortened and disorganized in the beagles in contrast to the coyotes. Research with the Norway rat indicated that domestic rats exhibited greater docility, less activity, and reduced reactivity to novelty or stimulus change in comparison to their wild counterparts (Price and Loomis 1973, Huck and Price 1976, Price and Huck 1976). Also, in a study of rat maternal behavior, Price and Belanger (1977) found significant quantitative differences in pup-retrieval and nest-building between wild and domestic rats. Domestic mothers were less efficient at pup-retrieval but more efficient at nest-building in comparison to their wild counterparts. With regard to gallinaceous birds, the domestic chicken exhibits decreased parental behavior in comparison to jungle fowl (Hale 1962, Immelmann 1980).

Some of these studies have also included wild-domestic hybrids with the subject groups. The results showed that F_2 and F_3 generation coyote-beagle hybrids, and F_1 generation wild-domestic rat hybrids were intermediate to the parental strains for the variables under consideration (Price and Loomis 1973, Boreman and Price 1972, Fox 1976). However, other evidence indicates that hybridization sometimes results in more vigorous hybrid offspring than either of the parent strains, due to the phenomenon of heterosis, or "hybrid vigor" (Strickberger 1968). Hybridization programs using different breeds of domestic sheep have led to increased productivity by improving traits such as fertility (Carter 1979). Previous research at the ISGI showed that heterosis occurred in the cases of body size and horn characteristics of the wild-domestic sheep crosses (Spillett et al. 1979).

The breeding of wild animals in captivity sometimes results in certain genetic changes, due to the differential selection pressure in the wild and captive environments (Price and King 1968). Price's (1967, 1970) observations of the deermouse indicated that even in the absence of conscious selection, laboratory breeding over successive generations produced genetic changes in reproductive performance and behavior. Laboratory-maintained animals showed an increased fertility and a reduced reactivity to unfamiliar stimuli in comparison to wild-caught individuals.

Changes in the morphology and physiology of animals due to domestication are less difficult to assess than are those associated with behavior. For example, it is apparent that certain reproductive physiological characteristics of sheep, such as length of the breeding season and fertility, have been altered in many breeds of domestic sheep as compared to wild sheep.

Most wild sheep species breed during the fall, although the Desert Bighorn sheep exhibits a very extended breeding season (Hansen 1965, Geist 1971). Wild sheep are generally regarded as less prolific than many domestic sheep breeds, but exceptions to this exist. For example, wild sheep from an Asiatic Mouflon x Urial hybrid zone in Iran display a higher lambing rate than do domestic sheep in Iran (Foote 1979). Domestic sheep breeds show considerable variation for these two characteristics. Breeds from more tropical regions are capable of breeding during any month (Hafez 1952, Foote 1979), and some breeds bear two or three young per lambing (Foote 1979). Selective breeding has also sought large body size and rapid growth rate in domestic lambs.

Table 1 gives further information on the three breeding parameters studied: season of breeding, length of estrous cycle, and length of gestation. Table 2 shows additional information on fertility and weight at birth.

Table 1. Information on three reproductive physiological characteristics of some sheep and goat species for which the traits have been measured.

Characteristic	Description	Species*	Measurement	Source
Season of breeding	the months when ewes or does are sexually receptive and hence, when mating occurs	Argali	Oct. thru Dec.	Hafez 1952
		Bighorn	Nov. thru Dec.	Asdell 1964, Geist 1971
		domestic sheep (Rambouillet breed)	throughout year, highest Oct. thru Jan.	Harris 1954
		Mouflon	Oct. thru Jan. or Oct. thru Nov.	Hafez 1952, Müller-Using 1972
		Urial	Sept. thru Nov. or Dec. thru Feb.	Bannikov and Heptner 1972
		domestic goat	Sept. thru Mar.	Geist 1960, Sadleir 1969
		Ibex	Oct. thru Nov. or Dec. thru Jan.	Hafez 1952, Grzimek and Nievergelt 1972
		Persian Wild Goat	Dec. thru Jan.	Schultze-Westrum 1972
Length of estrous cycle	the period from the beginning of one estrus (heat) to the beginning of the next estrus (Nalbandov 1958)	domestic sheep (Rambouillet breed)	$\bar{x}$=17.5 days range=13-21 days	Robinson 1959

Table 1. Continued.

Characteristic	Description	Species*	Measurement	Source
		domestic goat	$\bar{x}$=19.4 days range=12-24 days	Robinson 1959
Length of gestation	the period from conception to birth of the young	Bighorn	180 days or 174 days	Asdell 1964, Geist 1971
		domestic sheep	140-150 days	Hersher et al. 1963
		(Rambouillet breed)	143-159 days or 151 days	Asdell 1964, Robinson 1959
		Mouflon	146-161 days or 150 days	Kramer 1971, Müller-Using 1972
		Urial	147-188 days	Bannikov and Heptner 1972
		domestic goat	149 days 151 days	Shelton 1960, Asdell 1964
		Ibex	165-170 days or 150-180 days	Asdell 1964, Grzimek and Nievergelt 1972
		Persian Wild Goat	150 days	Schultze-Westrum 1972

*Species are fully identified by their scientific names in the Appendix.

Table 2. Information on two parturient physiological characteristics of some sheep and goat species for which the traits have been measured.

Characteristic	Description	Species*	Measurement	Source
Number of young born per female	The number of young born per female giving birth, whether dead or alive	Argali	most commonly 1, sometimes 2	Heptner et al. 1961 as noted in Geist 1971
		Bighorn	most commonly 1, very rarely 2	Welles and Welles 1961, Geist 1971
		domestic sheep	most commonly 1 or 2, occasionally 3, rarely 4	Robinson 1959, Asdell 1964
		Mouflon	most commonly 1, rarely 2	Bannikov and Heptner 1972
		domestic goat	most commonly 2, frequently 1 or 3, rarely 4 or 5	Robinson 1959, Asdell 1964
		Ibex	most commonly 1, rarely 2	Grzimek and Nievergelt 1972
		Persian Wild Goat	most commonly 1 or 2, occasionally 3	Schultze-Westrum 1972
Weight at birth	The weight of the young, taken 2 to 24 hours after its birth	Bighorn	$\bar{x}$=3.3 kg	Geist 1971
		domestic sheep	$\bar{x}$=4.5 kg for single lambs, $\bar{x}$=4.0 kg for twin lambs	Ewbank 1967
		domestic goat	$\bar{x}$=1.5 kg	Galeon 1951

*Species are fully identified by their scientific names in the Appendix.

The Influence of a Single or Twin Birth on Ewe and Lamb Behaviors

Few studies have compared the behavior and growth of single lambs and twin lambs, or their interactions with their mothers, and only domestic sheep have been used for subjects. Munro (1956) and Ewbank (1964, 1967) found that twins suckle more frequently than do singles, although Morgan and Arnold (1974) did not observe this distinction. Twin offspring receive less milk per lamb than do single offspring, and thus twins gain less weight than do singles during the preweaning period of growth, despite greater milk production in mothers of twins than in mothers of singles (Hafez and Scott 1962, Slen et al. 1963, Ewbank 1967). Ewbank (1967) also observed that ewes with twins appeared to prevent their young from suckling more frequently than did ewes with singles. Morgan and Arnold (1974) found differences between singles and twins in the distances they maintained from their mothers for different behaviors. They suggested these differences were due to ewes with twins "requiring" their young to stay closer in order to care for both of them, or to twins keeping closer in competition for maternal care. Observations of the activity patterns in large flocks of sheep indicated that singles were generally more active than twins (Gluesing et al. 1980).

General Relationships Between Ewes and Their Lambs

Lent (1974, p. 36), in his review of mother-young relationships in ungulates, notes that "ungulate mothers and their infants form closed social bonds to the exclusion of other individuals." The rapid, early formation of a specific bond between a ewe and her newborn lamb has been recognized by several workers (Collias 1956, Hersher et al. 1963, Smith 1965, Smith et al. 1966, Sharafeldin and Kandeel 1971). Morgan and Arnold (1974) observed the spatial and behavioral relationships between ewes and their single or twin young during the young's first month of life. Their study demonstrated that the maternal-filial attachment continues throughout this period, as shown by the maintenance of close contact between a ewe and her lamb, especially when both are lying or walking. However, Morgan and Arnold (1974) and other workers (Munro 1956; Ewbank 1964, 1967; Grubb 1974; Graves et al. 1977) have also observed signs of an increasing independence in the growing lamb, and a decreasing responsiveness in the ewe.

Information about the development of the mutual recognition process between ewes and their lambs, and the roles of sensory cues in the process, contributes to an understanding of the sheep's rare behavioral patterns. Ewes recognize their offspring within a day of parturition by relying on olfactory and visual cues at close quarters, and on auditory and different visual cues at greater distances (Collias 1956, Tschanz 1962, Hersher et al. 1963, Smith et al. 1966, Lindsay and Fletcher 1968, Morgan et al. 1975, Shillito and Alexander 1975, Alexander 1977, Alexander and Shillito 1977, Walser 1978). As well as playing a part in the recognition process, the vocalization of lambs attracts attention and helps ewes to locate their lambs' positions (Lindsay and Fletcher 1968, Morgan et al. 1975, Shillito 1975, Shillito and Alexander 1975, Alexander 1977, Alexander and Shillito 1977, Walser 1978). The relative importance of olfactory, visual, and auditory cues in the lambs' recognition of their mothers is unclear, but it is apparent that most lambs cannot identify their mothers until 11 days after birth (Tschanz 1962, Morgan and Arnold 1974, Arnold et al. 1975, Shillito 1975, Shillito and Alexander 1975, Alexander 1977, Alexander and Walser 1978).

METHODS

The study was conducted at joint facilities of the Utah State University Animal Science department and the International Sheep and Goat Institute. The seven enclosures where the animals were kept averaged 12 m x 15 m in size, and shelter was available within each pen. A daily feeding took place prior to 0800, when alfalfa was placed in mangers or feed troughs. Water in metal basins was always available. All the ewes and does were at least 3 years of age.

Parental Strains

American Rambouillet

The Rambouillet was bred primarily as a fine wooled sheep, with excellent body conformation. It originated from several strains of Spanish Merino which were imported to France from 1786 to 1803. Initial development of the breed took place only on a government-owned, experimental farm at Rambouillet. Rambouillet were imported to America from France during the period of 1840-60, and from Germany during the period of 1882-1900. The American Rambouillet produces a very acceptable fleece and satisfactory mutton, and it responds well to range conditions (Briggs 1969, Mason 1969).

Karakul

The primary virtue of the Karakul breed is its ability to produce fur pelts from young lambs, although its milk is also valued in its native country. It is native to Uzbekistan, a republic of the U.S.S.R.

in central Asia. The breed's origins are obscure, but it was probably formed by the crossing of the long-tailed Danadar sheep and the fat-tailed Arabi breed. The few Karakuls introduced in America were imported from 1909-14. The Karakul is a hardy breed noted for longevity. Its ability to survive under adverse circumstances is due partially to the broad, fat tail, which serves as a nutrient reserve (Briggs 1969, Mason 1969).

Barbados

The Barbados, or West Indian Blackbelly, is a haired breed which was imported to the West Indies from West Africa in the early 1900's. Its ancestral stock was probably the West African Long-legged sheep. After the Barbados was brought to America in the mid 1900's, it underwent further selective breeding. The breed is noted for its high fertility (Mason 1969, Terrill 1979).

European Mouflon

Most workers hold the view that the European Mouflon's original range covered much of the mountainous lands of southern Europe, but their numbers on the mainland were decimated, leaving only a small population on the islands of Sardinia and Corsica (Zeuner 1963, Walker 1964). Zeuner (1963) and others maintain that the Mouflon was the ancestor of certain European domestic breeds. However, on the basis of hemoglobin alleles and other evidence, it also has been hypothesized that the European Mouflon originated from an introduction of an archaic domestic sheep to the islands about 500 B.C. This strain then rapidly reverted to a feral and later to a wild form (Bunch et al. 1978). Whichever the case, the island strain is the ancestral stock of populations introduced in Europe during the 1800's, and of captive populations maintained in America.

Hawaiian Blackbuck

The European Mouflon was intentionally introduced in Hawaii from 1954-62. Later, Mouflon were bred with existing feral domestic stock as part of a program to reduce vegetational damage, and the resulting Mouflon-domestic hybrid was called the Hawaiian Blackbuck. The Hawaiian Blackbucks living under captive conditions on the mainland are descendants of the feral hybrid population (Kramer 1971).

Alpine and Toggenburg

The Alpine breed of goat originated in the Swiss Alps, although the Alpine goats which were introduced for breeding stock in the United States came from the French Alps. The Toggenburg was first bred in Switzerland, and is the oldest breed of dairy goats in America. The does of both breeds are excellent milk producers (Pegler 1965, Briggs 1969).

Behavioral Traits

Data collection

Identification and placement of ewes and lambs

Two to 24 hours after the birth of each lamb, metal, coded tags were fastened into the lamb's ears. To aid in differentiating the young, distinctive markings were recorded, or colored plastic bands were tied to the ear tags. All the ewes were identified by large, numbered ear tags. The sheep were placed in five pens so that the animal density was approximately equal, and the ages and genotypes of the lambs were varied in each pen.

Observations

Animals were observed 1600 hours, from which 608 hours of quantitative data were gathered for the present analysis. Observations of the behavior of ewes and lambs were made at 5 day intervals until each lamb was 30 or 31 days old. Each age category encompassed 2 days so that the individual young could be observed at the appropriate age periods. Thus, the first age category corresponded to 0 or 1 day of a lamb's age, the second category to 5 or 6 days, the third category to 10 or 11 days, the fourth category to 15 or 16 days, the fifth category to 20 or 21 days, the sixth category to 25 or 26 days, and the seventh category to 30 or 31 days.

Each ewe-lamb set (one set equaled one ewe with her young of the year) was observed for 1 to 4 hours at generally each of the seven age categories. Observations of each set were made at random between the hours of 0800 and 1800.

Data types

Two types of data were collected. The first type was termed a common behavioral pattern and the second type was called a rare behavioral pattern. A common behavioral pattern referred to an activity which was frequently displayed or which was usually of long duration. Observations of the common behavioral patterns were made at 5 minute intervals. The recorded counts were then transformed to the percentages of time that the ewe or lamb or both engaged in particular activities. These behaviors formed the basis of time budget analysis, or how the animals allocated their time in various activities.

A rare behavioral pattern referred to an activity which was infrequently displayed and which was of short duration. Observation of the rare behavioral patterns was continuous. The recorded counts were then transformed to the number of occurrences per hour that the ewe or lamb exhibited certain behaviors.

Behavioral patterns

Common behavioral patterns

The possible common activities of the ewe were: (1) lying (without feeding), (2) standing (still without feeding), (3) feeding (from a manger), and (4) moving (walking or running). With regard to the nursing and suckling activities, emphasis was placed on the offspring's role rather than the mother's. The percentage of time that the ewe spent nursing was included within the percentage for the standing behavior. The possible common behaviors of the lamb were: (1) lying (without feeding), (2) standing (still without feeding), (3) feeding (from a manger), (4) moving (walking or running), (5) playing (this activity had priority over any simultaneous activity), and (6) suckling (this behavior had priority over any simultaneous behavior). Combinations of these behavioral patterns of the mother and young were statistically discrete. In addition to the ten individual activities given above, a combined behavior was also calculated--the percentage of time that each ewe-lamb set spent simultaneously engaged in the same behaviors, or the amount of time that both a ewe and her lamb spent lying, standing, feeding, or moving.

Distance categories

The percentage of time that individual animals spent at varying distances from each other, regardless of the activity, also was analyzed. Three distance categories were established: (1) close--1 m or less, (2) intermediate--between 1 and 3 m, and (3) far--greater than 3 m. These meter lengths were used so that any bias owing to varying pen size was minimized. Distances were analyzed between mother and young for the three distance categories, between siblings for close distance, and between alien young for close distance.

Rare behavioral patterns

Six rare behavioral patterns were observed. (1) The ewe sniffing the lamb was an occurrence of sniffing by the mother when the young was not suckling. (2) The lamb sniffing the ewe was an occurrence of sniffing by the young when it was not suckling. (3) The ewe vocalizing was an occurrence of calling by the mother while sniffing the young, in answer to the young's call, while searching for the young, or under undetermined circumstances. (4) The lamb vocalizing was an occurrence of calling by the young while being sniffed by the mother, in answer to the mother's call, while searching for the mother, or under undetermined circumstances. (5) The ewe horn threatening or butting an alien lamb was an occurrence of the mother lowering her head and aiming the frontal area at a lamb other than her own, or actually pushing an alien lamb with her head. (6) The ewe preventing her own lamb from suckling was an occurrence of the mother not allowing her young to suckle by walking forward a few paces, by stepping over her young, by turning away sharply, or by flexing a hind leg.

Ewe-lamb sets

Number and genotype of ewe-lamb sets

Table 3 indicates the five genotypic groups and the number of ewe-lamb sets observed during the study of ewe and lamb behavioral patterns. One set (one ewe with her offspring of the year) equaled one experimental unit. Each twin was a subsample.

Statistical tests

Analysis of variance and planned comparisons

For each behavior, at each of the seven age categories, the ewe-single lamb sets and the ewe-twin lamb sets of the five genotypes (a total of ten groups) were compared by one-way analysis of variance with completely randomized design. If a primary test of a behavior at a specific age category indicated a significant difference (at $P<.01$ or at $P<.05$), five major planned comparisons were made using the *F* test at the specific age.

For a significant age period, the average of all the ewe-single lamb sets and the average of all the ewe-twin lamb sets were compared for the first of the planned comparisons. The mother-single young sets and the mother-twin young sets were combined within each genotypic group for the remaining four comparisons: (1) a comparison of the five genotypic groups (MM vs. MR vs. BR1 vs. BR2 vs. KR), (2) a comparison of the three groups with Rambouillet ewes and half-Rambouillet lambs versus the group with Mouflon ewes and Mouflon lambs [(MR + BR1 + KR) vs. MM], (3) a comparison of the group with Rambouillet mothers and

Table 3. The genotypic groups and number of ewe-lamb sets* observed in a study of ewe and lamb behavior during the lambs' first month of life.

Age of young (days)	Genotype									
	BR1[a]		BR2[b]		KR[c]		MR[d]		MM[e]	
	Single	Twin	Single	Twin	Single	Twin	Single	Twin	Single	Twin
0-1	2	4	3	3	3	2	2	4	4	2
5-6	2	4	3	3	3	2	2	4	4	2
10-11	2	4	3	3	3	2	2	4	4	2
15-16	2	3	3	3	3	2	2	4	4	2
20-21	2	4	3	3	3	2	2	3	4	2
25-26	2	4	3	3	3	2	2	4	4	2
30-31	2	4	3	3	3	2	2	3	4	2

*One set equaled one ewe with her young of the year, which equaled one experimental unit, i.e., one ewe with a single offspring counted as much in statistical tests as one ewe with twin offspring.

[a] A lamb in this group had a Barbados sire and a Rambouillet dam.

[b] A lamb in this group had a Barbados-Rambouillet sire and a Barbados-Rambouillet dam.

[c] A lamb in this group had a Karakul sire and a Rambouillet dam.

[d] A lamb in this group had a Mouflon sire and a Rambouillet dam.

[e] A lamb in this group had a Mouflon sire and a Mouflon dam.

Mouflon-Rambouillet young versus the group with Mouflon mothers and Mouflon young (MR vs. MM), and (4) a comparison of the group with Rambouillet ewes and F_1 Barbados-Rambouillet lambs versus the group with F_1 Barbados-Rambouillet ewes and F_2 Barbados-Rambouillet lambs (BR1 vs. BR2).

Thus, for a significant age period, the first planned comparison showed if the ewe-single lamb sets were significantly different from the ewe-twin lamb sets. The second comparison indicated if significant differences existed between any of the genotypic groups. The third comparison showed if the combined group of Rambouillet ewes and their crossbred young was significantly different from the group of Mouflon ewes and their purebred young. The fourth comparison was more group specific, since it considered only a possible difference between the Rambouillet, Mouflon, Mouflon-Rambouillet genotypes. The fifth comparison was also more group specific, since it involved pure and crossbred ewes, and first and second generation hybrid lambs with the same genotype.

t distribution

In addition, paired *t* tests were used to reveal if significant differences existed between the ewe-single lamb sets and the ewe-twin lamb sets, for the overall month.

Physiological Traits

Breeding

Length of breeding season

Data collection and number of animals. A sterilized

Mouflon-Rambouillet ram was placed with 16 Mouflon ewes on 20 August 1973 and with 19 Mouflon ewes on 25 August 1974. Each year, the beginning of the estrous season was observed with all the ewes present. After some of the ewes were removed to other pens to be bred (six ewes in 1973 and eight ewes in 1974), the remaining ewes were observed until the anestrous season began. In addition to observations of breeding activity, the brisket of the ram was painted with successively different colors to mark the rumps of estrous ewes.

Length of estrous cycle

Data collection and number of animals. A sterilized Dorset-Landrace ram was placed with two Karakul ewes from 28 October to 17 November 1974. Two sterilized Dorset-Landrace rams were placed with 30 Rambouillet ewes from 7 December 1973 to 13 February 1974. In conjunction with the observations for the season of breeding, data on the length of the estrous cycle of six Mouflon ewes were gathered from 24 September to 10 December 1973. Two Barbados ewes which were also in the Mouflon's pen were observed for breeding activity from 18 September to 22 October 1973. A sterilized Nubian buck was placed with 14 Alpine and Toggenburg does from 21 September to 10 December 1974. As in the observations for the breeding season, observations for the length of the estrous cycle were aided by painting the briskets of the rams and buck.

Statistical tests. One female equaled one experimental unit. Each estrous cycle was a subsample. The means and standard deviations of the lengths of the estrous cycle were calculated for the five groups, and the mean estrous cycle lengths were compared by one-way analysis of variance with completely randomized design. In addition, planned comparisons within the ewe groups and between the ewes and does were made using the F test.

Length of gestation

Data collection and number of animals. To measure gestation length, the dates of breeding and parturition were recorded for the individual females, and then the number of days between the dates was calculated. Table 4 presents the number of females observed in nine genotypic groups.

Table 4. The number of ewes or does used in nine genotypic groups for the measurements of gestation length and fertility.

Genotype of females	Number of females	
	Gestation length	Fertility
Barbados	2	2
Barbados-Rambouillet	7	7
Hawaiian Blackbuck	2	3
H. Blackbuck-Rambouillet	15	22
Karakul	2	2
Mouflon	5	19
Mouflon-Rambouillet	3	3
Rambouillet	37	55
Domestic goat (Alpine and Toggenburg)	12	18

Statistical tests. One female equaled one experimental unit. Each gestation was a subsample. The means and standard deviations of the lengths of gestation were calculated for the nine groups. The mean gestation lengths for five groups (BR1, BR2, KR, MM, MR) were compared by one-way analysis of variance with completely randomized design. Planned comparisons were made using the *F* test.

Parturition

Number of young born per female

Data collection and number of animals. As a measurement of fertility, the number of young born per female giving birth each year was recorded, including young which were dead at birth. Table 4 shows the number of females observed in nine genotypic groups. One female equaled one experimental unit. Each birth was a subsample.

Weight of young at birth

Data collection and number of animals. Each young was weighed 2 to 24 hours after birth. Table 5 indicates the number of single, twin, and triplet young observed in 12 genotypic groups.

Statistical test. One young equaled one experimental unit. The mean weights for five groups (BR1, BR2, KR, MM, MR) were compared by one-way analysis of variance with completely randomized design.

Weight of young at four ages

Data collection and number of animals. Certain lambs were weighed 2 to 24 hours after birth, at 2 days of age, at 7 days of age, and at 14 days of age. Table 5 shows the number of single and twin lambs observed in six genotypic groups.

Table 5. The number of single, twin, and triplet young used in 12 genotypic groups for the measurement of weight at birth, and the number of single and twin lambs used in six genotypic groups for the measurement of weight at four ages.

Genotype of young: Sire	Genotype of young: Dam	1, 2, or 3 in litter	Number of young: Weight at birth	Number of young: Weight at four ages
Barbados	Barbados	Single	0	
		Twin	2	
Barbados	Rambouillet	Single	8	5
		Twin	20	6
Barbados-Rambouillet	Barbados-Rambouillet	Single	6	4
		Twin	10	6
Hawaiian Blackbuck	Hawaiian Blackbuck	Single	2	
		Twin	3	
Hawaiian Blackbuck	Rambouillet	Single	2	2
		Twin	10	6
H. Blackbuck-Rambouillet	H. Blackbuck-Rambouillet	Single	12	
		Twin	6	
Karakul	Karakul	Single	2	
		Twin	0	
Karakul	Rambouillet	Single	5	3
		Twin	6	4
Mouflon	Mouflon	Single	13	2
		Twin	8	2
Mouflon	Rambouillet	Single	2	2
		Twin	9	6
Mouflon-Rambouillet	Mouflon-Rambouillet	Single	4	
		Twin	2	
Wild-domestic goat	Alpine and Toggenburg	Single	5	
		Twin	18	
		Triplet	12	

RESULTS

Behavioral Traits

Presentation of figures

Due to the volume of figures involved in the presentation of the results concerning lamb and ewe behavior, all the figures are grouped together at the end of the Results section. Figures 1 through 16 depict the percentages of daytime spent in common behaviors by lambs and ewes in single sets and twin sets through the first month of life for lambs. Figures 17 through 23 present the number of occurrences per hour of rare behaviors displayed by lambs and ewes in single and twin sets. Figures 24 through 27 show the percentages of daytime spent in selected common behaviors by lambs and ewes in genotypic sets through the first month of life for lambs. Figures 28 through 34 depict the number of occurrences per hour of rare behaviors displayed by lambs and ewes in genotypic sets. The remaining common behaviors, Figures 36 through 47, are given in the Appendix. The rare behaviors occurred while the common behaviors were in progress.

Single and twin sets

Common behavioral patterns

Percentages of daytime single lambs and their mothers spent engaged in common behaviors. On the average, of their first month of daytime life, single lambs spent 51 percent lying, 25 percent standing, 10 percent feeding, 8.5 percent moving, 2.8 percent playing, and 2.6 percent suckling (Figures 1-6). Of their daytime life during this month, mothers of singles spent 37 percent feeding, 31 percent standing, 26 percent lying, and 6.9 percent moving (Figures 7-10).

Random simultaneous percentages expected and simultaneous percentages observed, in common behaviors of singles and their mothers. By random chance, singles and their mothers should have lain simultaneously 13.3 percent of the time (51 percent x 26 percent), but they actually lay simultaneously 23.2 percent of the time. By random chance, singles and their mothers should have stood simultaneously 7.8 percent of the time (25 percent x 31 percent), but they actually stood simultaneously 13.4 percent of the time. By random chance, singles and their mothers should have fed simultaneously 3.7 percent of the time (10 percent x 37 percent), but they actually fed simultaneously 9.1 percent of the time. By random chance, singles and their mothers should have moved simultaneously 0.59 percent of the time (8.5 percent x 6.9 percent), but they actually moved simultaneously 4.2 percent of the time. In total, singles and their mothers should have simultaneously engaged in the same behaviors 25 percent of the time by random chance, but they actually spent 50 percent of the time simultaneously engaged in the same behaviors (Figure 11).

Percentages of daytime twin lambs and their mothers spent engaged in common behaviors. On the average, of their first month of daytime life, twin lambs spent 43 percent lying, 33 percent standing, 9.8 percent feeding, 9.7 percent moving, 1.3 percent playing, and 3.8 percent suckling (Figures 1-6). Of their daytime life during this month, mothers of twins spent 42 percent feeding, 28 percent standing, 21 percent lying, and 8.3 percent moving (Figures 7-10).

Random simultaneous percentages expected and simultaneous percentages observed, in common behaviors of twins and their mothers. By random chance, twins and their mothers should have lain simultaneously 9.0 percent of the time (43 percent x 21 percent), but they actually lay simultaneously 18.8 percent of the time. By random chance, twins and their mothers should have stood simultaneously 9.2 percent of the time (33 percent x 28 percent), but they actually stood simultaneously 16 percent of the time. By random chance, twins and their mothers should have fed simultaneously 4.1 percent of the time (9.8 percent x 42 percent), but they actually fed simultaneously 8.9 percent of the time. By random chance, twins and their mothers should have moved simultaneously 0.81 percent of the time (9.7 percent x 8.3 percent), but they actually moved simultaneously 3.7 percent of the time. In total, twins and their mothers should have simultaneously engaged in the same behaviors 23 percent of the time by random chance, but they actually spent 48 percent of the time simultaneously engaged in the same behaviors (Figure 11).

Distance categories

Percentages of daytime lambs and their mothers spent at close, intermediate, and far distances to each other. Twin young tended to stay closer to their mothers than did single young. During the lambs' first month of life, single lambs and their mothers spent an average of 53 percent of the daytime at close distance to each other (1 m or less), whereas twin lambs and their mothers averaged 62 percent of the daytime at close distance to each other (Figure 12). For the intermediate distance category (between 1 and 3 m) singles and their mothers averaged 18 percent of the daytime at this distance, and twins and their mothers spent an average of 16 percent of the daytime at this distance (Figure 13). Singles and their mothers spent an average of 29 percent of the daytime at far distance to each other (greater than 3 m), but twins and their mothers averaged 22 percent of the daytime at far distance to each other (Figure 14).

Percentages of daytime lambs spent at close distance to sibling and alien lambs. Sibling lambs spent more time together than did alien lambs. Twin young spent an average of 83 percent of the daytime at close distance to each other during their first month of life (Figure 15). Single lambs averaged 21 percent of the daytime and twin lambs averaged 22 percent of the daytime close to alien lambs (Figure 16).

Statistical treatments

By month. On a month-long basis, the single young spent significantly more time engaged in certain behaviors than did the twin young at $P<.05$: single lambs lay more, they played more, and they spent more time at far distance from their mothers. On the other hand, twin lambs stood more during their first month of life ($P<.01$).

By age class. The suckling behavior and distance categories indicated significant differences within an age class between single and twin young. Twin lambs suckled more at 20-21 days ($P<.05$), and twins were closer to their mothers at 20-21 days ($P<.01$) and at 30-31 days ($P<.05$). Single young were more often at intermediate distance to their mothers at 20-21 days ($P<.05$), and singles were more often at far distance from their mothers at 20-21 days ($P<.05$), at 25-26 days ($P<.05$), and at 30-31 days ($P<.10$).

Rare behavioral patterns

Number of occurrences per hour of lambs sniffing mothers and vocalizing. On the average, during their first month of daytime life, both lamb types sniffed their mothers at similar rates: 0.17 times per hour for the singles and 0.15 times per hour for the twins (Figure 17). Twin young vocalized more frequently than did single young: On the average, individual twins called 1.41 times per hour, whereas singles called 0.78 times per hour (Figure 18).

Number of occurrences per hour of ewes sniffing offspring, vocalizing, horn threatening or butting alien lambs, and preventing own lamb(s) from suckling. During the lambs' first month of daytime life, mothers of singles sniffed their lambs an average of 0.45 times per hour (Figures 19 and 20). Ewes with twins sniffed each lamb only 0.25 times per hour. In total, however, the number of occurrences per hour of maternal sniffing was slightly greater for mothers of twins (0.49 times per hour) than for mothers of singles (0.45 times per hour). Ewes with twins vocalized an average of 2.95 times per hour; ewes with singles vocalized only 1.21 times per hour (Figure 21). Mothers of twins also horn threatened or butted alien lambs more often than did mothers of singles, at 0.38 times per hour versus 0.25 times per hour (Figure 22). Ewes with twins prevented each of their lambs from suckling 0.47 times per hour, while ewes with singles prevented their lambs from suckling 0.32 times per hour (Figure 23).

Statistical treatments

By age class. Significant differences between the rates of the single and twin sets were found within certain age categories for three ewe behaviors: vocalizing, horn threatening or butting alien young, and preventing own lambs from suckling. Ewes with twins vocalized significantly more frequently than did ewes with singles at 0-1 days ($P<.01$). Mothers of twins horn threatened or butted alien lambs significantly more often than did mothers of singles at 0-1 days ($P<.05$), but mothers of singles horn threatened or butted more than did mothers of twins at 15-16 days ($P<.10$). At 0-1 days, ewes with twins prevented their own young from suckling significantly more often than did ewes with singles ($P<.10$).

Genotypic sets

Selected common behavioral patterns

Playing. Of the five genotypic groups, the F_2 Barbados-Rambouillet (BR2) lambs played the most during their first month of daytime life--3.0 percent (Figure 24). The Karakul-Rambouillet (KR) young and the Mouflon-Rambouillet (MR) young both played the same amount--2.1 percent. The F_1 Barbados-Rambouillet (BR1) lambs played 1.8 percent. At 1.1 percent, the purebred Mouflon (MM) young played the least during their first month of daytime life.

Suckling. Lambs with Rambouillet mothers suckled the most (Figure 25). The groups, ranked from most to least amount of suckling were KR at 4.9 percent, MR at 4.7 percent, BR1 at 3.6 percent, BR2 at 2.0 percent, MM at 1.4 percent.

Percentages of daytime lambs and their mothers spent simultaneously engaged in the same behaviors. The ewes and lambs of the MR and BR1 groups both spent the least amount of time, 43 percent, simultaneously engaged in the same activities during the young's first month of daytime life (Figure 26). The KR and BR2 groups had higher overall percentages, with 48 percent and 52 percent, respectively. Despite the fact that Mouflon young and their mothers spent less time at close distance to each other than did the other groups (see below), they still spent the greatest amount of time, 57 percent, simultaneously engaged in the same behaviors.

Distance category

Percentage of daytime lambs and their mothers spent at close distance to each other. The ewes and lambs of the two Barbados-Rambouillet groups spent the greatest overall amounts of the daytime at close distance to each other, at 62 percent for the BR2 group and 61 percent for the BR1 group (Figure 27). The KR and MR groups followed with the lesser, similar amounts of 56 percent and 55 percent, respectively. The Mouflon mothers and young, at 53 percent, spent the least amount of the daytime close to each other.

Statistical treatments

By age class. Significant differences between the percentages of the genotypic groups were found within certain age classes for three behaviors: suckling, simultaneously engaging in the same activities, and spending time at close distance.

The hybrid lambs with Rambouillet mothers suckled 44 percent more than did the Mouflon lambs with Mouflon mothers at 20-21 days ($P<.05$).

At two age periods, the Mouflon ewes and lambs spent significantly more time simultaneously engaged in the same behaviors than did the mothers and young of the combined group (MR + BR1 + KR), or of the MR group alone. At 5-6 days the Mouflon ewes and their lambs spent about twice as much time simultaneously engaged in the same activities as did the Rambouillet ewes and their hybrid lambs ($P<.05$), or as the Rambouillet ewes and their Mouflon-Rambouillet lambs ($P<.01$). The MM group also had a higher percentage than the (MR + BR1 + KR) group or the MR group at 30-31 days ($P<.05$). Concerning another comparison of interest at 30-31 days, the F_1 Barbados-Rambouillet ewes and their F_2 generation lambs spent twice as much time simultaneously engaged in the same behaviors as did the Rambouillet ewes and their F_1 Barbados-Rambouillet lambs ($P<.01$).

At 20-21 days, the ewes and lambs of the BR1 group spent 50 percent more time at close distance to each other than did the ewes and lambs of the BR2 group ($P<.10$).

Rare behavioral patterns

Number of occurrences per hour of lambs sniffing mothers. During their first month of daytime life, the lambs of the KR group sniffed their mothers the most, at 0.28 occurrences per hour (Figure 28). The Barbados-Rambouillet lambs followed with the two next highest rates: 0.19 times per hour for the BR1 group and 0.16 times per hour for the BR2 group. The MR group had the fourth highest rate, 0.14, and the MM group came last, at 0.05 occurrences per hour.

Number of occurrences per hour of lambs vocalizing. The lambs of the BR2 group vocalized the most, at 1.75 times per hour during the lambs' first month of daytime life (Figure 29). Young with Rambouillet mothers vocalized at intermediate rates: 1.20 for the KR group, 1.18 for the MR group, and 1.09 for the BR1 group. The lambs of the MM group vocalized 0.29 times per hour, the lowest rate.

Number of occurrences per hour of ewes sniffing offspring. The number of times per hour that ewes sniffed each lamb during the lambs' first month of daytime life was highest for the BR2 group, at 0.57 (Figure 30). The KR group followed with the next highest number of occurrences per hour--0.35. The last three groups had similar overall rates: 0.29 for the MM group, 0.28 for the MR group, and 0.24 for the BR1 group. The BR2 group and the KR group also had the two highest total number of occurrences per hour that ewes sniffed their young, at 0.69 and 0.46, respectively (Figure 31). The ewes of the MR and BR1 groups both sniffed their lambs 0.42 times per hour in total, while the ewes of the MM group sniffed their lambs 0.37 times per hour in total. The total rate of sniffing shown by the BR2 group was especially high at 0-1 days, when the F_1 Barbados-Rambouillet ewes sniffed their lambs over twice as much as did the other ewes.

Number of occurrences per hour of ewes vocalizing. During the lambs' first month of daytime life, the ewes of the BR2 group vocalized the most, at 3.44 times per hour (Figure 32). The BR1 group had the second highest number of occurrences per hour--2.60. The MR and KR groups followed next, at 1.91 times per hour and 1.74 times per hour, respectively. The ewes of the MM group vocalized the least, at 0.78 times per hour.

Number of occurrences per hour of ewes horn threatening or butting alien lambs. The number of times per hour that ewes horn threatened or butted alien lambs was highest for the BR1 group, at 0.61 (Figure 33). The rates of the next three groups were 0.30 for the MR group, 0.27 for the BR2 group, and 0.23 for the KR group. The ewes of the MM group horn threatened or butted alien young at the lowest number of times per hour--0.18.

<u>Number of occurrences per hour of ewes preventing each of their own lambs from suckling</u>. At a rate of 0.17, the ewes of the KR group displayed the lowest number of occurrences per hour for the prevention of suckling of each lamb (Figure 34). The MR, MM, and BR2 groups followed with similar rates of 0.34, 0.35, and 0.37, respectively. The BR1 group had the highest number of occurrences per hour for preventing each lamb from suckling, at 0.72.

Statistical treatments

<u>By age class</u>. Significant differences between the rates of the genotypic groups were found within certain age categories for three ewe behaviors: vocalizing, horn threatening or butting alien young, and preventing own lambs from suckling.

For the vocalizing of ewes, a comparison of the BR2 group versus the combined group of (MM + MR + BR1 + KR) revealed a significant difference at 0-1 days ($P<.10$). The F_1 Barbados-Rambouillet ewes called about two and a half times more frequently than did the other ewes (see Figure 32).

Two of the Rambouillet ewe groups horn threatened or butted alien lambs at rates significantly greater than those of the other groups at two age periods (see Figure 33). At 0-1 days, the Rambouillet ewes with F_1 Barbados-Rambouillet lambs horn threatened or butted two and a half times more frequently than did the F_1 Barbados-Rambouillet ewes ($P<.10$), and over four times more often than did the average ewe ($P<.01$). At 15-16 days, Rambouillet ewes with Mouflon-Rambouillet lambs horn threatened or butted four times more often than did Mouflon ewes ($P<.10$), and over three times more frequently than did the average ewe ($P<.05$).

The Rambouillet ewes with F_1 Barbados-Rambouillet lambs prevented each young from suckling significantly more often than did the other ewes at two age categories (see Figure 34). At 0-1 days, the BR1 group's rate was about seven times greater than the BR2 group's rate ($P<.05$), and about ten times greater than the average rate of the combined group (MM + MR + BR2 + KR) ($P<.01$). At 20-21 days, the BR1 group's rate was about 30 times greater than the BR2 group's rate ($P<.01$), and about three and a half times greater than the average rate of the combined group (MM + MR + BR2 + KR) ($P<.01$).

Physiological Traits

Breeding

Length of breeding season

In 1973-74, the first instance of observed breeding among the Mouflon took place on 10 September and the last instance of observed breeding occurred on 22 January. In 1974-75, the first instance of observed breeding among the Mouflon occurred on 24 September and the last instance of observed breeding took place on 16 January.

Length of estrous cycle

Table 6 indicates the sample sizes, the mean lengths of the estrous cycle in days, and the standard deviations in days for four groups of sheep and one group of goats. With regard to the sheep groups, the mean length of the estrous cycle varied according to the species or breed, but not significantly so. The goats exhibited a significantly longer estrous cycle than did the sheep ($P<.01$).

Table 6. The mean length of the estrous cycle exhibited in ewes and does of different genotypes.

Genotype	n	$\bar{x}$ (days)	S D (days)
Barbados	2	17.0	0.0
Karakul	2	16.5	0.71
Mouflon	6	17.0	2.45
Rambouillet	30	17.9	1.11
Alpine and Toggenburg	14	19.7	1.69

Length of gestation

Table 7 presents the sample sizes, the mean lengths of gestation in days, and the standard deviations in days for 11 groups of sheep and one group of goats. The gestation length of the BR2 group was significantly shorter than the gestation length of the combined group (BR1 + KR + MM + MR) ($P<.01$).

Parturition

Number of young born per female

Table 8 shows the number of young born per female giving birth for 11 groups of sheep and one group of goats.

Weight of young at birth

Table 9 indicates the litter size, the sample sizes, the mean weights in kg at birth, and the standard deviations in kg for 11 groups of sheep and one group of goats. If the birth weights of the singles

Table 7. The mean length of gestation exhibited by ewes or does of different genotypes after they were bred to males of the same or different genotypes.

Genotype		n	$\bar{x}$ (days)	S D (days)
Male	Female			
Barbados	Barbados	2	153.00	0
Barbados	Rambouillet	17	152.24	1.79
Barbados-Rambouillet	Barbados-Rambouillet	7	148.57	1.77
Hawaiian Blackbuck	Hawaiian Blackbuck	2	152.25	1.77
Hawaiian Blackbuck	Rambouillet	7	151.29	2.29
Hawaiian Blackbuck-Rambouillet	Hawaiian Blackbuck-Rambouillet	15	150.20	2.08
Karakul	Karakul	2	148.00	1.41
Karakul	Rambouillet	6	152.67	4.37
Mouflon	Mouflon	5	153.40	0.89
Mouflon	Rambouillet	7	152.86	2.27
Mouflon-Rambouillet	Mouflon-Rambouillet	3	152.17	1.89
Wild-domestic goat	Alpine and Toggenburg	12	154.33	2.43

Table 8. The number of young born per ewe or doe after females of different genotypes were bred to males of the same or different genotypes.

Genotype		Number of young born per female
Male	Female	
Barbados	Barbados	1.50
Barbados	Rambouillet	1.59
Barbados-Rambouillet	Barbados-Rambouillet	1.43
Hawaiian Blackbuck	Hawaiian Blackbuck	1.50
Hawaiian Blackbuck	Rambouillet	1.85
Hawaiian Blackbuck-Rambouillet	Hawaiian Blackbuck-Rambouillet	1.18
Karakul	Karakul	1.00
Karakul	Rambouillet	1.60
Mouflon	Mouflon	1.42
Mouflon	Rambouillet	1.90
Mouflon-Rambouillet	Mouflon-Rambouillet	1.33
Wild-domestic goat	Alpine and Toggenburg	2.11

Table 9. The mean weights found at birth for single, twin, or triplet lambs and kids of different genotypes.

Genotype of young		1, 2, or 3 in litter	Birth weights (kg)		
Sire	Dam		n	$\bar{x}$	S D
Barbados	Barbados	Single	0		
		Twin	2	2.64	0.771
Barbados	Rambouillet	Single	8	4.22	0.584
		Twin	20	3.84	0.560
Barbados-Rambouillet	Barbados-Rambouillet	Single	6	3.25	0.518
		Twin	10	3.38	0.591
Hawaiian Blackbuck	Hawaiian Blackbuck	Single	2	3.30	0.071
		Twin	3	2.50	0.201
Hawaiian Blackbuck	Rambouillet	Single	2	4.60	0.071
		Twin	10	3.31	0.389
Hawaiian Blackbuck-Rambouillet	Hawaiian Blackbuck-Rambouillet	Single	12	3.51	0.878
		Twin	6	3.55	0.472
Karakul	Karakul	Single	2	4.80	0.035
		Twin	0		
Karakul	Rambouillet	Single	5	4.98	0.673
		Twin	6	4.10	0.532
Mouflon	Mouflon	Single	13	2.84	0.553
		Twin	8	2.86	0.249
Mouflon	Rambouillet	Single	2	5.30	0.636
		Twin	9	3.95	0.702
Mouflon-Rambouillet	Mouflon-Rambouillet	Single	4	4.02	0.544
		Twin	2	2.41	1.610
Wild-domestic goat	Alpine and Toggenburg	Single	5	3.22	1.070
		Twin	18	2.86	0.702
		Triplet	12	2.26	0.505

and twins within each of the five primary groups are averaged, the following order from the highest to the lowest weight is obtained: (1) KR at 4.50 kg, (2) MR at 4.20 kg, (3) BR1 at 3.95 kg, (4) BR2 at 3.33 kg, (5) MM at 2.85 kg. No significant differences were found between the mean birth weights of the five groups.

Weight of young at four ages

Table 10 presents the litter size; the sample sizes; the mean weights in kg at 0, 2, 7, and 14 days of age; and the standard deviations in kg for six groups of sheep. A calculation of the average weight gains shown by the lambs of the five primary groups from birth to 2 weeks of age indicates the following high to low ordering: (1) KR at 2.89 kg, (2) BR1 at 2.86 kg, (3) BR2 at 2.78 kg, (4) MR at 2.39 kg, (5) MM at 2.21 kg. Figure 35 depicts the weight gain in kg of 18 single lambs and 30 twin lambs over the 2 week period following birth.

Table 10. The mean weights found at four ages for single or twin lambs of different genotypes.

Genotype of young		1 or 2 in litter	n same all ages	Weights (kg) at four ages							
				0 days		2 days		7 days		14 days	
Sire	Dam			$\bar{x}$	S D	$\bar{x}$	S D	$\bar{x}$	S D	$\bar{x}$	S D
Barbados	Rambouillet	Single	5	4.23	0.43	4.51	0.47	5.78	0.30	7.35	0.42
		Twin	6	3.89	0.66	4.14	0.60	5.20	0.69	6.52	0.91
Barbados-Rambouillet	Barbados-Rambouillet	Single	4	3.38	0.53	3.59	0.62	5.10	0.56	6.60	0.82
		Twin	6	3.00	0.38	3.10	0.50	4.24	0.49	5.48	0.85
Hawaiian Blackbuck	Rambouillet	Single	2	4.60	0.07	4.92	0.09	6.03	0.04	7.66	0.09
		Twin	6	3.19	0.45	3.37	0.37	4.52	0.11	5.38	0.39
Karakul	Rambouillet	Single	3	5.07	0.93	5.53	1.09	6.91	1.58	8.68	2.19
		Twin	4	4.12	0.69	4.31	0.64	5.28	0.83	6.48	1.29
Mouflon	Mouflon	Single	2	3.25	0.40	3.85	0.42	4.73	0.42	5.85	0.42
		Twin	2	3.10	0.06	3.48	0.16	4.14	0.23	4.92	0.23
Mouflon	Rambouillet	Single	2	5.30	0.64	5.54	0.62	6.06	0.30	8.98	2.77
		Twin	6	3.72	0.40	3.82	0.36	4.66	0.75	5.69	0.86

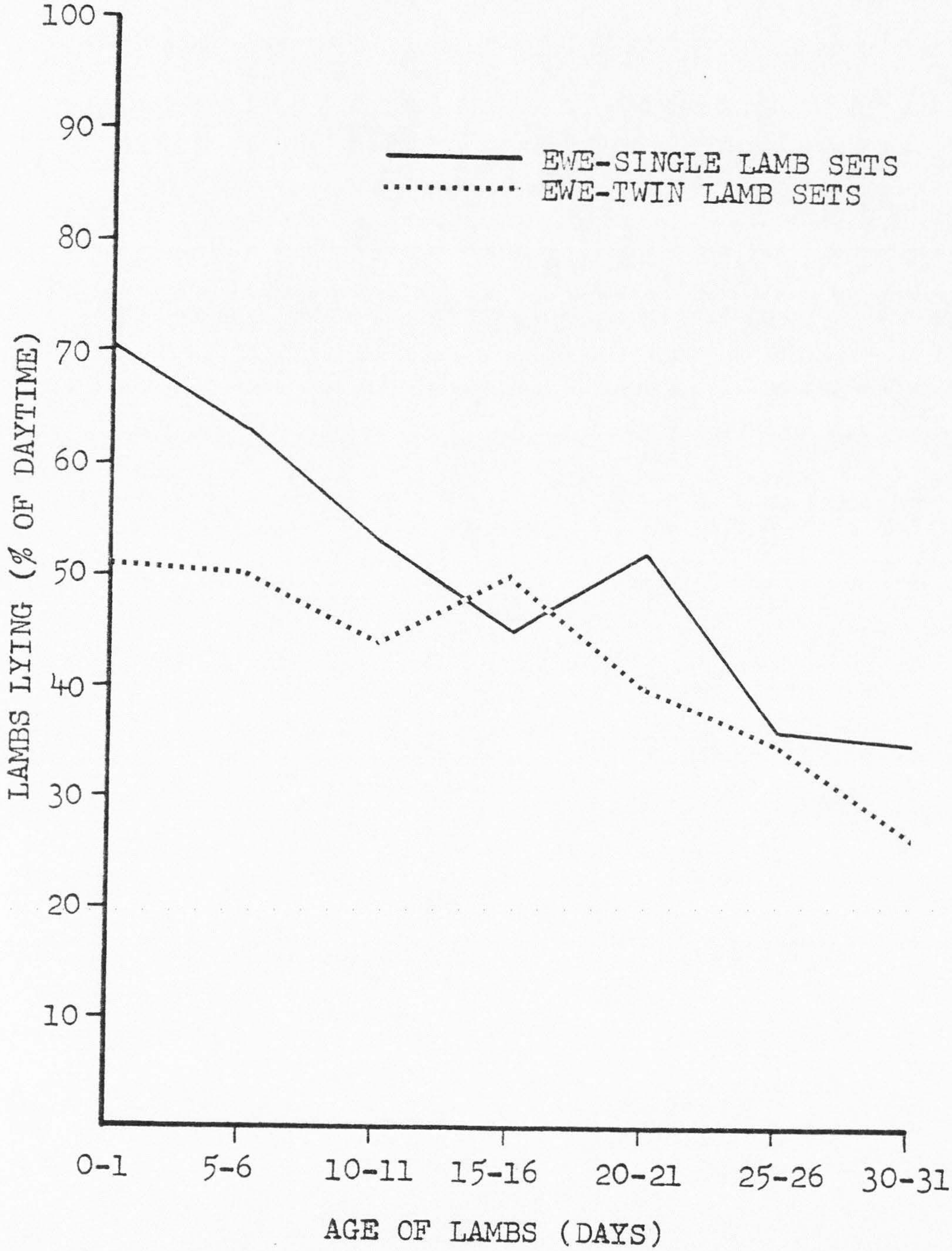

Figure 1. Percentages of daytime that lambs spent lying, in ewe-single lamb sets and ewe-twin lamb sets by age of lambs. Over the month, singles lay more than did twins ($P<.05$).

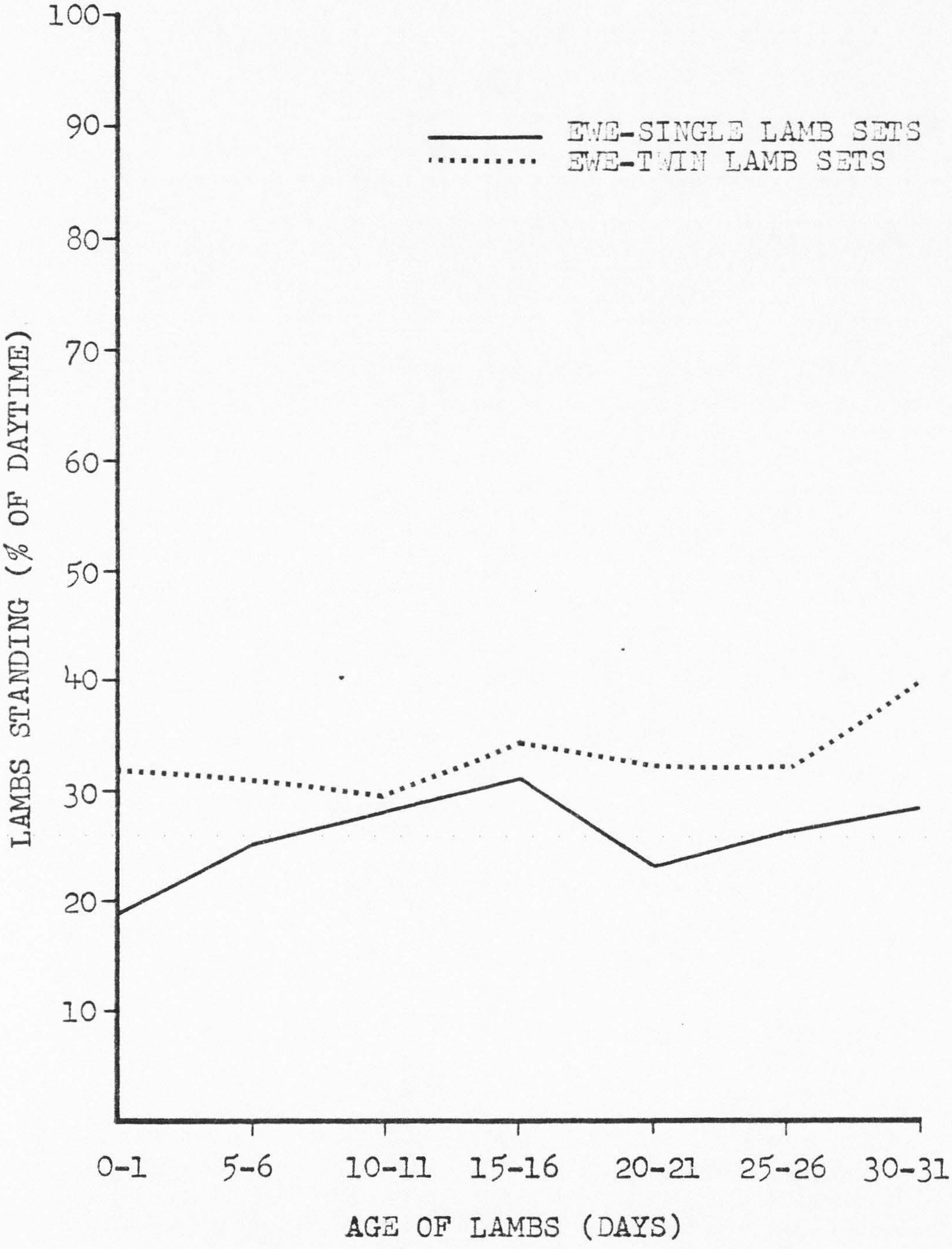

Figure 2. Percentages of daytime that lambs spent standing, in ewe-single lamb sets and ewe-twin lamb sets by age of lambs. Over the month, twins stood more than did singles (P<.01).

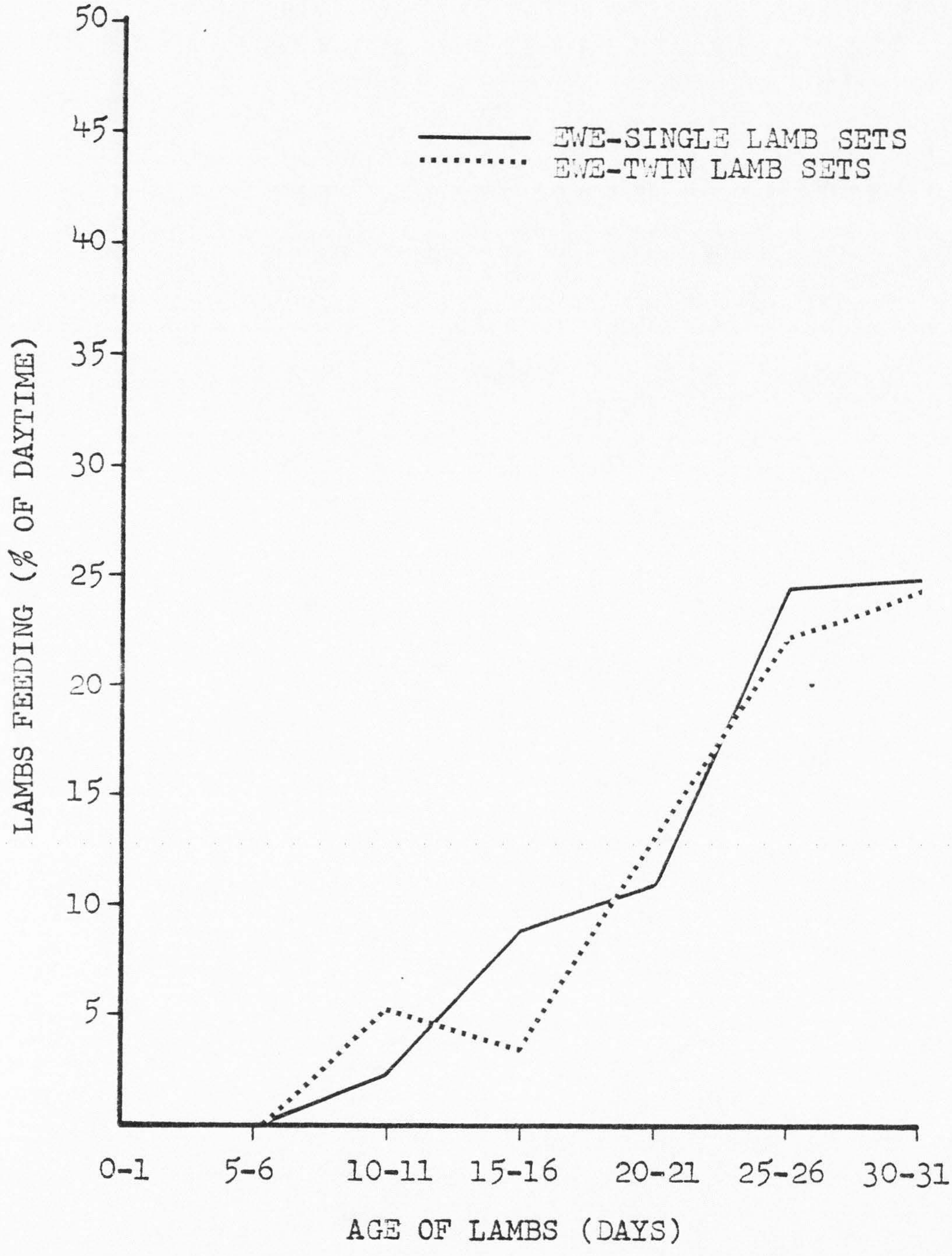

Figure 3. Percentages of daytime that lambs spent feeding, in ewe-single lamb sets and ewe-twin lamb sets by age of lambs.

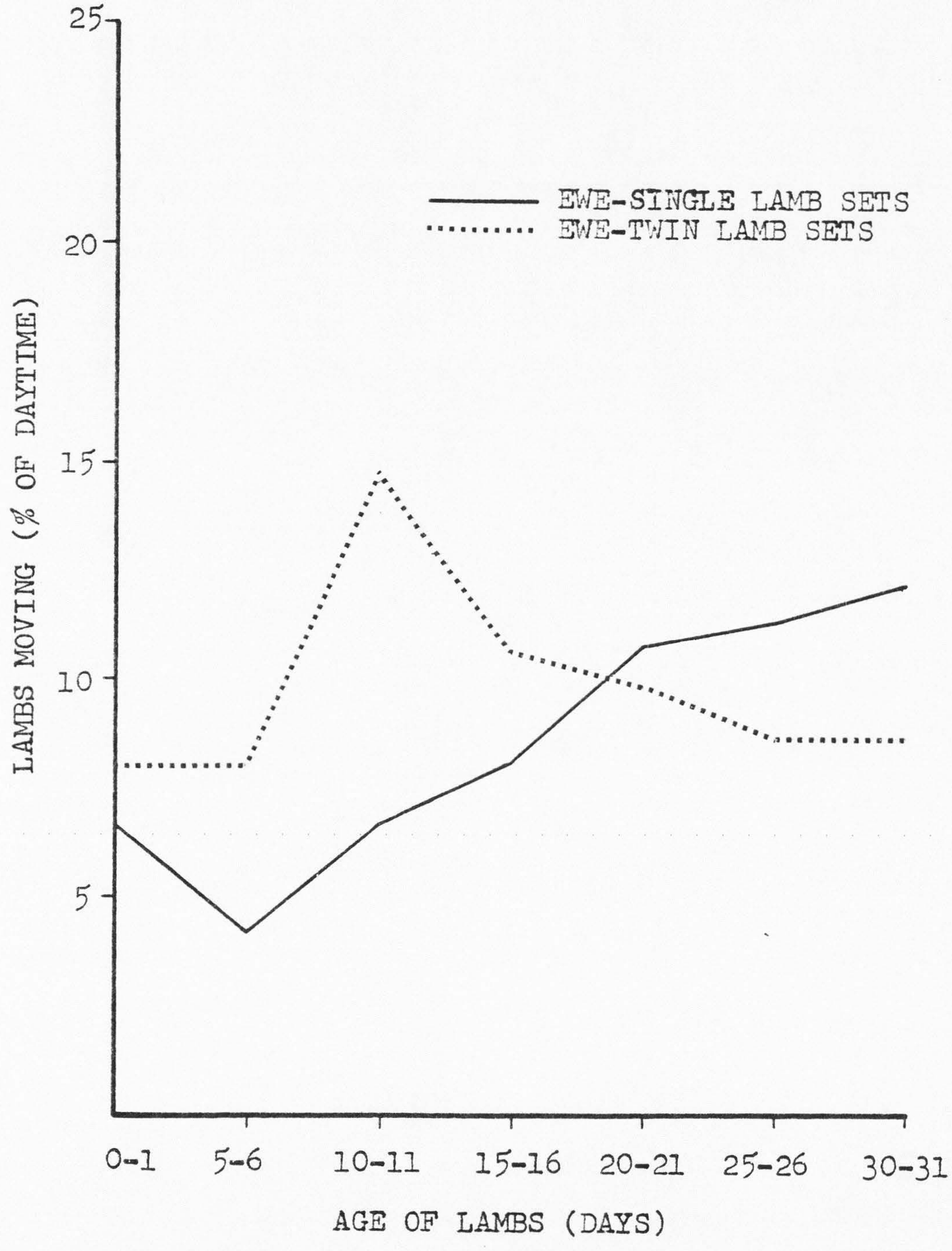

Figure 4. Percentages of daytime that lambs spent moving, in ewe-single lamb sets and ewe-twin lamb sets by age of lambs.

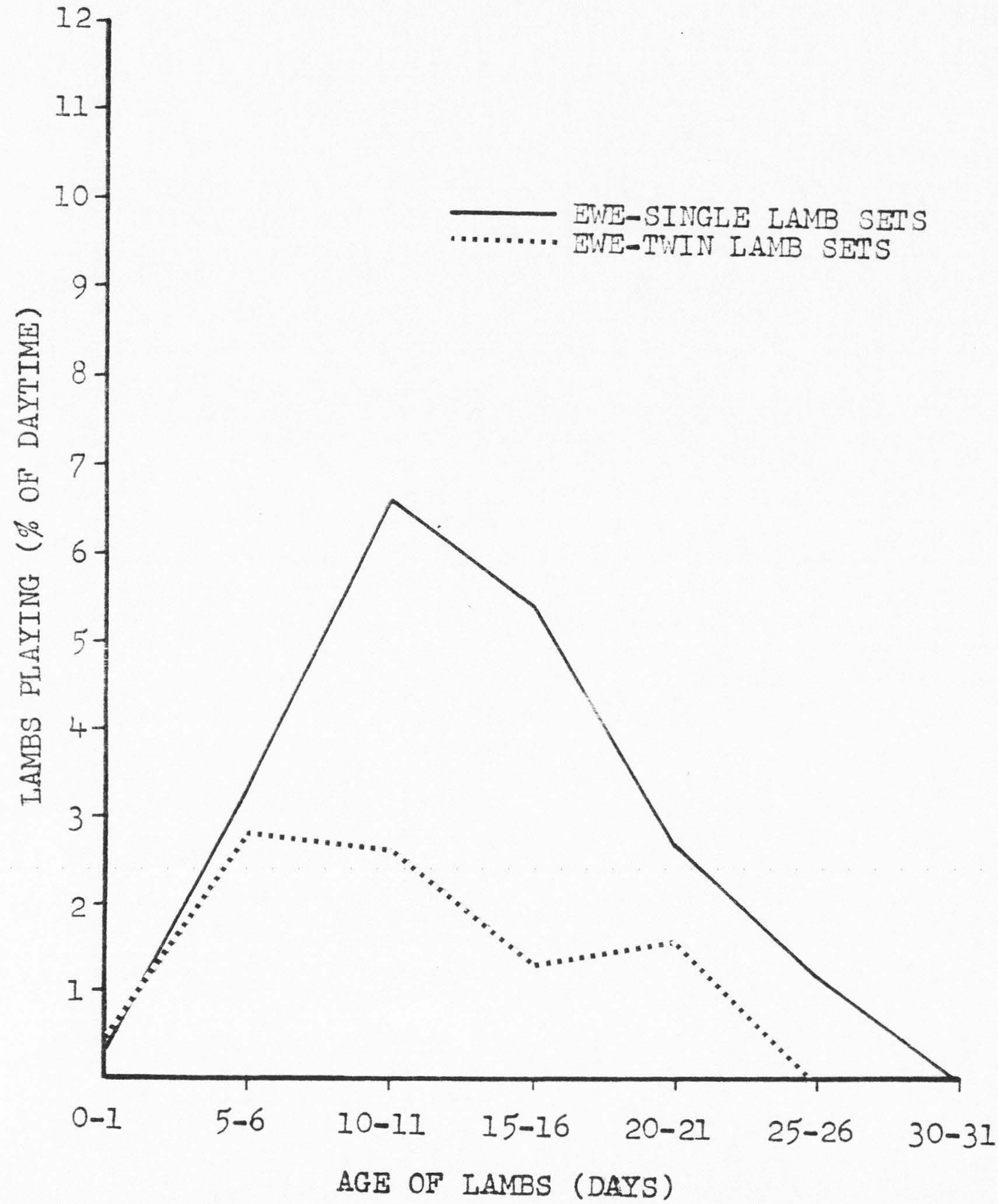

Figure 5. Percentages of daytime that lambs spent playing, in ewe-single lamb sets and ewe-twin lamb sets by age of lambs. Over the month, singles played more than did twins ($P<.05$).

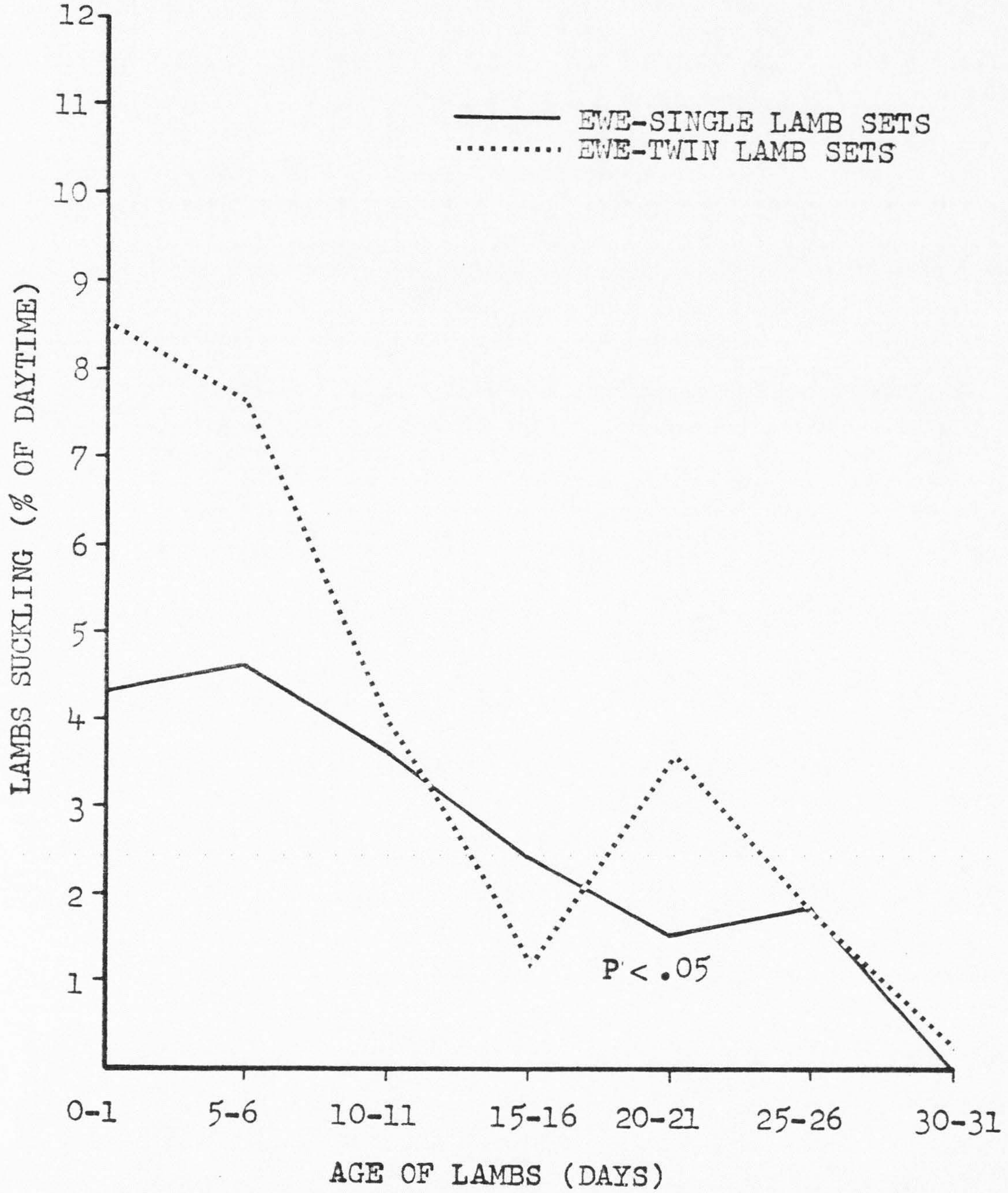

Figure 6. Percentages of daytime that lambs spent suckling, in ewe-single lamb sets and ewe-twin lamb sets by age of lambs.

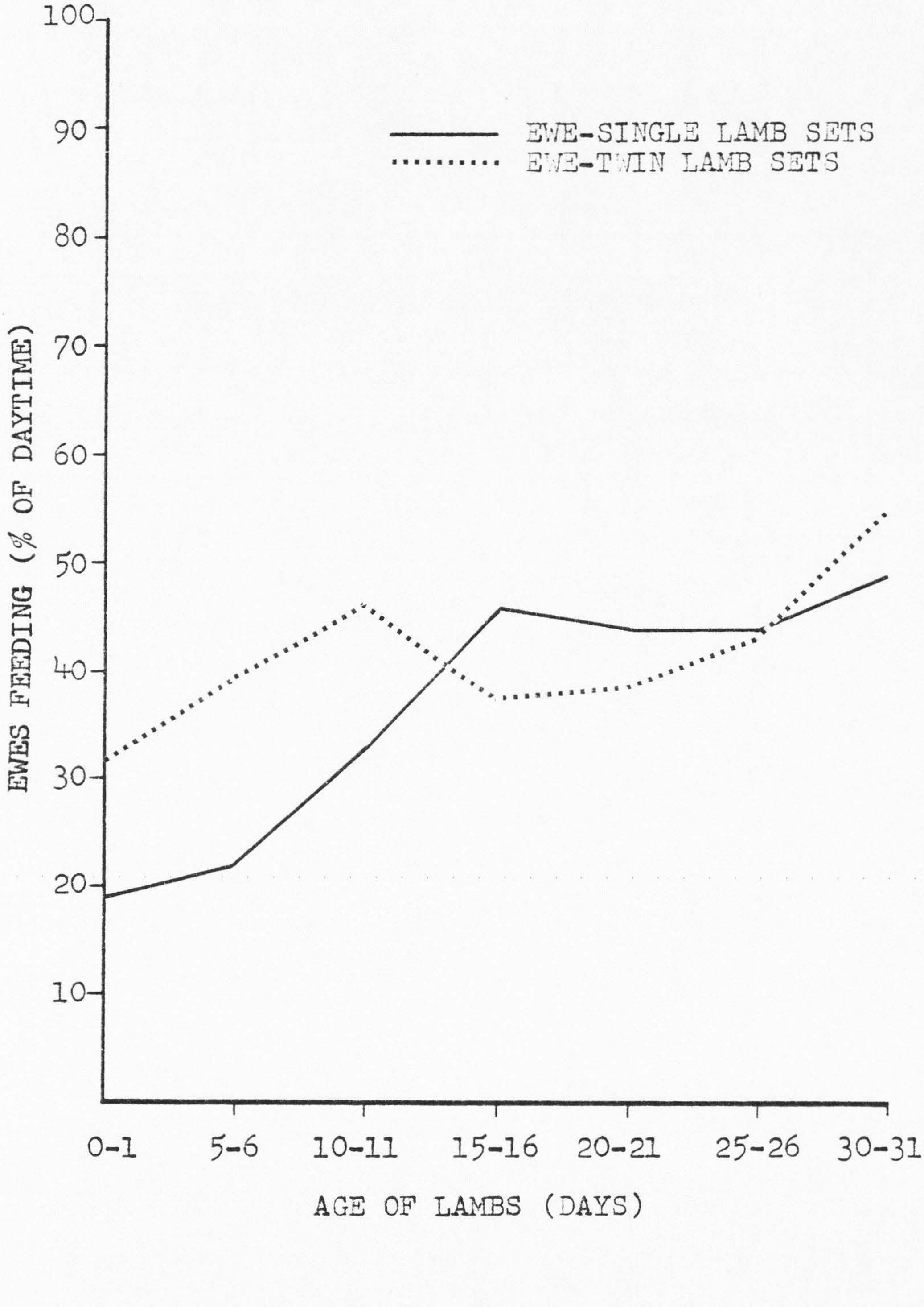

Figure 7. Percentages of daytime that ewes spent feeding, in ewe-single lamb sets and ewe-twin lamb sets by age of lambs.

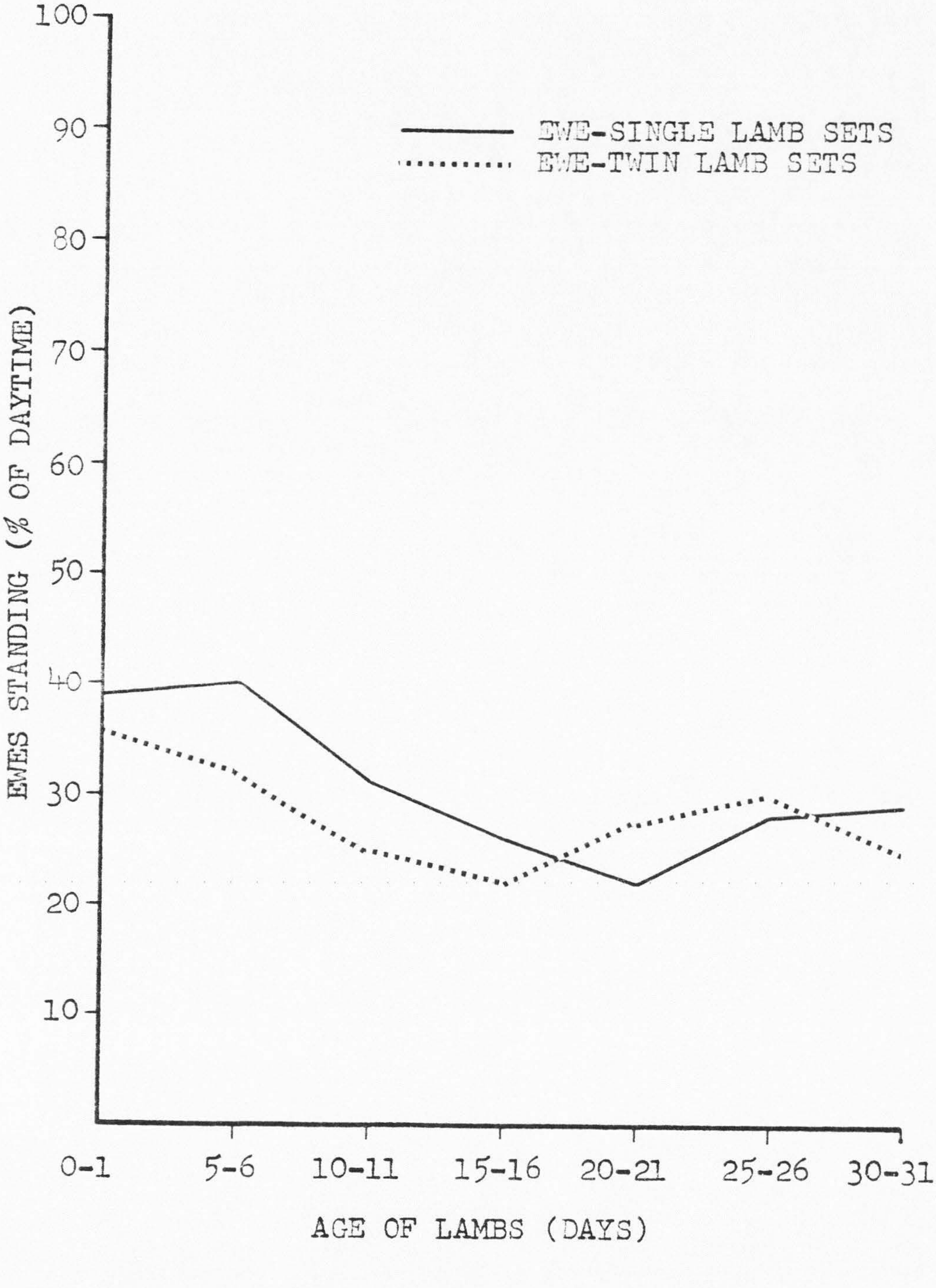

Figure 8. Percentages of daytime that ewes spent standing, in ewe-single lamb sets and ewe-twin lamb sets by age of lambs.

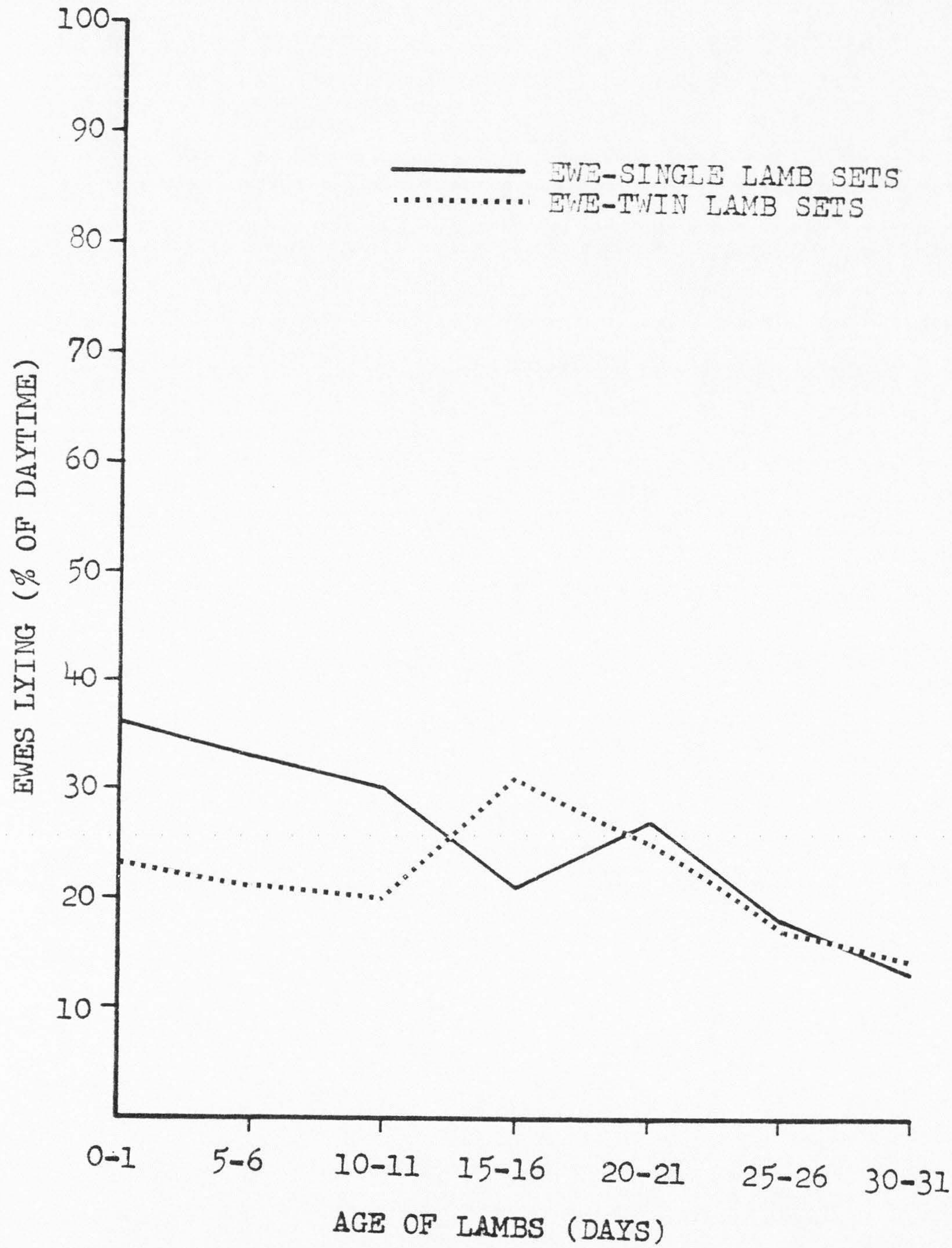

Figure 9. Percentages of daytime that ewes spent lying, in ewe-single lamb sets and ewe-twin lamb sets by age of lambs.

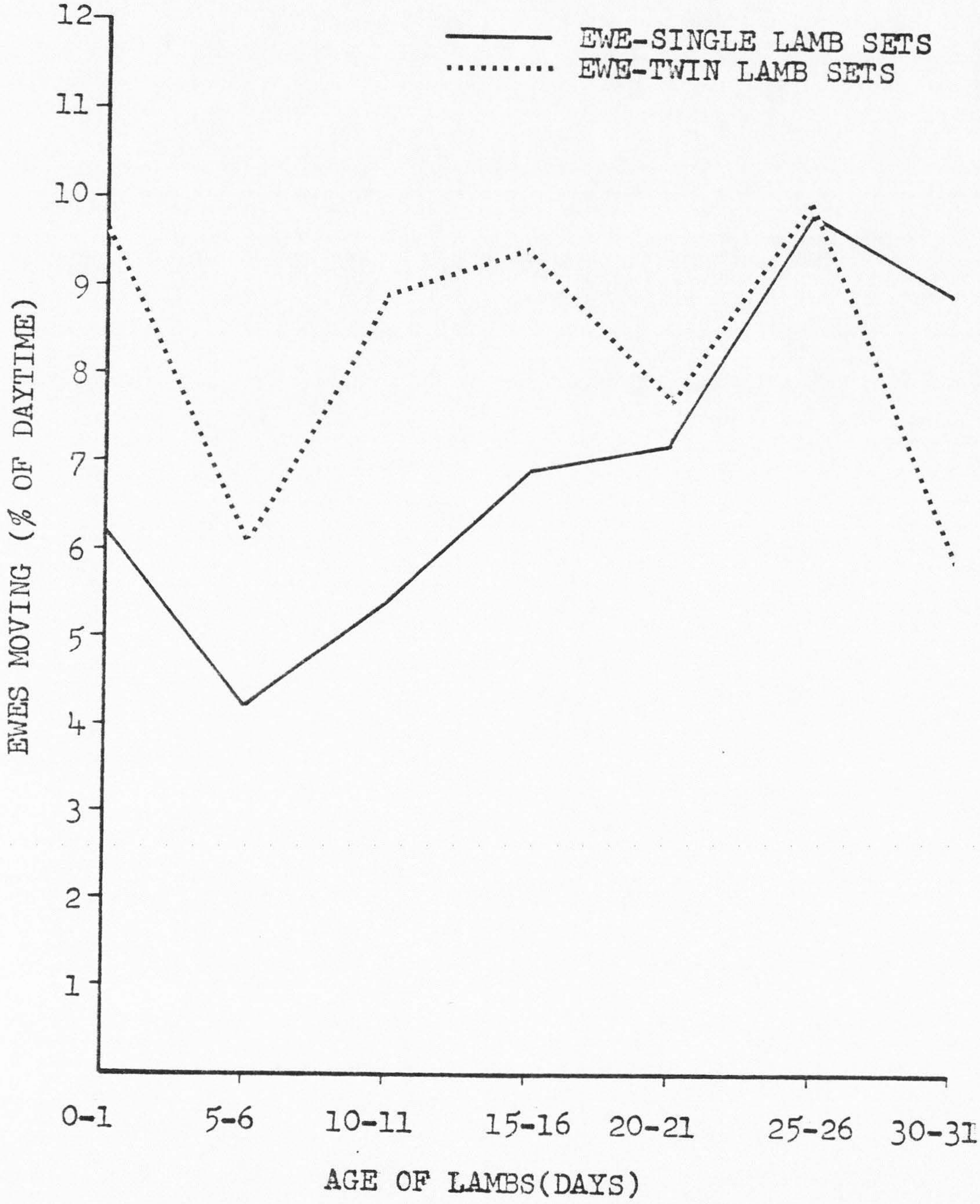

Figure 10. Percentages of daytime that ewes spent moving, in ewe-single lamb sets and ewe-twin lamb sets by age of lambs.

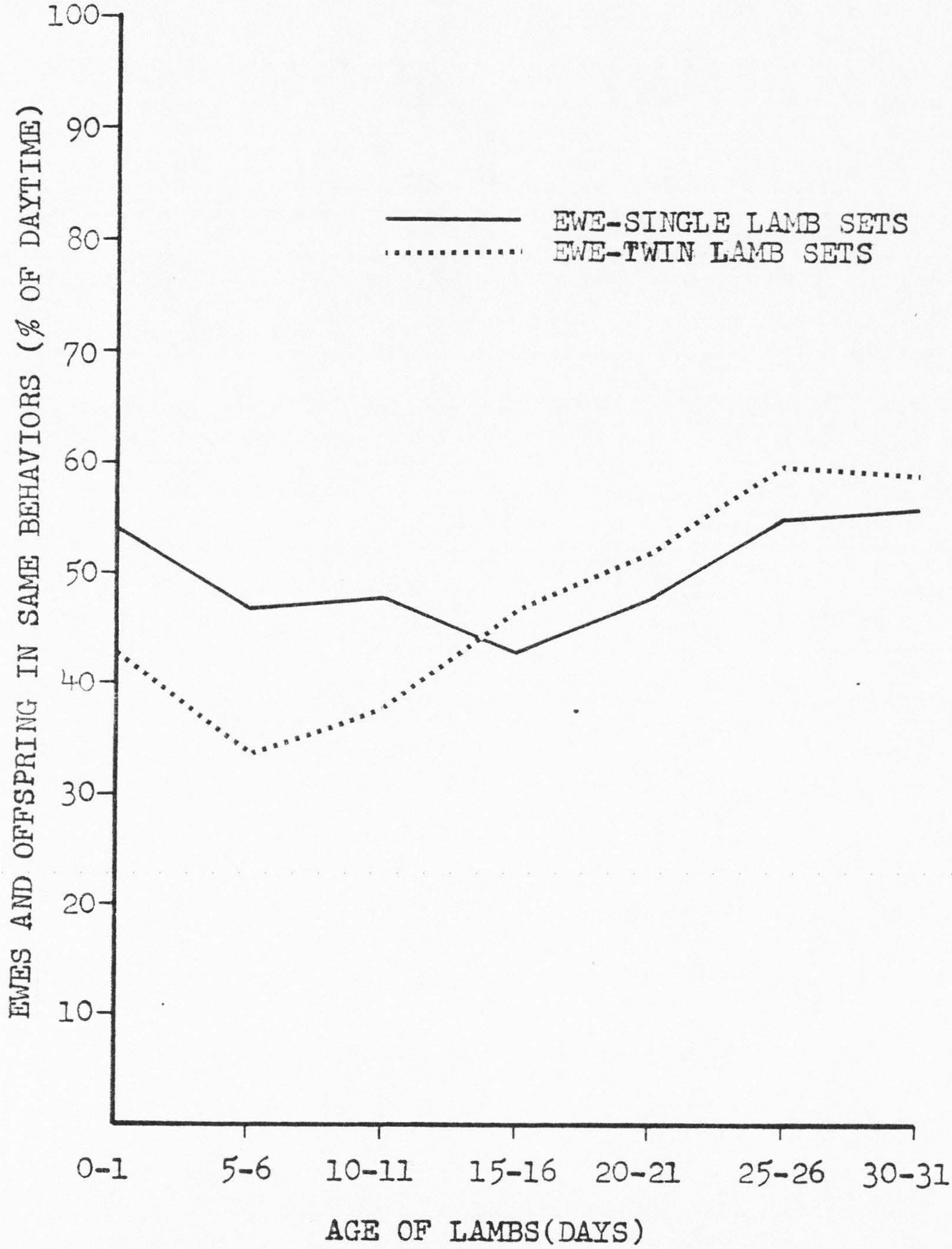

Figure 11. Percentages of daytime that ewes and their offspring spent simultaneously engaged in the same behaviors, in ewe-single lamb sets and ewe-twin lamb sets by age of lambs.

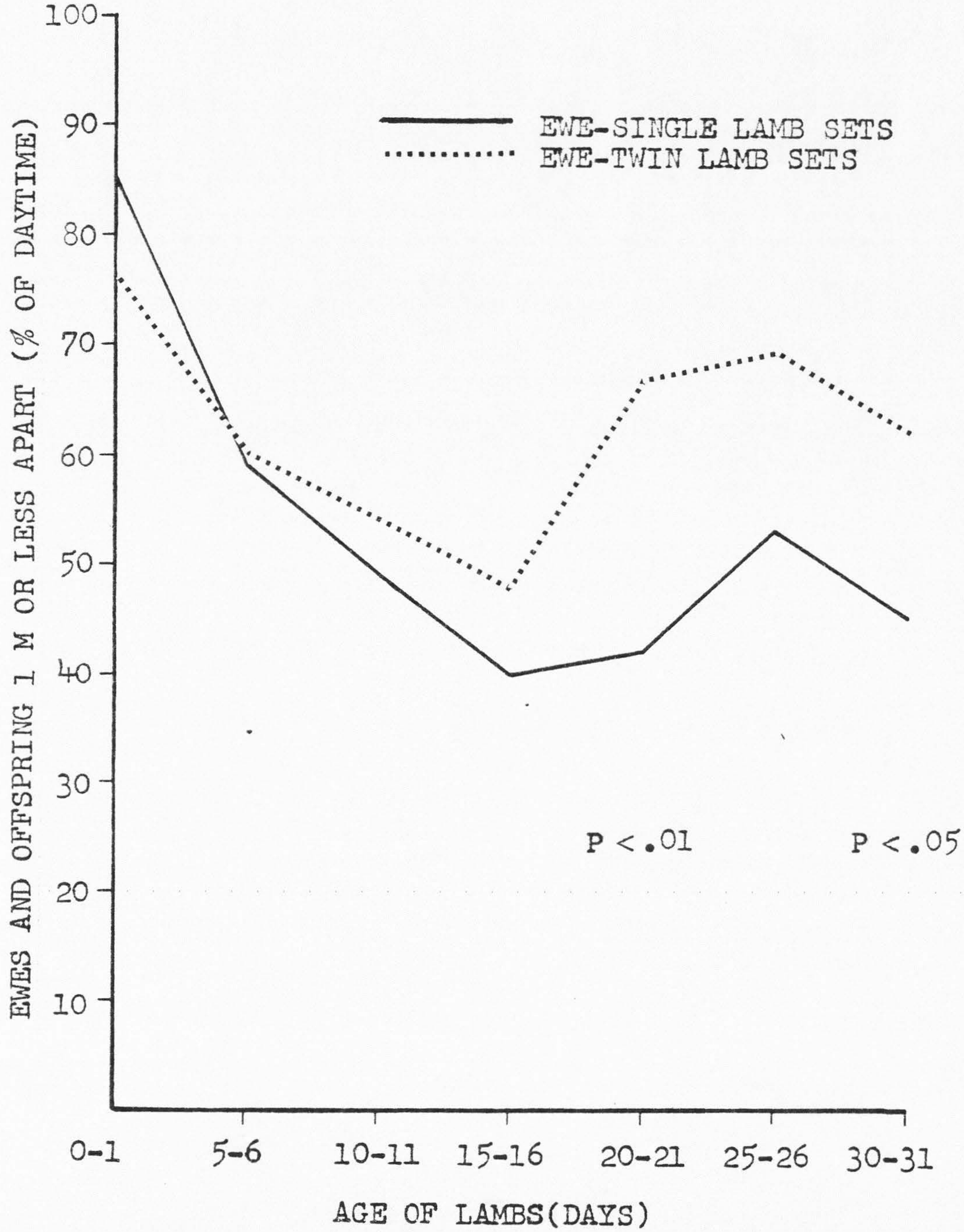

Figure 12. Percentages of daytime that ewes and their offspring spent at 1 m or less from each other, in ewe-single lamb sets and ewe-twin lamb sets by age of lambs.

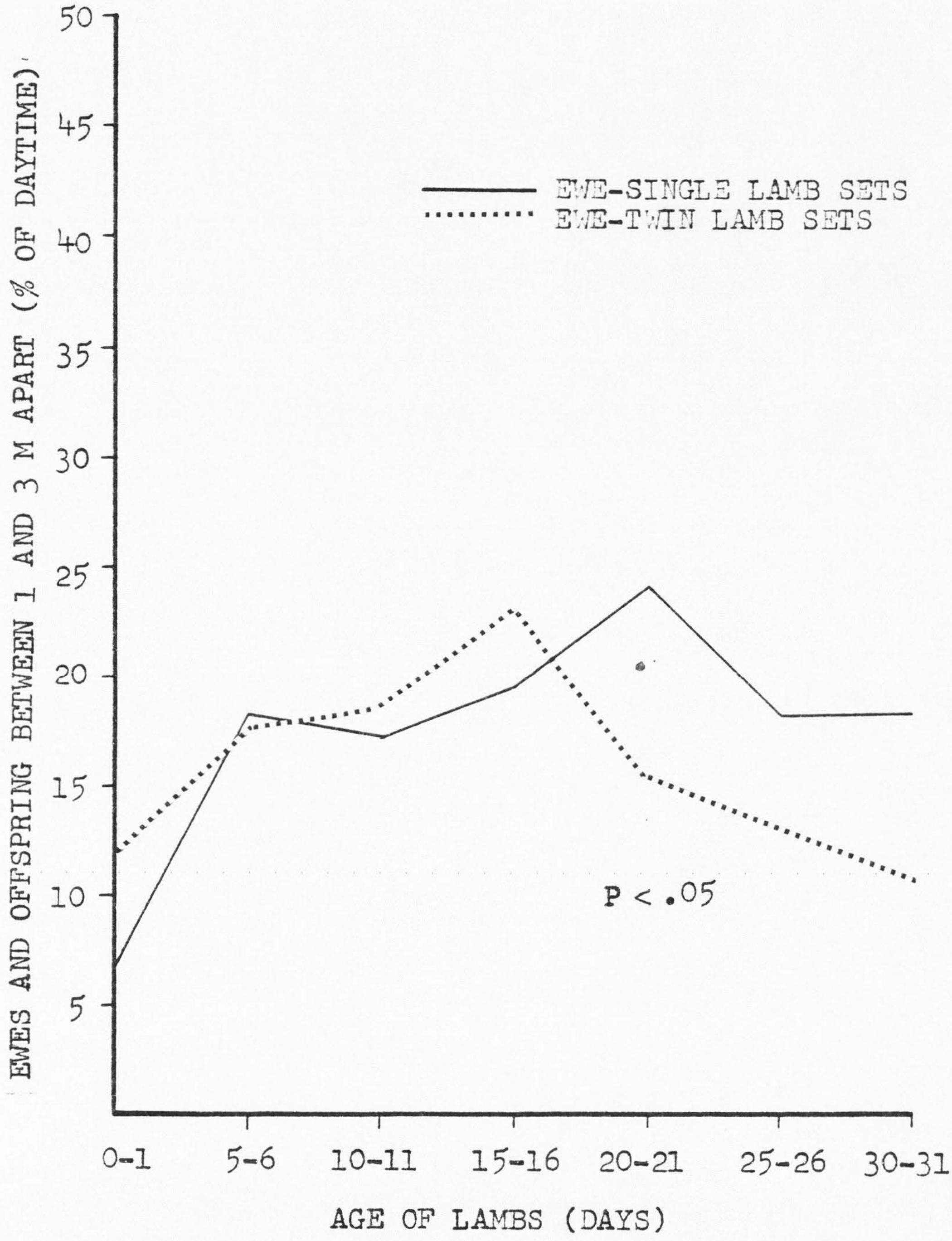

Figure 13. Percentages of daytime that ewes and their offspring spent between 1 and 3 m from each other, in ewe-single lamb sets and ewe-twin lamb sets by age of lambs.

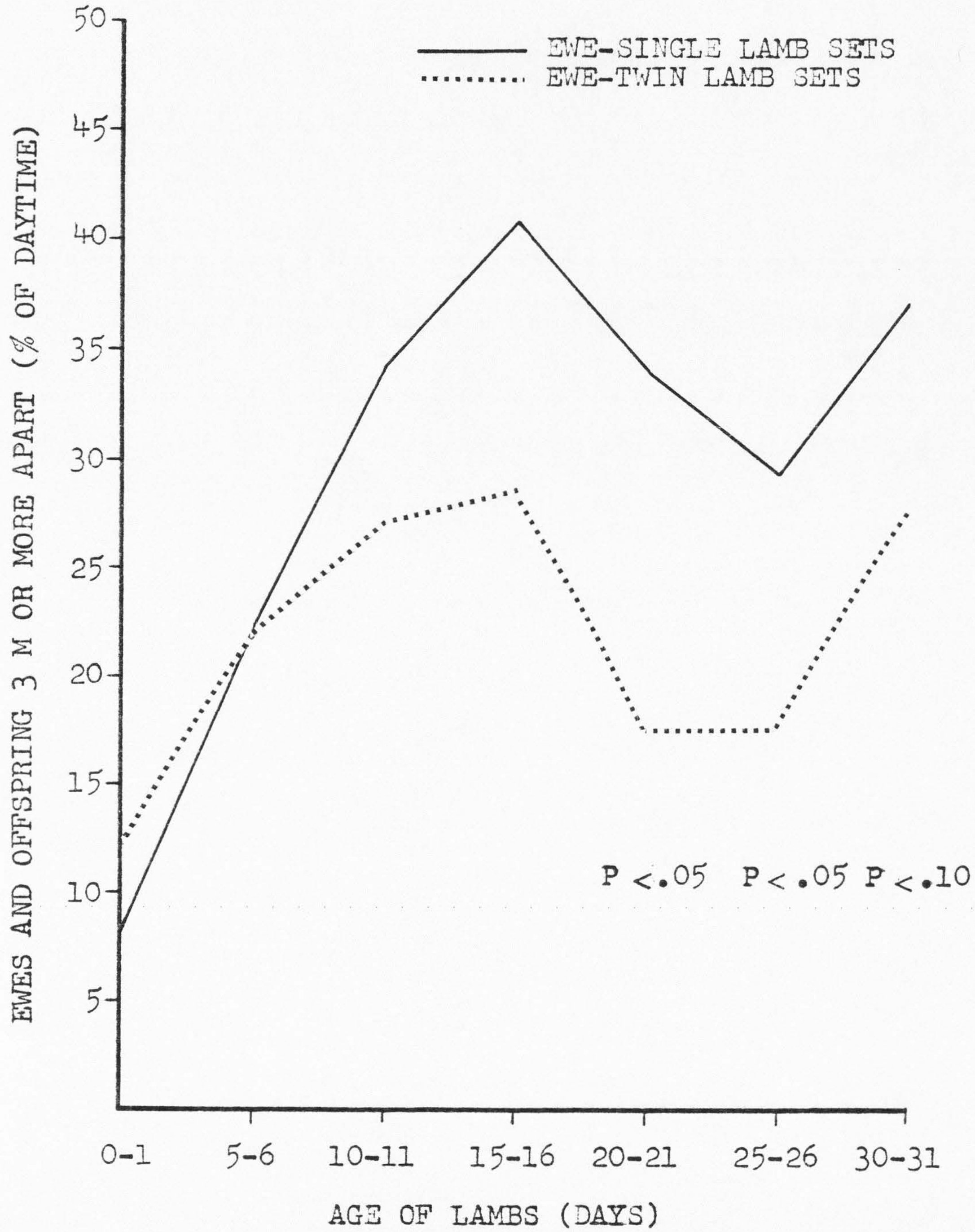

Figure 14. Percentages of daytime that ewes and their offspring spent at 3 m or more from each other, in ewe-single lamb sets and ewe-twin lamb sets by age of lambs. Over the month, singles and their mothers spent more time at 3 m or greater from each other than did twins and their mothers ($P<.05$).

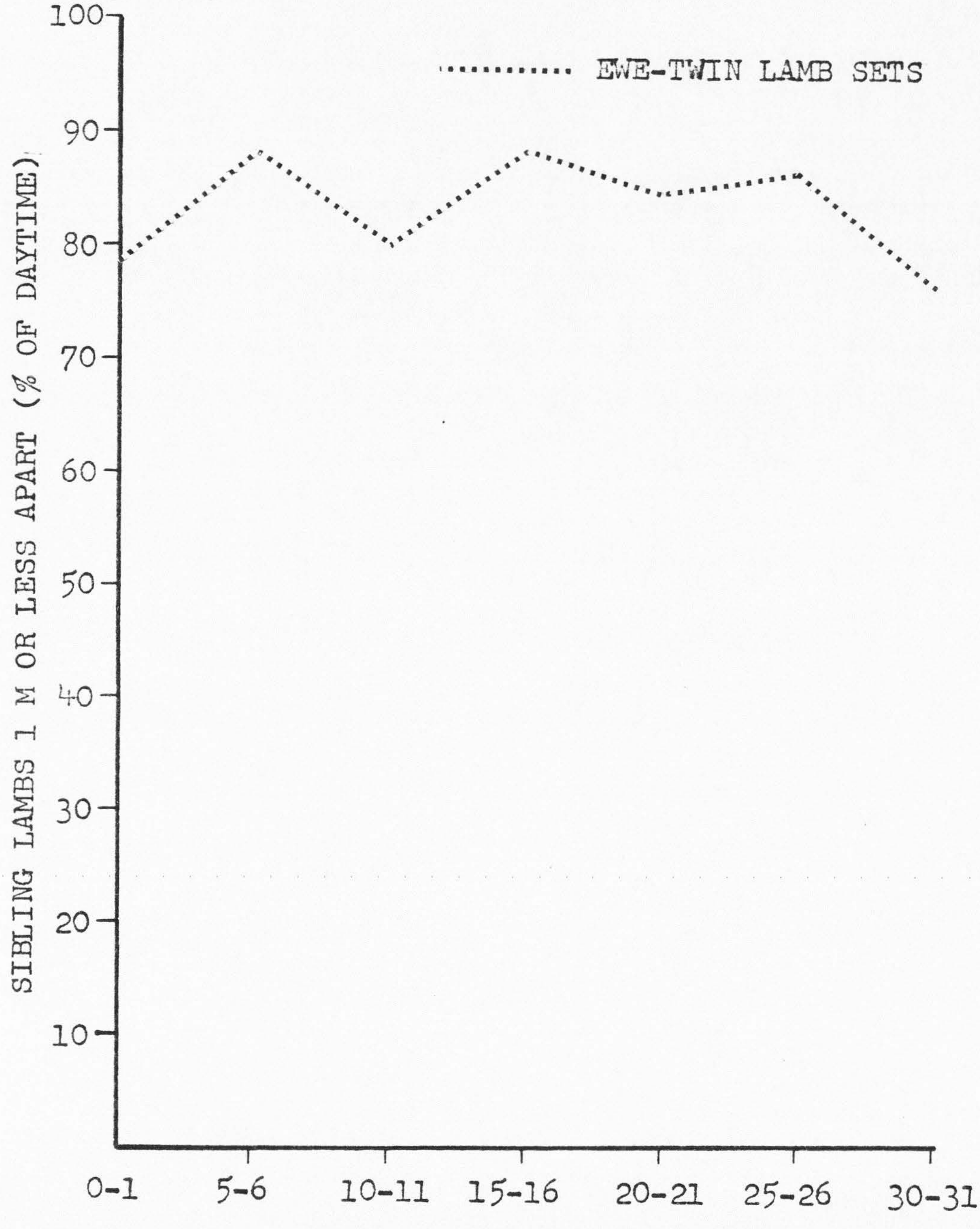

Figure 15. Percentages of daytime that sibling lambs spent at 1 m or less from each other, in ewe-twin lamb sets by age of lambs.

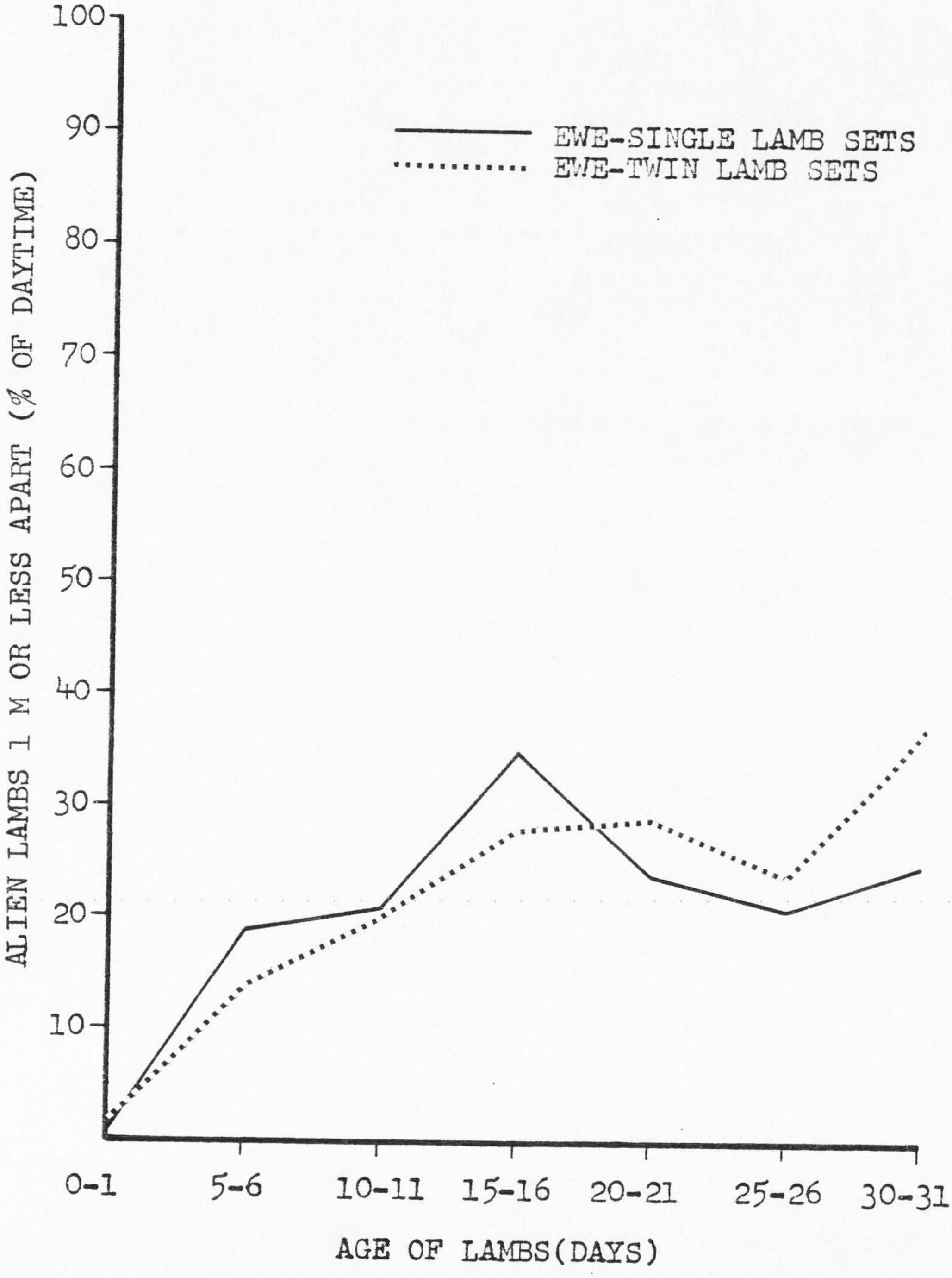

Figure 16. Percentages of daytime that lambs spent at 1 m or less from alien lambs, in ewe-single lamb sets and ewe-twin lamb sets by age of lambs.

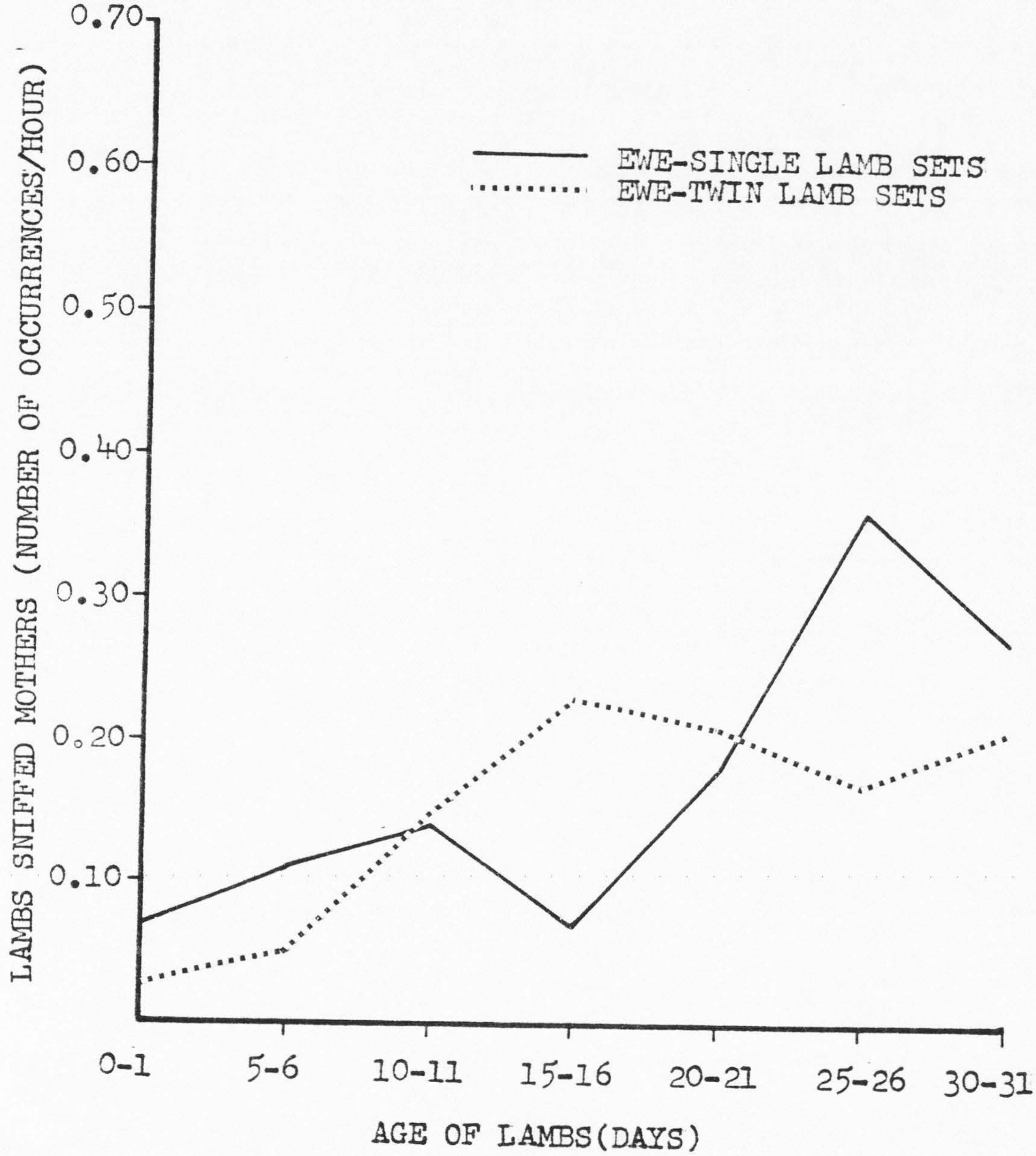

Figure 17. Frequencies at which lambs sniffed their mothers, in ewe-single lamb sets and ewe-twin lamb sets by age of lambs.

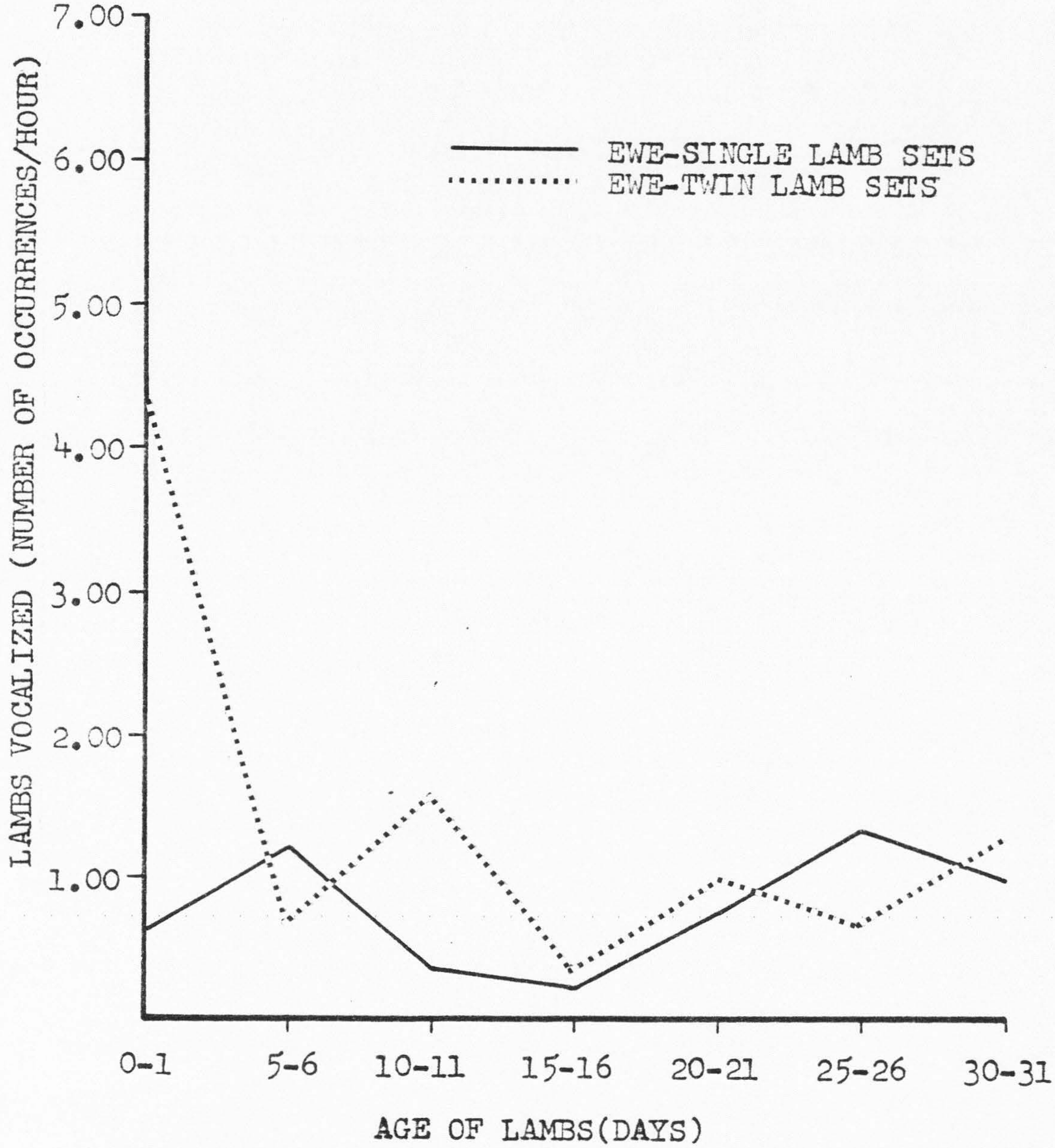

Figure 18. Frequencies at which lambs vocalized, in ewe-single lamb sets and ewe-twin lamb sets by age of lambs.

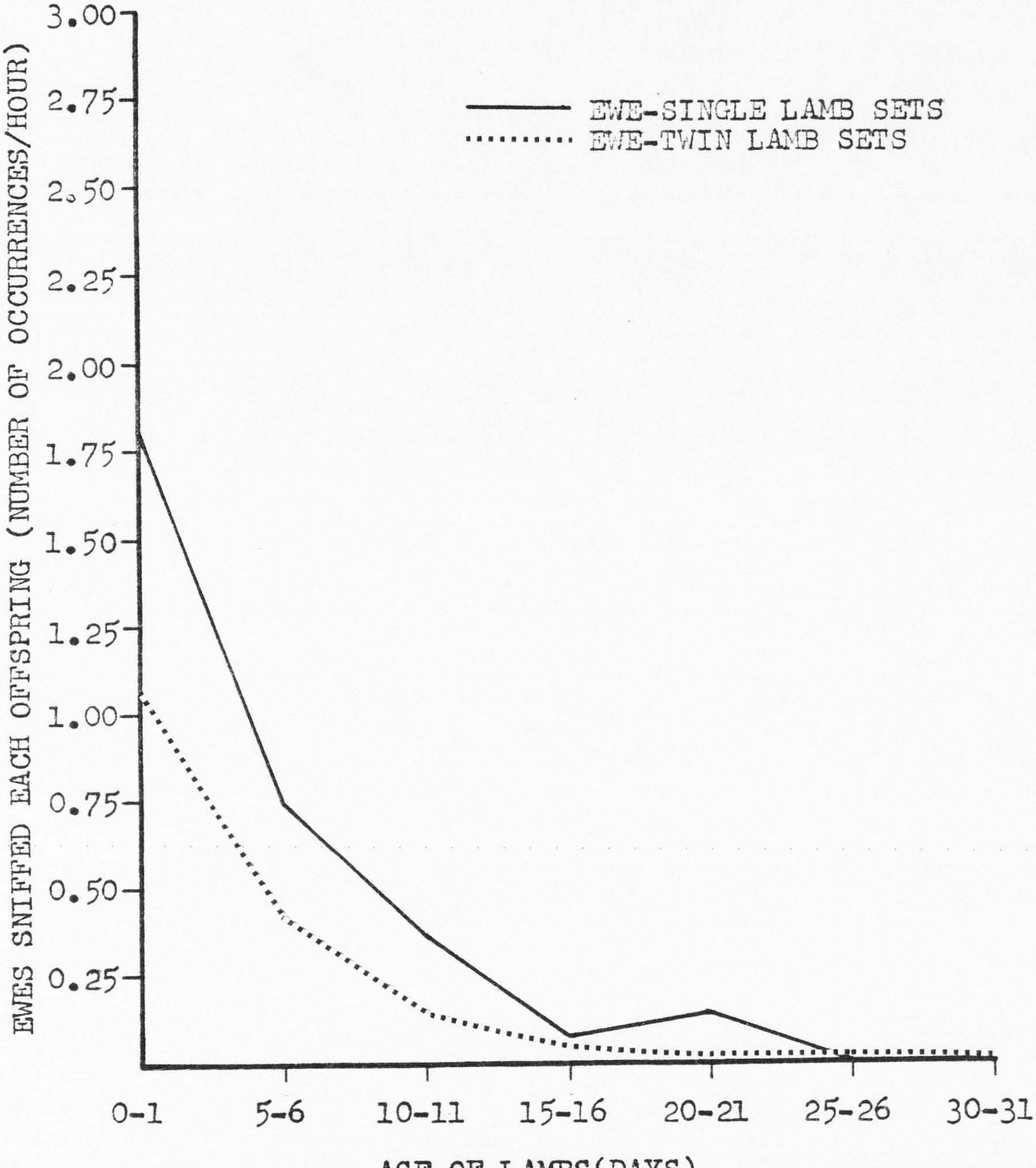

Figure 19. Frequencies at which ewes sniffed each individual offspring, in ewe-single lamb sets and ewe-twin lamb sets by age of lambs.

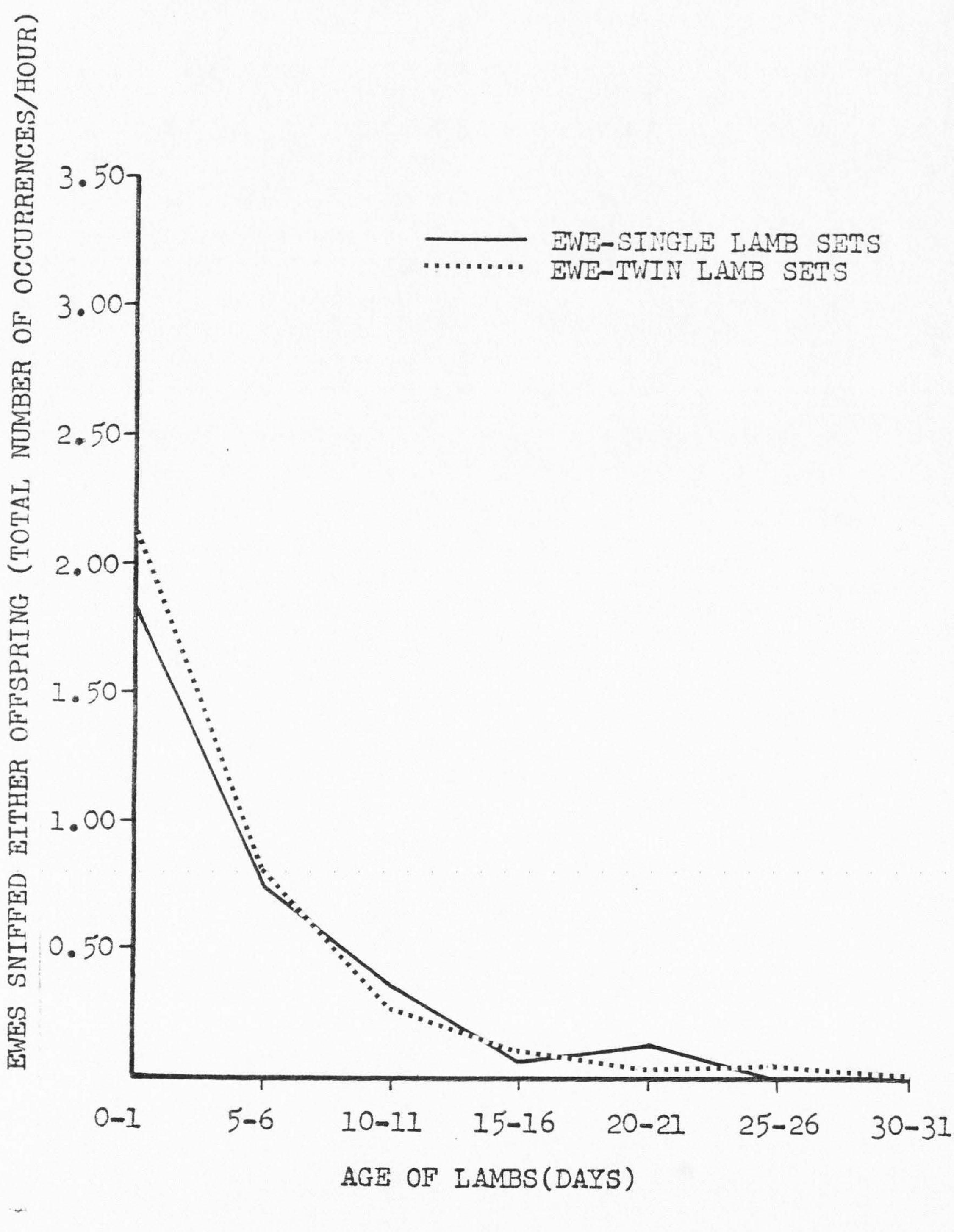

Figure 20. Frequencies at which ewes sniffed either of their offspring, in ewe-single lamb sets and ewe-twin lamb sets by age of lambs.

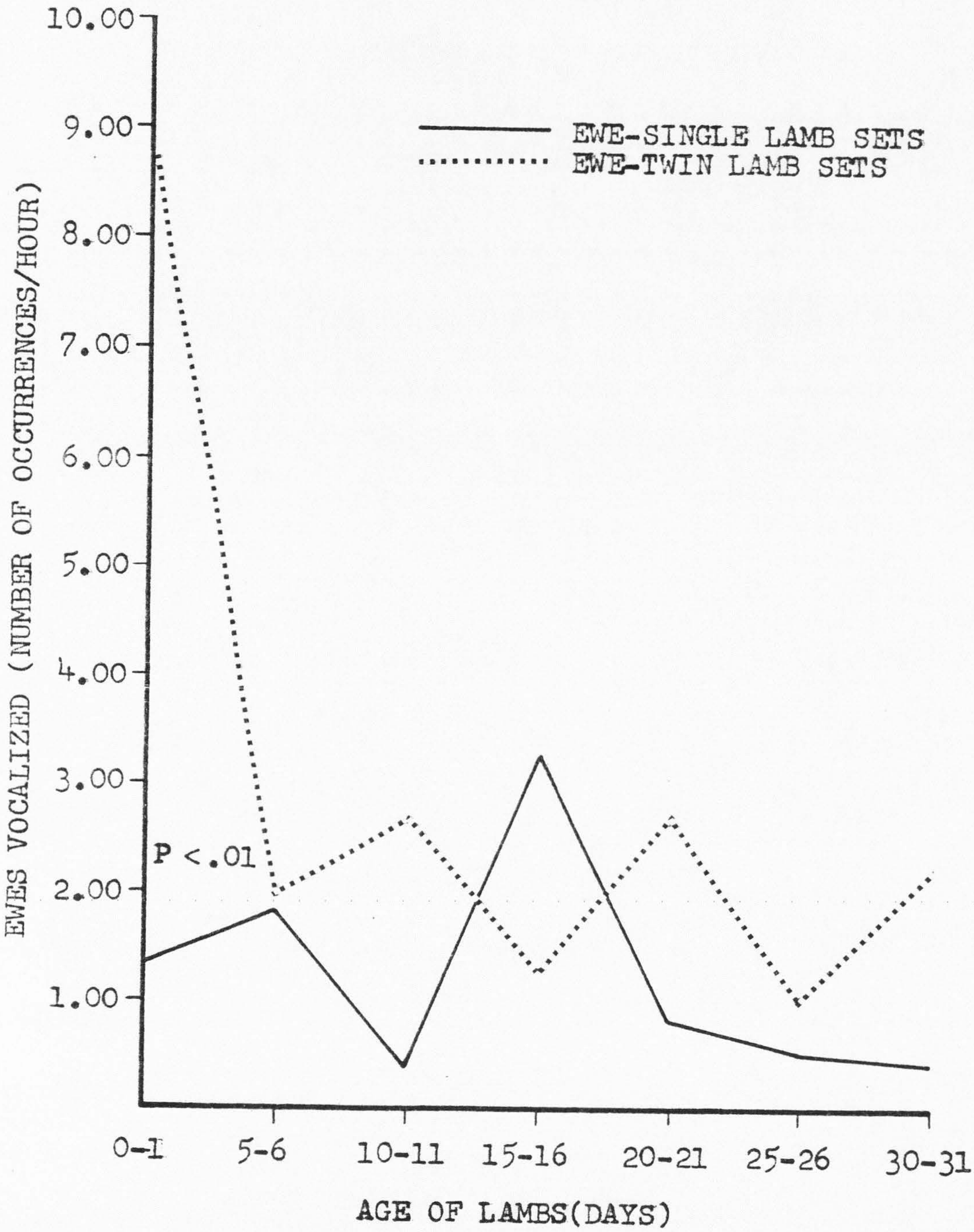

Figure 21. Frequencies at which ewes vocalized, in ewe-single lamb sets and ewe-twin lamb sets by age of lambs.

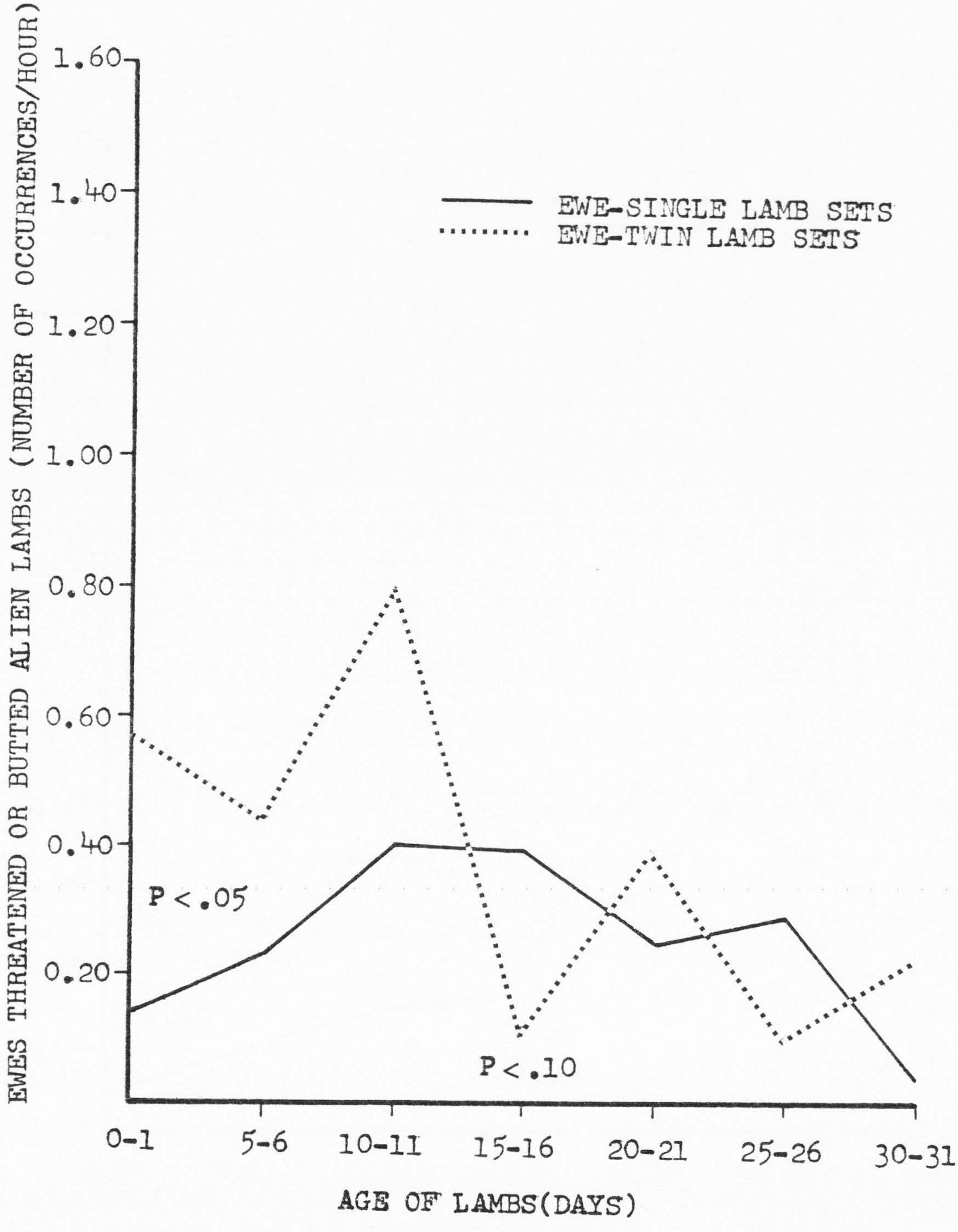

Figure 22. Frequencies at which ewes horn threatened or butted alien lambs, in ewe-single lamb sets and ewe-twin lamb sets by age of lambs.

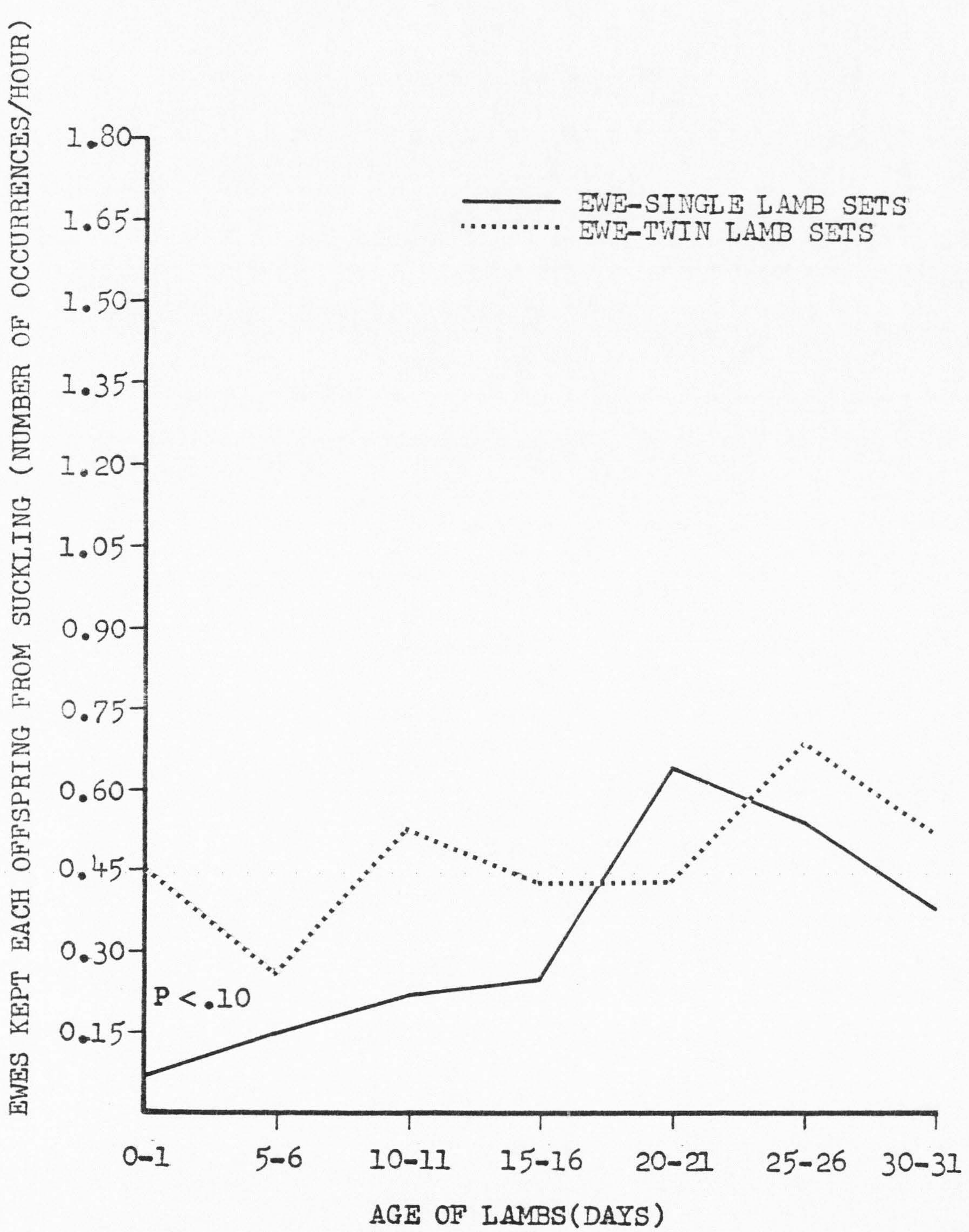

Figure 23. Frequencies at which ewes prevented each individual offspring from suckling, in ewe-single lamb sets and ewe-twin lamb sets by age of lambs.

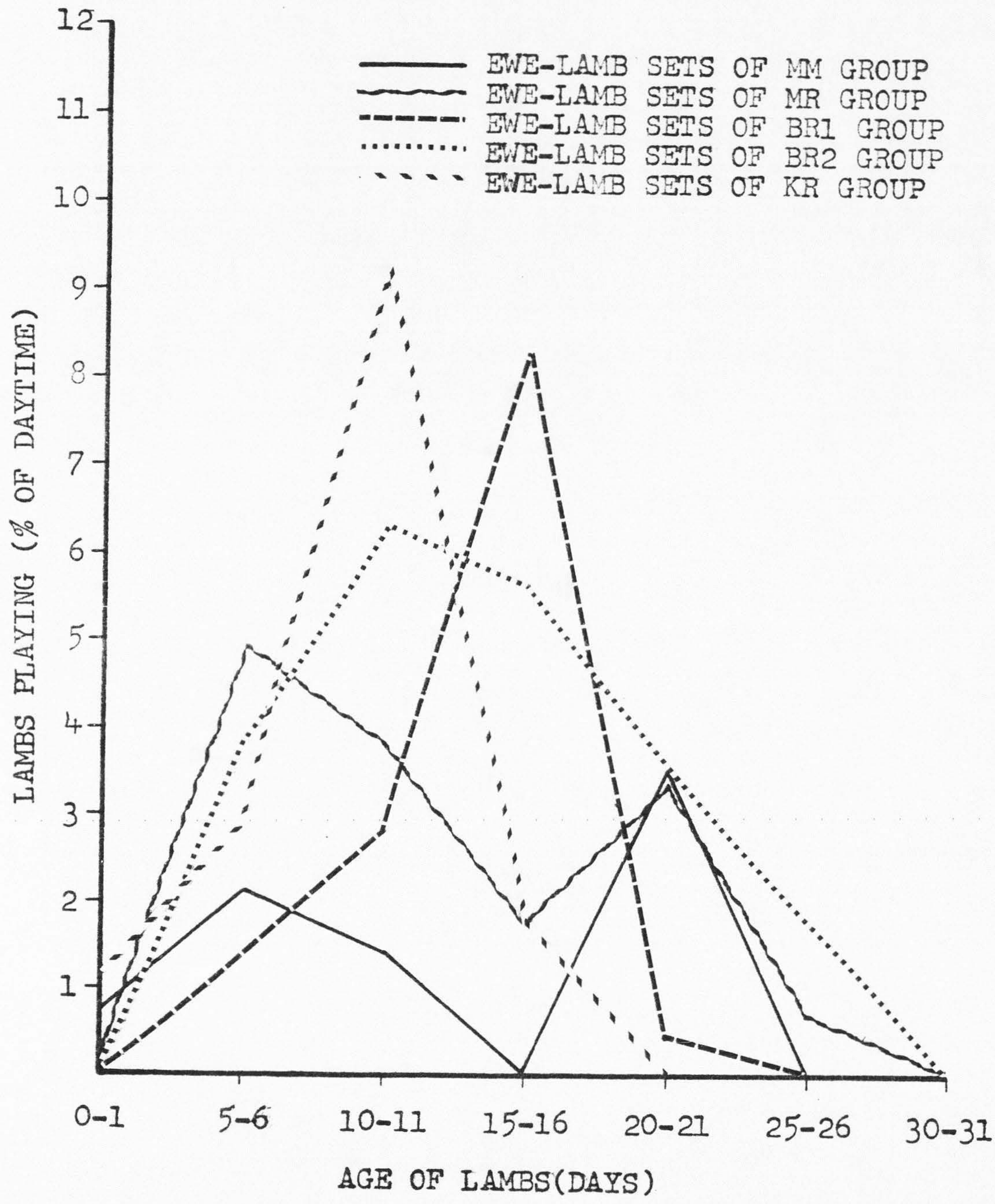

Figure 24. Percentages of daytime that lambs spent playing, in ewe-lamb sets by genotype and age of lambs.

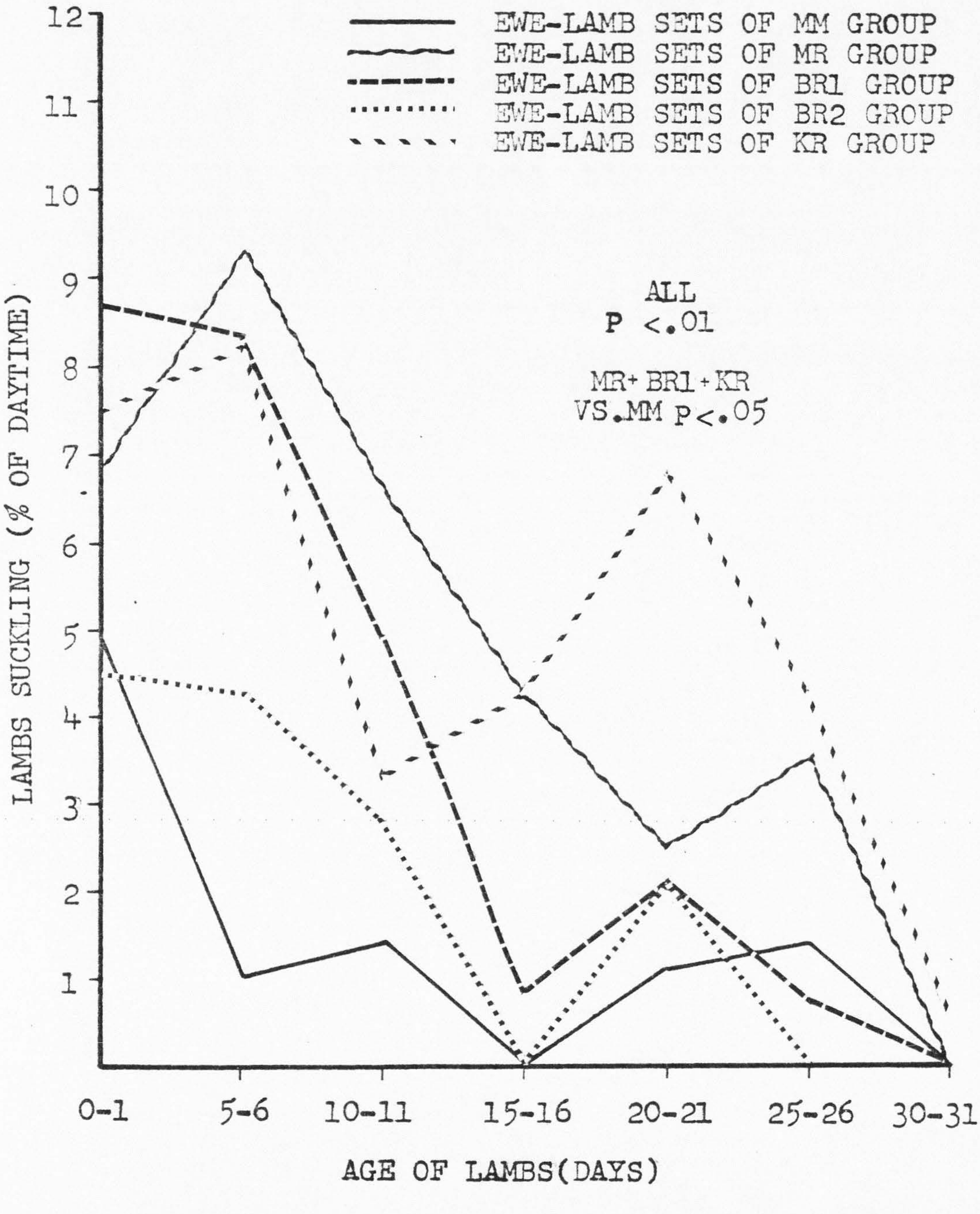

Figure 25. Percentages of daytime that lambs spent suckling, in ewe-lamb sets by genotype and age of lambs.

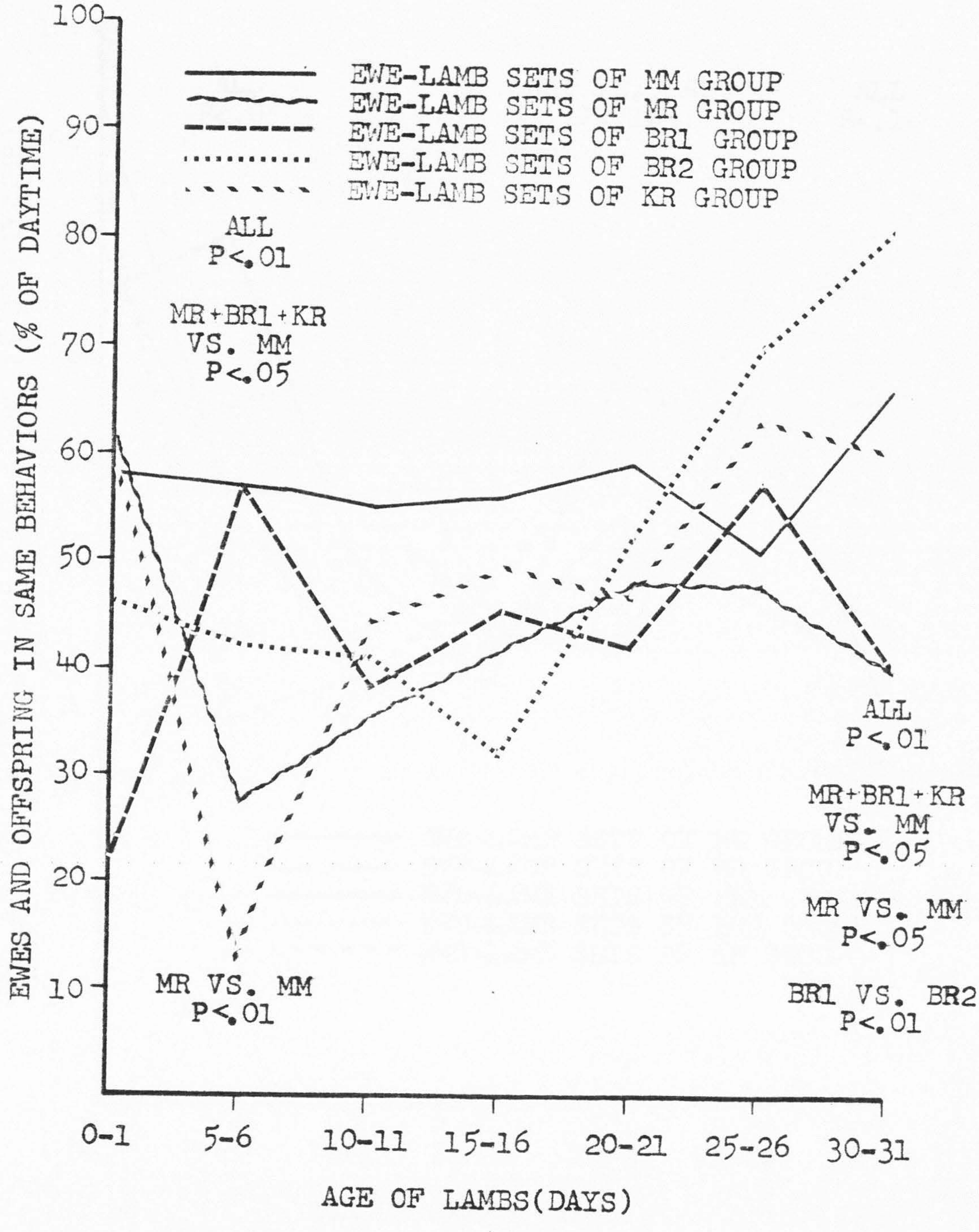

Figure 26. Percentages of daytime that ewes and their offspring spent simultaneously engaged in the same behaviors, in ewe-lamb sets by genotype and age of lambs.

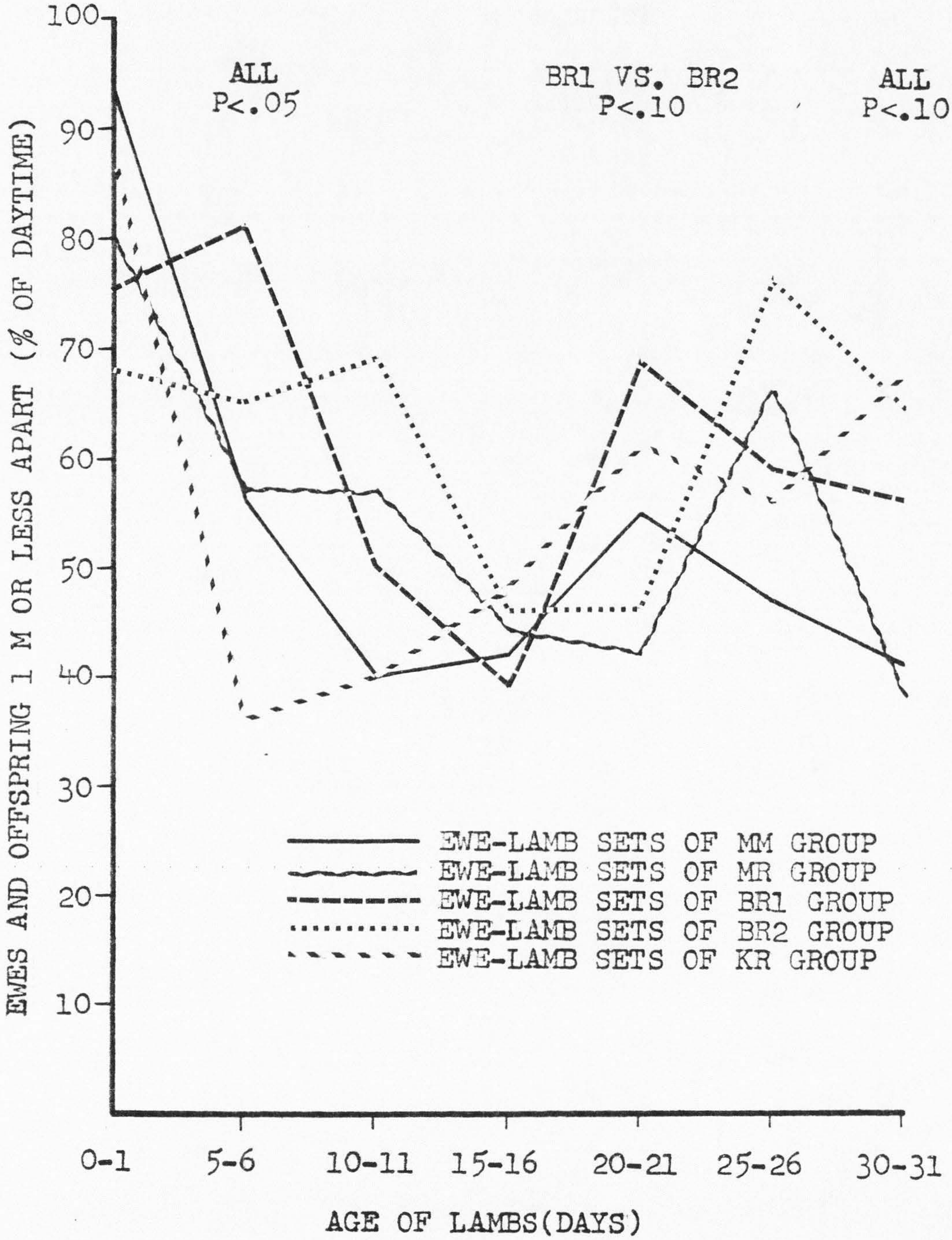

Figure 27. Percentages of daytime that ewes and their offspring spent at 1 m or less from each other, in ewe-lamb sets by genotype and age of lambs.

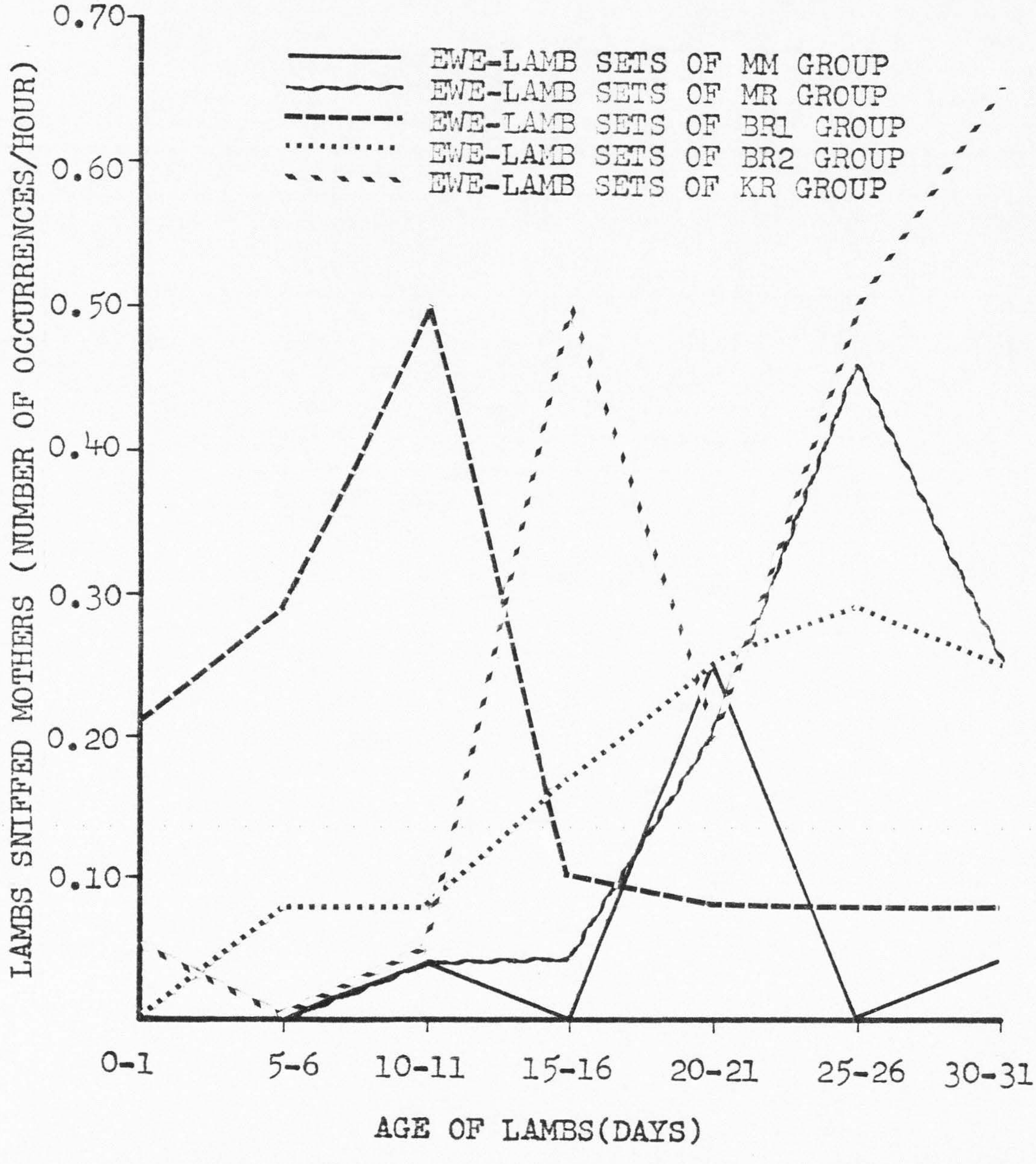

Figure 28. Frequencies at which lambs sniffed their mothers, in ewe-lamb sets by genotype and age of lambs.

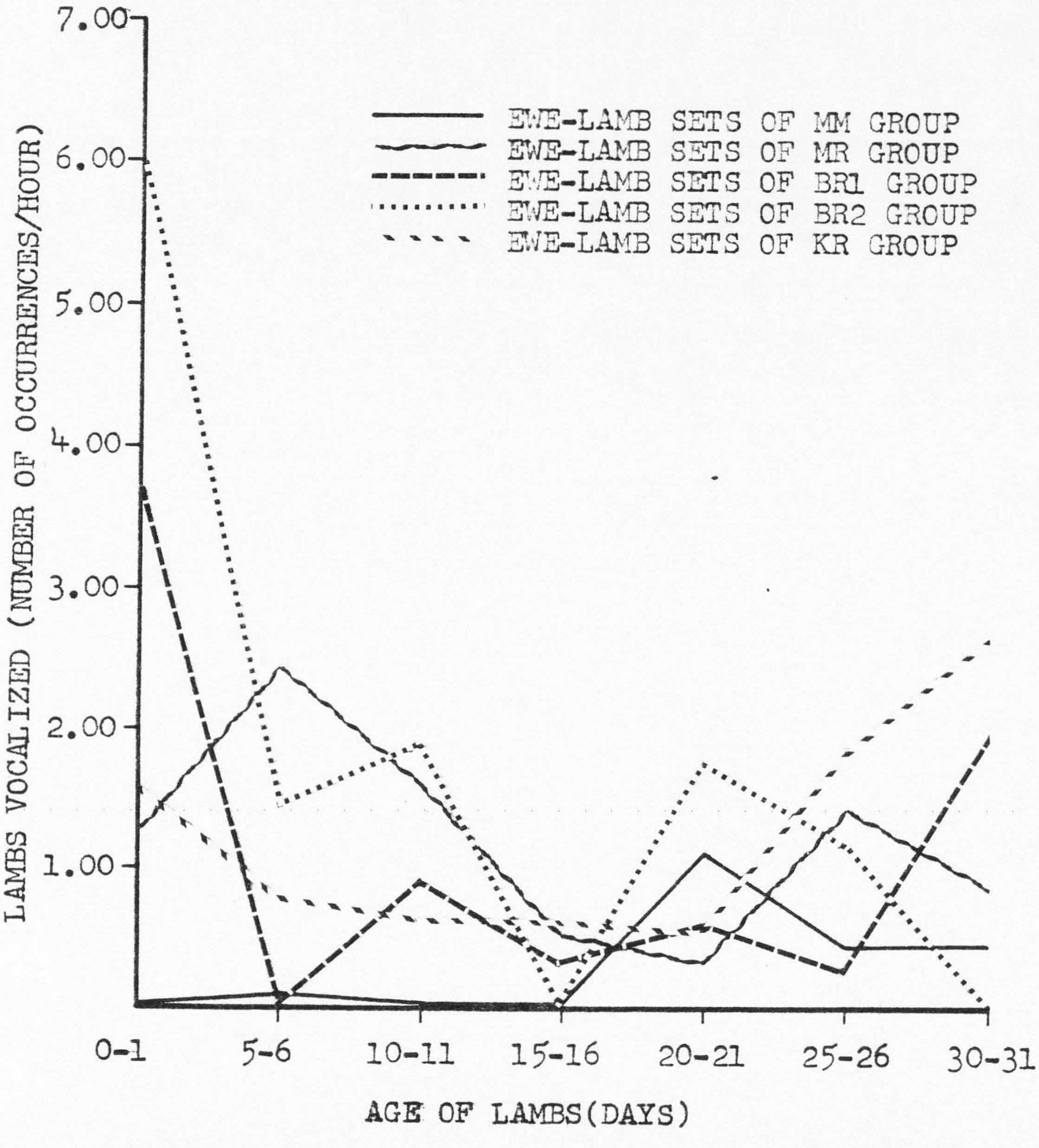

Figure 29. Frequencies at which lambs vocalized, in ewe-lamb sets by genotype and age of lambs.

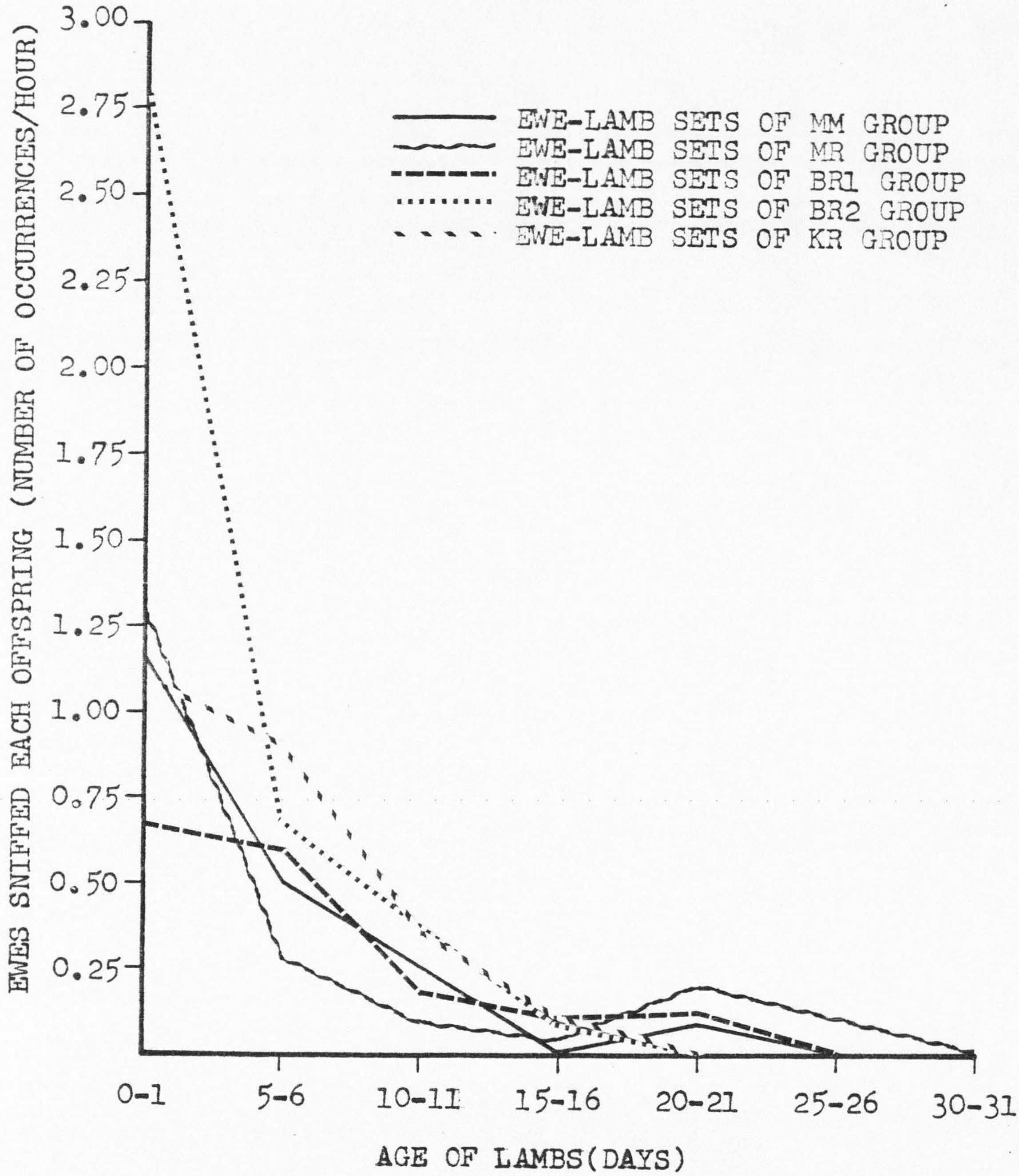

Figure 30. Frequencies at which ewes sniffed each individual offspring, in ewe-lamb sets by genotype and age of lambs.

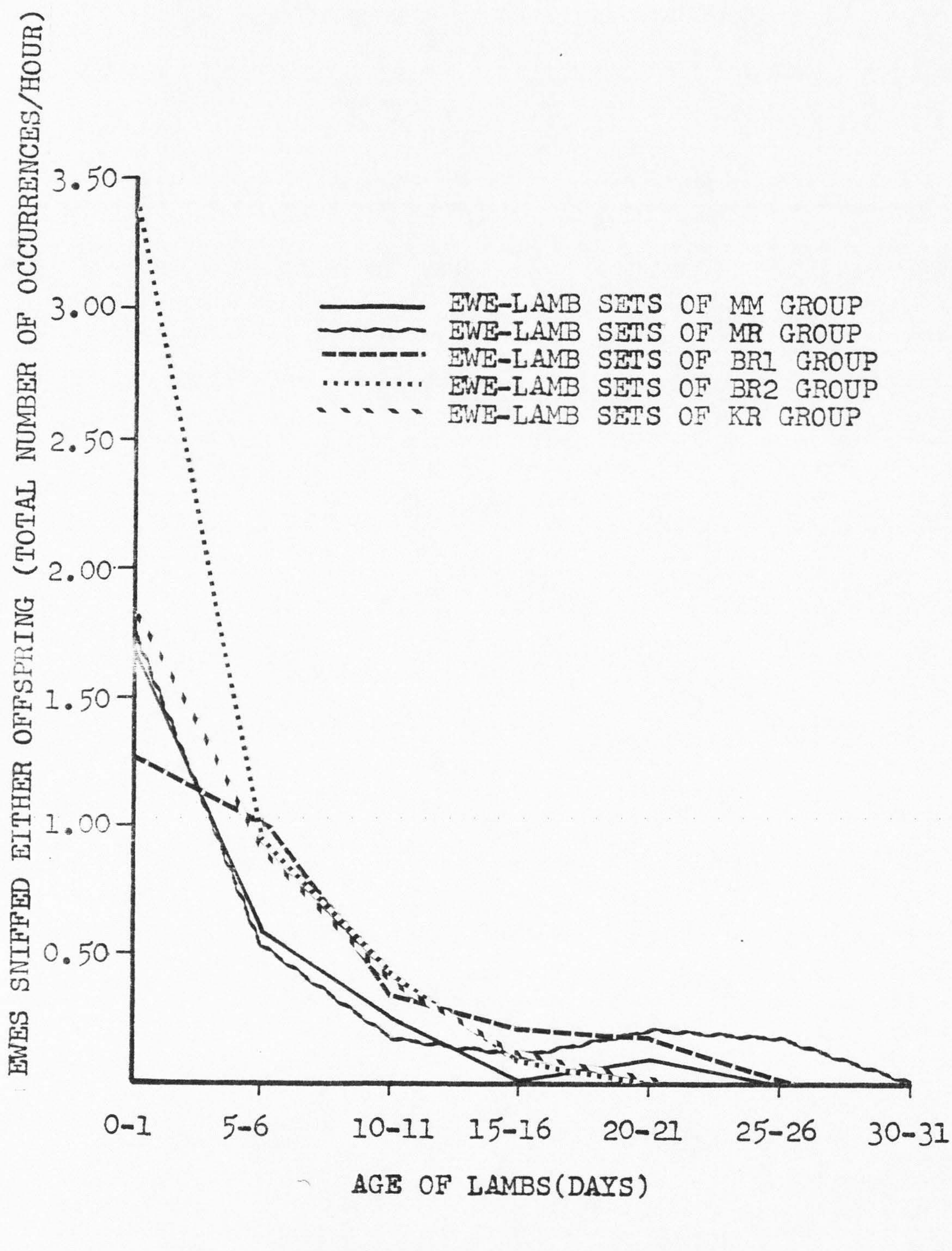

Figure 31. Frequencies at which ewes sniffed either of their offspring, in ewe-lamb sets by genotype and age of lambs.

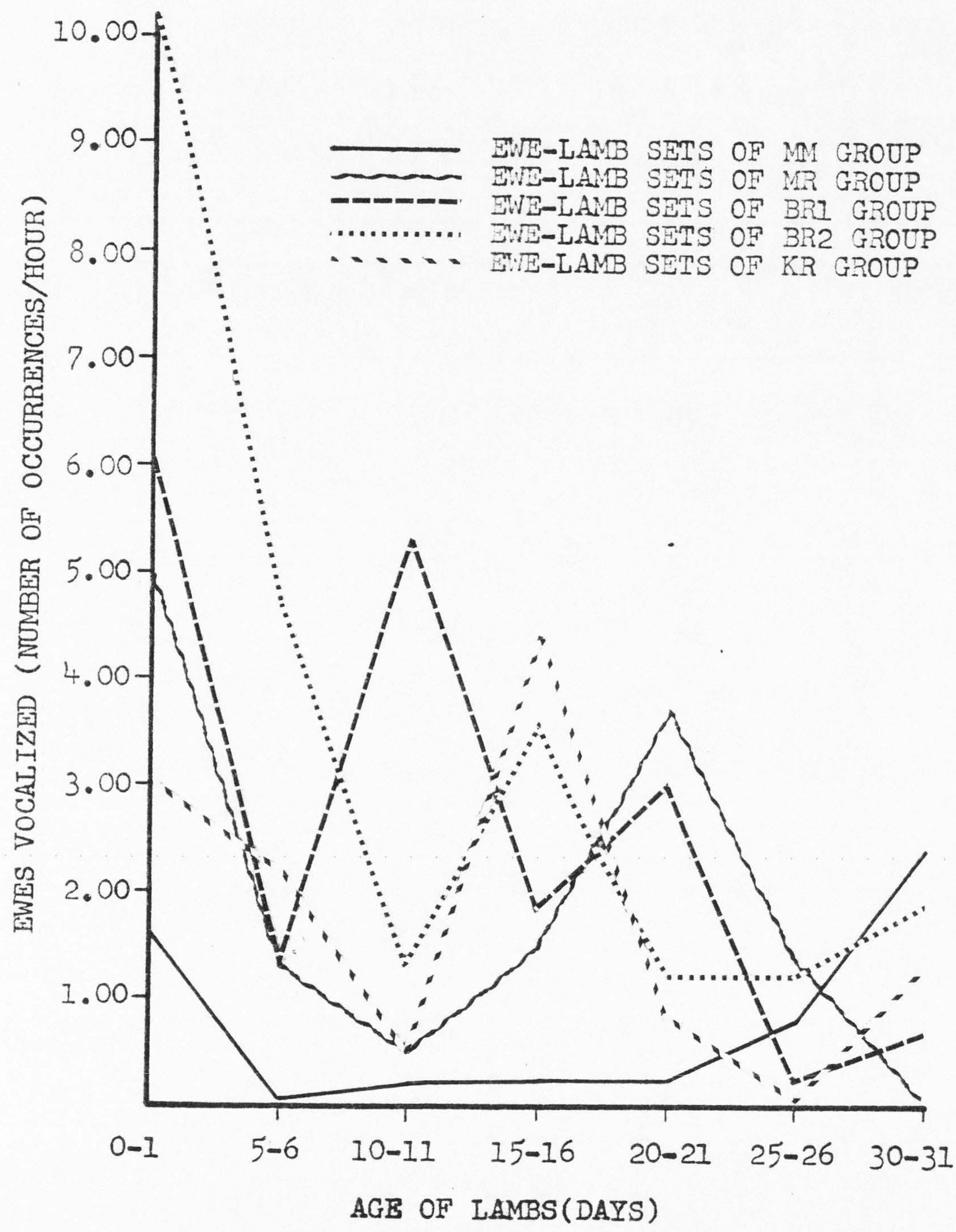

Figure 32. Frequencies at which ewes vocalized, in ewe-lamb sets by genotype and age of lambs.

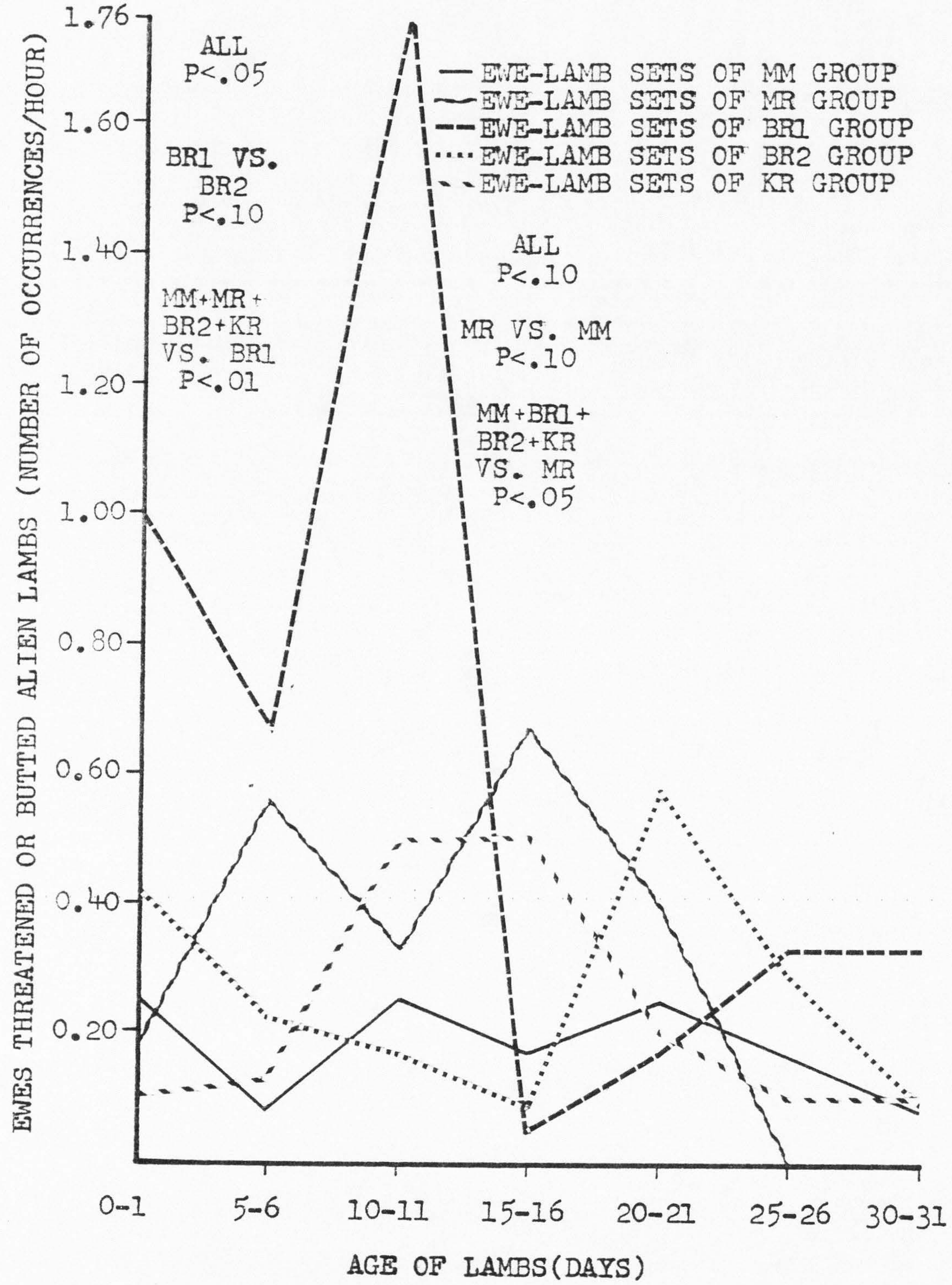

Figure 33. Frequencies at which ewes horn threatened or butted alien lambs, in ewe-lamb sets by genotype and age of lambs.

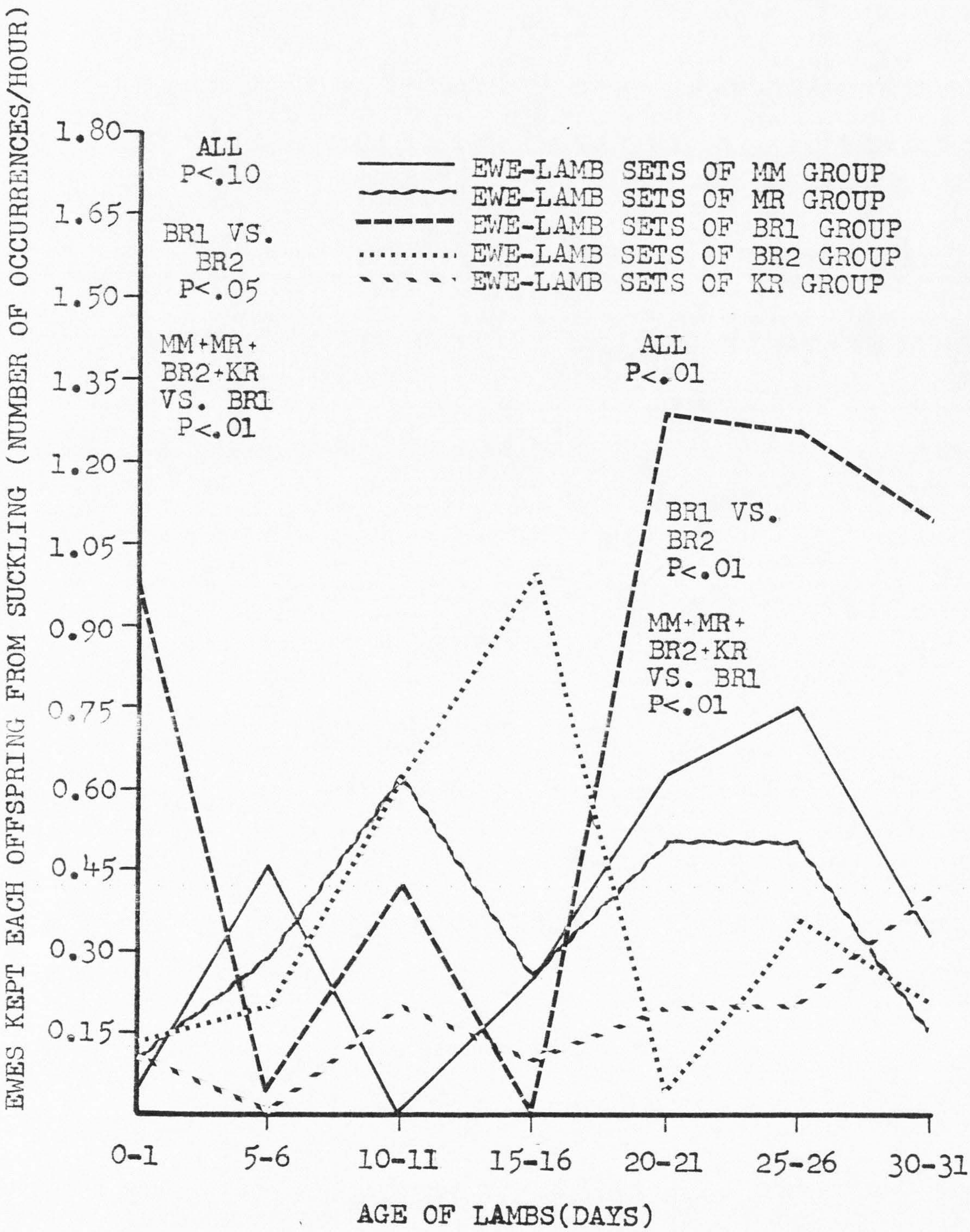

Figure 34. Frequencies at which ewes prevented each individual offspring from suckling, in ewe-lamb sets by genotype and age of lambs.

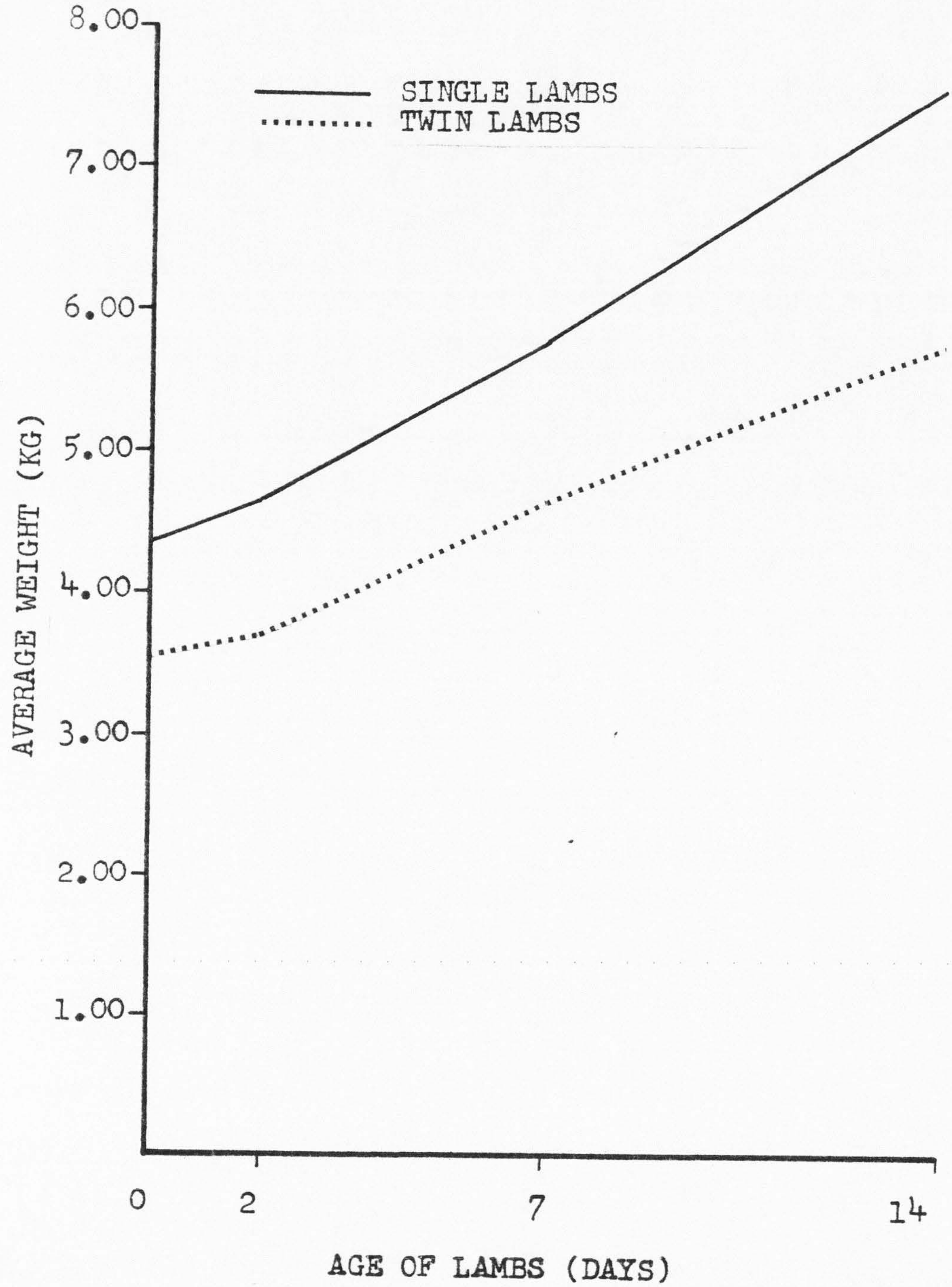

Figure 35. Weight gain by 18 single lambs and 30 twin lambs over the 2 week period following birth.

DISCUSSION

The Influence of Domestication on Ewe and Lamb Traits

Maternal care

Six rare behaviors and one common behavior were used as indicators of maternal care in this study. Ewes sniffing offspring, lambs sniffing mothers, ewes vocalizing, lambs vocalizing, ewes horn threatening or butting alien lambs, and ewes not preventing their own lambs from suckling were the rare behaviors, and lambs suckling was the common behavior. As given in the Results section, differences in the degree of maternal care exhibited by the genotypic groups were assessed in two ways. First, significant differences between the groups were found at certain age classes for four of the behaviors. Second, the groups were individually ranked using their month-long rates or percentage for the seven behaviors.

Ewes sniffing offspring

Ewes rapidly form a closed bond with their offspring within hours, or even minutes, of parturition (Collias 1956, Hersher et al. 1963, Smith et al. 1966, Shillito and Alexander 1975). For maternal bonding to successfully occur, the ewe must learn to distinguish her offspring from other young. The lambs' olfactory cues are of primary importance in the recognition process used by mothers, although other sensory cues are significant (Tschanz 1962, Lindsay and Fletcher 1968, Morgan et al. 1975, Shillito and Alexander 1975, Alexander 1977, Alexander and Shillito 1977, Walser 1978). Parturient ewes lick and sniff their lambs very intensely. Even beyond the postpartum period, ewes sometimes sniff their lambs' anogenital areas as a final verification of the correct identity. Experimental evidence indicates that anosmic ewes lack discriminative behavior at suckling between their own and alien young (Poindron and Le Neindre 1980). In addition, olfactory stimuli have a nonspecific influence on maternal behavior by increasing the level of interest ewes display toward their lambs (Lent 1974, Poindron and Le Neindre 1980). For example, suppression of the sense of smell in ewes leads to disturbances in the maternal response (Poindron and Le Neindre 1980). Thirdly, naso-nasal contacts initiated by mothers to their lambs apparently strengthen the young's following response (Lent 1974). Thus, olfactory stimulation helps to ensure the maintenance of maternal care. Such a factor is particularly important in the more crowded conditions of the domestic environment.

Results showed that the groups' ordering from the highest to the lowest total number of occurrences per hour that ewes sniffed their offspring was BR2, KR, MR and BR1, MM.

Lambs sniffing mothers

With regard to lambs, the role of olfactory cues in bond formation and ewe recognition has not been studied. The process of maternal identification develops slowly in lambs, taking as long as 21 days after birth to complete (Tschanz 1962, Morgan and Arnold 1974, Arnold et al. 1975, Shillito 1975). The present results showed a general increase in the young's sniffing of their mothers as they grew older (see Figure 28), so olfactory information may contribute to the recognition process. It is probable that the lambs' nasal contact, which mothers permit from their own young and prevent from alien young, contributes to the exclusive character of the ewe-lamb bond. Such stimulation also may elicit maternal responses from the ewe.

The groups' ordering from the highest to the lowest number of occurrences per hour that lambs sniffed their mothers was KR, BR1, BR2, MR, MM.

Ewes vocalizing and lambs vocalizing

Vocalization between ewes and their lambs helps them to locate each other, and it probably also functions in the bonding and recognition processes. Lindsay and Fletcher (1968, p. 416) suggested that the calling of lambs only served as "a non specific alerting signal," and Morgan et al. (1975) concluded that auditory cues helped ewes to locate their lambs, but not to identify them. However, the work of Shillito (1975), Shillito and Alexander (1975), Alexander (1977), Alexander and Shillito (1977), and Walser (1978) indicated that the vocalization of both ewes and lambs not only served as an attractant, but also aided in the discrimination process. Ewes probably recognize the vocal patterns of their lambs within 24 hours of parturition, but the lambs' ability to recognize their mothers' vocal cues may not fully develop until 3 weeks of age (Shillito and Alexander 1975). Like nasal contact, vocal contact is also important in the stimulation of maternal interest, and in strengthening the young's following response.

Vocalization is thus another important factor in the maintenance of maternal behavior, especially in the domestic environment. Calling helps to prevent lambs from becoming separated from their mothers in situations of higher animal densities. However, in the wild environment, it would not be adaptive to attract the attention of predators by frequent vocalization between mothers and their young.

The groups' ordering from the highest to the lowest number of occurrences per hour that ewes vocalized was BR2, BR1, MR, KR, MM. The ranking for the number of occurrences per hour that lambs vocalized was BR2, KR, MR, BR1, MM.

Ewes horn threatening or butting
alien lambs

Lent (1974, p. 38) noted that "Mothers play an active role in strengthening and maintaining maternal-infant bonds by driving away strange infants that approach them." This behavior also reduces competition to the ewe's own lamb and so increases the lamb's chances of survival. Such protection against competition is especially important in crowded domestic flocks. On the other hand, this horn threatening or butting behavior is less adaptive among wild sheep, since wild sheep often occur in small kinship groups in which all the members are closely related.

The groups' ordering from the highest to the lowest number of occurrences per hour that ewes horn threatened or butted alien lambs was BR1, MR, BR2, KR, MM.

Ewes preventing their own lambs
from suckling

Young lambs are usually allowed to suckle at will, but there is an increasing tendency for their mothers to prevent suckling attempts as the lambs grow older (Ewbank 1967). Although this behavior is a normal part of the weaning process when the lamb is 3 to 5 months old, infrequent prevention during the lambs' first month of life reflects better quality maternal care. An early, lower incidence of ewes preventing their lambs from suckling results in more frequent suckling periods, which are beneficial to the young's growth and health. More frequent suckling permits more milk consumption immediately, and may also induce the ewe's milk production to increase (Blaxter 1961).

The groups' ordering from the lowest to the highest number of occurrences per hour that ewes prevented each of their lambs from suckling was KR, MR, MM, BR2, BR1.

Lambs suckling

Nursing behavior is one of the most important aspects of maternal care, and the amount of time a lamb spends suckling reflects the strength of the dam's nursing tendency. Lambs which suckle more grow more rapidly and have a better chance of survival than lambs which suckle less.

The groups' ordering from the highest to the lowest percentage of time that lambs suckled was KR, MR, BR1, BR2, MM.

Integration of behaviors associated
with maternal care

The Rambouillet ewes of the BR1 and MR groups showed a strong defense of the immediate space around them, and in turn, of access to their milk. They displayed significantly more frequent horn threatening or butting of alien young in comparison to the other ewes at early periods of their lambs' life, when bonding and suckling were especially important ($P<.01$ at 0-1 days and $P<.05$ at 15-16 days). In addition, all the Rambouillet ewes spent more time engaged in nursing behavior than did the other ewes, particularly in comparison to the Mouflon ewes ($P<.05$ at 20-21 days). However, in contrast to the Rambouillet breed's favorable tendencies, one of the Rambouillet ewe groups (BR1) exhibited the highest rates of suckling prevention toward their own lambs at two age periods ($P<.01$ at 0-1 days and at 20-21 days). Since the BR1 group's high rates of horn threatening or butting of alien lambs and preventing suckling of their own lambs occurred at the same or similar age periods, the former behavior may have inadvertently interfered with suckling attempts by the ewes' own lambs.

The F_1 Barbados-Rambouillet ewes of the BR2 group exhibited the highest use of vocal ($P<.10$ at 0-1 days) and olfactory contact with their young during the first postpartum days. Also, the F_2 Barbados-Rambouillet lambs of the BR2 group vocalized more in comparison to the other lambs during the first days after birth. Such behaviors contribute to a strong bond between mother and young, and they help insure the young's survival during this critical time. The high degree of sensory contact shown by the BR2 group may be a behavioral indication of hybrid vigor. However, since purebred Barbados and Rambouillet groups were not included in this study, a substantiated conclusion on heterosis must await future work.

The rankings of each group for the seven behaviors averaged as follows: the KR group, 2.14; the BR2 group, 2.43; the MR group, 2.79; the BR1 group, 2.93; the MM group, 4.71. Thus, the observations on significant differences and rankings generally supported the suppositions concerning the first objective. The pure domestic group showed the most activity associated with maternal care, while the pure wild group exhibited much less activity associated with maternal care, in comparison to the other groups. The groups with partially domestic lambs were intermediate in their display of maternal behaviors. Of these three groups, the BR2 group with half-domestic mothers showed the most activity associated with maternal care, possibly owing to hybrid vigor.

Learning in the young

In Kummer's (1971, p. 127) general discussion of acquired behaviors he noted that discovery learning is "appropriate if the information is relevant only to the individual who has the experience and if this information is easy to discover." Discovery learning is particularly important for the growing domestic animal, which is often moved or sold to a new locale or flock by its owner.

On the other hand, imitative learning is more advantageous in the wild environment, because the experiences of older animals with factors such as local topography, food and water sources, and migratory routes are perpetuated within the group without the risks of discovery learning (Kummer 1971). Tradition plays an important role in wild sheep societies, and a primary means through which tradition learning takes place is by directly imitating more mature and experienced individuals (Geist 1971).

Lambs and their mothers simultaneously engaged in the same behaviors

The amount of time young and their mothers spend simultaneously lying, standing, feeding, or moving is one indication of the amount of imitative learning the young display. Imitative learning perpetuates traditions, and is the opposite of discovery learning.

At both early and late periods of the lambs' first month of life, the Mouflon ewes and their lambs spent significantly more time simultaneously engaged in the same behaviors than did the Rambouillet ewes and their hybrid lambs ($P<.05$ at 5-6 days and at 30-31 days). The BR2 group showed a significantly higher percentage than did the BR1 group for this behavior when the lambs were a month old ($P<.01$).

The groups' ordering from the lowest to the highest percentage of time that lambs and their mothers spent simultaneously engaged in the same behaviors was BR1 and MR, KR, BR2, MM.

Lambs playing

Play, primarily an activity of young animals, tends to have negative effects on an individual's immediate fitness (Fagen 1977). It diverts energy and time from other allocations such as suckling and feeding. Animals at play may become injured, may not notice an approaching predator, and may actually attract a predator. The positive effects of play result from delayed or cumulative benefits (Fagen 1977). One of the benefits of play is that a young animal learns about its environment through discovery (Eibl-Eibesfeldt 1970). This function is especially positive for the immature domestic animal. For example, through play with its conspecifics the young domestic animal learns about its very diverse and unstable social environment (Price and King 1968). Moreover, the domestic situation presents few of the negative aspects associated with play. However, in the wild environment the drawbacks connected with play--energy loss, injury, predation--are more relevant. Sachs and Harris (1978) suggest that the dangers of the wild sheep's mountainous environment result in a reduction of play tendencies in wild lambs. Also, for wild sheep species, gaining information independently through frequent play would tend to be counterproductive to learning traditions through imitative behavior.

The groups' ordering from the highest to the lowest percentage of time that lambs played was BR2, MR and KR, BR1, MM.

Integration of behaviors associated with learning in the young

The rankings of each group for the two behaviors averaged as follows: the MR group, 2.00; the BR2 group, 2.50; the KR group, 2.75; the BR1 group, 2.75; the MM group, 5.00. When the significant differences and rankings are considered together, it is evident that the wild group showed much more activity associated with imitative learning and less activity associated with discovery learning than any of the other groups. Results indicated that the F_1 generation hybrid lambs showed stronger inclinations toward behavior associated with discovery learning, with this inclination being more prominent in the MR group rather than the KR group. The F_2 Barbados-Rambouillet lambs spent a high percentage of time in simultaneous behaviors with their mothers, and yet they played the most. Their strong tendency toward activities associated with imitative and discovery learning was perhaps due to the more varied genetic combinations of F_2 generation hybrids in comparison to F_1 generation hybrids. Thus, the partially domestic groups were not intermediate to the domestic and wild groups for play and time spent in simultaneous activities.

Proximity of conspecifics

One of the behavioral traits which favored domestication in sheep was their social structure in flock formations rather than small family units. The natural structure of the flock is easily managed by humans, and it provides a sizeable grouping to produce wool and meat in large quantities (Hale 1962). It is likely that changes in the flock structure were induced through selective breeding. One such change probably was toward maintenance of a spatially tight flock: Less dispersed sheep are more readily managed by a herder than are widely dispersed sheep.

Therefore, members of domestic and semi-domestic breeds should spend more time close to other sheep than do members of wild species. One way to assess differences in this trait is to consider the amounts of time that the ewes and lambs of the genotypic groups spent close to each other. The groups' ordering from the highest to the lowest percentage of time that ewes and their lambs spent at close distance to each other was BR2, BR1, KR, MR, MM.

The results of the close distance category supported the first but not the second supposition concerning the first objective. The domestic and semi-domestic groups displayed a greater tolerance or inclination for close affiliation than did the wild group. However, the Barbados-Rambouillet groups exhibited a greater tendency for closeness than did the most domestic group (KR), and consequently the partially domestic groups were not all intermediate to the domestic and wild groups. Perhaps the first place ranking of the BR2 group was due to hybrid vigor.

Breeding parameters

Length of breeding season

The Mouflon ewes observed in this study exhibited a breeding season 1 to 3 months longer than the seasons noted by Hafez (1952) and Müller-Using (1972). Wild sheep generally have a short breeding season, which occurs primarily during the fall. In the wild, breeding by fertile rams usually results in pregnancy, and hence, a cessation of estrous cycles in the ewes. The longer breeding season observed in the present study was probably due to the use of sterile rams. The use of these rams created an artificial situation for the Mouflon ewes, and they exhibited repeated estrous cycles. It is still of interest to note that the breeding season of the study's captive Mouflon occurred during the fall and early winter, and did not show the extreme lengthening of the season exhibited by many domestic breeds (Hafez 1952). Also, the dates of initiation and cessation of estrous activity in the Mouflon ewes were relatively constant from year to year, and were probably closely tied to photoperiod (Hafez 1952).

Length of estrous cycle

Because the mean lengths of the estrous cycles were not significantly different for the Rambouillet, Karakul, Barbados, and Mouflon, domestication apparently has not influenced this physiological trait in these breeds. The goats' longer estrous cycle in comparison to the sheep's ($P<.01$) is a characteristic difference between the two genera (Robinson 1959).

Length of gestation

The mean length of gestation shown by the Mouflon ewes was not significantly different than the mean length measured for the Rambouillet ewes. However, the Karakul and F_1 Barbados-Rambouillet ewes ($P<.01$) exhibited shorter gestation lengths in comparison to the other ewes. Thus, although domestication apparently has not generally altered the length of gestation, the length varies between certain breeds.

Integration of measurements associated with breeding parameters

Although domestication has modified the length of the breeding season in many breeds of sheep, it apparently has had less effect on length of gestation and no effect on length of estrous cycle.

Fertility

The measurement of fertility which was used in this study was the number of young born per female giving birth. The groups' ordering from the highest to the lowest number of lambs born per ewe was MR, KR and BR1, BR2 and MM.

In previous studies, crossing different domestic breeds has resulted in higher fertility (Carter 1979). Apparently crossing wild rams and domestic ewes (MR) or semi-domestic rams and domestic ewes (BR1), produces a similar effect. However, the hybrid cross of F_1 Barbados-Rambouillet rams and ewes (BR2) exhibited a reduced lambing rate when compared to the rate of Barbados rams and Rambouillet ewes (BR1). Perhaps the optimum benefits for greater fertility occur when crossing species or breeds, and the effects are not retained when mating the hybrids.

Domestic sheep usually display higher lambing rates than do wild sheep (Foote 1979), and they did so in the present study. Still, the MM group's rate of 1.4 was higher than that observed in the wild, where Mouflon only occasionally bear more than one lamb (Bannikov and Heptner 1972). A lambing rate higher than in wild populations has been noted in other captive or introduced groups. Dr. Thomas D. Bunch (pers. commun., September 8, 1981, Research Associate Professor of Animal Science, Utah State University) observed a rate of 1.2 in a captive flock, and a Mouflon population which was introduced in Crimea exhibited a lambing rate of 1.5 (Pfeffer 1967). The MM group's increased fertility was probably due to the higher level of nutrition available in the captive environment. In addition, a genetic change may be involved, as in the increased fertility associated with captive deermouse populations (Price 1967, 1970).

These results supported the supposition that groups which have been under domestication longer exhibited the greatest departure from wild populations in fertility: The groups with domestic ewes showed higher lambing rates than did the group with wild ewes. The results did not support the supposition that the offspring of domestic and semi-domestic parents were intermediate to domestic and wild stock in fertility.

Crossing a wild-domestic buck with domestic does did not noticeably raise the birth rate of the goats. The number of kids born per doe, 2.1, is comparable to the common occurrence of twins in domestic goats (Robinson 1959, Asdell 1964).

Birth weight

The groups' ordering from the highest to the lowest weight of the lambs at birth was KR, MR, BR1, BR2, MM. Although the domestic group had the highest average birth weight, the birth weight of the wild-domestic cross was almost as great. Also, the F_2 generation hybrid had a lower birth weight in comparison to its F_1 generation counterpart. The observation that the MM group displayed the lowest birth weight concurs with previous work on the birth weight of wild sheep. For example, a domestic lamb weighs at least 1 kg more at birth than does a bighorn lamb (Ewbank 1967, Geist 1971).

Therefore, these results supported both of the first objective's suppositions. The domestic group (KR) had a higher birth weight than did the wild group (MM), and the birth weights of the partially domestic lambs were intermediate to those of the domestic and wild lambs.

The average birth weight of the wild-domestic kids was 2.8 kg, almost twice as much as the mean birth weight of 1.5 kg which Galeon (1951) observed for domestic kids. This finding indicates a beneficial consequence of crossing a partially wild buck with domestic does.

Growth rate

The groups' ordering from the highest to the lowest weight gain of the lambs from birth to 2 weeks of age was KR, BR1, BR2, MR, MM. Thus, the domestic group showed the greatest weight gain and the wild group showed the least. The partially domestic groups were intermediate in their weight gains.

The Influence of a Single or Twin Birth on Ewe and Lamb Behaviors

Ewe-lamb bond

Some results seemingly indicated that ewe-single lamb sets had a stronger intraset attachment than did ewe-twin lamb sets. From 0 to 11 days of the lambs' life, singles and their mothers were more often simultaneously engaged in the same behaviors than were twins and their mothers (see Figure 11). Also, mothers of singles sniffed each offspring more frequently than did mothers of twins (see Figure 19). In addition, ewes with singles prevented their lambs from suckling less often than did ewes with twins (see Figure 23).

On the other hand, other results seemingly indicated that ewe-twin lamb sets had a stronger intraset attachment than did ewe-single lamb sets. Twins and their mothers spent more time close to each other (see

Figure 12) and less time far from each other (see Figure 14) than did singles and their mothers. Also, in terms of total occurrences per hour, ewes with twins sniffed their young more often than did ewes with singles (see Figure 20). Furthermore, twins spent a higher percentage of time suckling than did singles (see Figure 6). In addition, from 0 to 11 days of the lambs' life mothers of twins horn threatened or butted alien lambs more frequently than did mothers of singles (see Figure 22). Finally, twins and their mothers both vocalized at higher rates in comparison to their single set counterparts (see Figures 18 and 21). This pattern was especially striking during the first 48 hours of the lambs' life.

Thus, ewes and their single young apparently did not form a stronger bond than did ewes and their twin young. The results indicated no consistent pattern of stronger attachment in one set type than in the other. Behavioral differences between the sets arose from other causal factors, which are considered in the following sections.

Physical development

The results of the present study suggest that physical developmental differences between singles and twins caused some of the behavioral differences. Singles averaged 4.37 kg at birth and 7.52 kg at 14 days of age, while twins averaged 3.52 kg at birth and 5.75 kg at 14 days of age (see Figure 35). Ewbank (1967) noted similar differences in the weights of single and twin lambs which he observed. Although singles and their mothers spent more time simultaneously engaged in the same activities than did twins and their mothers from 0 to 11 days of the lambs' life, after 11 days, the two set types spent similar amounts of time simultaneously engaged in the same behaviors (see Figure 11). Thus, as the twins became stronger they were able to participate more fully in activities with their mothers. Also, the overall percentage of daytime that mothers and young spent simultaneously engaged in the same activities was essentially the same for the single and twin sets. Furthermore, the ratio for expected versus actual time spent simultaneously engaged in the same behaviors was the same for the two sets.

Greater physical and emotional development apparently enabled singles to spend more time at far distance from their mothers during their first month of life ($P<.05$), especially after 3 weeks of age ($P<.05$ at 20-21 days and at 25-26 days, and $P<.10$ at 30-31 days) (see Figure 14). Similarly, singles spent more time at intermediate distance to their mothers than did twins, again most notably after they were 3 weeks old ($P<.05$ at 20-21 days) (see Figure 13). The observation that singles played more than twins during their first month of life ($P<.05$) may be another indication of the singles' more advanced physical state (see Figure 5). Gluesing et al. (1980) also found that singles were generally more active than twins. For example, they too observed that singles played significantly more than twins.

Mothering capacities, sibling competition, and a sibling bond

Several lines of evidence support the supposition that mothering capacities, sibling competition, and a sibling bond caused behavioral differences between ewes and their single young and ewes and their twin young. Twins spent 17 percent more time at close distance to their mothers than did singles, and this intraset difference increased as the lambs grew older (P<.01 at 20-21 days and P<.05 at 30-31 days) (see Figure 12). The study of Morgan and Arnold (1974) also found that twin lambs tended to stay closer to their mothers than did single lambs. The authors suggested that ewes with twins "may require" their young to stay closer, or that twins may compete for maternal care. By staying close to its mother, an individual twin would lose less of its mother's attention to the sibling twin. The results of the present research seem to indicate that twins were competing for maternal care during a variety of the ewes' activities, rather than the ewes somehow inducing twins to stay closer to them.

The findings that twins stood more than singles (P<.01), and that singles lay more than twins (P<.05) during their first month of life, indicates indirectly that twins were in a greater state of readiness for their mothers' attentions than were singles.

Despite the twin lambs' efforts to stay closer to their mothers and the greater state of readiness of twins, the average twin still received only 56 percent as much individual olfactory contact from its mother as did a single (see Figure 19). Also, twins were unable to gain enough nutrition to grow as fast as singles, despite more effort at suckling.

During their first 4 weeks of life, individual twin lambs spent 49 percent more effort suckling than did single lambs (see Figure 6), but twins still grew at a slower rate than did singles. More specifically, from 0 to 16 days of age, individual twins spent 44 percent more time suckling than did singles (see Figure 6), although from 0 to 14 days of age, individual twins gained weight only 71 percent as fast as did singles (see Figure 35). Other researchers noted that individual twins suckled more than did singles (Munro 1956; Ewbank 1964, 1967), but that individual twins grew more slowly than did singles (Slen et al. 1963, Ewbank 1967). Although milk production in mothers of twins is greater, the difference does not compensate for the doubled needs of two offspring (Hafez and Scott 1962, Slen et al. 1963, Ewbank 1967). The greater suckling efforts of twin lambs, for the insufficient quantities of milk, caused mothers of twins to prevent their lambs from suckling 47 percent more often than did mothers of singles (see Figure 23). Ewbank (1967) also observed that ewes with twins seemed to prevent their young from suckling more frequently than did ewes with singles. A twin can outcompete its sibling for the insufficient milk supply, if the twin is ready to suckle whenever suckling is permitted, and if the twin initiates suckling more often and so gets more of the currently available milk.

The observation that twins averaged 83 percent of the daytime at close distance to each other during the first month of their life (see Figure 15) appeared to be at least partially due to their competition for maternal care. By staying close to their mother, twins naturally were close to each other. Also, by staying close to each other, each twin could watch the other's activities, and thus be able to share potential interactions with their mother.

However, since twins spent even more time close to each other than they did close to their mothers--34 percent more time--it is also possible that the tendency to remain close to each other derived in part from a sibling bond. Another indication of the occurrence of a sibling bond is the observation that twins spent only one-fourth as much time at close distance to alien lambs as to each other.

A benefit of the sibling bond is its contribution to flock cohesion. Since twins maintain such a marked degree of close contact, a higher proportion of twins in a flock would probably result in greater cohesion and better synchronization of flock activities.

One of the positive consequences of play is its socialization effects (Fagen 1977). During their first month of life, twin lambs played 55 percent less, on the average, than did single lambs ($P<.05$) (see Figure 5). This marked difference in the amount of playing behavior may be because twins already have peer contact and intense interactions with each other; thus twins have less need to seek out and play with other lambs.

The study's results do not allow us to draw any firm conclusions on the relative strength and interplay of the sibling bond and competition. Further research on these factors would be useful.

Suckling and agonistic behavior

Mothers of twins horn threatened or butted alien young four times more often than did mothers of singles at 0-1 days ($P<.05$), 91 percent more often at 5-6 days, and 100 percent more often at 10-11 days (see Figure 22). The more frequent suckling by twins, which was particularly high during the first 11 days of life (see Figure 6), influenced horn threatening or butting of alien young. When alien lambs saw suckling, the strange young often approached and attempted to suckle too, and then the ewes horn threatened or butted the alien lambs. The rate of horn threatening or butting by ewes against alien lambs was correlated with the percentage of time that the ewe's young spent suckling ($r^2 = .36$). Since the early, agonistic actions of ewes with twins sometimes disrupted the suckling of their own lambs, the quality of the ewes' nursing was diminished during this period.

Vocalization

The number of lambs born per ewe also influenced the frequency of vocalization given by lambs and their mothers. Previous research has not compared the vocalization of single and twin lambs and their mothers, but it does indicate that vocalization helps mothers and young to locate each other, and it probably serves in the identification process as well (Lindsay and Fletcher 1968, Morgan et al. 1975, Shillito 1975, Shillito and Alexander 1975, Alexander 1977, Alexander and Shillito 1977, Walser 1978).

At 0-1 days of the lambs' age, mothers of twins called seven times more often than did mothers of singles ($P<.01$) (see Figure 21), and individual twins also called seven times more often than did singles (see Figure 18). Ewes with twins may call more frequently to stimulate more frequent calling in their young. Since mothers of twins must learn the identities of two lambs during the first hours following parturition, it is reasonable that a greater degree of vocalization would be necessary for the ewes to distinguish the auditory cues of the voices of two lambs.

The early, frequent calling of ewes with twins also may indirectly help the ewes to learn the olfactory and visual cues of their lambs. Close contact appears to be needed in the perception of olfactory cues (Shillito and Alexander 1975, Alexander 1977), and relevant visual cues may only be perceived at relatively close quarters (Alexander

1977). The attractant properties of the ewes' vocalization may be the reason that their lambs stayed closer.

Twins and their mothers continued to vocalize more than did singles and their mothers after 0-1 days. From 5 to 31 days, ewes with twins vocalized an average of 1.97 times per hour, while ewes with singles vocalized an average of 1.20 times per hour. From 5 to 31 days, each twin vocalized an average of 0.92 times per hour, while each single vocalized an average of 0.80 times per hour. Two factors may be involved in the continuing tendency of ewe-twin lamb sets to call more: (1) Ewes with two offspring may call more to induce both lambs to follow, since vocalization strengthens the young's following response; (2) ewes initiate nursing periods by calling to their lambs (Ewbank 1964, 1967), and ewes with twins nursed more often.

General Relationships Between Ewes and Their Lambs

Changes in the ewe-lamb bond

The ewe's bond to her young develops within hours, or even minutes, of parturition, but the lamb's bond to its mother develops during the first 2 or 3 weeks after birth. The ewe—lamb bond possibly decreases slightly in the second half of the lamb's first month of life.

The rapid, early formation of the ewe's bond to her newborn lamb has been observed by previous workers (Collias 1956, Hersher et al. 1963, Smith 1965, Smith et al. 1966, Sharafeldin and Kandeel 1971). The ewe recognizes her young through a discrimination process involving primarily the lamb's olfactory stimuli at close quarters, and its auditory and visual stimuli at greater distances (Collias 1956, Tschanz 1962, Hersher et al. 1963, Smith et al. 1966, Lindsay and Fletcher 1968, Morgan et al. 1975, Shillito and Alexander 1975, Alexander 1977, Alexander and Shillito 1977, Walser 1978).

In the present study, the rate that the ewe sniffed her lamb was high at 0-1 days and then steadily decreased with increasing lamb age (see Figures 19 and 20). The frequent sniffing immediately after parturition possibly helped the ewe to bond to her offspring. The sniffing certainly permitted the ewe to learn her lamb's scent. As the ewe came to know her lamb's scent perfectly, her sniffing decreased to that amount necessary to identify her lamb. Later, as the ewe relied more on senses other than olfaction to locate and identify her lamb, reliance on olfactory contact decreased.

Previous workers have shown that most lambs can identify their mothers by 11 days after birth, but some individuals do not complete the process of maternal identification until 21 days of age (Tschanz 1962, Morgan and Arnold 1974, Arnold et al. 1975, Shillito 1975). The ewes' olfactory stimuli may contribute to the lambs' recognition process. The present study showed a general increase in the young's sniffing of their mothers as they grew older (see Figure 28). Also, the frequency of the ewes' horn threatening or butting alien lambs fell after their lambs were 11 days old (see Figure 22), probably because most young had learned the correct identities of their dams.

In the present study two types of measurements indicated that the ewe-lamb bond developed and remained strong during the lamb's first month of life. First, ewes and their lambs averaged 49 percent of the daytime simultaneously engaged in the same behaviors: twice as much time as was expected by random chance. Furthermore, the amount of time they spent simultaneously engaged in the same activities generally increased over the first month of the lambs' life, so that the highest percentage for simultaneous behavior, 58 percent, occurred at 30-31 days. Second, lambs and their mothers averaged 58 percent of the daytime within 1 m or less of each other during the lambs' first month of life (see Figure 12). In contrast, they spent an average of 17 percent of the daytime between 1 and 3 m of each other (see Figure 13), and they averaged 26 percent of the daytime at more than 3 m from each other (see Figure 14). Morgan and Arnold (1974) also observed that most lambs and their mothers stayed near one another, even though considerable separation was possible in the large paddock used for their study.

A slight weakening of the ewe-lamb bond may have occurred in the second half of the lambs' first month of life. The rate of the ewes' prevention of suckling by their own lambs increased slightly after the lambs reached about 3 weeks of age (see Figure 23). After the first 1 to 2 weeks of the lambs' age, Ewbank (1967) noted incidents where the lambs tried to suckle but their mothers walked or ran forward. The study's lambs suckled less and spent more time close to other lambs as they grew older, but these tendencies reflected changes in diet and formation of peer groups, and probably were not due to a decreasing bond to their mothers.

The ewe-lamb bond and flock cohesion

The occurrence of simultaneous behaviors and the maintenance of close contact between ewes and their lambs not only result from and strengthen the maternal-filial bond, but they also contribute greatly to flock cohesion. Social facilitation within the ewe-lamb sets promotes the synchronization of flock activities.

For the lying, standing, and feeding behaviors, ewes and their lambs spent about twice as much time simultaneously engaged in each of the behaviors as was expected by random chance. The ratio was even greater for the moving activity: The single lambs and their mothers simultaneously moved seven times more often than was expected by random chance, and the twin lambs and their mothers simultaneously moved four times more often than was expected by random chance. Such unison in moving would be especially important in maintaining flock cohesion.

Since the ewes and their lambs spent more time at close distance to each other than they did at intermediate and far distances (see Figures 12, 13, and 14), the close proximity increased the opportunities for social facilitation to occur, because the ewes and their lambs were likely to be more aware of each others' activities.

Similarly, Morgan and Arnold (1974) found that when both ewes and their lambs were lying or walking, they generally stayed close together. Also, when the ewes stood, the lambs remained nearby, either lying or standing. Morgan and Arnold (1974) also suggested that these mutual and close activities formed a basis for the flock organization.

SUMMARY

1. This study had three objectives: (1) to document differences between various sheep genotypes in several behavioral and physiological traits which are important in ungulate production, (2) to compare the behaviors of ewes and their single offspring with the behaviors of ewes and their twin offspring during the lambs' first month of life, and (3) to estimate general relationships between ewes and their lambs during the lambs' first month after birth.

2. The primary sheep groups studied were the Karakul-Rambouillet, F_1 Barbados-Rambouillet, F_2 Barbados-Rambouillet, Mouflon-Rambouillet, and Mouflon-Mouflon.

3. Animals were observed 1600 hours, from which 608 hours of quantitative data were gathered for the present analysis. For the behavioral data, each ewe-lamb set (one set equaled one ewe with her offspring of the year) was observed for 1 to 4 daytime hours at 5 day intervals until each lamb was 1 month old. Analyses showed the percentages of daytime hours that ewes and lambs spent engaged in common behaviors (frequently displayed or long lasting activities) and at varying distances from each other. The number of occurrences per hour of rare behaviors (infrequently displayed, short lasting activities) was also determined.

4. Physiological measurements on breeding and parturition were taken by recording dates of breeding and parturition; recording the number of young born; and weighing the young at 0, 2, 7, and 14 days of age.

5. The results supported the supposition that domestication has caused the intensities of observed traits to diverge greatly from the tendencies shown by wild populations. Domestication has produced increases in activities or measurements associated with maternal care, discovery learning, tolerance or inclination for closeness with conspecifics, length of the breeding season, fertility, birth weight, and growth rate. Behaviors associated with imitative learning have decreased with domestication. Domestication has not altered length of estrous cycle nor length of gestation.

6. Results supported the supposition that the partly domestic groups were intermediate to the most domestic and wild groups--at least for three of the traits: maternal care, birth weight, and growth rate. However, other hybridization factors apparently altered the intermediate position of the partly domestic groups for the remaining traits: learning in the young, proximity of conspecifics, and fertility.

7. The study's findings indicated that the development of new crossbreeds is an advantageous method of improving sheep and goat productivity. Also, sheep ranchers should consider breeding their domestic ewes to Mouflon rams, because the resulting first generation offspring are much more numerous and only slightly smaller than pure domestic young.

8. Certain behavioral differences between ewe-single lamb sets and ewe-twin lamb sets resulted from the earlier physical development of singles as compared to twins, e.g., singles spent less time close to their mothers and singles played more than did twins.

9. Mothering capacities, sibling competition, and a sibling bond caused behavioral differences between ewes and their single young and

ewes and their twin young. Twins suckled more and made more attempts to suckle than did singles, yet twins gained less weight. Twins spent more time close to their mothers and stood more than did singles, but each twin received less olfactory contact from its mother than did each single. Twins spent more time close together than did alien lambs. Twins spent even more time close to each other than they did close to their mothers. Twins played less than did singles.

10. Twins and their mothers vocalized more frequently than did singles and their mothers.

11. The ewe-lamb bond did not vary between ewe-single lamb sets and ewe-twin lamb sets.

12. The ewe's bond to her young develops within hours of parturition, but the lamb's bond to its mother develops during the first 2 or 3 weeks after birth.

13. The high occurrence of simultaneous behaviors, especially moving, and the maintenance of close contact between ewes and their lambs contributed to the cohesion and organization of the flock. The close contact between twins also contributed to flock cohesion.

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APPENDIX

Table 11. The scientific names of the sheep and goat species listed by their vernacular names in Tables 1 and 2.

Vernacular name	Scientific name
Argali	*Ovis ammon*
Bighorn	*O. canadensis*
Domestic sheep	*O. aries*
Mouflon	*O. musimon*
Urial	*O. orientalis*
Domestic goat	*Capra hircus*
Ibex	*C. ibex*
Persian Wild Goat	*C. aegagrus*

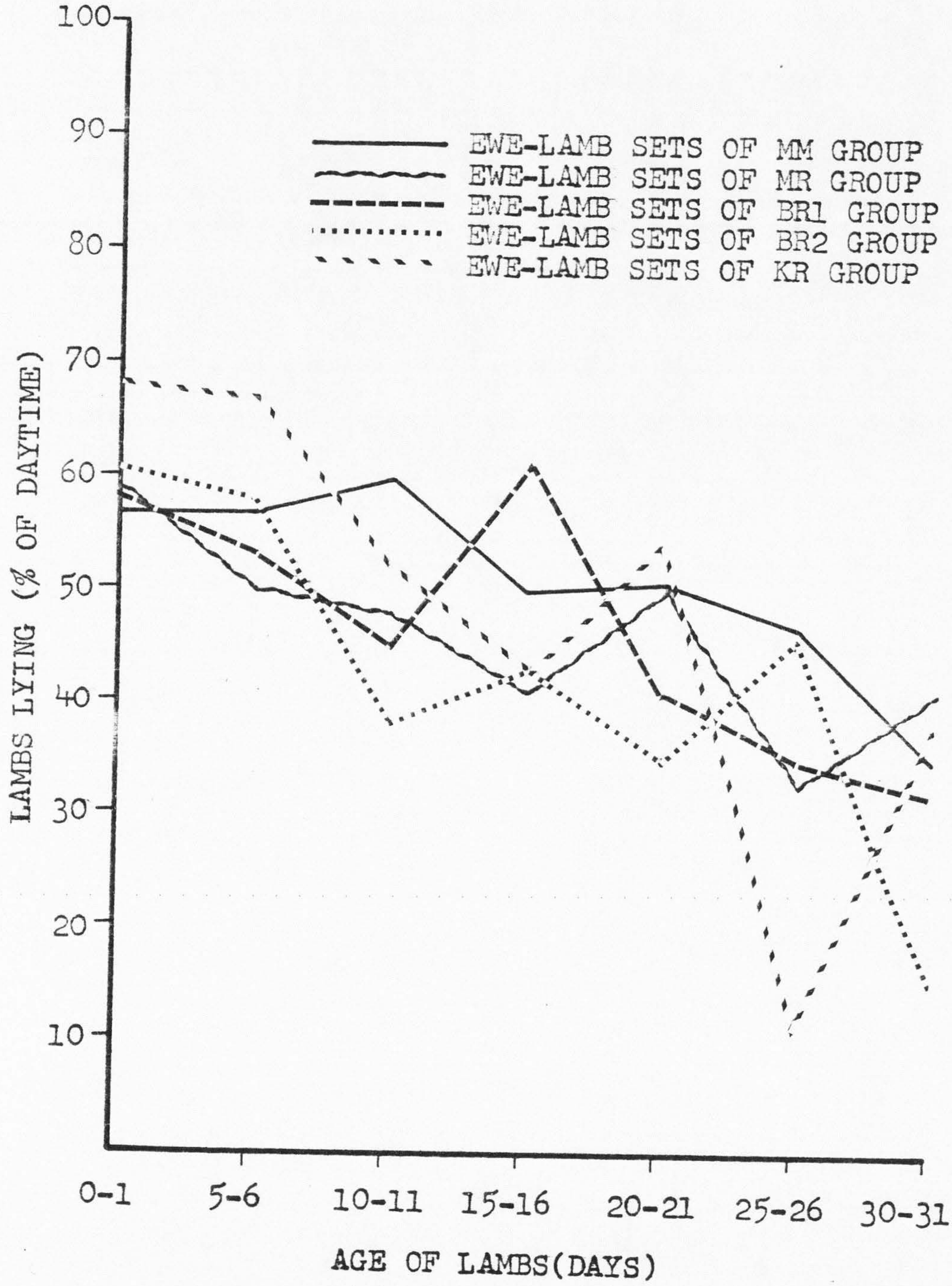


Figure 36. Percentages of daytime that lambs spent lying, in ewe-lamb sets by genotype and age of lambs.

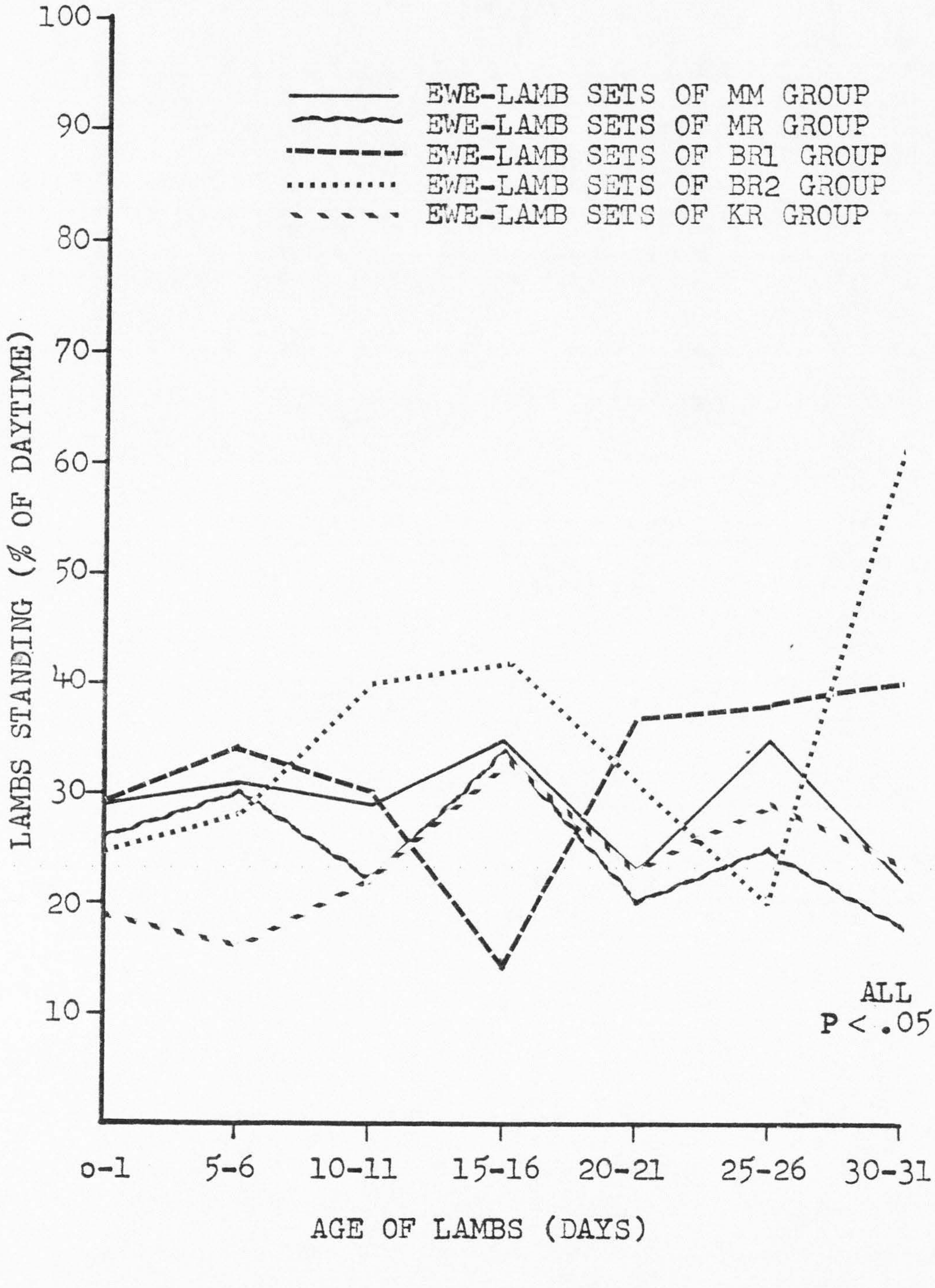


Figure 37. Percentages of daytime that lambs spent standing, in ewe-lamb sets by genotype and age of lambs.

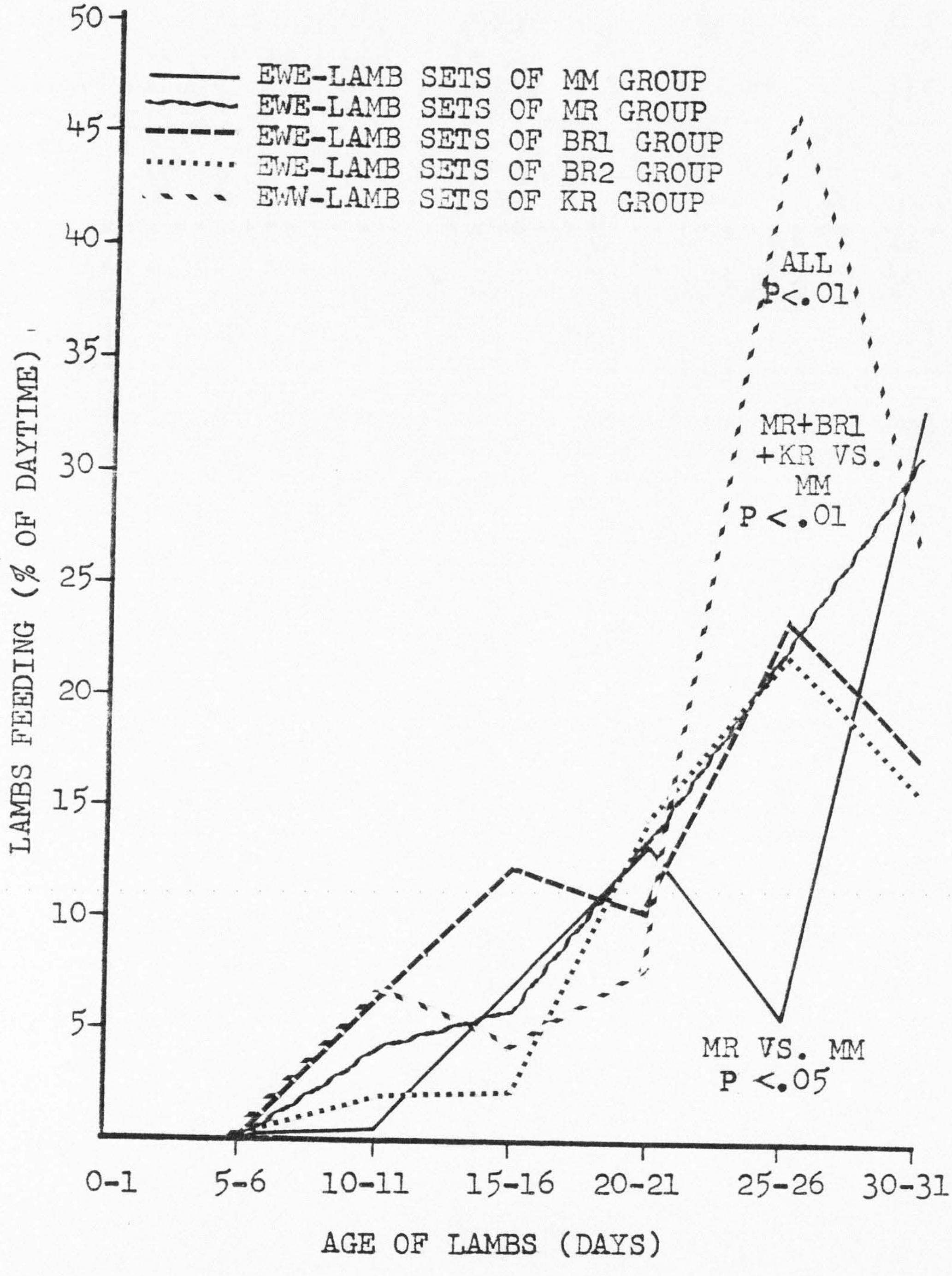


Figure 38. Percentages of daytime that lambs spent feeding, in ewe-lamb sets by genotype and age of lambs.

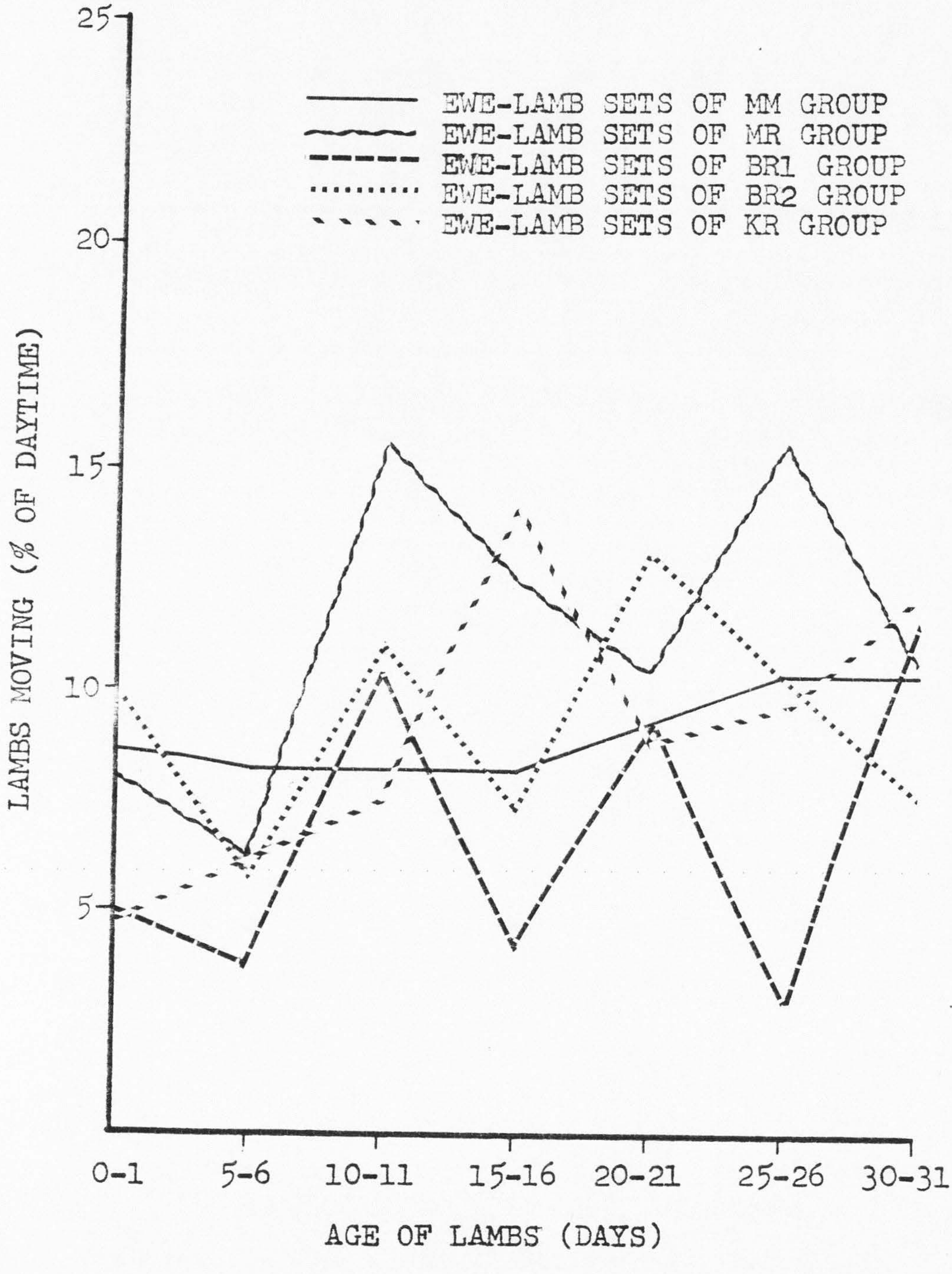


Figure 39. Percentages of daytime that lambs spent moving, in ewe-lamb sets by genotype and age of lambs.

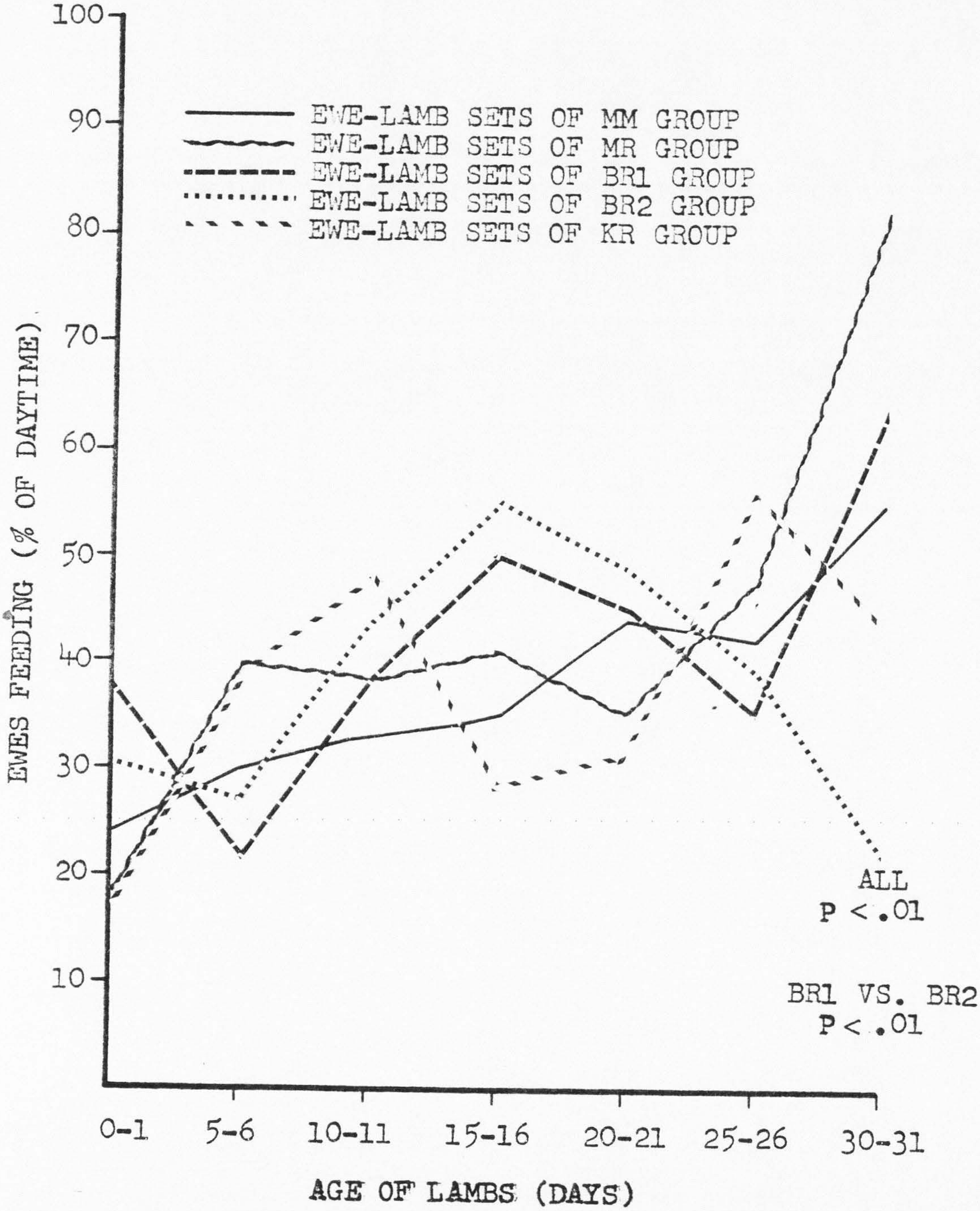


Figure 40. Percentages of daytime that ewes spent feeding, in ewe-lamb sets by genotype and age of lambs.

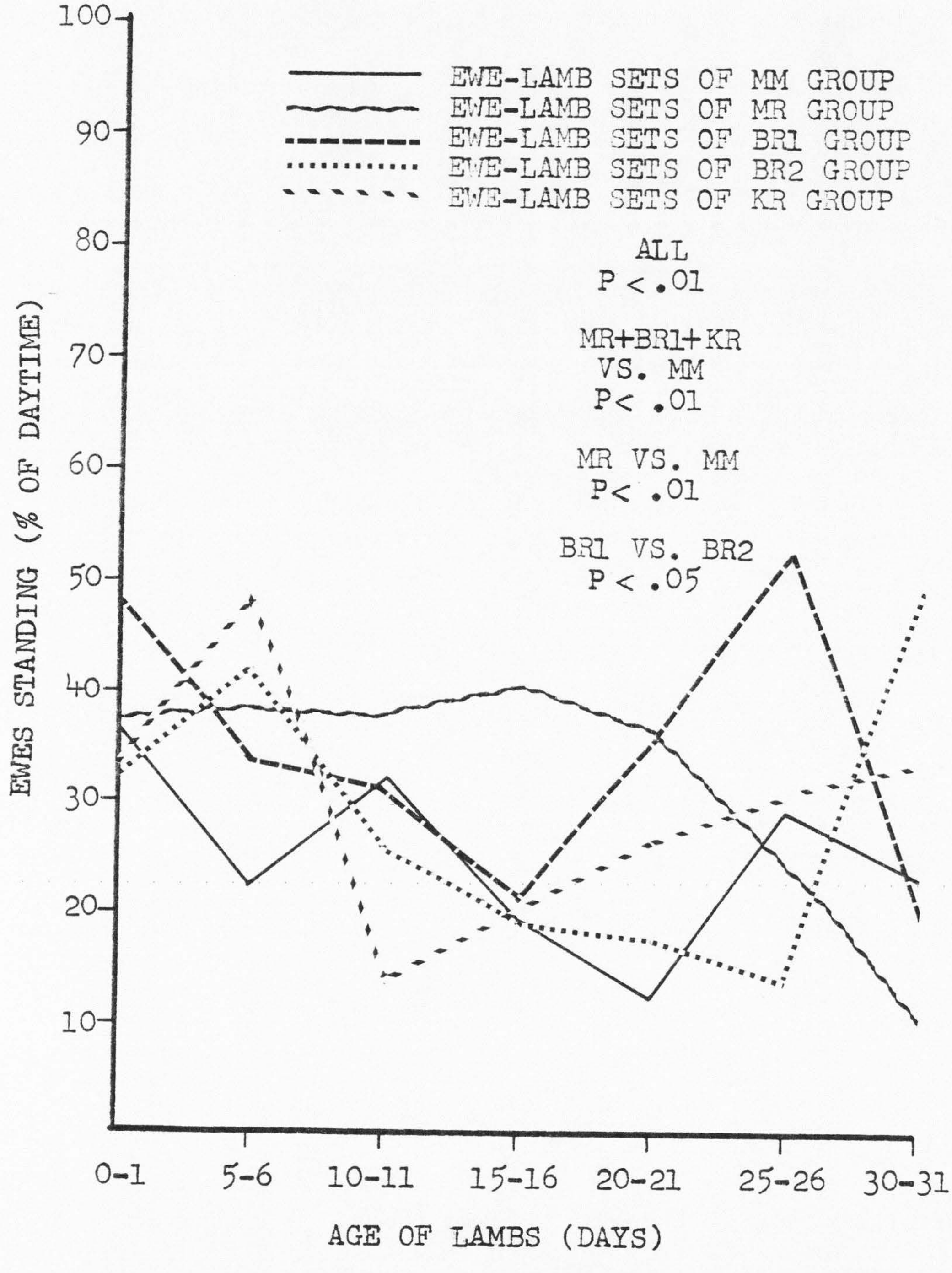


Figure 41. Percentages of daytime that ewes spent standing, in ewe-lamb sets by genotype and age of lambs.

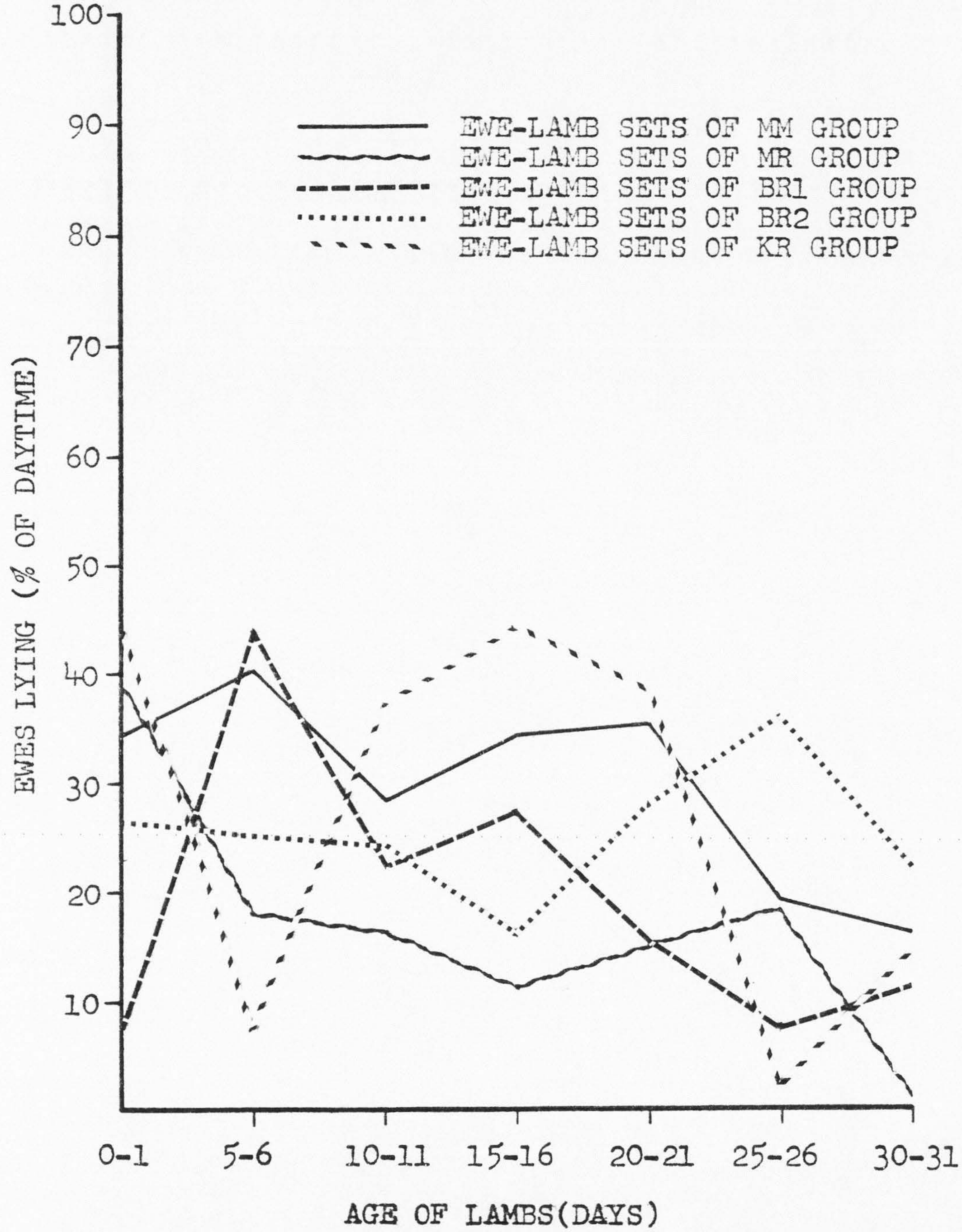


Figure 42. Percentages of daytime that ewes spent lying, in ewe-lamb sets by genotype and age of lambs.

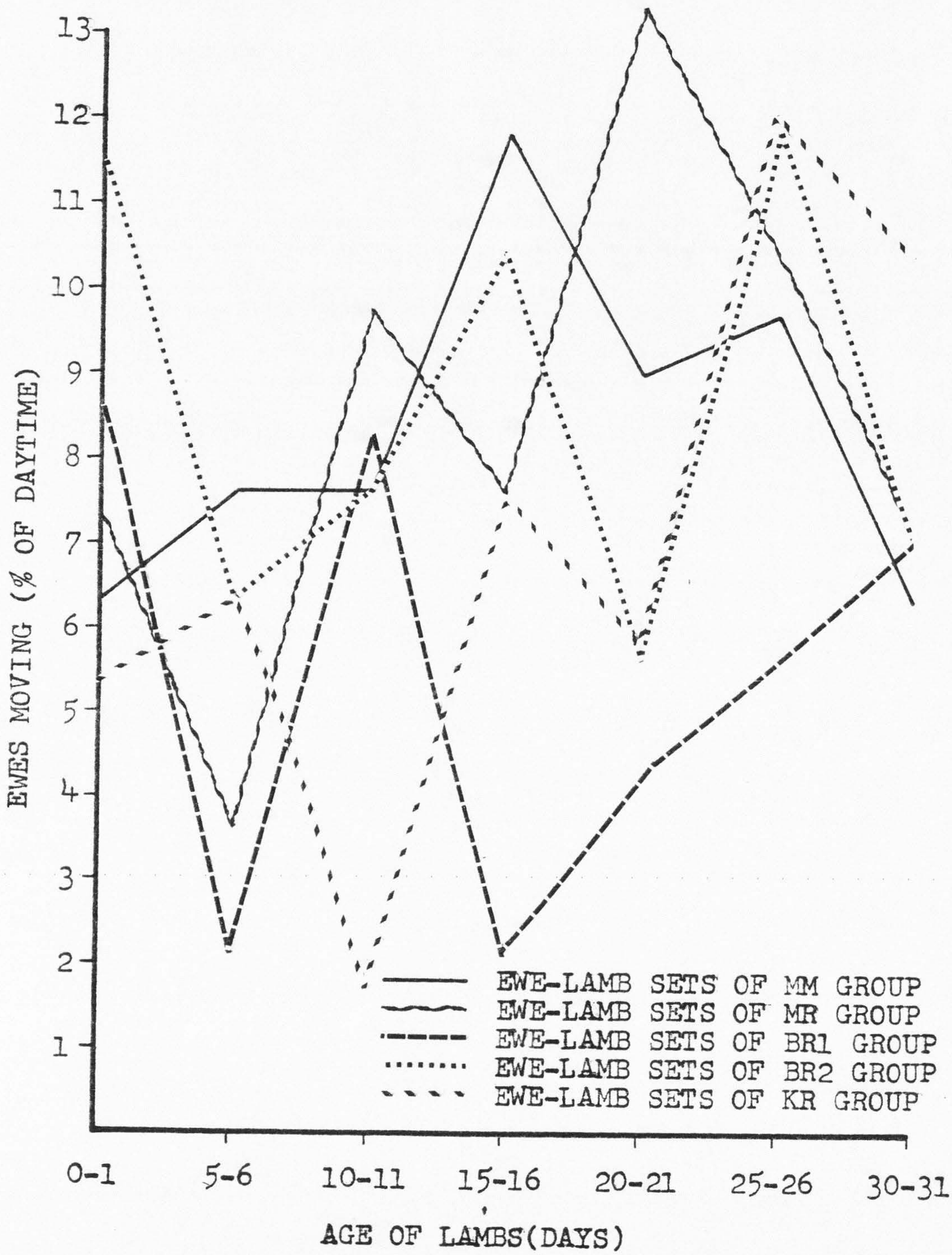


Figure 43. Percentages of daytime that ewes spent moving, in ewe-lamb sets by genotype and age of lambs.

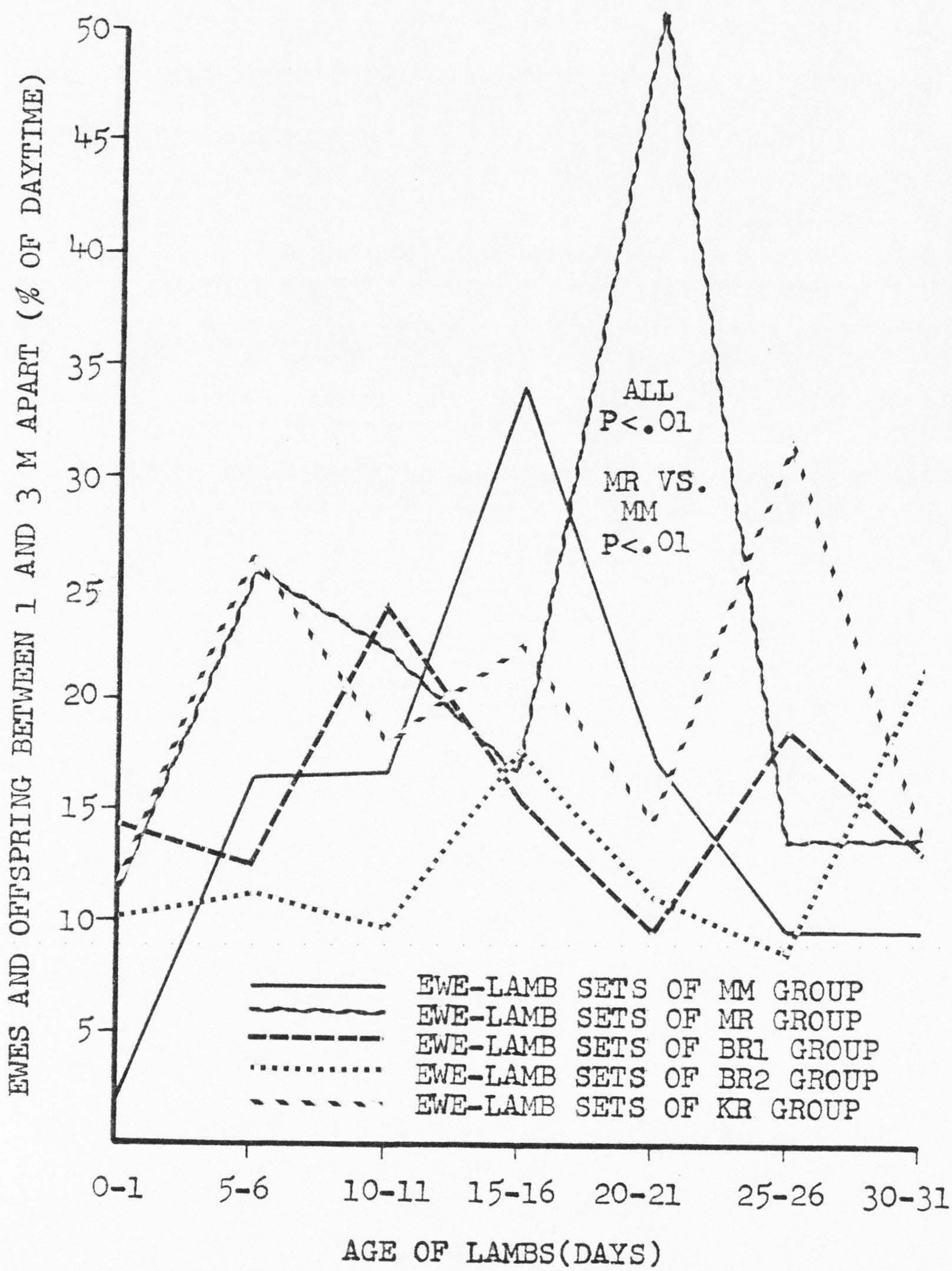
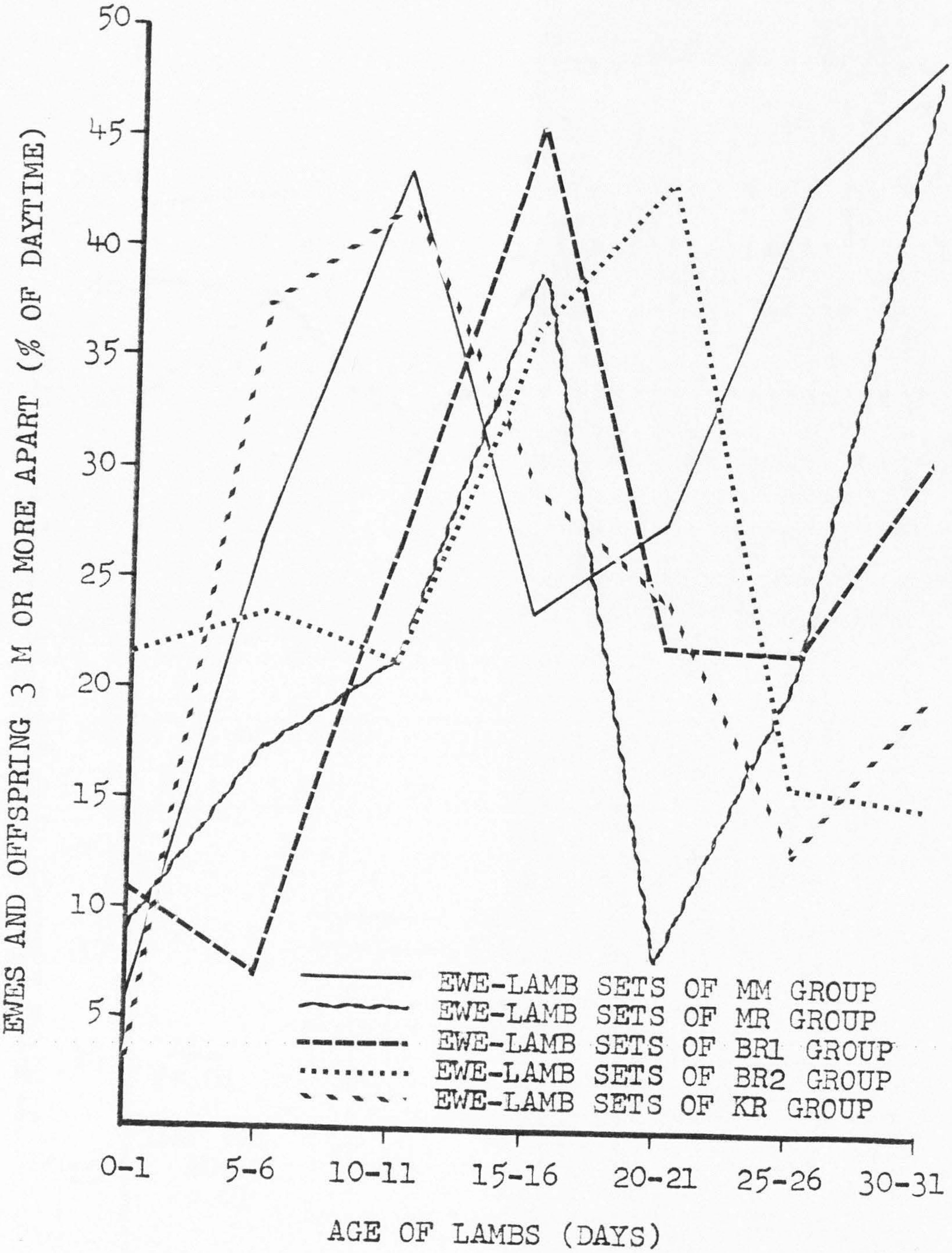


Figure 44. Percentages of daytime that ewes and their offspring spent between 1 and 3 m from each other, in ewe-lamb sets by genotype and age of lambs.



ALL GROUPS	P<.05	P<.05	P<.01
MR+BR1+KR VS. MM	NS	P<.01	P<.05
MR VS. MM	P<.05	P<.05	NS
BR1 VS. BR2	P<.05	NS	P<.10

Figure 45. Percentages of daytime that ewes and their offspring spent at 3 m or more from each other, in ewe-lamb sets by genotype and age of lambs.

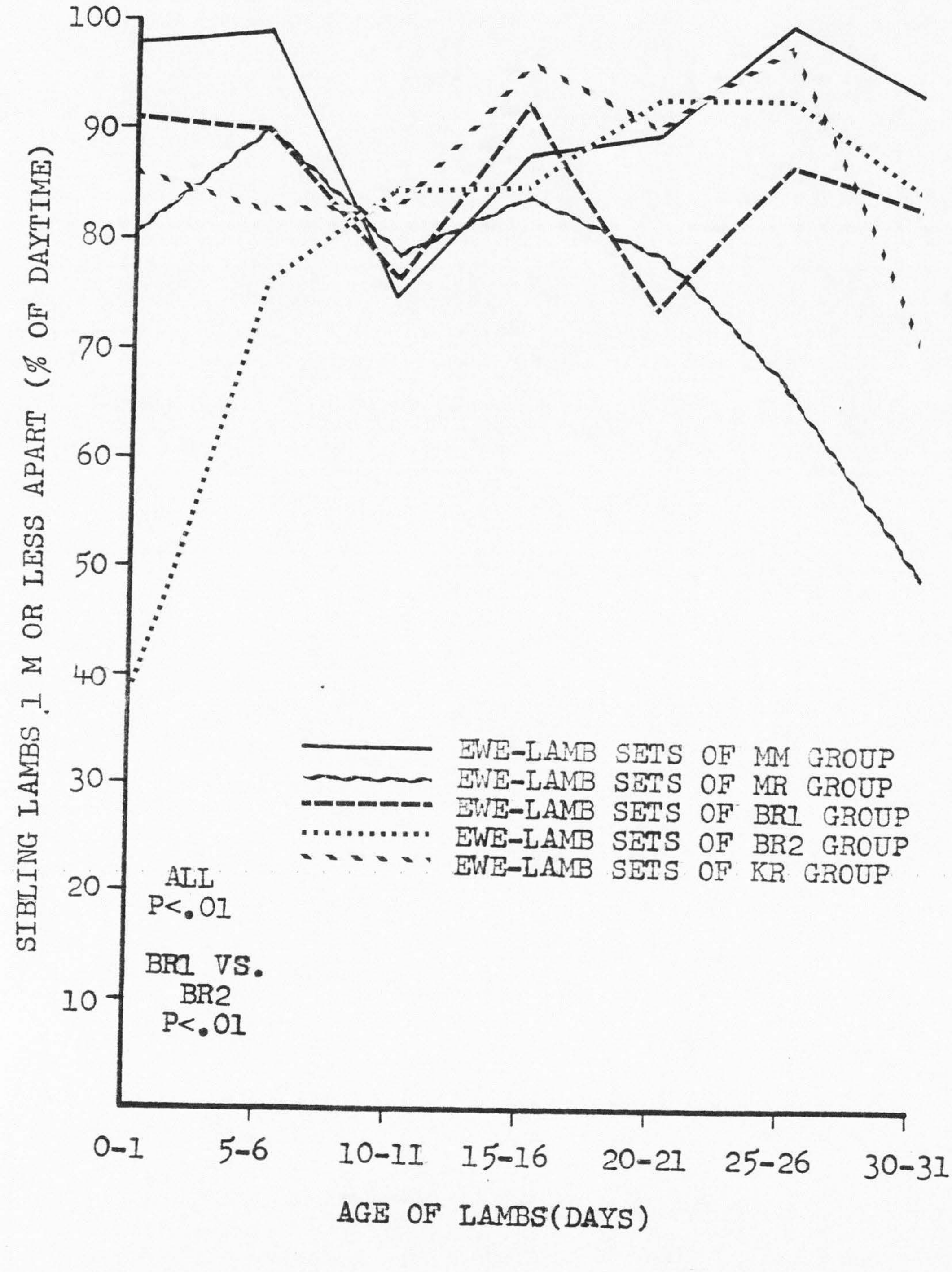


Figure 46. Percentages of daytime that sibling lambs spent at 1 m or less from each other, in ewe-lamb sets by genotype and age of lambs.

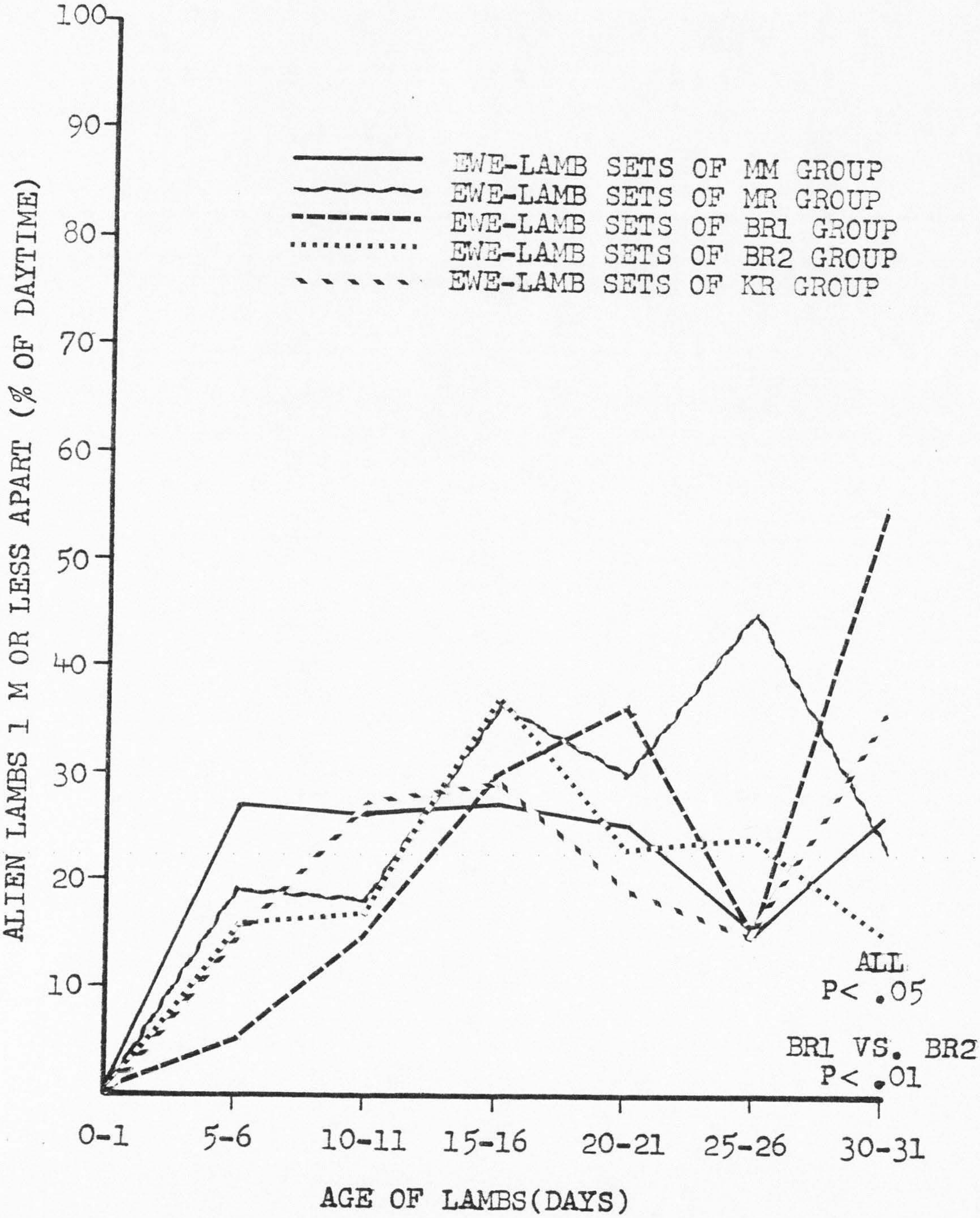


Figure 47. Percentages of daytime that lambs spent at 1 m or less from alien lambs, in ewe-lamb sets by genotype and age of lambs.