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ASPECTS OF THE BEHAVIOURAL ECOLOGY OF FERAL GOATS (*Capra* (domestic))

By

Simon Paul Christopher Pickering B.Sc. (Hatfield Polytechnic)

Thesis submitted to the University of Durham for the degree of Doctor of Philosophy, September 1983.

25. JAN. 1984

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ABSTRACT

Even though the goat was one of the first ruminants to be domesticated some 9,000 years ago, information on its social behaviour in domestication or the feral state is minimal. Aspects of the behavioural ecology of the population of feral goats in the Moffat hills were studied between 1979 and 1983.

The general social organisation was groups of females, their offspring and associated adult males (heft). Each heft occupied a discrete area of land. Movement between hefts was restricted to males during the rut.

Kids were born in late winter and perinatal survival was low. Kid production varied between years and hefts but not between age classes of adult females. It appeared that male survival was lower and more variable than female, resulting in a skewed adult sex ratio. For the first few weeks of life kids were left lying out while their mothers fed. Females returned to suckle their kids at intervals throughout the day. Male kids sucked more frequently and for longer periods than female kids. Female kids associated with their mothers after weaning whereas male kids tended not to, although they remained in their natal heft range.

During a short rutting period in the autumn males competed for access to oestrous females. Fighting success and mating success were both closely related to pre-rut body weight. The frequency of aggression appeared to be related to the potential costs and benefits of such behaviour. Subordinate males were more likely to leave rutting groups than dominant animals and go in search of other females. During the rut adult males lost 10-30% of their pre-rut body weight. This loss was probably the result of a decrease in time spent feeding and an increase in aggressive and social/sexual activity during this period.

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helping with fieldwork, typing and correcting my appalling spelling, for without her help I would still be writing now.

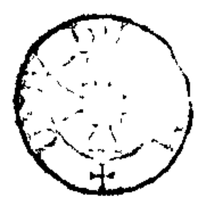
INTRODUCTION

Wild goats of the genus Capra occur from Spain eastwards through the Mediterranean basin and central Asia to the Himalayas. The wild ancestors of the domesticated goat are thought to be Capra hircus aegagrus of Greece and central Asia. This was probably one of the first ruminants to be domesticated. The earliest remains of domesticated goats to be found are from Asia on the Iranian plateau; they date from approximately 10000 B.P. (Bokonyi 1976).

Goats were first brought to the British Isles by Neolithic peoples. Remains of domesticated goats found at a Neolithic site in Wiltshire date from 2960±150 years B.C. (Jope and Grigson 1965). They were brought as domestic stock and were presumably used for their milk, meat, skins and to clear scrub.

These goats are believed to have been small, stocky and longhaired (Greig 1969), very similar to the Old English/Scottish breeds of goat. The Old English/Scottish breeds of goat became extinct in domestication before 1930 (Greig 1969, Whitehead 1972). This was due largely to two factors, the introduction of Saanan and Toggenburg breeds which have much higher milk yields and the increased demand for mutton and wool. The combination of these factors made the husbandry of Old English/Scottish goats uneconomical.

It is likely that because of their intractability, populations of feral goats became established soon after their introduction to



this country. In the Scottish Highlands the collapse of the sheiling system is thought to have been responsible for the establishment of feral populations, while in England and Wales the clearances and rural depopulation were important factors (Megaw 1963, Crook 1969, Greig 1969). In the Southern Uplands of Scotland most populations are believed to have been established for between one and two hundred years; their origins have been reported as stock owned by monks, miners, gypsies, railway workers or farmers. Some of the populations may have been deliberately established or maintained by farmers in the interests of their livestock. This is because feral goats are believed to kill adders, prevent contagious abortion in cattle and sheep, act as weather prophets, lead sheep to shelter during storms and eat luxuriant vegetation on cliffs where sheep would probably get stuck.

Feral ("wild") goats have been the subject of many tales and legends (Whitehead 1972). However, until recently there has been very little scientific attention paid to them. Work by Riney and Caughley (1959), Yocum (1967), Tomich (1969), Clarke (1976) and Rudge and William (1962) was largely concerned with their eradication or control. In this country most studies have been concerned with their status (Watt 1937, Darling 1937, Brown 1977, Brown and Lloyd 1981), their general ecology (Greig 1969, Crook 1969, McDougall 1975, Buckland 1977, Stevenson-Jones 1977), and their population dynamics (Boyd 1981). In a detailed study Bullock (1982) investigated the population dynamics, biometrics, diet and general spatial organisation of several populations in the Southern Uplands of Scotland. With the exception of Munton (1975) and

Maisels (1982), most studies of the behaviour of feral goats have been carried out in tropical or semi-tropical regions where breeding occurs throughout the year (Shank 1972, Gould 1979, Coblentz 1980). In view of this lack of detailed information on this aspect of the biology of feral goats I undertook a study of their behaviour and social organisation, with particular emphasis on mother-offspring behaviour and rutting behaviour. The population in the Moffat Hills was chosen for two reasons: firstly, it is a relatively small, unmanaged population that can be observed with relative ease and secondly, information on the population status and general spatial organisation had been obtained by Bullock (1982).

This thesis is divided into six chapters. The first briefly describes the study area and outlines the methods used to collect the data. Chapters 2, 3, 4, and 5 each have their own introduction, methods, results and discussion sections and deal with population dynamics, spatial organisation, mother-offspring behaviour and rutting behaviour. These are followed by a general discussion.

CHAPTER 1

THE STUDY AREA, DATA COLLECTION AND BEHAVIOURAL DESCRIPTIONS

1.1 STUDY AREA

The study area was in the Moffat Hills (NT1614) Dumfriesshire, Scotland (Fig. 1.1). The goats live in a series of rugged valleys, Capplegill, Blackhope, Spoonburn, Carrifran and Grey Mare's Tail which run into Moffat Water, a large glaciated valley (Fig. 1.2, Plates 1 and 2). The valley floors are approximately 100m above sea level and the sides rise to over 700m; the highest peak, White Coomb, reaches 821m. The underlying rocks consist largely of silurian greywackes and shales.

Grassland dominates the lower slopes: large areas of Festuca-Agrostis and Agrostis-Anthoxanthum grasslands occur with areas of Nardus and Juncus squarrosus on the wetter peatier soils. Extensive areas of Pteridium aquilinum also occur on the lower slopes. Molinia grasslands are restricted to flushed areas. Between 300m and 600m there is a zone composed of a heath community dominated by Calluna and Vaccinium which is dissected by steep craigs and lines of scree. A Nardus-Vaccinium community is present on the smoother slopes. Blanket-mire (Calluna-Europhorum) is extensive below some of the summits along with areas of Vaccinium

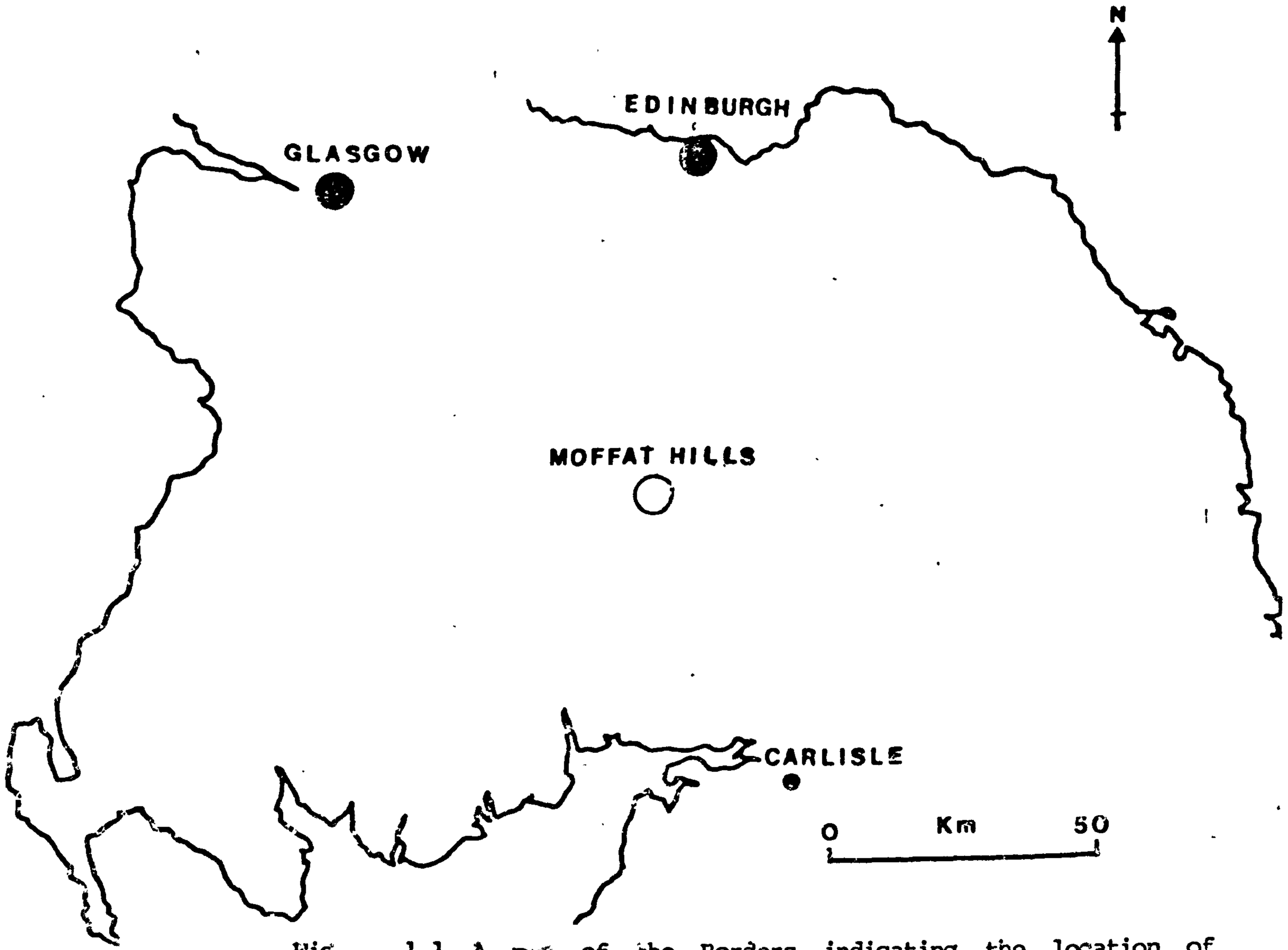


Fig. 1.1 A map of the Borders indicating the location of Moffatdale.

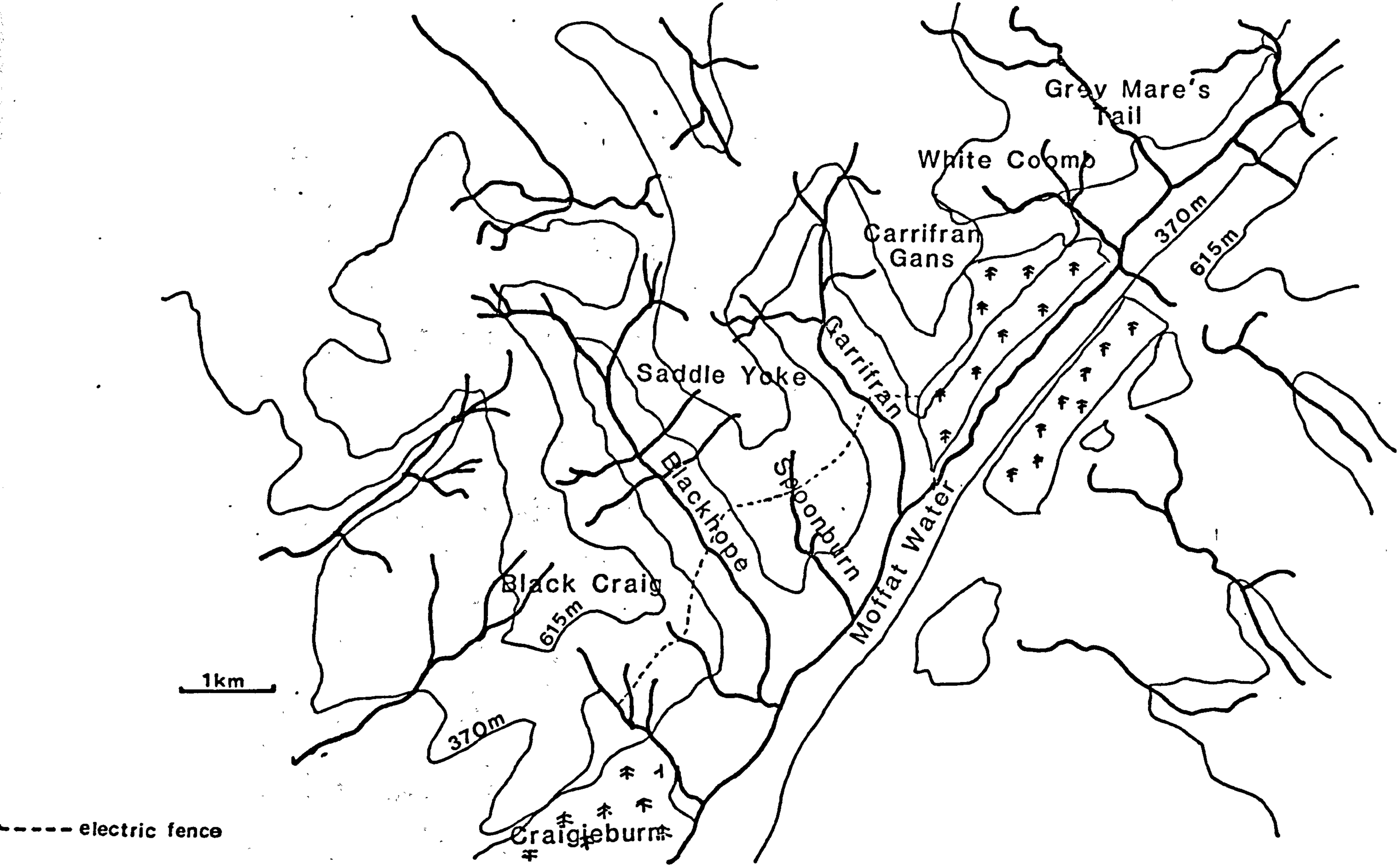


Fig. 1.2 A sketch map of Moffatdale indicating the major valleys and water courses.

Plate 1. Blackhope valley.

Plate 2. Carrifran valley.

and Empetrum nigrum. The summit vegetation is predominantly Festuca-Rhacomitrium heath along with areas of Erica cinera, Calluna and Luzula campestris. On the western slopes of Moffatdale, between Carrifran and Grey Mare's Tail, there is approximately 330ha of fenced conifer plantation from which goats were shot or driven out prior to planting in 1968 (Greig 1969). There is an extensive area of forestry plantation and mixed deciduous woodland on the southern boundary of the study area.

The Moffat Hills are mainly managed as a sheep walk with predominantly South Country Cheviots and Blackface breeds. The area is divided by an electric fence between Roundstone Foot burn and the forestry plantation to the west of Carrifran. There are numerous gates in the fence which are only closed when the fence is switched on during lambing (April-May) and tupping (male sheep are put out on the hill during November and December). During these periods goats could still get under the fence where it crossed burns.

1.2 DATA COLLECTION

1.2.1 Recognition of individuals

Prior to the study an identification sketch of each individual goat was drawn; notes were also made on their coat colour and shape and colour of horns. There was considerable variation in the pattern and colour of the coat of feral goats (Plates 3 and 4) and

Plate 3. Identification photograph of Male 79 .

Plate 4. Identification photograph of Female 7 , showing unique coat pattern.

after six visits to the study area every individual goat could be recognised without the aid of the identification sketches. Each kid was drawn when it was first seen. These sketches were modified as the kid grew and its coat colour changed. The coat of male kids usually became much darker and shaggier during their first two years. The coat colour and pattern of females changed little after their first year of life. When in the field the indentification sketches were always carried.

1.2.2 Census Data

A census of the population was made by walking the whole study area and scanning the hills from vantage points. On finding goats the location (eight figure grid reference), activity, and estimated distance to nearest neighbour of each individual was recorded. Distances between individuals were estimated in goat lengths; the length of an adult goat's back (base of neck to tail) is approximately 1m. Weather conditions and date were also noted. Goats were regarded as being in the same group if they were less than 100m apart. The route taken around the study area was similar each time but by necessity had to vary on occasions due to weather conditions and the location of goats. The route was walked in the opposite direction on successive visits. Each census was completed in one or two days depending on the weather and the time of year. The whole study area was censused 3 or 4 times each month between Febuary 1980 and March 1981 and then once each month between April

and August 1981. A further 16 complete censuses were made during September and October 1981 and single censuses were made in May, September and December 1982. F. Maisels also made a census in July and August 1982. A total of 83 censuses were made during the study.

When an individual was missed during a census an intensive search was made for that animal or its carcass. In spring, foxes (Vulpes vulpes), mink (Mustela vison), crows (Corvus corone corone) and ravens (Corvus corax) rapidly devour dead sheep and goats. Consequently the remains of several individuals that were thought to have died were never located. Extensive movements out of the study area were never recorded (Bullock 1982 and present study). Therefore it is unlikely that these individuals left the area.

During the 1981 kidding period (20 Febuary - 1 April) an attempt was made to locate each female every day. However, poor weather conditions meant that most females were actually located every 3 or 4 days during this period. Females suspected to have given birth were observed for a minimum of one hour to see if they returned to their hidden kid.

In order to monitor the movements of males and to record when each female came into oestrous the main study area (Capplegill, Blackhope, Spoonburn and Carrifran but not Grey Mare's Tail) was censused every second day between the 1 September and 30 October 1981.

1.2.3 Biometrics

The capture of goats provided data on the age, size, weight and

weight changes of individual goats. Goats were captured by building a temporary fence at 45 degrees to the electric fence which crossed the study area (see above and Fig. 1.1) to form a "V" on the valley side. A catching pen was built at the point of the "V" and the gates in the electric fence were closed to make it relatively goat-proof. A group of goats was then driven along the hillside by a line of people to the electric fence and then turned downhill and herded into the open end of the "V" which funnelled the group, hopefully, into the pen (see Plates 5, 6 and 7). Once in the pen, the goats could be examined at close quarters. Each goat was aged by counting the number of major horn rings (Greig 1969 and Plate 8, Figs. 1.3 and 1.4). The following measurements were made using a flexible tape measure; horn length, horn span, horn ring increment length, ear length, body length, tail length, height at shoulder and chest girth. Also the eruption of adult teeth was recorded and all females were checked for milk. Goats were weighed to the nearest 0.5kg using a Salter balance from which the goat was suspended in a weighing crate or in a sling put under its belly (Plates 9 and 10). Every goat caught was photographed from both sides. A total of 192 captures of 107 individuals were made during the study. Those adult goats not captured were aged in the field. With the aid of binoculars the major horn rings can be clearly seen on males, but they are much less conspicuous on females. Forty one (65%) of the females alive in 1979 were caught and aged during the study. Of the remainder, four were obviously still kids in autumn 1979 and five died during the study and were aged when their skulls were recoverd. The remaining 13 were all aged several times in the field at close

Plate 5. Line of people driving goats down the hillside.

Plate 6. Driving goats towards a temporary catching pen.

Plate 7. Goats confined in a temporary catching pen.

Plate 8. Close-up of an adult male showing the major horn-rings.

Plate 9. Weighing a goat in a weighing crate.

Plate 10. Weighing a goat using a sling placed under the belly.

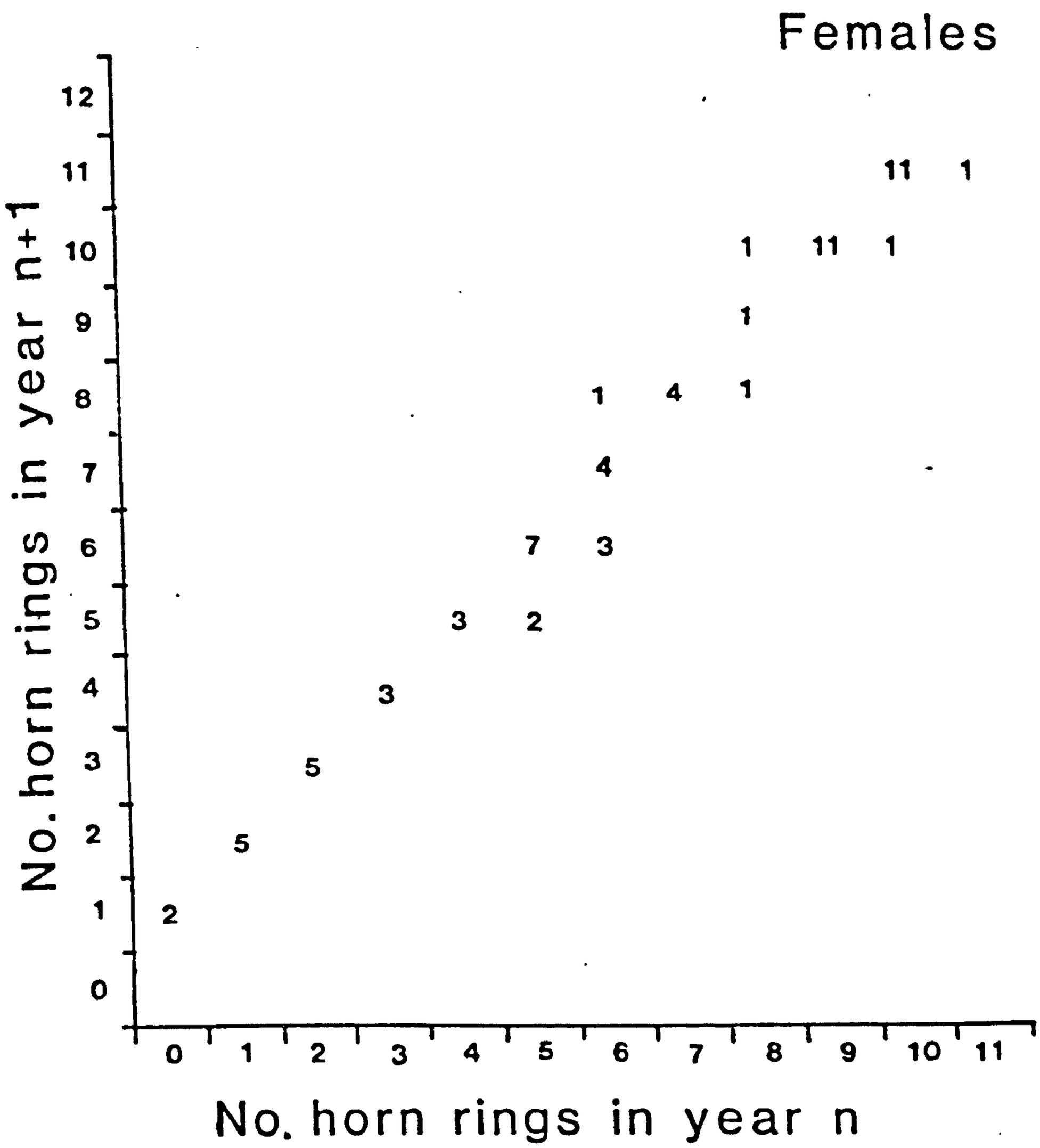


Fig. 1.3 Comparison of the number of horn rings counted when caught in year n and the number counted when caught the next year. Numbers indicate numbers of goats.

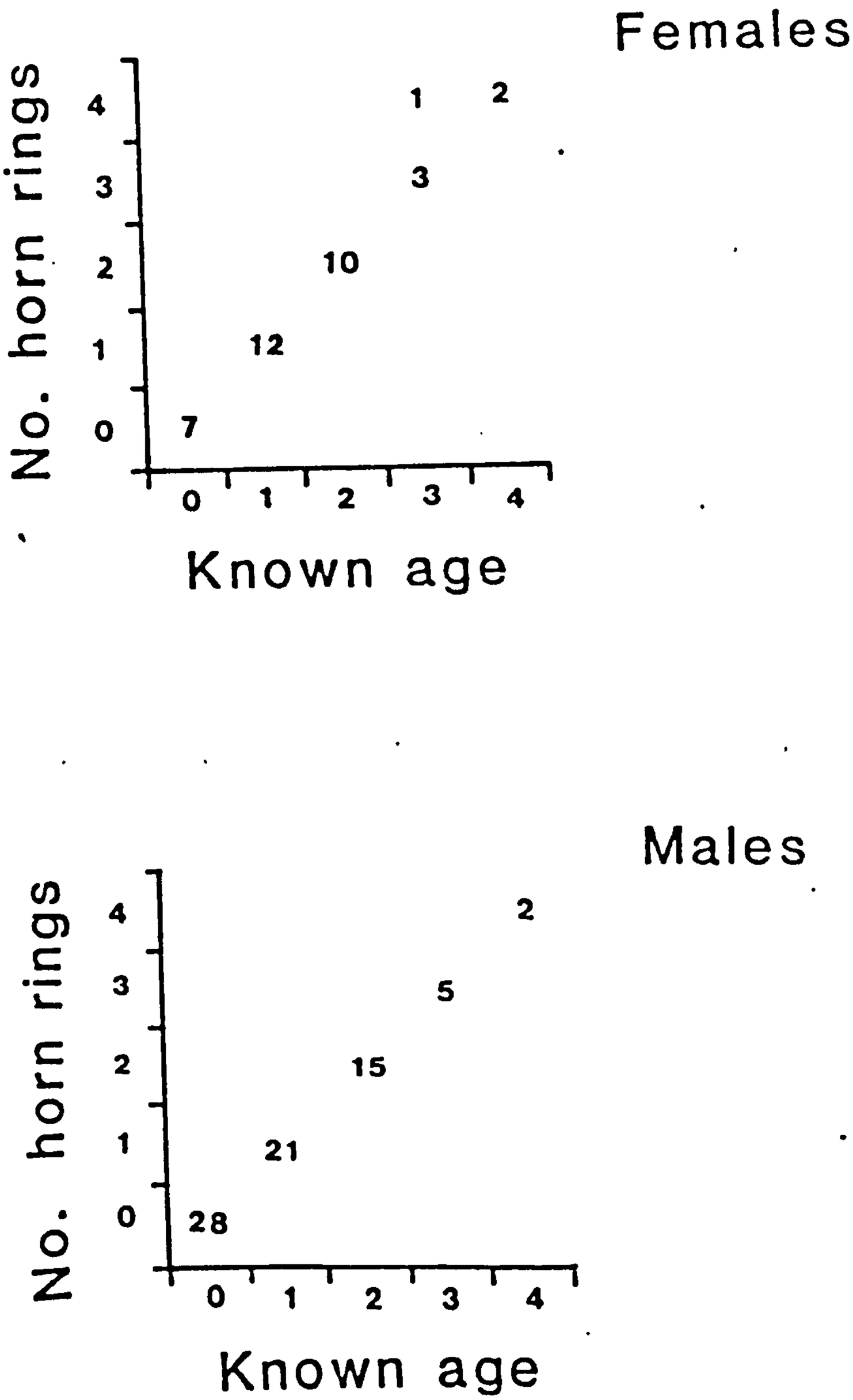


Fig. 1.4 Numbers of horn rings counted on captured goats of known date of birth. Numbers indicate numbers of goats.

range with the aid of a telescope. Goats between birth and one year of age were termed 'kids', while those between one and two years of age were called 'yearlings' and those animals greater than two years old 'adults'.

1.2.4 Continuous Watches of Individuals and Groups

In order to measure the activity patterns and obtain data on the frequency of behavioural interactions individual groups or goats were watched continually for a minimum of four hours and often for a whole day. The activity of each goat under observation was recorded every ten minutes (instantaneous scan sample, Altmann 1974) and classified into one of seven mutually exclusive categories:

1) Feeding: biting or chewing vegetation or moving between feeding spots with head down.

2) Walking: walking with head up, including walking while chewing.

3) Cudding: chewing cud, lying or standing.

4) Resting: lying down, not cudding, awake or asleep.

5) Aggressive: involved in an aggressive encounter or fight (see 1.4.1 and 5.5) with another goat.

6) Social/Sexual: interacting non-aggressively with another goat.

7) Standing: not cudding or interacting with another animal.

By using data collected during continuous watches it was shown that the proportion of time that an individual was recorded to be involved in a particular activity did not differ significantly between instant scan samples taken at 2min, 5min or 10min intervals.

Recording instant scan samples every ten minutes allowed enough time to complete a 5 minute focal animal watch (Altmann 1974) between scan samples. Five minute focal animal watches were used because this period of time was long enough to include most behaviour sequences and short enough for the observer not to suffer eye fatigue when observing goats through a telescope. Some behavioural sequences which lasted more than 5 minutes were watched continually from start to finish whenever possible. Continuous records were analysed separately from focal animal watch data. When watching a courtship sequence or a mother and kid, the behaviour of both individuals (focal pair) was recorded.

Individuals for focal animal watches were selected in a semi-random fashion. When the group under observation was first located the identity of each individual from left to right was recorded on a check sheet. Goats were selected to be watched by starting at the top of the sheet and working down. During the spring, females with kids were watched more frequently than other individuals, as were adult males during the rut. The frequency of behavioural acts for individuals or age/sex classes was expressed as the number per goat hour (g-hr) (2 g-hr = 1 goat observed for 2 hrs or 2 goats observed for 1 hr each).

A total of 718 hours of observations were made during the study, the majority being done during the spring and autumn (Fig. 1.6). Poor weather conditions during the 1981 rut made dawn-to-dusk continuous watches and dusk-to-dawn watches virtually impossible. To overcome this problem the day was divided into six mutually exclusive sequential blocks, each four hours in length. On any one

day, observations were made during one or two of these blocks. Activity budgets were expressed as the proportion of time involved in each activity per four hour block during the pre-rut period (20 August - 10 September), the rut (21 September - 28 October) and the post-rut period (4 - 9 November).

1.3 TREATMENT OF DATA

Standard parametric and, where necessary, non-parametric statistical tests were used (Siegel 1956, Sokal and Rohlf 1961, Snedecor and Cochran 1967). The null hypothesis was rejected at the probability level of 0.05 or less. Analyses were performed using hand calculators and the computing facilities of the University of Durham. Greenwich Mean Time was adopted throughout and the seasons of the year were defined as follows: Spring - March, April, May; Summer - June, July, August; Autumn - September, October, November; Winter - December, January, February.

1.4 DESCRIPTION OF BEHAVIOUR PATTERNS

A total of 23 distinct behaviours were recognised during this study and each is described below. In each case, the actor is the individual performing the behaviour and the recipient is the individual to which the behaviour is directed.

1.4.1 Aggressive Behaviour Patterns

Displace.....Actor approaches recipient showing no overt aggressive or sexual behaviour pattern and the recipient moves away.

Stare.....Actor stares directly at recipient while holding its body motionless. Used in aggressive encounters and appears to be a low intensity threat.

Horn point.....The actor's head is lowered with the horns pointed towards the recipient.

Butt.....Actor hits recipient's body with its horns.

Rush.....Actor rushes directly towards recipient with head lowered and chin tucked in, and either stops short, or delivers a butt if the recipient does not move out of the way. Recipient flees, occasionally first parrying the blow with its horns.

Chase.....As Rush, except that actor continues to follow after recipient moves away.

Clash.....Actor and recipient stand facing each other usually 1-2m apart and simultaneously strike forwards and downwards so that head-to-head contact is made with considerable force, the crack of impact

being audible from a long distance. Horns are usually interlocked.

Rear and clash.....As Clash except actor rears onto its hind legs and delivers the blow on descending.

Horn wrestle.....Opponents attempt to push each other backwards having interlocked horns in a Clash.

Neck wrestle.....Each opponent pushes against the other's neck, the two facing in opposite directions.

Shoulder push.....Opponents push against each other's shoulders while facing in the same direction.

Side swipe.....Following Clash in which opponents fail to lock horns so that their heads slide past each other, actor twists its head to bring horns horizontal and thrusts them rapidly into recipient's neck, abdomen or rump.

Horn thrash.....Actor bashes vegetation with its horns by swinging its lowered head from side to side.

1.4.2 Sexual Behaviour Patterns

Sniff/lick head.....Actor sniffs or licks recipient's head. Usually performed by female to male, but

sometimes by male to female or male to male.

Sniff/lick external genitalia.....Male sniffs/licks vulva of female during courtship.

Approach.....Male walks up to rear of female.

Low stretch approach..As Approach but male holds head low and horizontal, straining muzzle towards female.

Leg kick.....Actor raises one front leg stiffly, kicking to the side of, or between the hind legs of, recipient. Usually performed by male to female during courtship but also occasionally by victorious male to defeated male opponent.

Gobble.....Actor lunges head or whole body towards recipient and makes deep guttural moan with flapping of the tongue. Usually performed by male to female but also occasionally by dominant male to subordinate male, especially one just beaten in a fight.

Mount.....Actor approaches recipient from behind, extends penis, rears up onto hind legs and clasps recipient with forelegs. Normally male to female, occasionally male to male.

Scent urinate.....Male with erect penis bends head down between forelegs and urinates onto beard, head and forelegs.

Lick penis.....Male licks or nuzzles penis during scent urination. Usually followed with flehmen.

Flehmen.....Male holds muzzle elevated with upper lip curled back for 10-31 sec. Occurs as response evoked by taking urine (usually female's but occasionally his own) into mouth.

Tail wag.....Actor wags tail rapidly from side to side. Usually performed by receptive female in response to male courtship, but also sometimes by fighting males.

Tail raise.....Actor holds tail vertical or bent back over rump. Males always have their tails raised when courting a female.

CHAPTER 2

POPULATION DYNAMICS

2.1 INTRODUCTION

A population is normally defined as a group of individuals of the same species living in a particular area with limited genetic exchange with other groups of the same species.

There have been few detailed studies of the population dynamics of feral goats in Britain. Crook (1969) and Greig (1969) provided basic population information for Scotland and Wales respectively. This was summarised by Whitehead (1972) and added to by McDougall (1975) and Stevenson-Jones (1977) in the Southern Uplands, also by Brown (1977) and Brown and Lloyd (1981) in North Wales. Buckland (1978), and Boyd (1981) have censused the population of feral goats on the Island of Rhum. Boyd (1981) found that the population on Rhum had apparently fluctuated in a cyclical manner since 1960 showing three peaks at approximately six year intervals. Bullock (1982), in a detailed study of seven populations in the Southern Uplands, found that the size of unmanaged populations appeared to fluctuate about mean levels and showed no long term trends or cycles in their numbers.

2.2 HISTORY AND DESCRIPTION OF THE MOFFAT GOATS

The origin of the goats in the Moffat hills is rather uncertain. Ribble (1972) recounts a tale that the wild goats in the Moffat Hills are descended from goats owned by monks in the time of King David I circa 1200. Goats were kept near to the sulphur spar at Moffat during the 18th century (Sinclair 1791). The whey from the milk of those goats grazed by the spar was thought to have great healing powers. Feral goats were certainly present in the area at the turn of this century (J.Dalglish and J.Mitchell pers. comm.). It is clear that there have been domestic and probably feral goats in the area for a considerable time. However it is uncertain whether the present feral goats are descended from these ancient introductions or are of more recent origin. The goats in the Moffat Hills are now one of eight populations of feral goats in the Southern Uplands. All appear to be isolated from one another with apparently no movement between them. The nearest population to the Moffat Hills is on Roan Fell some 24km away.

The goats in the Moffat hills show the characteristics of the old British breeds. They are small and light, with males measuring less than 70cm at the shoulder and weighing less than 80kg. Both males and females possess horns and lack the neck tassles of the modern breeds of goat. In common with most feral goats in Britain they are long-haired and often have a shaggy appearance. In addition to this long hair, short fine under hairs (Kashmir) may be present. The coat colour is highly variable ranging from black through various shades of grey, black and white patches, and browns

to completely white individuals.

The population was censused several times between 1964 and 1967 by Lockie (unpublished data) and his counts varied between 30 and 74. In 1969 Grieg (1969) recorded a total of 60 individuals in the area.

2.3 METHODS

Measures of survival and kid production were obtained from censuses and the recovery of carcasses (see 1.2.2). The population counts for 1978 and the ages of the animals that died during the 1978/79 winter were provided by D. Bullock. In the spring of 1981 estimates of age specific fecundity (number of live kids born to females of different age-classes) and perinatal survival (survival to one month of age) were obtained. Kid production was defined as the number of kids reared to weaning per female.

Any animal found dead was identified and examined for any obvious cause of death. A sample of tibia marrow was examined and the skull was collected. Bone marrow fat is the last fat reserve to be mobilized in large herbivores suffering malnutrition, and it has been shown that visual estimates of marrow reflect actual differences in fat levels and therefore condition of the animal (Sinclair and Duncan 1972). The tibia marrow was asssigned to one of three categories.

1) White or cream and firm to touch (high fat).

2) Pink, firm and wet.

3) Red or yellow, gelatinous and translucent (low fat).

In 1982 the goat population was subjected to management. Feral goats are occasionally reported as causing economic damage to young conifer trees (J. Walsham pers. comm.). The Forestry commission planned to replant part of the Craigieburn plantation, and they believed that the number of goats using the plantation in the spring constituted an unacceptable risk to their young trees. Therefore in May 1981, 13 goats (six females, five males and two kids) were driven out of the plantation, captured, and given to the Hill Farming Research Organisation. In September 1982, two white male kids and a white male yearling were taken from the population for research into managing feral goats for Kashmir production. These goats have been included in the 1982 totals.

2.4 RESULTS

2.4.1 Population changes

The number of adult goats decreased from 94 in 1978 to 76 in 1979. Since then, the number has increased to 103 by autumn 1982 (Fig. 2.1). This represents a 34% increase in three years. There are more females in the population than males. The adult sex ratio fluctuated between 1:3.27 to 1:1.76 (males:females) during the study, and appeared to be due to fluctuation in the number of males rather than the number of females (Table 2.1). The sex ratio of kids was biased in favour of males in three of the four years for which data were available, but it did not differ overall from a 1:1

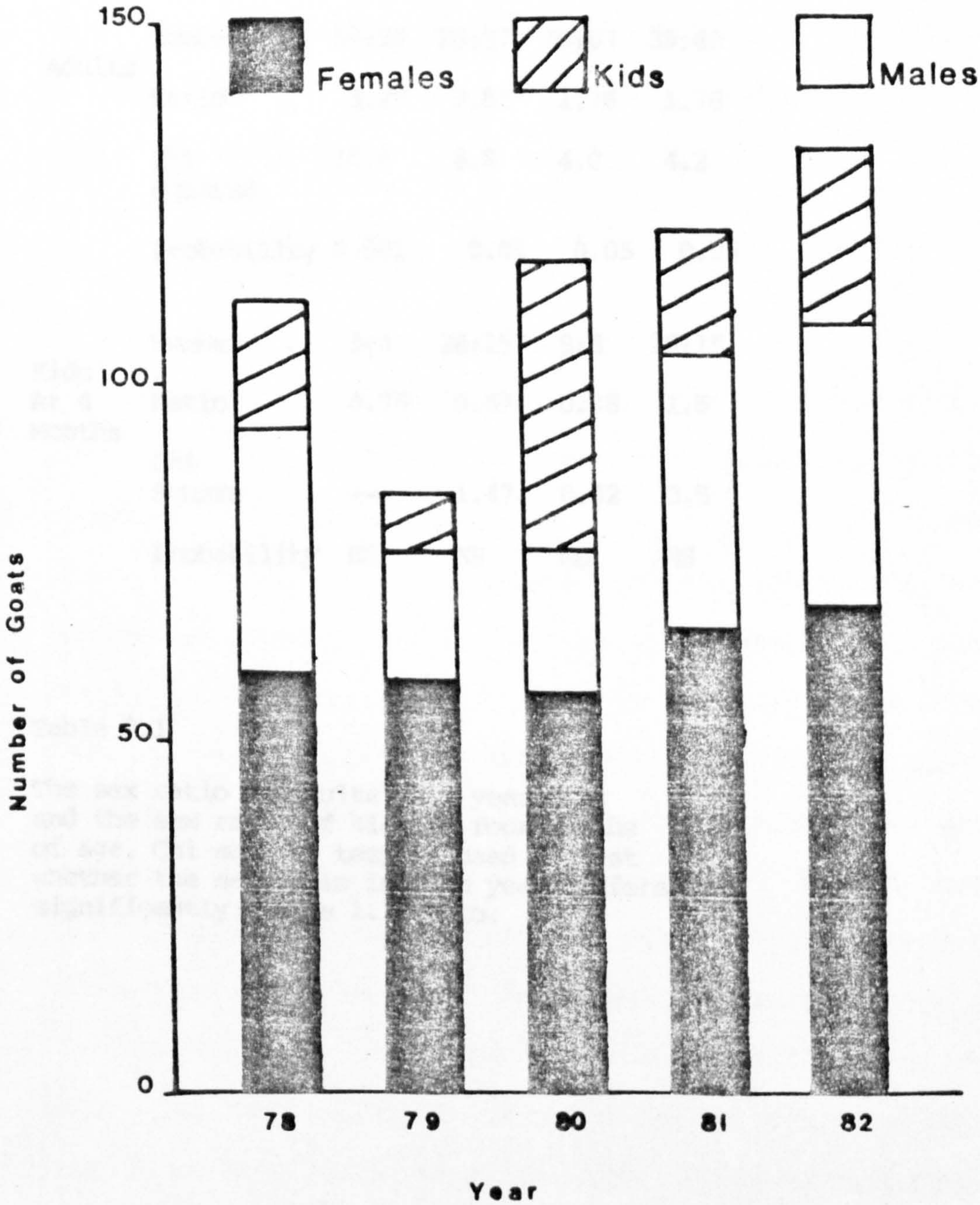


Fig. 2.1 The number of goats present in the Moffat Hills each autumn between 1978 and 1982.

		1979 M:F	1980 M:F	1981 M:F	1982 M:F
Adults	Number	18:59	20:57	38:67	39:69
	Ratio	3.27	2.85	1.76	1.76
	Chi Squared	10.9	8.8	4.0	4.2
	Probability	0.001	0.01	0.05	0.05
Kids At 4 Months	Number	3:4	26:15	9:8	10:15
	Ratio	0.75	0.57	0.88	1.5
	Chi Square	---	1.47	0.02	0.5
	Probability	NS	NS	NS	NS

Table 2.1

The sex ratio of adults plus yearlings and the sex ratio of kids at four months of age. Chi squared test is used to test whether the sex ratio in each year differs significantly from a 1.1 ratio.

ratio (Table 2.1). The number of adult females decreased by 4% between 1978 and 1979, while the number of males in the population was halved over the same period. Between 1979 and 1982 the number of adult males increased by 117%, while the number of adult females only increased by 17%.

2.4.2 Fecundity and Kid production

Estimates of age specific fecundity were only obtained in 1981 (Table 2.2). The fecundity of yearling females was significantly less than that of older females (χ^2=9.04, d.f.=1, P<0.01). However, after two years of age there was no clear difference in fecundity between age classes. It can be seen from Fig. 2.2 that kid production was significantly higher in 1980 than in the other four years (χ^2=19.03, d.f.=1, p<0.001). There was also a significant difference in kid production between hefts of females (Friedman two way anova: χ^2=7.16, d.f.=4, p<0.001, Table 2.3). Females belonging to the Capplegill heft produced more kids per female each year than females in other hefts. Kid production by yearling females was significantly lower than by adult females (χ^2=31.7, d.f.=1, p<0.001, Fig. 2.3). Although adult kid production was highly variable there were no age specific trends (Fig. 2.3). There was no difference in the probability of a female rearing a kid in any year between those females which had successfully reared a kid in the previous season, and those that had not (χ^2=0.16, d.f.=1, N.S., Table 2.4). The probability of rearing a kid showed no significant difference if the female had reared a male kid, rather than a female kid in the

Age	No.of Females	No.of Kids	Estimated Fecundity
1	15	3	0.20
2	4	3	0.75
3	8	5	0.60
4	5	3	0.63
5	8	6	0.75
6	10	7	0.70
7	9	5	0.55
8	4	3	0.75
9	4	3	0.75
10	4	3	0.75
11	2	1	0.50

Table 2.2

Estimated age specific fecundity of females in spring 1982.

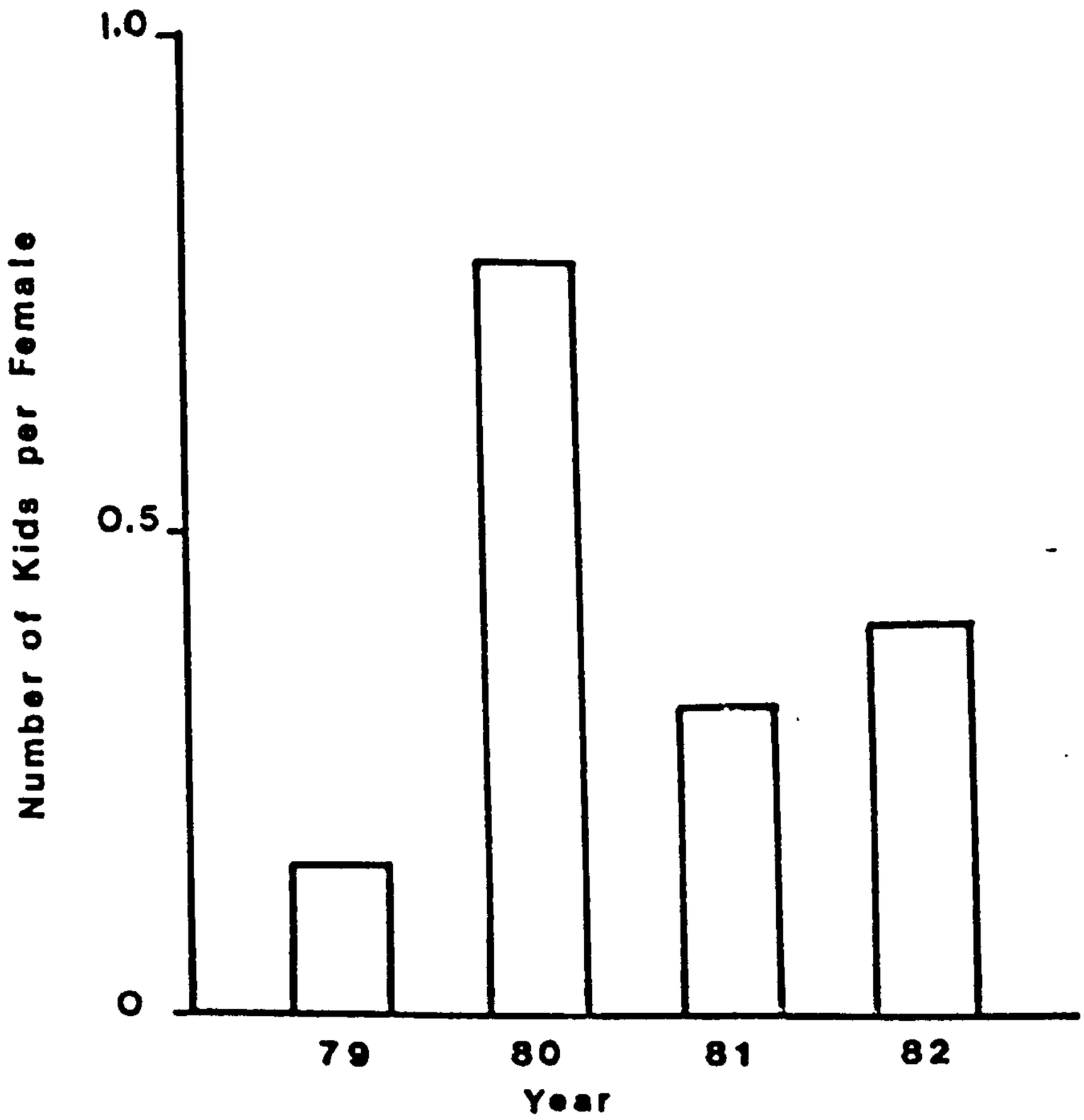


Fig. 2.2. Kid production of adult females between 1979 and 1982. Chi squared test comparing 1980 with other years, χ^2=19.03, d.f.=1, p<0.001.

Heft	1979 No. F.	1979 No. Kids /F.	1980 No. F.	1980 No. Kids /F.	1981 No. F.	1981 No. Kids /F.	1982 No. F.	1982 No. Kids /F.	Mean	s.e.
Grey Mare's Tail	11	0.00	11	0.90	14	0.70	18	0.38	0.49	0.19
Carriferan	10	0.00	9	0.55	10	0.10	9	0.55	0.30	0.14
Spoonburn	15	0.07	14	0.78	17	0.11	16	0.50	0.36	0.16
Capplegill	7	0.40	9	1.00	9	0.42	12	0.55	0.59	0.13
Blackhope	16	0.18	16	0.47	17	0.25	14	0.16	0.24	0.08

Table 2.3

Kid production of each heft 1979-1982

Fig. 2.3 Age specific kid production. Each point indicates four year mean, and the vertical lines one standard error. Chi squared test comparing yearlings with adult females, χ^2=31.7, d.f.=1, p<0.001.

previous season (χ^2=0.23, d.f.=1, N.S., Table 2.4).

Most kids were born during late winter, but one kid was born in June 1981 and another in July 1982. Excluding the summer born kids the mean date of birth in 1980 was 8th April, s.d.=12.0 days, and in 1981 was 5th March, s.d=15.1 days (Fig. 2.4) Kid production was 0.73 and 0.34 in 1980 and 1981 respectively. In 1981 the perinatal mortality of kids born prior to the mean birth date was significantly higher than those born after this date (χ^2 =5.77, d.f.=1, p<0.01, Table 2.5).

2.4.3 Survival rates

The survival of kids during the first few weeks of life was low. In 1981, only 34% of kids born survived to six months of age. The survival rate of goats increased after the first six months of life, but showed considerable variation between years and was particularly low for males between 1978 and 1979 (Table 2.6). A four year mean survival rate was calculated by following known cohorts (Table 2.7). This information is presented in the form of age specific survival curves (Fig. 2.5). It can be seen from this figure that the mean female survival rate was high and approximately constant between the age of one and seven years, after which it decreased rapidly. The mean survival rate of males was (nonsignificantly) lower than that of females between the age of one and seven. Males also tended to die younger than females.

YEAR N		YEAR N+1 No.of females							
		Rearing kids				Not Rearing kids		Dying	
History	n	Male		Female					
		n	%	n	%	n	%	n	%
A) No kid Reared	83	21	23	17	19	39	46	6	7
B) Male Kid Reared	40	8	19	7	16	20	47	5	11
C) Female Kid Reared	28	6	21	7	25	13	46	2	7

Table 2.4

A Comparison of the breeding success of females in year N+1 that reared A) no kid, B) a male kid, C) female kid in year N.

Time Period	No.kids Born	No.kids Alive in May	Survival rate	Chi Squared
20 Feb-2 March	18	2	0.11	
				5.77
3 March-12 March	14	8	0.57	
				$p<0.05$
13 March-22 March	15	7	0.46	

Table 2.5

The perinatal survival of kids born in different periods in spring 1981.

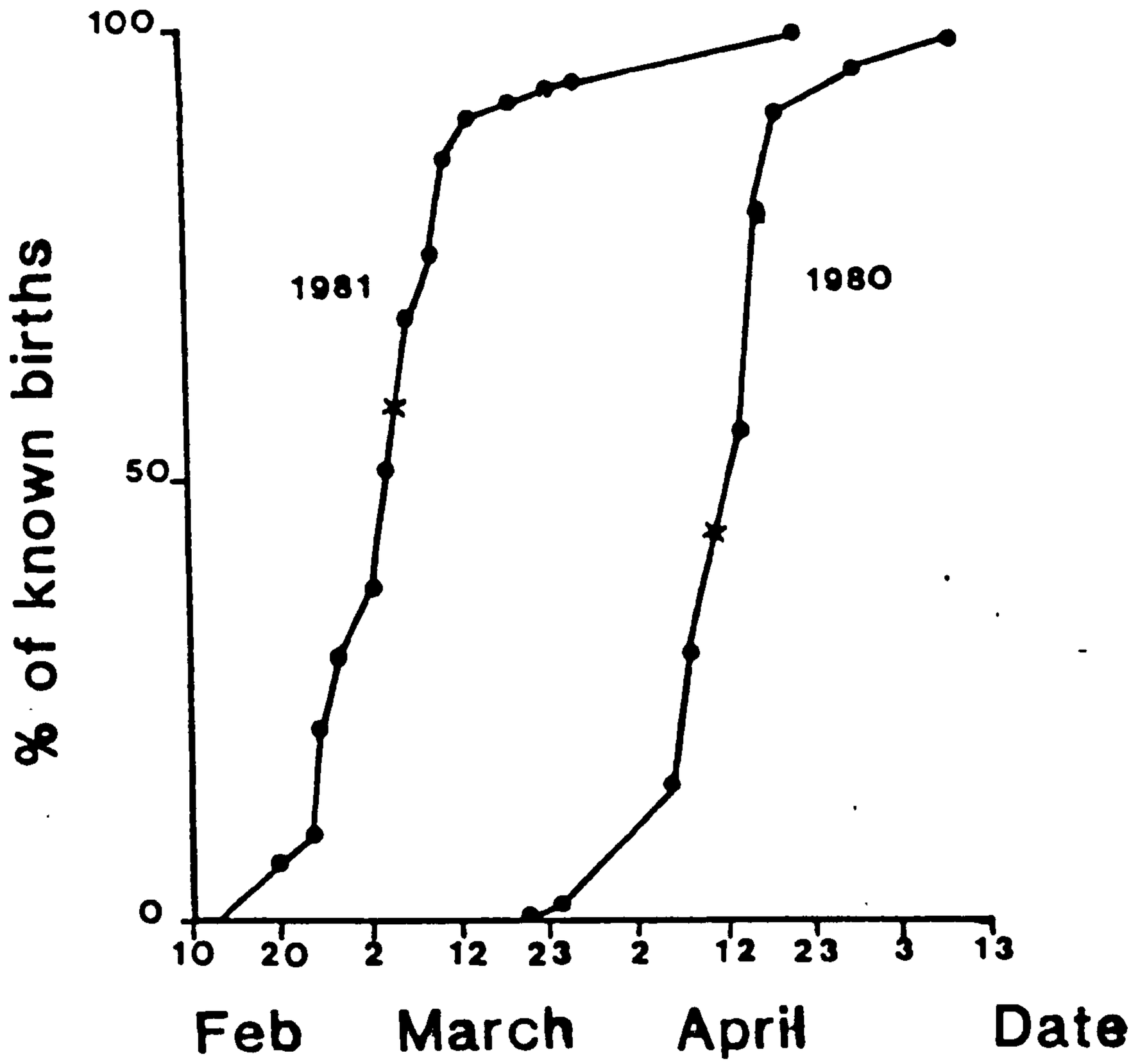


Fig. 2.4 Cumulative frequency of known births during the spring in 1980 and 1981. The cross indicates mean date of birth each year.

Survival Rates

	Adults		Kids		
Year	Male	Female	Male	Female	
78/79	12/34 0.35	53/60 0.88	6/9 0.67	5/9 0.56	Bullock 1982
79/80	17/18 0.94	54/59 0.91	3/3 1.00	4/4 1.00	Present Study
80/81	18/20 0.90	52/58 0.89	20/27 0.74	14/15 0.93	"
81/82	29/38 0.76	61/66 0.92	7/9 0.77	8/8 1.00	"
Mean	0.73	0.90	0.79	0.87	
Standard Error	0.13	0.001	0.07	0.10	

Table 2.6

Survival rates of adults plus yearlings and kids of both sex.The enumerator is the number alive in the autumn of the first year and the denominator is the number of goats alive in the following autumn.

Age Class	Number of female goats present in autumn each year 1979 N	1980 N	1981 N	1982 N
0-1	4	15	8	15
1-2	8	4	14	8
2-3	6	8	4	14
3-4	8	5	8	4
4-5	10	8	5	8
5-6	9	10	8	5
6-7	4	9	8	8
7-8	4	4	7	8
8-9	7	4	3	5
9-10	3	4	4	2
10-11	0	2	4	4
11-12	0	0	1	3
Total	63	73	74	84

Table 2.7a

Age structure of females 1979-82.

Number of male goats present in autumn each year.

Age Class	1979 N	1980 N	1981 N	1982 N
0-1	3	26	9	10
1-2	6	3	20	7
2-3	5	5	3	16
3-4	2	5	5	3
4-5	0	2	4	4
5-6	3	0	2	3
6-7	1	3	0	1
7-8	0	1	3	0
8-9	0	0	1	2
9-10	0	0	0	0
10-11	1	0	0	0
11-12	0	1	0	0
Total	21	46	47	48

Table 2.7b

Age structure of males 1979-1982.

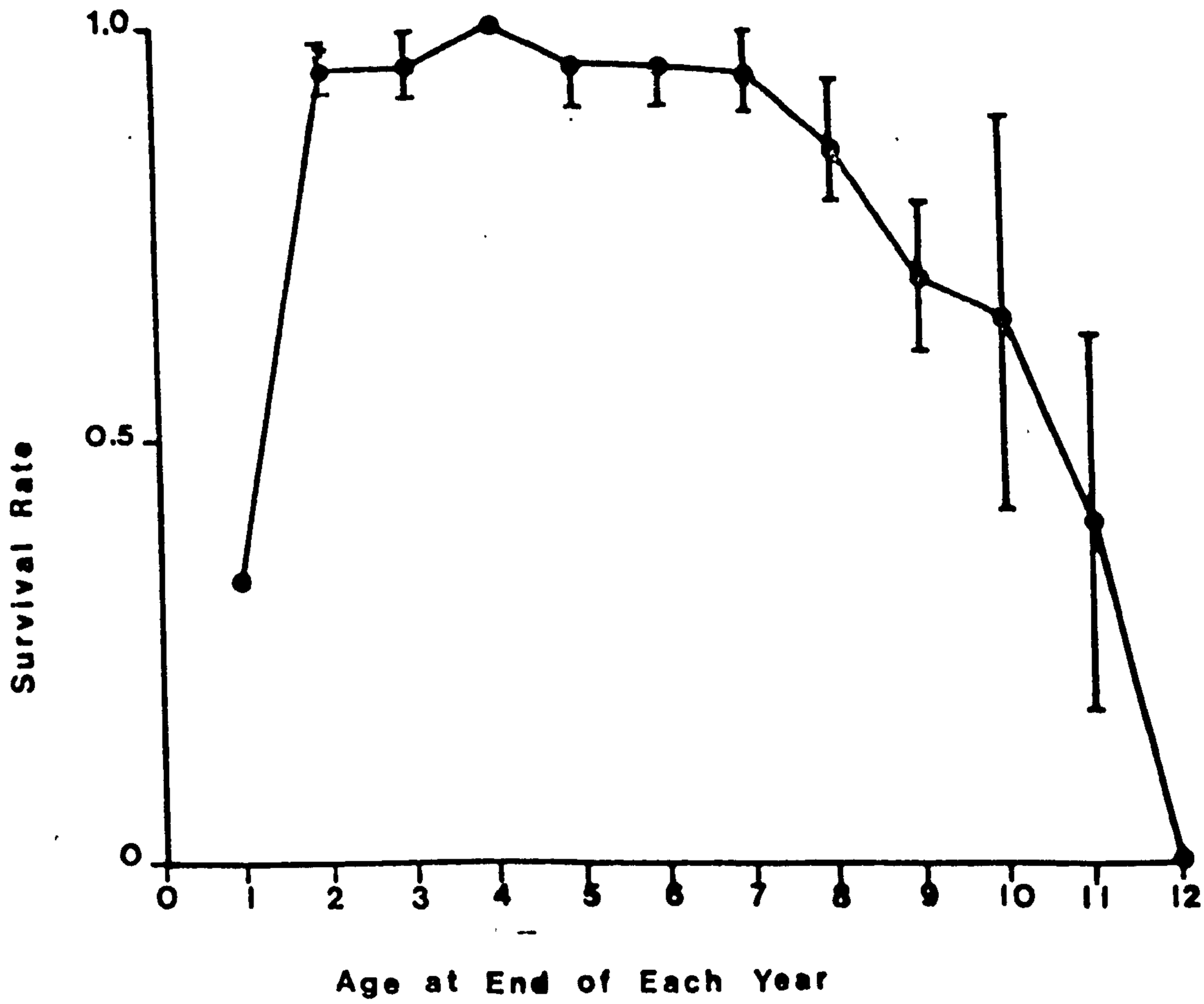


Fig. 2.5a. Female survival curve. Vertical lines indicate standard errors.

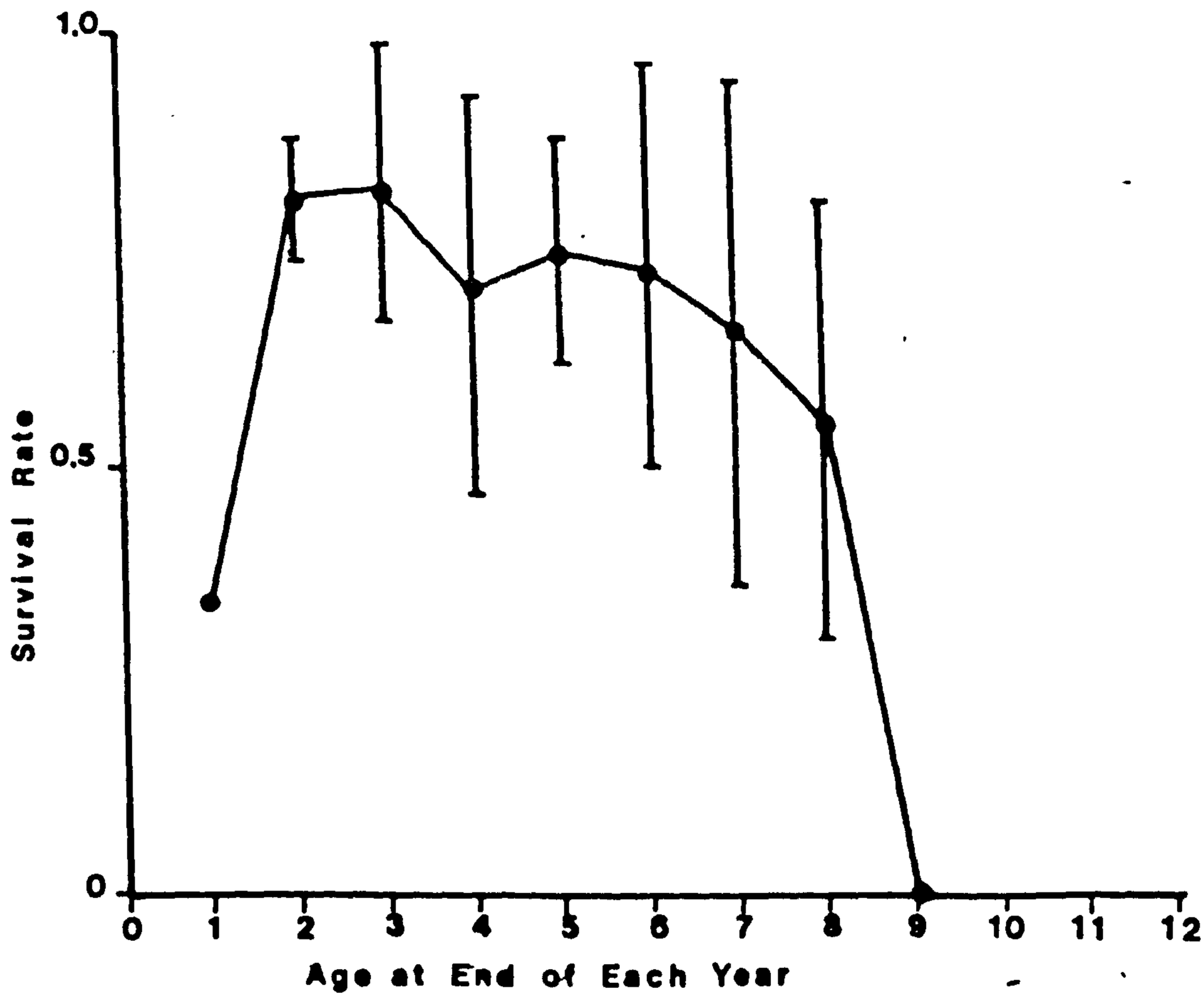


Fig. 2.5b. Male survival curve. Vertical lines indicate standard errors.

2.4.4 Causes of death

Fourteen goats were found dead between autumn 1979 and autumn 1981, seven were female and seven were male. The majority of males died during the winter months (Fig. 2.6). All except one appeared to be in poor condition with low marrow fat reserves (category 3). The one exception was a male found dead by the side of the road in June 1981. It appeared to have died from injuries (broken hind leg and hip, internal bleeding) sustained in a road accident. This animal appeared to have been in good condition prior to death with a high marrow fat level and fat reserves around the kidneys. All the female carcasses found were of animals that had died during spring or summer. Two appeared to be close to parturition, and may have died as a result of difficulties with parturition. The cause of death of the others was uncertain, one may possibly have died as a result of a fall. The remaining four were all old females in relatively poor condition, (marrow fat category 2 or 3) and had worn teeth.

Predation, although probably not the most important cause of kid mortality, did occur. Fox, mink and raven (twice) were all observed to unsuccessfully attack young kids. On each occasion the mother charged and drove off the predator.

In March 1981 three carrion crows were seen attacking a kid that had been observed to lie down in a hiding place some two hours previously. The attack continued for twenty minutes until the mother returned to find a dead kid. It is not certain whether the kid was alive at the time of the attack.

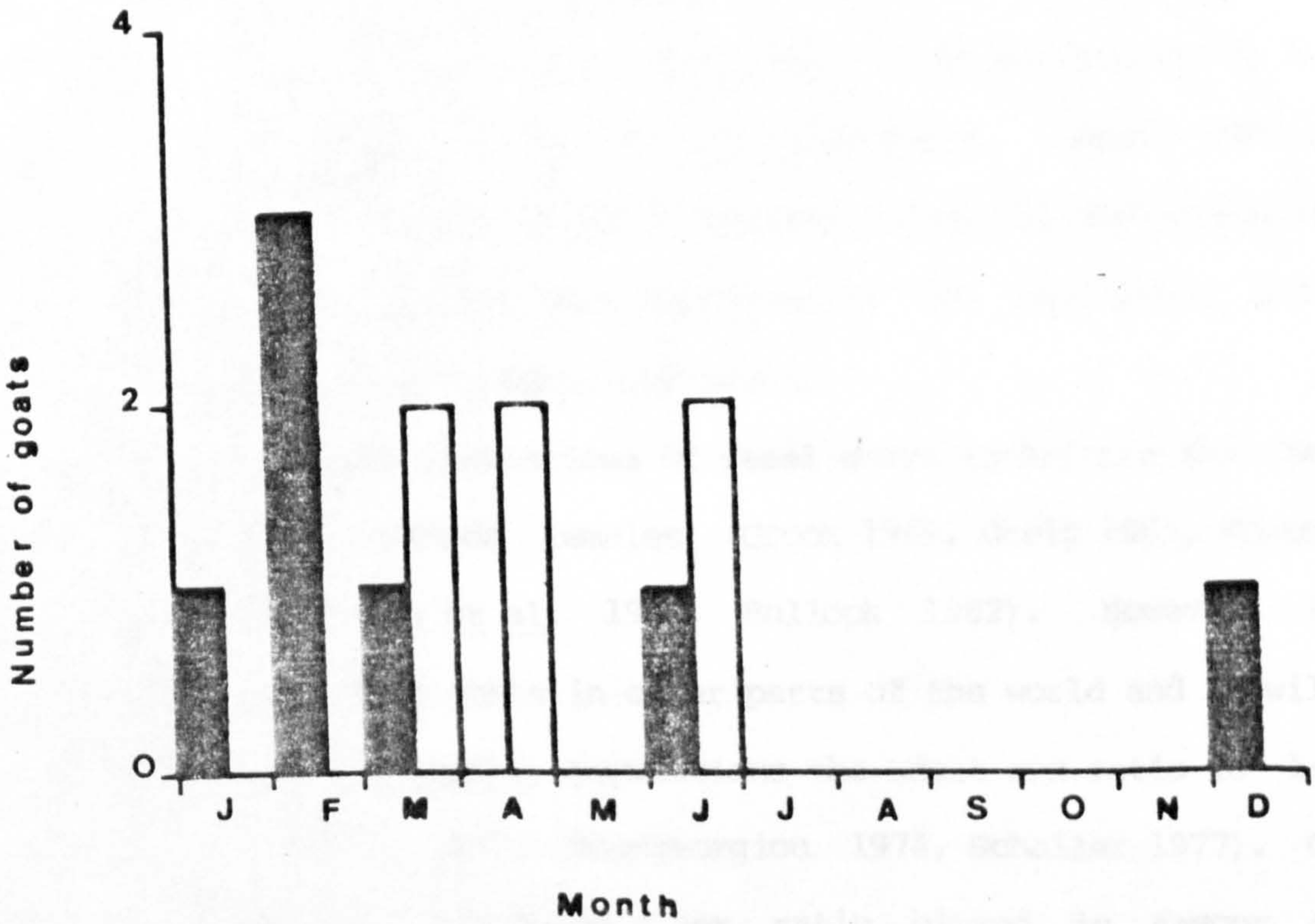


Fig. 2.6 Distribution of deaths of female (open) and male (shaded) goats throughout the year.

2.5 DISCUSSION

All the population counts during the period 1964-69 are lower than the totals between 1978 and 1983. This indicates that either the population has increased or that these earlier counts were actually underestimates. After the high mortality rate of goats, especially males, over the 1978/79 winter, the population has increased. This increase between 1979 and 1982 is due largely to an increase in the number of males in the population. Boyd (1981), found that the proportion of males increased when the population on Rhum was high, and suggests that decreases in the population were caused by changes in male mortality rates.

In all unmanaged populations of feral goats in Britain the sex ratio is biased towards females (Crook 1969, Greig 1969, Munton 1975, Boyd 1981, Brown et al. 1981, Bullock 1982). However, in populations of feral goats in other parts of the world and in wild goat (Capra hircus aegagrus) populations the adult sex ratio is 1:1 (Yocum 1969, Shank 1972, Papageorgiou 1974, Schaller 1977). On Aldabra, Gould (1979) has found a sex ratio biased in favour of males. The sex ratio of kids at birth or at six months does not differ significantly from a 1:1 ratio (Crook 1969, Greig 1969, Yocum 1969, Brown and Lloyd 1979, Boyd 1981, Bullock 1982 and present study). Therefore the biased sex ratio found in British populations appears to be due to differential mortality of the sexes. Mortality during the first few weeks of life was found to be very high but there was no evidence of male mortality being higher than that of female kids up to the age of six months. After this age the

mortality of males was found to be higher than for females in some years. Boyd (1981) and Bullock (1982) found a similar pattern of mortality. Females lived longer than males and the further life expectancy of yearlings was estimated to be 2.4 years for males and 5.6 years for females. This is similar to the median age at death of 3.75 years and 6.75 years of male and female goats found by Bullock (1982). On the island of Aldabra Gould (1979) found the mortality of females to be higher than that of males.

The number of animals found dead during this study was relatively low. However the yearly pattern of mortality whereby males tended to die in late winter and females in spring was similar to the findings of Bullock (1982). Although most males had relatively healthy dentition they had depleted fat reserves suggesting that they had died of starvation. It has been suggested that a reduction in time spent feeding and increased energy expenditure during the rut may be a primary factor contributing to the lower survival rate of males compared to females (Boyd 1981, Bullock 1982). Soay rams on Hirta have a higher mortality rate than ewes and this is thought to be for the same reason (Grubb 1971). Tropical populations of feral goats and those off the west coast of North America, where the adult sex ratio is 1:1, do not have one restricted breeding season (Yocum 1967, Shank 1972, Gould 1979, Coblentz 1980). Consequently the selection pressure on males to rut intensively for a short period of time is not present. This hypothesis is partially tested and discussed in Chapter 5.

Kid production varied between years. It was much higher in 1980 when the median date of birth was a month later than in 1981

and 1982. Those kids born early in 1981 suffered much higher mortality than those born later in that year. The exact cause of death of kids during the first few weeks of life is unknown but it could be related to when they were born. On British uplands forage availability decreases over the winter to a minimum in March and early April (Rawes and Welch 1969). All the goats found dead during this period were in a state of undernutrition. Many ungulates in northern regions cannot find sufficient food during late winter and show a marked decline in weight (Eadie 1970, Jewell et al. 1974, Mitchell et al. 1976). Therefore it is likely that most goats incur a negative energy balance at this time of year. It is suggested that because of their poor condition and the lack of forage many females cannot provide enough milk for their kids. These undernourished kids may easily succumb to the cold, wet conditions prevalent during the spring.

Kidding in late winter does not appear at first sight to be an adaptive breeding strategy. Most ungulates in northern latitudes breed seasonally, presumably in response to a well defined periodicity in available food (Geist 1974, Schaller 1977). The onset of the birth period appears to be determined by forage quality and quantity (Baker 1938, Skinner et al. 1977, Bunnel 1980, Thompson and Turner 1982), while the duration of the birth period is thought to be limited by the need for the young to attain adequate body size by winter (Bunnel 1980, 1982, Bullock 1982). In Scotland however, the kidding period of feral goats does not coincide with the period of vegetation development when the environmental regime might ameliorate neonate survival. Therefore other factors probably

influence the time of kidding.

It is known that decreasing daylength stimulates female goats to come into oestrus in September/October (Adsell 1964, Hafez 1969). However the fact that mean birth date in 1980 was a month later than in 1981 or 1982 indicates that this is not the only factor determining timing of oestrus In red deer (Cervus elaphus), females in poor condition tend to come into oestrus after females in good condition (Mitchell and Lincoln 1973) After the harsh winter of 1978/79 female goats may have been in poor condition and come into oestrus later than usual in 1979.

The feral goat's wild ancestors, Capra hircus aegagrus, still exist today in the Mediterranean and Middle East. Those in the Karchal hills in Pakistan rut between August and November (Schaller 1977). They kid at the end of the cool wet winter when the primary production is highest. Greig (1969) suggests that feral goats have not yet adapted to the northern seasonal pattern. However summer births are regularly recorded on Rhum (Buckland 1978), on Cairnsmore, Galloway (J. Theacker pers. comm.) and twice during this study, but there does not appear to be any shift towards summer breeding. This suggests that those early born kids that do survive have a marked advantage over summer born kids in terms of survival and reproductive success. There is no evidence from kids born in the same season that early born kids have a higher overwinter survival than late born kids. However, kids born in March 1981 did have a (nonsignificantly) higher overwinter survival than those born in April 1980 (see Table 2.6). Factors other than date of birth may account for these differences in survival rate of kids between these

two winters. In 1981 there were significant negative correlations between date of birth and body weight of male kids caught in September ($r=-0.88$, $df.=4$, $p<0.05$) and November ($r=-0.93$, $d.f.=4$, $p<0.01$) 1981. Large animals are more efficent thermoregulators than small (Kleiber 1961). Therefore early born kids may be at an advantage over late born kids for thermoregulatory reasons during their first winter. Artificial selection for females that kid early and therefore have a long lactation period between early spring and autumn may also have influenced the breeding period of feral goats (Bullock 1982).

In many mammal species female reproductive success increases with age for the first few years to reach a maximum before declining in later life, e.g. reindeer, Rangifer rangifer, (Preobrazhenski 1966), red deer (Clutton-Brock et al. 1982), while in other mammals female reproductive success increases with age until death, e.g. elephant seals, Mirounga angustirostris, (Reiter et al. 1981). Kid production was much lower for yearlings compared to adult females, possibly because of the much lower fecundity rate of the former. Boyd (1981) suggested that females between the ages of three and seven have a higher reproductive rate than other females and also that these females tend to produce more male kids. In this study there was no evidence of age specific variation in reproductive rate of females after their second year, or any age specific variation in the sex of kids produced. There was a consistent difference in the kid production between hefts of females. An explanation of this may lie in the fact that the females in the Capplegill heft made a seasonal migration. After spending late summer and autumn on the

open hill they moved into the Craigieburn forestry plantation to give birth. Although there is no quantitative evidence it is likely that the shelter provided by the trees, and the greater quantity of forage available in the plantation were the primary factors influencing the number of kids that they reared.

Food supply has been shown to be important in the regulation of several ungulate populations, eg. feral sheep on Hirta (Jewell et al. 1974), feral reindeer (Klein 1968, Leader-Williams 1981) and African Buffalo, Syncerus caffer, (Sinclair 1977). It is likely that the number of feral goats in the Moffat hills is also ultimately limited by the quantity and quality of available forage.

CHAPTER 3

HOME RANGE AND SPATIAL ORGANISATION

3.1 INTRODUCTION

Most animals do not roam at random over suitable habitat, but generally confine their activities to one or several restricted areas in the course of a year and, often a lifetime. This area is normally termed a home range and is generally considered to be the area over which an animal normally travels in pursuit of its routine activities (Jewell 1966). In this study I have used the term normal home range to include the area occupied by an individual between November and August inclusive, and rut home range to include the area occupied during September and October. Total home range is normal home range plus rut home range.

Work on Weaver birds, primates and African ungulates has shown that the number of individuals in a group, the relationship between individuals within a group and home range size are determined largely by the distribution and abundance of food and predators of that particular species (Devore 1965, Crook and Gartlan 1966, Bell 1970, Jarman 1974, Clutton-Brock and Harvey 1977, Jarman and Jarman 1979, Wrangham 1980).

The basic social organisation of feral goats is groups of females and their offspring with which adult males associate to a

variable degree (Riney and Caughly 1959, Rudge 1970, Shank 1972, MacDougall 1975, Coblentz 1980, Boyd 1981). These groups of females and associated males have been called hefts, a term used to describe similar groupings of hill sheep. Within each heft individuals have highly overlapping home ranges, but overlap between the home ranges of individuals in neighbouring hefts is less (Boyd 1981). Movement of individuals between hefts appears to be limited to adult males during the breeding season (Coblentz 1980). This chapter is concerned with variation in group size, group composition and the spatial organisation of feral goats.

3.2 METHODS

Data were collected by walking the study area and spot sighting groups of goats (see Chapter 1). Three types of group were recognised :

1) Female groups, consisting of adult and/or yearling females plus their kids of either sex.

2) Male groups, consisting of adult and/or yearling males.

3) Mixed groups, consisting of kids, yearlings and adult males and females.

The frequency distribution of group sizes was skewed to the left (Fig. 3.1). Jarman (1974) suggested that with such data, "typical group size" is more meaningful in describing the size of group containing, or experienced by, the average individual than mean or median group size (see Appendix 1). Mean and typical group sizes were calculated for each calendar month.

Individuals within the same group were considered to be

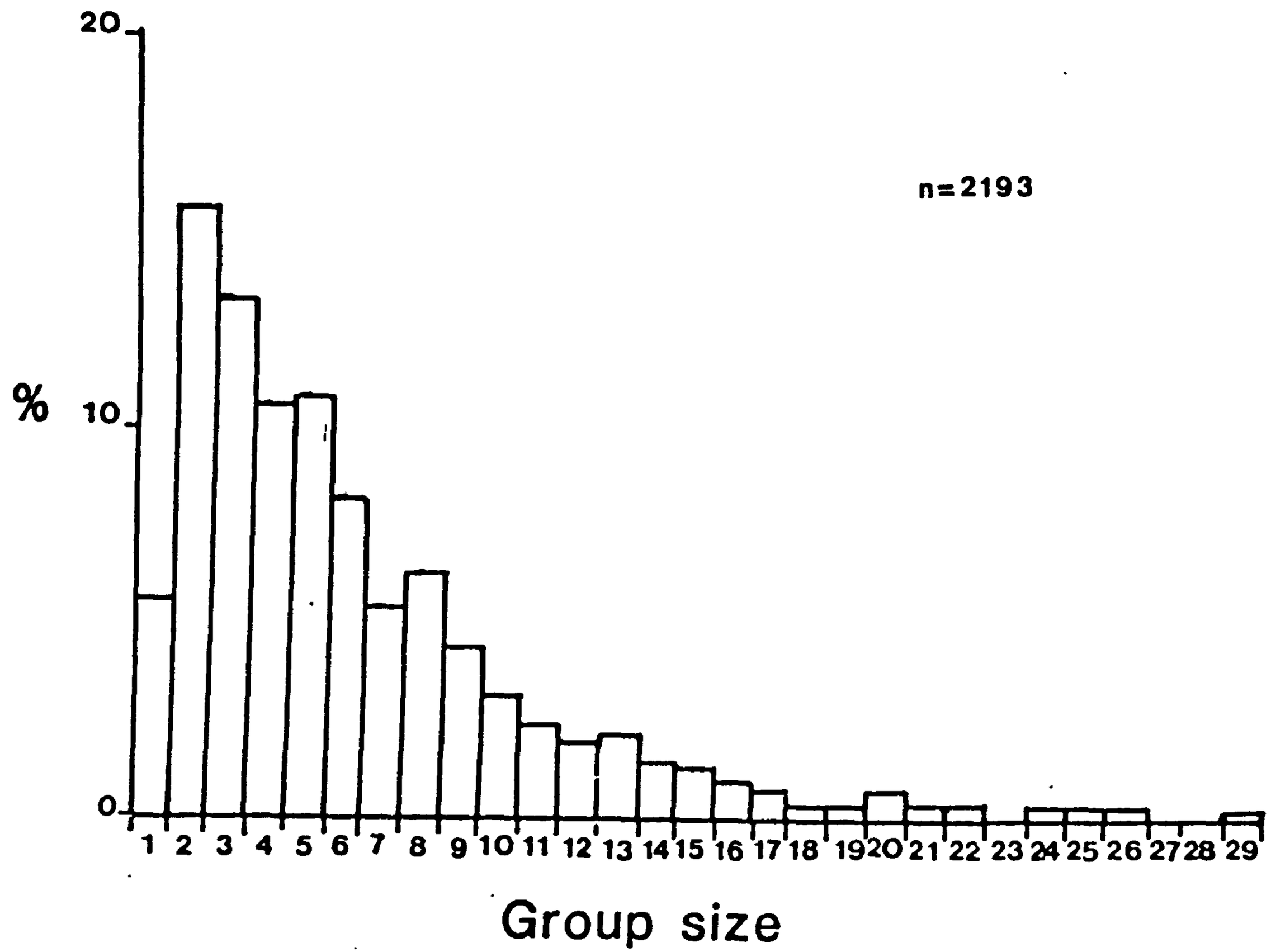


Fig. 3.1a Frequency distribution of all goat group sizes observed between January 1980 and October 1981.

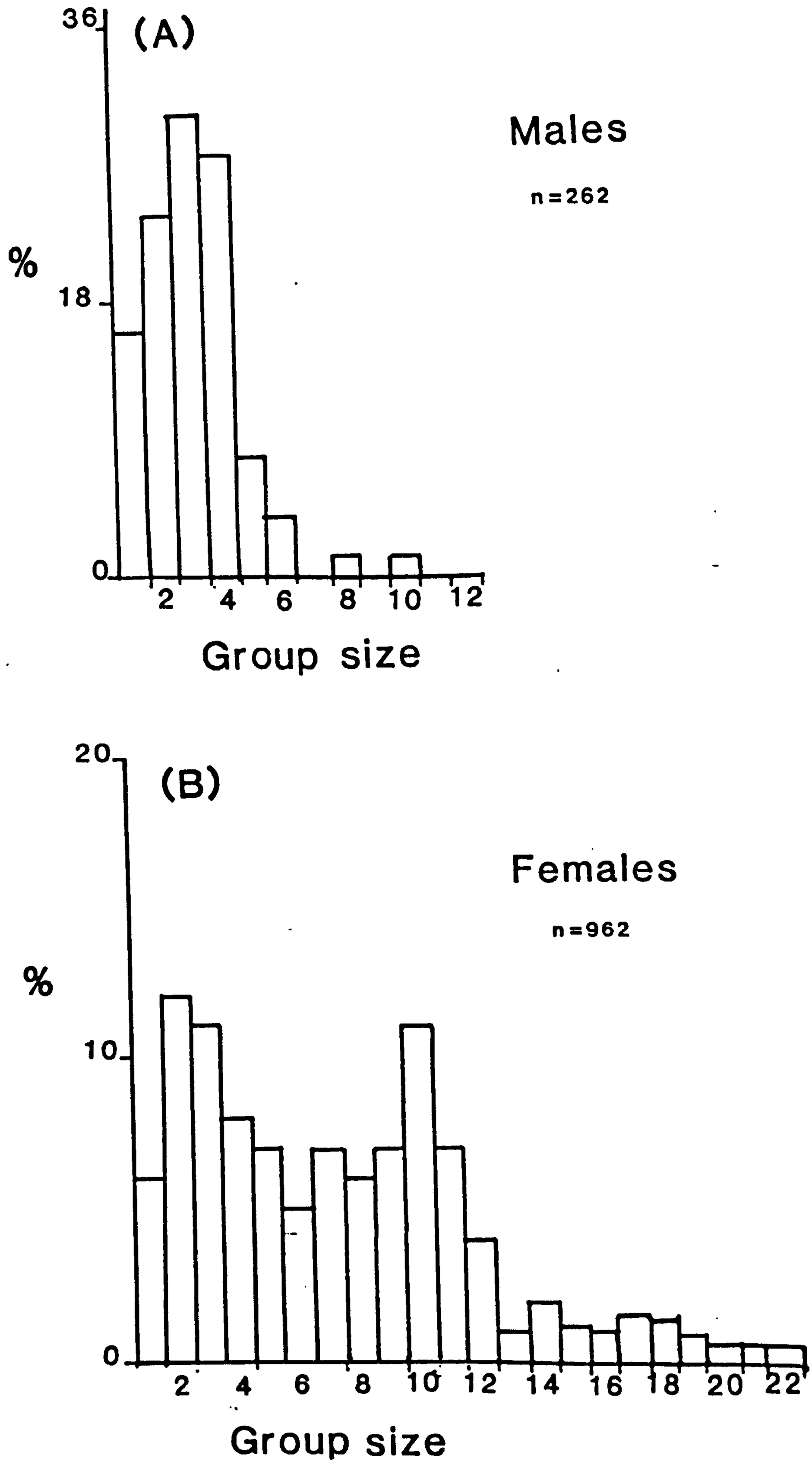


Fig. 3.1b Frequency distribution of male (A) and female (B) group sizes between January 1980 and October 1981.

associated. The frequency of association between individuals takes into account the number of sightings of each individual as follows (Dice 1945):

$$\text{Frequency of association} = \frac{\text{Total no. of sightings of goat A with goat B}}{\text{Total sightings of goat A} + \text{Total sightings of goat B}} \times 2$$

This measure of association formed the basis of the dendrogram, which was constructed using weighted-average cluster analysis.

The areas occupied by individuals (home range) or hefts (heft range) were calculated by plotting each sighting on a map and then enclosing all points with no re-entrant angles (minimum area method, Southwood 1978). The degree of overlap between individuals (or hefts) was calculated by measuring the area common to both and expressing this as a percentage of the home range area of the individual (or heft) concerned. The degree of home range overlap between each heft was measured by calculating the mean percent overlap of each individual from one heft with each individual of the neighbouring heft.

3.3 RESULTS

3.3.1 Group size and composition

Group size varied between 1 and 29 individuals during the study

period. Typical group size was larger than mean group size for each month but both measures showed the same changes during the year and there appeared to be no advantage in using typical group size rather than mean group size in describing changes in the size of groups of feral goats.

Overall group size (male + female + mixed) was smallest during the spring months March and April, but then increased during the summer to reach a maximum in September (Fig. 3.2a, b and c).

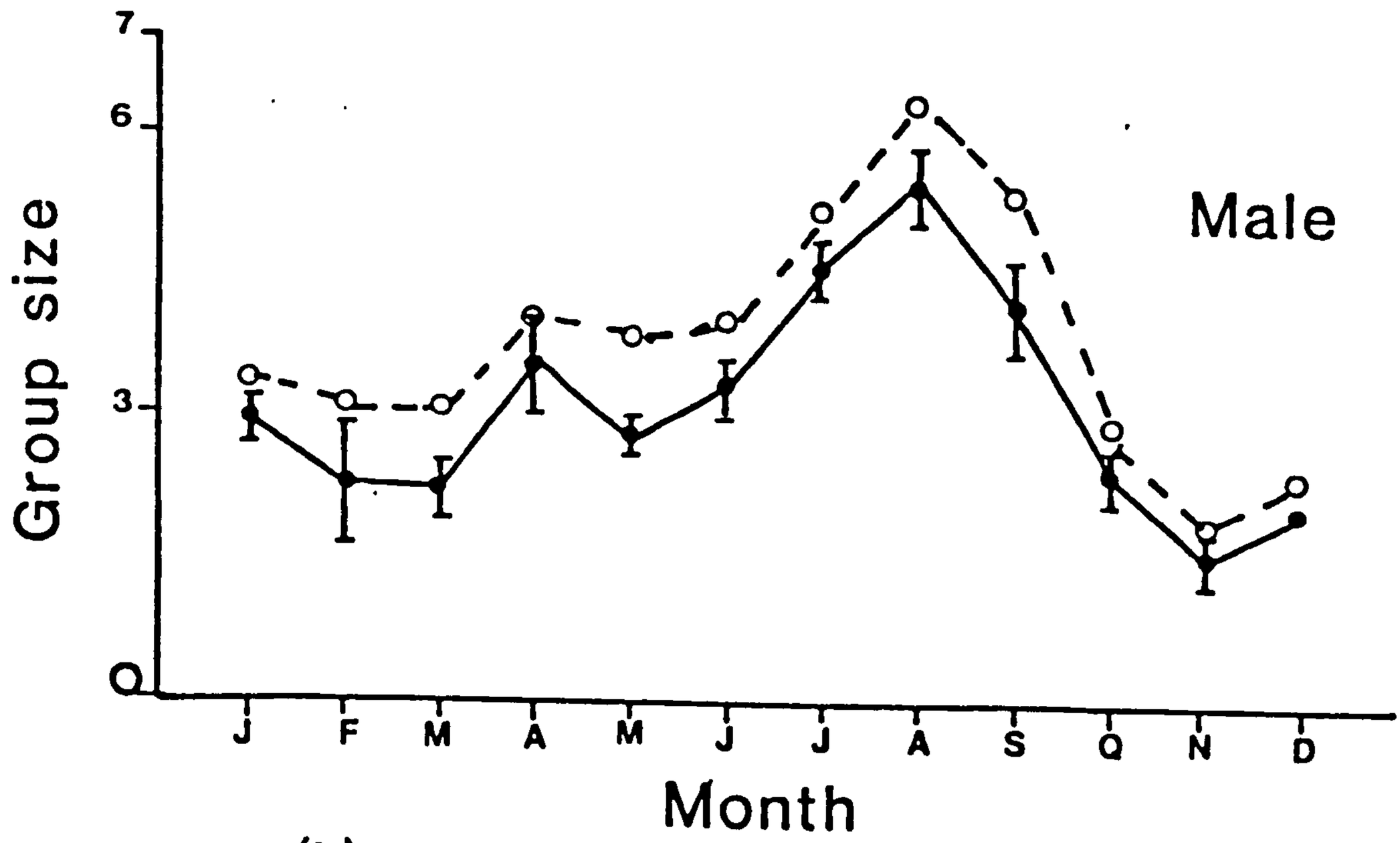
Female groups were always larger than male groups (Fig. 3.2). They both showed the same general trends in group size, with small groups in the spring and large groups in the autumn. However, the largest female groups were recorded in June and July (Fig. 3.2) and the largest male groups were observed in August and September. The size of mixed groups reached a maximum during the early part of the rut in September (Fig. 3.2).

It can be seen from Fig. 3.3 that during late spring and summer there was a degree of sexual segregation. In July, 36% of adult plus yearling males were to be found in mixed groups. This proportion increased during August and September and 97% of males seen during October were in mixed groups.

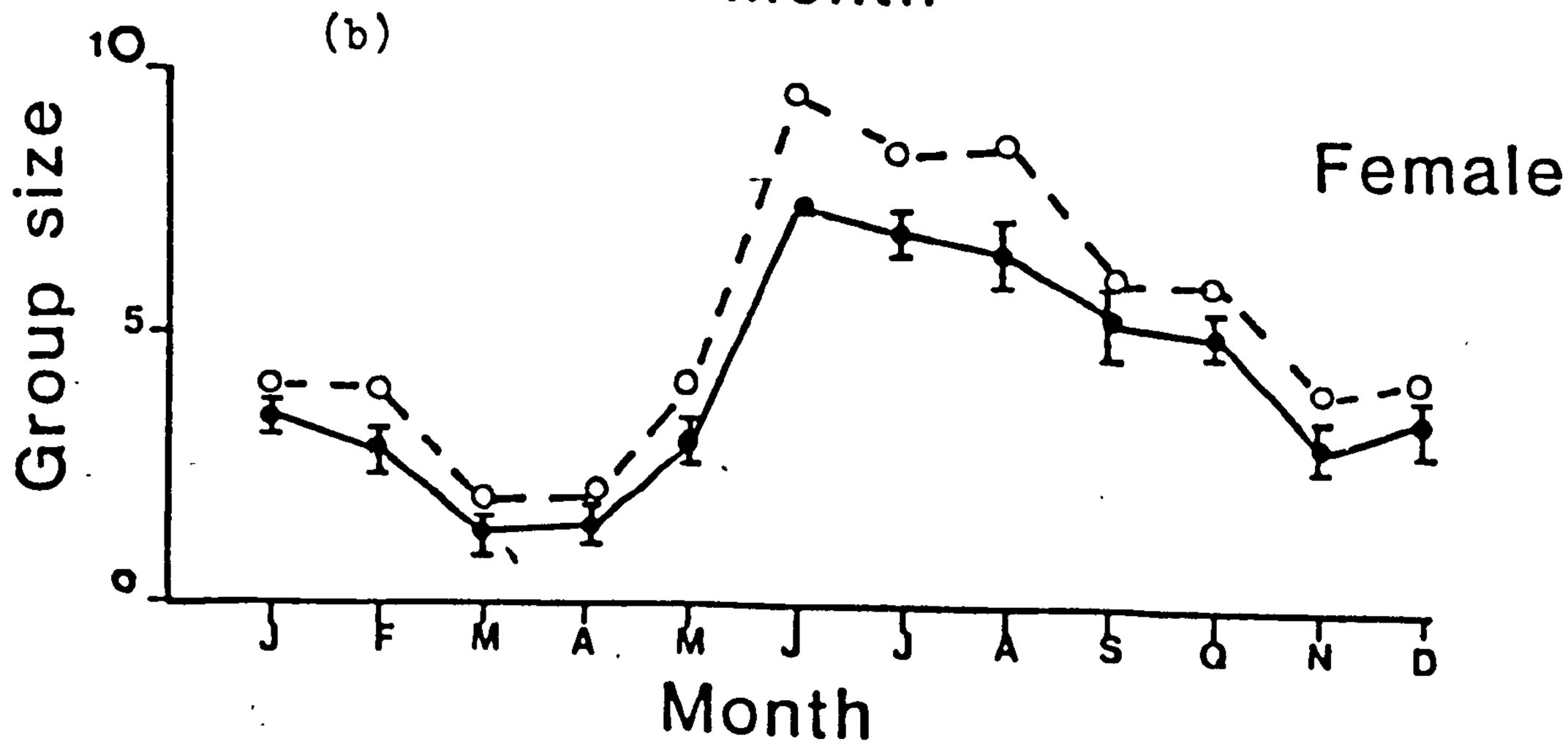
3.3.2 Grouping and home range

Fig. 3.4 shows the dendrogram of association between adult individual goats, taking the cut-off point at 20% association. This shows five main groupings, each containing between 8 and 20 adult goats. The dendrogram-defined groups correspond to the hefts

(a)


Group size
7
6
3
0
Male
J
F
M
A
M
J
J
A
S
O
N
D
Month

(b)


Group size
10
5
0
Female
J
F
M
A
M
J
J
A
S
O
N
D
Month

(c)

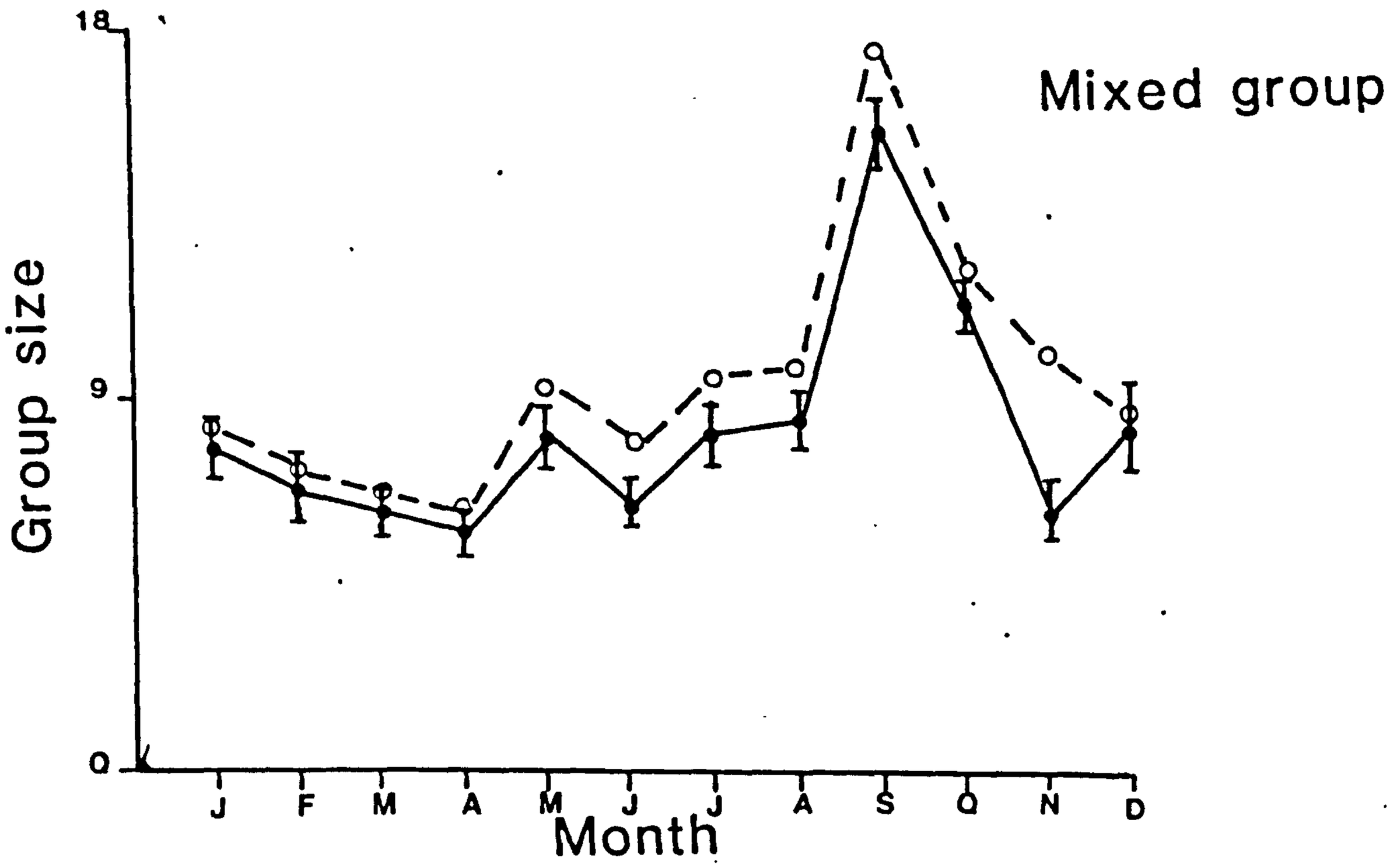


Fig. 3.2 Changes in typical o—o and mean ●—● group sizes during the year for (a) male, (b) female and (c) mixed groups. Bars indicate standard errors of means.

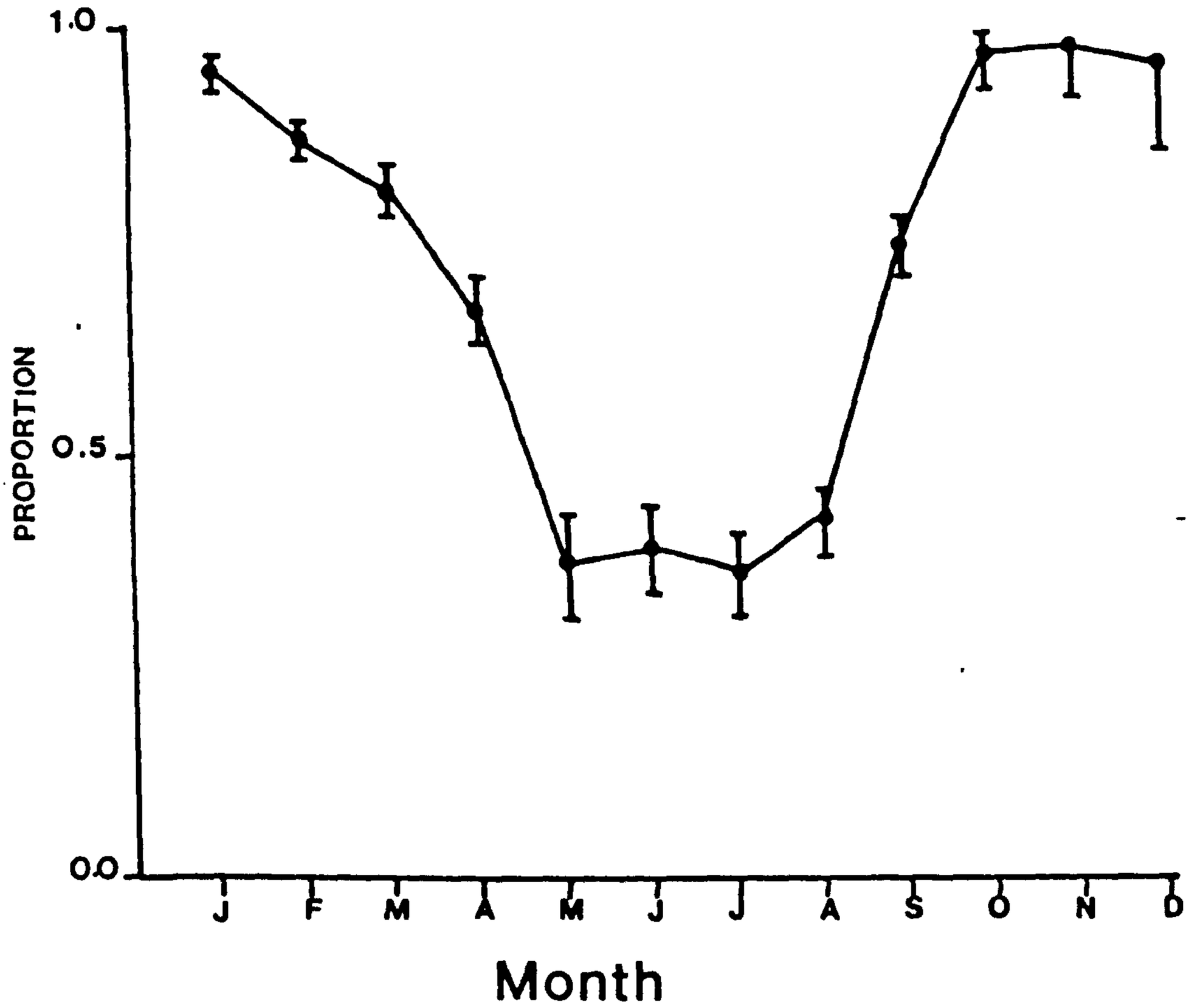


Fig. 3.3 The proportion of adult males in mixed groups throughout the year. The vertical lines indicate standard errors.

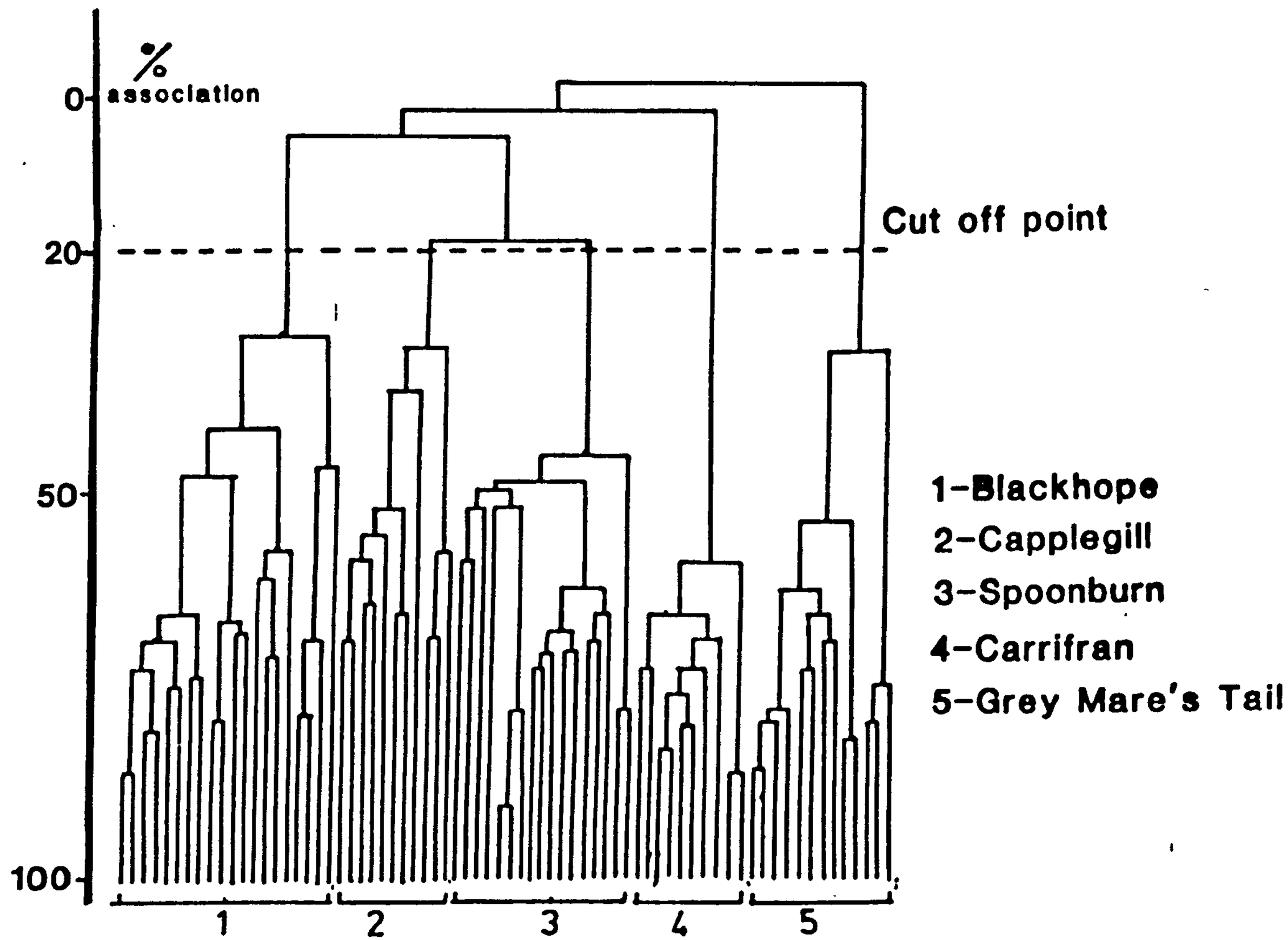


Fig. 3.4 Dendrogram indicating the frequency with which adult goats associated between January 1980 and October 1981, excluding sightings of males during the rut.

observed in the field during this study and by Bullock (1982) between 1977 and 1979 in the Moffat hills. Each heft was named after the watershed it was centred on. When 1980 kids were included in the analysis the overall picture of grouping remained the same, with the same five major units being distinguished (Fig. 3.5).

Within each major grouping in the dendrogram there are subgroups of goats which are closely associated. These are groups of females and their kids and also groups of adult males. The association of females and kids in the Blackhope heft was compared for each season. Fig. 3.6 shows that, except for these mother-daughter associations, no other permanent subgroupings of females within hefts could be recognised from the dendrograms or in the field during this study. Similar mother daughter associations were recognised in other hefts. Mother-daughter associations are discussed in more detail in Chapter 4.

3.3.3 Home range area

Cumulative area plots showed that for individual goats the normal home range area appeared to reach an asymptote after approximately 50 sightings over an eighteen month period (Fig. 3.7). It was assumed that when an individual was recorded on more than 50 occasions during the study period an accurate estimate of home range size had been obtained.

Total home range areas varied between 145 and 1023 hectares. Some of the variation depended on the sex of the individual and to

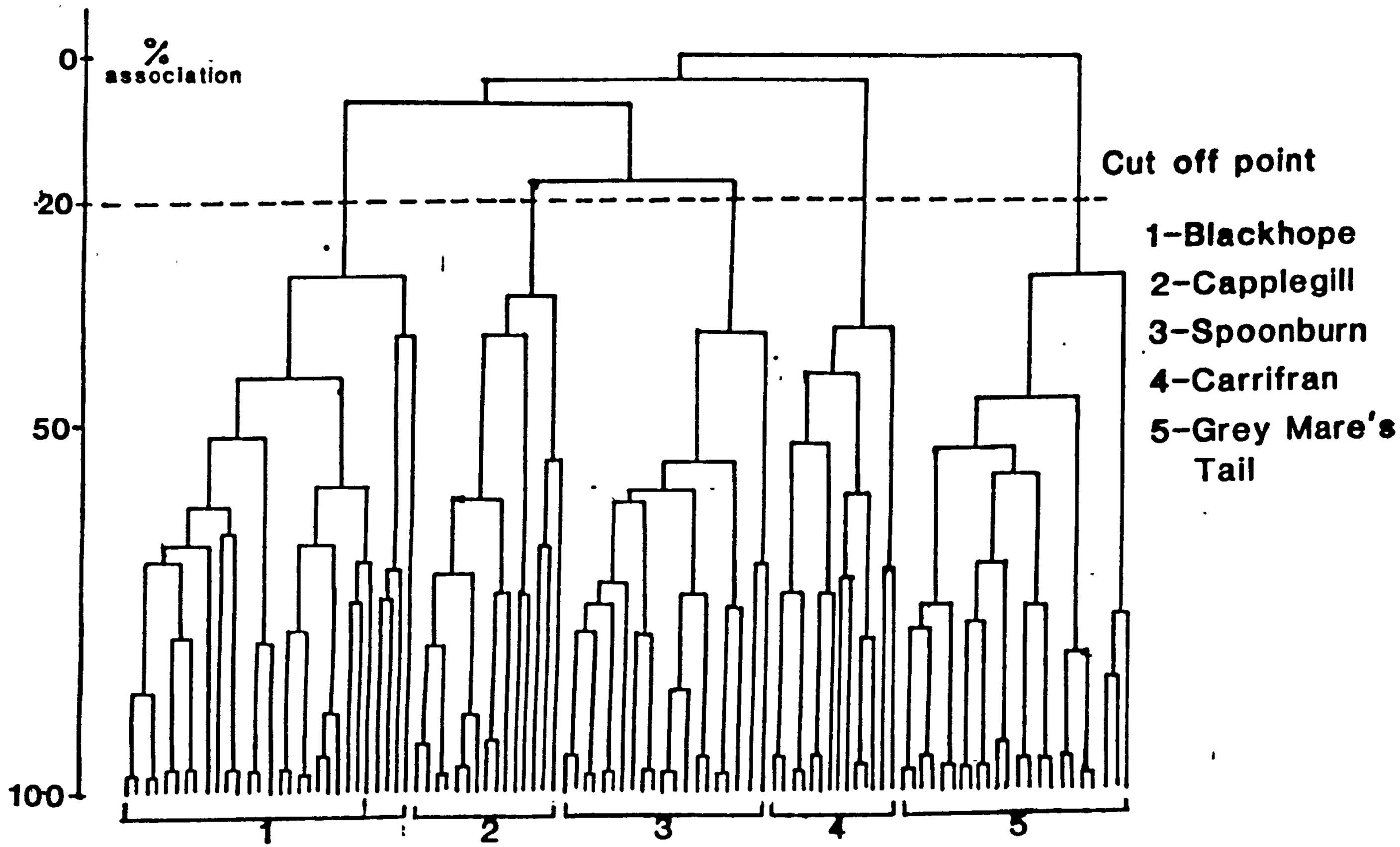


Fig. 3.5 As Fig. 3.4 but including kids born in 1980.

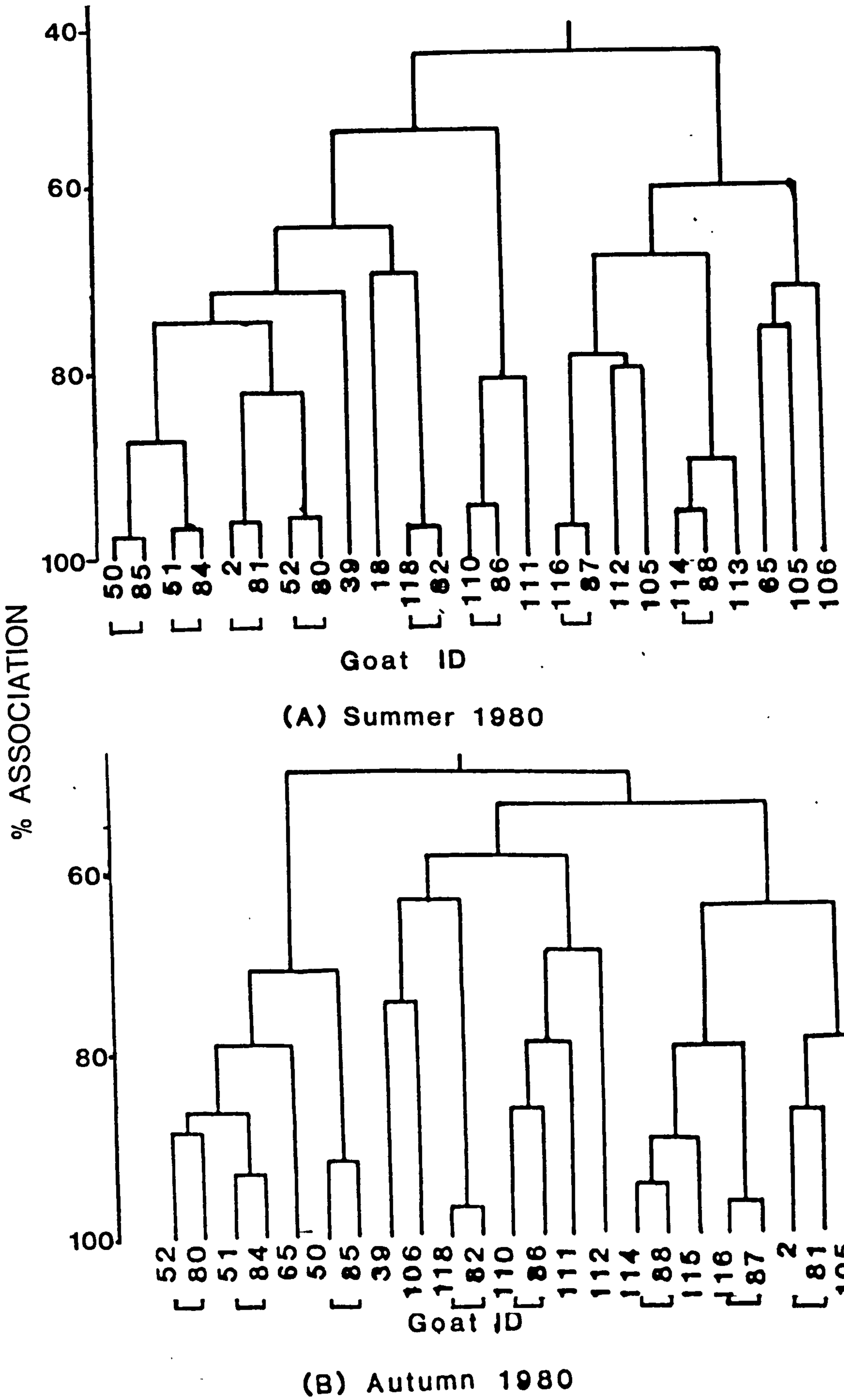
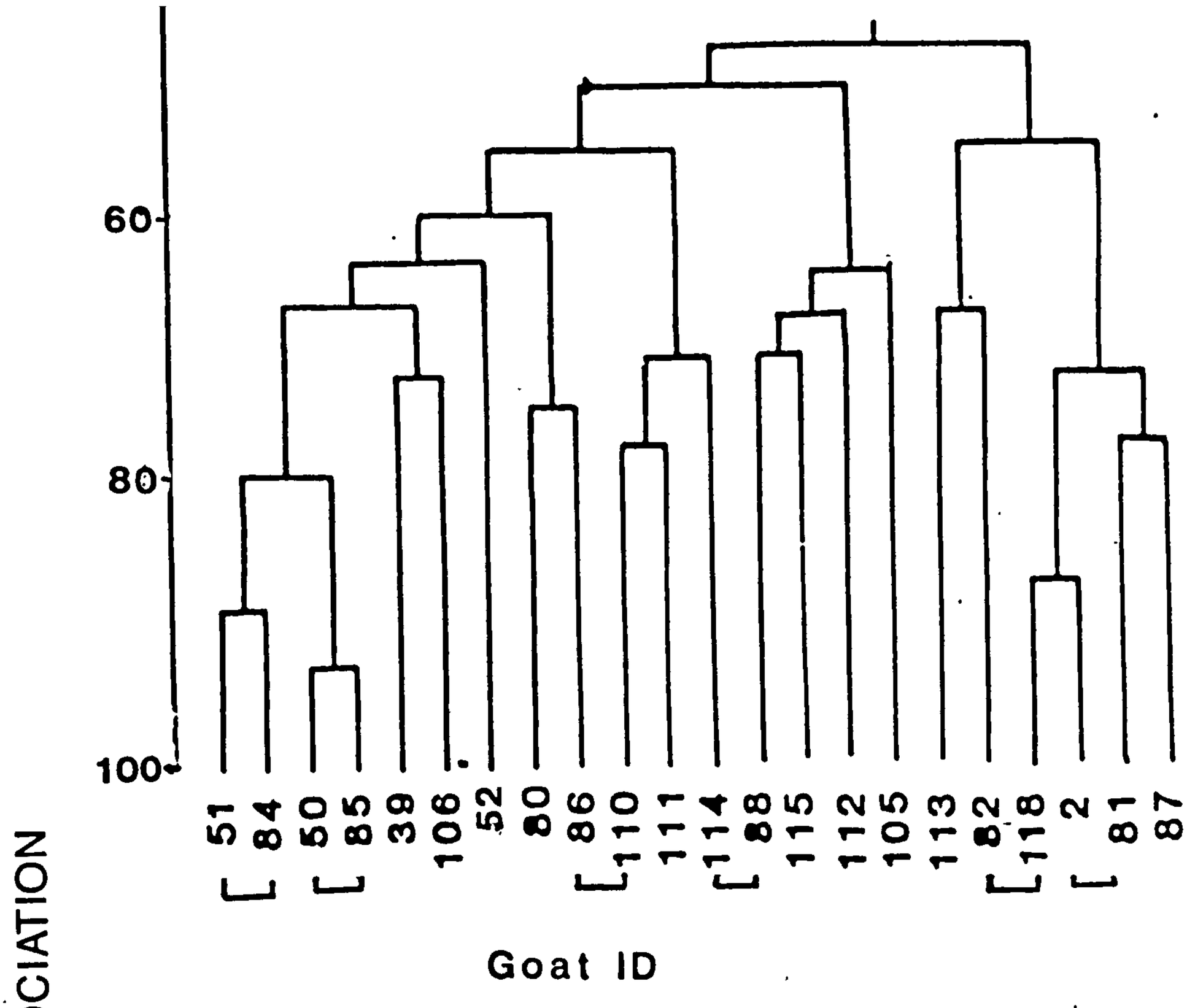
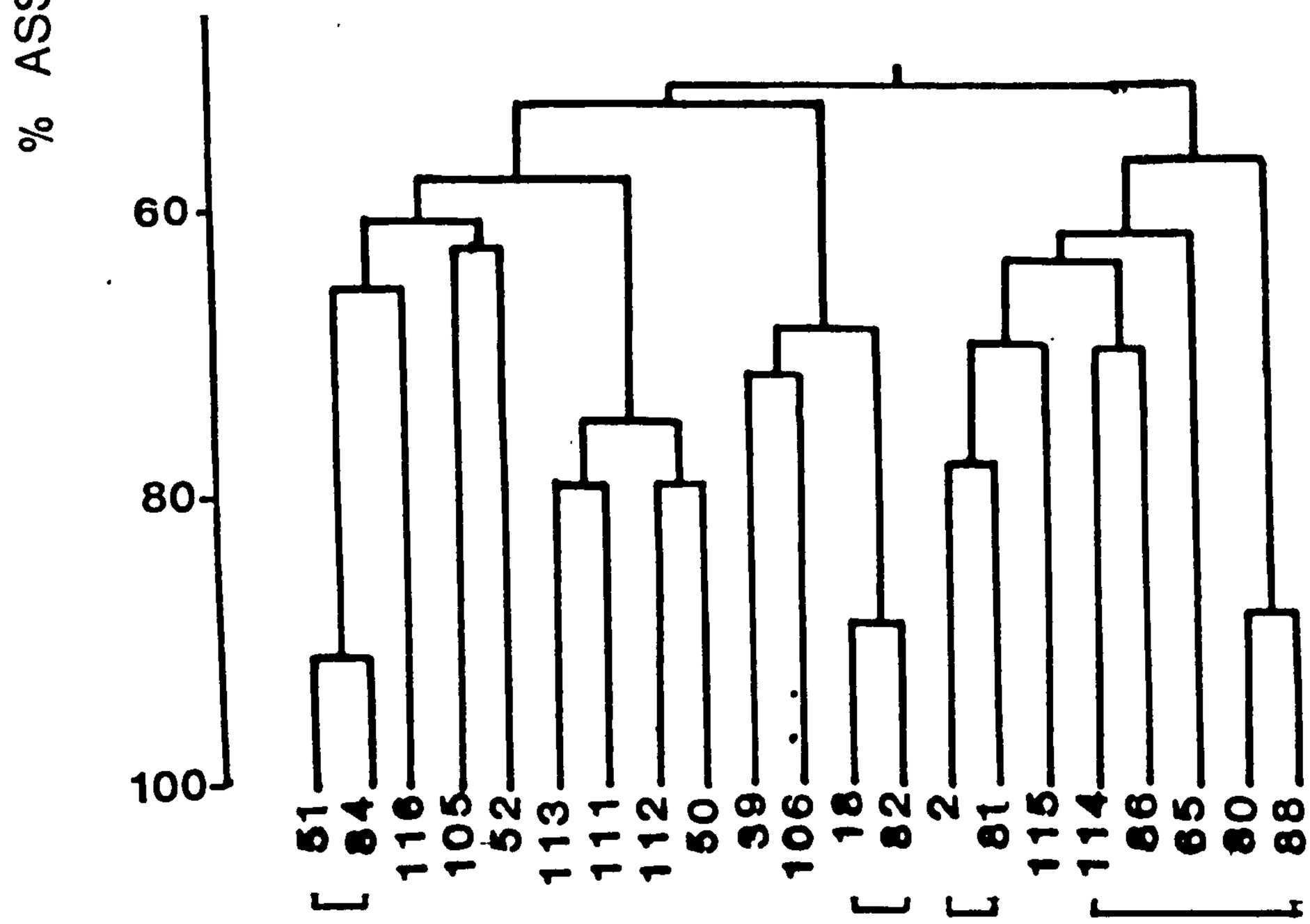


Fig. 3.6 Dendrogram indicating the frequency of association of females and their 1980 kids (relationships are indicated by brackets) in the Blackhope heft during (A) summer 1980, (B) autumn 1980, (C) winter 19881 and (D) spring 1981



(C) Winter 1980/1981



(D) Spring 1981

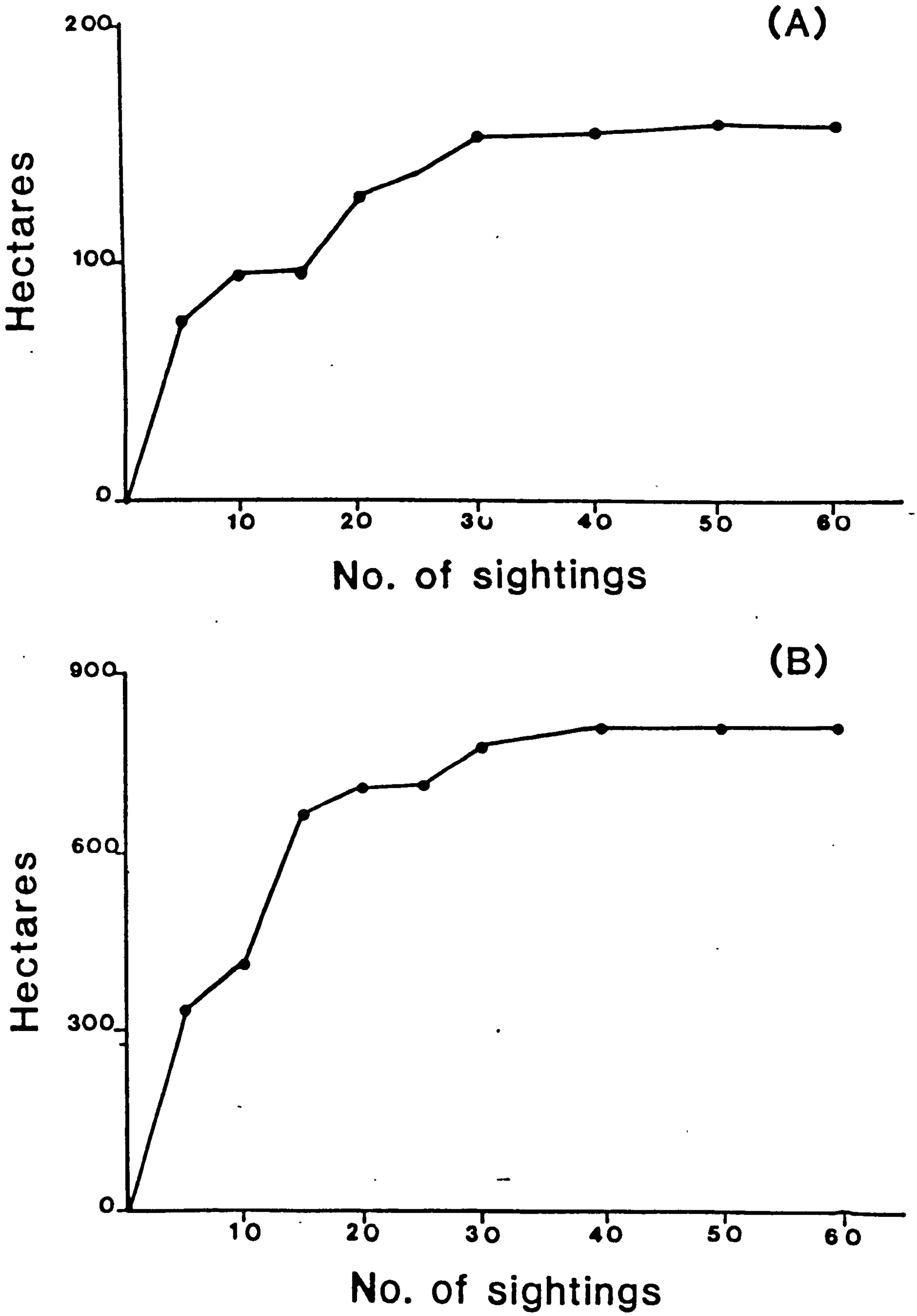


Fig.3.7 Cumulative total home range area plots for (A) female 36 belonging to the Spoonburn heft and (B) male 32 belonging to the Carrifran heft, from observations made over 18 months.

which heft it belonged (Table 3.1). Adult males always had larger total home ranges than females from the same heft. This was because males moved between hefts during the rut (see Chapter 5). There was no significant difference between the size of normal home ranges for males and females from the same heft (Table 3.1).

The sizes and locations of the home ranges of kids were the same as their mothers' during their first year of life. Females born in 1978 and 1979 still occupied the same range as their mothers in 1981 (Fig. 3.8). Most males known from birth also remained within the limits of their natal heft except during the rut (Fig. 3.9). There were three exceptions to this: male 33 was born in the Carrifran heft in 1978. After the 1980 rut he did not return to it but remained in the Spoonburn heft (Fig. 3.10). Two others, male 131 and male 133, both born in the Carrifran heft in 1980, moved to the Spoonburn heft after the 1981 rut rather than returning to their natal heft (Fig. 3.11 and 3.12.)

3.3.4 Home range overlap

All individuals within the same heft had highly overlapping home ranges, while the degree of overlap between individuals from different hefts was much lower (Table 3.2 and Fig. 3.13). However, the home ranges of goats belonging to the Capplegill heft did overlap to a certain extent with those of animals from the Blackhope and Spoonburn hefts (Fig. 3.14). It can be seen from Fig. 3.15 that the Capplegill goats made a seasonal migration between the forestry plantation at Craigieburn and the Blackhope and Spoonburn

	Home range in hectares								
	Females			Males					
				(a)			(b)		
Heft	$\bar{x}$	sd.	n	$\bar{x}$	sd.	n	$\bar{x}$	sd.	n
Blackhope	635	173	15	890	212	5	641	78	5
Capplegill	821	179	7	1031	131	3	851	71	3
Spoonburn	324	126	13	763	112	5	326	72	5
Carrifran	238	73	7	943	-	2	235	-	2
Grey Mare's Tail	295	50	10	300	14	3	300	14	3

Table 3.1

Mean home range size of adult female and male goats. Male (a): all sightings; Male (b) excludes sightings during September and October.

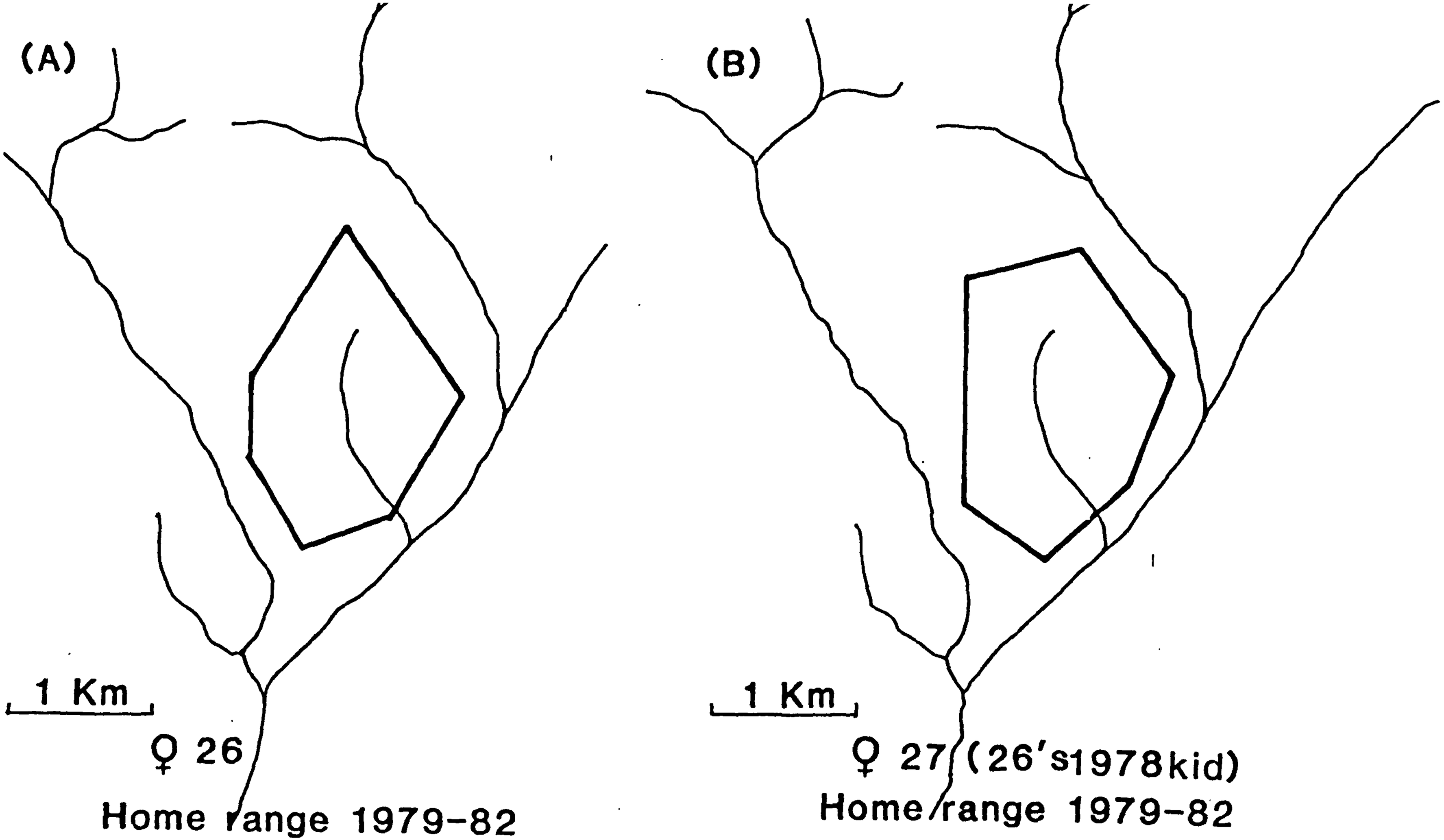


Fig. 3.8 An example of the total home ranges of a female (female 26) and her daughter (female 27, born in 1978).

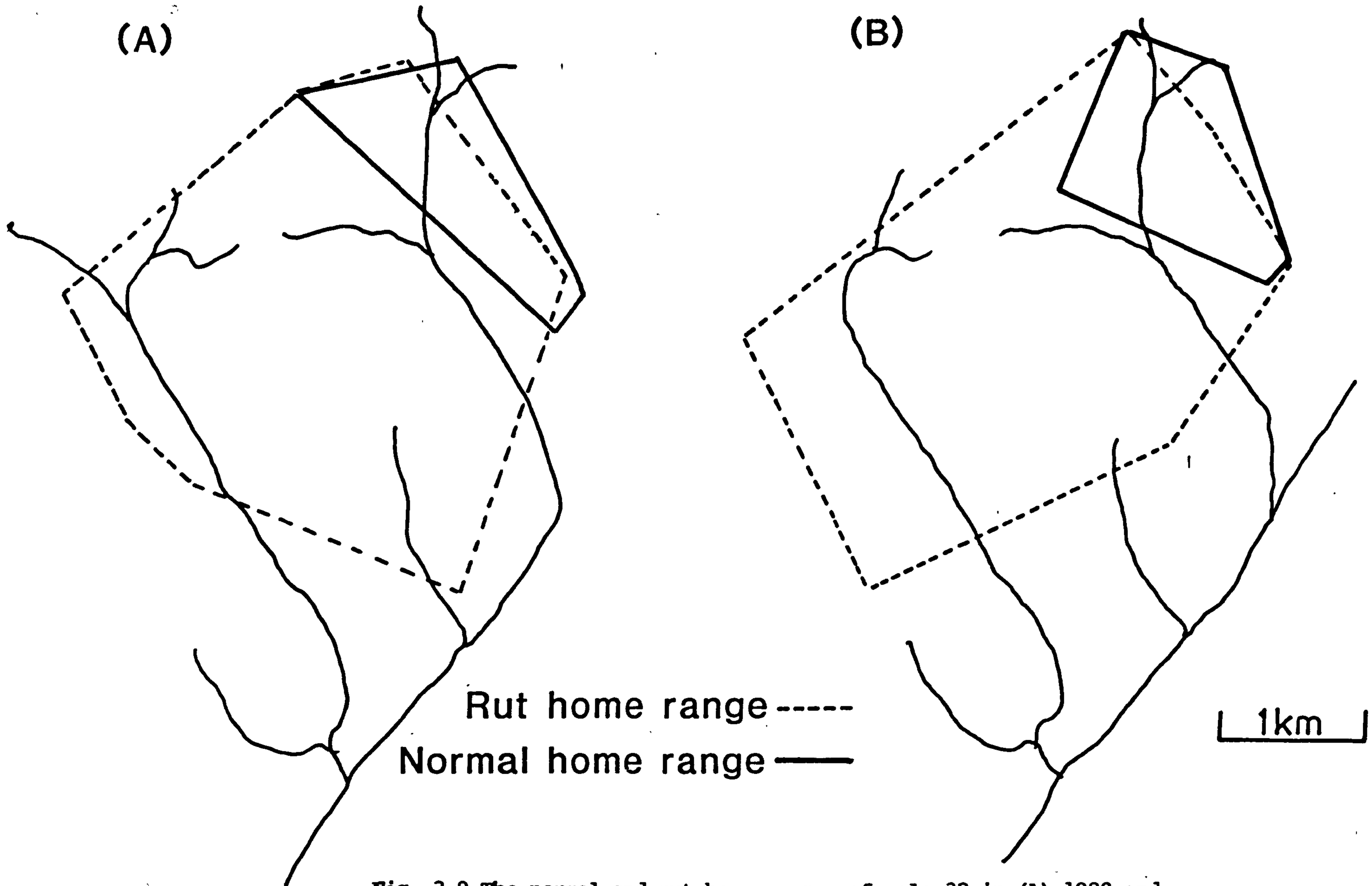


Fig. 3.9 The normal and rut home ranges of male 32 in (A) 1980 and (B) 1981.

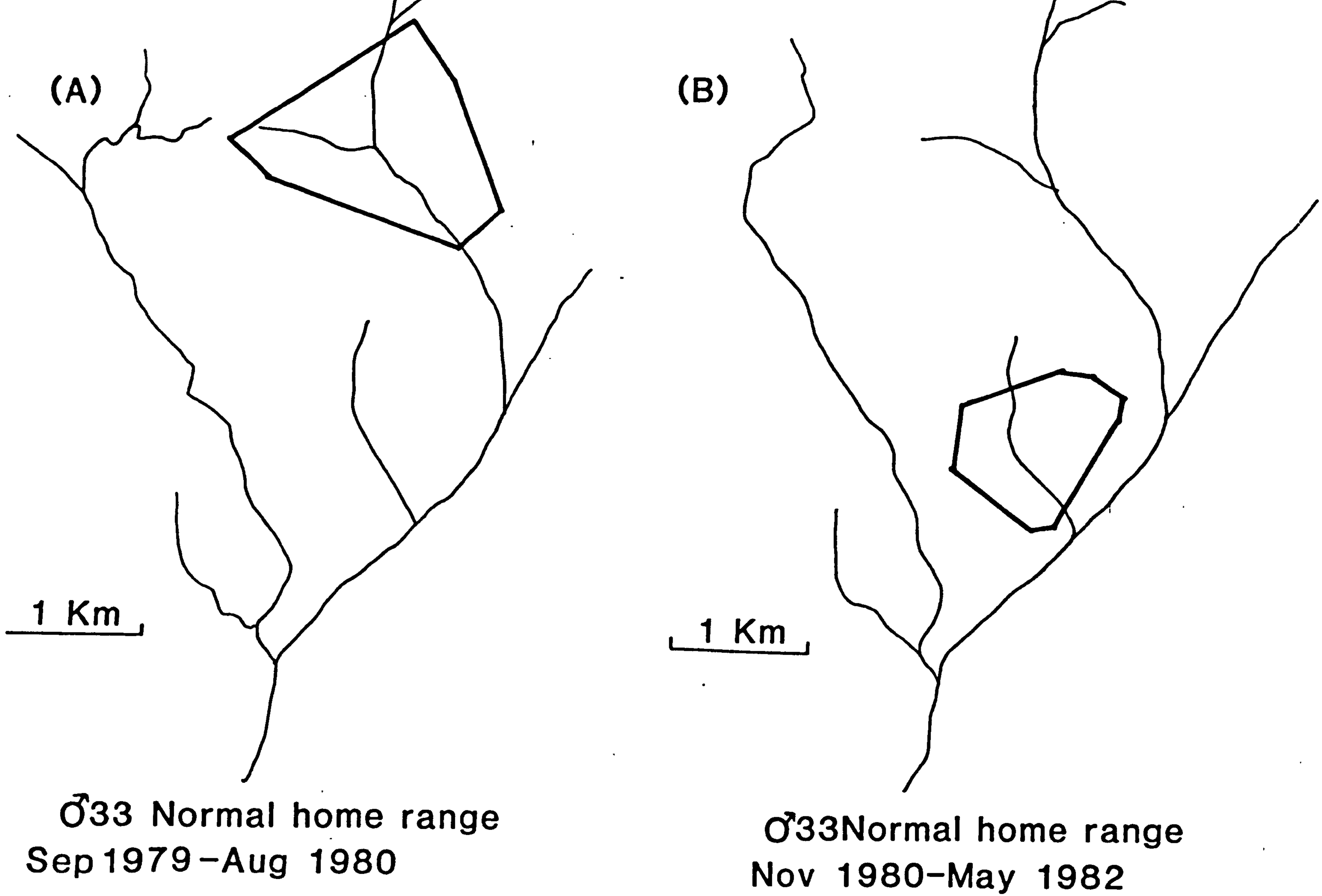


Fig. 3.10 Change in location of male 33's normal home range.

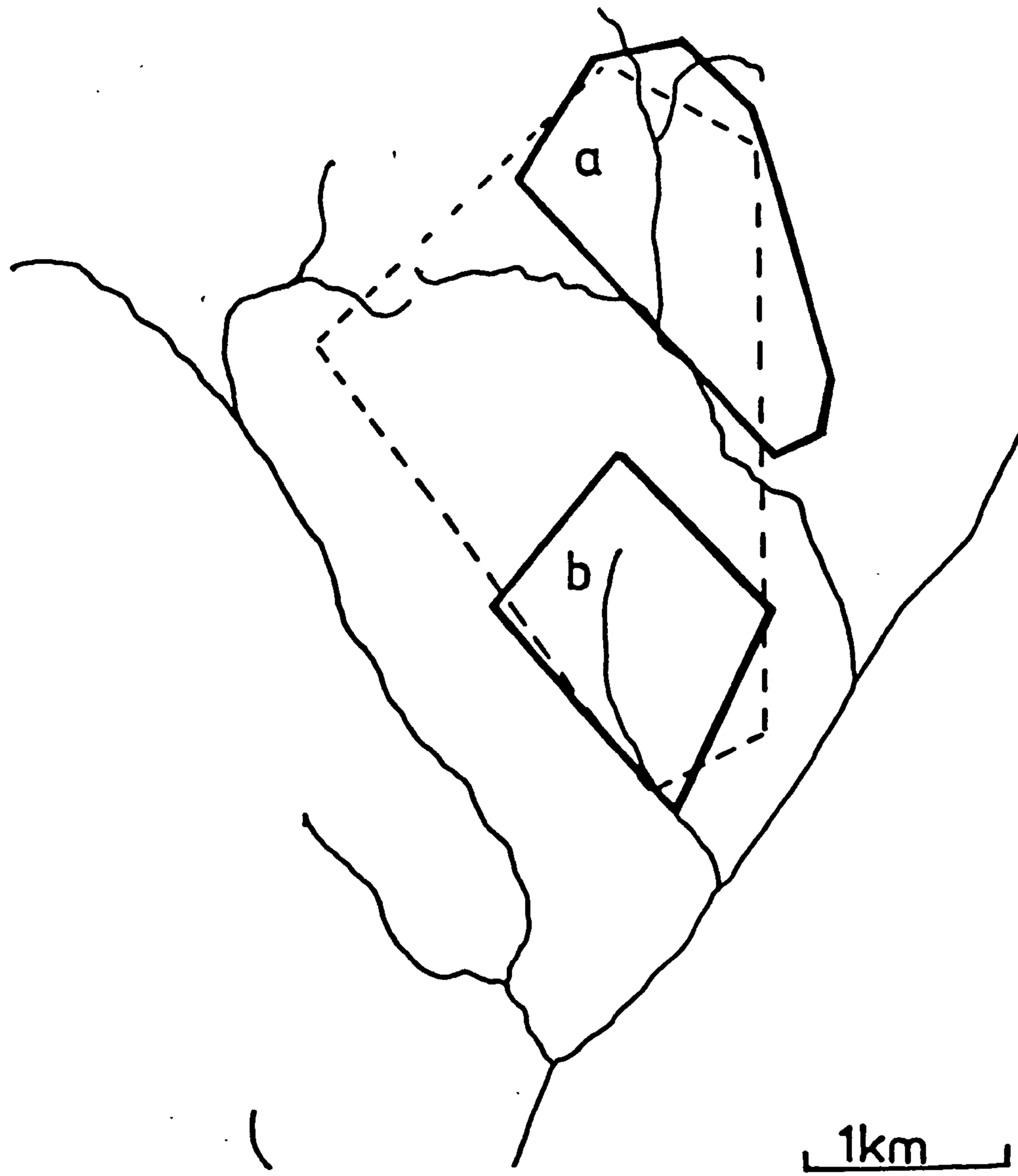


Fig. 3.11 Change in location of the normal home range of male 131. a = normal home range prior to October 1981, b = normal home range after 1981 rut. The dashed line indicates the extent of the 1981 rut range.

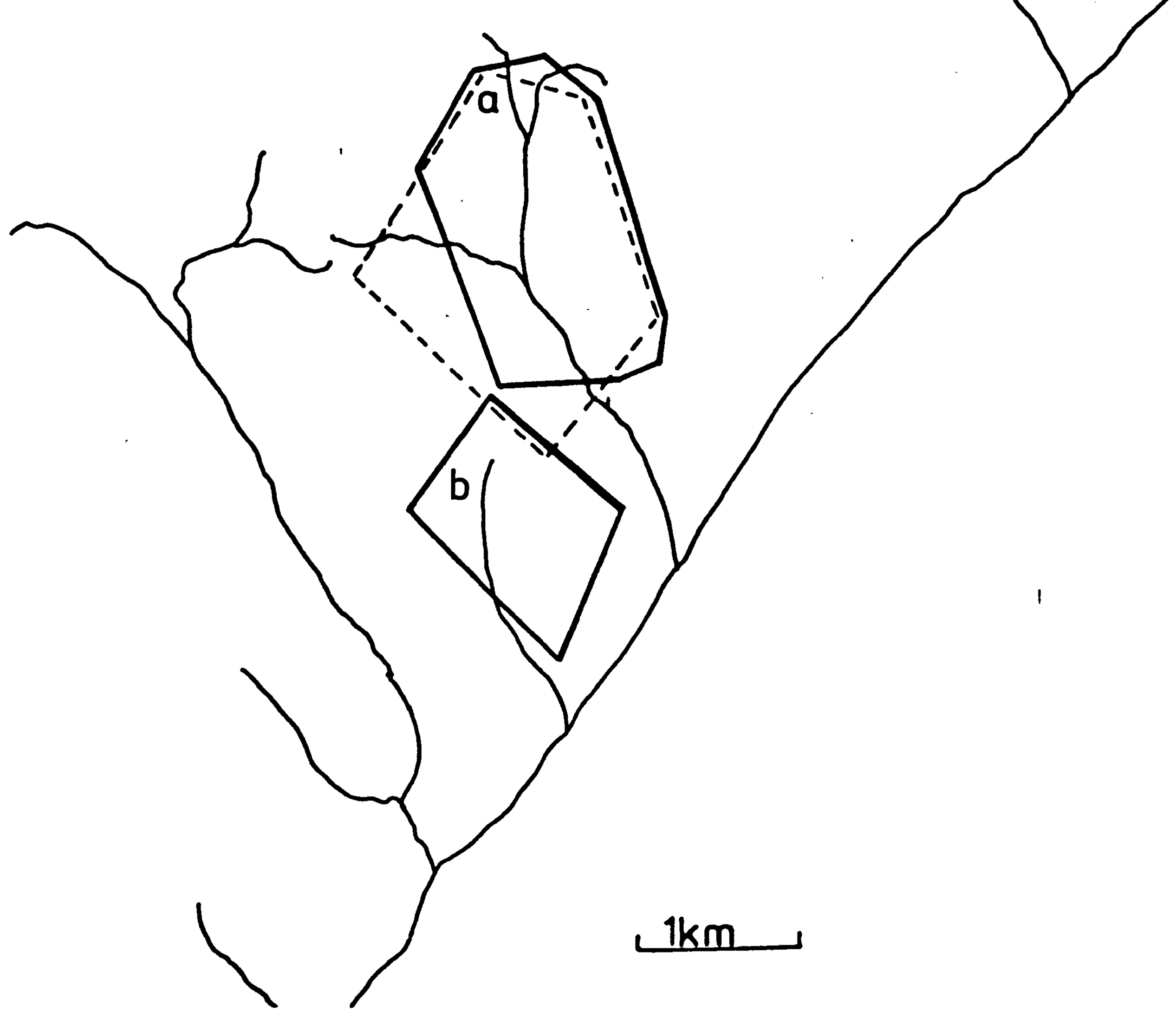


Fig. 3.12 Change in location of male 133's normal home range. a = normal home range prior to October 1981, b= normal home range after the 1981 rut.

		% Overlap Range	Mean
Carrifran	Carrifran	52.4-100	78.4
	Spoonburn	0.0-29.4	10.3
	Blackhope	0.0-27.3	12.7
	Capplegill	16.2-68.4	29.2
	Grey Mare's Tail	0	0
Spoonburn	Carrifran	2.6-22.8	8.8
	Spoonburn	52.3-100	78.4
	Blackhope	0.0-57.9	20.2
	Capplegill	43.2-82.1	66.4
	Grey Mare's Tail	0	0
Blackhope	Carrifran	0.0-15.2	5.5
	Spoonburn	15.0-35.0	28.2
	Blackhope	67.5-100	83.7
	Capplegill	48.0-65.0	59.4
	Grey Mare's Tail	0	0
Capplegill	Carrifran	0.0-10.1	5.1
	Spoonburn	15.0-35.0	28.2
	Blackhope	67.5-100	83.7
	Capplegill	75.9-95.2	87.2
	Grey Mare's Tail	0	0
Grey Mare's Tail	Carrifran	0	0
	Spoonburn	0	0
	Blackhope	0	0
	Capplegill	0	0
	Grey Mare's Tail	83.0-100	97.3

Table 3.2

The mean % overlap of the home range of all goats from one heft with each other and with all the individuals from each different heft.

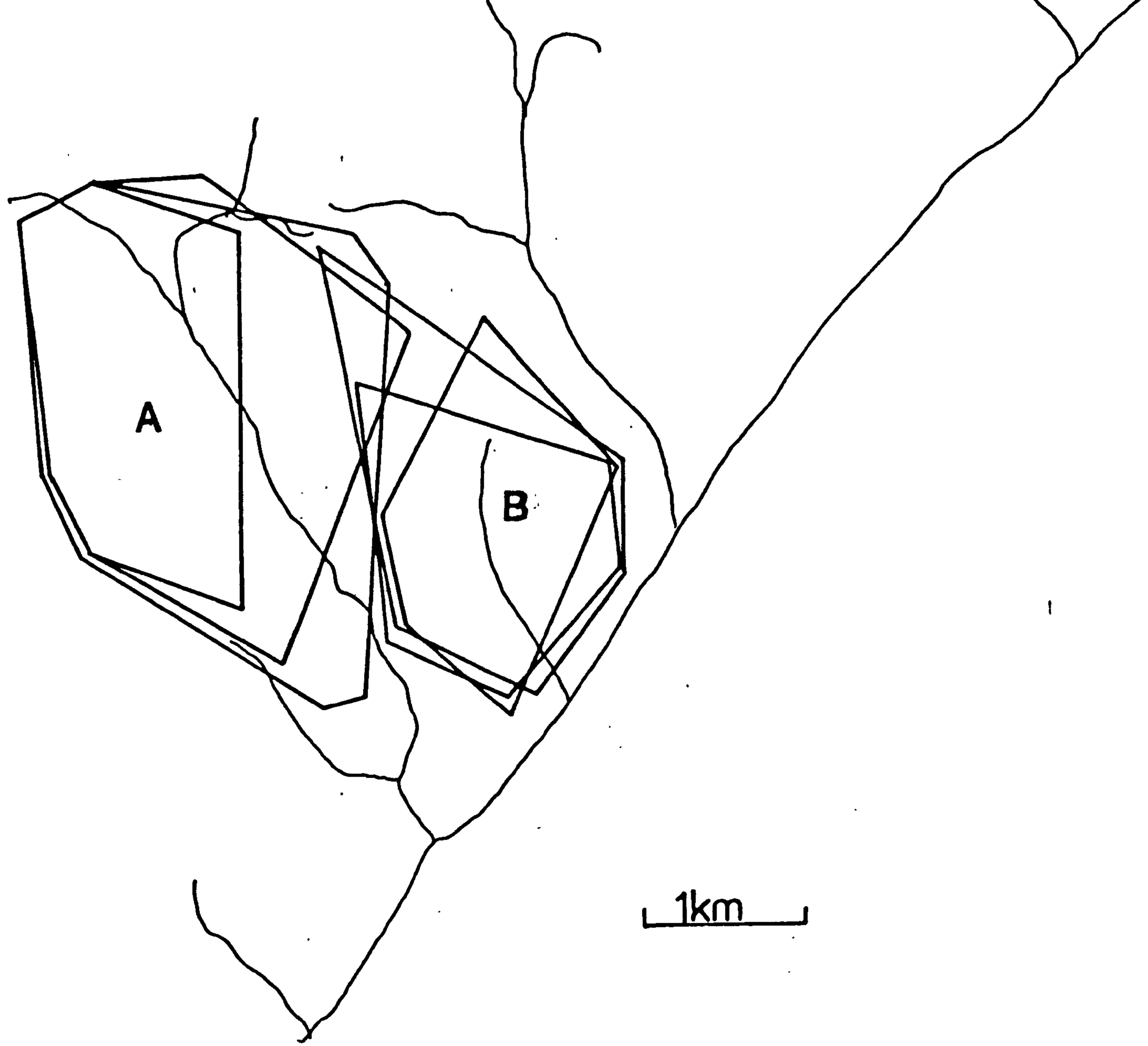


Fig. 3.13 Overlap of the total home ranges of (A) three Blackhope females and (B) three Spoonburn females.

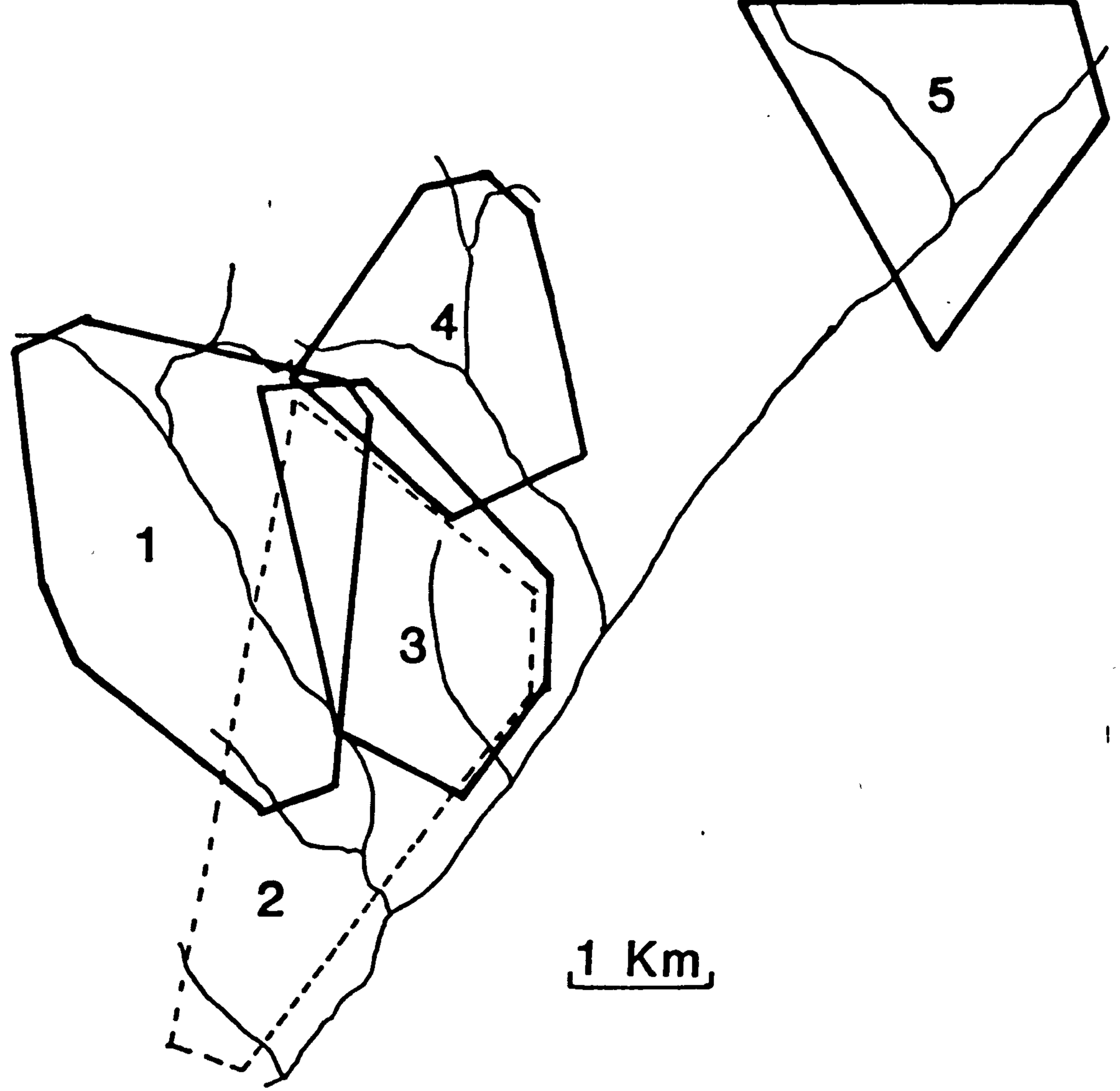


Fig. 3.14 A plot indicating the location and outer limits of each heft range (excluding males during rut): 1)Blackhope, 2)Capplegill, 3)Spoonburn, 4)Carrifran, 5)Grey Mare's Tail.

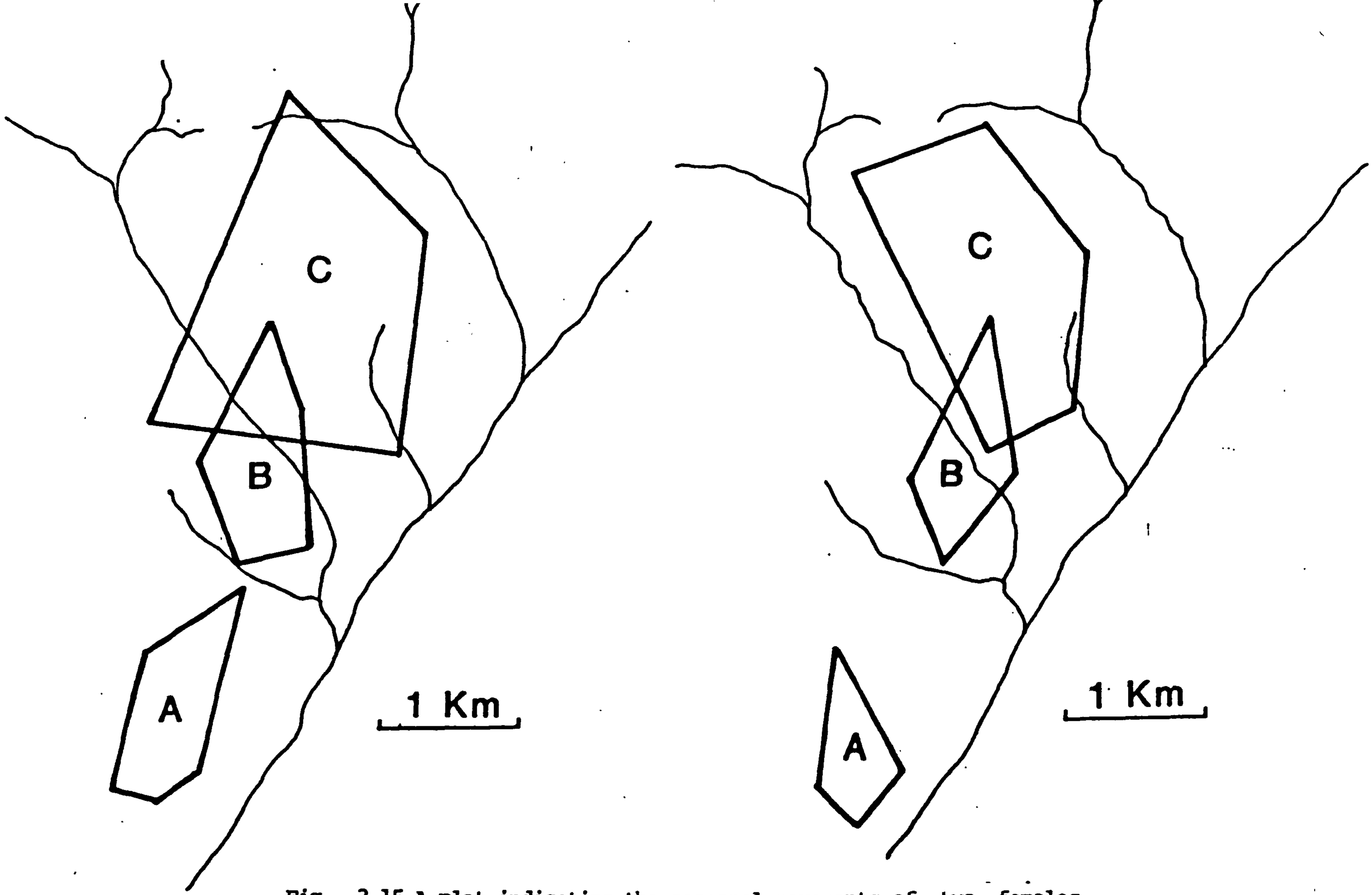


Fig. 3.15 A plot indicating the seasonal movements of two females belonging to the Capplegill heft. A = December - June, B = July and August, C = September and November.

hefts. These goats spent most of the winter months in the area by Roundstone Foot burn but during the summer they moved to the Capplegill burn, and just prior to the start of the rut they were found in the range of the Blackhope or Spoonburn hefts. After the rut the females moved back to the forestry plantation first and then in late winter the males followed. The extent of their movement in the Craigieburn plantation is not known and it is likely that their late winter and spring range is larger than that indicated in Fig. 3.15

The outer limits of the home ranges of individuals belonging to the same heft tended to coincide with each other on the peaks of hills dividing watersheds or at high stockproof fencing. The boundaries of each heft, except those of the Capplegill heft, were clearly defined and there was little mixing between individual females from different hefts. There was no evidence of territorial marking. Large groups made up of Capplegill and Blackhope, and Capplegill and Spoonburn goats were occasionally seen during the rut. When individuals from neighbouring hefts met they tended to ignore each other. However fighting between females from the Capplegill and Spoonburn hefts was observed twice, in 1979 and 1980. On both occasions it was probably the first time these groups of females had met since the previous rut.

3.4 DISCUSSION

The fluctuations in the size of all types of groups of goats

observed during this study were similar to those observed by Crook (1969) and Bullock (1982). The small size of female and mixed groups during the spring reflects the behaviour of females during this period. Females tended to isolate themselves from other goats just prior to parturation and sometimes remained away from other females until their kids were several days old (see Chapter 4). At this time of year the quality and quantity of forage is very low and feral goats, in common with hill sheep, may be suffering a negative energy balance (Eadie 1970). Appleby (1980) showed that feeding interference between ungulates is greater in larger groups. Therefore a decrease in group size may be expected in order to reduce intra-specific competition.

Except during the spring, mean female group sizes were larger than for males. This is probably a result of the skewed sex ratio in favour of females in the population. During much of the study period there was a maximum of five adult males in any one heft; male groups containing more than five individuals were unlikely outside the rut.

The increase in the size of female groups during the summer occured when females banded together after kidding. During this period forage is abundant so feeding interference is probably low. There may also be energetic advantages for lactating females, during this period of high metabolic demands, to being in a large group. Maisels (1982) has shown that as group size in feral goats increases group vigilance increases and the amount of time any individual is vigilant decreases, increasing the amount of time available for feeding.

The increase in male group size in August just prior to the rut was due to the Capplegill males leaving the forestry plantation and associating with the Blackhope males.

The peak in the size of mixed groups in September occurs at the begining of the rut. Males join these groups in search of oestrous females (Chapter 5). However it is less clear why females join these groups. It is known that dominant males tend to remain in groups where oestrous females are present and visit fewer groups than do smaller subordinate males. Assuming females prefer to mate with dominant males, females should remain in groups where such males are present until they have been mated.

Sexual segregation of feral goats has been recorded in Britain (McDougall 1975, Boyd 1981) and in New Zealand (Riney and Caughley 1959). However some tropical populations of feral goats show little sexual segregation (Yocum 1967, Gould 1979). Segregation of the sexes also occurrs in many wild ovids and cervids (Geist 1971, Mitchell et al. 1977, Shank 1979) and various explanations of this based on altruism (Geist and Petocz 1977) or difference in the nutritional requirements of each sex have been put forward and will be considered in the concluding discussion.

The general social organisation of the Moffat hills population, in common with other populations (McDougall 1975, Boyd 1981) is based on groups of females, their offspring and associated males which together form discrete hefts. Movement of individuals between hefts is largely restricted to males during the breeding season. The exception to this was the Capplegill heft which made seasonal movements between different areas. Bighorn sheep, Ovis canadensis,

use several different home ranges during the year (Geist 1971), but this has not been previously documented in other populations of feral goats. It is unclear why only the Capplegill heft made seasonal movements while the other hefts were more sedentary. However all female offspring used the same home range, and in the case of the Capplegill heft made the same seasonal movements, as their mothers. This, combined with the fact that no female was observed to change hefts during the study suggests that patterns of range use by particular hefts are unlikely to change rapidly. The patterns of range use observed today may have been established several generations ago when husbandry practices and land use by man differed from those seen today. For example the area now covered by forestry plantation between Carrifran and the Grey Mare's Tail was used by goats before 1969 but they were removed prior to planting in that year. Parts of the Craigieburn plantation have been established for over 50 years and it is known that goats did occupy some of that land prior to planting. However, it is uncertain whether these goats were shot or driven out prior to planting. The lack of movement of females between hefts also indicates that females belonging to the same heft were more closely related than females from different hefts.

CHAPTER 4

MOTHER-OFFSPRING RELATIONSHIPS

4.1 INTRODUCTION

Ungulates are the most precocial of all mammals. Most young ungulates can stand, and are capable of walking away from their mothers shortly after birth. It is important that the bond between mother and offspring is formed rapidly. Most of the work on mother-offspring relationships in goats has focused on this aspect of their behaviour. Maternal attachment in goats appears to be specific, rapidly formed, and fairly stable. It was originally thought to be analogous to imprinting in birds (Klopfer et al. 1964, Bateson 1966, Hess 1973) as there seems to be a sensitive postpartum period for the formation of maternal attatchment (Blauvelt 1955, Collias 1956, Herscher et al. 1963, Klopfer et al. 1964). Gubernick (1981), has shown that rather than being a form of imprinting female goats actually label their kids via their milk and by licking them.

Female feral goats can certainly recognise their own kids shortly after birth and will reject alien kids (Greig 1969, Rudge 1970, McDougall 1972, Munton 1975). This ability is especially important in goats because they tend to hide their young shortly after birth, returning at intervals during the day to suckle them (Rudge 1970 , McDougall 1972, Munton 1975). This behaviour has been

termed "lying out" by Walther (1961) who developed the concept of two distinct forms of maternal-infant behaviour in ungulates. These are the "Ablieger Typ" and the "Nachfolger Typ", which are known in English as the "hiders" and "followers". The wildebeest, whose young follow their mothers from birth (Talbot and Talbot 1963), is an example of the follower type whereas young reedbuck, hiders, may lie-out until four months of age (Jungius 1970). It is unclear whether a female goat actually leads her kid to a hiding place or, like true hider species (Leuthold 1977), the young determines the hiding place. The lying out phase in goats appears to be somewhat variable, ranging from the first three days of life (Rudge 1970) up to six weeks of age (McDougall 1972). There is little information on how frequently females return to their kids, or about their suckling behaviour. Munton (1975) noticed a decline in the length of suckling bouts during the summer. Weaning probably occurs in late summer (McDougall 1975).

The aim of the present study was to obtain quantitative data on lying out and suckling behaviour, and also to obtain information on kidding and on the maintenance of the mother-offspring bond.

4.2 METHODS

Data were collected by direct observation using the sampling techniques described in Chapter 1. A total of 165 hours of observation were made of mothers and offspring during spring and summer 1980 and 77 hours in spring 1981.

In order to establish whether the kid or mother determines

lying out, detailed observations were made. Four possible categories of the start of lying out were considered:

1) Kid walks away from mother and lies down.

2) Kid is either walking, standing, or playing near the mother who is feeding and the kid lies down as the mother moves away.

3) Mother walks to suitable lying out spot followed by kid, who lies down, and mother walks away (Rudge 1969).

4) Kid and mother lying together, and then mother gets up and walks away.

It was assumed that in categories 1 and 2 the kid determined the lying out spot and that the mother determined the lying out location in categories 3 and 4.

Data on mother-kid distance and association between females and their 1980 offspring were obtained from spot sightings (see Chapter 1). The percentage association between mother and offspring was calculated for each calendar month, where percentage association is defined as:

$$\text{Percentage association} = \frac{\text{No. of times mother and kid seen in same group}}{\text{No. of times seen in separate groups} + \text{No. of times seen in same group}} \times 100$$

Mothers of male and female kids were considered separately and then further subdivided into those that did and did not rear a kid in 1981. Data on females or kids which died were not included for the

month in which they died. The maintenance of proximity between mother and offspring was examined by recording the number of movements the mother and kid made towards each other during focal pair observation periods.

4.3 RESULTS

4.3.1 Kidding

Prior to kidding females tend to leave their normal group and are often seen separated from their previous year's kid (see 4.3.4). Only one female was observed actually kidding. Unfortunately weather conditions (low cloud and rain) and the position of the goat (approximately 350m away) made observation difficult. The female was first seen at 11.15hrs on 15th April 1980, lying partially on her side in a small gully. There were no obvious signs of physical exertion. The female turned and sniffed her hind quarters several times. Twenty minutes later she appeared to strain as the kid appeared. The mother immediately stood up and began to lick the kid vigorously. The kid lay motionless for approximately two minutes and then attempted to stand. At this point the clouds came down and obscured the goats from view. Thirty minutes later the kid was observed standing and attempting to suck.

Most females appear to choose secluded, sheltered locations to kid. Nineteen females were observed with kids only a few hours old (kids still wet or very unsteady on their legs). Most of these were

in gullies or in deep heather (Table 4.1).

4.3.2 Lying out

Even during the first day of life kids are left lying out while their mothers feed. Table 4.2 shows that kids determined the lying out spot significantly more often than mothers. The mother was never seen to lead her kid to a suitable lying out spot. No female with a kid thought to be less than one day old was seen to move more than 100m away from her kid or to leave it for more than 2hrs. However, after this age, females would move up to 600m away from their kids and leave them for up to 9hrs 20mins. The length of time that females left their kids, and the distance they moved away, was very variable. Time ranged from 10 to 580 mins (mean=214.8mins, s.d.=164.2, n=32), and distance ranged from 20 to 600m (mean=177.2m, s.d.=164.5, n=32). There was no change in the length of time the kid was left, or in the distance the mother moved away as the kid got older (Figs. 4.1 and 4.2).

All kids less than one week old which were observed for more than four hours on any one day were seen to lie out. This dropped to 50% in the second week, 20% in the third and only 5% in the fourth week of life.

Kids tended to lie out in sheltered situations, but were not necessarily hidden from view. Only 55% (11/20) of the kids under one week old observed to lie out actually disappeared from sight. Most of the kids lay down in deep heather (45%, 9/20) or behind rocks (40%, 8/20), while the other three lay down in dips or hollows

	HABITAT TYPE			
	Gullies	Craigs	Deep Vegetation	Grass, Scree and Short dwarf shrub
No. Females	11	3	5	1
%	57	15	26	5
% Habitat type in study area	< 1	< 1	30	47

Table 4.1

Habitat types in which females were seen with kids less than one day old.

Initiation of lying out

Category	Number	%
1.Kid walks away	14	33
2.Kid lies down as mother walks away	16	38
3.Mother leads kid to lying out place (Rudge 1969)	0	0
4.Lying out together and mother walks away	12	28

Table 4.2

The frequency with which mother or kid determines lying out.

χ^2 comparing categories 1 and 2 against 3 and 4:
$\chi^2 = 3.85$, d.f.=1, $p<0.05$.

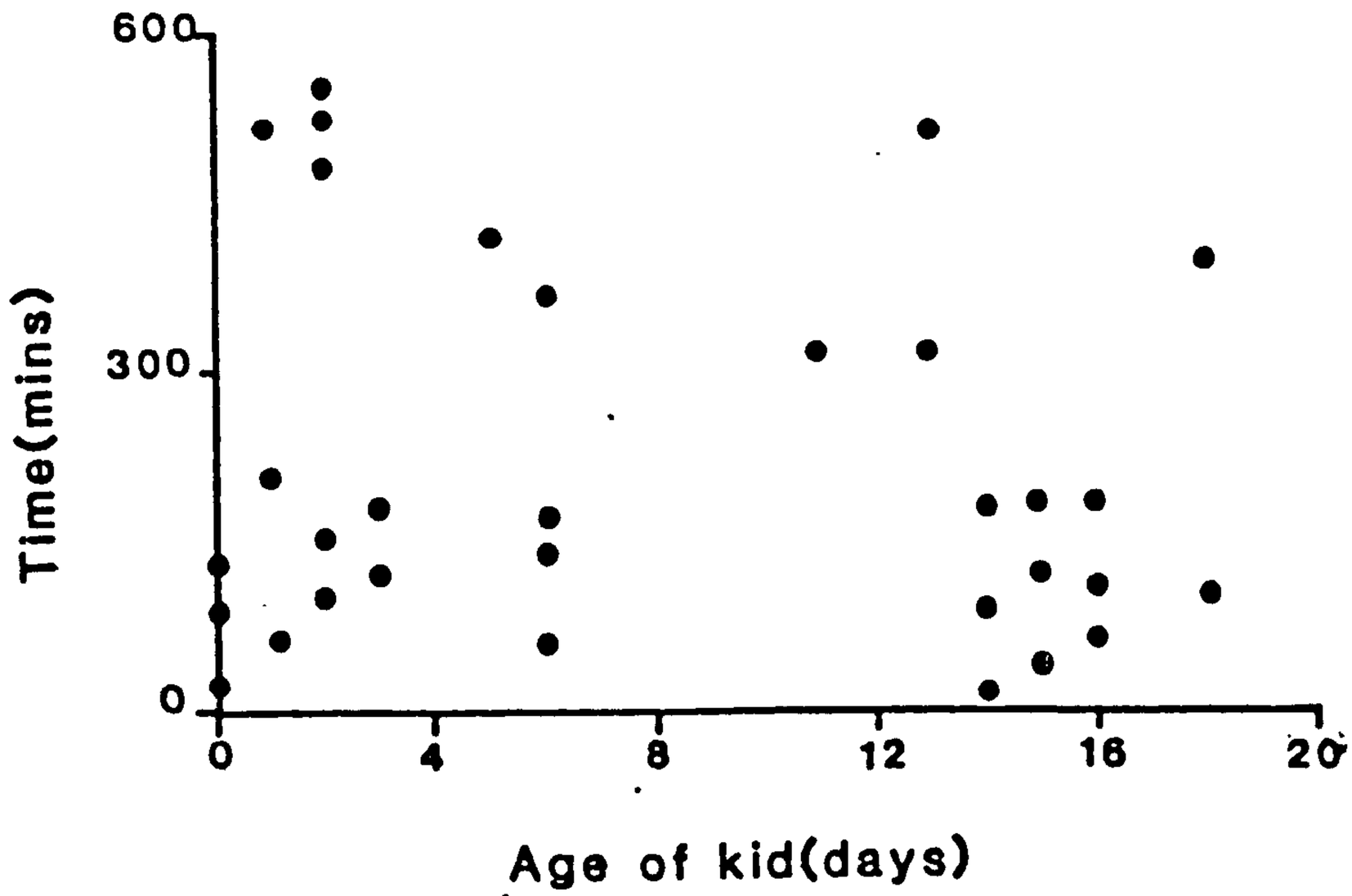


Fig. 4.1 Length of time that kids of various ages were left lying out by their mothers.

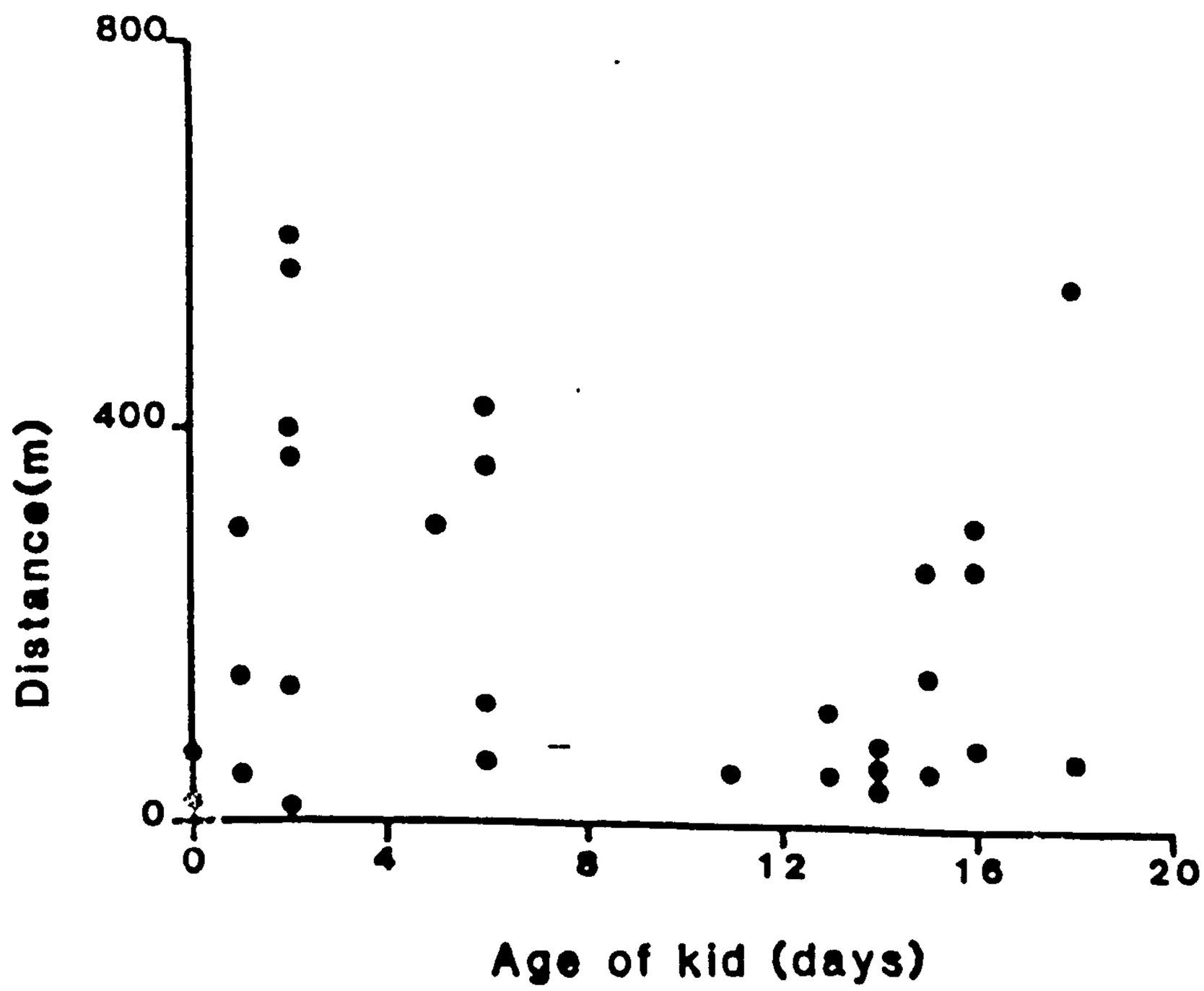


Fig. 4.2 Maximum distance between mother and kid during a lying out period.

on open grassland. During the first few days of life kids lie out alone but as they get older they tend to lie out with other kids. A maximum of eight kids were seen lying out together at any one time.

When a mother returned to her kid, she often began to call from some considerable distance. On hearing the female the kid would run to meet her. Kids would get up and run towards any calling female, and there was no evidence that either kids or their mothers could recognize each other by call alone. On five occasions a kid was observed to run towards a female who, after sniffing the kid, butted it away and continued to search for her own kid.

4.3.3 Suckling Behaviour

The normal position adopted for suckling is head-to-tail, the kid standing with its body at an acute angle to the female's. Occasionally the kid attempts to suck from behind, reaching between the mother's hindlegs. With young kids, females tend to lick the anal-genital region of the kid while it sucks. Both mother and kid stand while suckling, although older kids sometimes drop on their "knees" (carpel joints). Kids usually wag their tails vigorously while they suck. While sucking, kids push their noses upwards at intervals (bunting), which is thought to aid the milk flow (Leuthold 1977). As the young get older, bunting becomes more vigorous and appears to cause the female discomfort.

Kids often attempt to suck from females other than their own mothers. This is normally met with a horn threat or a butt from the female. However, one kid was seen to regularly suck from another

female. This female's own kid died at eight days of age and she suckled the second kid for approximately one month.

Suckling always occurred when a female returned to a kid that had been lying out, after the mother and kid had been disturbed, or occasionally after the kid had crossed some rough terrain to catch up with the female. Suckling was most frequent in early morning and late afternoon (Fig. 4.3). The frequency of suckling bouts decreased as the kids got older (Fig. 4.4). Male kids were suckled more frequently than female kids, but this difference was only significant in the first month of life (Mann-Whitney U-test $z= 1.72$, $n1=85$, $n2=25$, $p<0.05$). The mean suckling bout duration declined during the summer from 42 seconds in the first month of life to 18 seconds in month four and then increased again to 25 seconds in month five of life (Fig. 4.5). Fig. 4.6 shows that mean suckling bout duration was longer for male kids than female kids, although this difference was only significant during the first two months of life (month 1: $t=2.6$, $d.f.=121$, $p<0.05$; month 2: $t=2.5$, $d.f.=44$, $p<0.05$). There was no difference in mean suckling bout duration between mothers of different ages (Fig. 4.7). Mean time spent suckling per day (12hrs.) was calculated for each month by multiplying mean suckling bout duration by mean frequency of suckling. Fig. 4.8 suggests that male kids spent approximately three times more time sucking than female kids during their first two months of life (see 4.4).

Mothers tended to initiate most of the suckling bouts during the first day but kids initiated almost all bouts after the second day. Suckling bouts tended to be terminated more frequently by the

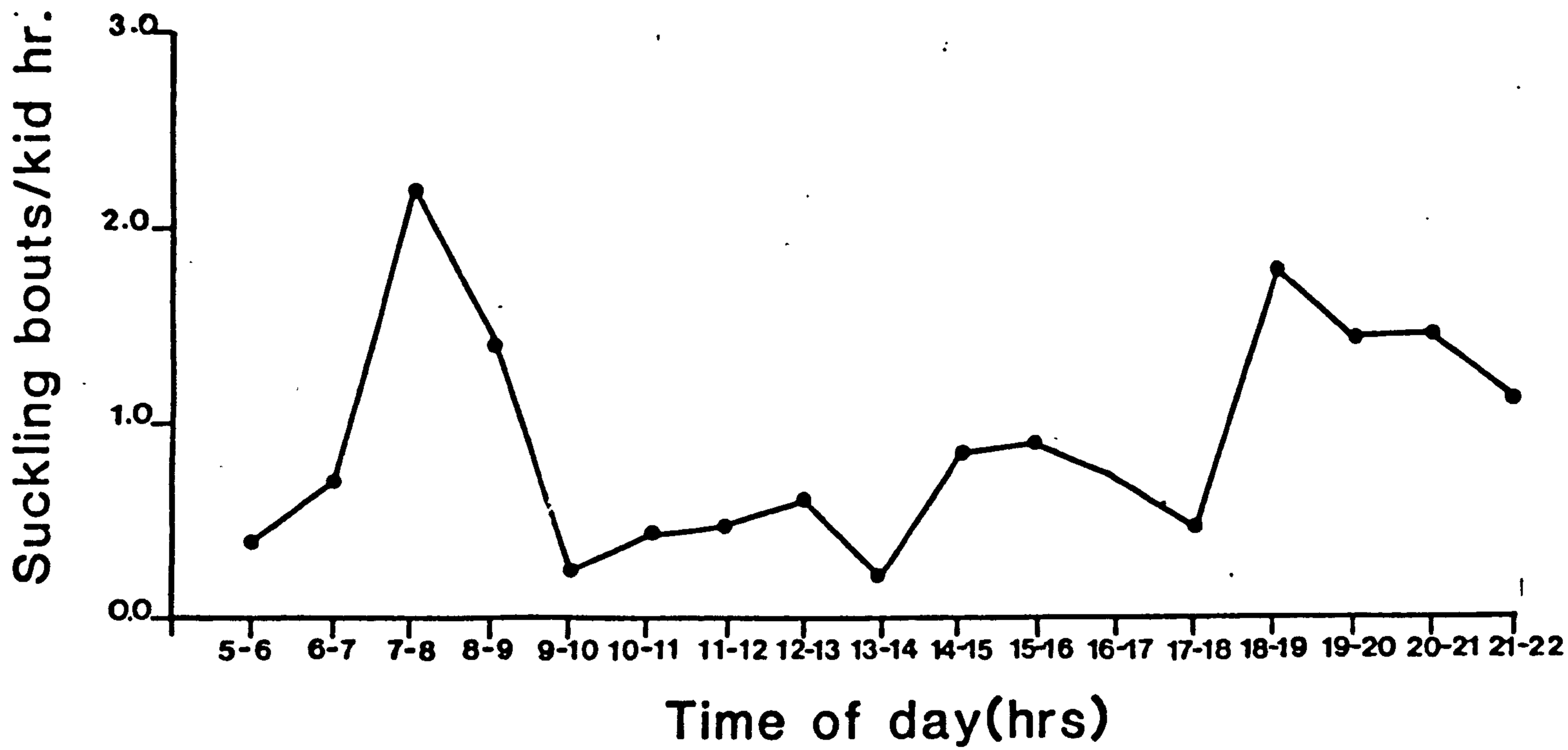


Fig. 4.3 Temporal distribution of suckling behaviour.

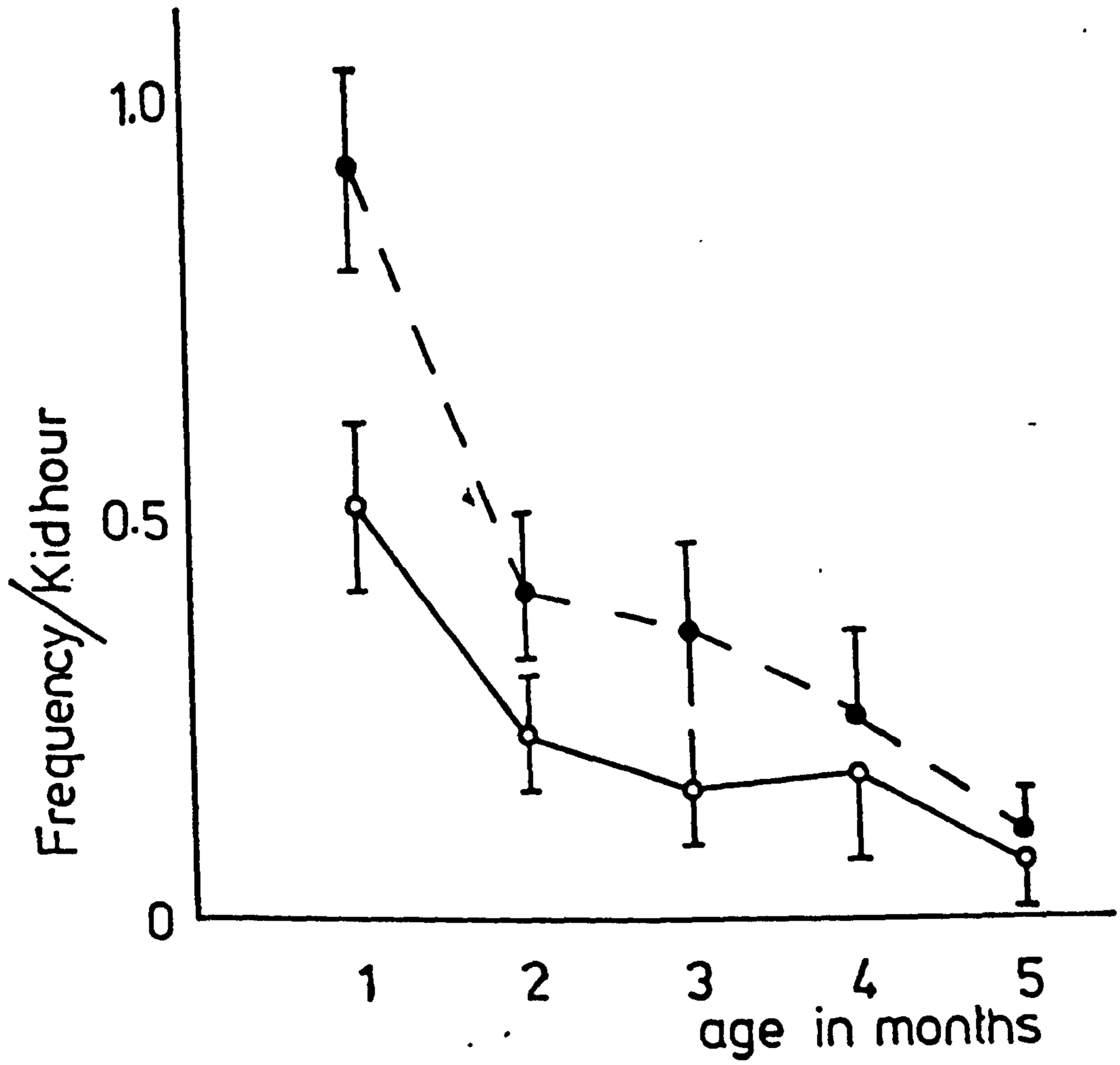


Figure 4.4 The change in mean frequency of suckling bouts, with age, of male ●—● and female ○—○ kids. Vertical lines indicate standard errors.

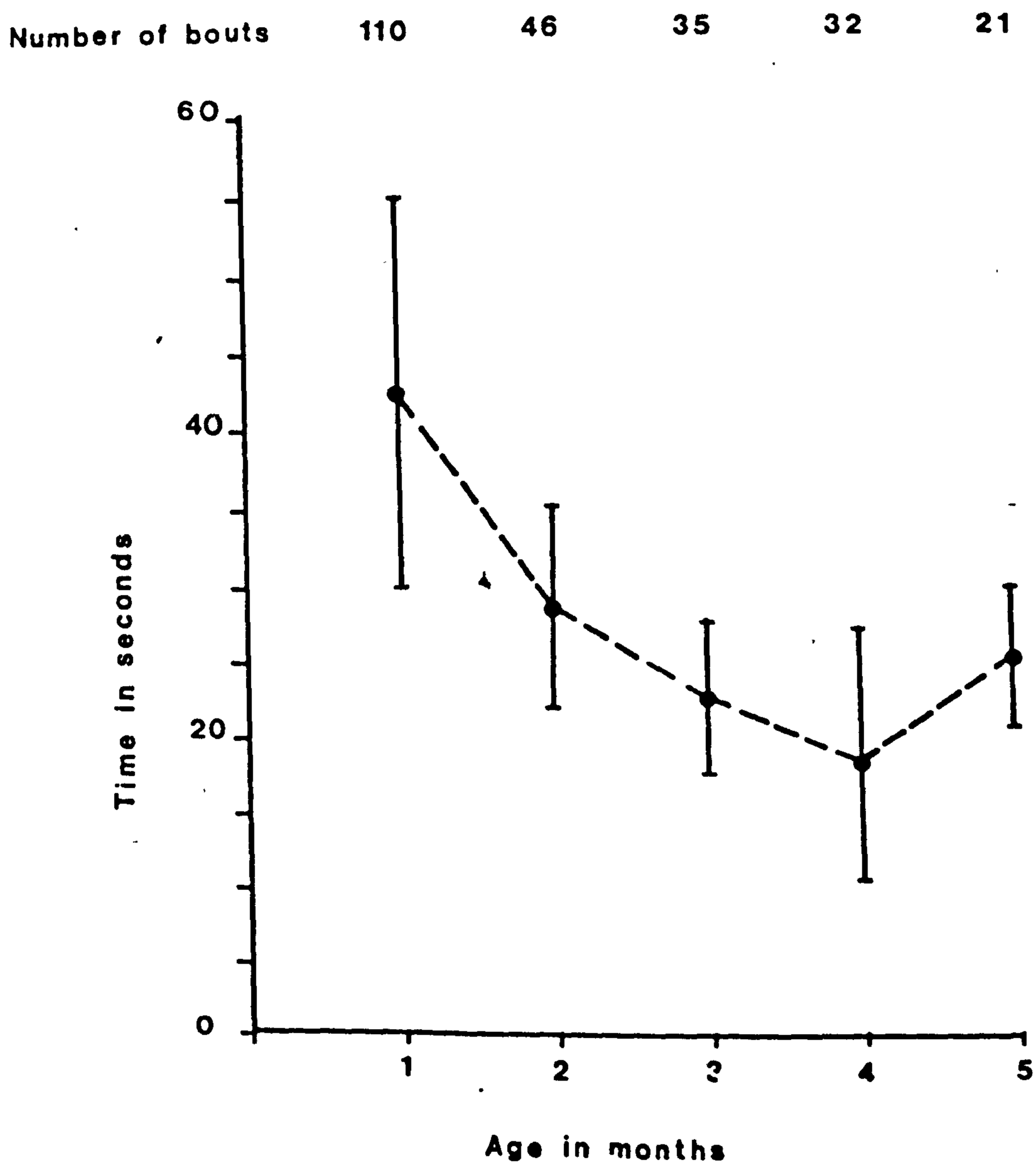


Fig. 4.5 The change in mean suckling bout duration in relation to age of kid. Vertical lines indicate standard errors.

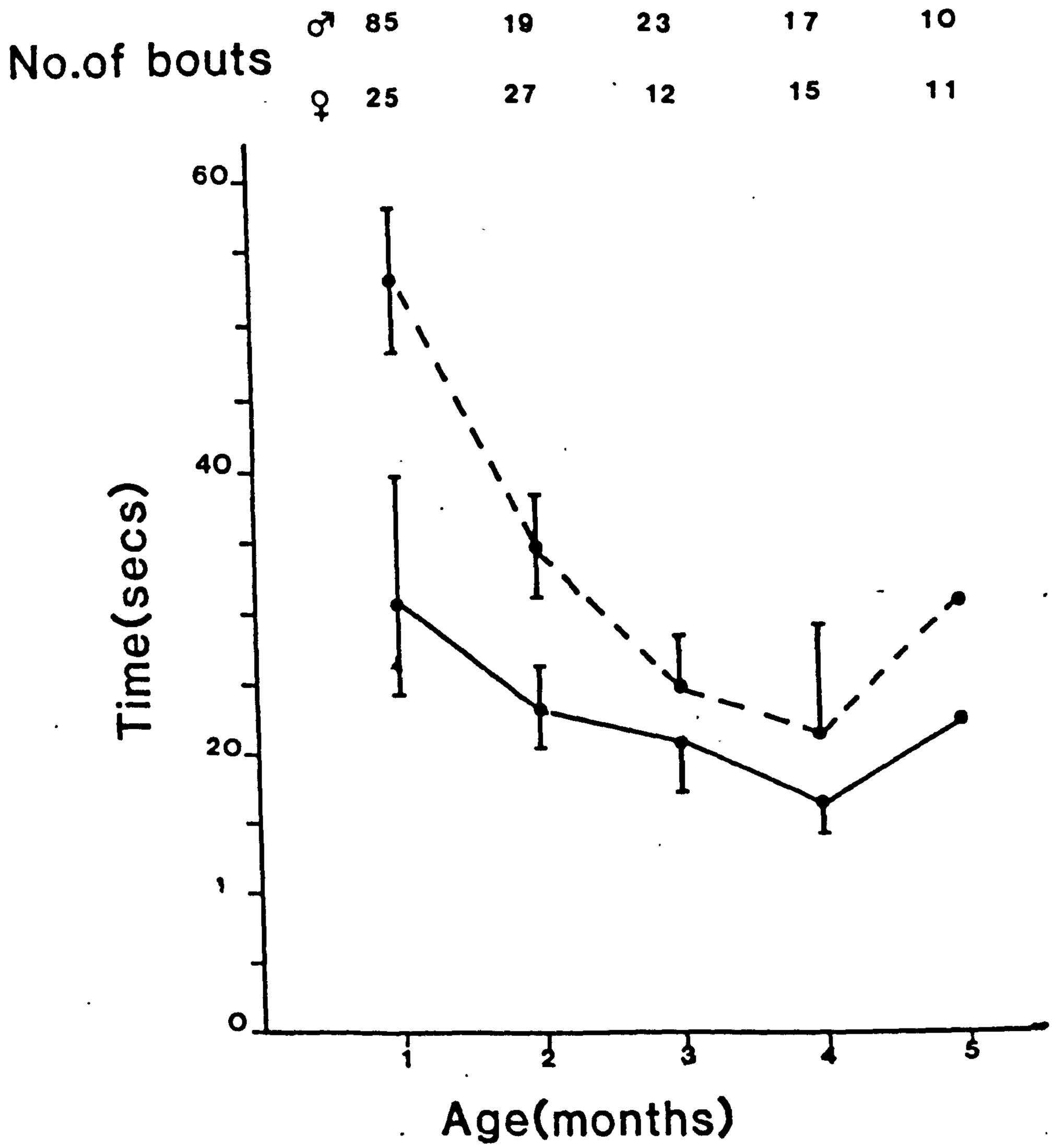


Fig. 4.6 The change in mean suckling bout length of male ●—● and female ●—● kids with age. The vertical lines represent standard errors.

Fig. 4.7 Mean suckling bout duration of females of different ages during the first two months (A) and months 3-5 (B) of their kid's life. Vertical lines indicate standard errors.

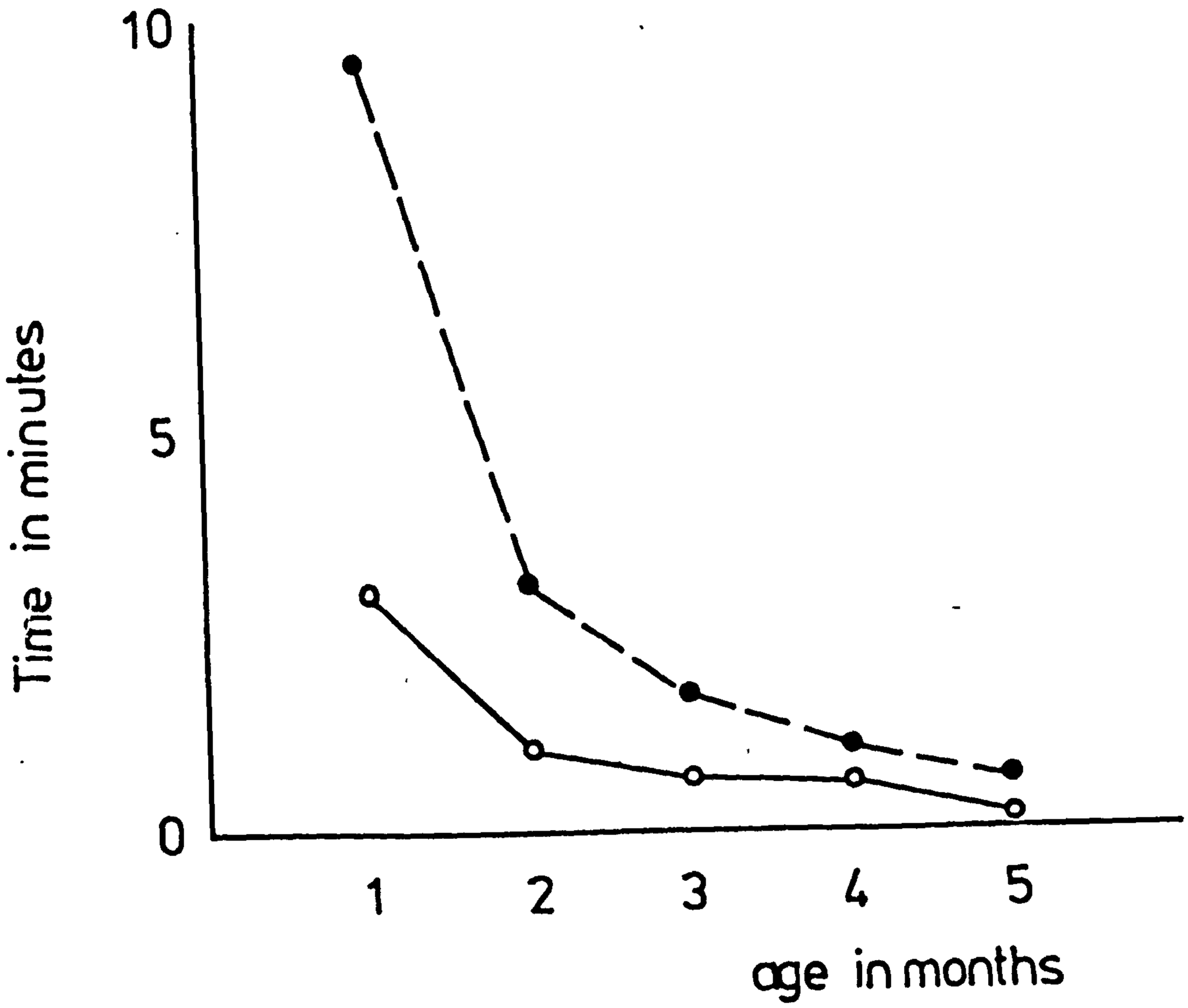


Fig. 4.8 Change in mean time spent sucking during daylight hours, by female O——O and male ●——● kids, with age.

kid during the first few days of life, after which there was a significant increase in the number of suckling bouts terminated by the mother (Table 4.3). The occurrence of unsuccessful sucking attempts was low during the first two months of life. However, between month two and five there was a significant increase in the number of unsuccessful sucking attempts (Table 4.4). At the age of five months, 69% of attempts to suck were unsuccessful. No kid was seen to suck after the fifth month, but 28% (4/14) of the females caught in November 1980 that had reared a kid that summer still had milk.

4.3.4 Mother-offspring distance and association.

It can be seen from Fig. 4.9 that, except when lying out, kids remained close (<3m) to their mothers during the first three months of life. Significant increases in the mother-kid distance occurred during the rut and in late winter when kids tended to be seen further away from their mothers. On average, male kids were seen further away from their mothers than female kids after the age of six months, with the exception of months 10 and 11 when there was no significant difference in the distance at which kids of each sex were seen from their mothers. These changes in mother-kid distances occurred during the same periods as changes in association between them occurred.

There was an increase in percentage association between mothers and kids of either sex between April and June 1980 (Fig. 4.10). Association remained high during the summer. It can be seen from

Age class of kid	No. of bouts terminated by mother	No. of bouts terminated by kid		Chi value for paired age classes	
	n	n	%		
0-14 days	22	40	65		
				13.60	p<0.001
15-30 days	38	15	28		
				32.14	p<0.001
Month 2	33	3	8		
Month 3	40	0	0		
Month 4	24	0	0		
Month 5	7	0	0		

Table 4.3

The change in proportion of suckling bouts terminated by mother and kid in relation to age of kids.

Age	Successful	Unsuccessful		χ^2 value for paired age class d.f=1	Probability
	n	n	%		
Month 1	122	8	6.2		
				0.23	N.S.
Month 2	36	4	10.0		
				2.73	N.S
Month 3	44	15	25.4		
				0.15	N.S.
Month 4	24	11	31.4		
				2.52	N.S
Month 5	7	10	58.8		

Table 4.4

The change in proportion of successful suckling attempts in relation to age of kids.

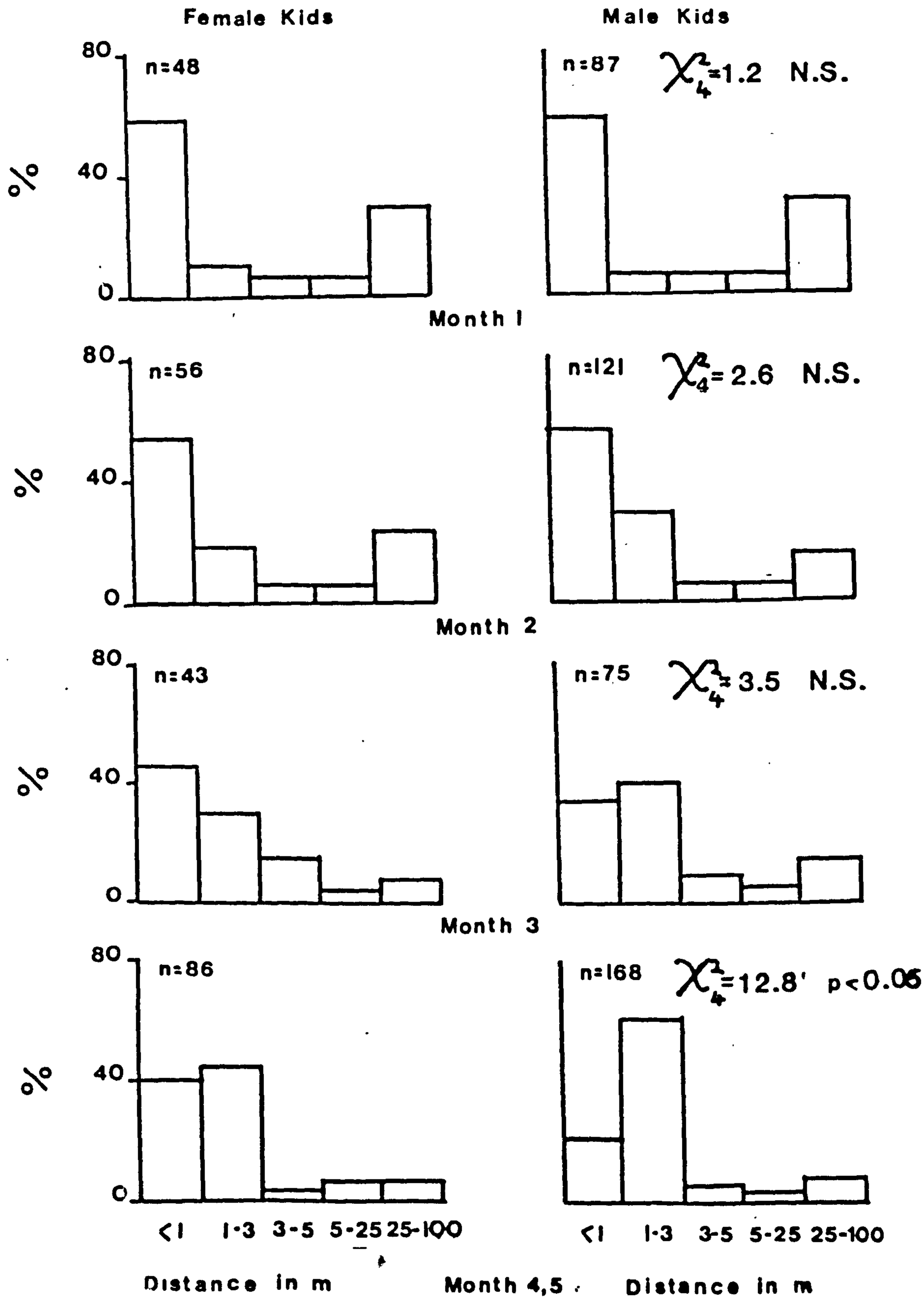


Fig. 4.9a Distance between mother and kid aged 1 - 5 months: distribution of spot sightings (as percentage) by age class. n = number of sightings. Chi squared compares male and female kids.

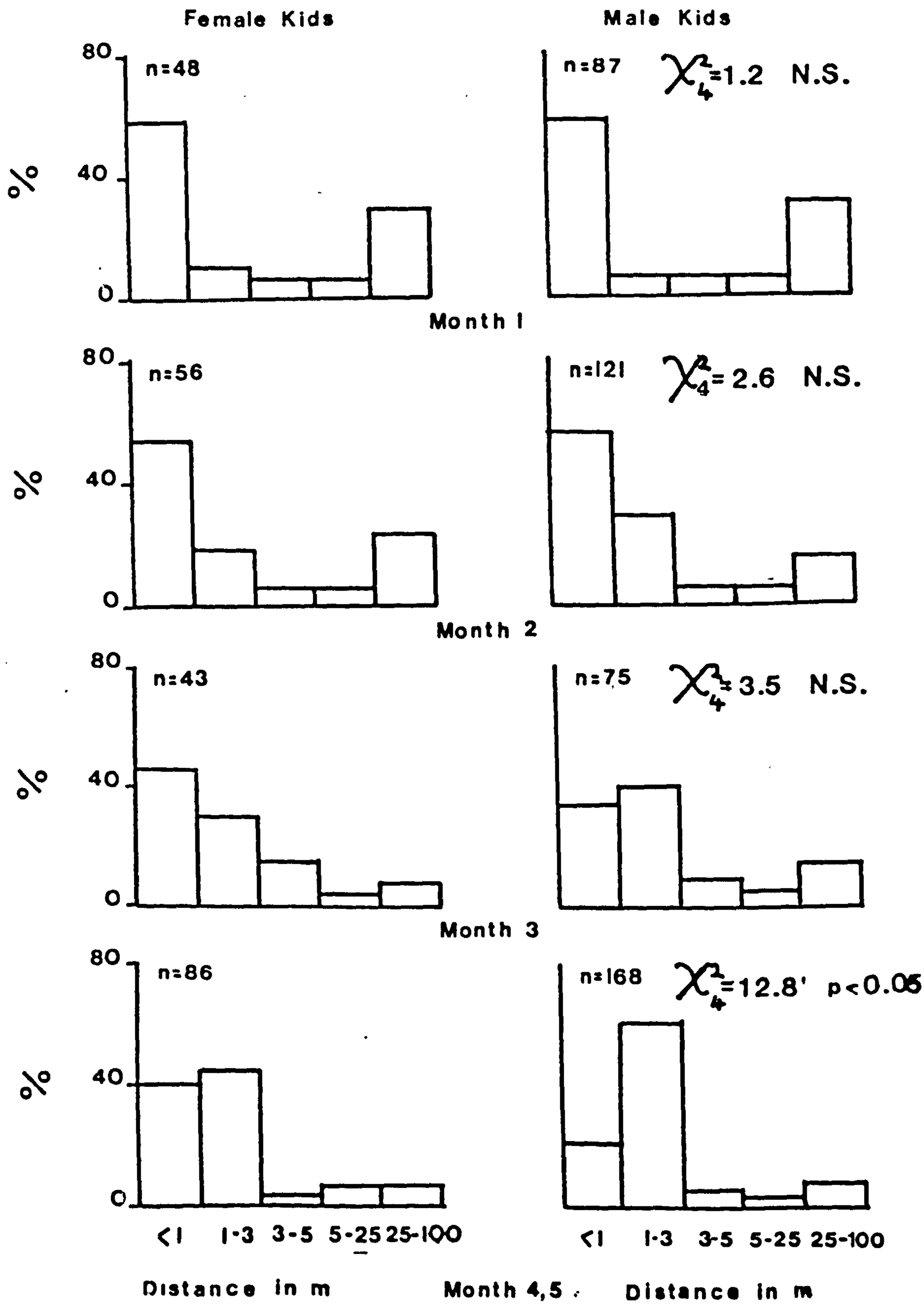


Fig. 4.9a Distance between mother and kid aged 1 - 5 months: distribution of spot sightings (as percentage) by age class. n = number of sightings. Chi squared compares male and female kids.

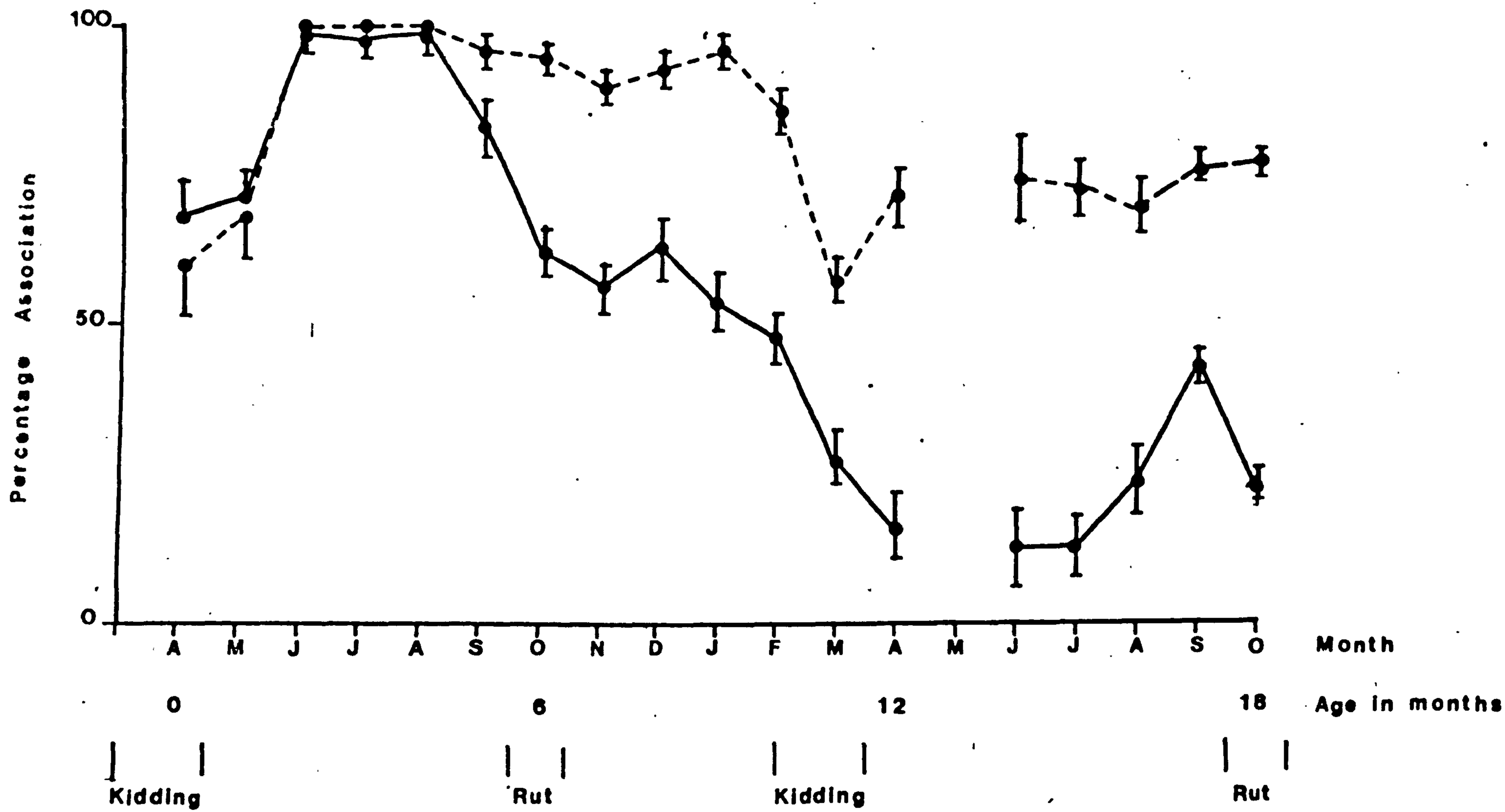


Fig. 4.10 Mean percentage association between mother and offspring, comparing male ●—● and female ●—● kids. The vertical lines indicate standard errors.

Fig. 4.10 that there was a marked decrease in the degree of association of mothers with their male kids between August and October. However there were no changes in the percentage association between mothers and their female offspring during this period.

During late winter (January to March) there was a decrease in association between mothers and their male and female offspring of the previous summer. Adult females that had a kid in April 1981 associated less with their female yearlings than adult females who did not have a kid in April 1981 (Fig. 4.11a). However, during the summer there was an increase in the degree of association between adult females with kids and their female yearlings and by October 1981 females with kids were seen in the same group as their yearlings in 70% of observations. Male yearlings only occasionally associated with their mothers during the summer. However, between July and August 1981 there was a significant increase in the percentage association between mothers and their male yearlings (Fig. 4.11b). During their third summer, males were only occasionally seen to associate with their mothers (Maisels, pers. comm.).

4.3.5 Maintenance of Mother-offspring proximity

During the lying out period the mother must clearly be responsible for determining the distance between herself and her kid. There was no difference in the proportion of movements made towards and away from their mothers between male and female kids

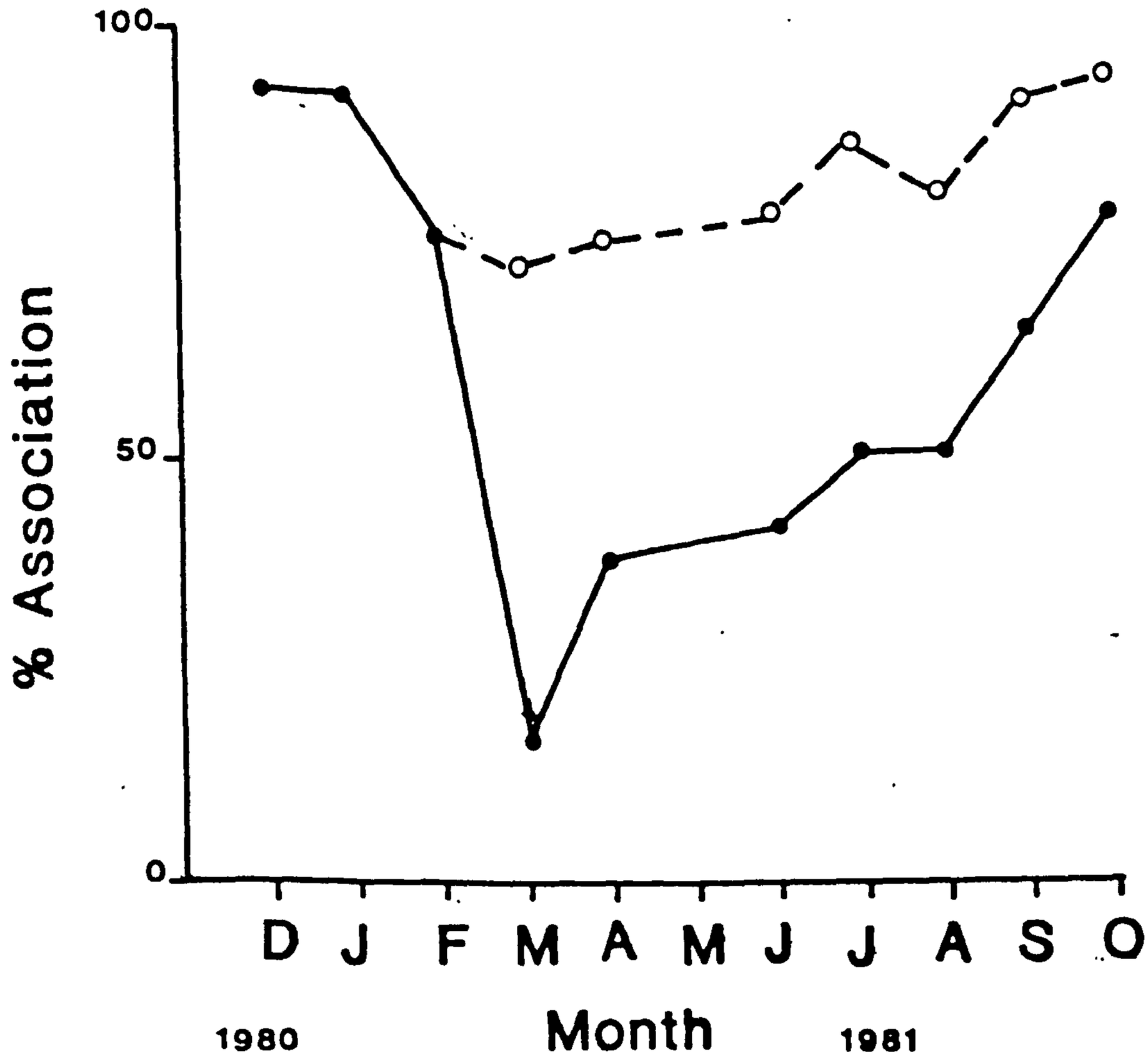


Fig. 4.11a Mean percentage association of mothers with female offspring, comparing those that had another kid in 1981 ●—● with those that did not rear another kid that year ○—○.

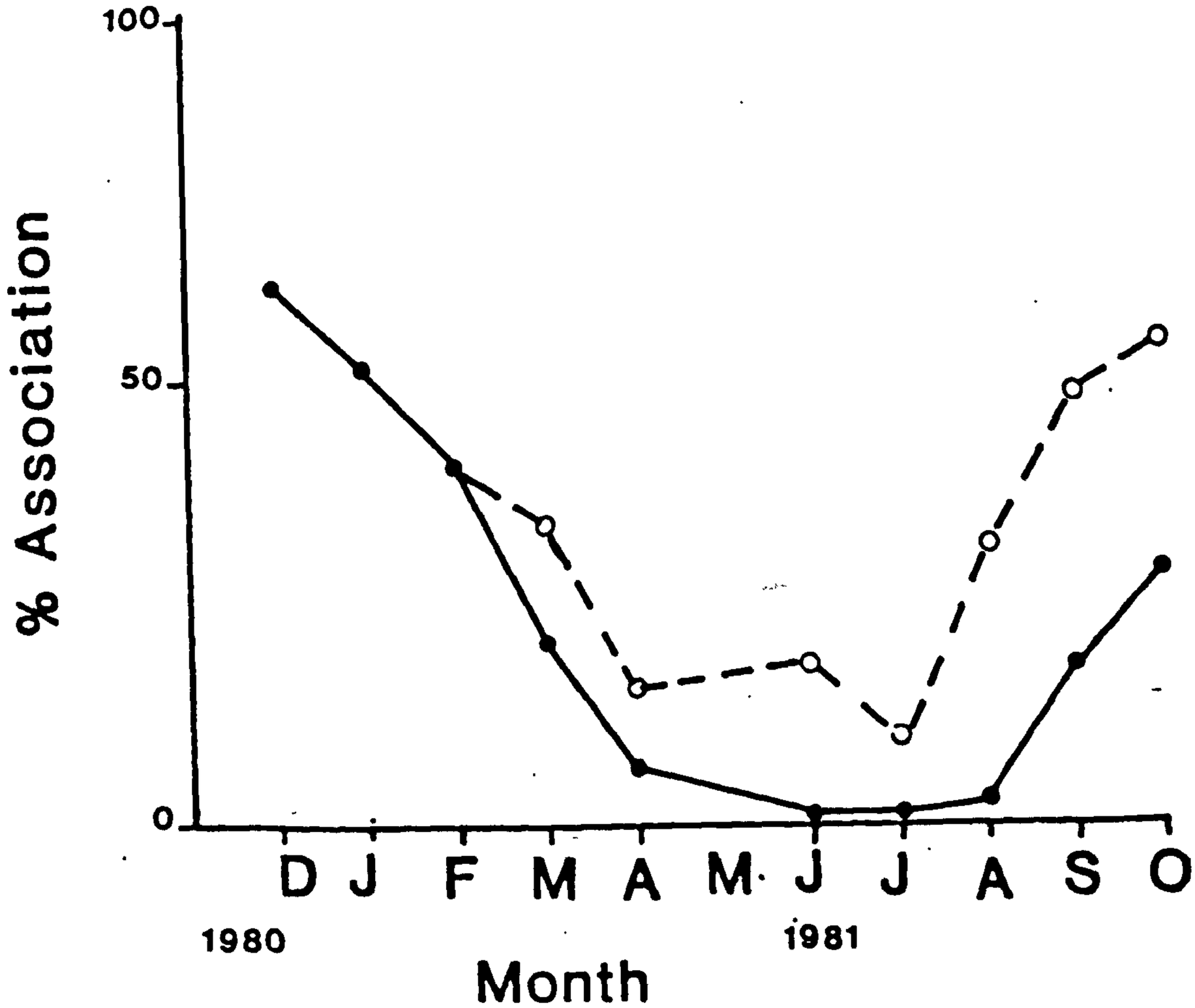


Fig. 4.11b Mean percentage association of mothers with male offspring, comparing those that had another kid in 1981 ●——● with those that did not rear another kid that year ○——○.

until month four, when male kids made fewer movements towards their mothers than female kids (χ^2=5.03, d.f.=1, $p<0.05$). During their first rut, male kids (aged 6 months) actually made more movements away from their mothers than movements towards them (Table 4.5). However,female kids continued to follow their mothers during this period.

4.4 DISCUSSION

The isolation from other females and the selection of secluded areas by female ungulates prior to parturition is thought to be an attempt to reduce predation (Gosling 1969, Leuthold 1977). Adult female feral goats have no predators, apart from man, in the Southern Uplands. However, newborn kids are probably taken by foxes and have been observed to be taken by golden eagles, Aquila chrysaetos, (R. Roxburgh pers. comm.). Therefore the selection of secluded sites to give birth may reduce the risk of kid predation. Also, by giving birth in a sheltered spot and licking the kid dry the mother may reduce the cold stress to which the kid is likely to be exposed in late winter. Pre-partum isolation may further be essential to ensure that the kid does not contact any other females during the critical period prior to the establishment of the mother-kid bond.

Hiding behaviour of young is also considered to be chiefly an anti-predator mechanism in many ungulates (Walther 1968, Gosling 1969, Lent 1971, Leuthold 1977). In feral goats however, there may be other advantages in adopting this behaviour. Kids appear to

Age of kid (mths)		Mother's movements in relation to kid				Kid's movements in relation to mother				x^2	p
		male		female		male		female			
		T	A	T	A	T	A	T	A		
1	n	11	62	3	18	102	38	31	8		
	%	15	85	14	86	68	26	79	21	0.20	NS.
2	n	7	69	3	31	78	5	36	3		
	%	9	91	9	91	94	6	92	8	0.03	NS.
3	ń	5	91	2	31	85	34	27	10		
	%	5	95	6	94	71	29	73	27	0.03	NS.
4	n	9	74	3	35	68	36	36	6		
	%	11	89	8	92	65	34	85	15	5.03	0.05
5	n	21	90	8	46	86	67	31	20		
	%	19	81	15	85	56	43	60	39	0.32	NS.
6	n	0	45	3	35	28	70	56	20		
	%	0	100	8	92	29	71	74	26	33.1	0.001

Table 4.5

Maintenance of proximity.The number of movements made towards (T) and away (A) by mother and kid in relation to each other. Chi Squared value comparing the frequency of movements by male and female kids in relation to their mother's

determine when and where they lie out. This is probably related to the rough terrain which goats inhabit. Kids may be physically incapable of following their mothers thoughout the day for the first few weeks of life. Even two week old kids were seen to have difficulty crossing some of the large boulder screes in the study area. Not all kids are hidden from view when they lie out, yet they always choose sheltered spots. This suggests that reduction of heat loss in cold weather may be more important to the survival of kids than a reduction of the risk of predation. Feral goats are similar to other caprids in that females do not ingest the urine and faeces of their young (Walther 1961). This behaviour is thought to be essential in antelopes, gazelles and deer which all hide their young from terrestrial predators, since it would remove the evidence of the young (Geist 1977).

The apparent inability of mother and kid to recognise each other by calls alone (Herscher et al. 1963 and 4.3.2) suggests that calling or bleating is a general contact call rather than a mechanism for individual recognition. Although there is good evidence in many birds that parents and offspring can recognise each other by their calls (Thorpe 1961, Shugart 1977, Howell 1978, Beer 1979) there is only circumstantial evidence of individual recognition by auditory means in ungulates, for example Dall sheep, Ovis dalli dalli, (Murie 1944), caribou, Rangifer tarandus, (Lent 1966), and cattle, Bos domesticus, (Schloeth 1958). Experiments with playback of vocalisations have produced no clear-cut evidence in Barbary sheep, Ammotragus lervia, (Hass 1959), mouflon, Ovis musimon, (Tschanz 1962), roe deer, Capreolus capreolus, (Kurt 1968)

and reindeer (Ericson 1971, Espmark 1971).

It was found that during the first week of life, the kid terminated most suckling bouts. This suggests that, at this time, the mother could produce, and allowed her offspring, as much milk as it required. After this period there was a marked decline in the duration and frequency of suckling bouts. This was accompanied by an increase in the proportion of bouts terminated by the mother and an increase in the proportion of unsuccessful sucking attempts (see 4.3.3). Therefore it appears that kids were attempting to obtain more milk than their mothers were able, or willing, to give to them.

It is widely accepted that with all other factors being equal, young which suck more frequently and for longer durations consume more milk (Munro 1962, Brown 1964, Graham and Seale 1970). Therefore the longer mean suckling bout length and higher frequency of sucking by male kids compared to female kids suggests that male kids obtain more milk from their mothers than female kids. I have no data on the weight of male and female kids at birth. However Greig (1969) found that in a sample of 47 near term foetuses (23 male, 24 female), male foetuses tended to be heavier than females but the difference was not significant. However, by the age of seven months male kids are significantly heavier (mean wt.=23.8 kg) than female kids (mean wt.=18.4kg), ($t=3.84$, $df.=38$, $p<0.01$). With a mean weight difference of only 22% between male and female kids it is difficult to believe that male kids actually spend over three times more time sucking than female kids (Fig. 4.8). This result may be due to the sample size or distribution of observations. Alternatively, female kids may be more efficient at sucking than

males or they may be suckled more frequently at night than males.

In domestic goats, male kids drink more milk than female kids. I have been told of one domestic male kid that apparently drank almost twice as much milk as its female sibling (M. Clark, pers. comm.).

There was no evidence of male kids being weaned later than females as occurs in elephant seals (Reiter at al. 1978). Weaning appeared to be completed by the age of five or six months. McDougall (1972) suggested that weaning in feral goats occurs at about six months of age, while Couturier (1962) states that ibex (Capra ibex) are frequently weaned by three months.

In the present study it was found that male kids tended to associate less frequently and stray further from their mothers than female kids during their first rut. The decrease in the association of mothers with their male offspring during the rut appeared to be due to a combination of aggression from high ranking males towards male kids (Chapter 5) and the onset of sexual maturity causing the young males to search for receptive females. In red deer, aggression by stags also results in a decrease in the association of male yearlings and their mothers during the rut (Guinness et al. 1979).

The decrease in association between adult females and their female offspring during February and March appears to be related to the female giving birth to another kid. Those females which reared a live kid in April 1981 associated less frequently with their previous year's offspring than females who did not rear a kid that year. There was insufficient data to determine whether this was a

passive or forced separation. Altmann (1963) found that in moose (Alces alces) and wapiti (Cervus canadensis), the birth of the new calf breaks the relationship between mother and offspring. A similar decrease in association between red deer hinds and their calves occurred if the female had another calf the following year, but if the hind did not produce a second calf she would continue to associate with her yearling (Guinness et al. 1979).

CHAPTER 5

THE RUT

5.1 INTRODUCTION

Feral goats in Britain mate during a short intense rutting period in the Autumn (Darling 1937). There are many anecdotal tales concerning the rutting behaviour of feral goats (Whitehead 1972), but there have been few detailed studies. Some authors have described feral goats as harem breeders similar to red deer (Darling 1937, Mackenzie 1957, Tegner 1970). However Geist (1960), Munton (1975) and Coblentz (1980) describe a mating system where males form a brief 'tending bond' with single oestrous females before mating with them and moving on to the next female. Shank (1972) in a study on Saturna Island, British Columbia, and Gould (1979) working on Aldabra in the Seychelles observed males forming tending bonds with females and also situations where one female was chased and repeatedly mounted by several males.

Folk tales of "majestic" dominant billy (male) goats with large curved horns and tremendous fighting ability seem to have influenced several authors when they refer to a dominance hierarchy amongst rutting males and claim that dominance is determined by age, fighting ability or horn size (Geist 1960, Tegner 1970, Greig 1969). During the rut older larger males were seen to be dominant to

smaller younger males in aggressive encounters and to form more tending bonds with females than younger males (Shank 1972, Munton 1975). However there is little quantitative information to support the assumption that dominance hierarchies develop amongst rutting males or that only a few dominant males do most of the mating (Geist 1960, Greig 1969, MacDougall 1975, Munton 1975).

There is good evidence that some male goats move considerable distances during the autumn (Crook 1970, MacDougall 1975) and then return to their pre-rut home range after breeding (Coblentz 1980) but it is still uncertain which males move, how far they move and what causes them to move. It has been suggested that a reduction in time spent feeding and increased energy expenditure by males during the rut may be primary factors contributing to the lower survival rate of male goats compared to females (Boyd 1981, Bullock 1982).

The aims of this study were to collect detailed quantitative information on the rutting behaviour, time budgeting and movements of individual feral goats in order to gain a functional understanding of such behaviour and to quantify the reduction in time spent feeding and changes in weight by goats during the rut.

5.2 METHODS

Information on the time of oestrous in females and the movement of males during the 1981 rut was collected by walking the study area and spot sighting goats (see Chapter 1). The minimum distance moved by each male was calculated by plotting successive sightings on a

1:25000 scale map and measuring the horizontal straight line distance between each successive sighting to the nearest 25m. Goats did not usually walk directly from one group to the next but they would tend to follow the contours of the land and walk around the ends of valleys rather than walking straight across. It was not always possible to follow these wanderings but when possible the actual route taken by a goat was recorded. From information on the actual routes taken by three males during a ten day period it was estimated that they walked 21%, 25% and 37% further than that calculated by joining the points with straight lines.

A male seen in a particular group one day but not seen in that group on the next census was recorded as leaving that group. The probability of adult males leaving a rutting group (a group with one or more females in oestrus on two successive censuses) or a non rutting group (no oestrous female present on two successive censuses) was calculated by the following method:

$$\text{Probability of moving per two days} = \frac{M}{N-1}$$

where M is the number of occasions males were recorded leaving a particular type of group and N is is the total number of occasions

males were seen in that type of group. The null hypothesis was that movement between groups by males during the rut was at random so the probability of a male leaving each type of group would not differ significantly from 0.5.

Data on behavioural interactions and time budgeting were collected by direct observation using instant scan and focal animal (or focal group) sampling methods (see Chapter 1).

During the rut it became clear that some individual males always displaced other individuals in aggressive encounters; that is there were relatively stable dominant-subordinate relationships. Dominance ranks were calculated using three methods for all the males over two years of age in the main study area during the 1981 rut. These were based on victories in aggressive encounters and fights (Table 5.1) and were calculated as follows:

Method 1: By arranging the males in order so that they were beaten by the smallest number of males beneath them. For any pair of males the one with the most victories over the other was regarded as the dominant male. It was assumed that if male A was dominant to B and B dominant to C, then A would be dominant to C even if they were never seen to interact. The animal beaten by the smallest number of goats was assigned rank one.

Method 2: A dominance ratio was calculated by taking the number of individuals beaten divided by the total number seen to be interacted with, and arranging them in order of magnitude of the ratio.

Method 3: A second dominance ratio was calculated by taking the

		LOSER													
MALE I.D.	101	7	19	14	34	117	36	33	37	38	32	18	46	35	20
101		4	16	4	2	5	4	3	4	13	24	5	18	11	3
7	0		2	6	16	10	2	1	18	4	2	10	5	11	-
19	4	0		4	7	4	6	-	5	5	26	10	5	1	-
14	0	0	1		-	2	1	1	2	2	4	5	16	3	-
34	0	0	0	-		3	5	3	1	1	4	-	2	-	-
117	0	0	3	0	0		1	3	3	3	-	3	2	1	-
36	0	0	0	0	0	0		1	2	3	1	2	3	1	8
VICTOR 33	0	0	-	0	3	3	0		-	2	-	1	1	-	-
37	0	0	0	0	0	0	0	-		2	3	6	5	9	-
38	0	0	0	0	0	2	0	0	-		-	1	3	-	-
32	0	0	0	0	0	-	0	-	2	-		-	1	2	-
18	0	0	0	0	-	0	0	0	0	0	0		3	6	-
46	0	0	0	0	0	0	0	0	0	0	0	2		4	-
35	0	0	0	0	-	0	0	-	0	-	0	0	0		0
20	0	-	-	-	-	-	-	0	-	-	-	-	-	-	-

Table 5.1

Interaction matrix indicating victors and losers in aggressive encounters and fights during the 1981 rut. A dash indicates the two males were never seen to interact.

number of encounters in which an individual was the victor and dividing it by the number of encounters in which it was involved. Animals were then ranked in order of magnitude of dominance ratio.

All three methods of calculating dominance rank produced very similar results (Table 5.2). The rank orders calculated by methods 1 and 2 were more similar to each other than they were to that produced by method 3. The ratio produced by method 2 was used because it did not depend on the assumptions made in method 1.

The term relative rank (RR) refers to the ranks of all the males in a particular group in relation to each other. For example in a group containing Males 7, 34 and 38, their absolute ranks are 2, 5.5 and 10, but their relative ranks would be 1, 2 and 3 respectively. The term dominant male is used to refer to the male with the highest rank in a particular group.

5.3 TIMING OF RUT

In 1980 and 1981 the rut occurred between the 20 September and the end of October. The rut was not observed in 1979. However counting back 150 days (average gestation period of goats) from known kidding dates in spring 1980 it must have occurred during the last two weeks of October and the first two weeks of November in 1979.

A female in oestrus is most easily recognised by the behaviour of male goats. Males approach and court females in oestrus more

Method 1		Method 2			Method 3		
Male	Rank	Male	Dominance Ratio	Rank	Male	Dominance Ratio	Rank
101	1	101	1.0	1	101	0.96	1
7	2	7	0.92	2	7	0.95	2
19	3	19	0.91	3	19	0.81	3
14	4.5	14	0.83	4	14	0.72	4
34	4.5	34	0.66	5.5	34	0.43	8
117	6	117	0.66	5.5	117	0.44	7
36	7	36	0.57	7	36	0.60	5
33	8.5	33	0.55	8	33	0.45	6
37	8.5	37	0.41	9	37	0.42	9
38	10.5	38	0.30	10	32	0.14	11
32	10.5	32	0.33	11	38	0.07	13
18	12	18	0.16	12	18	0.18	10
46	13	46	0.15	13	46	0.08	12
35	14.5	35	0.00	14.5	35	0.00	14.5
20	14.5	20	0.00	14.5	20	0.00	14.5

Table 5.2

Dominance as calculated by the three different methods for 1981 data.

frequently than non oestrous females (Fig. 5.1). Also at close range one can see a slight swelling of an oestrous female's vulva. Females were assumed to be in oestrus if they were approached more than 10 times per hour. During the 1981 rutting period the date of oestrus was recorded for 47 of the 51 females in the main study area. Thirty one were recorded in oestrus on only one day and 14 on two consecutive days. The remaining two females were recorded in oestrus on two separate occasions separated by six days in one case and nine days in the other. It can be seen from Fig. 5.2 that females from the same heft tended to come into oestrus at a similar time. There was a significant difference between the mean dates of oestrus of the four hefts (Table 5.3).

5.4 THE MOVEMENT OF MALES DURING THE RUT

5.4.1 Timing of movements

Prior to the first female coming into oestrus males approached and tested each female in a group for oestrus by sniffing and licking her vulva or by taking urine and performing a flehmen (see 5.6.1). In their search for oestrous females, adult males wandered between groups of females, often moving beyond the limits of their normal home range (Figs. 5.3 and 5.4). Adult males were first observed to leave their own home ranges in early September, but no yearling males or male kids were seen beyond the limits of their natal home ranges until the second week of October (Fig. 5.5).

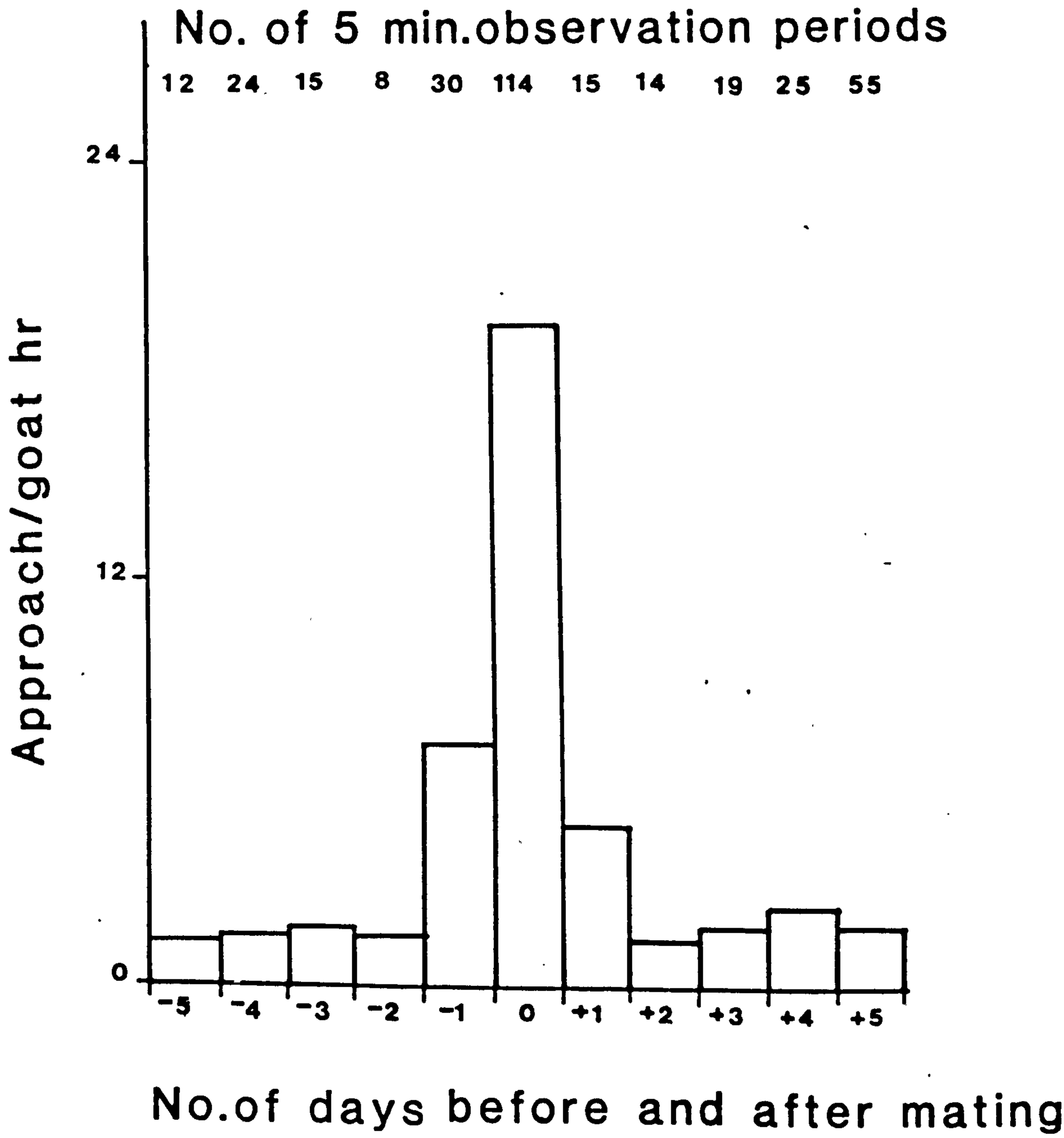


Fig. 5.1 The frequency of male approaches to females on the day they were seen to be mated and on days before and after.

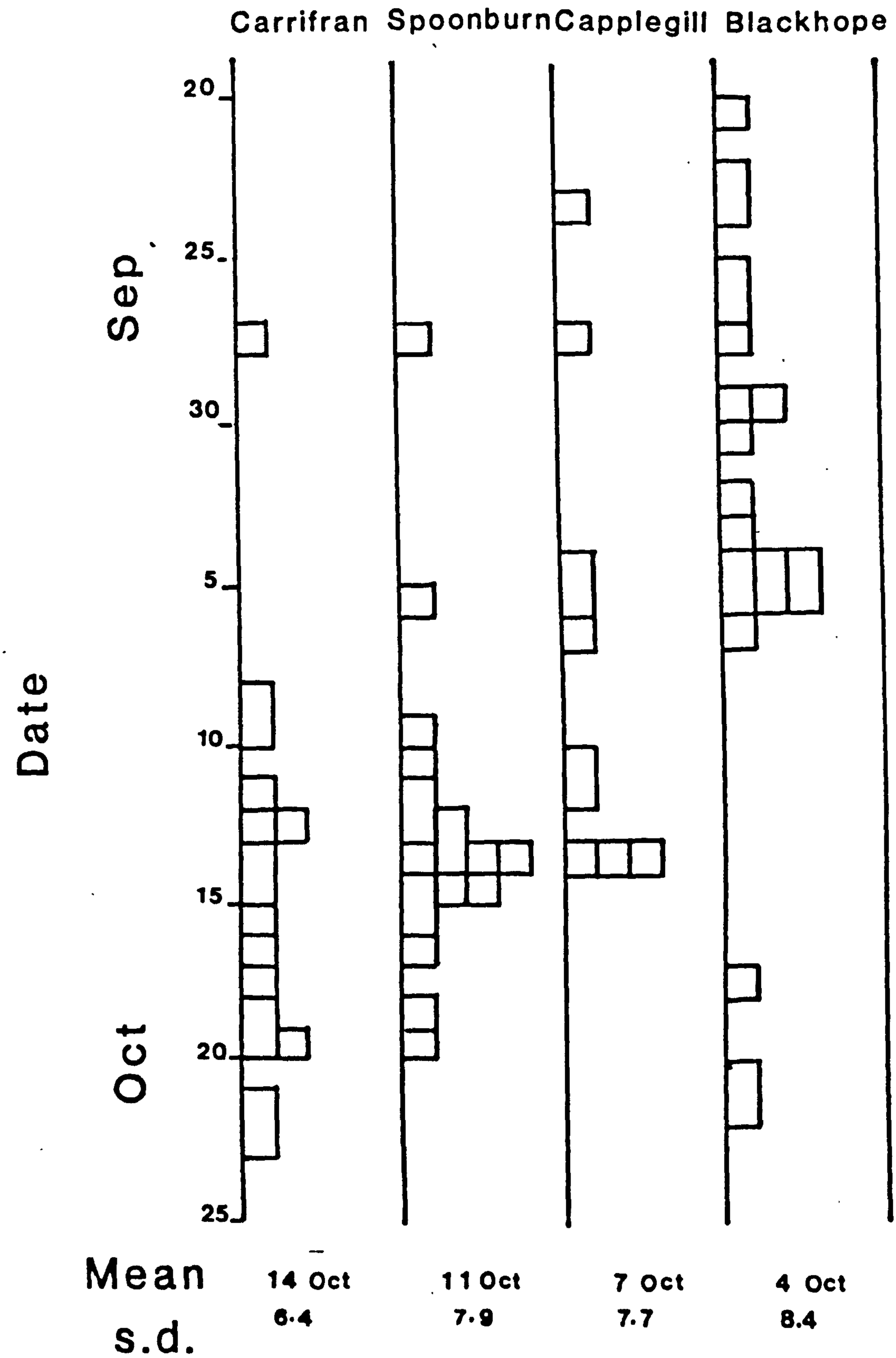


Fig. 5.2 Date of oestrus of females in each heft during the 1981 rutting period.

Source of variation in oestrus dates	Degrees of freedom	Sum of squares	Mean square	Variance ratio
Between hefts	3	1375	4581	9.16 ($p<0.001$)
Within hefts (residual)	42	2098	49.9	
Total	45	3473		

Table 5.3

Analysis of variance comparing the dates of oestrus of females from different hefts.

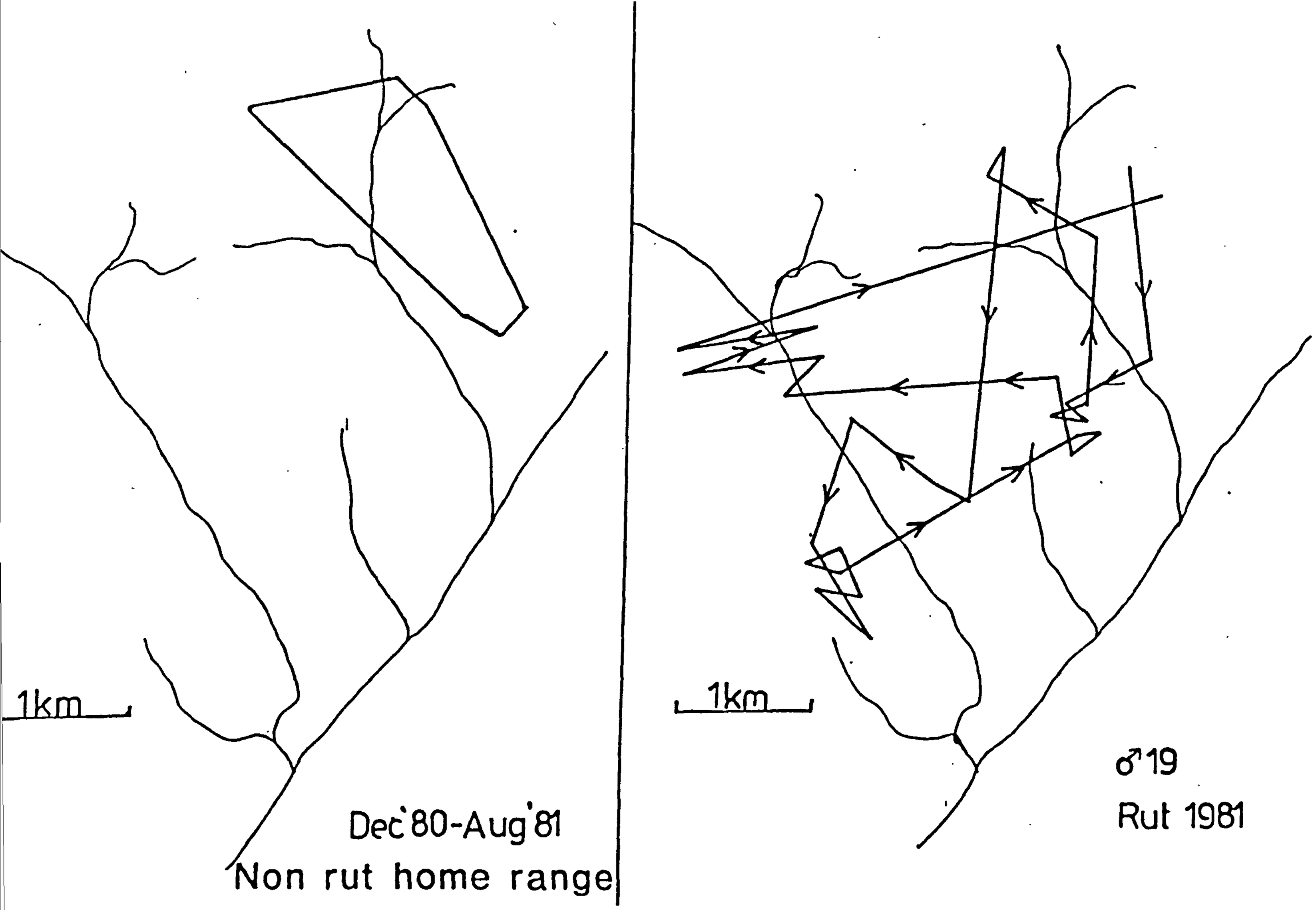


Fig. 5.3 Comparison of non-rut home range and movements during the rut by an adult male (male 19).

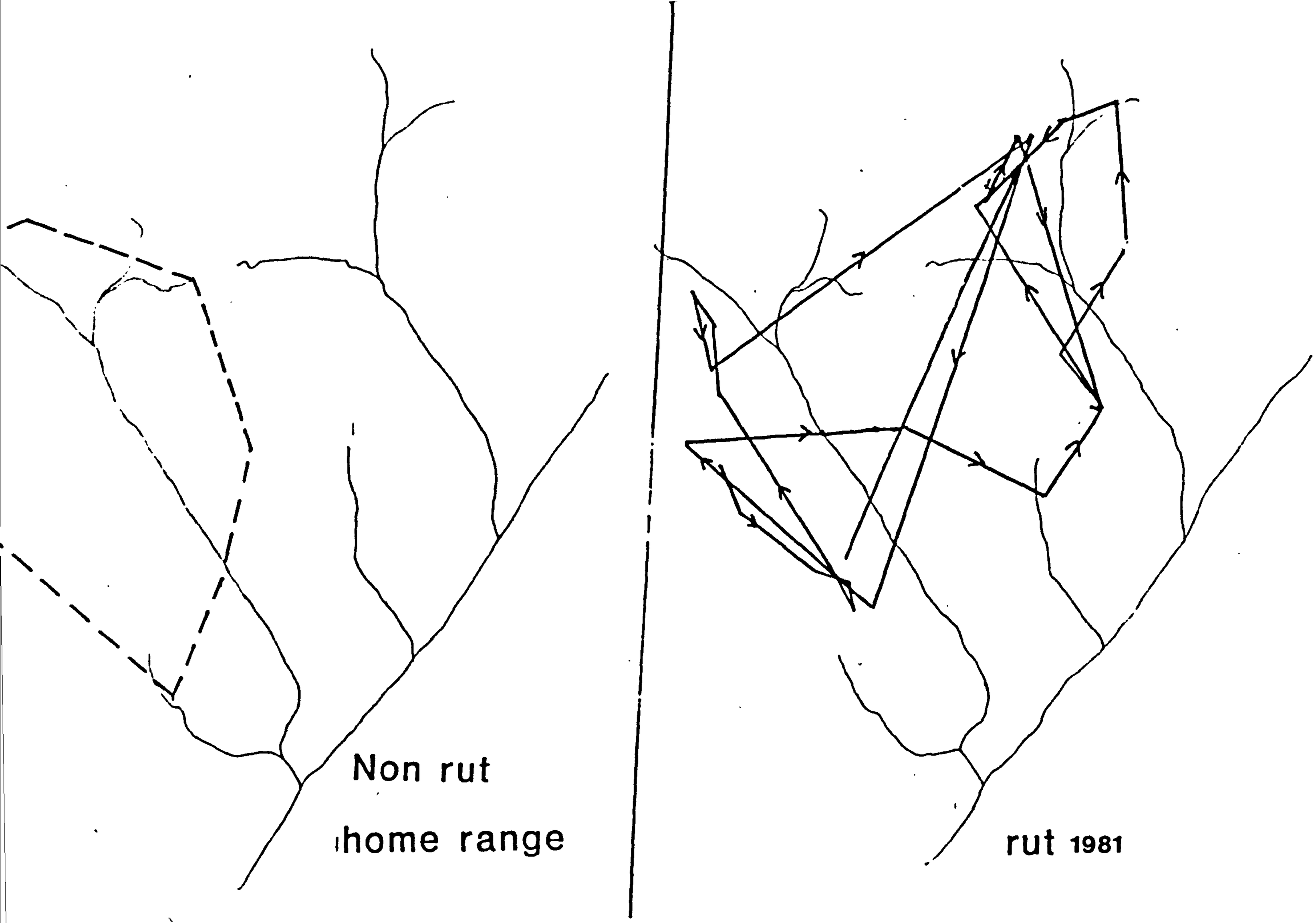


Fig. 5.4 As Fig. 5.3 for a second adult male (male 18).

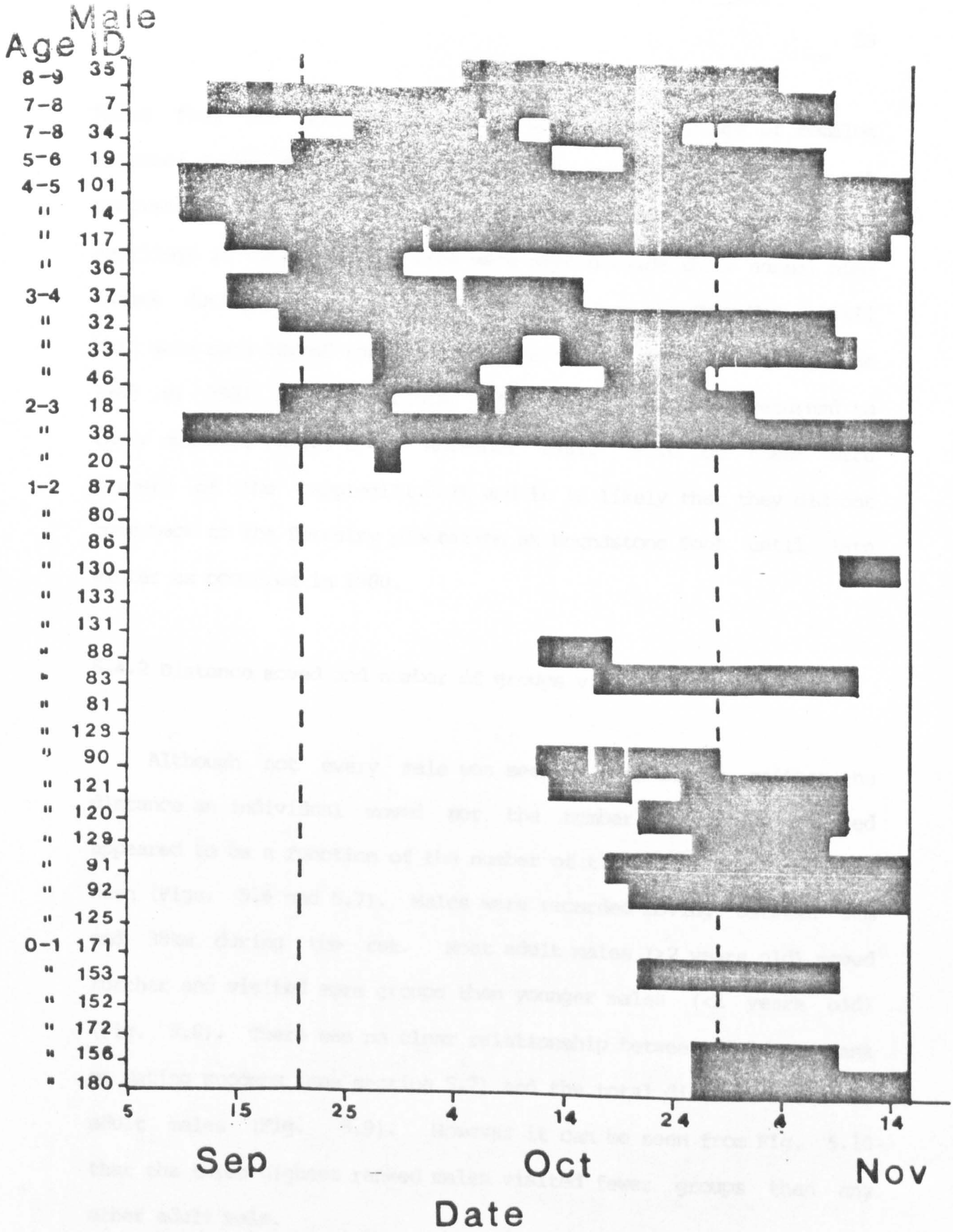


Fig. 5.5 Movement of males in the main study area beyond the limits of their non-rut home range during the 1981 rut. Shading indicates that males were seen outside their normal home ranges. The dashed lines indicate the first and last days on which a female was recorded in oestrus.

Males from the same heft tended to move between groups of females together during the early part of the rut, but split up as the rut progressed. Although all the adult males and 52 percent of the yearlings in the main study area were seen outside their normal home ranges during the rut, none of the males from the Grey Mare's Tail heft were seen beyond the limits of their home ranges during the 1980 or 1981 rutting periods. All but nine males had returned to their own heft ranges by 15 November 1981. Five of these were members of the Capplegill Heft and it is likely that they did not move back to the forestry plantation at Roundstone Foot until late winter as occurred in 1980.

5.4.2 Distance moved and number of groups visited

Although not every male was seen on each census, neither the distance an individual moved nor the number of groups visited appeared to be a function of the number of times each individual was seen (Figs. 5.6 and 5.7). Males were recorded moving between 5km and 38km during the rut. Most adult males (>2 years old) moved further and visited more groups than younger males (<2 years old) (Fig. 5.8). There was no clear relationship between dominance rank or mating success (see section 5.7) and the total distance moved by adult males (Fig. 5.9). However it can be seen from Fig. 5.10 that the three highest ranked males visited fewer groups than any other adult male.

The movement of a male between groups was influenced by the presence or absence of oestrous females and by the male's relative

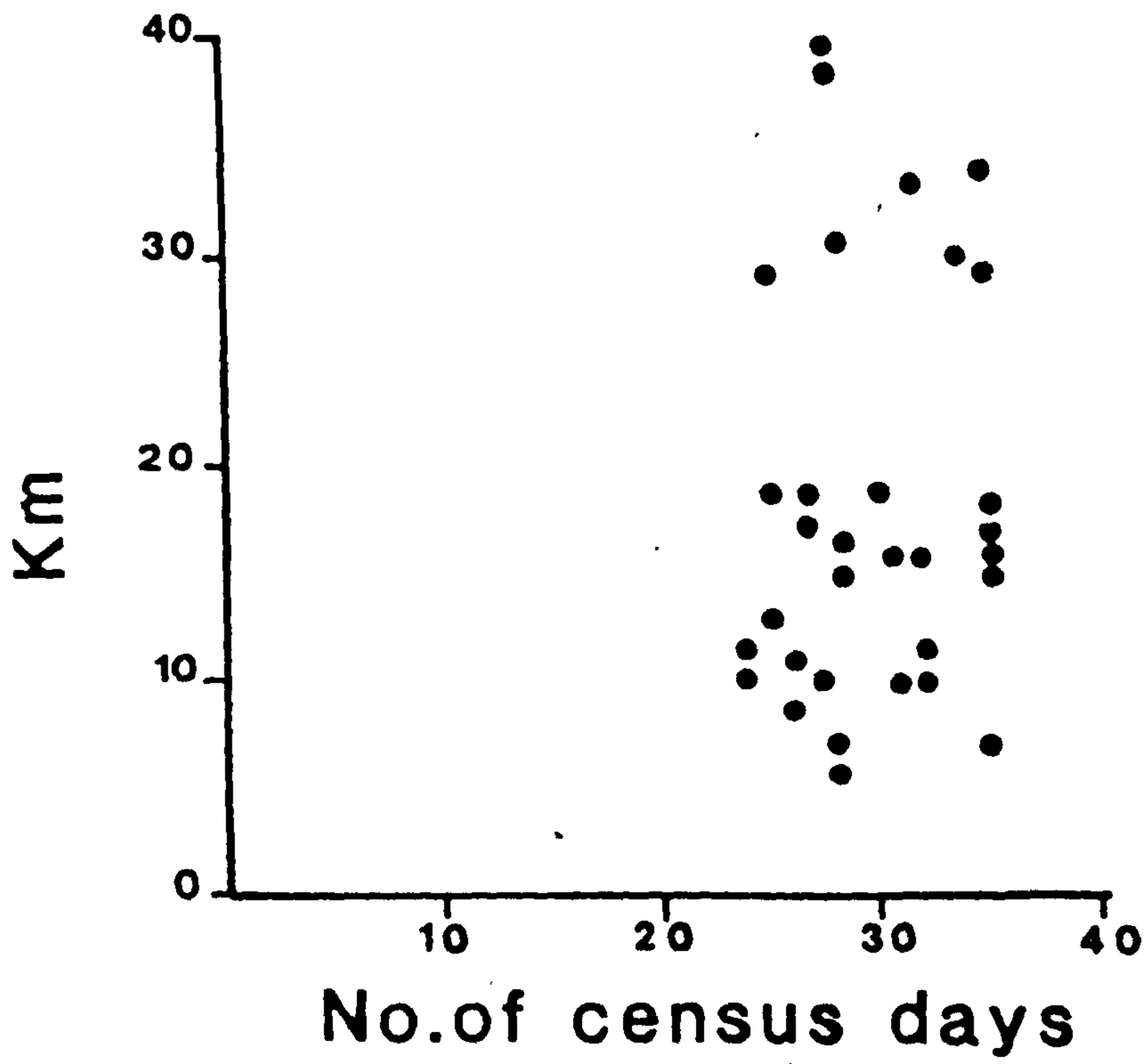


Fig. 5.6 The relationship between the number of census days on which a male was seen and the distance that male was estimated to have moved during the rut.

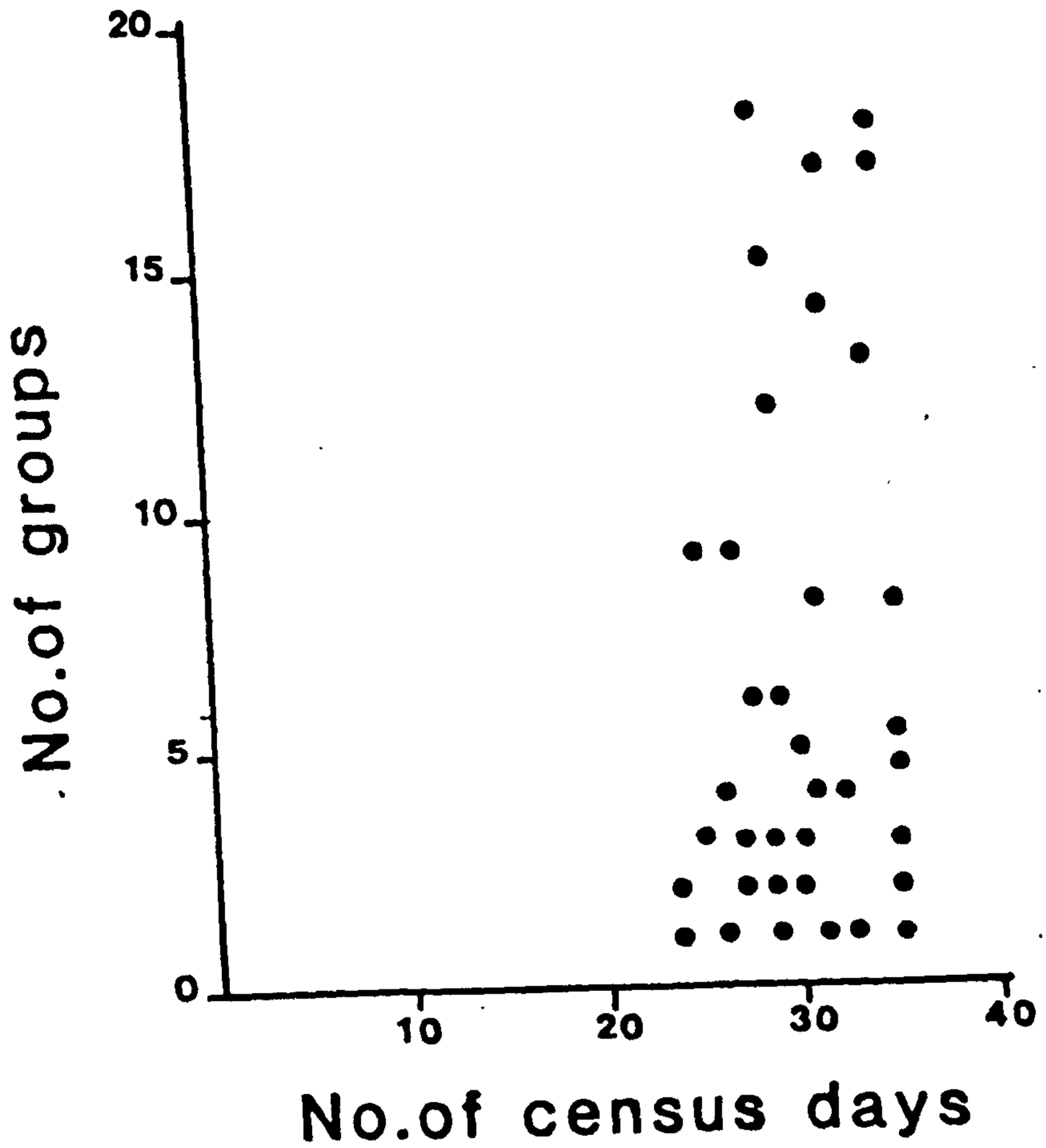


Fig. 5.7 The relationship between the number of census days on which an individual male was seen and the total number of groups visited by that male during the rut.

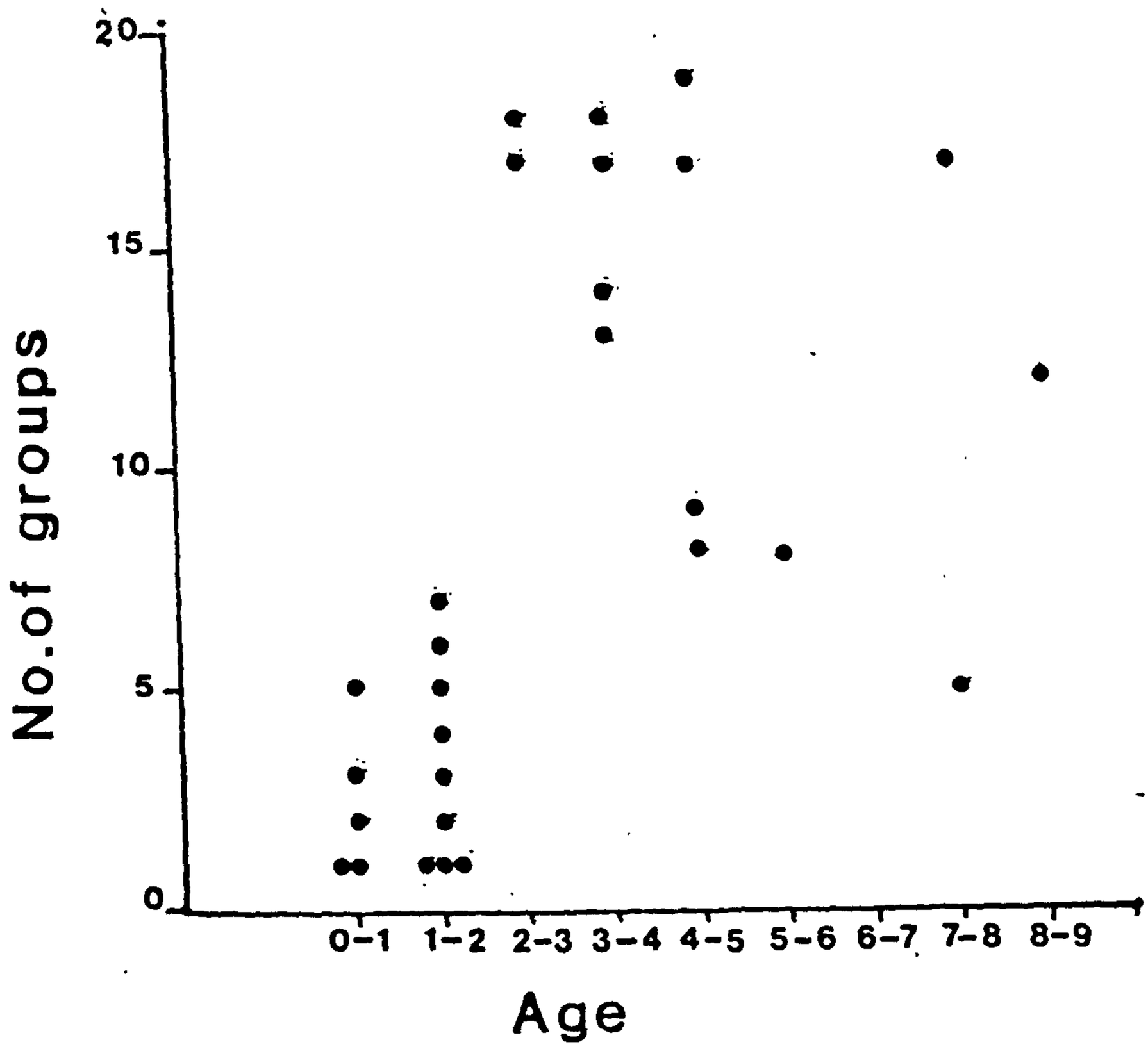


Fig. 5.8a The number of groups of females visited by males of different ages during the 1981 rut.

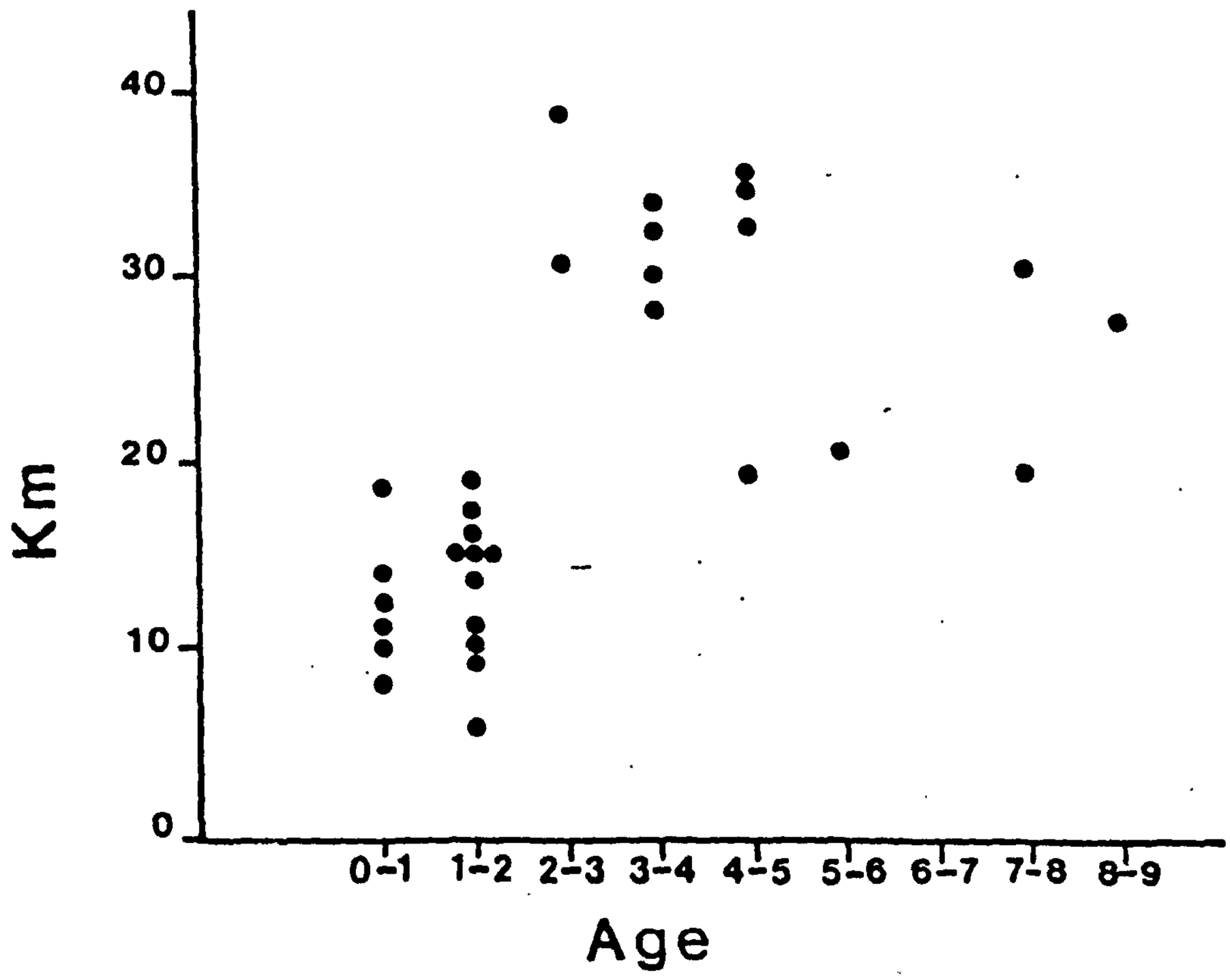
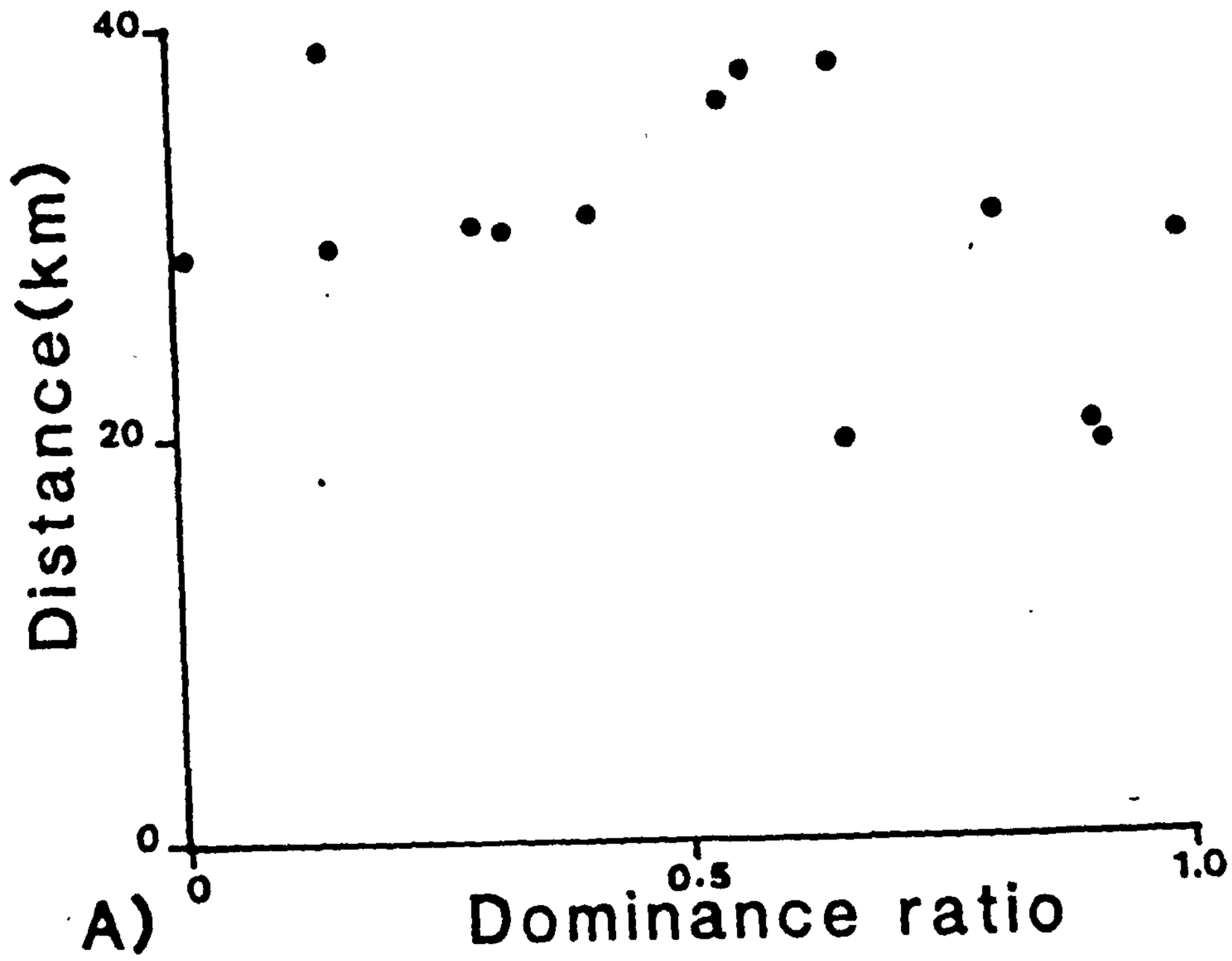


Fig. 5.8b The total distance moved by males of different ages during the 1981 rut.



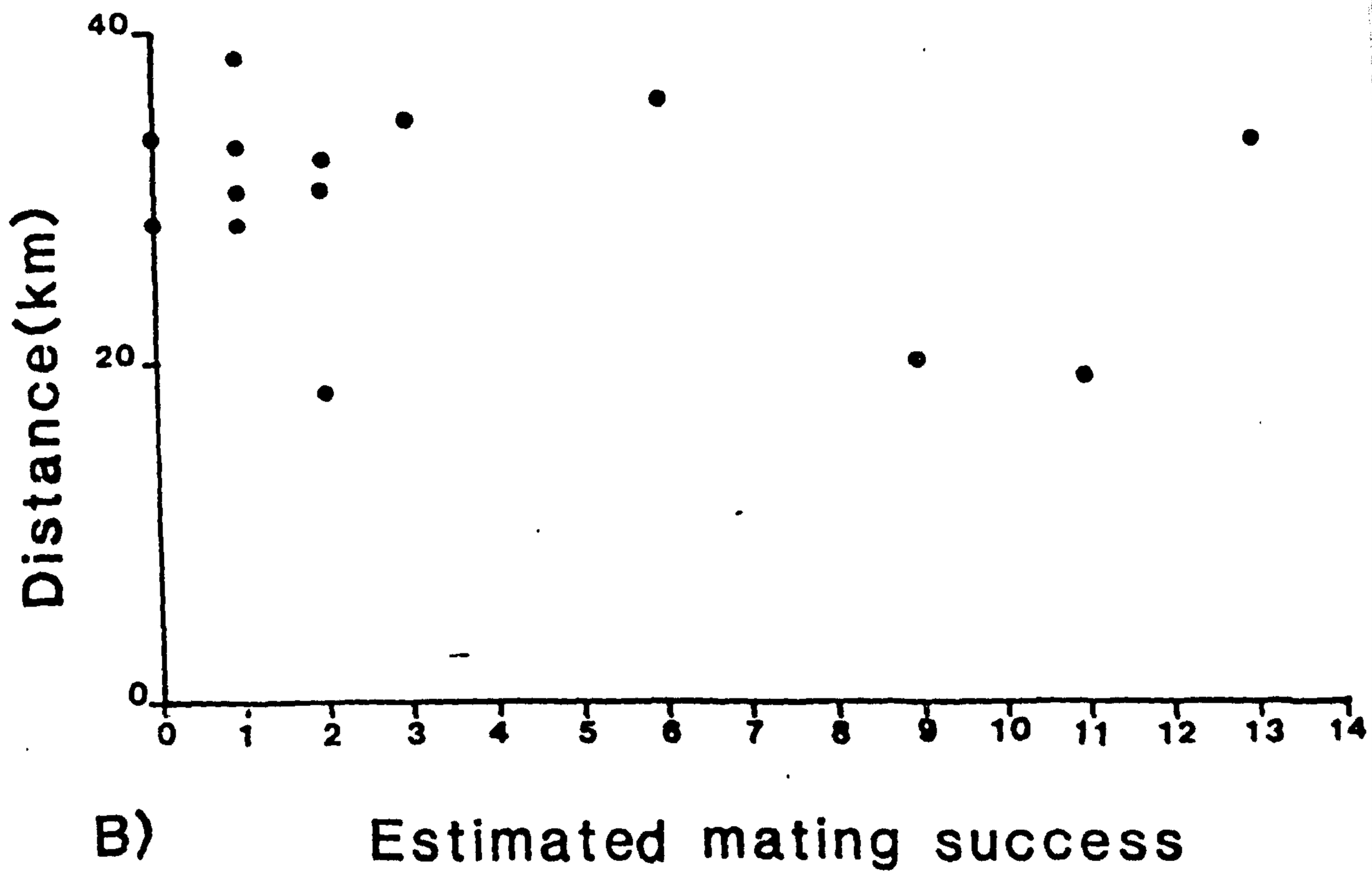
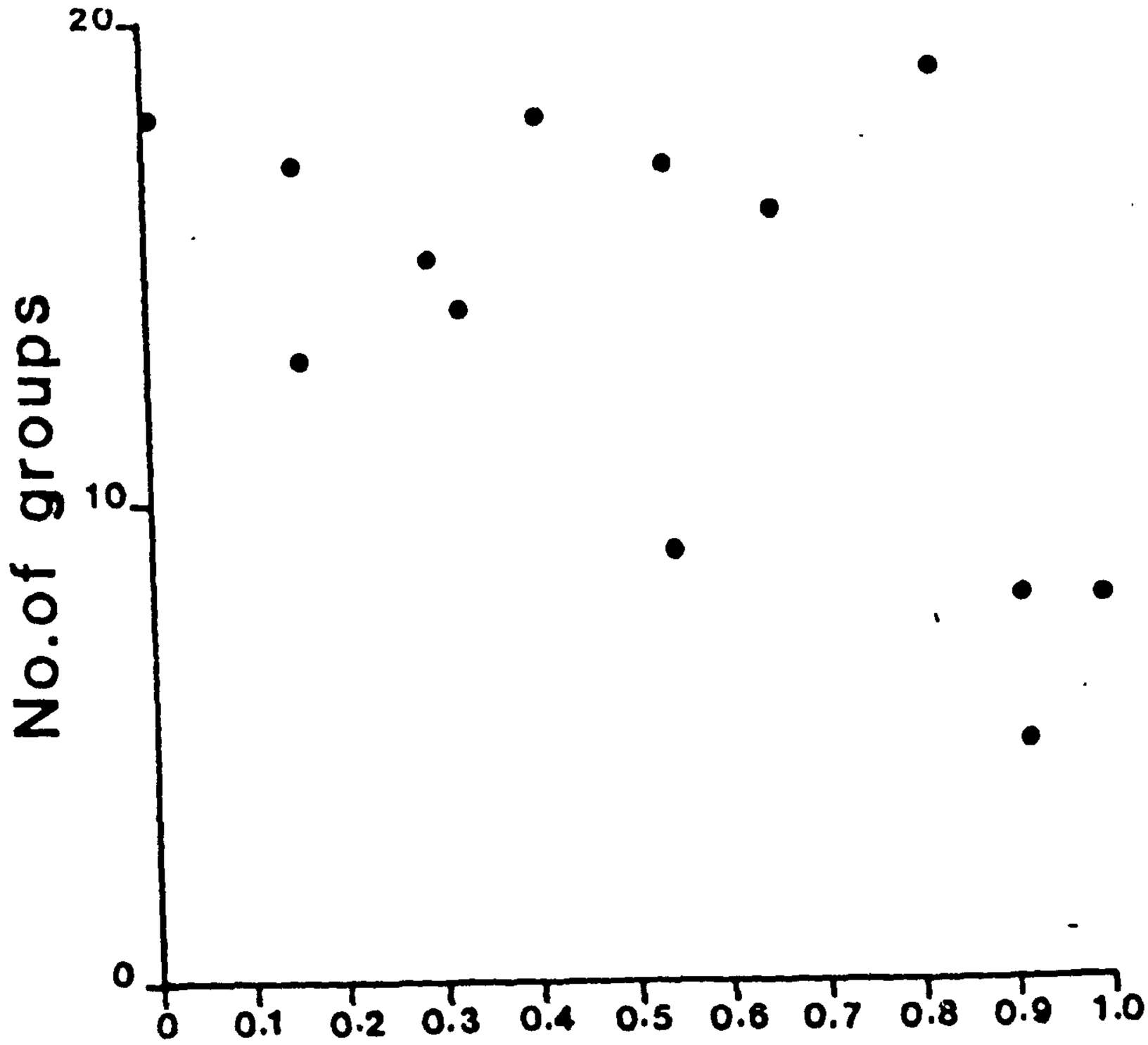
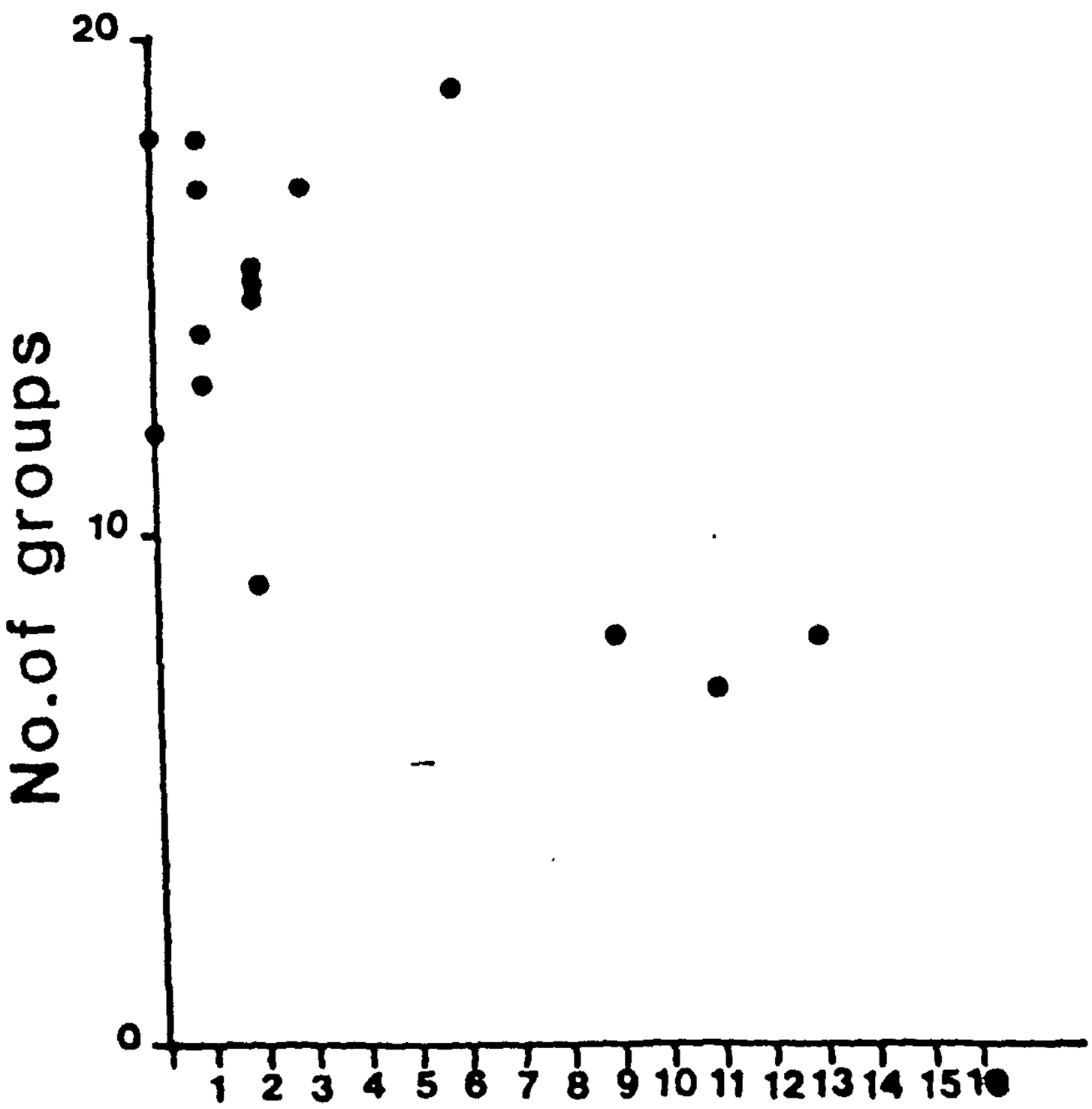


Fig. 5.9 The relationship of (A) dominance ratio and (B) estimated mating success to the total distance moved by males of two or more years of age during the 1981 rutting period.



(A) Dominance ratio



(B) Estimated mating success

Fig. 5.10 The relationship of A) dominance and B) estimated mating success to the number of groups visited by males during the 1981 rut.

rank in the group. Males were significantly less likely to leave a rutting group than a non rutting group, (χ^2=23.2, d.f.=1, p<0.001; Fig. 5.11). The probability of a high ranking male (relative rank 1 or 2) with access to an oestrous female leaving a rutting group was significantly less than would be expected by chance, (relative rank 1: χ^2=26.5, d.f.=1, p<0.001; relative rank 2: χ^2=5.92, d.f.=1, p<0.05; Figs. 5.12 and 5.13). The probability of a subordinate male leaving a rutting group did not differ significantly from that expected if movement between groups was random.

5.5 AGGRESSION AND FIGHTING

Two distinct forms of aggression were observed during the rut. I termed these 1) Aggressive Encounters and 2) Fights. Aggressive encounters were defined as those social interactions where one male delivered one or several of the following behavioural acts (see Chapter 1): a stare threat, horn threat, butt, rush or chase to a second male which might respond by either moving away or returning one or more of these behavioural acts. If the interaction escalated to a point where both males clashed head to head more than once then the interaction was defined as a fight.

Aggressive encounters tended to be short in duration (< 1 min). Fights were very variable in length and those seen lasted for between less than one minute and 2 hours 20 minutes. Fights develop from aggressive encounters in which the threatened male continues to return the threats until one male moves forward head lowered and

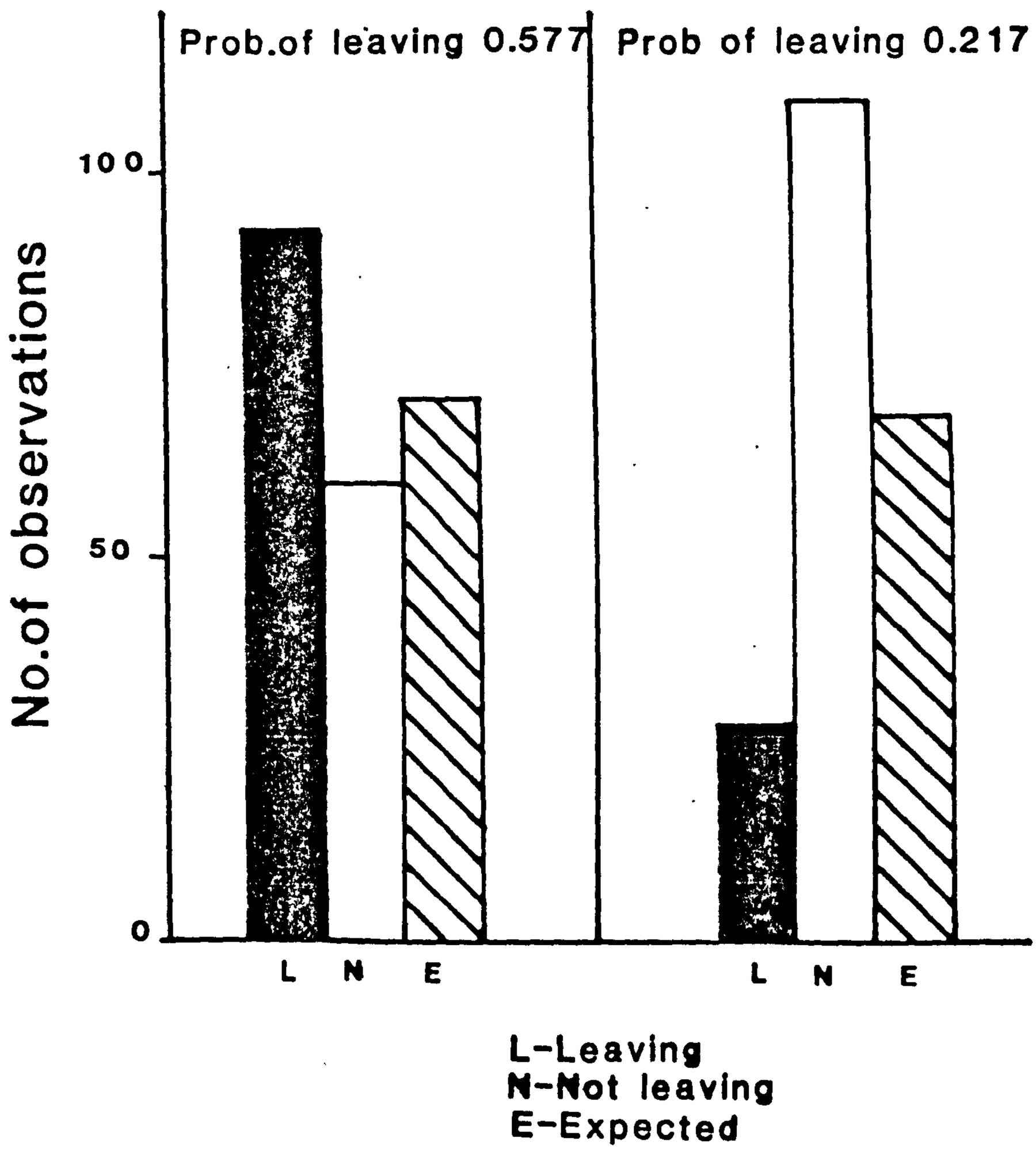


Fig. 5.11 Number of observations of males leaving rutting and non rutting groups. The probability of a male leaving a rutting group was significantly less than the expected value. (χ^2=23.2, d.f.=1, p<0.001).

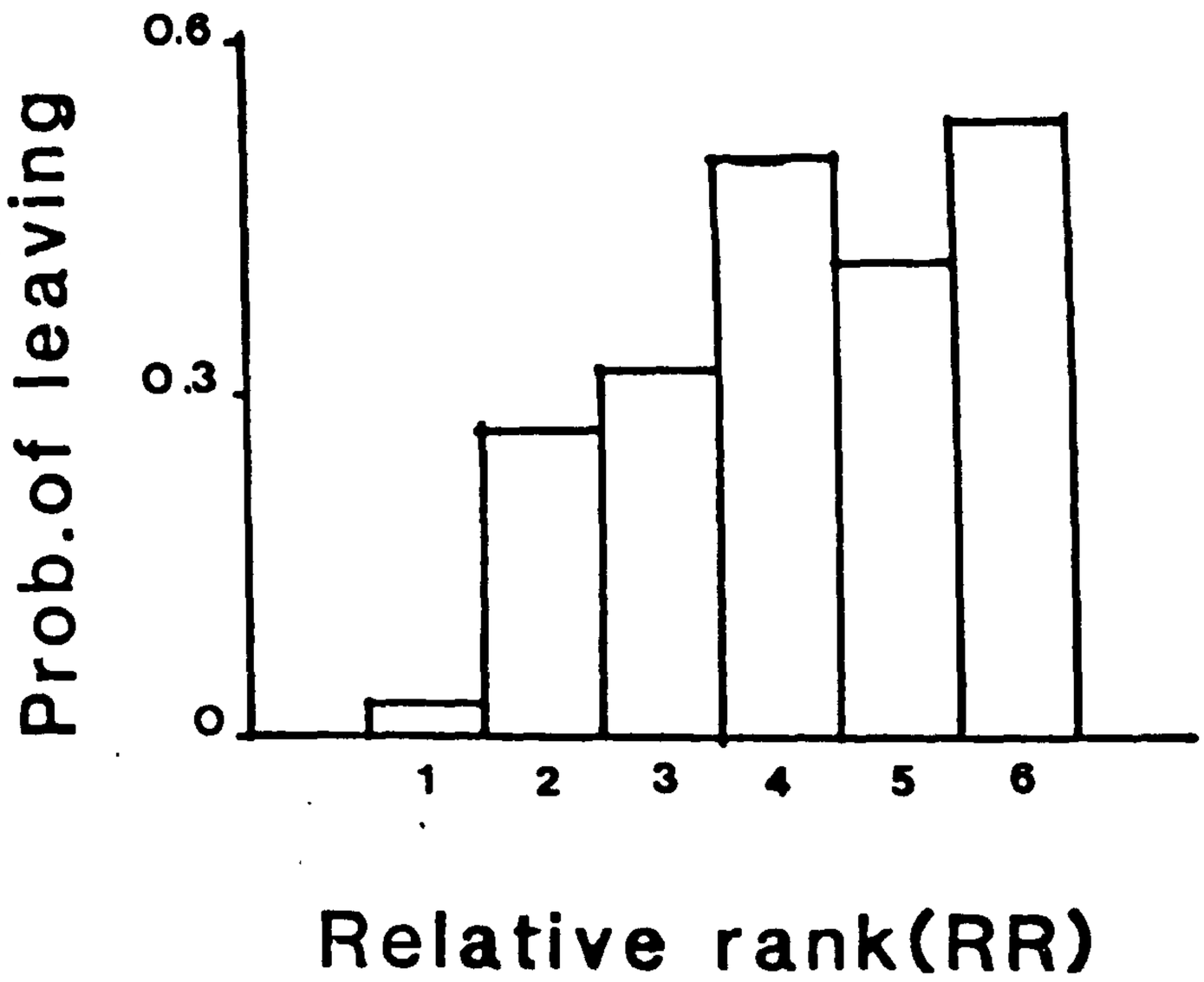


Fig. 5.12 The probability of males of different relative ranks leaving a rutting group.

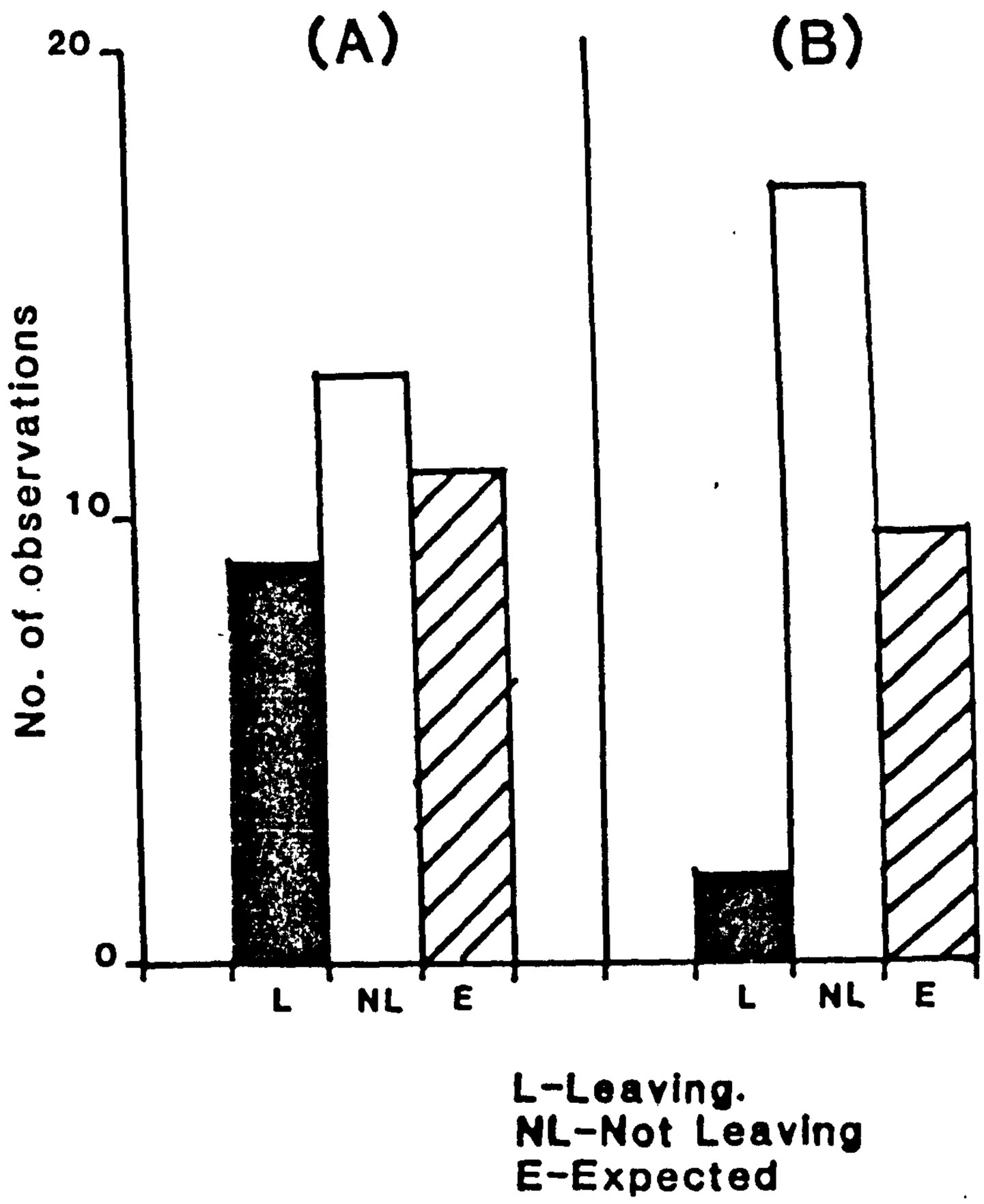


Fig. 5.13 The number of times a male of RR 2 was seen to leave a rutting group with A) one oestrous female present (p=0.40) and B) two oestrous females present (p=0.10).

clashes. At this point one male may withdraw but if not the two animals will continue to clash. In the early stages of a fight the two males lock horns for only short periods of time after each clash. They often clash several times in rapid succession. As the fight continues the two aggressors clash less frequently and spend more time with their horns locked trying to push each other backwards. If on clashing their horns do not lock but slide past each other's, they show no hesitation in delivering sideswipes with their horns into the flank, belly or neck of their opponent. Fights usually have a conclusive outcome with the loser walking or running away from the victor who may deliver gobbles or leg kicks to the loser.

5.5.1 Dominance among males

All males over two years of age were dominant to yearlings and yearlings were dominant to male kids. In 1981 the dominance rank of adult males was correlated with pre-rut body weight (r_s =0.89, d.f.=9, $p<0.001$; Fig. 5.14) and horn length (r_s= 0.70, d.f=9, $p<0.01$; Fig.5.15). However, males and their horns increase in size with age (Figs. 5.16 and 5.17) so a Kendal partial rank correlation analysis was carried out to investigate the effect of age. The Kendal correlation coefficient between pre-rut body weight and rank was 0.70. When age was partialled out the correlation between pre-rut body weight and rank was 0.67 which is not much smaller than 0.70 suggesting that the correlation between pre-rut body weight and rank is largely independent of age. However, when age is partialled

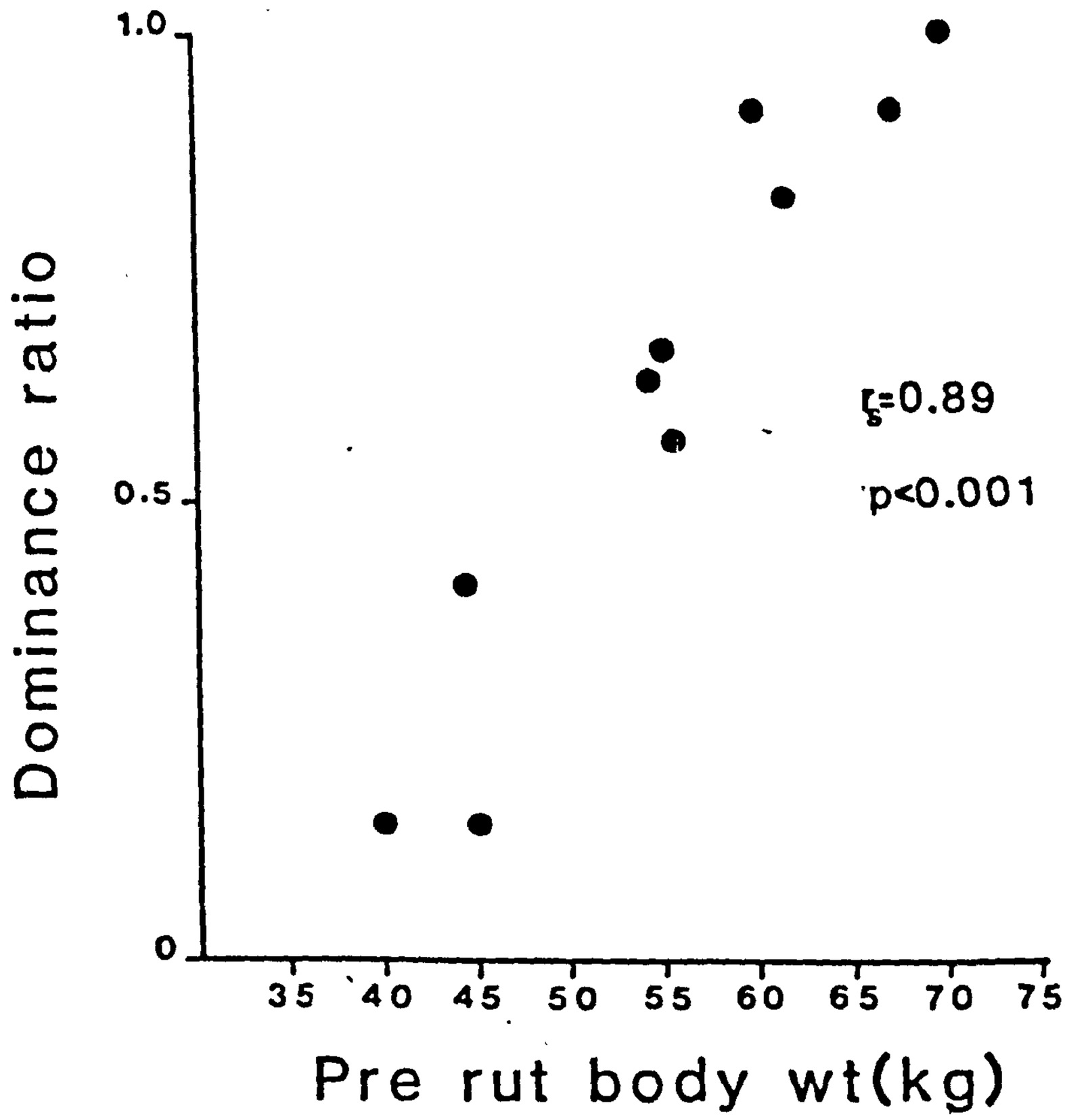


Fig. 5.14 The relationship between pre-rut body weight and dominance in adult males.

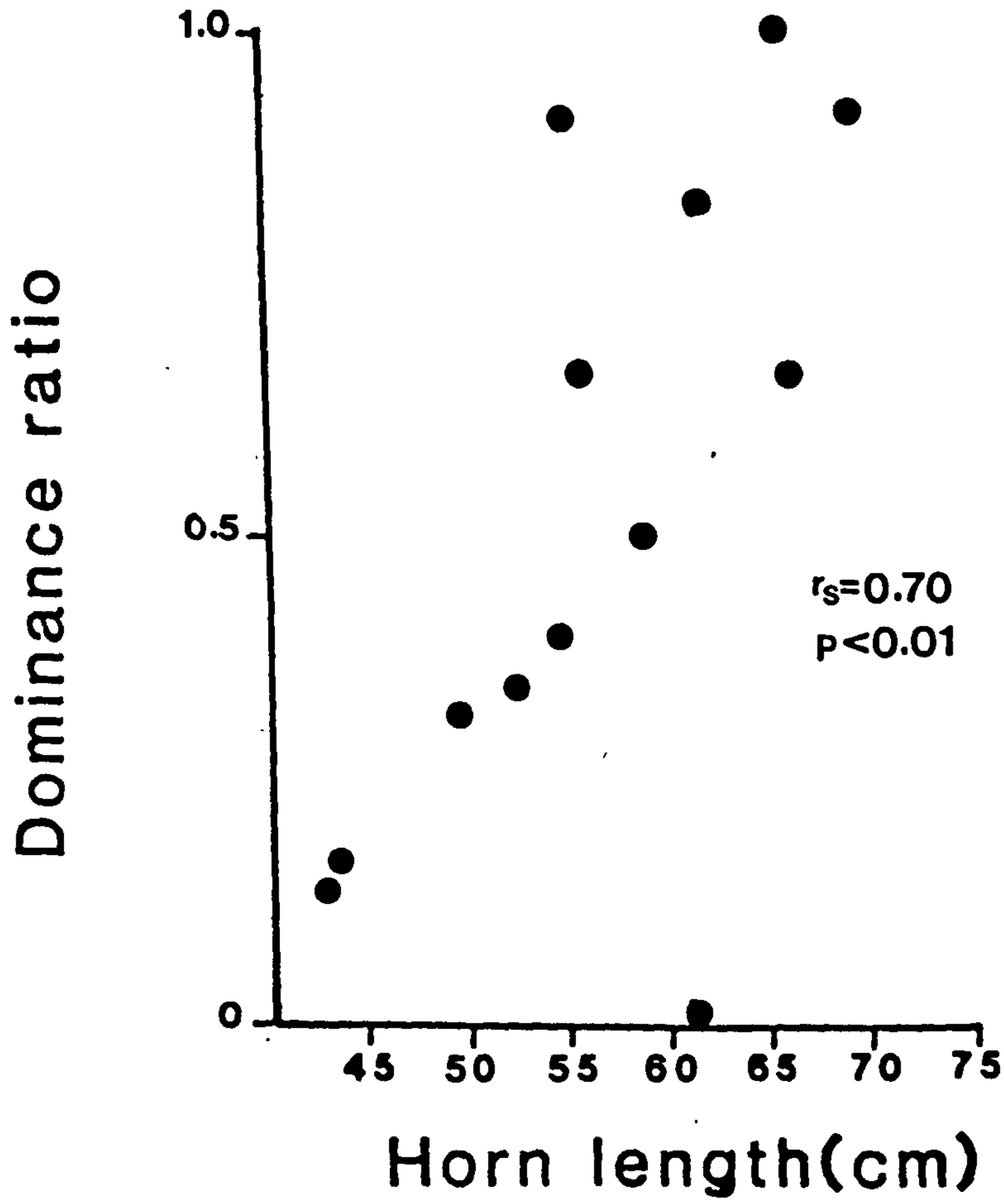


Fig. 5.15 The relationship between horn length and dominance in adult males.

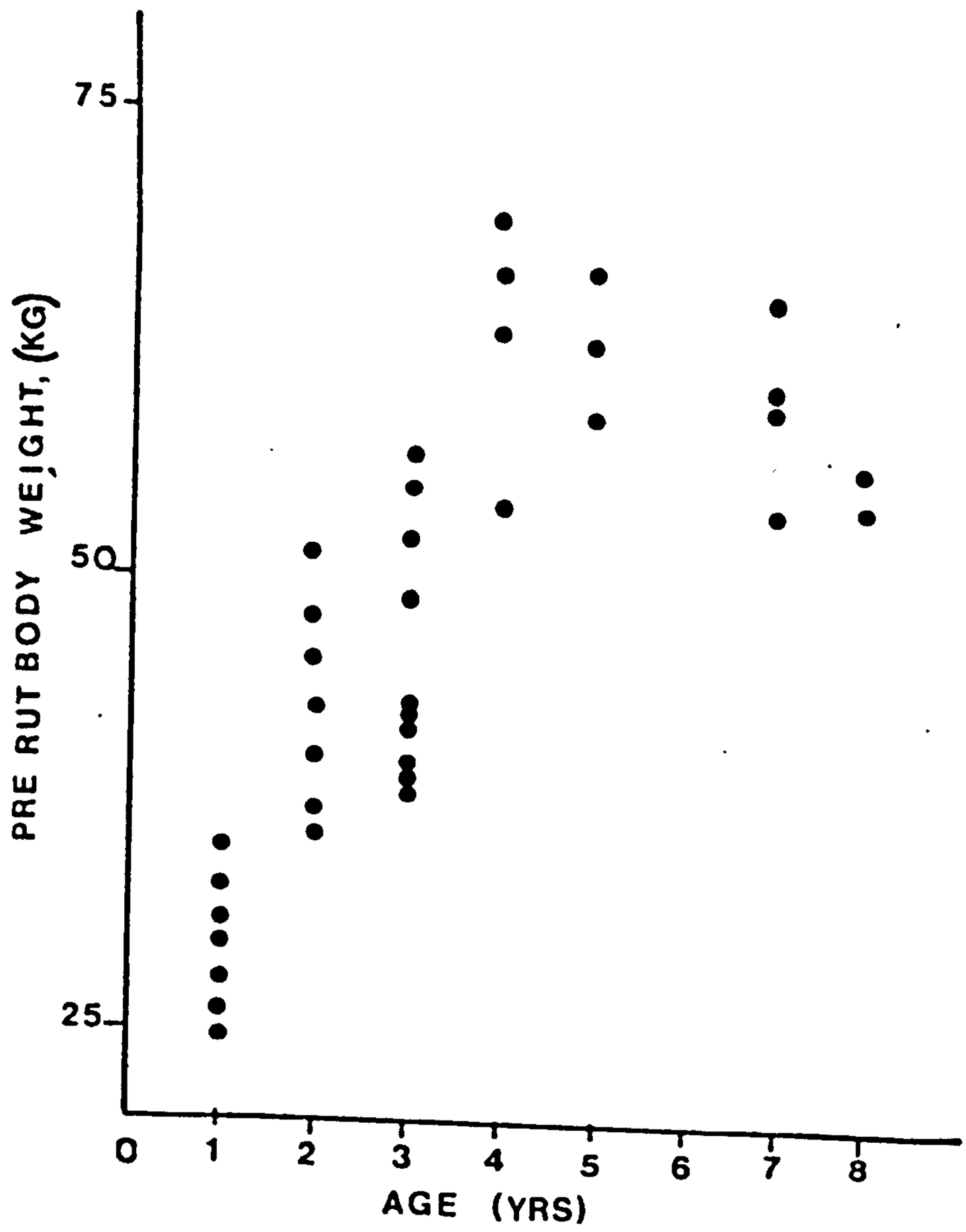


Fig. 5.16 The relationship between pre-rut body weight and age in male goats.

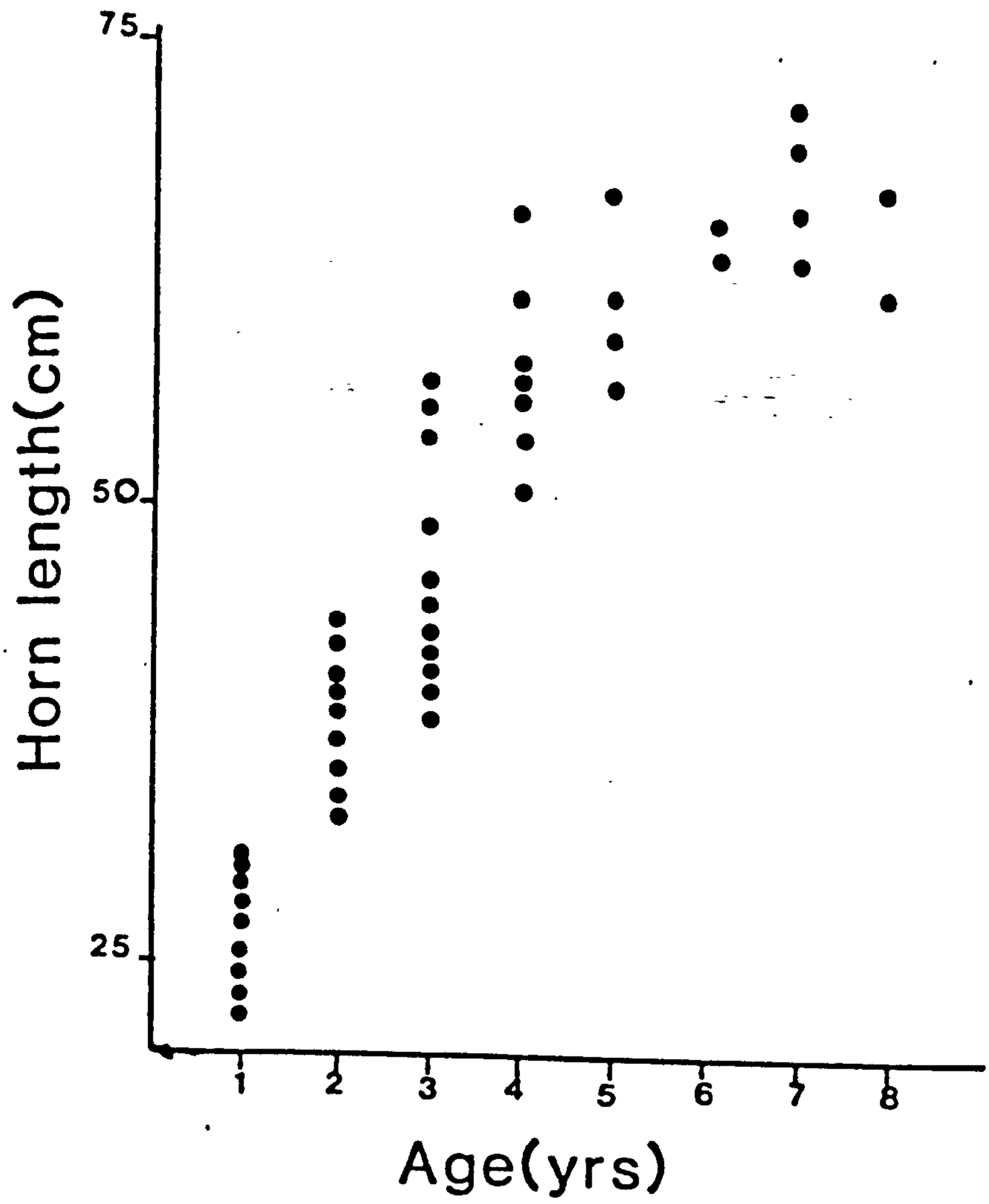


Fig. 5.17 The relationship between horn length and age in male goats.

out of the correlation between horn length and rank the correlation coefficient drops from 0.47 to 0.32, suggesting that this correlation is more dependent on age. If one considers only those males over four years of age (there is no increase in pre-rut body weight in males greater than four years old) then dominance rank is still significantly correlated with pre-rut body weight but not with horn length (Figs. 5.18 and 5.19)

5.5.2 Timing of fights and aggressive encounters

If males act aggressively during the rut to increase their chances of mating with an oestrous female then evolutionary theory would lead us to expect the level of aggression to vary in relation to the availability and distribution of this limited resource.

The level of aggression between male goats is much higher during the rut than the rest of the year (Fig. 5.20). The frequency of aggressive encounters between males in the main study area was correlated with the number of females in oestrus during each 10 day period between 20 August and 9 November (Fig. 5.21; r_s=0.78, d.f.=6, $p<0.05$). The level of aggression was significantly higher in groups with one or more oestrous females present ($\bar{x}$=39.4 acts/g-hr) than in groups where no females were in oestrus ($\bar{x}$=4.8 acts/g-hr; Mann-Whitney U-test: z=3.2, n1=196, n2=324, $p<0.001$). Most of these aggressive acts were delivered by a dominant male that was courting and defending an oestrous female (Fig. 5.22).

During her oestrous period a female appears only to be receptive for a short period. During this period a female will

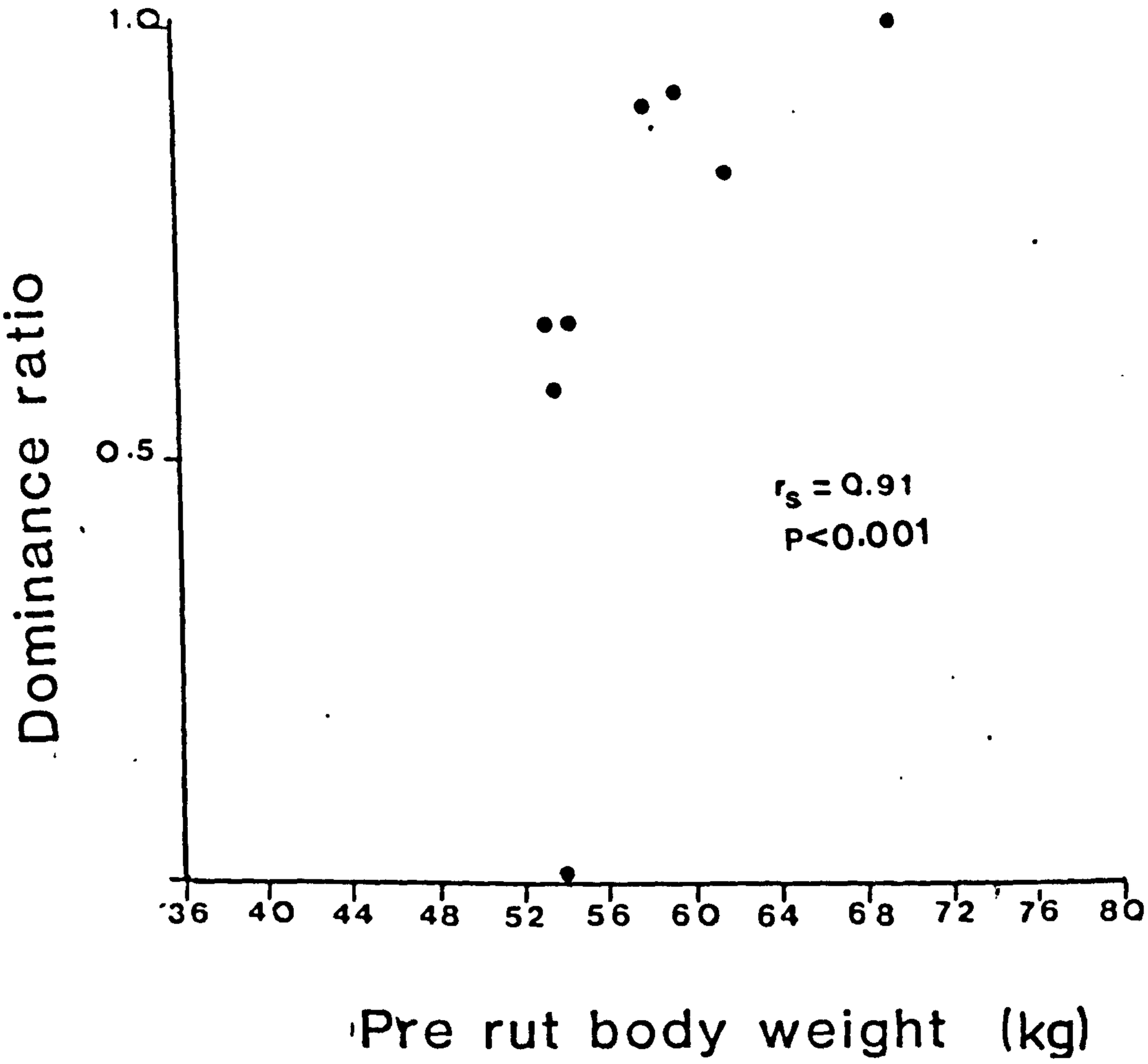


Fig. 5.18 The relationship between pre-rut body weight and dominance in male goats over four years old.

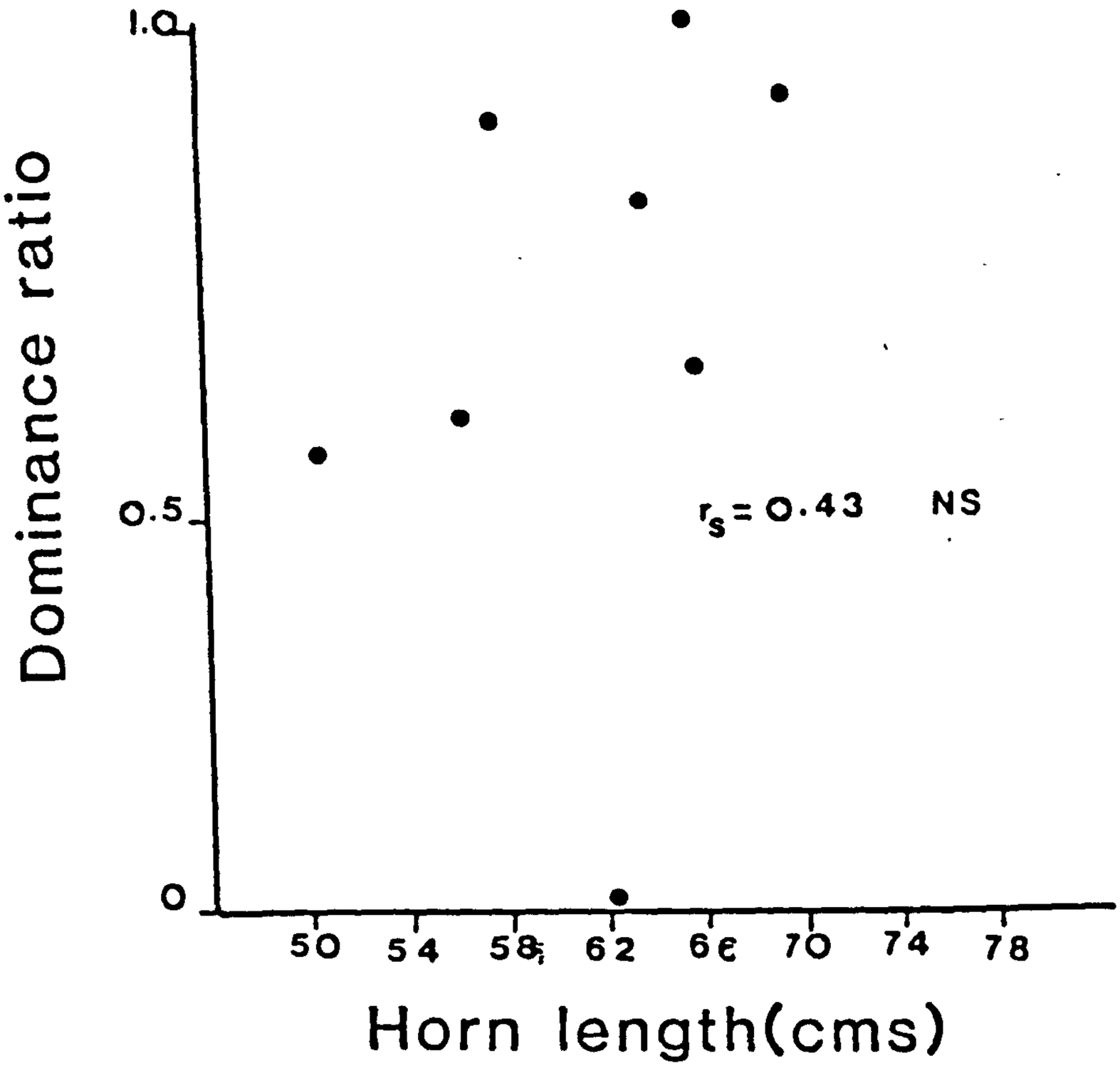


Fig. 5.19 The relationship between horn length and dominance in male goats over four years old.

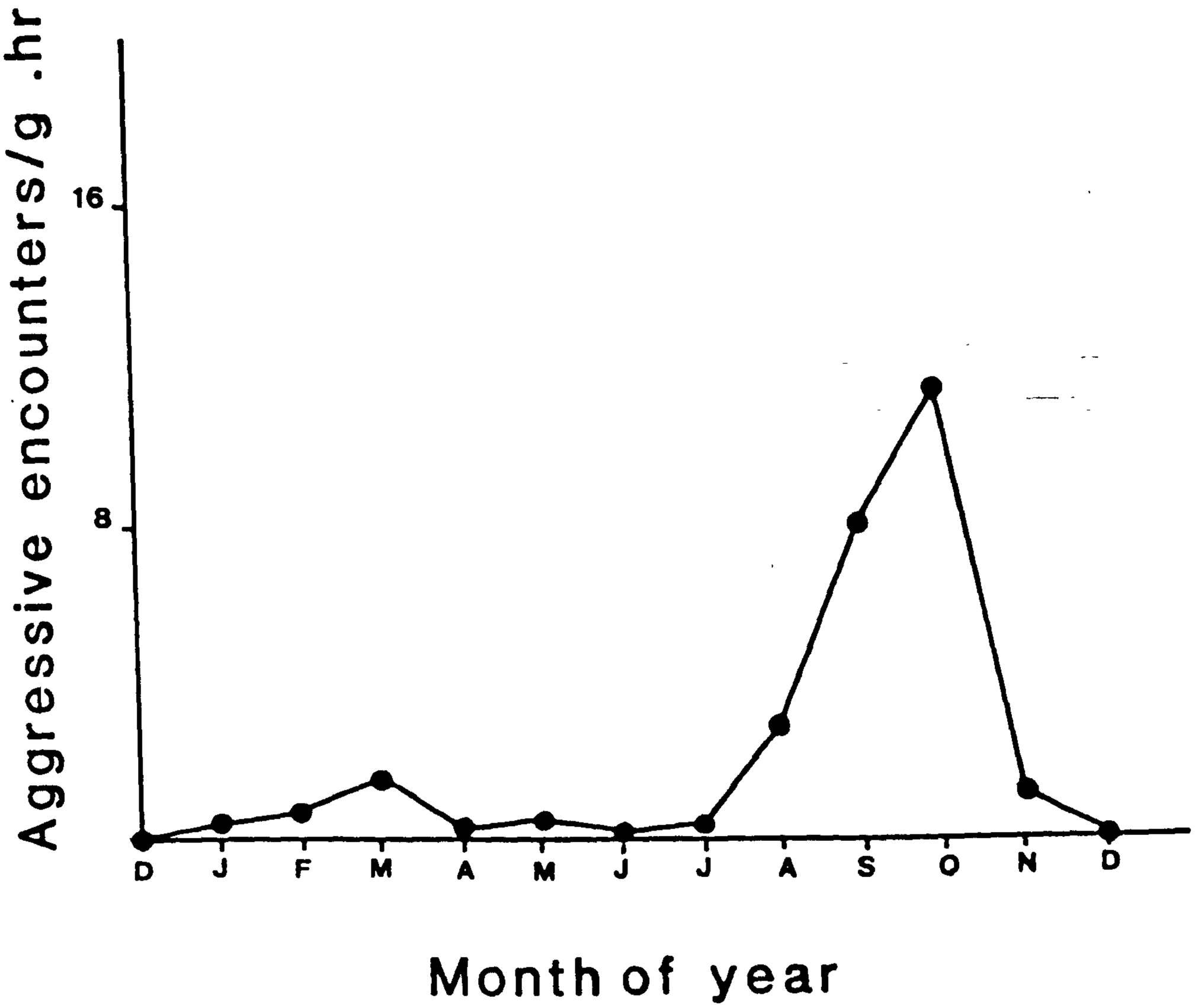


Fig. 5.20 The number of aggressive encounters between males throughout the year. Play fighting between male kids is not included.

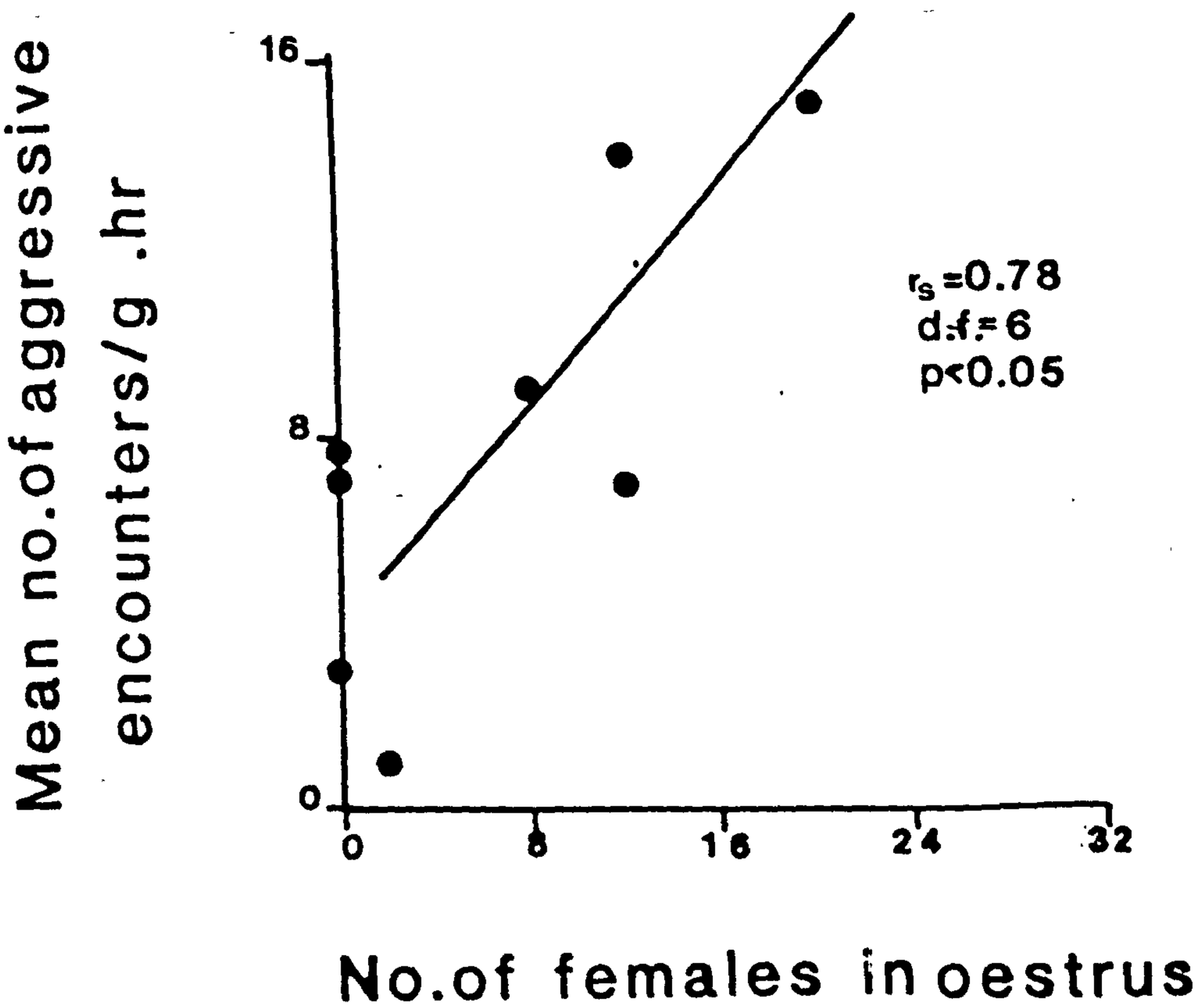


Fig. 5.21 The relationship between the number of females in oestrus and the frequency of aggressive encounters between males during each ten day period of the 1981 rut.

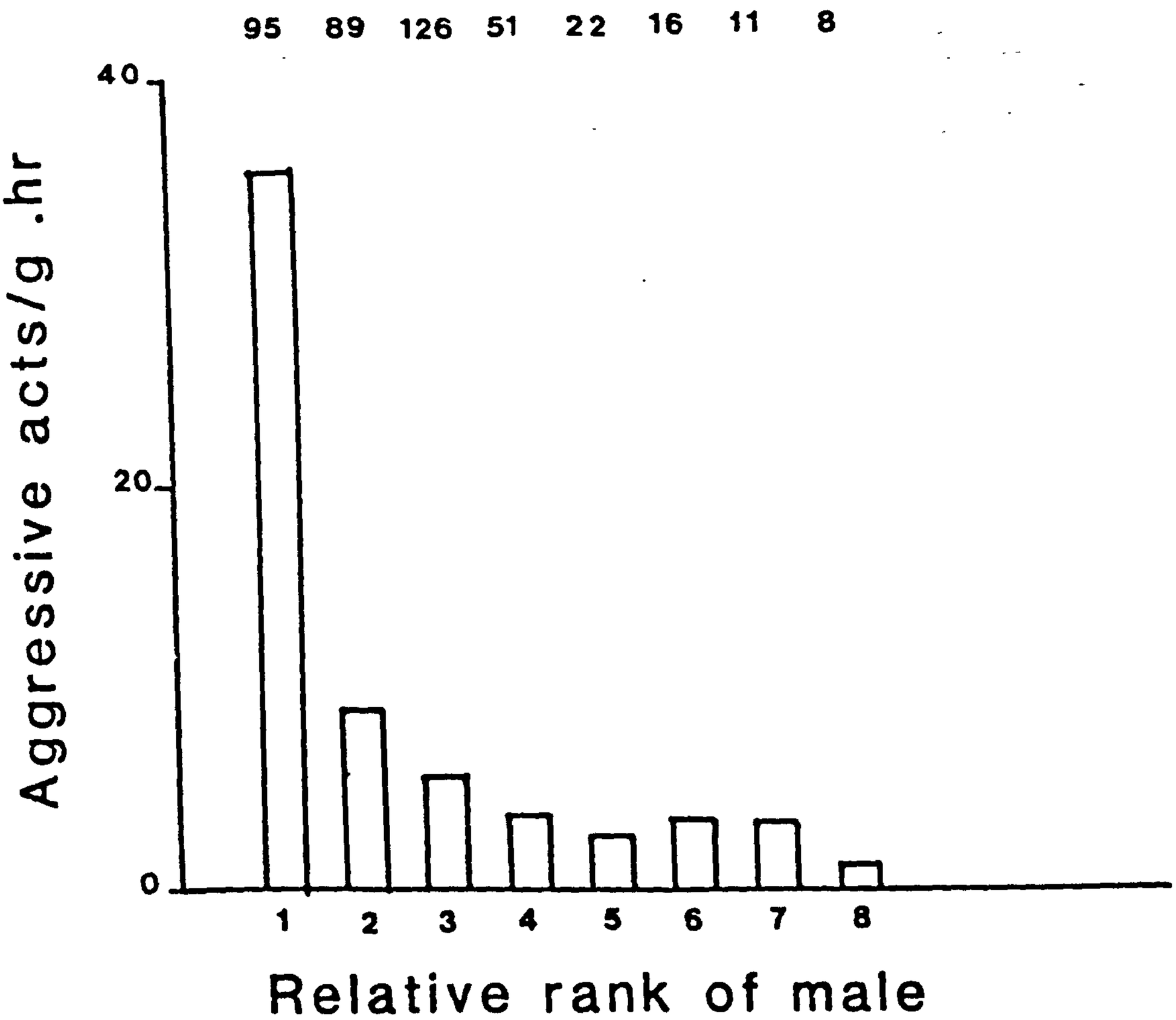


Fig. 5.22 The frequency of aggressive acts delivered by males in a group with a dominant male defending an oestrous female. The numbers above the columns indicate the number of five minute focal animal watches for each rank of goat.

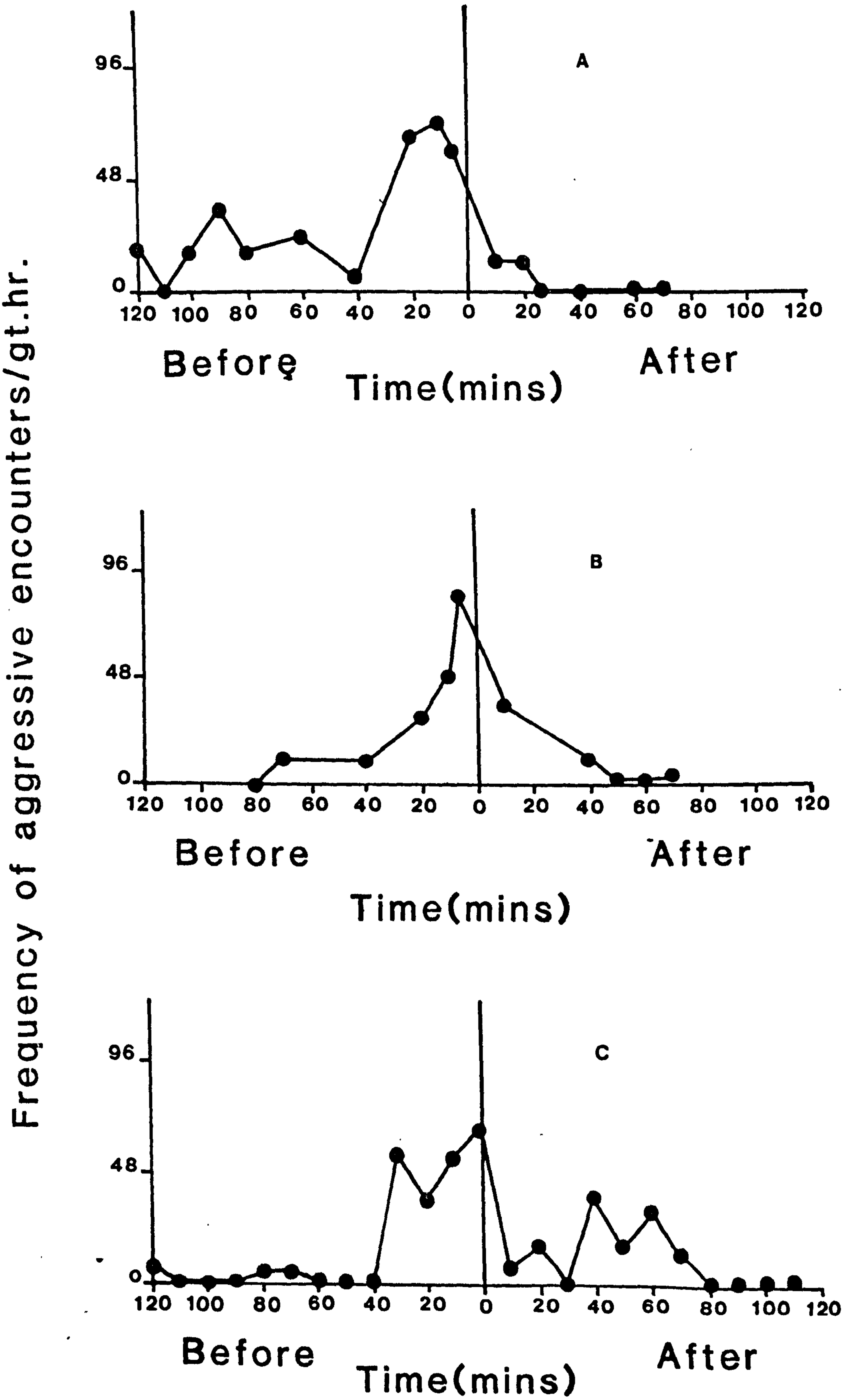
tail-wag in response to a male's sexual approaches and is willing to be mated by a courting male (see 5.6.2). After a successful mating no female was seen to be mated again for at least two hours. It can be seen in Fig. 5.23 that during the hour prior to a successful mating the frequency of aggressive encounters involving the dominant male was significantly greater than that during the 60 minute period two hours prior to mating and during the hour after successful mating (2 hours prior to mating: $U=45.5$, $p<0.01$; hour after mating: $U=51.5$, $p<0.01$).

Fights occurred much less frequently (0.02/male goat hr) than aggressive encounters (9.98/male goat hr) during the rut. A total of 40 fights between male goats were observed of which 31 were seen from start to finish. The frequency of fights increased during the rut with a peak coinciding with the peak in the number of oestrous females (Fig. 5.24).

5.5.3 Age and rank difference in opponents in aggressive encounters

In rutting groups there was no relationship between the frequency of aggressive acts directed at a particular male and that male's age or rank relative to the male delivering the behavioural acts, i.e. a dominant male defending a female did not direct more aggressive acts to the number two ranked male in that particular group than to a lower ranked male (Fig. 5.25). However it can be seen from Figs. 5.26 and 5.27 that the type of aggressive act given varies with the age and relative rank of the recipient. A dominant male defending a female gives proportionately more high intensity

Fig. 5.23 The frequency of aggressive encounters before and after a successful mating during three courtship sequences, A, B and C, involving different males and females.


Frequency of aggressive encounters/gt.hr.
A
96
48
0
120 100 80 60 40 20 0 20 40 60 80 100 120
Before
After
Time(mins)
B
96
48
0
120 100 80 60 40 20 0 20 40 60 80 100 120
Before
After
Time(mins)
C
96
48
0
120 100 80 60 40 20 0 20 40 60 80 100 120
Before
After
Time(mins)

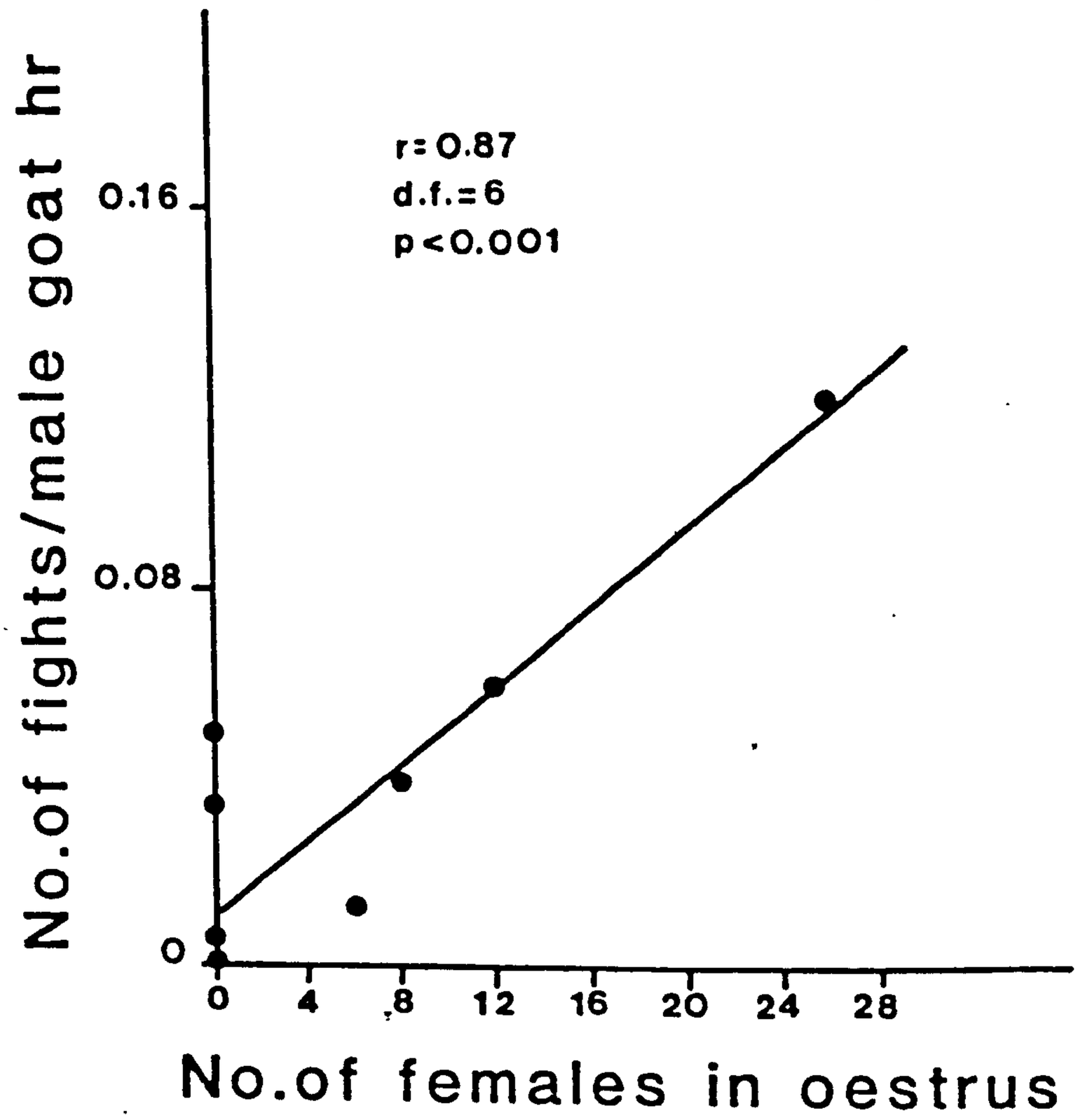


Fig. 5.24 The relationship between the frequency of fights and the number of females in oestrus during each ten day period of the rut.

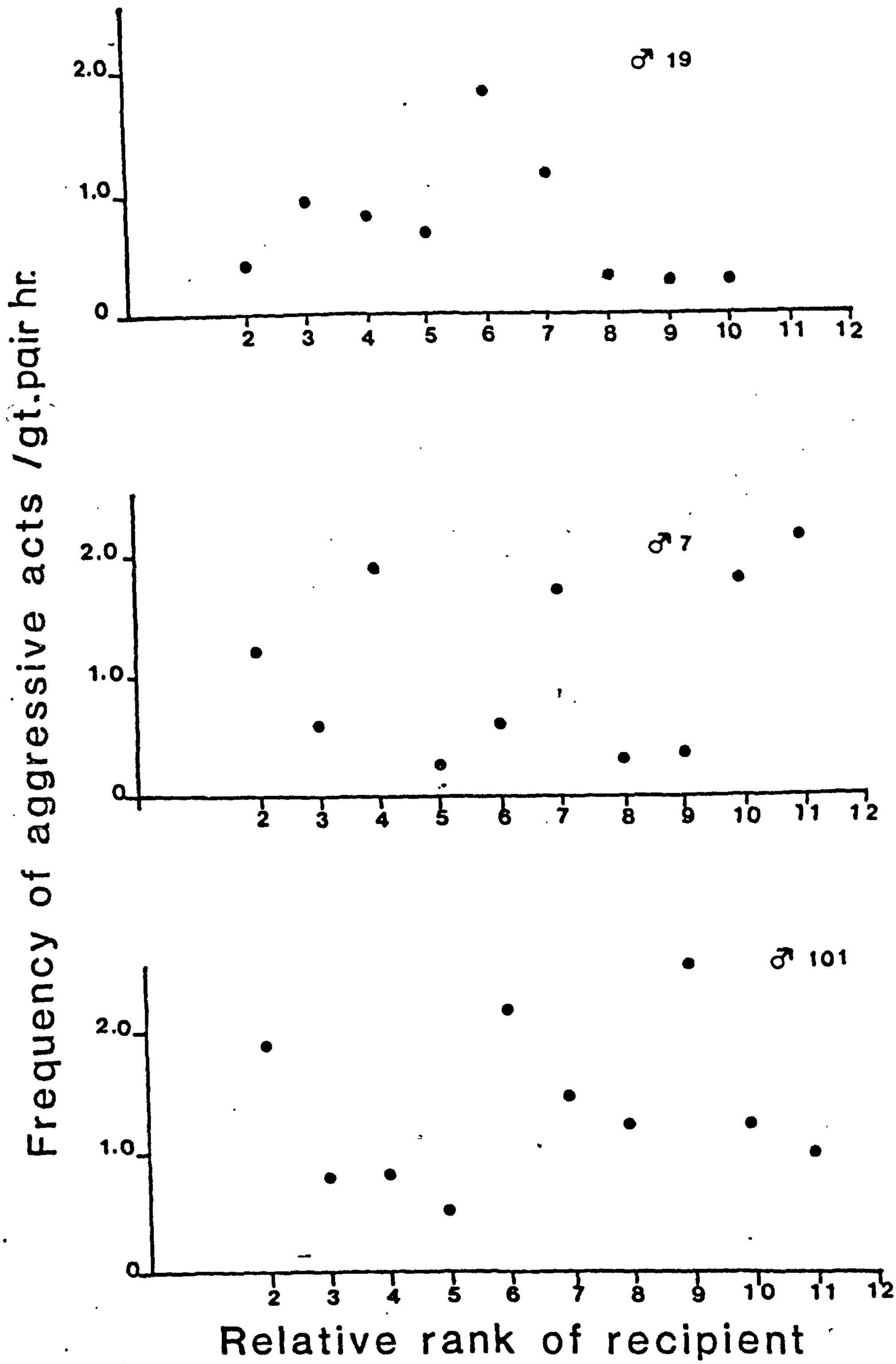


Fig. 5.25 The relationship between the frequency of aggressive acts delivered by three dominant males to other males. All frequencies were corrected for the amount of time each dominant male was seen with males of each relative rank.

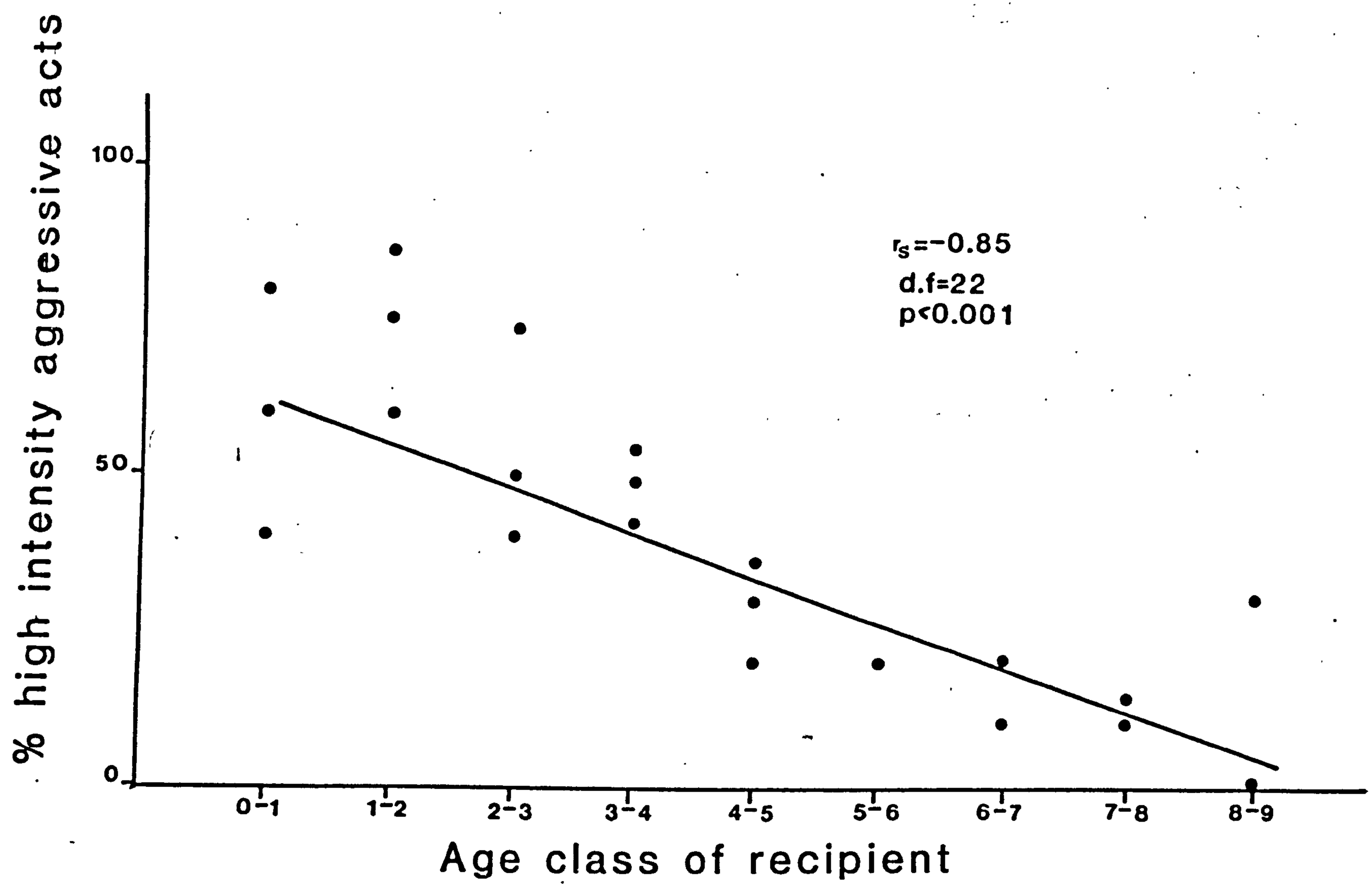


Fig.5.26 The relationship between the percentage of aggressive acts of high intensity (rush, butt, chase) delivered by a dominant male and the age of the recipient male.

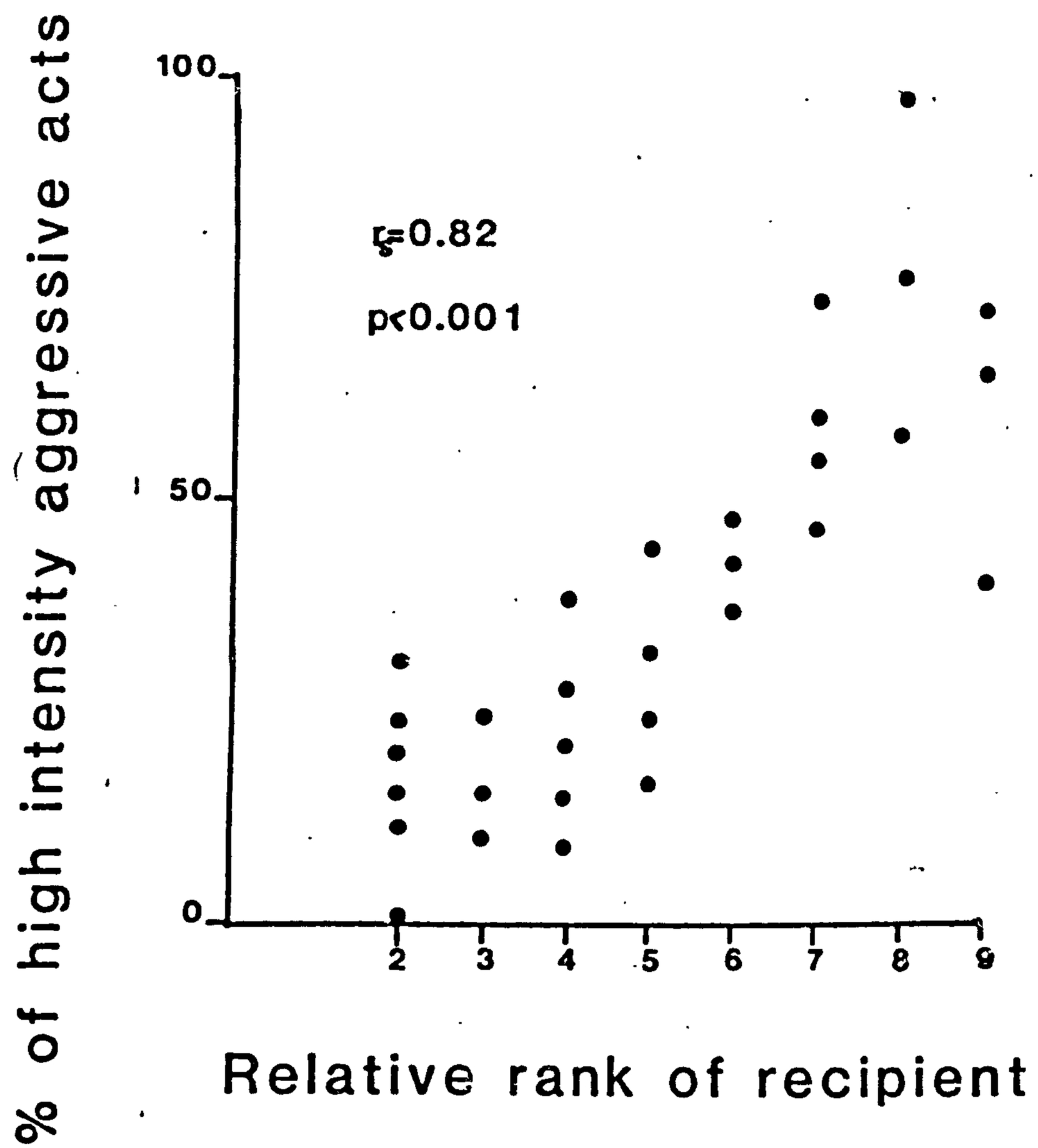


Fig. 5.27 The relationship between the percentage of aggressive acts of high intensity (rush, butt, chase) delivered by a dominant male and the relative rank of the recipient.

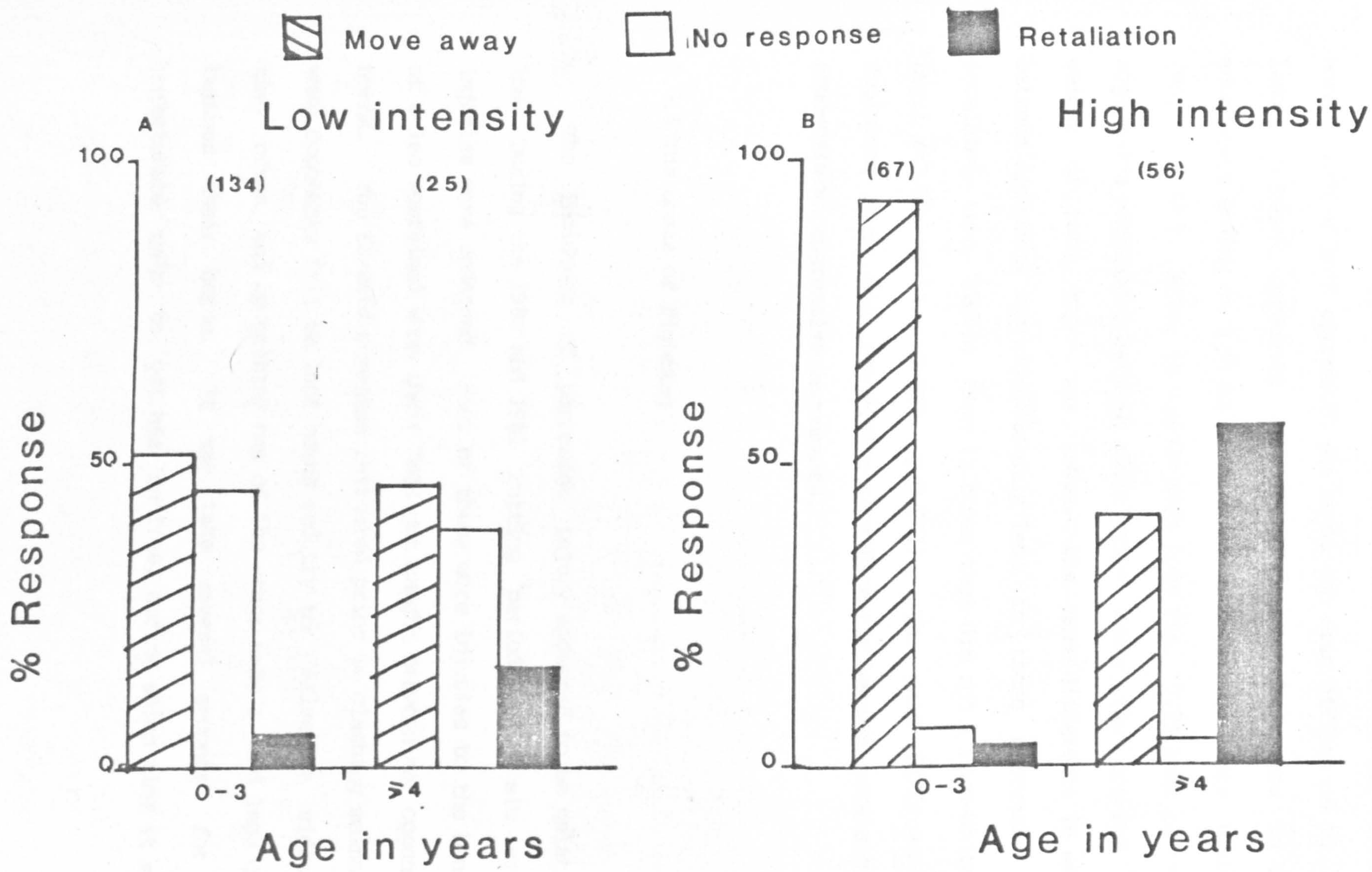
aggressive acts (butt, rush or chase) to younger, lower ranking males than to males of similar age and rank to himself.

The response by a male to these aggressive acts varies with his age and the type of aggressive act (high or low intensity). It can be seen from Fig. 5.28 that high intensity aggressive acts were significantly more likely to provoke a male under four years of age to move away than a low intensity act (0-3 year-old males: X^2 =32.4, d.f.=1, $p<0.001$). However males over four years of age appear to be less likely to move away in response to a high intensity aggressive act than a low intensity act although the difference is not statistically significant. There are probably considerable risks for a dominant male in directing a high intensity aggressive act to a male older than four years, because these older males are just as likely to return the aggressive act as to move away (Fig. 5.28).

In 25% (7 out of 28) of instances where a dominant male delivered a high intensity act towards a male over four years old the encounter escalated into a fight. Fights between males also develop from aggressive encounters where the reactor returns a horn threat. These periods of reciprocal horn threatening are usually rather short (< 1min) in duration, although on five occasions they lasted more than 20 minutes. These prolonged periods of horn threatening were interspersed with bouts of horn thrashing and feeding. Three of these encounters escalated into fights while in the other two one male withdrew.

In all aggressive encounters between one male less than two years and another greater than two years of age the younger male withdrew. However in aggressive encounters between adult males the

Fig. 5.28 The frequency of various responses (Move away, No response, Retaliation) by males to (A) low and (B) high intensity aggressive acts delivered by dominant males. The figures in brackets indicate the sample size for each class.


Move away
No response
Retaliation
Low intensity
High intensity
A
B
100
50
0
% Response
(134)
(25)
(67)
(56)
0-3
≥4
Age in years

average difference in age of opponents did not differ significantly between escalated and non-escalated aggressive encounters (Fig. 5.29). In 53 aggressive encounters between adult males where the horn length of both opponents was known the mean difference in horn length between opponents was (non-significantly) less in those encounters ending in a fight than in those when one male withdrew (Fig. 5.30). Also, it can be seen from Fig. 5.31 that in the 47 aggressive encounters between adult males where the pre-rut body weight of both males was known, the mean difference in weight between opponents was significantly less in those encouters that escalated into fights than in those that did not (Mann-Whitney U test: $z=3.59$, $n1=42$, $n2=268$, $p<0.001$). The mean difference in dominance rank did not differ significantly between escalated and nonescalated aggressive encounters.

5.5.4 The costs of fighting

The incidence of permanent injury appeared to be relatively low. During the 1980 and 1981 rutting periods only six serious injuries were observed. Four of these were injuries to the hind leg of males sustained when their legs got caught between an opponent's horns. The forward momentum initiated prior to clashing means that when opponents fail to lock horns and try to deliver a sideswipe, they often end up getting one of the other male's hind legs caught between their horns. It may take several seconds for the unfortunate male to get his leg free, during which time it may be

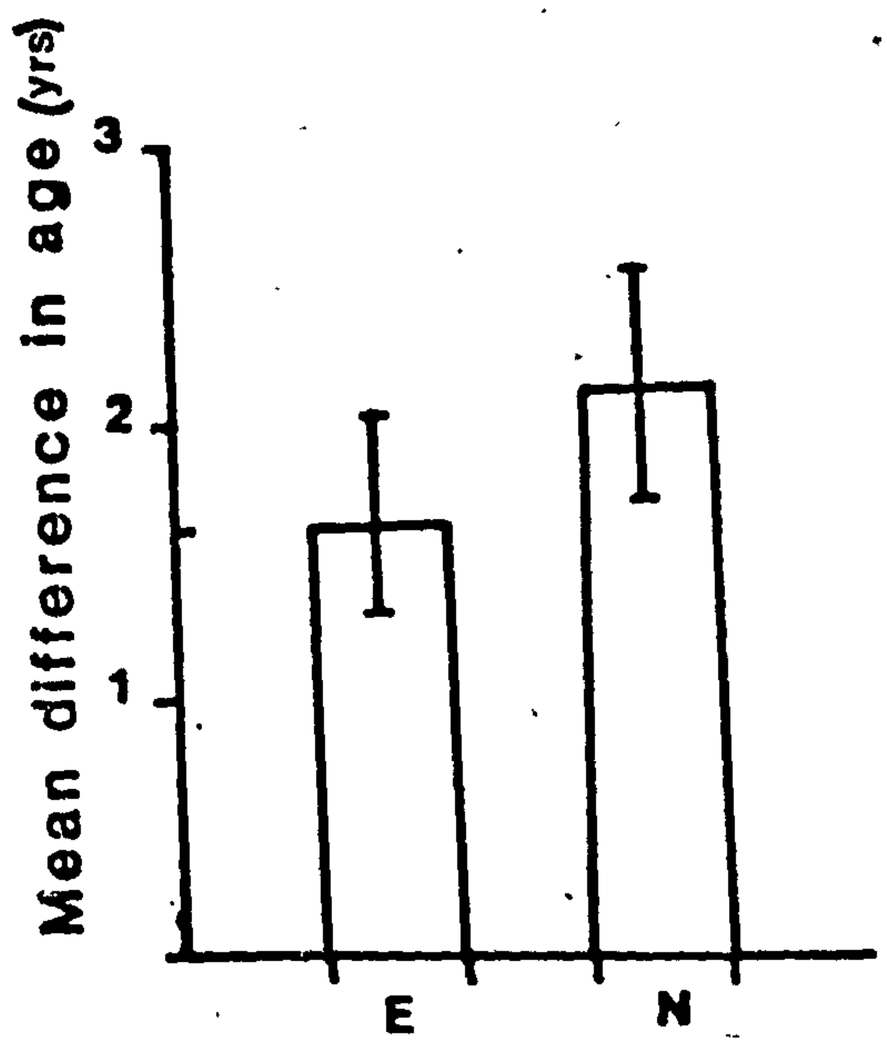


Fig. 5.29 Mean difference in age of opponents in escalated aggressive encounters (E) and non-escalated (NE) aggressive encounters. Vertical lines indicate 95% confidence limits.

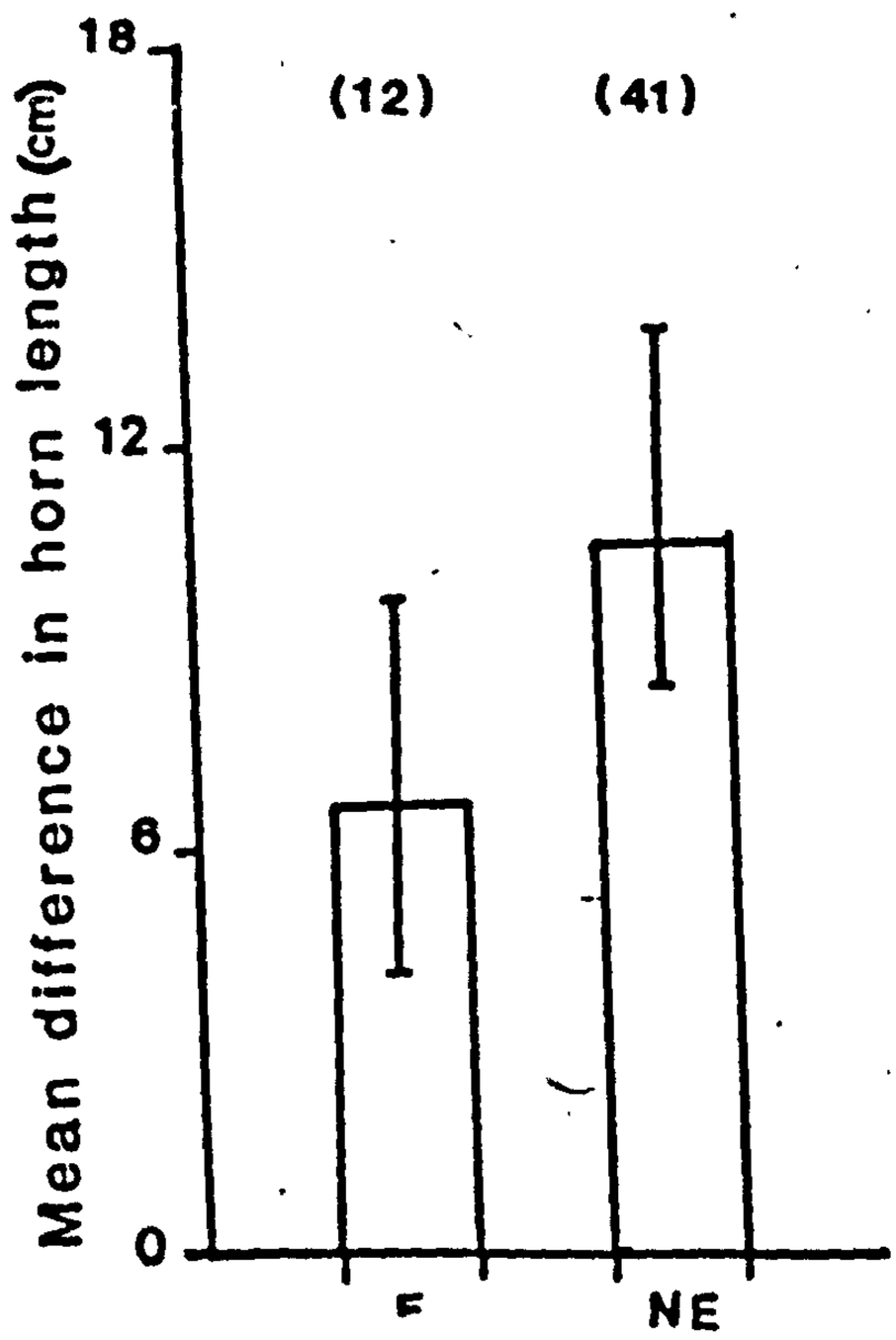


Fig. 5.30 Mean difference in horn length of opponents in escalated (E) and non escalated (NE) aggressive encounters. The vertical lines indicate 95% confidence limits and the sample size is given in brackets.

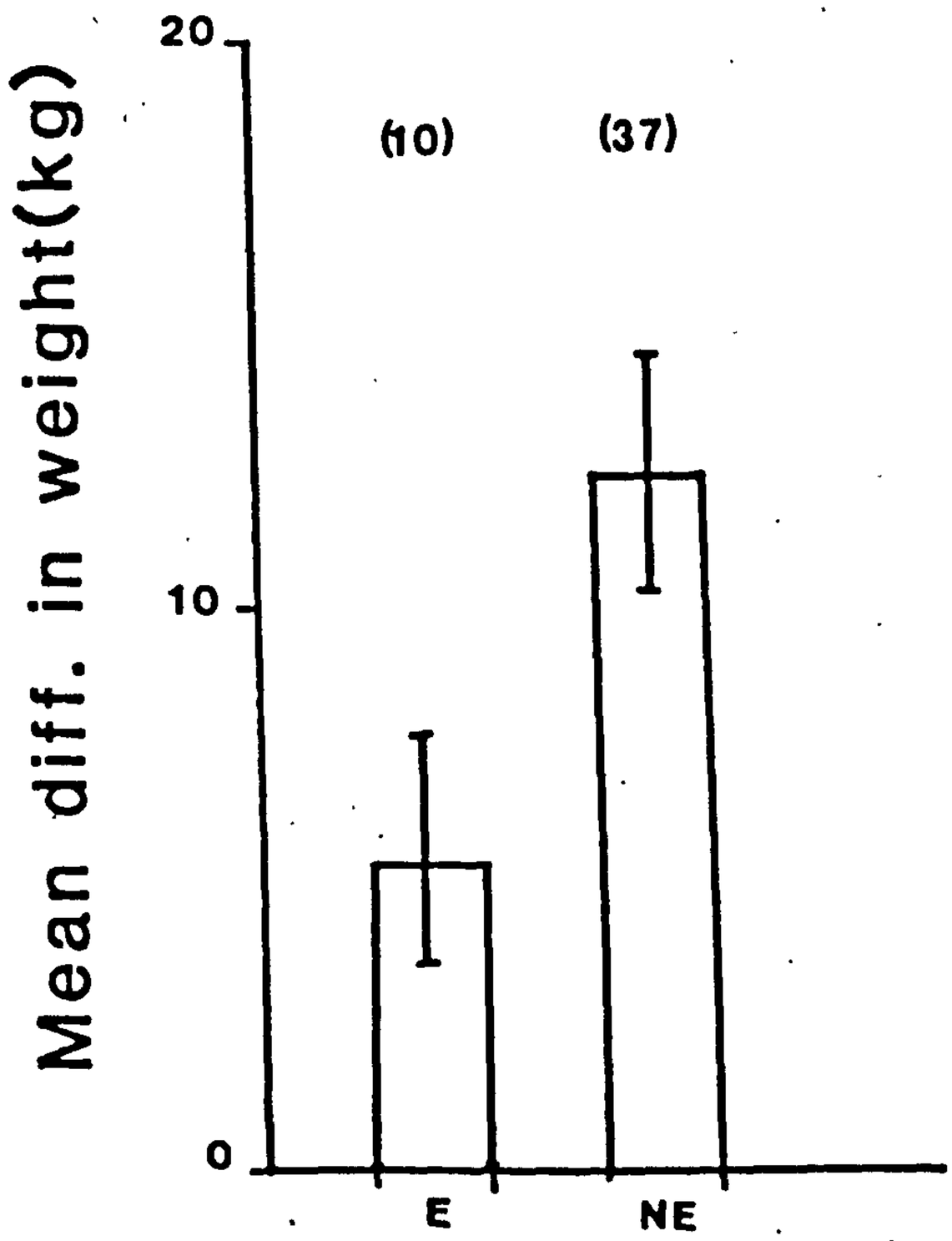


Fig. 5.31 Mean difference in weights of opponents in escalated (E) and non escalated (NE) aggressive encounters. The vertical lines indicate 95% confidence limits and the sample size is given in brackets.

twisted from side to side. The other two serious injuries observed were broken horns sustained by yearling males.

In addition to the costs of fighting due to energy expenditure and the risks of injury, fighting is also time consuming. Being involved in a long fight reduces the amount of time available for feeding, and for searching for and courting oestrous females. A dominant male involved in a fight cannot successfully defend an oestrous female. Twelve fights were observed which involved a dominant male which had previously been courting an oestrous female. During three (25%) of these fights another male successfully courted and mated the female while the fight was in progress.

There was no clear relationship between the difference in pre-rut body weight, horn length or age of opponents and the duration of the 31 fights observed from start to finish (Figs. 5.32, 5.33 and 5.34). However it can be seen from Fig. 5.35 that the duration of fights increased logarithmically with a decrease in the difference in the rank of the two opponents. In the 22 fights where the pre-rut body weight of each male was known the heavier males won more fights than would have been expected if there was no advantage in being heavier (Fig. 5.36). There was no clear relationship between age and success in fights (Fig. 5.37) and although there was a tendency for males with longer horns to beat males with shorter horns this was not a statistically significant trend (Fig. 5.38). Of the 12 fights over access to oestrous females mentioned above, 11 were won by the male originally courting the female. The pre-rut body weight of both males involved was known in nine of these fights and the heavier male was the victor in

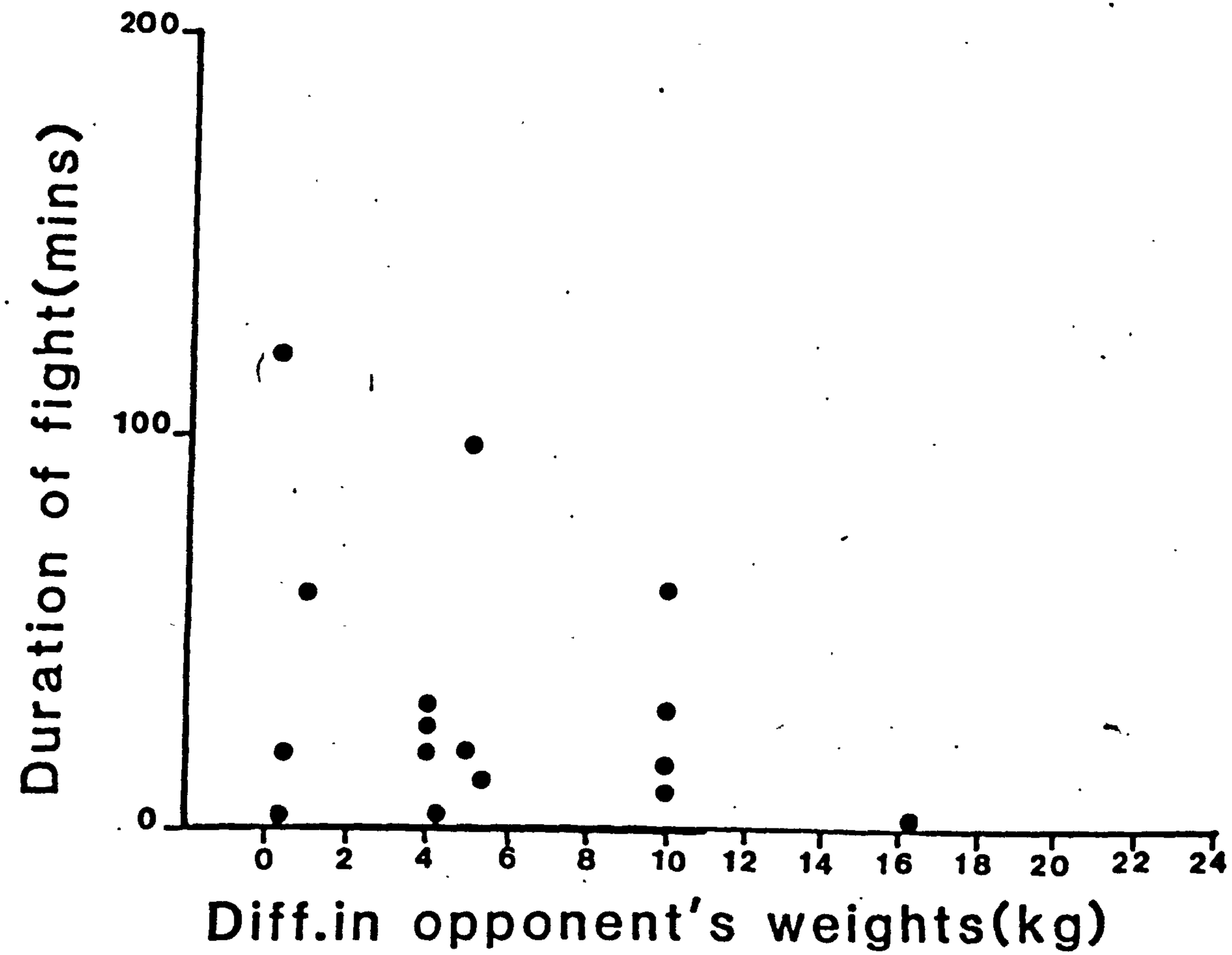
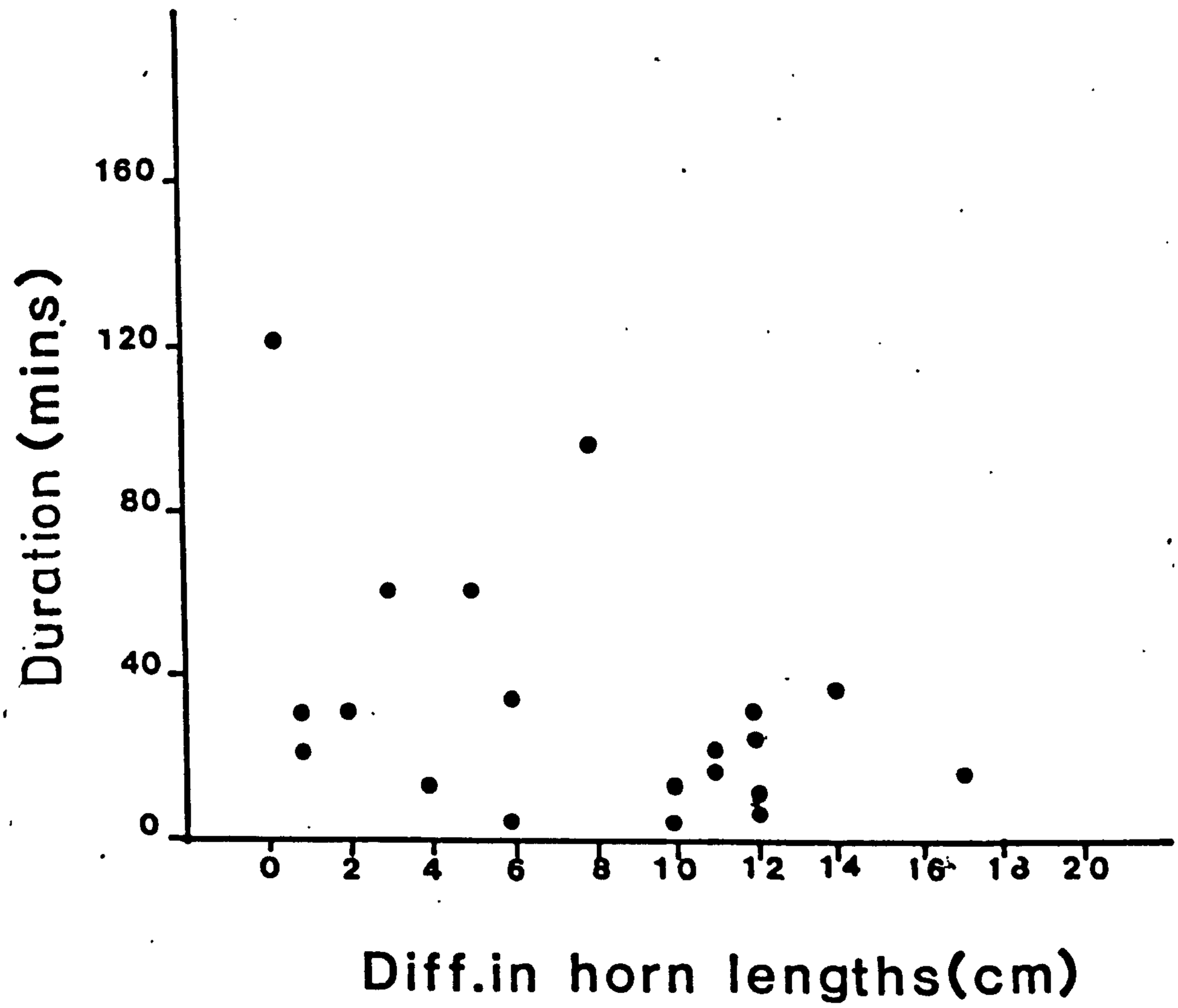
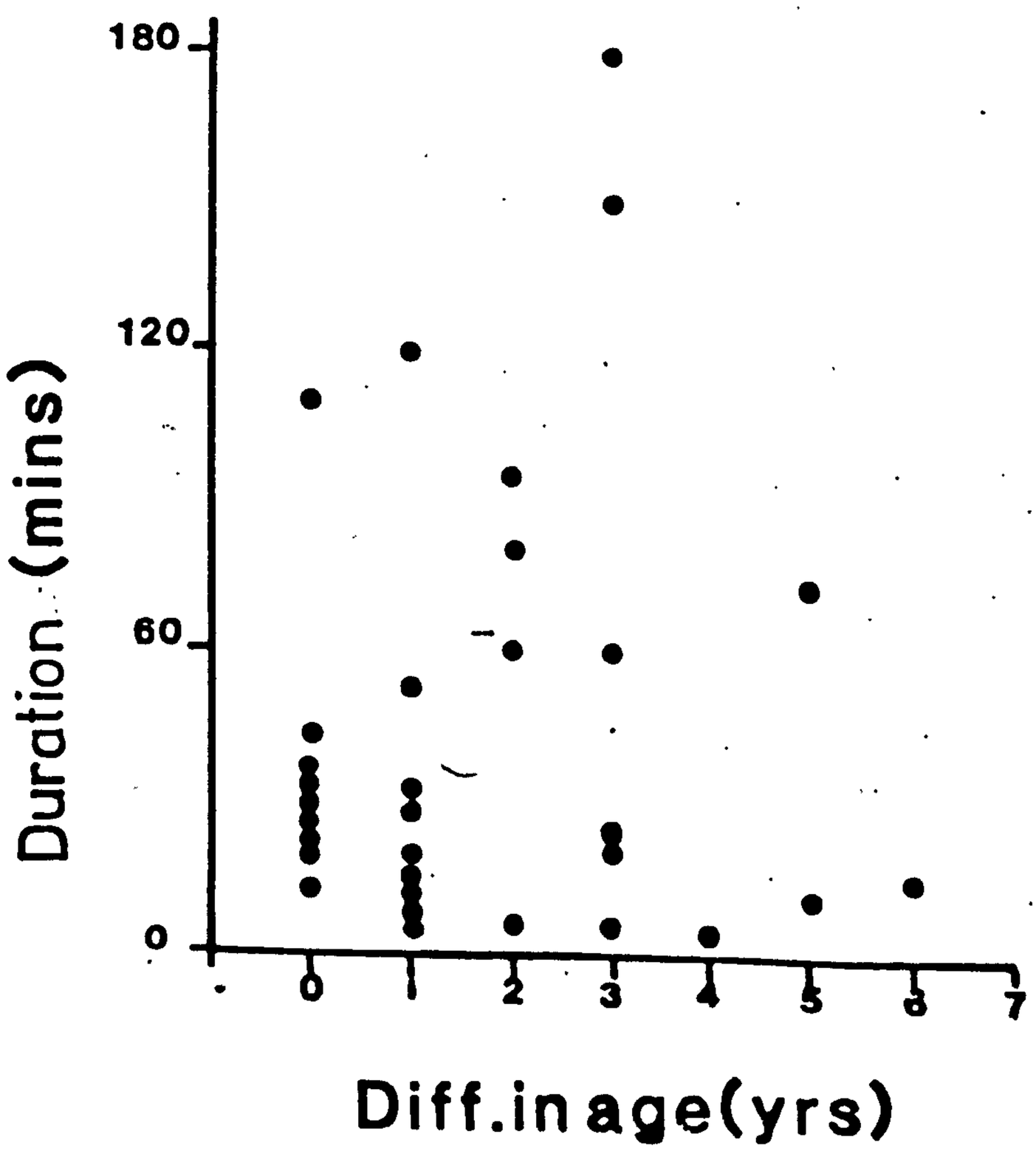


Fig. 5.32 The relationship between the difference in pre-rut body weight of opponents and duration of fights between males during the rutting period.

Fig. 5.33 The relationship between the difference in horn length of opponents and duration of fights between males during the rutting period.

Fig. 5.34 The relationship between the difference in age of opponents and the duration of fights between males during the rutting period.


Duration (mins)
160
120
80
40
0
0
2
4
6
8
10
12
14
16
18
20
Diff.in horn lengths(cm)


Duration (mins)
180
120
60
0
0
1
2
3
4
5
6
7
Diff.in age(yrs)

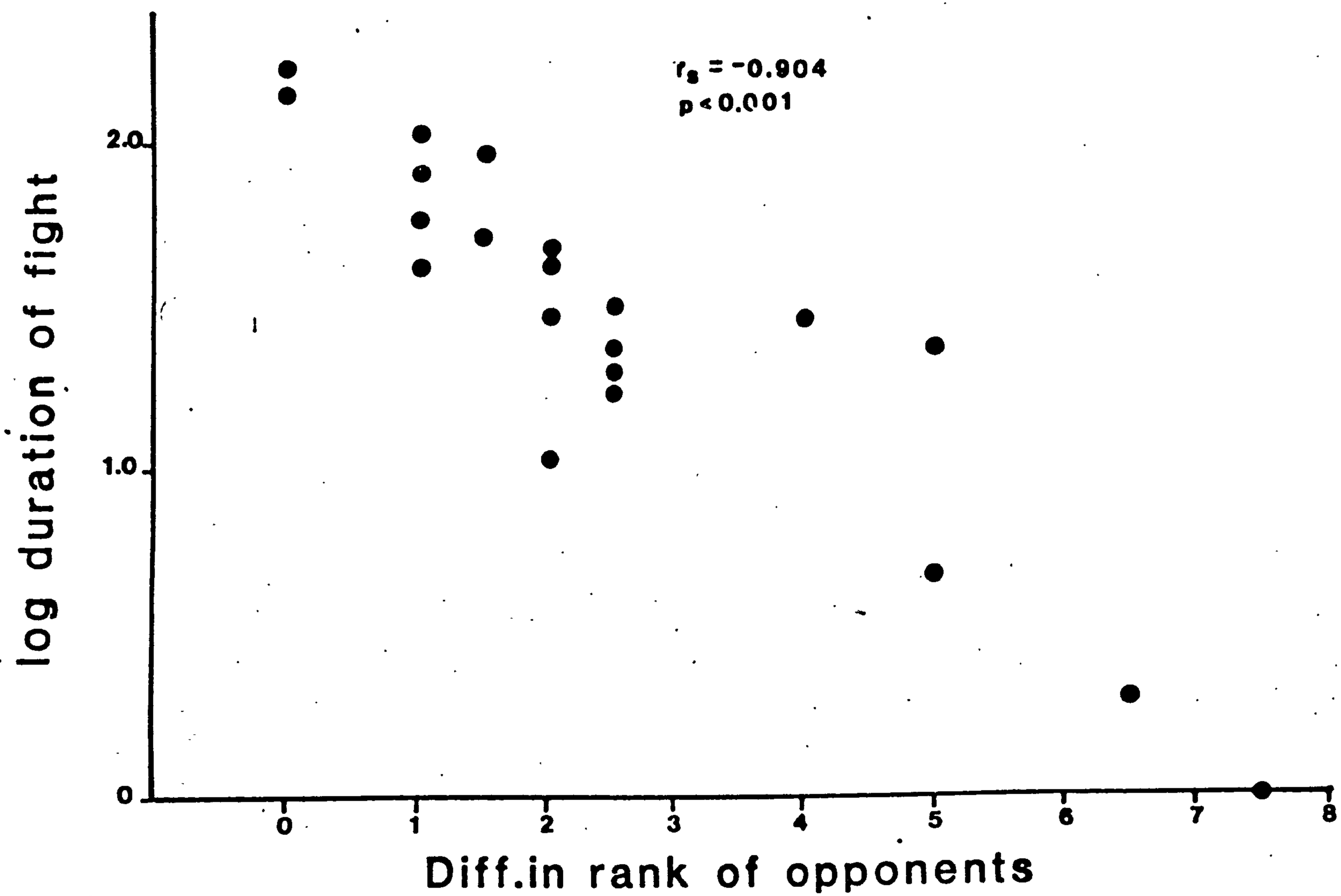


Fig. 5.35 The relationship between the difference in dominance rank and log. duration of fights between males during the rutting period.

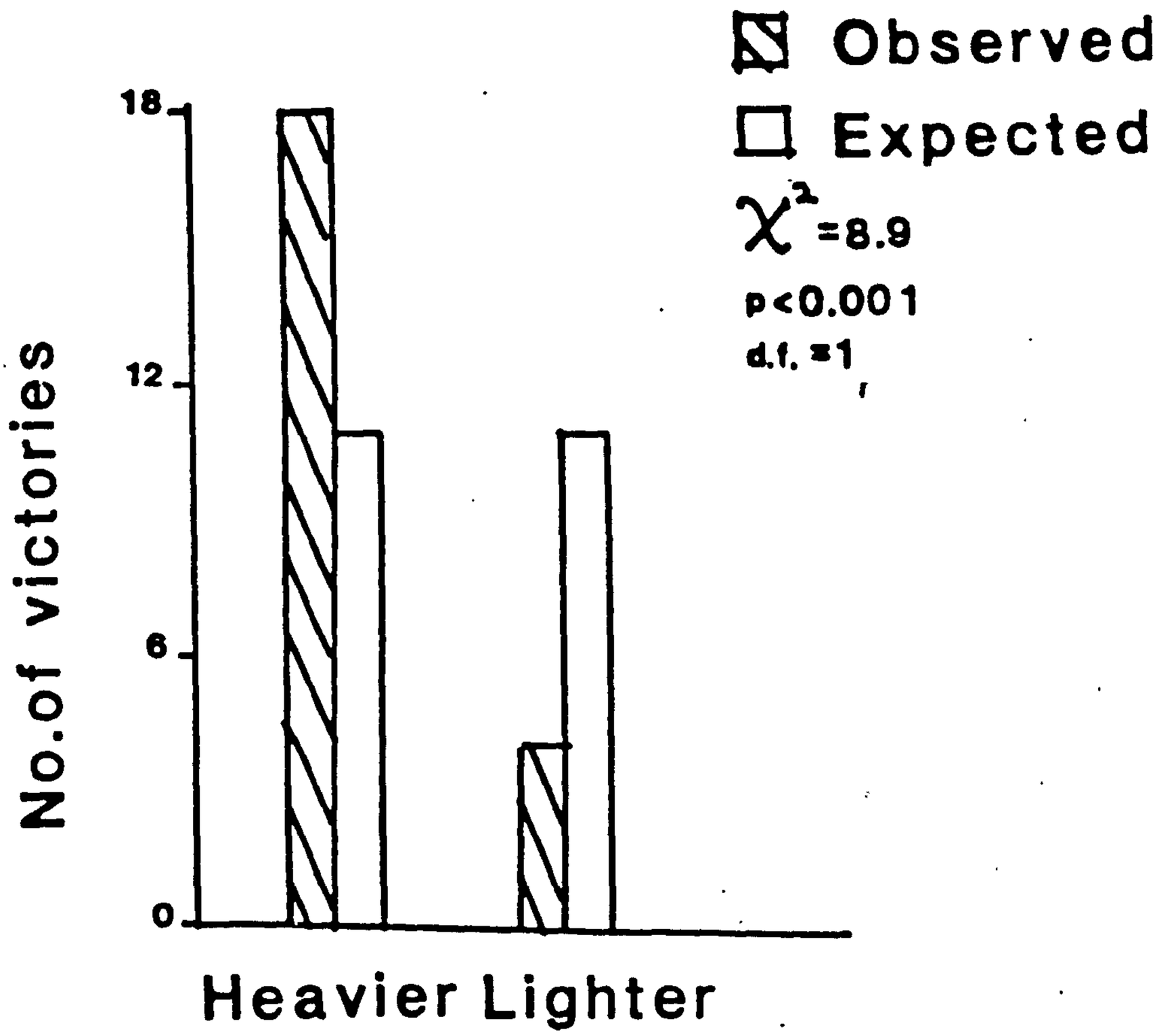


Fig. 5.36 Frequency of victories of heavier and lighter males in rutting fights.

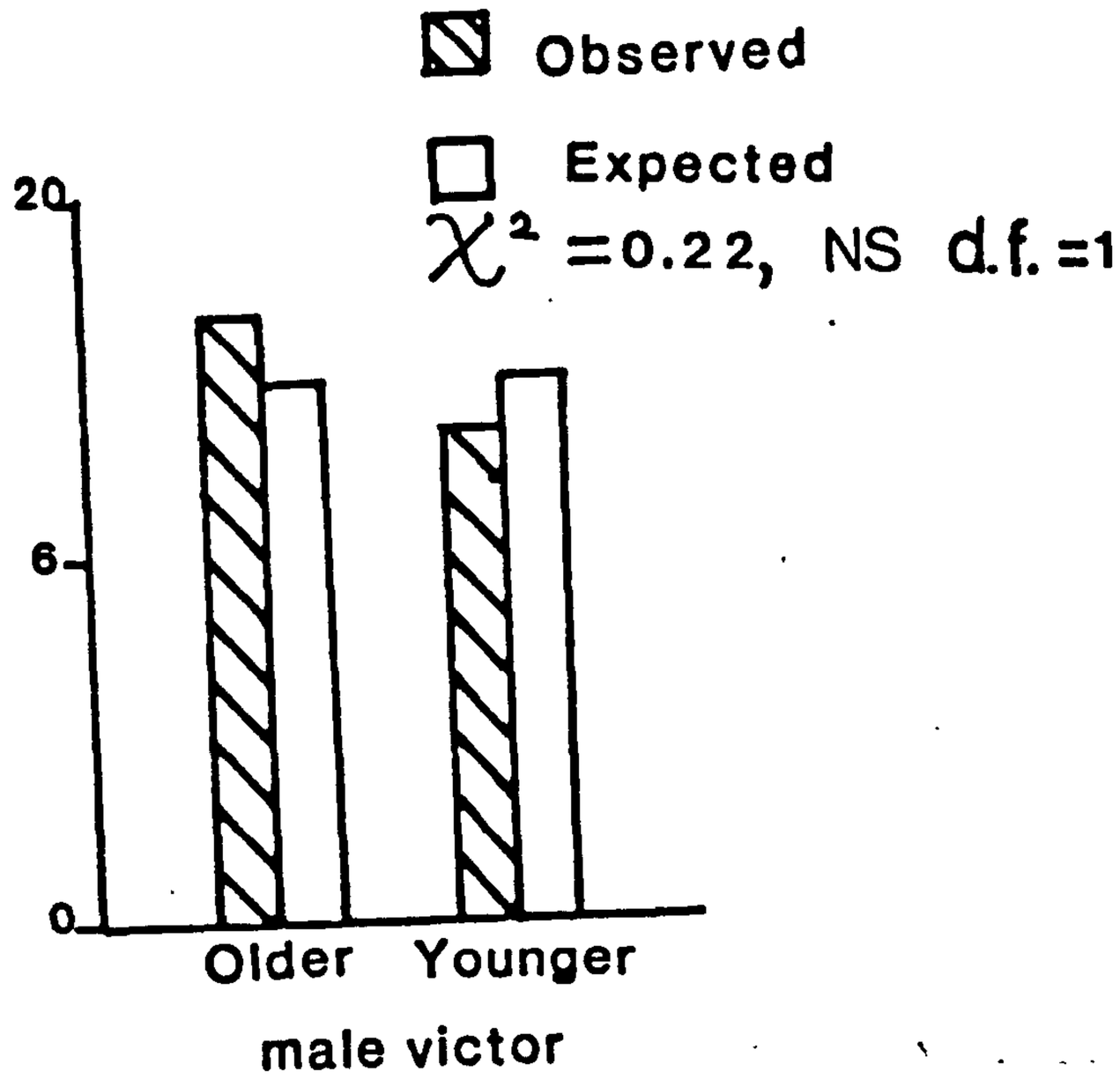


Fig. 5.37 Frequency of victories of older and younger males in rutting fights.

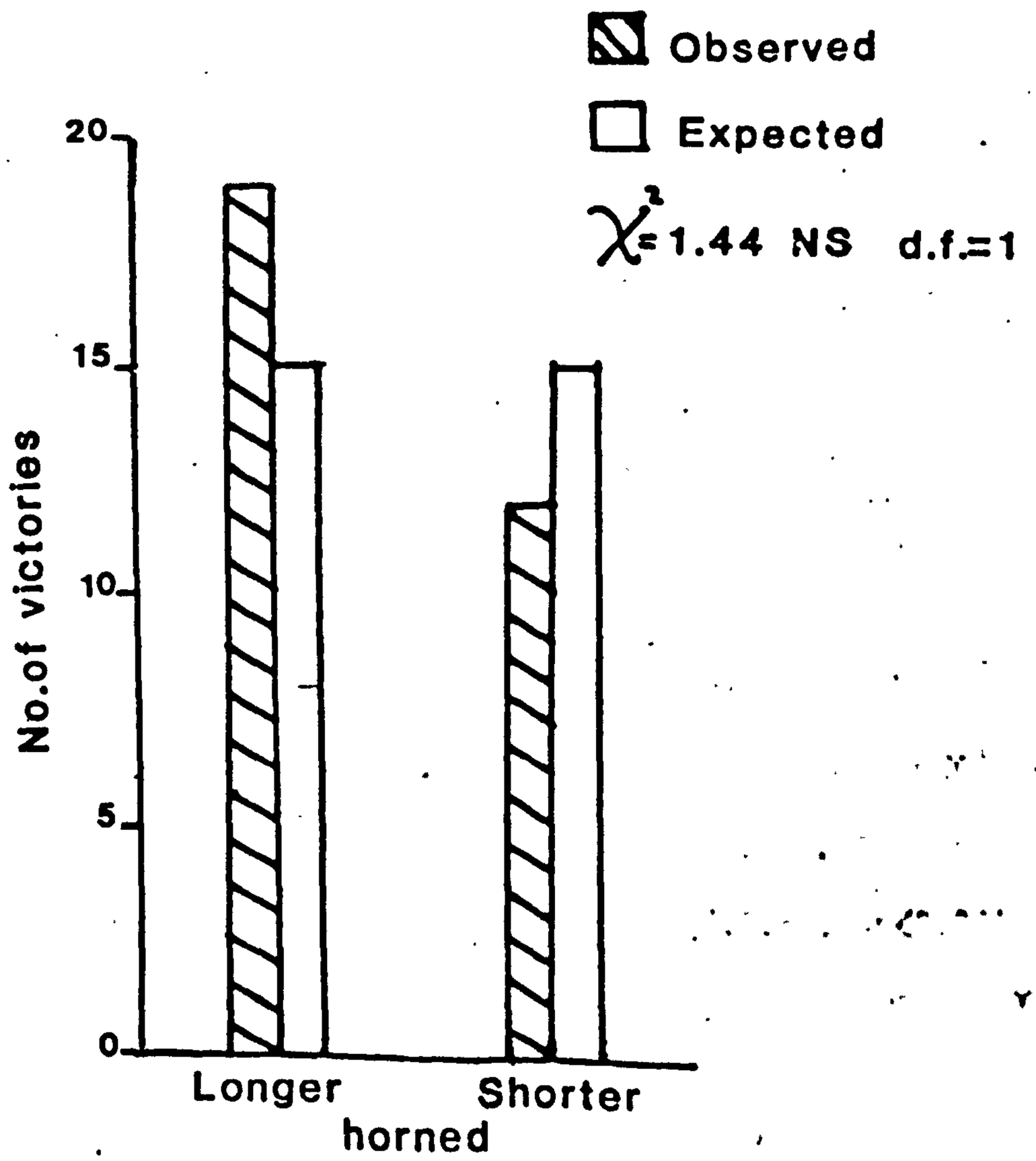


Fig. 5.38 Frequency of victories of the male with the longer or shorter horns in rutting fights.

six.

5.6 COURTSHIP AND MATING

5.6.1 Approach sequence

In 1981, males began to approach and court females at the end of August. The frequency of approaches increased during September and remained high until the end of October (Fig. 5.39). It can be seen from Fig. 5.40 that there was a tendency for older males (>3years old) to approach females more frequently than younger males. Amongst these older males there was no evidence to show that high ranking males approached females more frequently than subordinate males.

On 195 (19%, n=1028) occasions the approaching male adopted a low stretch posture. Fig. 5.41 indicates that males over three years of age adopted a low stretch more frequently than males younger than two years when approaching females.

Five different types of female response to male approaches were recognised: 1)Walk away, 2)Urinate, 3)Aggressive, 4)Tail wag, 5)No response (the female continues to do whatever it was doing before the male approached). The frequency with which each response was performed was influenced by the age of the male, whether the female was in oestrus and whether the male performed a low stretch. If a low stretch posture was adopted by a male when approaching a non-oestrous female she was significantly more likely to urinate

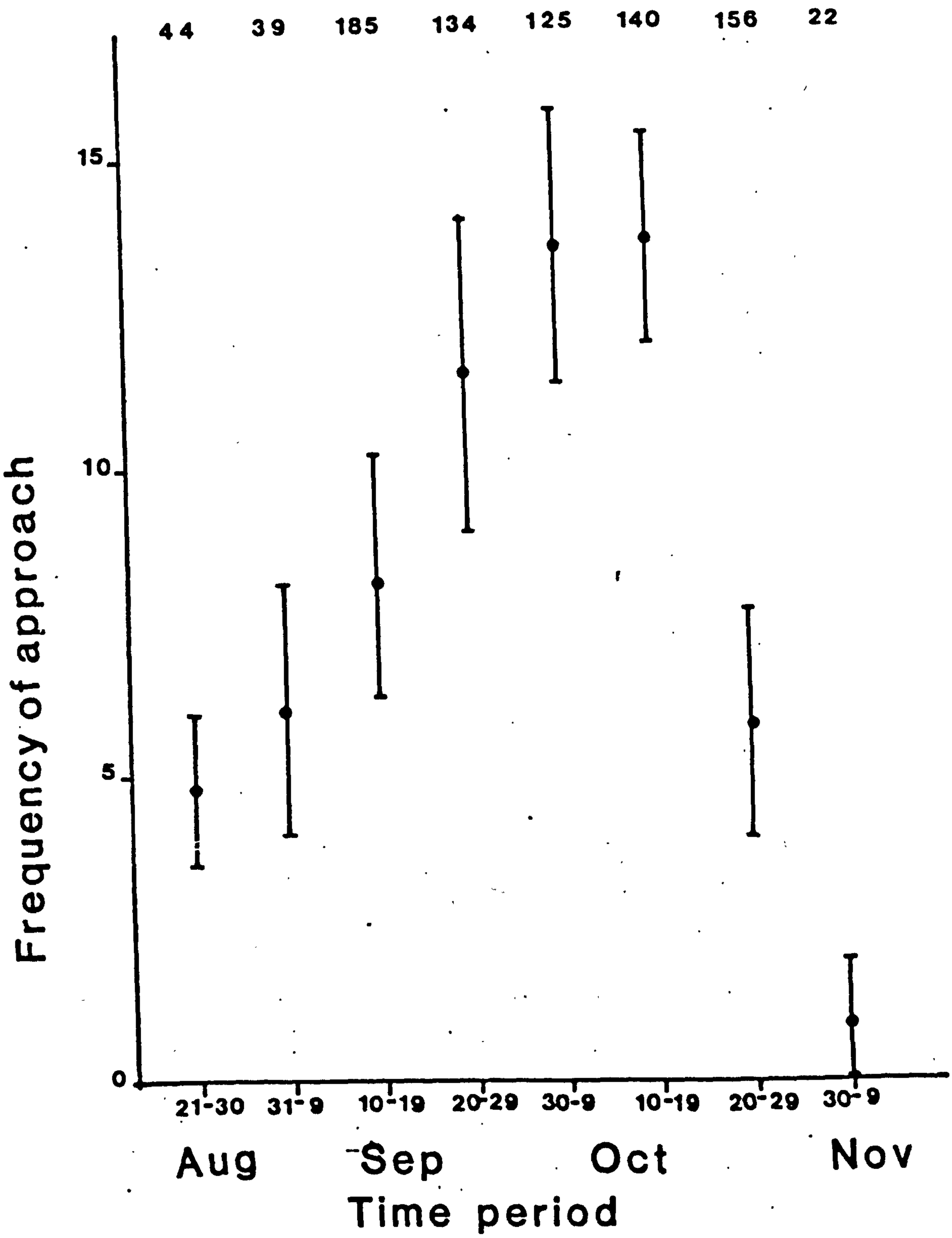


Fig. 5.39 The frequency of male sexual approaches to females during each ten day period in the autumn of 1981. The bars indicate 95% confidence limits and the number of five minute focal animal observation periods is given above each column.

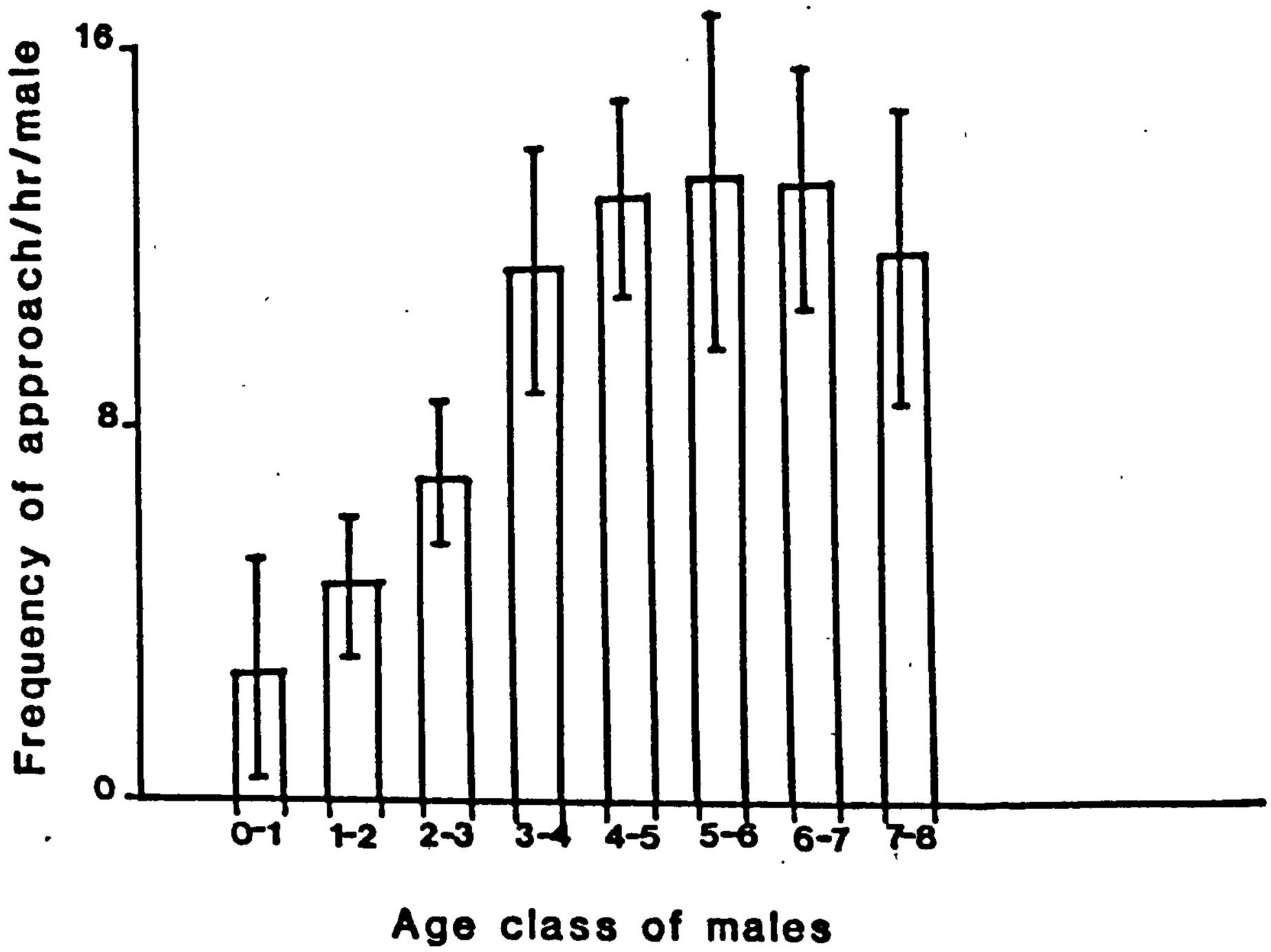


Fig. 5.40 The frequency with which males of different age approached females during the rut. Males in the 3-4 year age class approached females significantly more frequently than males in the 1-2 year age class ($t=16.6$, $d.f.=255$, $p<0.001$). The vertical lines indicate 95% confidence limits.

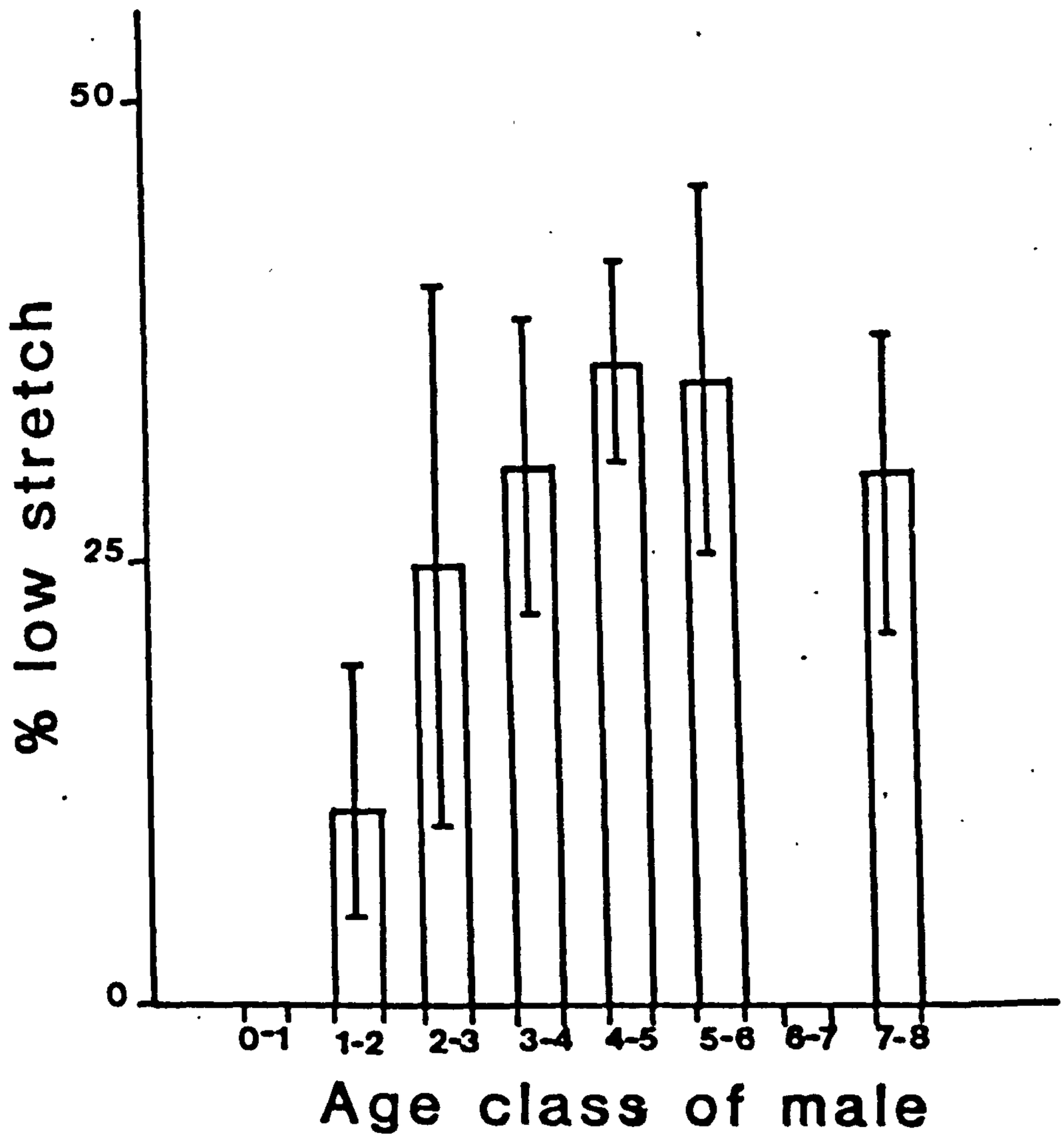


Fig. 5.41 The relationship between age and the number of low stretch approaches performed as a proportion or the total number of approaches towards females made by males of different ages. Vertical lines indicate 95% confidence limits. Younger males (1-2 years old) performed low stretch approaches significantly less frequently than males of over three years of age. (x =14.26, d.f.=1, $p<0.001$).

than when no low stretch posture was adopted (Fig. 5.42; χ^2 =18.87, d.f.=1, p<0.001). It can be seen from Fig. 5.43 that oestrous females walked away less frequently (χ^2=28, d.f.=1, p<0.001), and tail-wagged and responded aggressively more frequently (χ^2=144, d.f=1, p<0.001; χ^2=10.8, d.f.=1, p<0.001) than non oestrous females. Females responded aggressively more frequently to billy kids than to older males (Fig. 5.44).

Males usually lose interest in non-oestrous females and walk away after sniffing or licking a female once, but on 111 (15%) of such occasions the male followed the female and sniffed/licked her a second or third time. Non-oestrous females who were approached and then followed and approached again were more likely to urinate to the male than females approached only once. Females urinate by squatting and lowering their hind quarters. The male then dips his muzzle in the stream or licks it from the vegetation and performs a flehmen. Males were observed to flehmen for between 10 and 31 seconds ($\bar{x}$=22.3secs, s.d.=5.5, n=49). The length of flehmen did not appear to be dependent on the age of the male or whether the female was in oestrus . After performing a flehmen a male usually walked away from non oestrous females (86%) but always continued to court an oestrous female unless he was driven off by a more dominant male.

5.6.2 Courtship of oestrous females

High ranking males will court and defend (tend) oestrous females for many hours often remaining with them for one or two days. While a high ranking male is tending a female there are

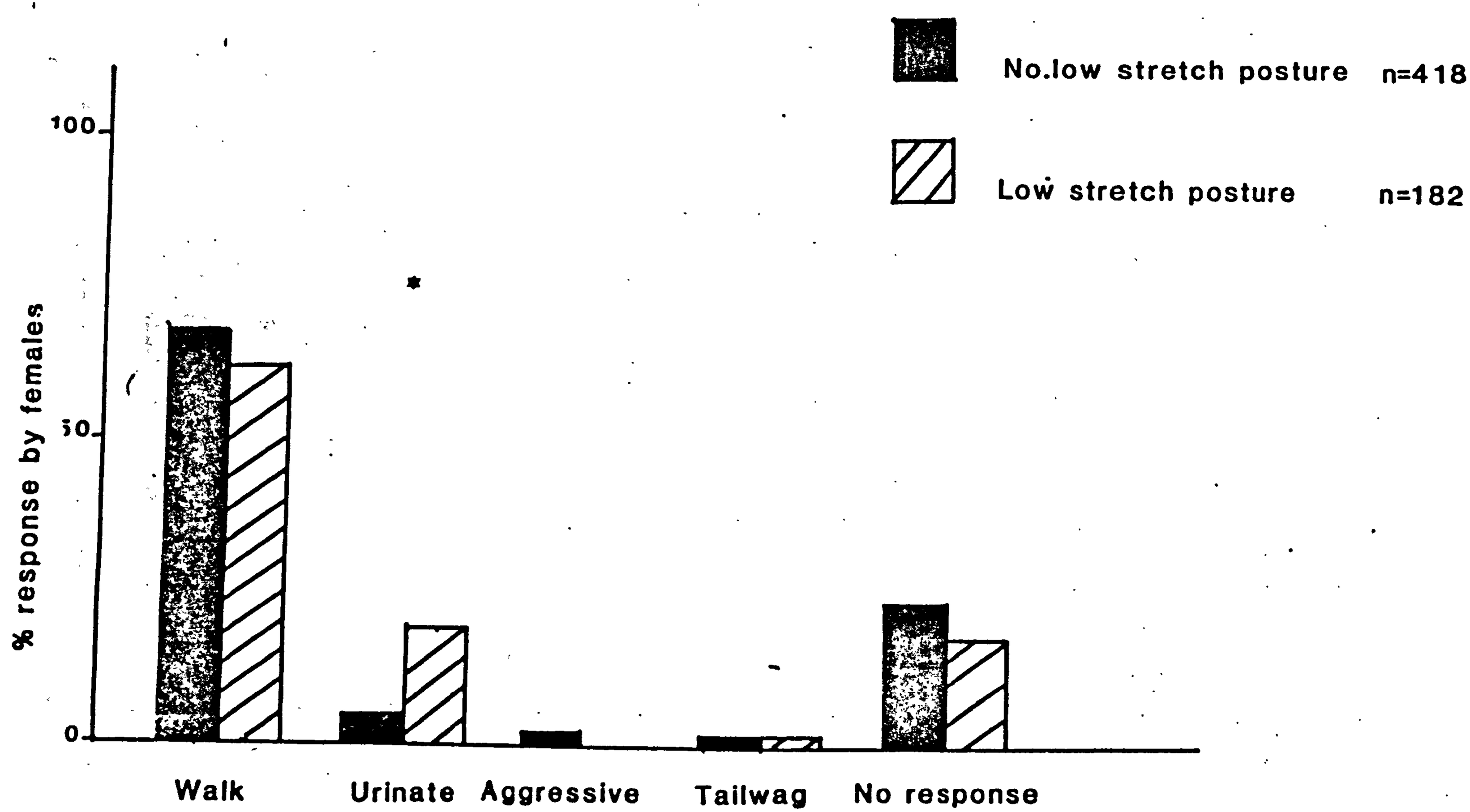


Fig. 5.42 The response of non-oestrous females to males that approached in a low stretch posture and to those that did not. The asterisk indicates a significant difference (see text).

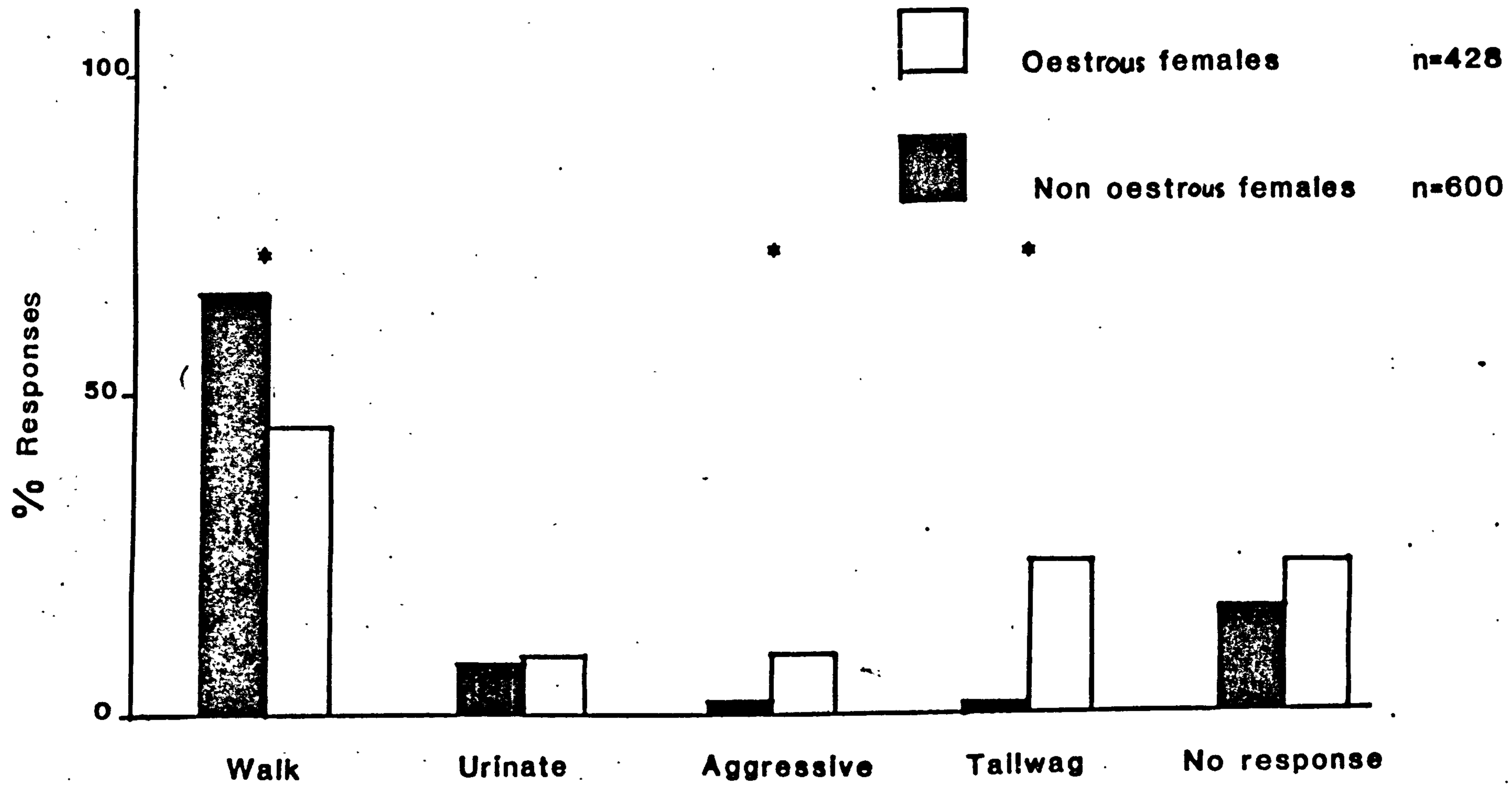


Fig. 5.43 The response of oestrous and non oestrous females to male sexual approaches as a proportion of the total number of responses. The asterisks indicate a significant difference between oestrous and non oestrous females (see text).

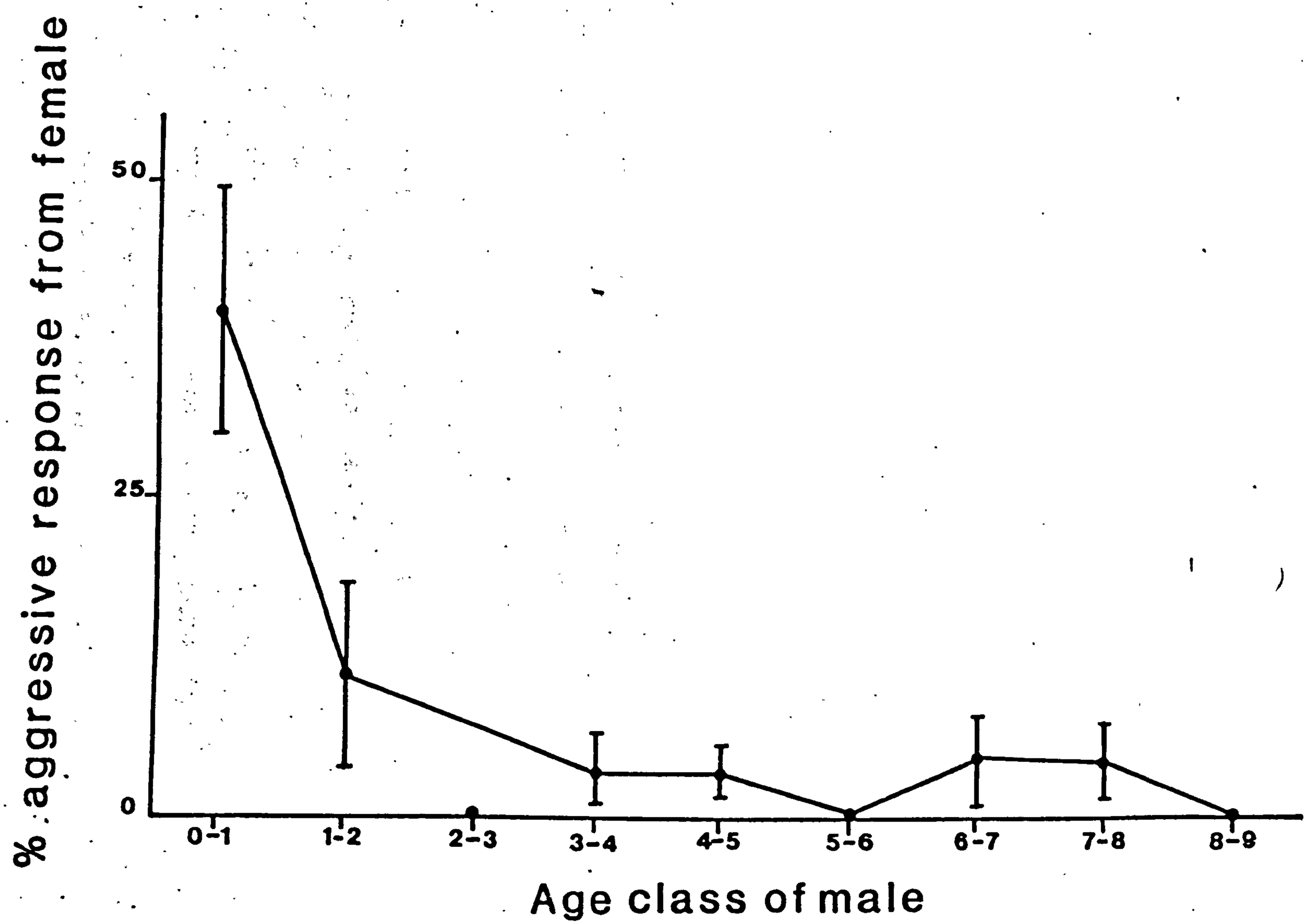


Fig. 5.44 The number of aggressive responses, as a proportion of all female responses, to the sexual approaches of males of each age class. Vertical bars indicate standard errors.

usually a number of subordinate males loitering and watching the oestrous female. If the tending male and the female become separated by more than a few metres the subordinate males will approach the female and court or mount her. This results in either the dominant male rushing the intruding individual or the female running back to the dominant male. Although a subordinate male may chase the female he will stop as she approaches the dominant male. On one of these occasions the female was chased and mounted repeatedly by six males. This stopped when the dominant male rejoined the female and fought off the other males.

While a male is tending a female he does not court her continually. Bouts of courtship are interspersed with periods of feeding or resting (Fig. 5.45). Bouts of courtship varied in length from a few seconds up to 30 minutes and involved up to 91 behavioural acts being made by a courting male.

Figs. 5.46a, b, c and d and 5.47 show the change in frequency of male and female courtship behaviour patterns during ten courtship bouts for which continous records were obtained. Bouts are divided into five minute periods between which behaviour frequencies are compared; three of the bouts lasted for four such periods, four for three periods, and three for two periods. Nine of the bouts ended with a successful mating and one in a cessation of courtship by the male. It can be seen that after an initial increase in the frequency of low stretch approaches there was a significant decrease between the second and last period ($t=2.6$, d.f=6 and 9, $p<0.05$). There was a significant increase in the frequency of gobbles and legkicks delivered during the courtship bouts (t test between second

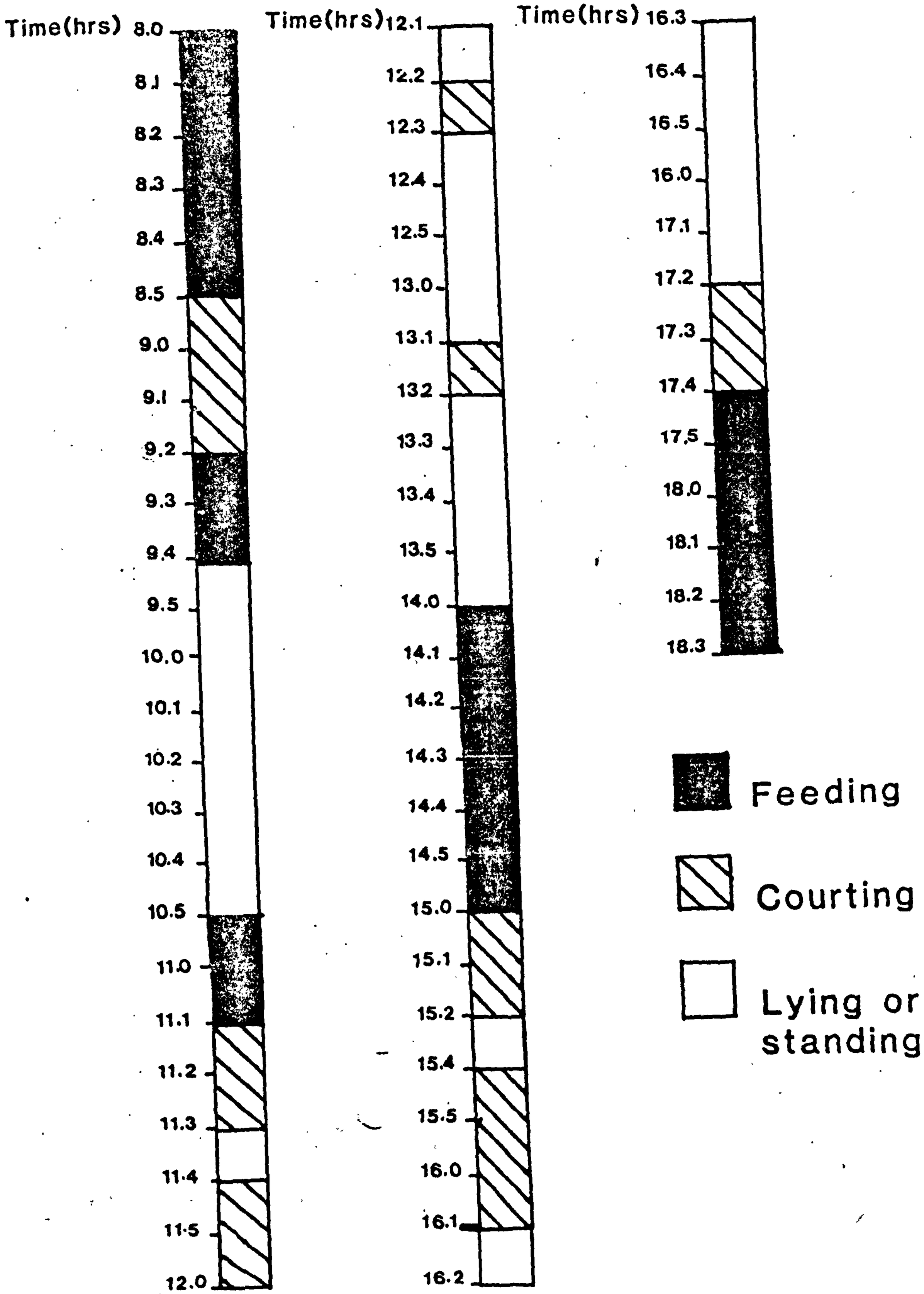


Fig. 5.45 The activity of an adult male (101) tending an oestrous female (112) throughout the day from ten minute instant scan samples.

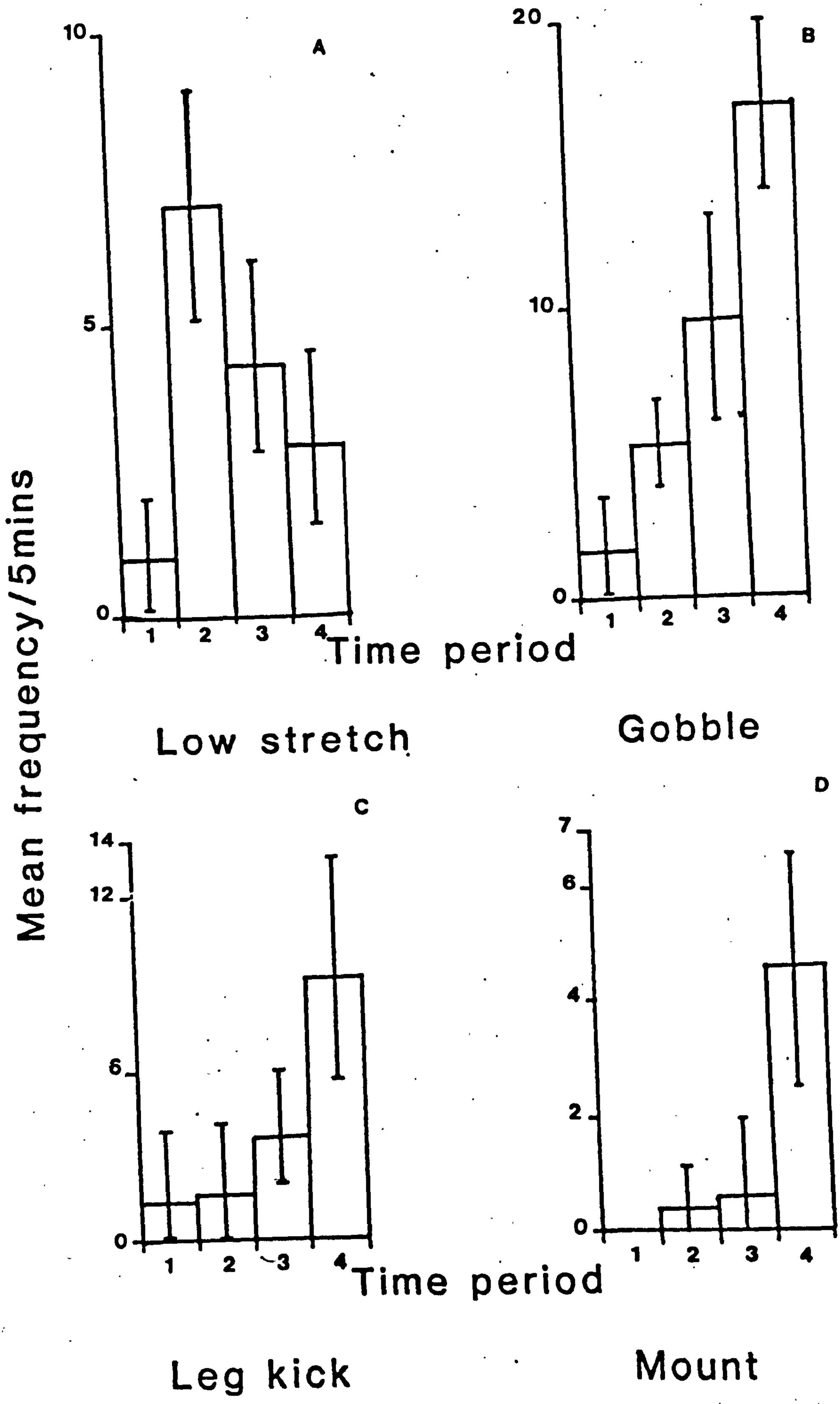


Fig. 5.46 The frequency of male courtship behaviour patterns during ten courtship bouts (see text). The vertical lines indicate 95% confidence limits.

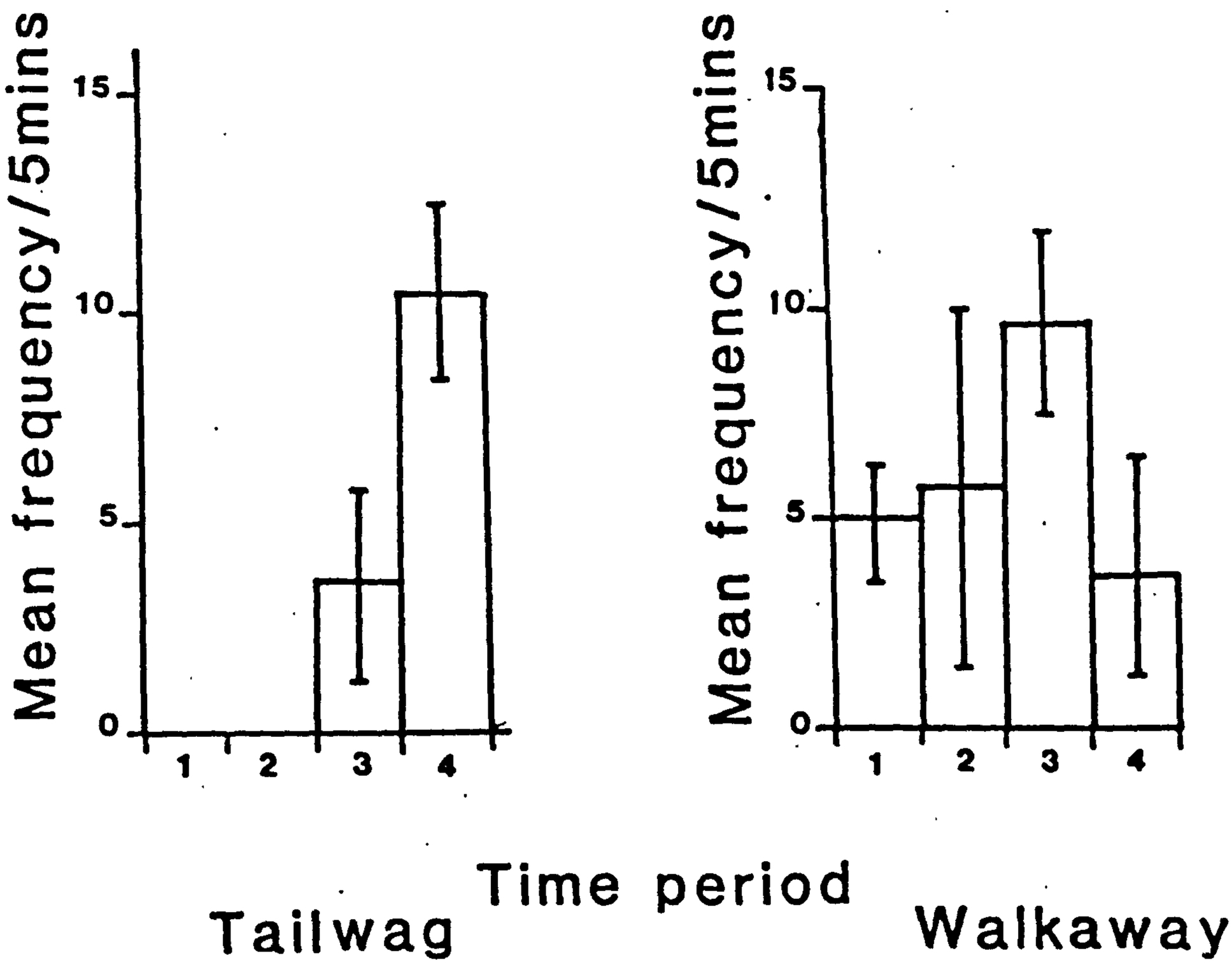


Fig. 5.47 The frequency of female courtship behaviour patterns during ten courtship bouts (see text). The vertical lines indicate 95% confidence limits.

and last periods: gobbles: $t=5.9$, d.f.=6 and 9, $p<0.01$; legkicks: $t=3.3$, d.f.=6 and 9, $p<0.01$). The frequency of mounts is significantly higher during the final five minute period of a courtship bout than any of the previous five minute periods ($t=3.5$, d.f= 9 and 9, $p<0.01$). The frequency with which females responded by walking away was significantly lower and the frequency of tail-wag response was significantly higher in the last five minutes of a courtship bout compared to the penultimate five minutes of a courtship bout (tail wag: $t=4.5$, d.f= 9 and 9, $p<0.01$; walk away: $t=3.5$, d.f= 9 and 9, $p<0.01$).

A male may mount a female several times in succession. If the female is not ready to copulate she will just walk forward a few paces when mounted and the male will fall off. This is followed by more gobbles and legkicks being delivered by the male before another attempt to mount is made. After several attempted mounts a receptive female will stand still and allow the male to mount. Mounting is followed by a series of short pelvic thrusts terminating when the male throws his head back and gives a final long thrust before dismounting. This long thrust was assumed to indicate ejaculation. After mating the female usually begins to feed. The male usually sniffs the female once or twice before either feeding (19.2%, n=26) or lying down close to the female (80.8%, n=26).

Females were observed to approach adult males on 55 occasions. Females usually ran to the side of high ranking males in response to an approach by another male. In every instance the male to which the female went was of higher dominance rank than the approaching male. Twenty seven (49%) of these approaches were by oestrous

females, and 55% (15) of these were to the male that was seen to mate with that female. On six occasions the approaching female licked and rubbed the male's head. This stimulated the male into courting the female, but on only one occasion did the courtship lead to a successful mating.

5.6.3 Homosexual behaviour

Male 4 is a large adult animal with large horns. When he was first captured in 1980 he was found to have no external testes. During the 1980 and 1981 rut Male 4 was never seen to court any females, even though, on two occasions he was seen to be approached and licked around the head by a female. Other males usually treated him as a subordinate male and would horn threat and rush him if he got too close to an oestrous female. However on three occasions Male 4 was seen to be courted and mounted by another male. When being courted Male 4 responded to gobbles and legkicks by wagging his tail in a similar manner to that of a receptive female.

5.7 MATING SUCCESS

A successful mating was recorded when a male was seen to give a long ejaculatory thrust followed by a cessation of courtship behaviour. A probable mating was recorded when no final ejaculatory thrust was observed but a male was observed tending a female and no male of higher rank was seen to be in that group or seen walking

towards that group during the following 24 hours. A total of 26 successful and 22 probable matings was observed. Matings were not distributed evenly throughout the day. There was a peak in the frequency of matings between 1600-1700hrs and a lesser peak between 1200-1300hrs (Fig. 5.48). There was a significant positive correlation between the number of successful and probable matings obtained by males (r_s =0.934, d.f.=9, p<0.01). The number of probable plus successful matings achieved by any male was taken as an estimate of that male's mating success for that season.

No male under two years of age was observed to obtain a successful mating. It is clear from Fig. 5.49 that some males were much more successful than others. Estimated mating success was highly correlated with dominance rank, pre-rut body weight, and horn length, but not with the age of the male (Rank: Fig. 5.50, r_s=0.92, d.f.=12, p<0.001; pre-rut body wt: Fig. 5.51, r_s =0.89, d.f.=9, p<0.001; horn length: Fig. 5.52, r_s=0.78, d.f.=12, p<0.01). Both horn length and pre-rut body weight of males increase with age up to four years old (Figs. 5.16 and 5.17). In order to eliminate the age effect one can consider only those males over four years of age, amongst which there was no increase in body weight with age. Males over four years of age achieved 96% of observed matings and 82% of probable matings. Amongst this group of males there was no significant correlation between horn length and estimated mating success (r_s =0.41, n=8, NS), but both pre-rut body weight and dominance rank were correlated with estimated mating success (pre-rut body weight: Fig. 5.53, r_s=0.86, n=8, p<0.01; rank: Fig. 5.54, r_s=0.98, n=8, p<0.01).

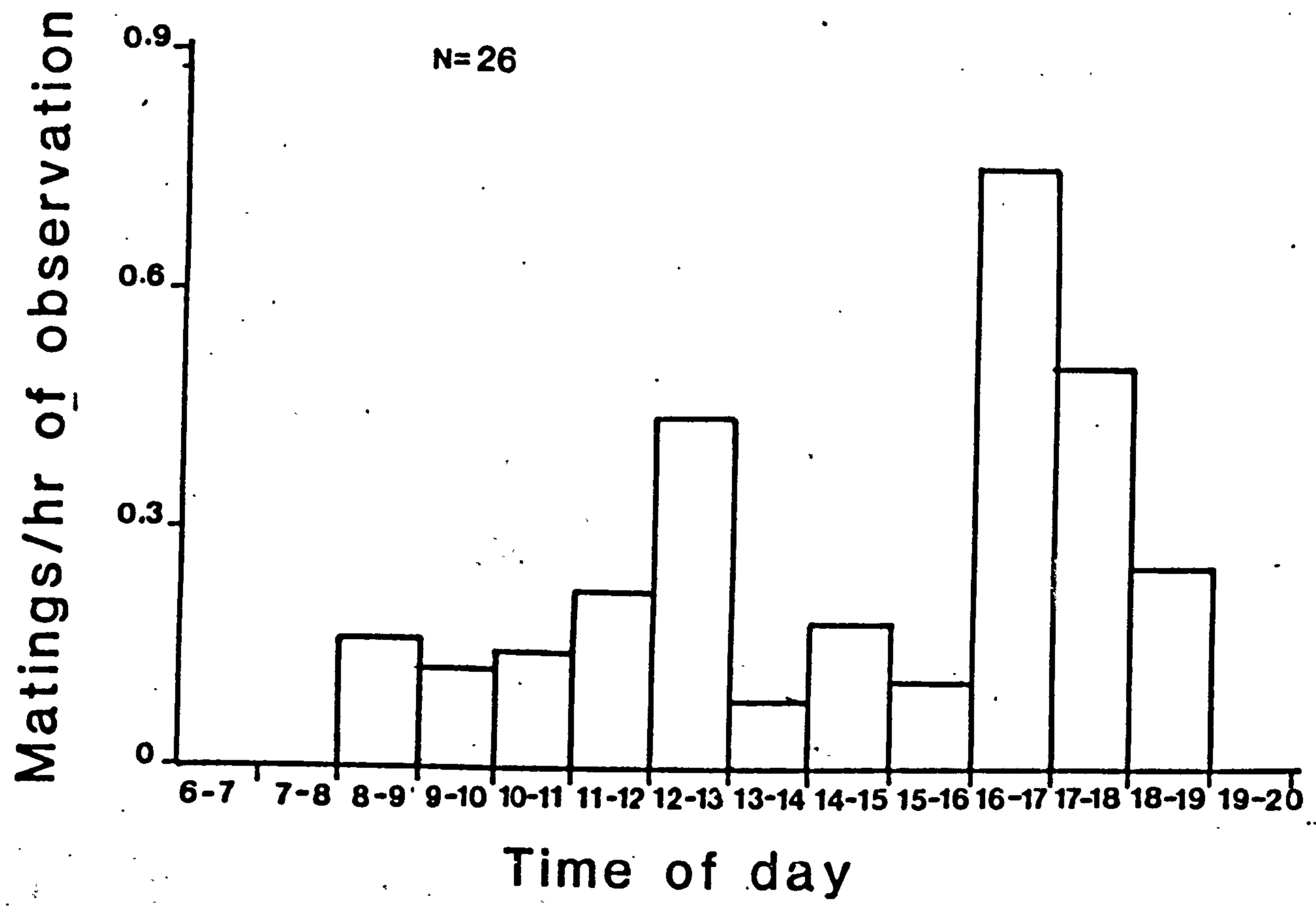


Fig. 5.48 The distribution of mating throughout daylight hours during the 1981 rutting period.

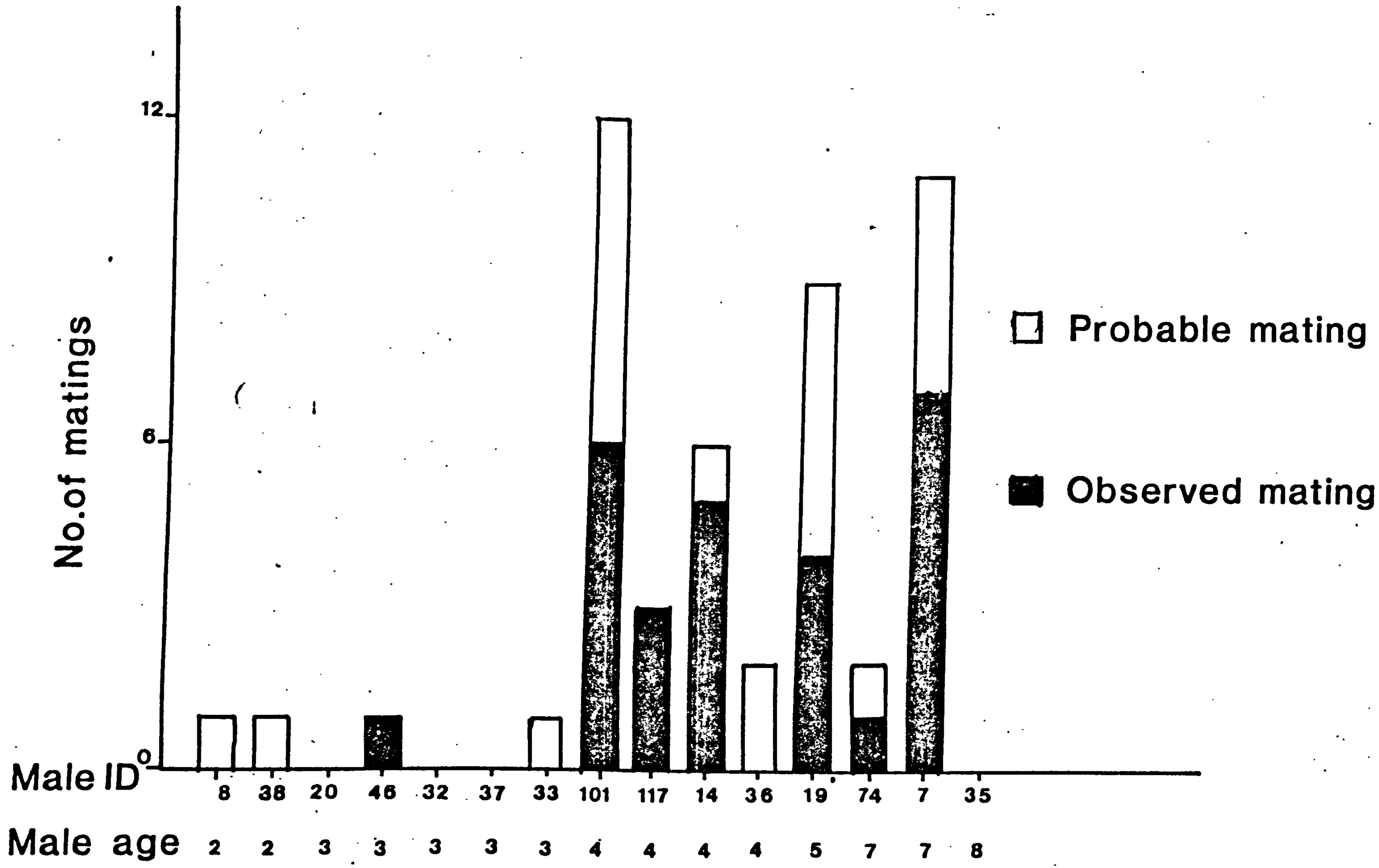


Fig. 5.49 The estimated mating success of adult male goats during the 1981 rutting period.

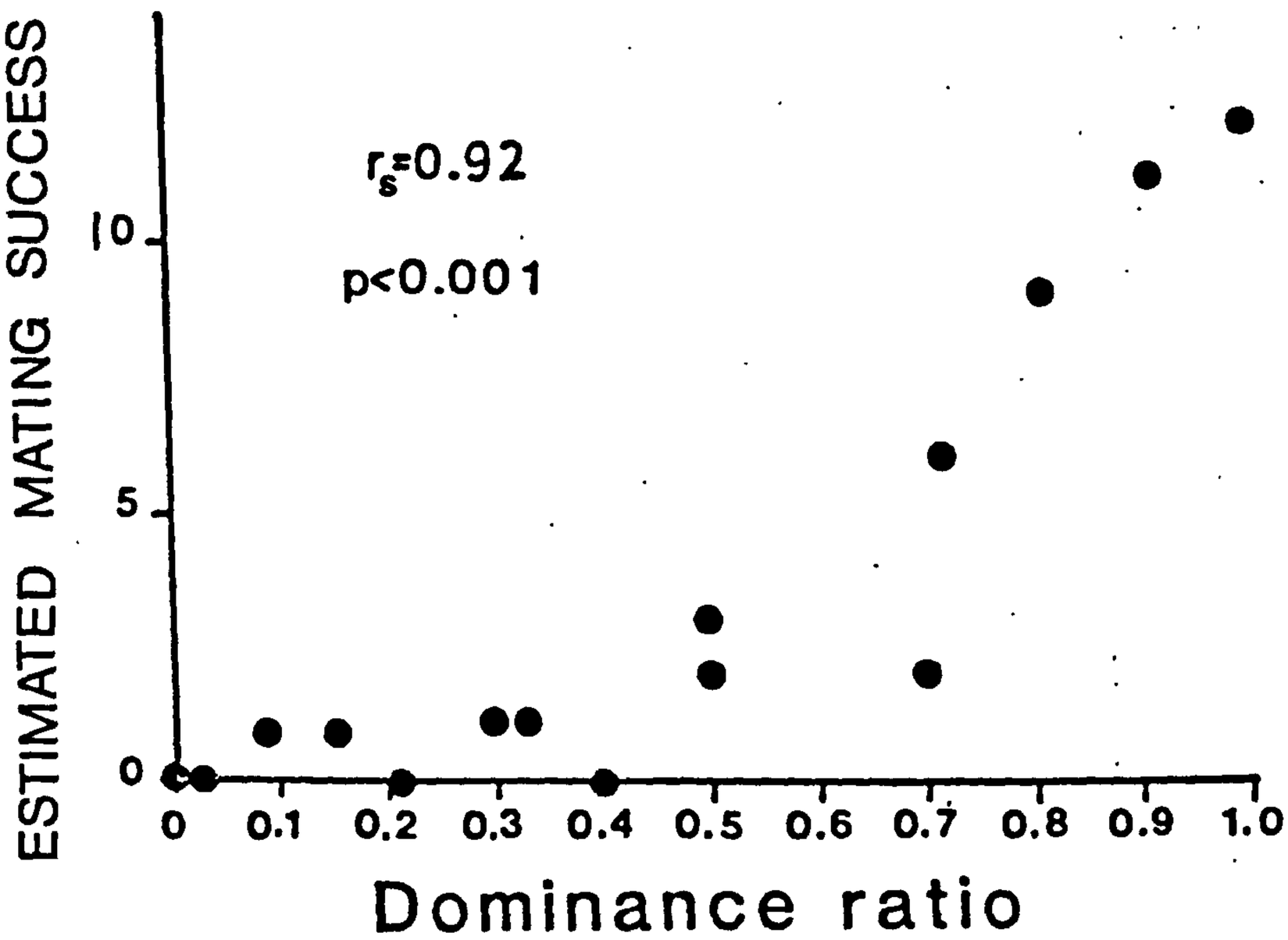


Fig. 5.50 The relationship between dominance ratio and estimated mating success of males over two years of age during the 1981 rut.

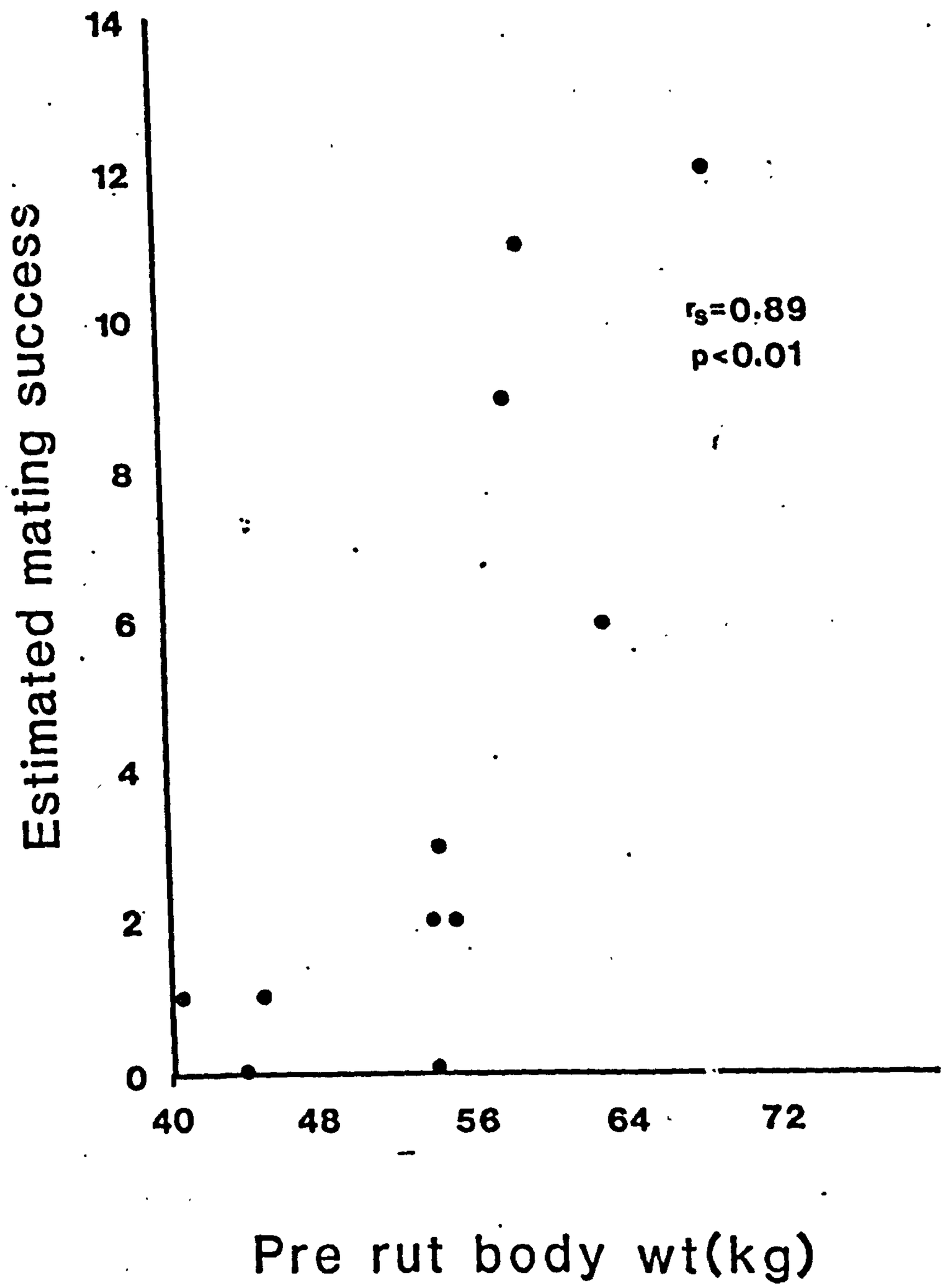


Fig. 5.51 The relationship between pre-rut body weight and estimated mating success for males over two years of age during the 1981 rut.

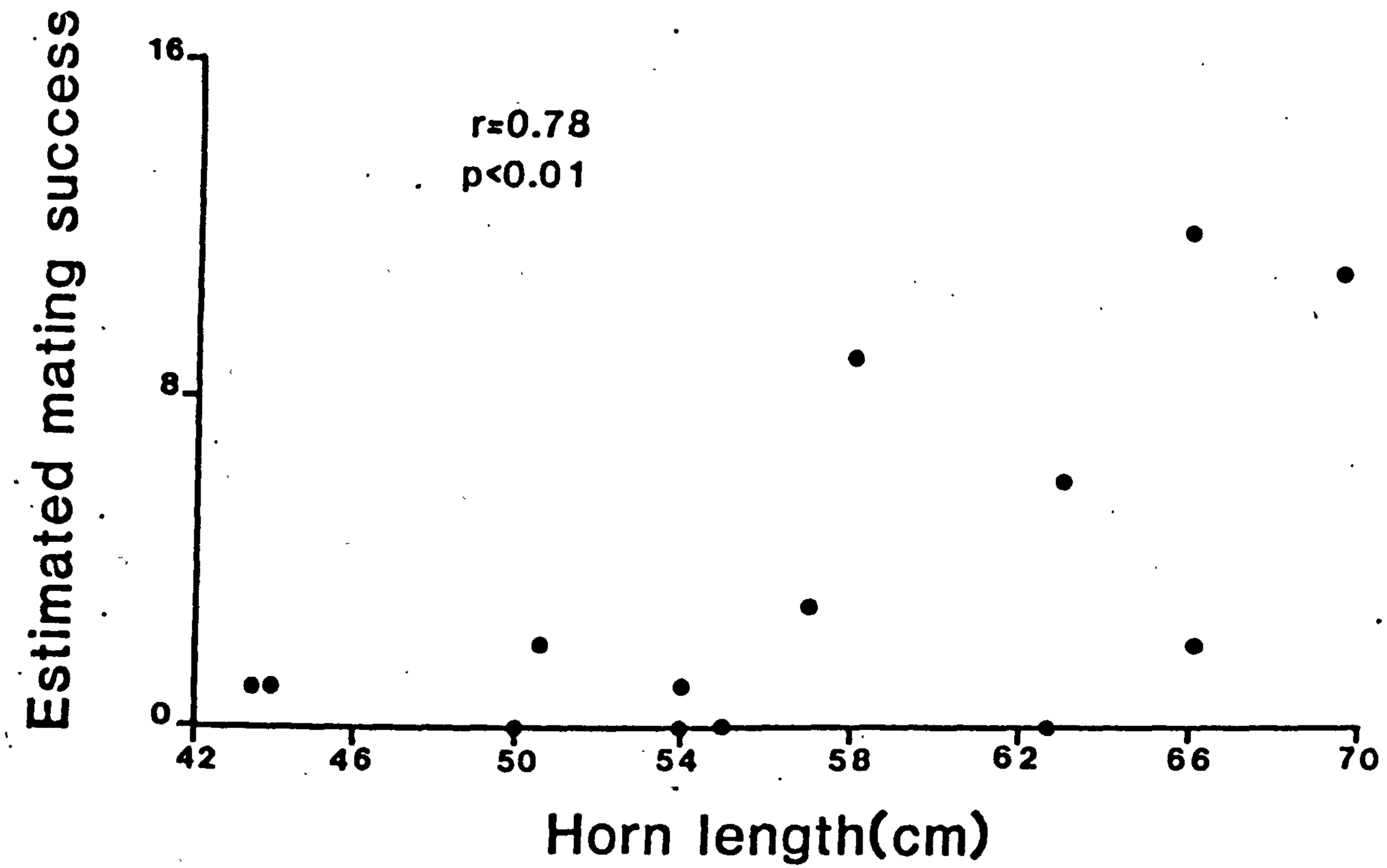


Fig. 5.52 The relationship between horn length and estimated mating success of males over two years of age during the 1981 rut.

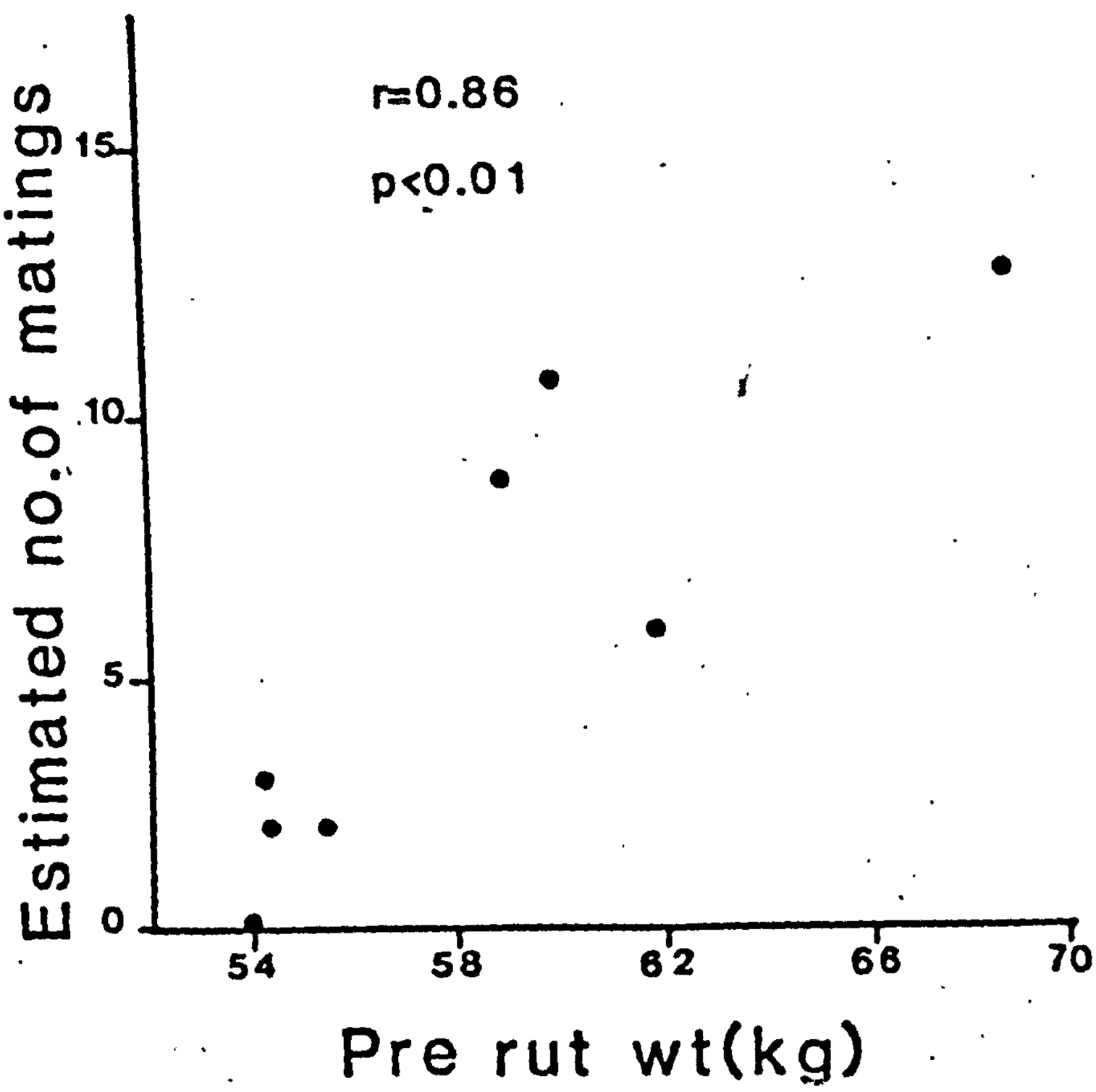


Fig. 5.53 The relationship between pre-rut body weight and mating success of males over four years old.

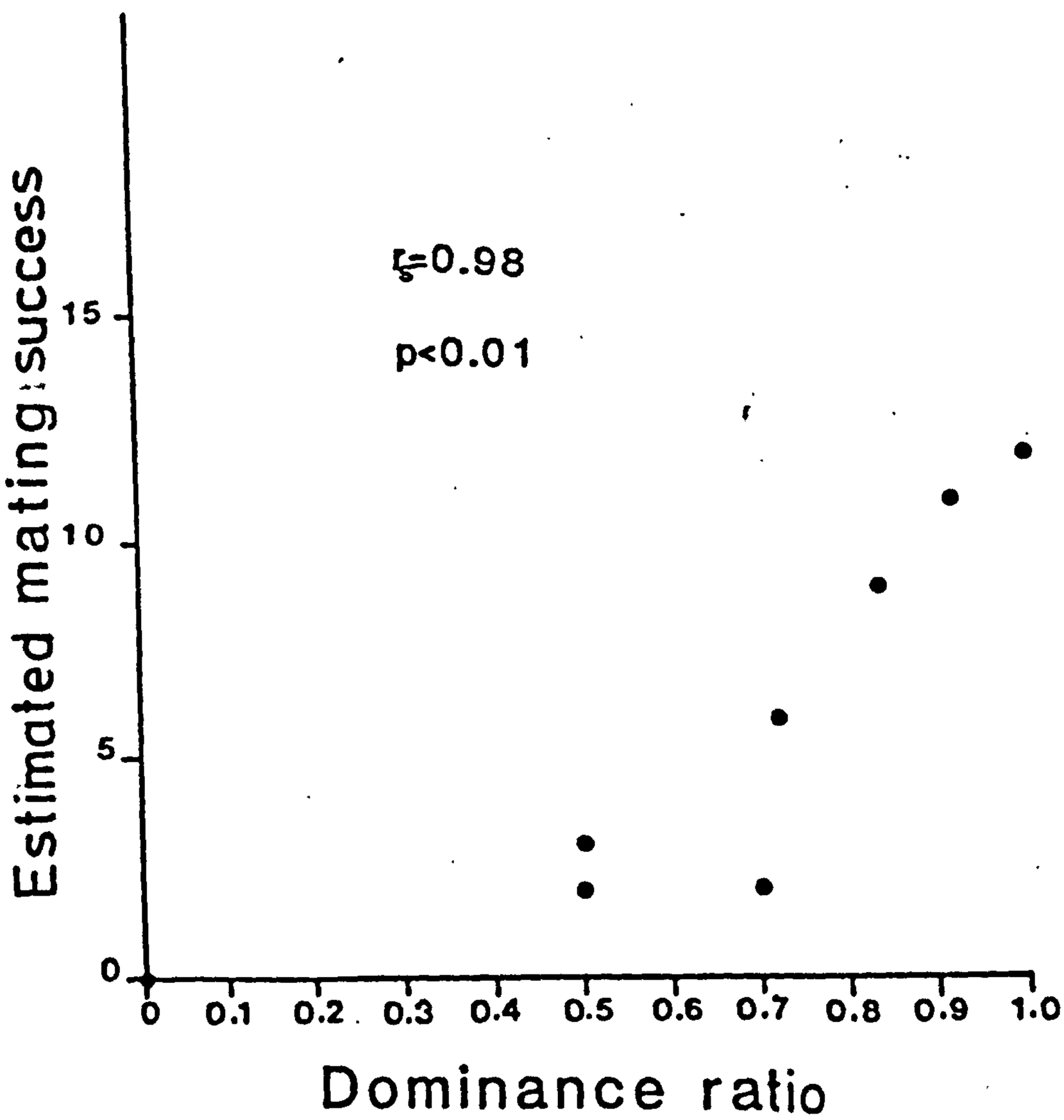


Fig. 5.54 The relationship between dominance ratio and mating success of males over four years old.

Estimates of reproductive success for adult males can be obtained by comparing which females they mated with and which successfully reared kids in 1982. No detailed observations were made during the 1982 kidding period to check on the exact kidding dates of individual females. However because only two females came into oestrus a second time it was assumed that most females conceived when they were seen, or presumed, to be mated by a particular male. It can be seen (Table 5.4) that estimated reproductive success was much lower than estimated mating success. However high ranking males did have a higher reproductive success than subordinate males (Fig. 5.55).

5.8 THE COST OF BREEDING TO MALES

5.8.1 Loss of feeding time

The census data show that adult males were seen feeding more frequently than females during July and August (Fig. 5.56; July: χ^2 =7.45, d.f.=1, $p<0.01$; August: χ^2=11.75, d.f.=1, $p<0.001$). However, during September and October adult males were seen feeding less frequently than adult females (September: χ^2=66.1, d.f.=1, $p<0.001$; October: χ^2=45.4, d.f.=1, $p<0.001$). These observations suggest that there was a large drop in the amount of time spent feeding by males during the rut.

Detailed observations made in 1981 confirmed this suggestion. During the pre-rut period (August 20-September 10) adult males spent

MALE ID	ESTIMATED NUMBER OF MATINGS	NUMBER OF KIDS SURVIVING TO SIX MONTHS PROBABLY SIRED
101	12	4
7	11	3
19	9	4
14	6	0
34	2	1
117	3	0
36	2	2
33	1	0
18	1	1
46	1	0

Table 5.4

Estimated reproductive success of adult males in the year 1981/82.

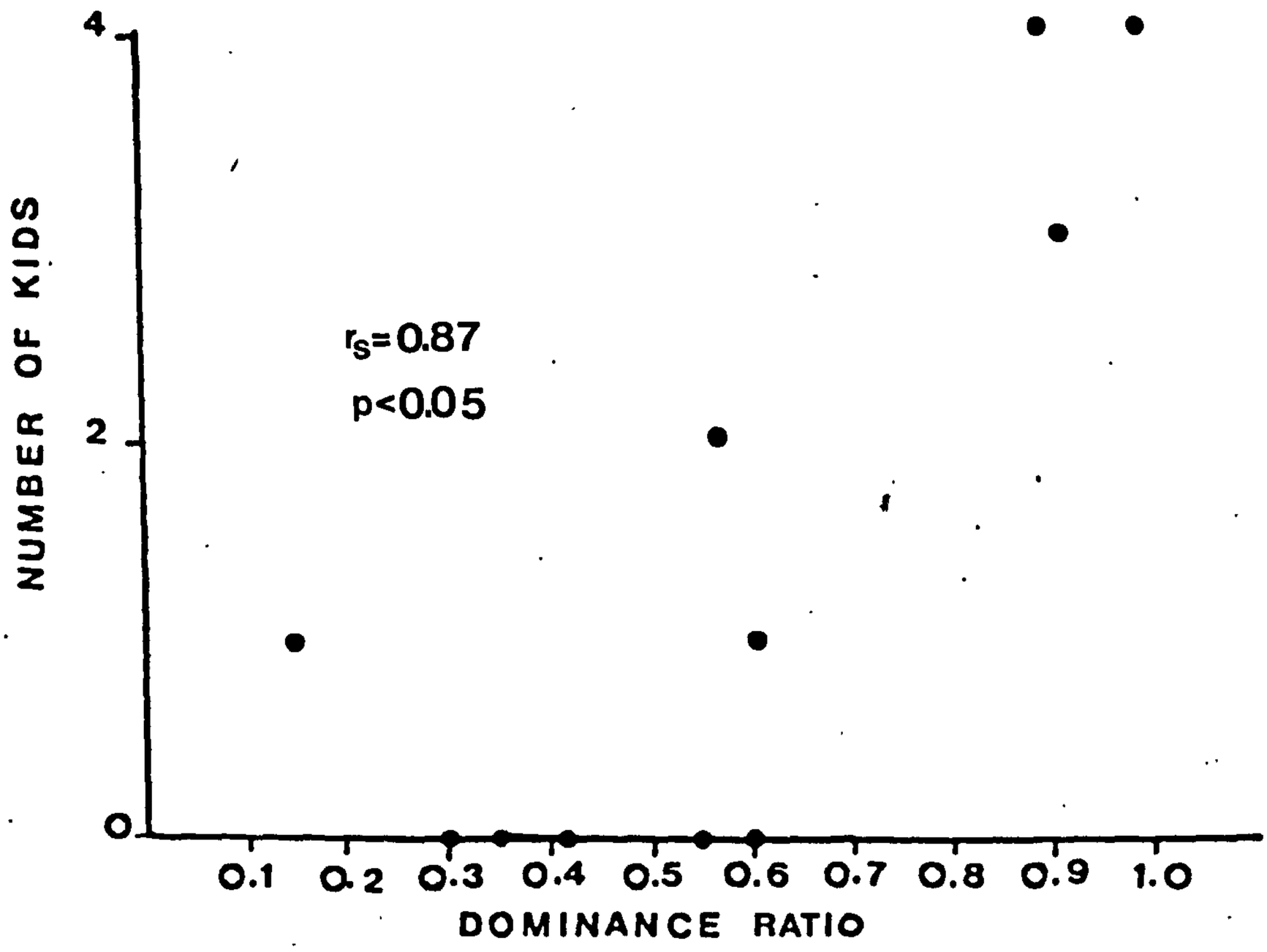


Fig. 5.55 The relationship between dominance ratio and reproductive success amongst adult males.

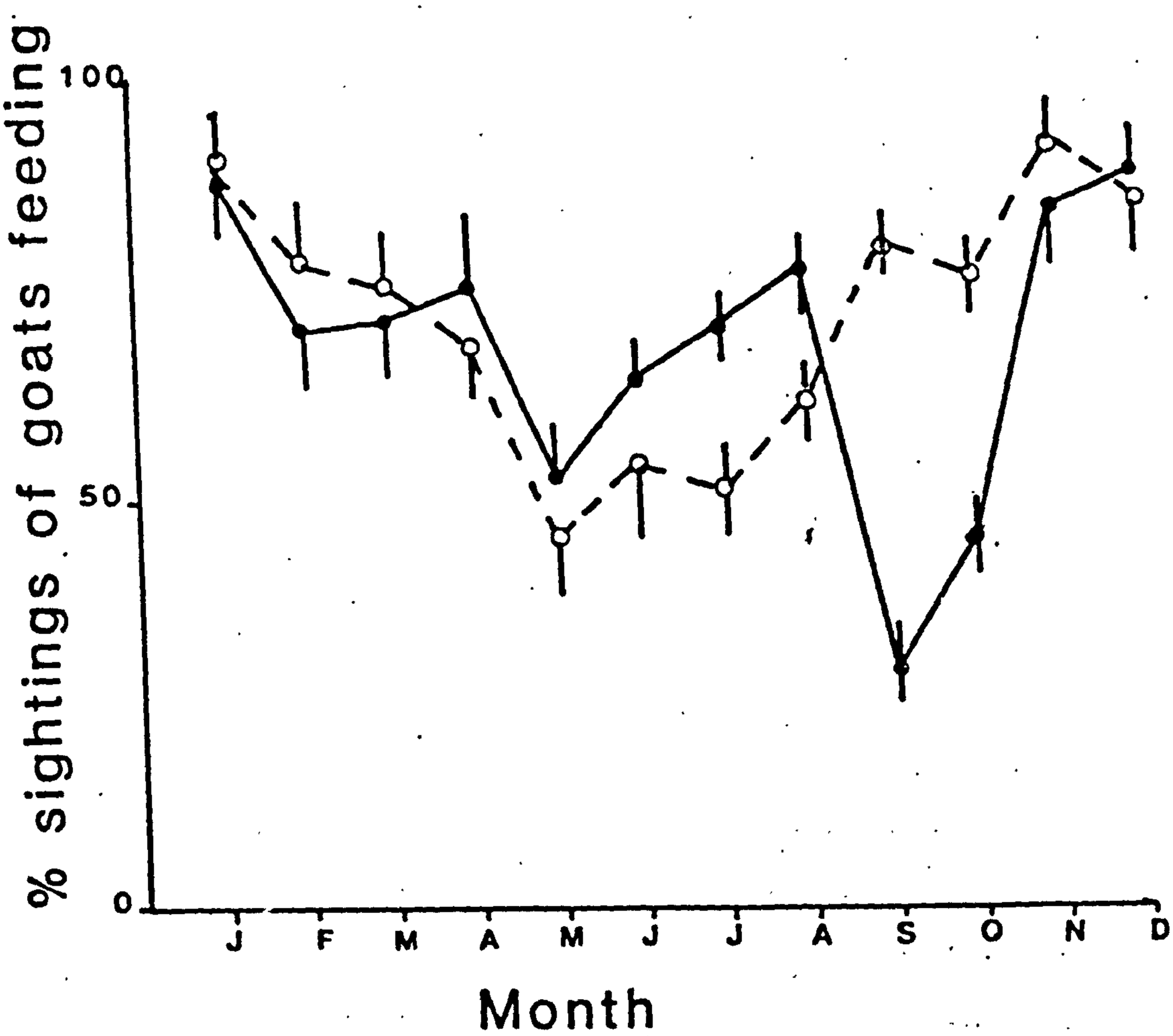


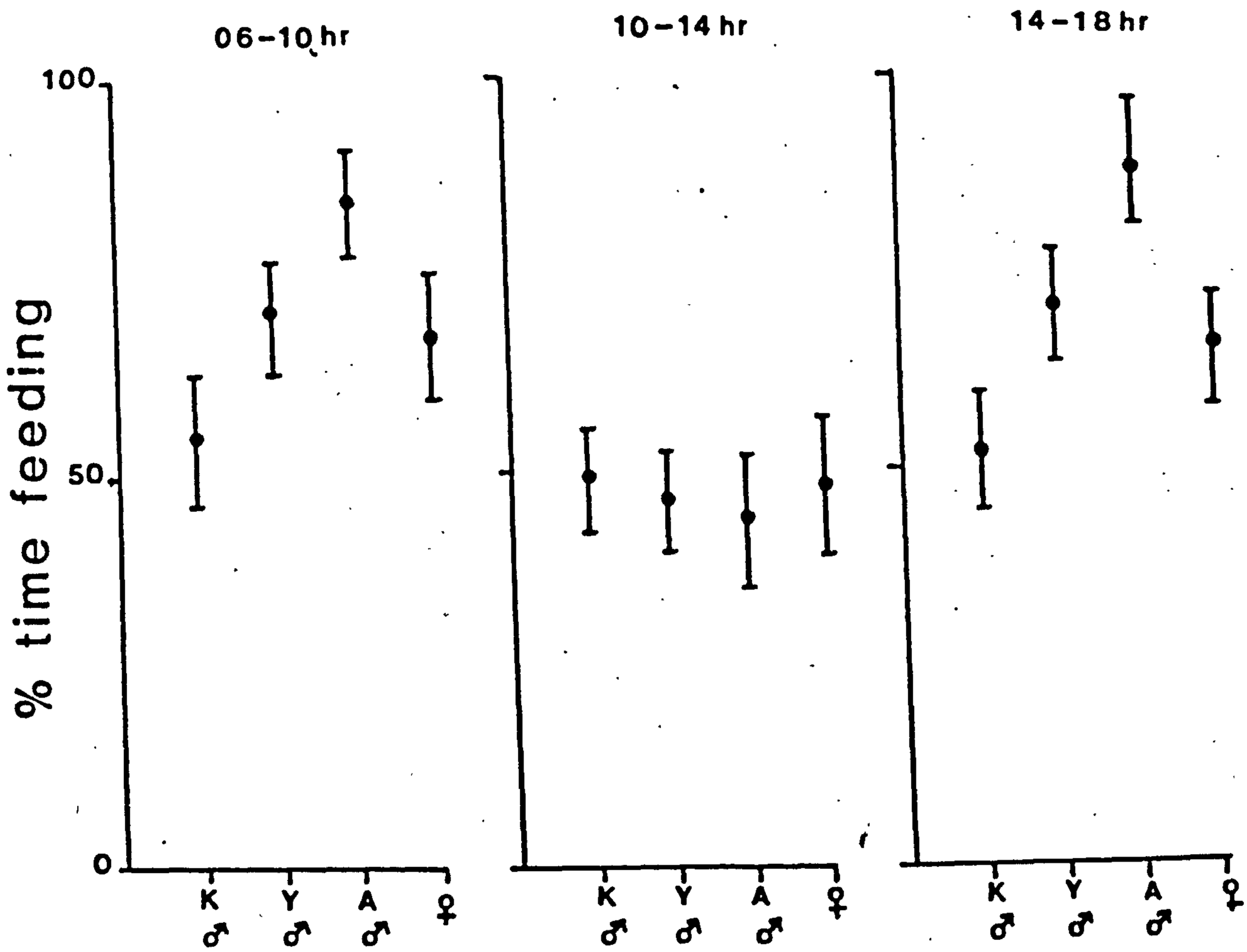
Fig. 5.56 Percentage of sightings of males ●—● and females ○—○ feeding throughout the year. The vertical lines indicate standard errors.

an average of 84% and 88% of their time during the morning and afternoon periods of the day feeding. This was significantly more than male kids, yearling males or females (Fig. 5.57). It should be noted that goats do not feed at night during this period of the year. Figure 5.58 shows that adult males spent on average between 15% and 31% of their time feeding in any four hour period. This is significantly less than the other age/sex categories of goat. Also it can be seen from Fig. 5.58 that males did not make up for lost feeding time during the day by feeding at night.

During the rut adult males spent up to 38% of their time during the afternoon period involved in rutting activities (Social/Sexual + Aggressive), which was significantly more than male kids or yearlings, or females (Fig. 5.59). Amongst these adult males there was a tendency for dominant males to spend less time feeding and more time involved in rutting activities than subordinate males (Fig. 5.60). However only during the middle period of the day (10.00-14.00) was there a significant negative correlation between dominance ratio and the percentage of time spent feeding ($r_s = -0.74$, $n=11$, $p<0.01$). During the afternoon period of the day (14.00-18.00) there was a positive correlation between dominance ratio and the proportion of time involved in rutting activities ($r_s = 0.70$, $n=10$, $p<0.05$).

In November, after the rut, the proportion of time spent feeding by adult males increased, and during the morning and afternoon periods of the day all age/sex categories of goat spent approximately 80% of their time feeding (Fig. 5.61).

Fig. 5.57 The proportion of time spent feeding during each four hour period in the pre-rut period. K=male kids, Y=male yearlings, A=adult males, ♀=adult and yearling females, N=number of goat hours. Chi squared compares yearling and adult males. Morning period 06-10hrs: χ^2=14.2, d.f.=1, $p<0.001$ and afternoon period 14-18hrs: χ^2=21.9, d.f.=1, $p<0.001$. Vertical lines indicate 95% confidence limits.


06-10 hr
10-14 hr
14-18 hr
% time feeding
100
50
0
K ♂
Y ♂
A ♂
♀

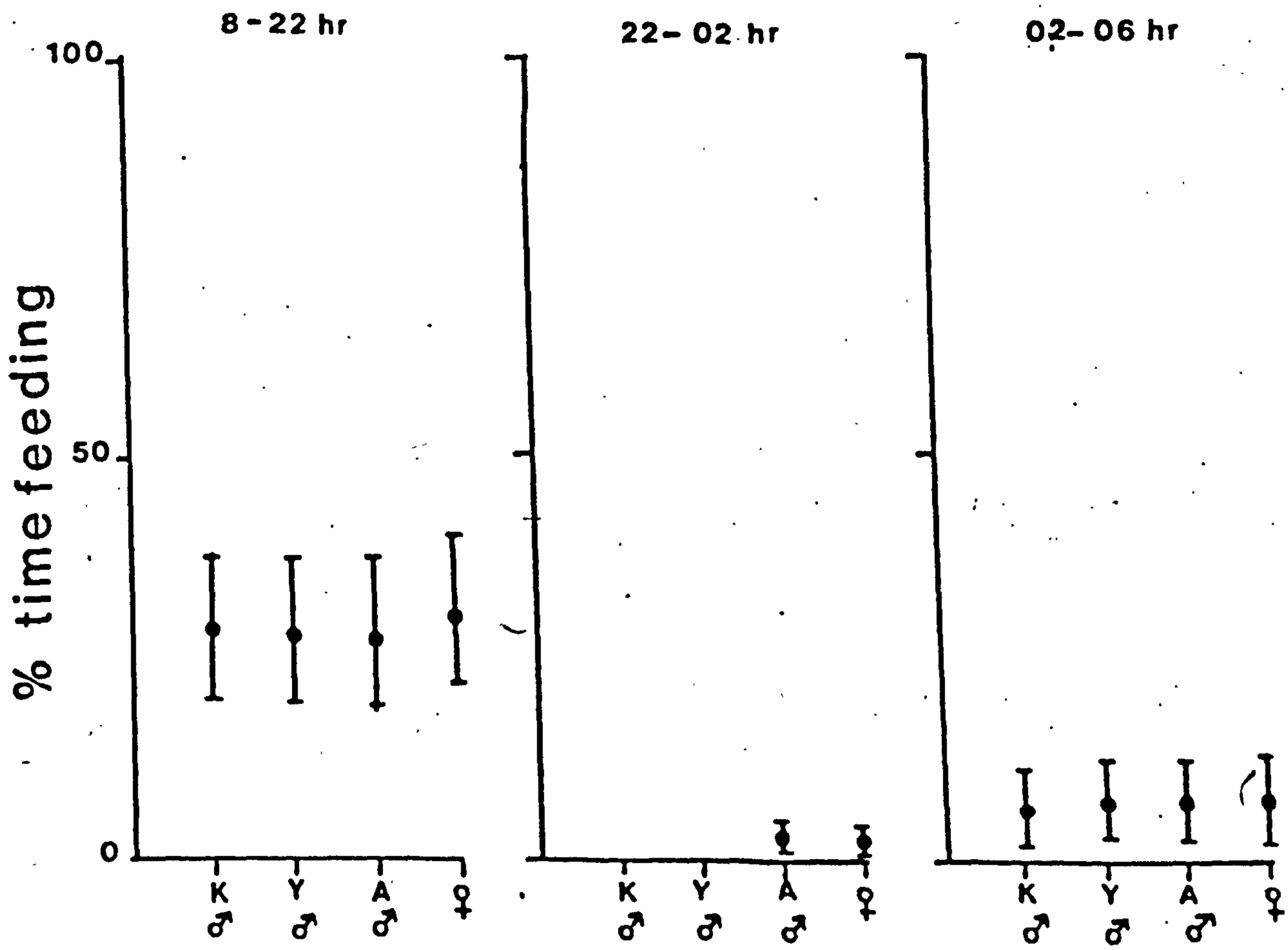
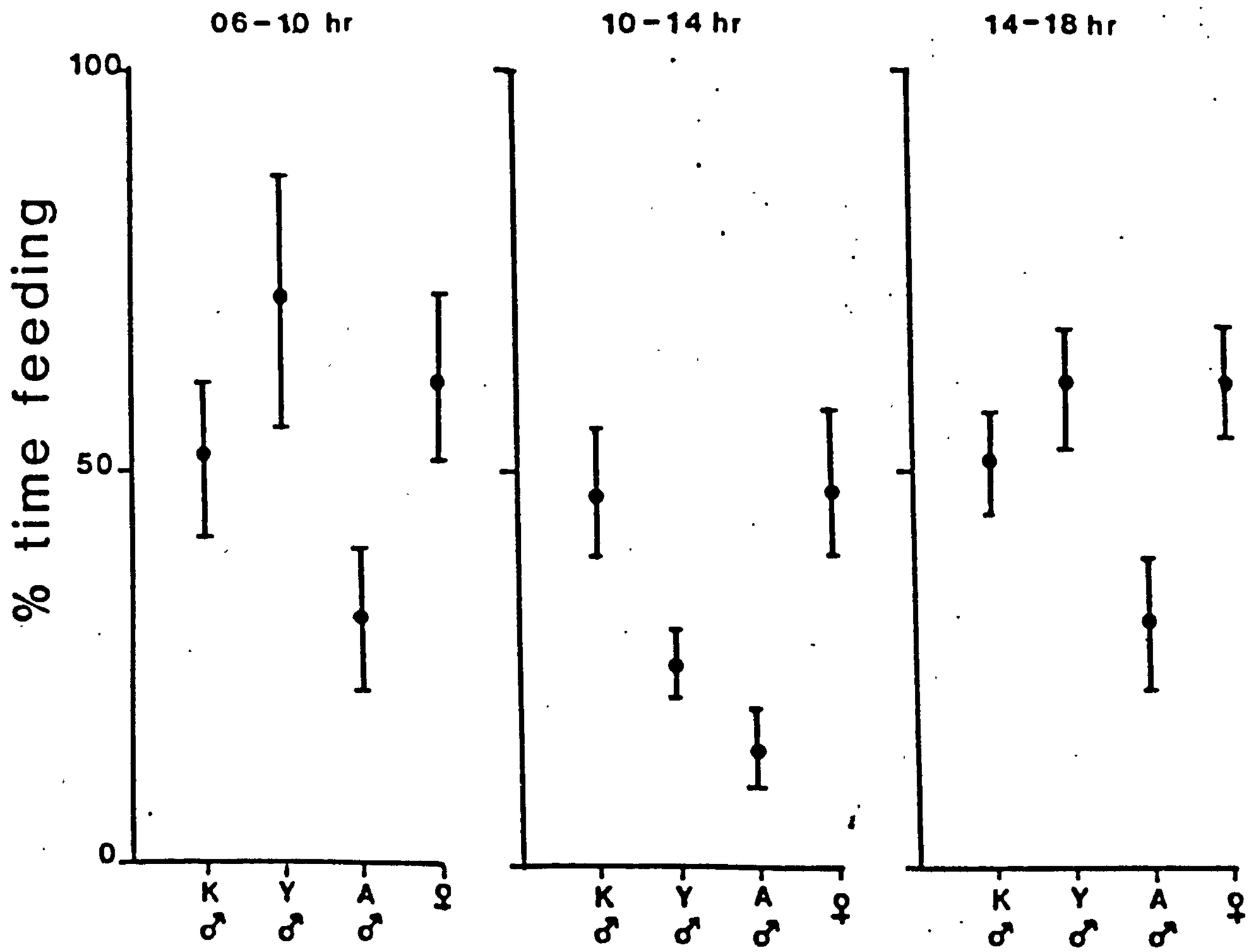

8-22 hr
22-02 hr
02-06 hr
% time feeding
100
50
0
K ♂
Y ♂
A ♂
♀

Fig. 5.58 The proportion of time spent feeding during each four hour period in the rut. K=male kids, Y=yearling males, A=adult males, ♀=adult and yearling females, N=number of goat hours. Chi squared compares adult males with male kids during the morning period, 06-10hrs: χ^2=15.5, d.f.=1, $p<0.001$, and the afternoon period, 14-18hrs: χ^2=21.5, d.f.=1, $p<0.001$. Vertical lines indicate 95% confidence limits.


06-10 hr
10-14 hr
14-18 hr
% time feeding
100
50
0
K ♂
Y ♂
A ♂
♀

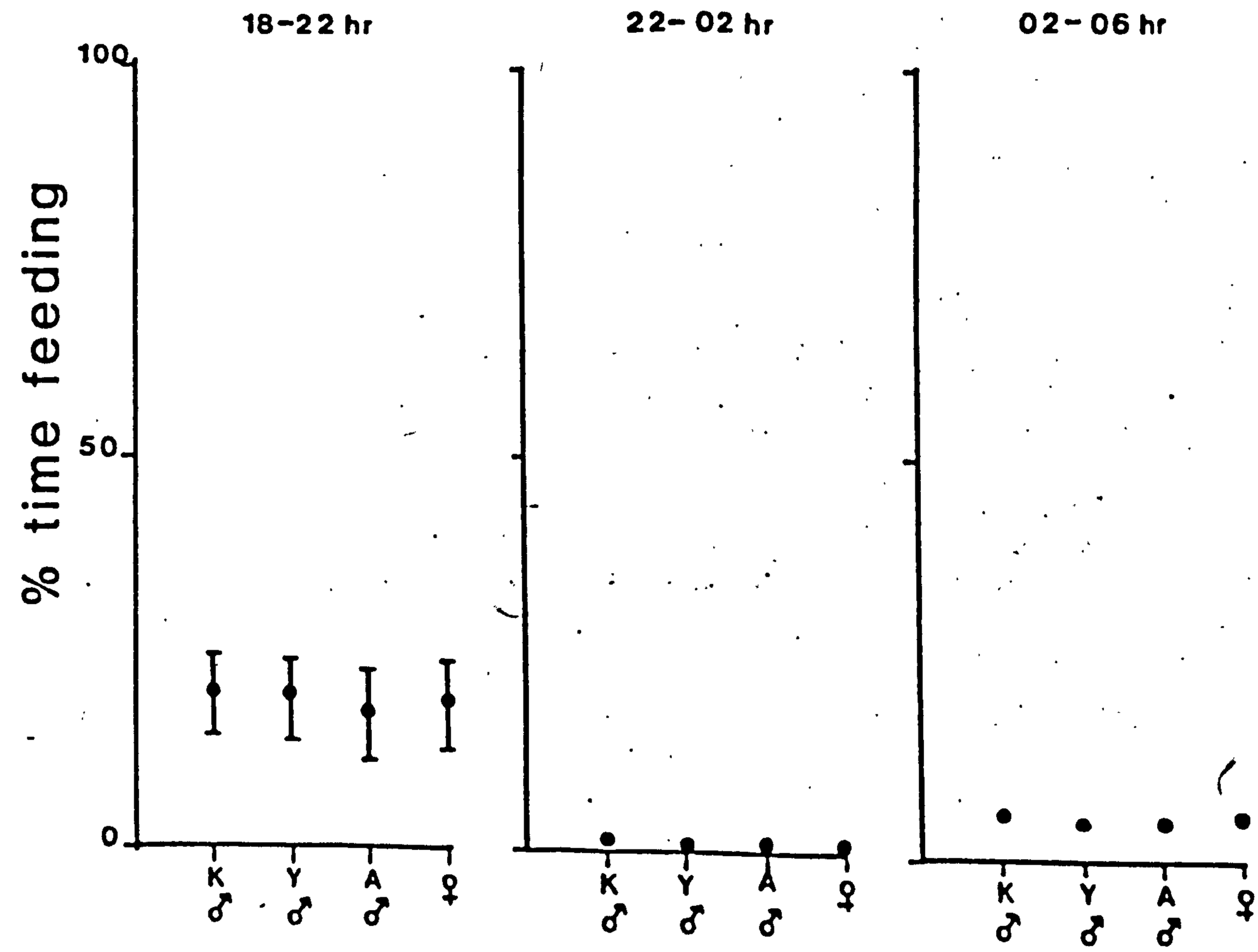
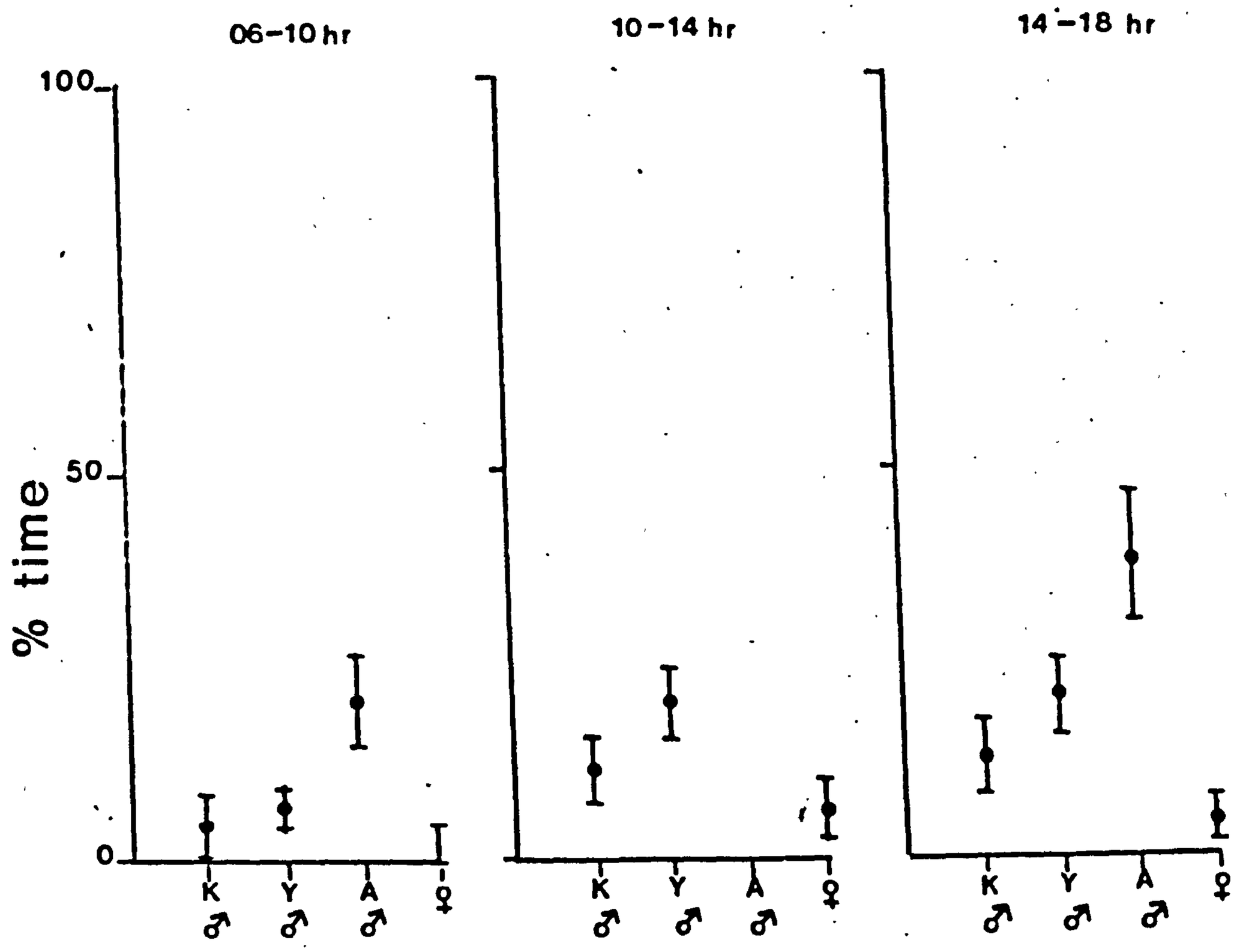

18-22 hr
22-02 hr
02-06 hr
% time feeding
100
50
0
K ♂
Y ♂
A ♂
♀

Fig. 5.59 The proportion of time spent involved in social/sexual and aggressive activities, during the rut, in each four hour period of the day. K=male kids, Y=yearling males, A=adult males, ♀=adult and yearling females. Chi squared compares adult males with yearlings during the morning period, 06-10hrs: χ^2=13.0, d.f.=1, $p<0.001$, and during the afternoon period, 14-18hrs: χ^2=21.31, d.f.=1, $p<0.001$. Vertical lines indicate 95% confidence limits.


06–10 hr
10–14 hr
14–18 hr
100
50
0
% time
K ♂
Y ♂
A ♂
♀

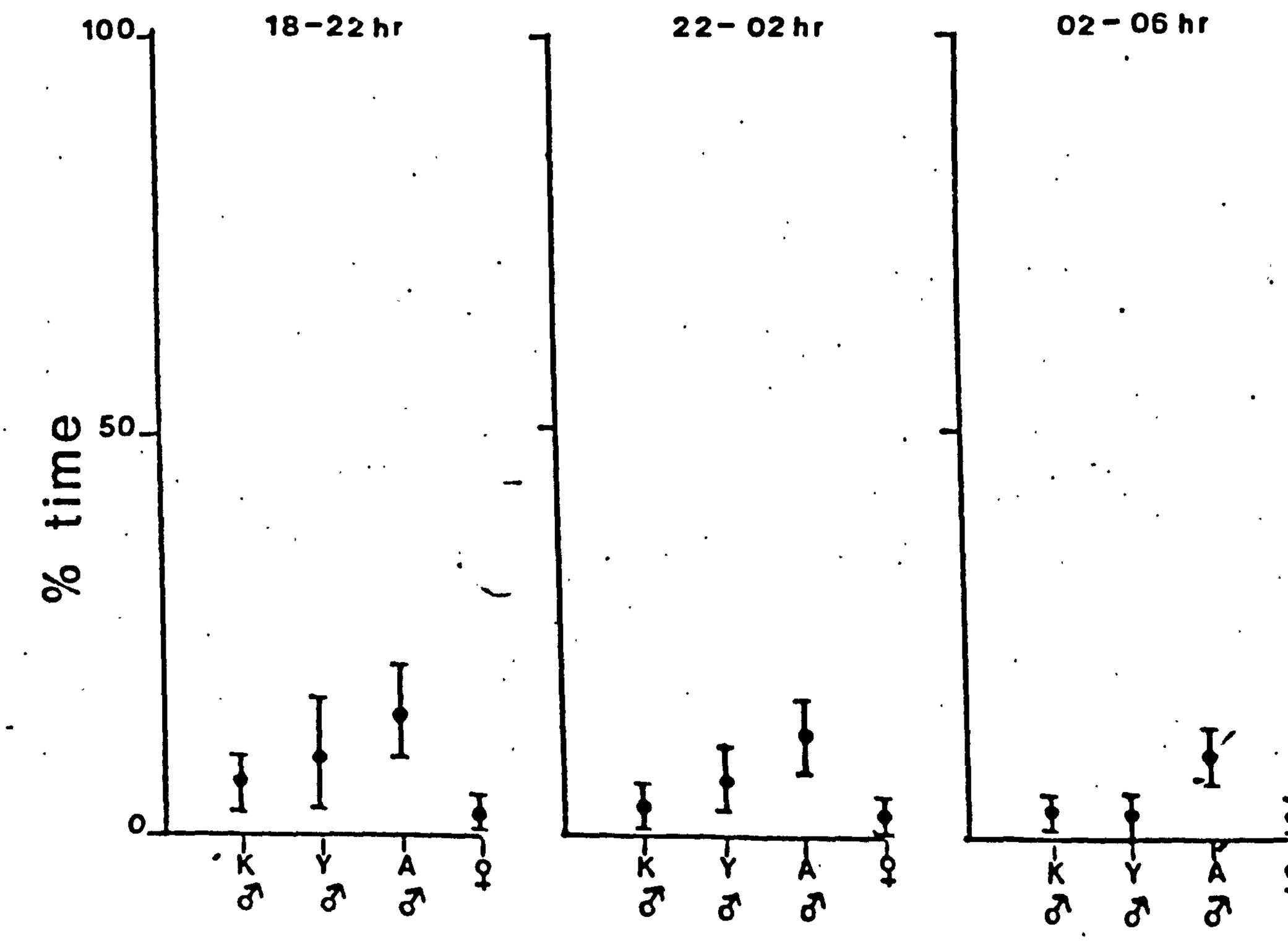
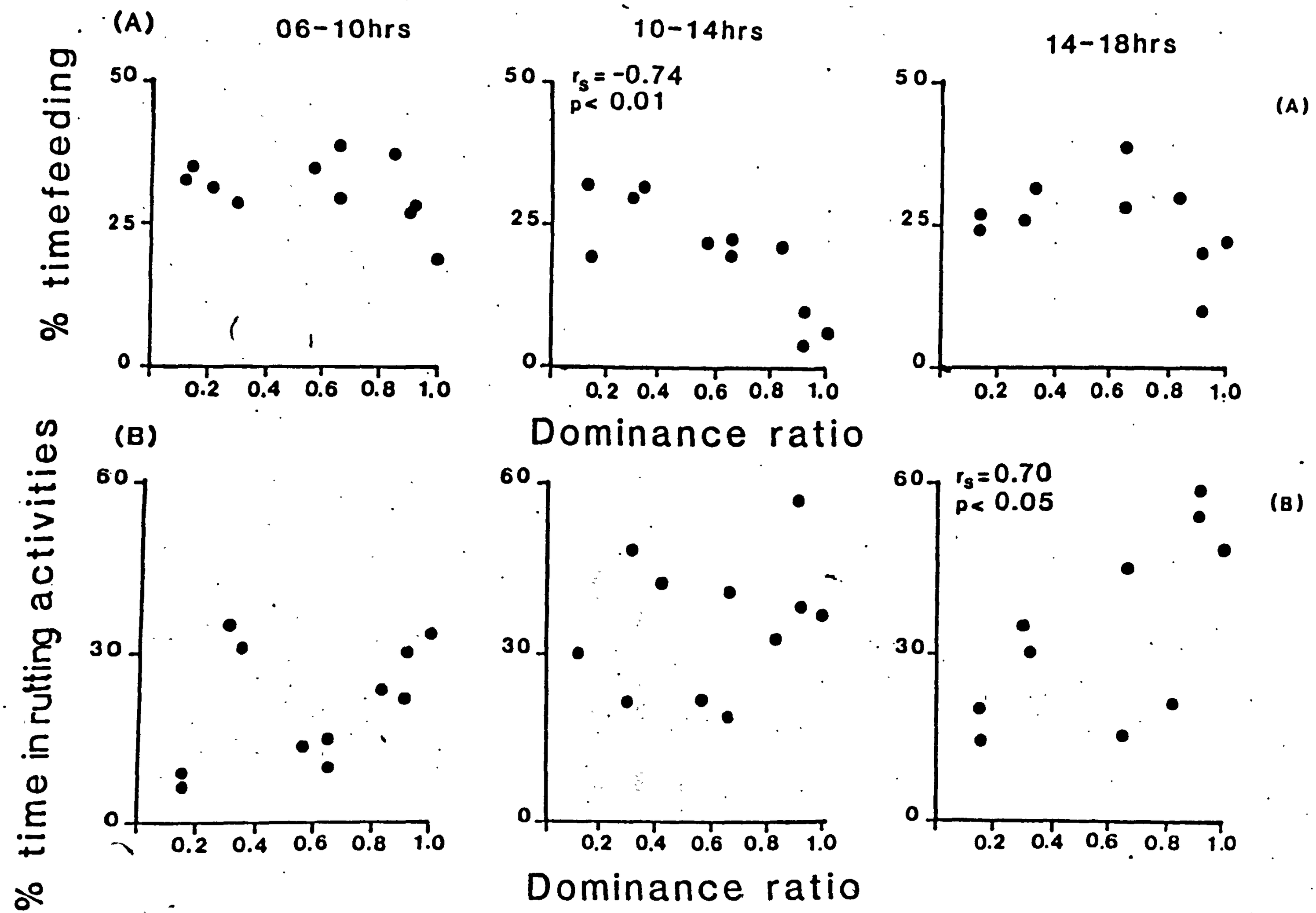

18–22 hr
22–02 hr
02–06 hr
100
50
0
% time
K ♂
Y ♂
A ♂
♀

Fig. 5.60 The relationship between dominance rank and the proportion of time spent feeding (A) and involved in rutting activities (B) during daylight hours in the rut.


(A)
06-10hrs
10-14hrs
14-18hrs
% timefeeding
50
25
0
0.2 0.4 0.6 0.8 1.0
$r_s = -0.74$
$p < 0.01$
(A)
Dominance ratio
(B)
% time in rutting activities
60
30
0
$r_s = 0.70$
$p < 0.05$
(B)
Dominance ratio

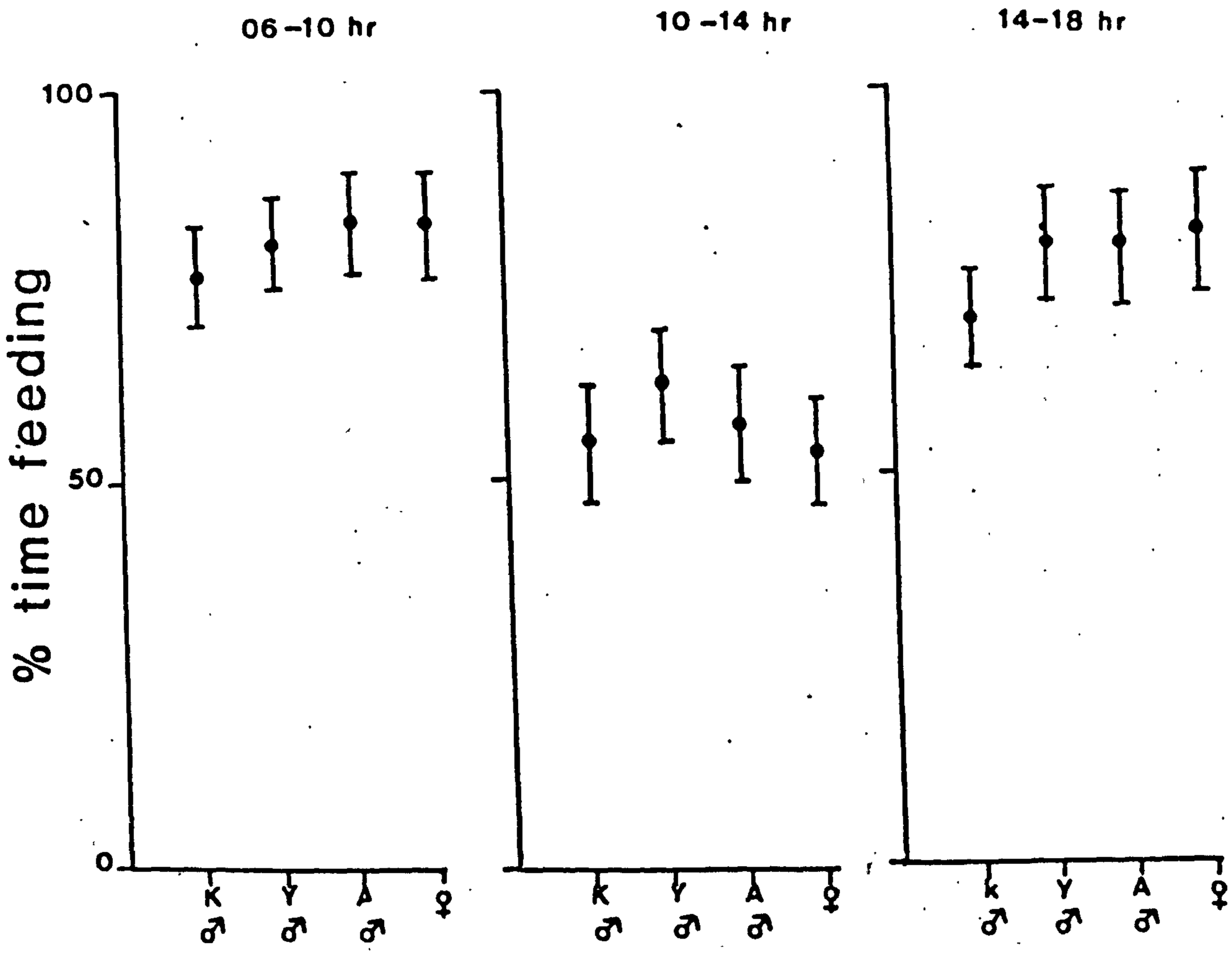


Fig. 5.61 The proportion of time spent feeding during the post rut period. K=male kids, Y=yearling males, A=adult males, ♀=yearling and adult females. Vertical lines indicate 95% confidence limits.

5.8.2 Weight loss

A total of 37 individual goats (19 males and 16 females) were caught both before and after the rut. Fig. 5.62 shows that all but one of the females and all male kids gained weight during the rut. One male yearling gained weight during the rut while others either lost weight or remained the same. All adult males except male 4 lost between 6kg and 20kg during this period, that is between 10-30% of their pre-rut body weight. Male 4 is a large seven year old animal with large horns but with no external testes (see 5.6.3). He did not take an active part in the rut and remained at the same weight. The fact that adult males were spending approximately 80% of their time feeding in early November prior to capture indicates that the weight loss was not entirely due to a reduction in the amount of forage in their rumens.

There was no clear relationship between percent weight loss and dominance rank or mating success. However there was a significant correlation between actual weight loss and mating success and dominance ratio of males (Figs. 5.63 and 5.64)

During the 1980/81 winter yearling and adult males suffered a higher mortality rate (yearling 20%, adult 17%) than yearling or adult females (yearling 0%, adult 10%). However there was no relationship between the amount of weight lost and mortality (Table 5.5).

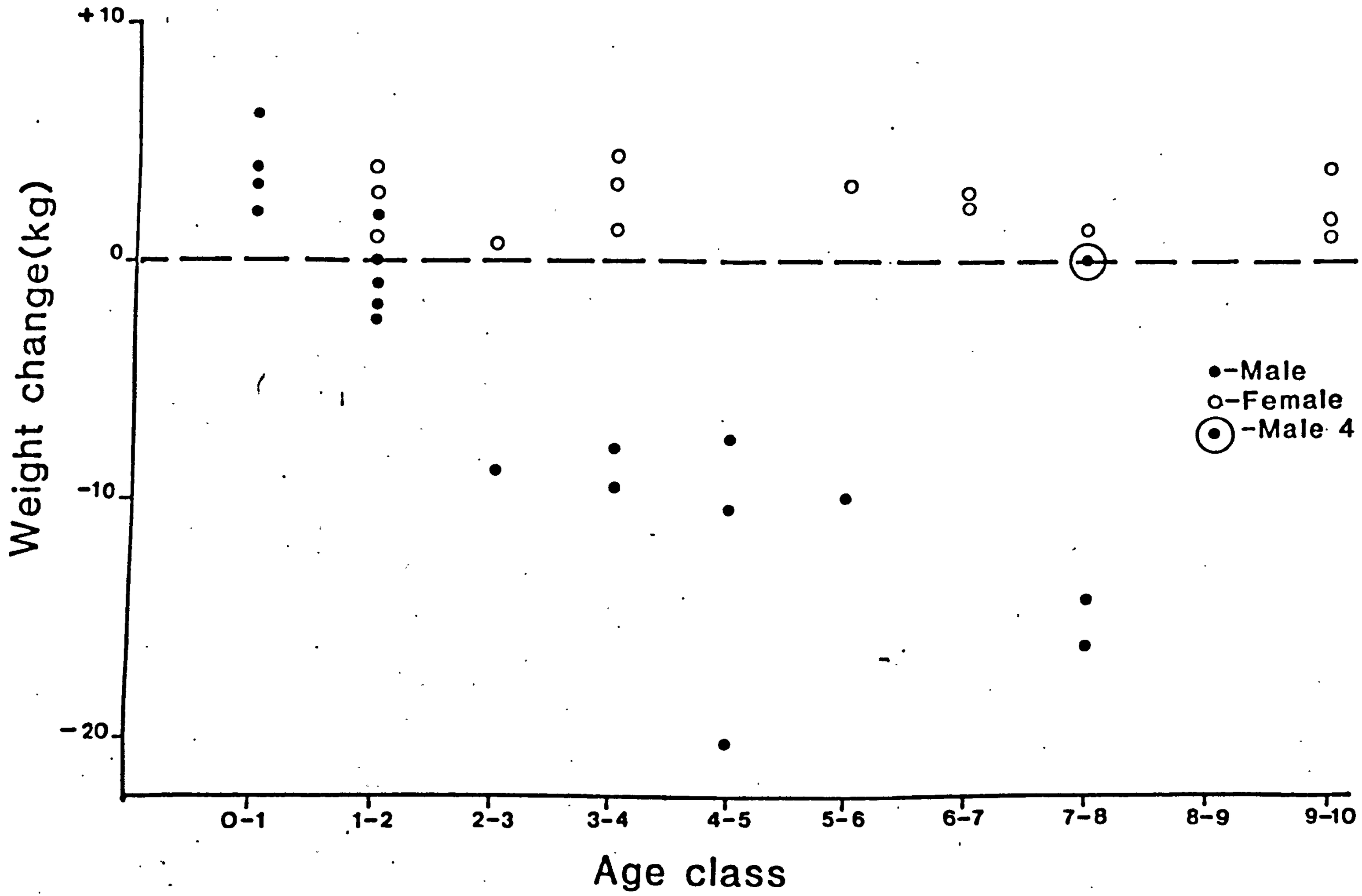


Fig. 5.62 The change in weight of male and female goats in relation to their age during the 1981 rut.

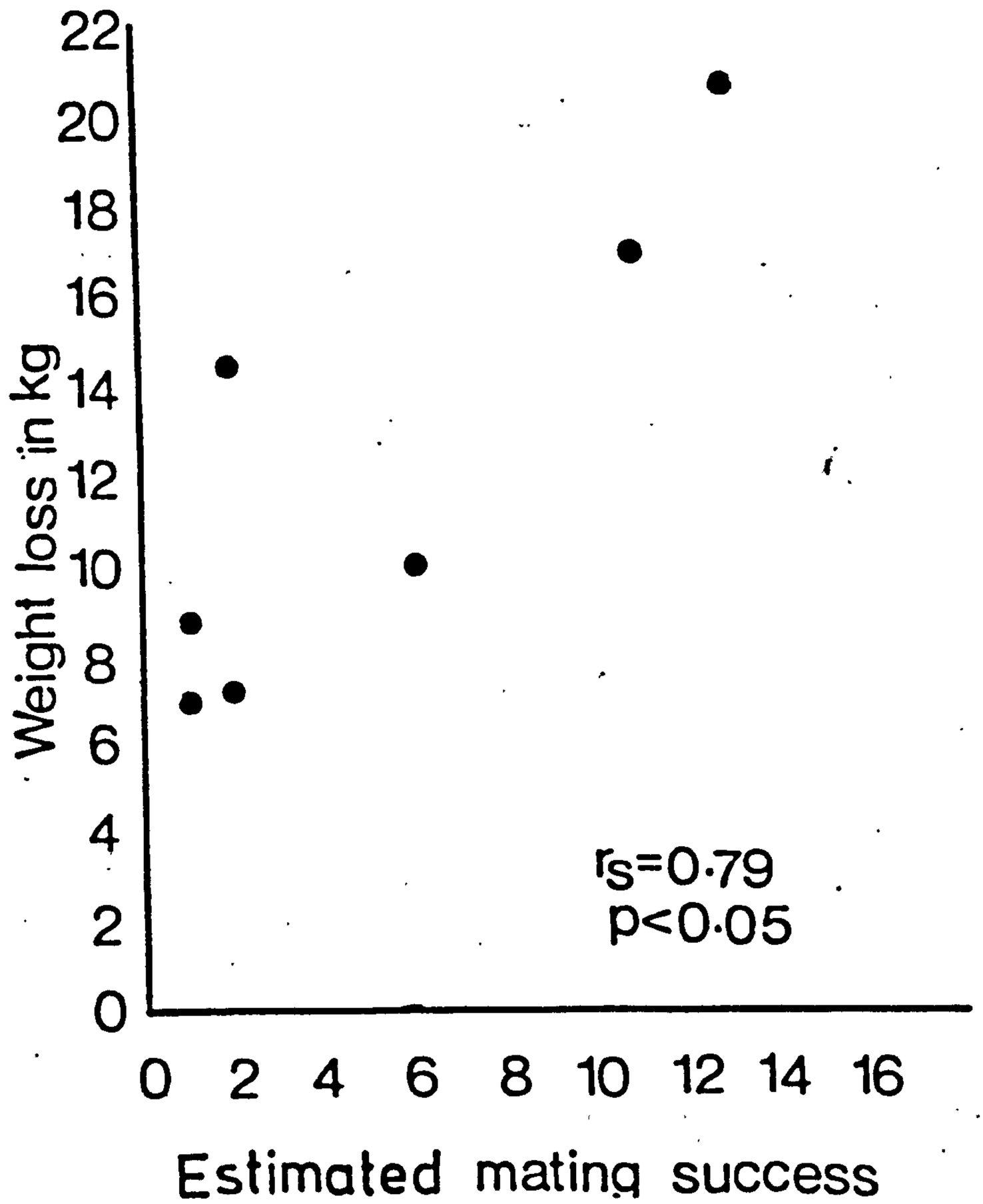


Fig. 5.63 The relationship between estimated mating success and weight loss by adult males during the 1981 rut.

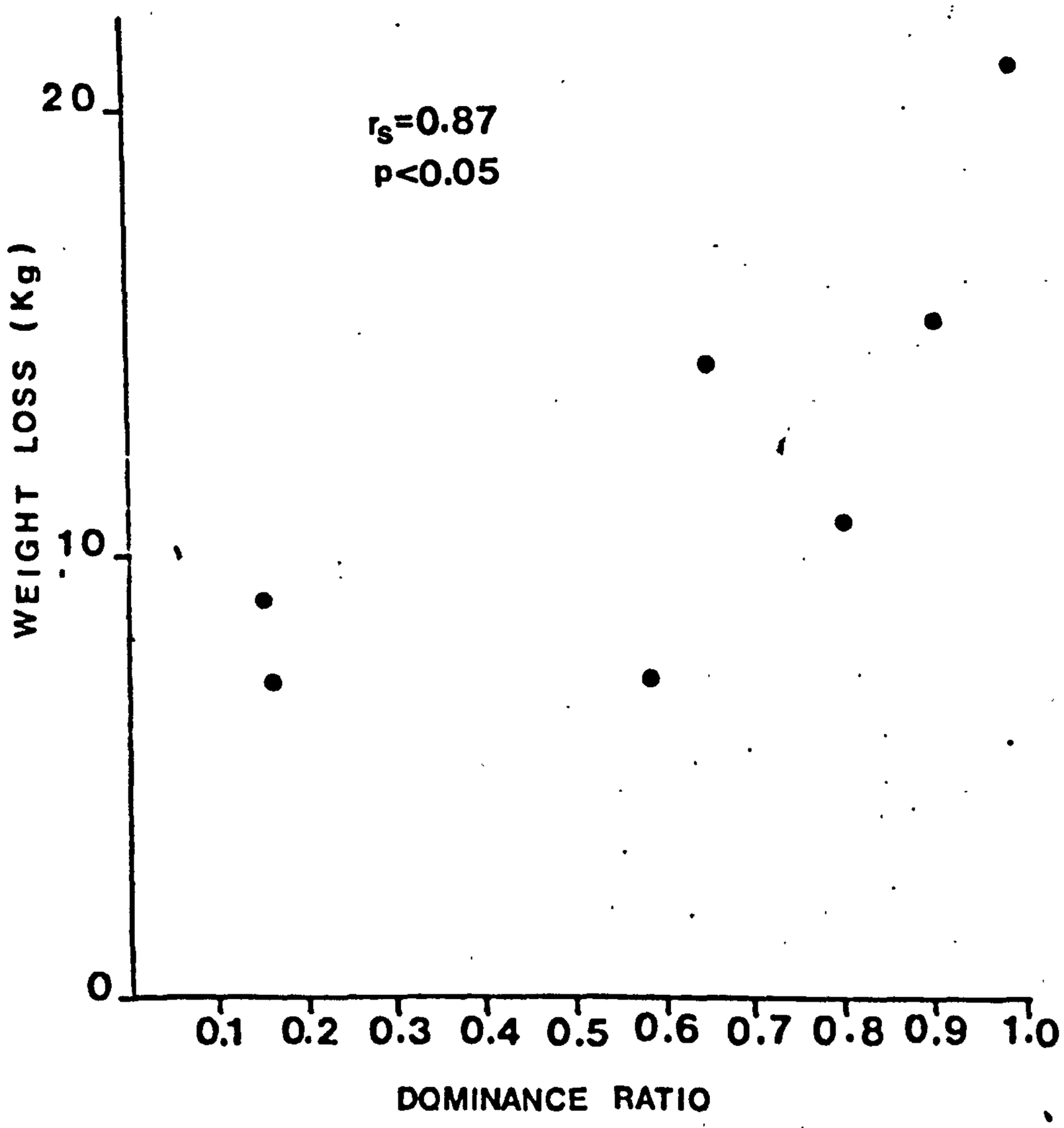


Fig. 5.64 The relationship between dominance ratio and weight loss by adult males during the 1981 rut.

Male ID.	Age	Dominance ratio	Weight change Kg.	%	Survival
83	1	-	+1.0	5	No
129	1	-	0.0	0	Yes
4	7	-	0.0	0	Yes
79	1	-	-0.5	1	Yes
87	1	-	-1.0	4	No
88	1	-	-2.2	10	Yes
46	3	0.15	-7.2	17.7	Yes
36	4	0.57	-7.2	16.2	Yes
18	2	0.16	-8.6	19.0	Yes
10	5	-	-9.2	15.1	Yes
14	4	0.83	-10.9	17.2	No
34	7	0.66	-14.5	26.4	No
7	7	0.92	-15.1	25.1	Yes
101	4	1.00	-20.9	29.8	Yes

Table 5.5

Weight loss, age and dominance ratio of male goats in relation to their survival over the 1980/1981 winter.

5.9 DISCUSSION

The mating system of the feral goats observed in this study was a form of successive polygny similar to that described by Geist (1960), Greig (1969), Crook (1970), Munton (1975), and Coblentz (1980). There was only one observation of a single female being chased and mounted by several males as reported by Shank (1972) and Gould (1979).

The timing of oestrous in goats is thought to be largely controlled by decreasing daylength (Yoshioka et al. 1952, Greig 1969, Hafez 1969, Mackenzie 1967). In 1980 and 1981 the rut occurred between late September and the end of October, with the kids being born after a gestation period of approximately 150 days in late February and March. In 1980 the kids were born between late March and the end of April, indicating that the rut in 1979 must have been almost one month later than in the following two years. The 1978/79 winter was severe and the spring was very late in 1979 (Bullock 1982). Mitchell and Lincoln (1973) have shown that in red deer hinds, those in poor condition come into oestrus and conceive later in the year than hinds in good condition. The combination of the hard winter and late spring in 1979 may have left all the females in relatively poor condition, resulting in their all coming into oestrus much later in the year than in 1980 or 1981.

There was greater synchrony in timing of oestrus between females from the same heft than females from different hefts. Jewell and Grubb (1974) found that Soay ewes from the same home range groups tended to come into oestrus at the same time. Odours

from other females have been shown to induce synchrony of oestrous cycles of mice (Whitten 1959).

In a species with a polygynous mating system that is achieved by mate defence (rather than resource defence) one would expect male biased dispersal (Greenwood 1980). The movement of males between groups in search of available oestrous females does appear to be a form of breeding dispersal. These movements appeared to be determined by whether or not a male had access to an oestrous female. High ranking males were less likely to leave a rutting group than low ranking males.

Considering that some males walked a minimum of 30km between hefts in the main study area and the Grey Mare's Tail heft is only 2km from the Carrifran heft it is somewhat surprising that there was no movement of males between the Grey Mare's Tail heft and the main study area. There are no physical barriers such as fences to stop males moving between these two areas. The females belonging to the Grey Mare's Tail heft came into oestrous after those in the main study area in 1980 and 1981. Adult males from the main study area had already been rutting for almost a month and would have lost considerable amounts of weight. They were probably not in good enough condition to continue rutting.

The present age structure of males in the Grey Mare's Tail heft may have been a factor limiting the movement of males out of this heft to the main study area. In 1980 and 1981 there were only two males over two years old present in the Grey Mare's Tail heft. The remaining males were all kids in 1980 and yearlings in 1981. In the main study area it was found that high ranking males were unlikely

to leave a group if they had access to an oestrous female. The three most high ranking males visted fewer groups than any other adult males during the rut. Male kids and yearlings in the main study area began to move between hefts much later, visited fewer groups and walked much shorter distances than adult males. Therefore taking into consideration; a) the timing of the rut in the Grey Mare's Tail heft, b) the probable small number of movements out of groups by adult males due to the low level of competition for females (22 between two adult males3 and c) the known lack of mobility of young males, then the absence of male movement between the Grey Mare's Tail and the main study area is not entirely unexpected. However if these arguments are correct one would predict that there is likely to be breeding dispersal of males from the Grey Mare's Tail heft to the main study area in the future.

In this study during two rutting seasons, four males suffered serious injuries to their legs which inhibited their mobility, and two males suffered permanent injuries (horn breakages). So in any one year up to 7% of all males over one year old may be expected to receive a serious or permanent injury each year. In areas where large predators still exist a large proportion of their kills are of ill or injured animals (Schaller 1972, Kruuk 1972). Therefore the cost of an injury to a leg would presumably be much higher in populations where large predators are present. Fighting was also found to carry costs in terms of a loss of mating opportunities. In 25% of fights over oestrous females a third male was observed to successfully copulate with the female while the fight was in

progress.

This study provides some evidence that both frequency and intensity of aggression is affected by the variation in the benefits and costs of aggressive behaviour. The frequency of both aggressive encounters and fights was highest during the period when most females were in oestrus . Aggressive encounters were more frequent in rutting groups than in non-rutting groups. Studies on other mammals have shown an increase in male:male aggression when females are most likely to conceive (Geist 1971, LeBoeuf 1974, Clutton-Brock et al. 1979, Packer 1979). However, Hausfater (1975) observed a decrease in the rate of agonistic interactions between adult male yellow baboons when at least one female was in oestrus .

If fights carry a risk of much higher cost than aggressive encounters, then one would not expect individuals to escalate aggressive encounters into fights with animals they are unlikely to beat (Maynard Smith 1974, Parker 1974). In this study, fighting success was found to be related to pre-rut body weight. The heavier male was the victor in 82% of fights where the weights of the contestants were known. Amongst adult males the mean difference in weight between opponents was significantly less in those encounters that escalated into fights than in those that did not. This suggests that male goats may be able to assess their opponents' weight and therefore fighting potential.

Horn size in male goats has been suggested to be a symbol of rank and fighting ability by Crook (1969) and Greig (1979). However, in this study there was no clear evidence that fighting ability was related to horn size. Also, there was only weak

evidence that males avoided fighting males with larger horns than themselves. Body size (length x height x width) is correlated with pre-rut body weight ($r_s = 0.89$, df = 9, $p<0.001$), so presumably males could assess each other's body weight and fighting potential from overall body size.

If a male fails to assess his opponent's fighting ability correctly and the aggressive encounter escalates into a fight, one would expect a male to willingly give up when it is clear that he is losing. Therefore fights between evenly matched males should be longer than those between unequally matched males. Also if the costs of fights increase with their duration, fights should be longest and most intense when the potential gains are greatest (Parker 1974). There was a tendency (non-significant) for fights between males of similar weight to be longer than those between males of dissimilar weight. However there was a significant increase in the duration of fights with a decrease in the difference in the rank of the two opponents.

Dominance amongst male goats appeared to be related to pre-rut body weight. Dominance or fighting success has been found to be determined by body size in many other vertebrates (dairy cattle: Schein and Fohrman 1955, Bouissou 1972; reindeer: Espmark 1964; toads: Davies and Halliday 1977; red deer: Suttie 1983).

High ranking male goats achieved higher mating success in one season than lower ranking males. Studies on other polygynous mammals have shown that fighting success and dominance plays a major part in deciding reproductive success of males (Buechner 1961, LeBoeuf 1974, Clutton-Brock et al. 1982). There are costs to

achieving high mating success. Adult males lost between 10% and 30% of their body weight during the rut, and there was a positive correlation between mating success and weight loss during the rut. This loss in weight was probably due to a reduction in the amount of time spent feeding, together with an increase in activity, during the rut. This contrasts with an increase of 6% in body weight by female goats during the rut. The prediction that weight loss by males during the rut results in males suffering a higher over-winter mortality rate than females was not conclusively demonstrated. The mortality rate of adult males was higher than that of females during the 1981/82 winter. However, of the nine adult males for which I have information on weight changes during the rut, there was no clear evidence that males that lost more weight were less likely to survive the winter.

In feral goats, as in many other mammals, males play a more active role in courtship than females. The first step usually involves locating and identifying an oestrous female. Male feral goats move considerable distances in search of oestrous females during the rut. Males identify an oestrous female by sniffing her vulva and "testing" her urine. Shank (1972) suggested that much of the courtship behaviour of goats is actually urine soliciting behaviour. Schaller and Laurie (1974) claim that female wild goats urinate less frequently in response to a low stretch, gobble or leg-kick than to a normal approach. However, in the present study, females urinated more frequently to low stretch approaches than to normal approaches. This suggests that the low stretch is a more efficient method of eliciting a urination response in female feral

goats. Also, older males adopted a low stretch posture more often than younger males.

Having detected an oestrous female the male continues to approach and touch the female in preparation for mating, while at the same time ensuring that the female does not leave. The actual courtship of ungulates often consists of a mixture of slightly aggressive and distinctly non-aggressive elements (Walther 1971, Leuthold 1977). The low stretch posture consists of both aggressive and appeasing elements. The lying of the horns along the back can be interpreted as a form of weapon hiding (opposite to the horn point threat posture) while the approach itself is aggressive as it encroaches on the female's individual distance. The normal female response is to walk forward, and the male then follows and approaches again. As the courtship proceeds the frequency of approach decreases and the frequency of gobbles and leg-kicks increases. The decrease in the frequency of male approaches is due to a decrease in female withdrawal possibly indicating the female's acceptance of the male's transgression of her individual distance.

The leg-kick is a form of contact behaviour common to many ungulates. Walther (1971) suggests that the leg-kick has evolved from a form of aggressive behaviour. However, the leg-kick could equally well be a ritualized form of an attempt to mount. The gobble, the most common courtship behaviour, has been described as a ritualized form of an attempt to bite (Walther 1971). Alternatively, it is more likely to be a ritualized form of lick. Males frequently lick a female's perineum during courtship. Towards the end of courtship, females tail-wag more frequently.

The movement of females towards males during the rut is suggestive of female mate choice. By remaining close to a high ranking male a female might increase her chances of being mated by that male and also avoid the continual harassment of younger subordinate males which might otherwise reduce the time available for feeding and increase energy expenditure by females during the rut.

CONCLUDING DISCUSSION

It is now widely accepted that natural selection operates through the differential reproductive success of individuals. This results in the spread and maintenance of advantageous traits, leading to the evolution of different adaptations in species occupying various habitats. If this is correct we should expect to find individuals behaving in such a way as to increase the propagation of their genes. In mammals this is usually achieved by individuals attempting to maximize their lifetime reproductive success.

Sexual reproduction usually involves the fertilization of a large female egg by a small male sperm. Females produce relatively few large gametes and males produce many small ones. Because of this males can potentially fertilize eggs at a faster rate than they are produced. Females, or rather the eggs they produce, are therefore in most species a scarce resource for which males compete. A male can increase its reproductive success by finding and fertilising many different females, but a female can only increase her success by turning food into eggs or offspring faster. However care for the zygote does not end with gamete investment. In many animals there is some form of parental care in the form of a prolonged gestation period, incubating and guarding eggs, or feeding the young. Parental care may be done by both parents e.g. wandering albatross, Diomedea exulans, (Tickell 1968), where both

parents incubate the egg and feed the chick, by the male alone e.g. sea-horse, Hippocampus, (Breder and Rosen 1966) where the male carries the fertilised eggs around in his brood pouch or by the female alone e.g. Northern elephant seal, Mirounga angustirostis, (Bartholomew 1952) where there is a prolonged period of gestation and once the young are born they are fed on milk and only the female lactates. The reproductive success of male seahorses and wandering albatross is clearly going to be influenced by the behaviour of the male after fertilisation but not in the elephant seal.

In "The Descent of Man" Darwin (1871) noted that in a species where males compete intensively with each other for access to breeding females there are often differences between the sexes quite unconnected with the primary reproductive organs. These traits, such as larger body size, strength and pugnacity of the male, weapons of offence or defence against opponents, gaudy colouring or song are termed secondary sexual characteristics. They are thought to have evolved by the process of sexual selection which "depends on the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction" (Darwin 1871).

In Scotland female feral goats only produce one or occasionally two kids in late winter each year. There is no paternal assistance in the rearing of the kids. Therefore for a male goat to maximize his own reproductive success he must mate with as many females as possible.

On any one day during the rut there were between zero and eight females in oestrus in the main study area, where there were 15 adult males and 16 yearling males all probably capable of

inseminating a female. Therefore competition amongst males during the rut was not entirely unexpected.

There are however potential costs to acting aggressively and fighting. In this study it was found that fighting had potential costs in terms of loss of mating opportunities and of injury. Up to 7% of males per year suffered visible physical injury (see 5.5.4). Estimates of the cost of fighting in the Caprinae are scarce. However, Darwin (1871) reports of a male feral goat that killed several other males in combat, while Wilkinson and Shank (1977) suggest that between 5 and 10% of adult male musk oxen (Ovibos moschatus) may die each year as a result of rutting injuries. The cost of fighting in deer is known to be high. Geist (1971) reports that in a sample of mature male mule deer (Odocoileus hemionus) 10% showed some signs of injury each year, and Clutton-Brock et al. (1979) found that up to 6% of adult red deer stags suffered permanent injury each year.

The potential benefits of aggressive behaviour during the rut can be measured in terms of mating success. During the 1981 rut success in fights and aggressive encounters (dominance ratio) was strongly correlated with estimated mating success, even when the age of each male was taken into account (see 5.7). Studies on other polygynous mammals have shown that fighting success played a major role in determining reproductive success in males (LeBoeuf 1974, Gibson and Guinness 1980a and 1980b).

Evolutionary theory suggests that where aggression does occur, its occurrence and intensity should be affected by the potential costs and benefits of such behaviour (Maynard-Smith and Price 1973,

Parker 1974, Maynard-Smith 1976, Parker 1978).

This study provides some evidence to support these predictions. The frequency of both fights and aggressive encounters was greatest during the period when most females were in oestrus Aggressive encounters were much more frequent than potentially more costly fights. The frequency of aggressive encounters was higher in rutting groups than in non-rutting groups and reached a peak in rutting groups just prior to a successful mating (see 5.5.2). Studies on red deer (Clutton-Brock et al. 1982) and Southern elephant seals, Mirounga leonina, (MacCann 1983) have also found the frequency of aggressive behaviour to be related to the potential benefits.

Success in fights and aggressive encounters was strongly correlated with the pre-rut body weight and horn length of males, but with body weight alone when age was taken into account (see 5.5.1). Male goats fight by clashing head to head and then locking horns and trying to push their opponent back. The horns of a male feral goat need to be large enough and strong enough to take the considerable force of each clash and not to break on impact. As fighting success appears to be ultimately determined by the weight and strength of an individual and its ability to push an opponent back it is likely that there is selection for horns to be larger than a certain minimum size but not a selection pressure to maximise horn size.

There was evidence that male goats tended to avoid escalating aggressive encounters into fights with males that they were unlikely to beat. Males under two years of age always withdrew in aggressive

encounters with males more than two years old as they were always considerably smaller than the older males. Mean difference in weight of opponents in escalated aggressive encounters was significantly less (5.6kg) than in aggressive encounters which did not escalate into fights (11.4kg) (see 5.5.3). This suggests that male goats can assess an opponent's fighting ability by assessing his weight. (The observer learnt to assess the weight of goats by sight with reasonable accuracy during the course of the study so it seems likely that goats could also make use of this information.)

Other animals use various attributes and ritualized displays to assess an opponent's fighting ability, for example: horn size in bighorn sheep (Geist 1974), croak pitch in the common toad, Bufo bufo, (Davies and Halliday 1978) and roaring contests and parallel walking in red deer stags (Clutton-Brock and Albon 1977). As already mentioned in Chapter 5, horn size (Crook 1969, Greig 1969) and rutting odour (Coblentz 1976) have been suggested as possible symbols of fighting ability in goats. However, in this study there was little evidence that horn size was used in this way although odour may have been important.

It is clear that large male goats are at an advantage over smaller males in terms of competition for access to, and defence of, oestrous females. However large body size alone does not ensure a high mating success. Before a male mates with a female there is normally a period of courtship. The actual courtship in ungulates often consists of a mixture of slighty aggressive and distinctly non-aggressive elements (see 5.6.1). The exact function and evolution of specific courtship behaviour patterns in ungulates has

been subject to much discussion. Walther (1971) and Leuthold (1977) both argue that the aggressive tendencies in courtship are necessary for two reasons: 1) The male must remain active, advance towards the female and transgress her individual distance and face evasive and/or repulsive actions; 2) The male must also assert some form of dominance over the female as he will quite literally subdue her during the act of copulation.

The suggestion that males must dominate females during courtship seems to have come from a rather anthropomorphic male chauvinistic interpretation of the courtship behaviour of ungulates. Male goats are physically much larger than females, and in terms of fighting ability highly superior to females. However during courtship there is no advantage to a male in dominating a female because a male ungulate cannot successfully copulate with an unwilling female. The female must stand still to allow intromission. Females can quite easily avoid being mated by stepping forward as the male attempts to mount or simply by lying down. In populations of feral goats where there are multi-male chases of females (Gould 1979, Shank 1972), the pursuing males apparently perform few if any typical courtship behaviour patterns and try and mount the female without any prior courtship. Gould (1979) reports that in these situations females are chased to the point of exhaustion. It is suggested that as a direct result of these multi-male chases females suffer a higher mortality rate than males. Murder of a potential mate is probably not an evolutionarily successful mating strategy.

I suggest that courtship in feral goats and presumably in other

ungulates is a process of co-operation, as in many species of birds (Tinbergen 1951), rather than a dominant-subordinate relationship. If, as Hediger (1941) has stated, animals tend to maintain a certain inter-individual distance, then this tendency must be overcome for copulation to occur. Courtship behaviour may function to overcome this tendency and bring animals together. As each courtship bout proceeded there was a decrease in the frequency of movements away from the male by the female suggesting acceptance by the female of the male's transgression of her individual distance. The simultaneous increase in the frequency of gobbles and legkicks performed by the male and of tail-wagging by the female during courtship may indicate a synchronization of the sexual behaviour of the male and female.

Theoretically courtship could also allow the female to assess a male for qualities important for increasing her own reproductive success. Recent work on birds suggests that females may use attributes such as body size (Yasukawa 1981) or tail length (Andersson 1982) to assess the quality of males. In ungulates female choice appears to occur in those species which lek such as the Uganda Kob (Buechner and Schleoth 1965, Leuthold 1966) although the basis on which females choose males or whether this really is a form of female choice is uncertain. Red deer hinds tend to avoid mating with immature stags but do not select particular stags with which to mate (Gibson 1978). Female elephant seals react to mating attempts by subordinate males with loud vocalizations that usually attract a dominant male who then displaces the subordinate male. Cox and LeBoeuf (1977) suggest that this behaviour ensures that the

female is mated by a genetically superior male and they predict that incitement of male:male competition is widespread among mammals. During the rut female goats were observed to run away from subordinate (and usually younger) males to dominant males whenever the former attemped to court or mount them (see 5.6.2). However it was unclear whether this was mate choice on the part of females or seeking refuge from the harrassment of subordinate males.

Female reproductive success in mammals is determined by ability to successfully rear offspring to weaning. In red deer this is influenced by the fecundity of the female, the survival of the calves and the female's lifespan (Clutton-Brock et al. 1982). These are all affected by the habitat quality. In the present study those females belonging to the Capplegill heft consistently produced more kids per female each year than females from the other hefts. This heft of females migrated to the Craigieburn forestry plantation prior to kidding. Although there were no quantitative data it was clear to the most casual observer that there was a greater quantity and quality of forage and more shelter in the forestry plantation than on the open hill. This suggests that habitat quality may be an important factor in determining female reproductive success.

However the large variation in kid production between years indicates that climatic factors and possibly timing of breeding may also play an important role in determining female reproductive success. Clearly the protection and nutrition given to a kid will affect its survival. However by imparting a large amount of resources to an offspring a female may increase the chances of survival of that particular kid but may decrease her own chances of

survival and future reproductive success. After the first month of a kid's life all of the suckling bouts were initiated by the kid and most were terminated by the female, and as the kid got older there was an increase in the number of unsuccessful sucking attempts (see 4.3.3). This reflects a conflict of interests, with the offspring wanting more resources than the female is willing to give. Work on other vertebrates indicates that this weaning conflict (Trivers 1974) is widespread (e.g. De Vore 1963, Jay 1963, Hinde and Spencer-Booth 1971).

During this study male kids sucked more frequently and for longer each time than female kids during their first two months of life. Evolutionary theory suggests that where the variance in reproductive success is greater in one sex than the other, and this variation is influenced by the amount of parental investment the individual receives, parents can maximize their reproductive success by investing more heavily in the sex that shows a greater variance in lifetime reproductive success (Maynard Smith 1980). I have no evidence concerning lifetime reproductive success in feral goats but in a single mating season there was much greater variation in male reproductive success than in that of females, large males being much more successful than smaller males (see 5.7).

Work on domestic mammals has shown that a slow growth rate during the first month of life cannot normally be compensated for by an increased growth rate later in life and such individuals often have smaller than average adult body size (Gunn 1964 and 1965, William et al. 1974, Fraser et al. 1975). The birth weight of domesticated goats is dependent on the mother's body weight

(Devandra and Brown 1970) but not her age (Prasad et al. 1971). The growth rate of domestic goat kids is linearly correlated with their intake of milk during the first month (Morand-Fehr 1981). Therefore by investing a large amount of resources in individual male kids a female should be able to produce large kids at weaning which may develop into large adult males which are likely to have a high mating success. Work on other polygynous mammals has shown that females do tend to invest more in individual sons than daughters, for example Northern elephants seals (Reiter et al. 1978) and red deer (Clutton-Brock et al. 1981).

Evolutionary theory also predicts that, where the cost of producing sons is greater than that of producing daughters, parents should divide their investment equally between the two sexes by producing fewer males (Fisher 1930). It appears from the present study that female goats may actually invest more resources (milk) in individual sons than individual daughters. However, there was no evidence that the sex ratio at birth or weaning was biased in favour of females; in fact there tended to be more male kids. Studies on elephant seals and red deer also found that the sex ratio at weaning was unity or slighty biased in favour of males (Clutton-Brock et al. 1981, LeBoeuf and Brigg 1977). This may be because the conception ratio in mammals is fixed at unity and that subsequent selective abortion or resorption would only reduce a female's reproductive success (Maynard-Smith 1980).

Clutton-Brock et al. (1982) suggest that female red deer may continue to invest in their daughters (but not their sons) after the weaning period. They argue that because female offspring continue

to occupy their mother's range, hinds are actually continuing to invest in their daughters by allowing these female offspring to eat forage which they themselves could have consumed. In feral goats both female and most male offspring continue to occupy their mother's range after weaning. Although after their first year of life males tended not to associate with their mothers and used different parts of the heft range at different times to their mothers, this does not rule out the possibility of competition for food by male as well as female offspring with their mothers. Therefore it appears that female goats may invest more in individual sons than daughters. It should be noted that in this study there was no evidence to show differential reproductive success in females after rearing male and female kids. By continuing to associate with their mothers young females presumably learn the location of good feeding areas and shelter essential for their survival and future reproductive success, while male kids presumably wander further away from their mother in preparation for their movements in search of oestrous females in later life. However aggression from dominant males during the rut may also be responsible for the breakdown in association between male kids and their mothers (see 5.5.2).

The general spatial organisation of the population of feral goats in the Moffat hills appeared to be based on groups of closely related females, their kids and associated males (a heft). Individuals within hefts had highly overlapping home ranges but overlap between the home ranges of individuals from neighbouring hefts was much less, except for males during the rut (see 3.3.4). Work on other populations of feral goats has yielded similar

findings (Riney and Caughly 1959, McDougall 1975, Boyd 1981, Bullock 1982). Although females from neighbouring hefts rarely met and the common limits to their hefts were fairly well defined on the tops of hills there was no evidence of territorial behaviour.

Studies on other species indicate that the distributon and variation in the size of female groups is closely related to the distribution of food (Altmann 1974, Estes 1974, Jarman 1974, Clutton-Brock and Harvey 1977, Owen-Smith 1977). Where food supplies can be defended, females typically occupy feeding territories which males try to defend and occupy with one or several females. Where food supplies are too widely distributed in time and space to be economically defensible females tend to live in sizeable groups. The diet of feral goats consists largely of dwarf shrubs with increasing amounts of grasses, sedges and rushes during the summer (Bullock 1982). These are widely dispersed and do not occur in defensible patches.

The detection and avoidance of predators is probably the most important advantage to ungulates aggregating in open country. In this study typical group size varied throughout the year, being smallest during the kidding period and increasing to a maximum during the rut (see 3.3.1). Work on several ungulate species has shown that as group size increases to an optimum size individual vigilance decreases and foraging efficiency increases (Berger 1981, Lipetez and Bekoff 1982). Maisels (1982) has shown that there was no increase in overall vigilance of feral goat groups larger than nine. In the present study typical female and mixed group size varied between six and 10 individuals throughout the year except

during the rut when it was much larger and during the kidding period when females tended to isolate themselves from other goats to give birth (see 4.3.1).

The movement of males in search of potential mates appears to be common in most vertebrates with a polygynous mating system where the distribution of females is not primarily determined by males (Greenwood 1980). Feral goats differ from many other species showing male biased dispersal in that most male goats appear to return to their natal heft after each breeding season. This may be because they have learnt the areas of good feeding and shelter in their natal heft and can increase their chances of survival by returning. Studies on primates have shown a decline in feeding efficiency of dispersing individuals (Pollock 1977).

During much of the spring and summer adult male and female goats were partially segregated. Sexual segregation has been recorded in several studies on feral goats (Riney and Caughly 1959, Crook 1969, McDougall 1975, Bullock 1982) and in wild caprinids (Geist 1971, Schaller 1977, Green 1978, Dunbar and Dunbar 1981) and in cervids (Mitchell et al. 1977). Geist and Petocz (1977) suggest that by segregation, males reduce the likelihood of attracting predators to the females (because the latter are usually larger and more conspicuous) and also reduce competition with females for food and thereby maximize the reproductive success of breeding individuals. However in many polygynous mammals only a few males are responsible for siring most of the offspring in any one year and there seems to be little advantage for unsuccessful males in segregating. Morgantini and Hudson (1981) recently suggested that

if bighorn sheep rams continued to associate with ewes after the rut this would cause a higher frequency and intensity of sexual and agonistic behaviour when reproduction was not possible. Such behaviour is energetically expensive and could be detremental to the ram's chances of survival in harsh winter conditions. However, there are many seasonally breeding ungulates where the sexes associate throughout the year (Jarman 1974, Estes 1974). For red deer, in which males are larger than females, it has been suggested that sexual segregation is a result of different nutritional requirements by stags and hinds causing them to use different areas (Clutton-Brock et al. 1982, Staines et al. 1982). They argue that stags are forced to feed less selectively and eat larger amounts of more abundant but less nutritious forage because they are unable to obtain sufficient digestable material from the heavily grazed swards on which the females feed. This theory is untested in feral goats, although it was noticed that males tended to remain within the dwarf shrub communities during the summer while the females were often seen feeding on the lower slopes on sedges and rushes in flushed areas.

It has been shown in this study that mating success among males in one season was largely determined by body size, but natural selection operates on lifetime reproductive success. There are considerable costs associated with achieving a high mating success. It was found that during the rut males reduced the amount of time they spent feeding and appeared to increase their energy expediture. This resulted in adult males losing between 10-30% of their pre-rut body weight prior to the winter. It has been suggested that this

accounts for the apparently higher mortality rate among male goats resulting in the skewed adult sex ratio found in all British populations of feral goats (Crook 1969, Greig 1969, McDougall 1975, Boyd 1981, Bullock 1982).

In other polygynous mammals the increased energy expenditure during the rut by males is thought to be a principle factor in the increased mortality rate compared to females (Grubb 1974, Flook 1970, Clutton-Brock et al. 1982). This may also be partially due to the larger body size of males in these species. The larger body size of the male great-tailed grackle (Quiscalus mexicanus) makes them less efficient foragers than females and exposes them to a greater risk of starvation than females (Selander 1965, 1972). When the reindeer population of Saint Matthew Island crashed from around 6,000 to 42 individuals only one male survived, and this appeared to be infertile because the population died out (Klein 1968). Fighting may also contribute to the increased mortality amongst males; mortality due to injuries received in rutting fights in cervids is not infrequent (Heptner et al. 1961, Muller-Using and Schloeth 1967, Bergerud 1973). Therefore it appears that a combination of increased energy expenditure, aggression and possibly large body size per se may contribute to the apparent higher mortality rate of males in sexually dimorphic polygynous mammals especially during periods of environmental stress.

In the present study there was a positive correlation between mating success and weight loss during the rut. If weight loss and large body size do contribute to an increased mortality rate of males then large successful males are likely to die younger than

smaller less successful peers. This then begs the question could a smaller male attain a similar lifetime reproductive success to a larger male by living longer and getting a few matings each year. It was shown in this study that subordinate males visited more groups during the rut than high ranking males and occasionally found and mated with oestrous females before high ranking males. Studies on mountain sheep suggest that males that are highly successful in breeding competition may die younger than less successful individuals (Geist 1971) and it is possible that this reduction in lifespan could have been compensated for by increased success in these individuals' short breeding life. However in red deer there was no evidence that reproductive success each year was related to age at death (Clutton-Brock et al. 1982).

If the 1981 rut can be taken as representative of an average rutting season then one can speculate on this possibility. Males appear to be able to compete successfully for females after the age of four years. The three most successful males had a mean estimated mating success of 10.4 matings, and the mean estimated mating success of the remaining five males over four years old was 2.4 matings. Mean kid production per adult female/year was 0.42 (see 2.4.2). Therefore on average a successful male may sire four surviving kids and less successful males only one surviving kid each year. This suggests that a smaller male would need to breed in four times as many seasons as a larger more dominant peer to achieve the same lifetime reproductive success. Assuming successful males breed during at least two seasons (all three high ranking males in 1981 survived through the 1982 and one to the 1983 rut) then a smaller

male would have to survive at least eight breeding seasons to achieve the same reproductive success as a large successful male. The youngest male observed to obtain a successful mating was two years old but only two males survived beyond their eighth year during the study which suggests that this is unlikely.

It should be remembered that although successful males actually lost more weight during the rut than less successful males there was no relationship between percentage weight loss and mating success or between weight loss and overwinter survival. There was also some evidence that although dominant males were larger than subordinate males they were also heavier size for size than subordinate males. This suggests that they may actually put on more weight prior to the rut than subordinate males and be able to tolerate a greater weight loss than subordinate males. This seems to suggest that large male goats may have a higher lifetime reproductive success than smaller individuals as would be predicted by evolutionary theory assuming large male body size is a result of sexual selection (Darwin 1871).

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APPENDIX 1

Typical Group Size

Jarman (1974) noted that, while mean group size may be a useful measurement in certain circumstances, such as where an observer's relationship to groups of animals is being investigated, it does not indicate the size of group which the average animal experiences. This can be derived from the following formula:

$$\text{Typical group size} = \frac{n_1^2+n_2^2+n_3^2+\ldots\ldots n_i^2}{N}$$

where n_1, n_2, n_3, etc. are the numbers of animals in each group and N is the total population.

APPENDIX 2

Approach and sniff

Low stretch approach

Gobble

A successful mating

Rush