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THE UNIVERSITY OF ALBERTA

DISPERSAL OF YEARLING COLUMBIAN GROUND SQUIRRELS

by

DAVID F. HACKETT

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

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THE UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled DISPERSAL OF YEARLING COLUMBIAN GROUND SQUIRRELS submitted by DAVID F. HACKETT in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

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ABSTRACT

Yearling Columbian ground squirrels (Spermophilus columbianus) from four sites in montane habitat of southwestern Alberta were studied during early May to mid-August of 1982-4. Yearlings were radio-collared and followed to monitor their excursions, dispersal movements, and fates. Body weights of dispersers and nondispersers were measured weekly. Rates of chases among adult females, and chases directed at yearlings by adult females, were determined in order to test the hypothesis that maternal aggression triggers yearling dispersal. The experimental design included seven reference plots to document normal dispersal, two plots where all adult females were sedated to reduce aggression, and a plot where adult females were temporarily sterilized to eliminate reproduction and maternal aggression. In Summer 1985, the sterilizer treatment and an adults-removed treatment were applied in a brief follow-up to the previous intensive study.

Dispersers and nondispersers of both sexes made excursions of up to 700 m from their natal home ranges. Eventually, 74% (31/42) of yearling males and 31% (9/29) of yearling females dispersed over distances ranging between 62-980 m, typically settling on edges of forest where the increased hunting success of predators apparently created vacant home ranges. The distribution of dispersal distances did not differ greatly from that predicted by competition models, provided that males and females were considered

separately. Dispersal was not significantly more dangerous than remaining philopatric.

Male dispersers were no heavier than nondispersers at the time of emigration but were as much as 100 g heavier by fall; the extra weight may have reflected escape from social pressure and competition for food, and represents a potential benefit for dispersing males. Female dispersers tended to weigh less than nondispersers early in the season and gained no weight advantage by dispersing.

Dispersers from each of seven reference plots typically emigrated within a two-week period closely associated with maternal aggression, juvenile emergence, and maximum numbers of wounds found on yearlings; the reproductive cycle was relatively late on three reference plots, and dispersal there was correspondingly delayed. Sedation of adult females was associated with delayed yearling dispersal, whereas sterilization of adult females eliminated maternal aggression and yearling dispersal.

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I. GENERAL INTRODUCTION

Dispersal can be viewed as a behaviour of individual organisms, but demographic and genetic consequences may result through the movement of individuals affecting population regulation, gene flow, colonization of new areas, and maintenance of species' ranges (Lidicker 1975, Krebs 1978a, Gaines and McClenaghan 1980). There is a rapidly growing literature associated with dispersal of vertebrates, reviewed by Greenwood (1980), Dobson (1982) and Holekamp (1984a). Greenwood (1980) divided dispersal phenomena into two classes - those dealing with movements of reproductive adults between breeding sites (breeding dispersal) and those dealing with emigration of young from their birthplaces (natal dispersal). Holekamp (1983, 1984a) emphasized that two analytical levels must be differentiated in attempting to study dispersal: there are "ultimate" explanations that deal with evolutionary forces shaping dispersal, and "proximate" factors thought to cause or cue dispersal on an immediate basis.

Historically, much effort has been invested in attempting to explain small mammal dispersal, particularily that of microtine rodents which exhibit 2-4 year cycles in population density. As a result we have terms such as "innate" and "environmental" dispersal dating back to Howard (1949, 1960), and four behavioural hypotheses that have been proposed as proximate mechanisms underlying dispersal. The four hypotheses - Social Subordination (Christian 1970, 1971), Genetic-Behavioural Polymorphism (Krebs 1978b), Presaturation-Saturation (Lidicker 1975), and Social Cohesion (Bekoff 1977) - are not mutually exclusive. These hypotheses were formulated when fewer and less precise dispersal data were available, and their arguments are stated at different levels (e.g. behavioural versus genetic viewpoints) making comparisons among the four difficult (Gaines and McClenaghan 1980). Furthermore, each hypothesis was presented as a coherent explanation involving chains of premises, meaning that the falsification of one link could lead to the premature rejection of the entire hypothesis. For these reasons, I concur with Holekamp (1983) in suggesting that individual proximate factors be studied without initial regard to the sequences represented by historical hypotheses. Once the key components have been identified, it may be possible to combine demonstrated proximate factors into parsimonious explanations or hypotheses.

The current literature contains many references to ultimate or evolutionary explanations of dispersal. Most authors appear to favour one of either avoidance of inbreeding (Packer 1979, Pusey 1980, Cockburn _et al._ 1985), competition for mates (Dobson 1982, Moore and Ali 1984), or competition for resources (Lidicker 1975, Boutin _et al._ 1985) as the primary evolutionary force underlying dispersal, although a number of authors have stressed that different combinations of these factors may be involved for different species (Greenwood 1980, Holekamp 1983, Dobson and Jones 1985). Some researchers have attempted to evaluate ultimate hypotheses through experimentation; for instance, Dobson (1979) rejected the Competition for Mates hypothesis on the basis that young male California ground squirrels (S. beecheyi) continued to disperse normally without the presence of adult male competitors. Whether evolutionary mechanisms thought to operate over thousands of generations can be expected to respond to manipulations within the confines of a short-term experiment remains to be determined. At the moment, much of the controversy surrounding ultimate hypotheses stems from deductive reasoning (Greenwood 1980, Dobson 1982, Liberg and von Shantz 1985) or extrapolations from laboratory work (Haigh 1983). More conclusive field data are needed.

A good deal of the information on small mammal "dispersal" has been derived from animals appearing on removal plots or disappearing from study sites. Removal studies require the assumption that individuals arriving on a trapped-out area are typical dispersers and are not simply responding to the newly created vacant space (Myers and Krebs 1971, Tamarin 1977, Stafford and Stout 1983). In fact, a number of studies have demonstrated that removal plots sample animals on excursions, those expanding nearby home ranges, and other individuals <u>not representative</u> of typical dispersers (Dobson 1981, Boutin <u>et al.</u> 1985, Krohne and Miner 1985). Thus, the most elaborate analyses of removal data (e.g. Gaines and Johnson 1984) still describe mixed groups of dispersers and nondispersers, and do not identify actual dispersers. Other studies have focussed on animals disappearing from study sites, employing the caveat that it was impossible to differentiate between disappearance through death or dispersal (Dunford 1977, Pfeifer 1980, 1982, Festa-Bianchet and King 1984). The problem here is that much of the information purported to describe dispersal was gained using animals that may not have been dispersers.

Precise details are essential to our understanding and quantification of dispersal. Reliable answers to simple "who?", "when?", "where?" and "cost/benefit" questions would contribute much toward unravelling proximate and ultimate hypotheses, and determining the extent to which dispersal may affect demographic and genetic processes. For example, some authors have assumed that dispersers have a poor chance of survival (Lidicker 1975, Gaines and McClenaghan 1980) - this view leads to different conclusions concerning the causes and consequences of dispersal than does a view that presumes reasonable survival of far-ranging, advantage-seeking dispersers. Are dispersers forced out or do they leave voluntarily? If either case could be shown to be true, certain proximate and ultimate hypotheses would be supported while others would be weakened. Unfortunately, precise details of dispersal are often lacking (Gaines and McClenaghan 1980; Greenwood 1980).

My interest in dispersal began in 1975-8 as I wondered what was happening to young eastern chipmunks (Tamias striatus L.) born on my study area in Sudbury; they seemed to wander away into the bush at a certain age, but I was tied to the project at hand and could not follow them. The research scheme described herein took shape in 1981 after Jan Murie convinced me that ground squirrels (Spermophilus spp.) were ideal animals for a dispersal study due to their convenient size, diurnal habits, observable behaviours and grassland habitat. Most ground squirrels were known to disperse as juveniles (Slade and Balph 1974, Dunford 1977) but Boag and Murie (1981) had shown that Columbian ground squirrels (Spermophilus columbianus) delayed their dispersal to the yearling summer in Alberta. There had been much speculation about ground squirrel dispersal and mortality (Michener and Michener 1977, Michener 1979, Schmutz et al. 1979), but few details were known since no radio-telemetric studies had been completed. Holekamp (1983, 1984b) was in the process of radio-tracking dispersing juvenile Belding's ground squirrels (S. beldingi) in California; I resolved to use telemetry to study the relatively unusual yearling dispersal of Columbian ground squirrels and learn all I could about their midseason movements and fates. Meanwhile, Festa-Bianchet and King (1984) had demonstrated that yearling Columbian ground squirrels disappeared from study sites at a time coinciding with aggression from adult females. Ground squirrel literature seemed to weigh against aggression as a cause of dispersal (Yeaton 1972, Dunford 1977), but interesting possibilities remained that the yearling dispersal of Columbian ground squirrels might be different; that maternal aggression and adult female territoriality, already described for a variety of rodents, might be tied to dispersal; that experimental treatments such as chemosterilization with Mestranol (Goulet and Sadlier 1974) might help to tease apart various factors potentially related to dispersal. Thus, beyond hopes of gaining much-needed details for testing general assumptions and hypotheses related to dispersal, the work of other ground squirrel biologists had put me in a position to aim at the proximate roots of dispersal.

A number of developments had a large impact on my research and writing. Some authors suggested that aggression might only affect dispersal in patchy habitat or at high population densities (Webb 1981, Festa-Bianchet and King 1984); this necessitated behavioural study of populations in continuous habitat and at a variety of densities. Holekamp (1984b) concluded that juvenile _S. beldingi_ dispersed when an "ontogenetic switch" was activated by a critical body weight; I have specifically addressed this issue in terms of _S. columbianus_. The information that _S. columbianus_ in Washington disperse as juveniles, not yearlings, is quite new (pers. comm. J. Murie, B. Weddell) and encouraged me to reflect on the significance of intraspecific differences in dispersal behaviour.

This thesis is composed of three papers and two summary chapters ("General Introduction" and "Conclusion") intended to place my findings in context with current dispersal literature. The first paper presents a detailed description of dispersal based on movements and fates of radio-collared yearlings as they explored their surroundings and moved away from natal sites. The second deals with the relationship between dispersal and body weight; hypotheses associating a critical weight with dispersal are evaluated using weekly weight data gathered on three cohorts of known dispersers. The third paper addresses some of the proximate causes of dispersal, particularly the role of maternal aggression, and attempts to clarify relationships between proximate cues and ultimate forces governing dispersal of yearling Columbian ground squirrels. Additional information, and solutions to various problems encountered during the study, appear in appendices.

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II. Paper 1 - A DESCRIPTION OF DISPERSAL IN COLUMBIAN GROUND SQUIRRELS

A. ABSTRACT

The dispersal of yearling Columbian ground squirrels (*Spermophilus columbianus*) living in continuous montane habitat of southwestern Alberta was monitored from 1982-1984 using a combination of radio-tracking, observation and live-trapping. Yearlings made excursions and located distant burrows before becoming dispersers or nondispersers; 74% of yearling males and 31% of yearling females dispersed, typically to edges of meadow near shrub cover where predators apparently created vacant home ranges. Risks of dispersal appeared to be associated with settling in relatively dangerous locations, not with transit through unfamiliar terrain. More nondispersers than dispersers survived through subsequent seasons although differences were not statistically significant; representatives of both groups lived to reproductive age. Dispersal distances appeared to conform to "competition" models provided that the sexes were analyzed separately. Assumptions related to competition models and to the disappearance of animals from study sites were examined in view of information on ground squirrel movements provided by means of telemetry. Twenty-five percent of dispersing yearlings settled in close proximity to a littermate; consequences of this nonrandom dispersal were considered.

B. INTRODUCTION

The dispersal of ground squirrels (Spermophilus spp.) has been discussed by a number of authors, but most previous studies were limited to documenting the disappearance of animals from study sites (Slade and Balph 1974, Dunford 1977, Pfeifer 1980, 1982, Festa-Bianchet and King 1984). Large-scale trapping projects (Sherman 1977, 1980, Boag and Murie 1981) supplied information on dispersal distances but could not pinpoint the timing of dispersal or differentiate between losses due to emigration or death. There has been much speculation about fates and destinations of dispersers (Carl 1971, Michener and Michener 1977, Michener 1979, Schmutz *et al.* 1979), but few clear answers have emerged. Recently, Holekamp (1984a,b) provided many details of the dispersal of juvenile Belding's ground squirrels (*S. beldingi*) through a combination of observation, trapping and radio-telemetry. Answers to questions about which animals disperse, when, where they go, risks faced in transit, and success at settling elsewhere are important to our understanding of ground squirrel biology. Many of these questions have not been answered satisfactorily for any small mammal (Gaines and McClenaghan 1980) and can probably be approached most directly by studying observable diurnal species such as ground squirrels (Holekamp 1984b).

A number of hypotheses, assumptions and models related to dispersal could be evaluated critically if accurate details were known about dispersers. For example, are dispersers forced into marginal habitat where most will perish (Anderson 1980), or do they emigrate to suitable habitat where they increase their chances to reproduce? Can dispersal distances be predicted by competition models (Murray 1967, Waser 1985), or is there evidence to support a polymorphism of dispersal tendencies (Howard 1960, Lidicker 1975)? Is dispersal a single movement into novel terrain or a more complex series of comparisons among different areas? Answers to these questions would help to indicate how much dispersers contribute to gene flow, colonization of unoccupied habitat and maintenance of species ranges (Krebs 1972, Gaines and McClenaghan 1980).

The purpose of this paper is to provide a detailed description of the dispersal of Columbian ground squirrels (S. columbianus), focussing on fates and locations of the emigrants. A study of S. columbianus in Alberta has potential to add new information to that obtained by Holekamp (1984a,b) since yearlings are the dispersing age-class (Boag and Murie 1981, Festa-Bianchet and King 1984); most other ground squirrels disperse as juveniles, including some S. columbianus at lower elevations and latitudes in Washington (pers. comm. J. Murie, B. Weddell).

C. METHODS

Four study sites, each approximately one hectare in area, were established on a private ranch 10 km southwest of Chain Lakes Provincial Park in southwestern Alberta (50 06' N, 114 33' W, elevation 1400 m). All sites were in open pasture periodically grazed by horses and cattle (Fig. 1.1). Sites 1 and 2 were in flat terrain with good visibility in all directions; Site 3 was flat but flanked by shrubs to the south and east; Site 4 was adjacent to Site 1 on a west-facing slope where it abutted a strip of shrubs and trees bordering an intermittent stream. Water bodies consisted of small streams swollen into ponds by beaver dams. An infrequently used dirt road and several barbed wire fences crossed the open meadow. The northwest corner of the meadow had been cleared and burned approximately 5 years before my study began but had not yet been invaded by ground squirrels; the remaining open meadow (stippled in Figure 1.1) was occupied by ground squirrels. Shrubby areas consisted of various low willows (<u>Salix</u> spp.) and scattered aspen trees (<u>Populus</u> <u>tremuloides</u>). The forested areas were mixed stands of aspen and white spruce (<u>Picea</u> <u>glauca</u>) penetrated by many cowpaths and small meadows leading to larger meadows beyond the area illustrated in Figure 1.1.

From May to August 1982-1984, ground squirrel populations of Sites 1-4 were monitored through a combination of live-trapping, radio-telemetry and behavioural observation. Ground squirrels were trapped in

National live-traps (15X15X50 cm) baited with peanut butter. Captured animals were examined for wounds and reproductive condition, weighed to the nearest 5 g using a Pesola spring scale, eartagged with serially numbered metal tags, and marked with distinctive numbers or letters on their pelage with Lady Clairol blue-black hair dye. Yearlings (n=75) were outfitted with radio-collars designed for this study by AVM Instruments (Appendix 1) and subsequently located at least once per afternoon by observers using a handheld antenna and receiver. Animals that were making excursions, dispersing, or establishing themselves at postdispersal locations were followed and observed from a distance of approximately 100 m or from hidden vantage points where woodland cover was available. Each yearling was radio-tracked every evening after 2100 hours to determine the location of its current sleeping burrow. "Dispersers" were yearlings that moved to new sleeping burrows away from their natal burrows and home ranges; the shortest case accepted as dispersal involved an individual that moved to new sleeping quarters 62 m away, and changed its activities so that it was no longer seen on the study site. This definition of dispersal achieves similar results to that of Lidicker (1975), "any movement in which individuals leave their home areas . . . this does not include short-term exploratory movements, or changes [that include] part of the former [home range]", except that focussing on sleeping burrow locations provides precise dispersal dates and distances, and allows for visits back to the natal area by animals that have moved to new locations. "Nondispersers" continued to sleep in or near their natal burrows, and maintained home ranges that overlapped their natal home ranges.

Survival of previously radio-collared animals was followed through intensive trapping and observation in the spring (mid-April to late May) and fall (mid-July to mid-August) of each season until May 1985, when many squirrels were collected for the Provincial Museum of Alberta (Edmonton). These searches provided information on the minimum number of dispersers and nondispersers known to be alive. The three cohorts radio-collared as yearlings in 1982-1984 were pooled to produce a composite survival curve describing attrition of numbers from the yearling spring through subsequent years.

Terminology

The use of specific terms, aside from "dispersers" and "nondispersers" given above, is as follows. *Natal burrow* is the burrow from which a litter of juveniles first emerged. *Natal home range* is the home range used by a juvenile within its first summer, approximately 30 m in diameter and containing the natal burrow (Waterman 1986). *Spring burrow* is the burrow in which a yearling initially slept with surviving littermates in the spring of its second season; this burrow was the same as, or within a few metres of, the natal burrow of the previous season. *Distant burrow* is a burrow used by a dispersing yearling outside its natal home range. *Dispersal distance* is the straight line distance between a yearling's spring burrow and the final burrow it occupied prior to hibernation. *Dispersal date* is the date on which an animal stopped using sleeping quarters in its natal area, provided that it was located alive elsewhere.

Competition models are mathematical models based on the premise that animals compete to remain philopatric, and that individuals that must disperse move to the nearest vacant home range. In Murray's (1967) model, animals search for hexagonal home ranges in randomly chosen straight lines from the natal site. The probability, p_n, of settling in the nth ring of home ranges is:

$$p_n = t(1-t)^n \qquad (1)$$

in which "t", the probability that a home range is available, can be approximated by the proportion of nondispersers. In Waser's (1985) model, animals are assumed to search in a spiral path or have additional information (through listening and watching, for instance) so that they can assess when space becomes vacant in the nth ring of hexagonal home ranges surrounding their natal site. In that case, the probability of settling in the nth ring is:

$$p_n = (1-(1-t)^{6n})(1-t)^{1+3n^2-3n} \qquad (2)$$

in which the first term is the likelihood that at least one of the home ranges in the nth ring is available, and the second term is the probability that no closer home ranges are available.

D. RESULTS

Early Season Activities

In the spring (April-May) of each field season, yearlings lived within their mother's home ranges close to their natal burrows. Several weeks before new litters emerged in mid-June, yearlings began making excursions away from their natal areas for distances of up to 700 m. Animals making excursions seemed exceedingly wary, travelling in short bursts punctuated by long bouts of sitting upright and looking around. They investigated most burrows that they encountered, but were sometimes pursued vigorously by squirrels occupying a burrow or by a series of residents while fleeing across several home ranges. Animals on excursions crossed streams, traversed woodlands, and climbed a variety of objects such as fence posts, trees and shrubs as if to reconnoitre. Upon finding a burrow where they were not challenged, yearlings spent a great deal of time sitting erect looking in various directions, twist-marking the ground (Steiner 1974, Betts 1976), and digging; former burrows of ground squirrels, pocket gophers, foxes and badgers were renovated in this manner. Some yearlings travelled to and from the same distant burrow regularly for days or weeks before finally dispersing there; others invested considerable time and energy on burrows away from the natal site but did not disperse. Animals that focussed excursions on a particular area followed a similar path everyday, winding their way between occupied home ranges *en route*. Only 10% of the radio-collared yearlings (n=40) dispersed to areas where they had not been observed making previous excursions (Fig. 1.2).

Who Dispersed?

All yearlings undertook excursions but only 74% (31/42) of the males and 31% (9/29) of the females dispersed to new burrow sites away from their natal areas. Four yearlings that were killed within natal home ranges before the end of the dispersal period were not included with the 71 yearlings of known dispersal status, except to determine that **disappearance** from study sites during the dispersal period involved 76% (34/45) of yearling males and 33% (10/30) of yearling females.

Ninety-three per cent (37/40) of the dispersers left "decisively", meaning that once they slept at a distant burrow they never reinhabited their spring burrow although some continued to make daytime visits to the natal area. The remaining three dispersers (2 males, 1 female) were "indecisive", sleeping away and at home alternately over a period of days or weeks before dispersing. Three yearlings (2 males, 1 female) that left during the typical dispersal period but returned to reinhabit their spring burrows before hibernation were considered to be nondispersers since they did not in effect change their neighbours and surroundings.

After dispersing, many yearlings continued to undertake excursions to new areas and make occasional daytime visits to the natal site. Sixty per cent (24/40) of the dispersers made subsequent moves to new sleeping burrows after the initial move to a distant burrow. One individual made a dozen such moves in the course of its yearling summer and did not stabilize the location of its sleeping burrow until early August.

Where Did Dispersers Go?

Some dispersers moved considerable distances from study sites, occasionally settling in smaller meadows away from continuous pasture (e.g. 7,44,47 - Fig. 1.2). Four yearlings moved near the ranch buildings (13,14,42,43 - Fig. 1.2) - this area was in effect a dispersal sink since the rancher shot and poisoned squirrels in the vicinity of his garden. A few dispersers settled in open terrain, but most moved to edge areas where grassland bordered trees or shrubs. Based upon a minimum estimate of 30 m for the diameter of spring home ranges of yearling Columbian ground squirrels (unpublished data, J. Waterman pers. comm.), I tested the hypothesis that the number of collared yearlings dispersing to within a home-range diameter of shrub-woodland was the same as the number dispersing into adjacent open meadow inhabited by ground squirrels. Seventy-seven per cent (24/31) of dispersing males and 62% (5/8) of dispersing females moved into the 24-ha strip of meadow within 30 m of shrub cover, and the remainder settled in the 43 ha of open habitat. The null hypothesis was rejected for the sexes combined ($X^2=25.07$, $P<0.005$) and for males ($X^2=23.36$, $P<0.005$), but not for the small sample of females ($X^2=2.38$, $0.25<P<0.10$). Apparently, dispersing males tended to settle within a home-range diameter of shrub or tree cover.

Each year dispersers showed a preference for edge areas near study sites, sometimes occupying the same burrows used by previous dispersers. We trapped those areas in the spring and found densities of 0-15 ground squirrels per ha despite surplus unoccupied burrows. In comparison, most burrows on study sites were occupied and spring densities ranged between 22 and 52 animals per ha (Paper 3). During the course of the study, 18 radio-collared yearlings were killed by predators; 94% (17/18) of them had burrows located within 30 m of shrub cover. It was significantly more dangerous to be one of the 50 yearlings that lived in, or dispersed to, locations near cover than to be one of 25 yearlings that remained in open grassland ($G=7.90$, $P=0.005$), and particularly dangerous to have a burrow within 10 m of shrubs or trees (Table 1.1).

Sources of Mortality

Radiocollared yearlings were preyed upon by coyotes (5 cases), weasels and mink (4), burrow-digging badgers (3), and raptors (1). One yearling was poisoned in the rancher's garden, and another was mortally wounded by conspecifics.

Two additional animals disappeared in the postdispersal phase although they had been radiolocated and observed only hours earlier - I attributed this to surface-hunting badgers since such attacks had recently been witnessed in the area and because badgers were the only predators known to sever the specially constructed R-collars (Appendix 1). Another radio-collar was traced to a small area on a densely forested hillside but could not be pinpointed because of signal distortions among overhanging conifers; the loss of this squirrel was attributed to an unknown predator. Further details of predator assessments are described in Appendix 2.

Is Dispersal Dangerous?

No radio-collared yearlings were killed during dispersal movements; all 18 deaths occurred either within natal home ranges (4 early-season deaths and 3 confirmed nondispersers) or after yearlings had been sleeping at postdispersal locations for an average of 16.4 ±3.6 days. Living close to shrub cover carried the same potential penalties for all yearlings. Thirty-four percent (10/29) of yearlings that dispersed near cover were killed, compared to 33% (7/21) mortality among animals that did not disperse and lived near cover. Only one of 25 yearlings that remained in open-meadow habitat (a disperser) was killed.

Twenty-eight per cent (11/40) of the dispersers died within their yearling summers, compared to 10% (3/31) of yearling nondispersers, but the difference was not statistically significant (G=2.6, P=0.11). Overwinter mortality experienced by dispersers (20%) and nondispersers (22%) was similiar in the first year and maintained the disparity between the two groups (Fig. 1.3). In the second summer and winter, comparatively few nondispersers disappeared, increasing the difference between the two survival curves (G=4.1, P=0.04). The third summer and winter are represented by relatively few cases since only the 1982 yearling cohort was monitored for that length of time (Table 1.2). Overall, more nondispersers than dispersers were known to be alive in all seasons subsequent to the initial spring when study of each cohort of yearlings commenced.

Survival was apparently influenced by a combination of dispersal status and gender (Fig. 1.4, Table 1.2). Proportionally more female dispersers than male dispersers survived to the end of the first winter (G=4.8, P=0.03), although this difference disappeared by the end of the second winter. I suspect that high first-winter survival resulted from 5 of 9 female dispersers belonging to the 1984 cohort, 87% (14/16) of which survived their first winter (Table 1.2). Only three female dispersers were included in the 1982 and 1983 cohorts which experienced 64% (9/14) and 70% (19/27) survival during their first winter (the fourth female disperser died prior to the first winter). Male and female nondispersers survived in similar proportions until the end of the second winter; percentage values determined after this time are not considered to be reliable since the

1982 cohort had only one male nondisperser and two female dispersers. In general, it appears that males and females that dispersed were at a greater risk than male and female nondispersers, although differences in proportions surviving were not significant at these sample sizes (P>0.11). Nondispersers tended to live longer than dispersers, and females longer than males; differences among these groups approached significance (Table 1.3).

Dispersal Distances and Competition Models

On average, males that dispersed settled 339 m ±50 (SE) from the spring burrow (n=31, range 62-980, median=230) whereas females that dispersed moved 394 ±101 m (n=8, range 93-940, median=325). The distribution of male dispersal distances was skewed with more than half of the dispersers settling within 250 m of their spring burrows (Fig. 1.5). Half of the female dispersal distances were within 250 m but this skewness is less obvious with the smaller sample size. There were no significant differences between means or medians (corrected Wilcoxon rank sum Z=-0.5, P=0.61) of male and female dispersal distances.

Most of the yearlings that dispersed less than 350 m were near edges of shrub-woodland and meadow in the vicinity of the study sites (Fig. 1.2). Half of the animals that dispersed between 400-650 m settled near ranch buildings. Two yearlings from different study sites dispersed more than 850 m to the same well-trampled area near a cattle gate. In short, dispersing yearlings were not distributed randomly as if in a homogeneous environment; the result was a discontinuous pattern of dispersal distances (Fig. 1.5).

The observed distribution of all yearlings (dispersers and nondispersers of both sexes) and the expected distributions based on "competition" models of Murray (1967) and Waser (1985) are compared in Figure 6. The value of "t" was approximated by the proportion of yearlings that did not disperse, 0.44; home-range diameters were estimated to be 50 m. The curve generated by Equation 1 appears to be a reasonable fit within the first 10 home range diameters; however, yearlings tended to disperse farther than predicted by the model after 5 home ranges. Consequently, differences between observed and expected curves approached significance (Kolmogorov-Smirnov Z=1.11, P=0.17). Equation 2 predicts that most yearlings should settle one home-range diameter away from their natal sites and that virtually all yearlings should remain within four home-range diameters. This was not true of observed values, and differences between the two curves were highly significant (K-S Z=1.74, P=0.005).

Separation of male and female yearlings improved the ability of Equation 1 to predict the observed distributions (Fig. 1.7). The value of "t" was approximated by the proportion of male and female nondispersers: 0.26 and 0.69, respectively. Murray's (1967) model described the observed male distribution (K-S Z=0.95, P=0.33) better than when both sexes were combined. The model accurately predicted female distribution for the first few home ranges, although more females than expected dispersed beyond 6 home-range diameters (K-S Z=0.63, P=0.82).

Nonrandom Dispersal by Littermates

Five pairs of littermates (two male, one female, two mixed-sex pairs) emigrated to distant locations where they shared a burrow or slept within 10 metres of their littermate. In each case, one member of the pair dispersed alone initially; upon returning to visit the natal area, the disperser associated with and was followed by a sibling. The two male pairs were particularly amicable: brothers sat and fed together, travelled as a pair, and slept within a few metres of each other until just before hibernation. The mixed-sex pairs slept together initially but moved to sleeping burrows 10 and 40 m apart after June and were rarely seen associating. Members of the female pair had overlapping home ranges, slept in separate burrows 10 m apart, and followed each other during excursions and visits to the natal area 220 m away. There were an additional seven cases in which two or more yearlings dispersed from the same litter but did not settle near a sibling. Thus 5 of 12 (42%) groups with two or more dispersing littermates were involved in the movement of siblings to a new area together.

E. DISCUSSION

Dispersers were not a class of homeless travellers in search of a vacancy as envisioned by Lidicker (1975), and the dispersal process was not a simple one-way trip as Quanstrom (1971) and others suspected. Most yearlings made a number of excursions and many began preparing a distant burrow before dispersing. Animals had "dispersed" when they stopped returning to sleep at the natal site. Holekamp (1984a,b) also found dispersal to involve a series of exploratory movements to and from natal areas and used locations of sleeping burrows to define dispersal dates and distances. After yearlings emigrated, many continued to make excursions, change burrow locations, and visit home areas; a few managed to re-establish themselves on their natal home range. In short, most cases of dispersal appeared to involve sampling and comparison among potential sites, as well as a degree of preparation.

The 10% of emigrants that settled in areas where they had not been observed making previous excursions were long-distance dispersers. Three likely reached their destinations by following cow trails and vehicle tracks leading from areas they were known to use; trail-following has been reported for dispersing black-tailed prairie dogs (Garrett et al. 1982). The fourth animal extended its former travels across approximately 100 m of open field uninhabited by ground squirrels. It may have been relatively risky and energetically expensive to return to natal areas once having reached these distant locations.

Values of 74% and 31% dispersal by yearling males and females, respectively, are in general agreement with previous studies based on the disappearance of Columbian ground squirrels. Festa-Bianchet and King (1984) reported slightly greater disappearance (males 80%, females 46%) during the presumed dispersal period, but their 1-hectare study area was surrounded by forest which probably increased the proportion of yearlings lost to predators. In this study, there was little difference between numbers of yearlings disappearing during the dispersal period (76% and 33% of yearling males and females, respectively) and those known to have dispersed, but 33% (7/21) of yearlings that lived in natal home ranges near cover were killed during the three summers. Study sites surrounded by tree or shrub cover are likely to have discrepancies between dispersal and disappearance through increased loss to predators.

Previous authors thought that yearlings were the primary dispersing age-class among Columbian ground squirrels on the basis of their differential disappearance from study sites and records of long-distance movements between trap captures (Boag and Murie 1981, Festa-Bianchet and King 1984); disappearance among other age-classes left the possibility that dispersal was not restricted to yearlings. Murie and Harris (1984) reported shifts in activity centres of some adult squirrels, primarily males, which appeared to indicate dispersal subsequent to the yearling summer. In this study, two males that did not disperse as yearlings emigrated the following spring as two-year-olds. Juveniles made excursions of up to 300 m in August, and some travelled to the same areas regularly. Observation of nine radio-collared juveniles that made frequent excursions showed that they continued to sleep (and eventually hibernated) near natal burrows; in spring, all yearlings commenced their activities near natal burrows where they had been marked as juveniles. Emigration of juvenile Columbian ground squirrels in Washington (B. Weddell, J. Murie) suggests that young squirrels at lower altitudes and latitudes have time to disperse and gain sufficient weight to survive hibernation, in contrast to the situation in Alberta (Paper 3).

I have described the timing of yearling dispersal elsewhere (Papers 2 and 3). Briefly, most yearlings emigrated within a period of four weeks in mid-June to mid-July, closely associated with the timing of juvenile emergence. This is consistent with assumptions about the dispersal period based on disappearance of yearlings from study sites (Boag and Murie 1981, Festa-Bianchet and King 1984), and closely resembles the timing of dispersal among black-tailed prairie dogs, which also emigrate as yearlings (Garrett _et al._ 1982).

Dispersers settled where empty burrows were available. This included the rancher's yard where he shot and poisoned squirrels in the area of his garden. The edge of meadow near trees or shrubs had low ground squirrel densities and surplus burrows, apparently because predators were most successful when they could surprise ground squirrels from cover. Squirrels living in open terrain could see predators approaching or be warned by alarm calls of other ground squirrels. Those near tree or shrub cover had little warning and appeared to be habituated to noise and motion associated with the frequently wind-blown foliage. It was possible for a radio-tracker to crash through the forest quite clumsily and still startle ground squirrels upon emerging into the meadow.

Yearlings did not disperse to any location lacking a pre-existing burrow. Hence the cleared northwest corner of the meadow was not invaded. Yearlings did disperse to areas devoid of ground squirrels, provided that empty burrows of ground squirrels or other animals were present to be renovated.

A number of authors have suggested that dispersal is a risky stategy because dispersers may be more susceptible to predators while in transit (Rongstad 1965, Metzgar 1967, Schmutz _et_ _al._ 1979, Gaines and McClenaghan 1980). I found no evidence that yearlings perished while making excursions or dispersal movements. Their success may be accounted for by a number of factors. They were extremely wary while in transit, moving from burrow to burrow; when danger threatened they were able to take refuge even if a resident ground squirrel were present. Ninety percent of dispersing yearlings expanded their movements through a series of excursions thus gaining familiarity with the area to which they eventually immigrated. Ground squirrels that disperse as yearlings may be less naive than if they dispersed as juveniles.

Transit is presumably more dangerous in cases where animals must cross large stretches of inhospitable terrain. Leuze (1979) found that 50% of dispersing female watervoles (Arvicola terrestris) were preyed upon as they emigrated through marginal unoccupied habitat. Young pikas (Ochotona princeps) must move between isolated patches of talus during hot weather and apparently experience high mortality (Smith 1974). The Columbian ground squirrels in this study lived in fairly continuous ground squirrel habitat, and probably encountered lower risks than those dispersing from isolated populations such as those described by Festa-Bianchet and King (1984).

The increased mortality of dispersers appeared to result from their tendency to settle in relatively dangerous locations. Yearlings that immigrated to the empty burrows in these areas became susceptible to the same factors (predators, ranchers) that originally created the vacancies. Slade and Balph (1974) and Dunford (1977) pointed out the vulnerability of ground squirrels living in low density populations with few conspecifics to warn them or in edge areas where visibility may be limited. Male dispersers and nondispersers in my study experienced higher mortality than their female counterparts, possibly owing to the larger home ranges of male yearlings (Waterman 1986).

Seventy-two percent of the dispersers were alive at the end of their yearling summer, contrary to assumptions that most dispersers soon perish after dispersing (Lidicker 1975, Schmutz et al. 1979). Numbers of dispersers and nondispersers declined gradually through subsequent seasons (Fig. 1.3); more nondispersers than dispersers were known to be alive at all intervals but representatives of both groups lived to reproductive age. Female Columbian ground squirrels occasionally give birth as yearlings but are typically 2 years old when they have their first litters (Murie et al. 1980, Festa-Bianchet 1981). Males show external evidence of reproductive maturity at 2 years of age but may not participate in breeding until they are 3 or 4 years old (Murie and Harris 1978, 1984). Consequently, some dispersers of both sexes had the potential to contribute genes to future generations. Dispersers were not observed closely enough to assess their reproductive success, but they appeared to recruit into nearby populations as described by Murie and Harris (1984). I suspect that the values presented in Figures 1.3 and 1.4 underestimate typical survival past the third summer since the small 1982 cohort had few yearlings available to survive to subsequent trapping sessions (Table 1.2). Extensive efforts were made to locate all surviving study animals, but the possibility remains that some former dispersers may have eluded recapture by making further moves into areas that were not trapped or observed. The figures discussed above thus represent the minimum known survival of dispersers, and the maximum survival differences possible between dispersers and nondispersers.

Female dispersers tended to move at least as far as male dispersers, as reported previously by Boag and Murie (1981:Table 6). Some authors have suggested that male sciurids are the long-distance dispersers (Schmutz _et al._ 1979, Holekamp 1984a,b) but it is not always clear whether their estimates were restricted to animals that left natal home ranges. The distinction is an important one. Most female yearlings remained philopatric, but those that emigrated were scattered over a wide range of distances (Fig. 1.7b).

The models of Murray (1967) and Waser (1985) predict that in homogeneous habitat, animals that lose in competition to remain philopatric will move to the nearest available opening by searching in randomly chosen straight lines (Equation 1) or by searching one ring of home ranges at a time (Equation 2). Other strategies of searching should produce distributions that lie between those of Equations 1 and 2 (Waser 1985:1171). To locate available home ranges, yearling Columbian ground squirrels must traverse the territories of adult females who are at the peak of maternal aggression at the beginning of the dispersal period (Paper 3). These territories are approximately 30 m in diameter

(Festa-Bianchet and Boag 1982; unpublished data) but I increased the estimate to 50 m to allow for small gaps between territories (Waser 1985:1173). Using this value and Equations 1 and 2, both models underestimated the observed extent of yearling dispersal movements (Fig. 1.6). Equation 2 incorrectly predicted that most dispersers would settle in the first ring and all would settle within four, based on the assumption of perfect information within each ring of home ranges. Yearlings did not search in a spiral path or explore in all directions, and were probably incapable of assessing occupancy from afar as birds might be able to by using acoustical signals (Waser 1985). Yearlings made their excursions by means of long-distance exploration in a few different directions, even to the extent of retracing a similar path on further excursions to the same area. This stategy approaches the search pattern assumed by Equation 1. The fit of Equation 1 could be improved by assuming that yearlings had to travel 100 m to reach the next available opening, but this value is not reasonable in view of adult spacing behaviour at the time of dispersal. Adult females defended territories around their natal burrows against other ground squirrels, including their own yearlings; dispersers and nondispersers changed their movements and sleeping burrows as if to fit between female territories (Festa-Bianchet and Boag 1982, Paper 3, Wiggett pers. comm.). Murray (1967) speculated that nonhomogeneous habitat would cause some individuals to move farther than others before finding an unoccupied site. In this study, dispersers tended to be concentrated in certain patches of habitat as described earlier, which resulted in a discontinuous distribution of dispersal distances.

Waser (1985) found no reason to separate the sexes when analyzing distribution data of deermice (Peromyscus maniculatus) and White-crowned sparrows (Zonotrichia leucophrys). My data indicate that Equation 1 fits Columbian ground squirrel dispersal more accurately once the sexes are separated (Fig. 1.7). Why should this be so? Shields (1983) proposed two important questions to be asked regarding dispersal: 1. What determines whether an animal disperses or not; 2. Given that an animal has dispersed, what pressures affect dispersal patterns? Sex-related biases of either factor would cause male and female dispersal distributions to differ. Elsewhere I have shown that yearling males do not compete aggressively to remain philopatric but disperse if they have a reproductively active mother or a surviving sister (Paper 3). Males without such kin remain philopatric; dispersing males appear to be distributed as predicted by Equation 1, with some clumping caused by heterogenous habitat (Fig. 1.7a). Female yearlings do compete aggressively to remain philopatric (Paper 3), and their success is illustrated by the preponderance of female nondispersers (Fig. 1.7b). Only the losers of interactions among multi-female litters disperse (Paper 3), and they are apparently subject to the same forces that cause males to emigrate considerable distances. Thus, there appear to be sexual differences in Columbian ground squirrels regarding Shield's first question, but there may not be differences for his second question.

An inappropriate assumption of "competition" models is that all potential dispersers have an equal chance of occupying home ranges. This fails to recognize the possibility of sexual differences and allows no bias in favour of residents. We should expect sexual differences to Shield's first question since the majority of birds and mammals exhibit sex-biased philopatry (Greenwood 1980, Waser and Jones 1983, Liberg and von Schantz 1985). Resident young might be expected to have an advantage on familiar ground, whereas immigrant young are likely to be subjected to heightened aggression from unfamiliar neighbours (Dunford 1977). As reported elsewhere (Paper 3), yearling females competed with their own siblings (not immigrants) to retain occupancy of their natal home ranges. Yearlings of either sex that could not remain philopatric moved to vacant spaces between and beyond the territories of aggressive adult females.

Other assumptions that seem inappropriate for ground squirrels are that only one offspring can inherit the natal home range and that the opportunity to remain philopatric depends on the death of the resident adult. Single female yearlings were able to remain philopatric despite the continued presence of their reproductively active mothers, and as many as two males or females were able to be philopatric if their mother did not become pregnant or if she had disappeared (Paper 3). On the natal home range then, the number of openings available is probably best determined by the number of nondispersers (Waser 1985:1173) rather than by calculating theoretical turnover probabilities based on deaths of adults (Waser 1985:1171). Once yearlings move away from natal sites, they are strangers on unfamiliar ground and may require death-created vacancies, as assumed by competition models.

The movement of 25% (10/40) of all dispersing yearlings, or 42% (5/12) of litters with two or more dispersers, as littermate pairs was unexpected from study of ground squirrel literature. Littermates that disperse to the same area gain certain advantages, regardless of their gender. They arrive with a familiar individual in close proximity which may help them to become established, particularly in areas with few other ground squirrels to detect predators. Dispersing siblings are related to at least one other animal in their new population, and the number of relatives will increase when either or both have progeny (Cheney and Seyfarth 1983). Kin are more likely to cooperate than are unrelated individuals, possibly resulting in increased survival and reproductive success (Krebs and Davies 1981, Sherman 1981). Littermate pairs that disperse to unexploited habitat containing few reproductive competitors may achieve a "jackpot" contribution of their genes to future generations (Carl 1971, Futuyma 1979, Anderson 1980). It might be possible for a mixed-sex pair to found a new colony in a previously uninhabited area, thus effecting range expansion; there would be costs to close inbreeding but locally adapted gene complexes would be preserved and resulting progeny would have high relatedness (Packer 1979, Smith 1979, Haigh 1983, Shields 1983). Once a nucleus of ground squirrels was established in the new area, additional immigrants might have an increased chance of settling successfully (Wiggett and Boag 1986), thus adding new genes to the pool. Dispersal of littermate groups has been reported for various primates (Drickamer and Vessey 1973, Cheney and Seyforth 1977,1983) and carnivores (Frame and Frame 1976, Bygott et al. 1979), and has recently been noted for Columbian ground squirrels in Washington (B. Weddell, pers. comm.).

In terms of ultimate and proximate factors thought to cause dispersal, the observation that littermates can emigrate together illustrates that dispersers are not necessarily asocial individuals as suggested by Bekoff (1977). Nor are they avoiding inbreeding (Greenwood 1980, Cockburn et al. 1985), to the full extent possible. Following a sibling to its postdispersal location and settling nearby results in "nonrandom dispersal" which provides increased opportunities for a degree of beneficial inbreeding in subsequent generations (Cheney and Seyfarth 1983). Shields (1983) argued that most species disperse over relatively short distances in order to achieve "optimal inbreeding" through matings with distantly related kin; emigrating with a littermate might be viewed as another mechanism to ensure a degree of relatedness in the new environment, even if mating among close relatives does not occur.

In conclusion, the results of this study provide a detailed description of the dispersal of yearling Columbian ground squirrels that supports and extends earlier work based on trapping and disappearance studies. Most yearlings were found to sample and prepare distant burrows before dispersing from natal sites; many dispersers settled in edge areas near tree or shrub cover where they suffered higher mortality than yearlings that lived in open-meadow habitat, but some dispersers survived to reproductive age and recruited into nearby populations. The post-dispersal distribution of yearlings did not differ greatly from that expected for animals moving to the nearest vacancy by straight-line searches, provided that sexes were considered separately; this proviso is reasonable since most birds and mammals are known to have sex-biased dispersal tendencies. The incidence of dispersal by pairs of littermates suggests that there may be advantages, or at least not serious disadvantages, in ensuring a degree of relatedness in the new area.

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Table 1.1 - Mortality of yearlings in relation to the distance of their sleeping burrows from shrub cover.

Distance interval	Number of deaths	Number of squirrels	% deaths
1-10	9	17	53
11-20	4	21	20
21-30	4	12	33
>31	1	25	4

Table 1.2. - Survival of each cohort of yearlings marked during 1982-4, as determined by spring (S) and fall (F) trapping. Cohorts are aligned to the spring in which they were yearlings in order to compare their survival through subsequent seasons.

			Minimum number known to be alive						
Year	Group	Sample size	S	F	S	F	S	F	S
1982	Male dispersers	7	7	6	3	3	1	1	1
	M. nondispersers	1	1	1	1	1	0	0	0
	Female dispersers	2	2	2	2	1	0	0	0
	F. nondispersers	5	5	5	3	2	2	2	2
1983	Male dispersers	18a	18	13	8	6	5		
	M. nondispersers	6b	6	5	4	2	2		
	Female dispersers	2	2	1	1	1	1		
	F. nondispersers	8	8	8	6	6	6		
1984	Male dispersers	6	6	2	2				
	M. nondispersers	4	4	3	3				
	Female dispersers	5	5	5	5				
	F. nondispersers	7	7	6	4				

a Sample size changed from 18 to 20 when two yearling "nondispersers" emigrated as two-year-olds after the second spring.

b Sample size changed from 6 to 4 after the second spring, as explained in "a" above.

Table 1.3. - Mean number of years (SE) that dispersers and nondispersers survived after the spring in which they were yearlings. Study animals were accredited with 0.5 years for each subsequent fall (mid-July to mid-August) and spring (mid-April to late May) trapping session in which they were known to be alive. Comparisons are by Mann-Whitney U-tests (MW) or Kruskall-Wallis one-way analysis of variance (KW).

Group	n	Mean years of continued survival	P
Dispersers	40	0.88 (0.12)	0.10 (MW)
Nondispersers	31	1.19 (0.15)	
Male dispersers	31	0.82 (0.15)	
Female dispersers	9	1.06 (0.18)	0.19 (KW)
M. nondispersers	11	1.00 (0.20)	
F. nondispersers	20	1.30 (0.20)	
Males	42	0.87 (0.12)	0.06 (MW)
Females	29	1.22 (0.15)	

Fig. 1.1 - Location of the four study sites in relation to features of surrounding habitat. Symbols SS1 to SS4 represent the four sites. Areas populated by ground squirrels are indicated by stippling.

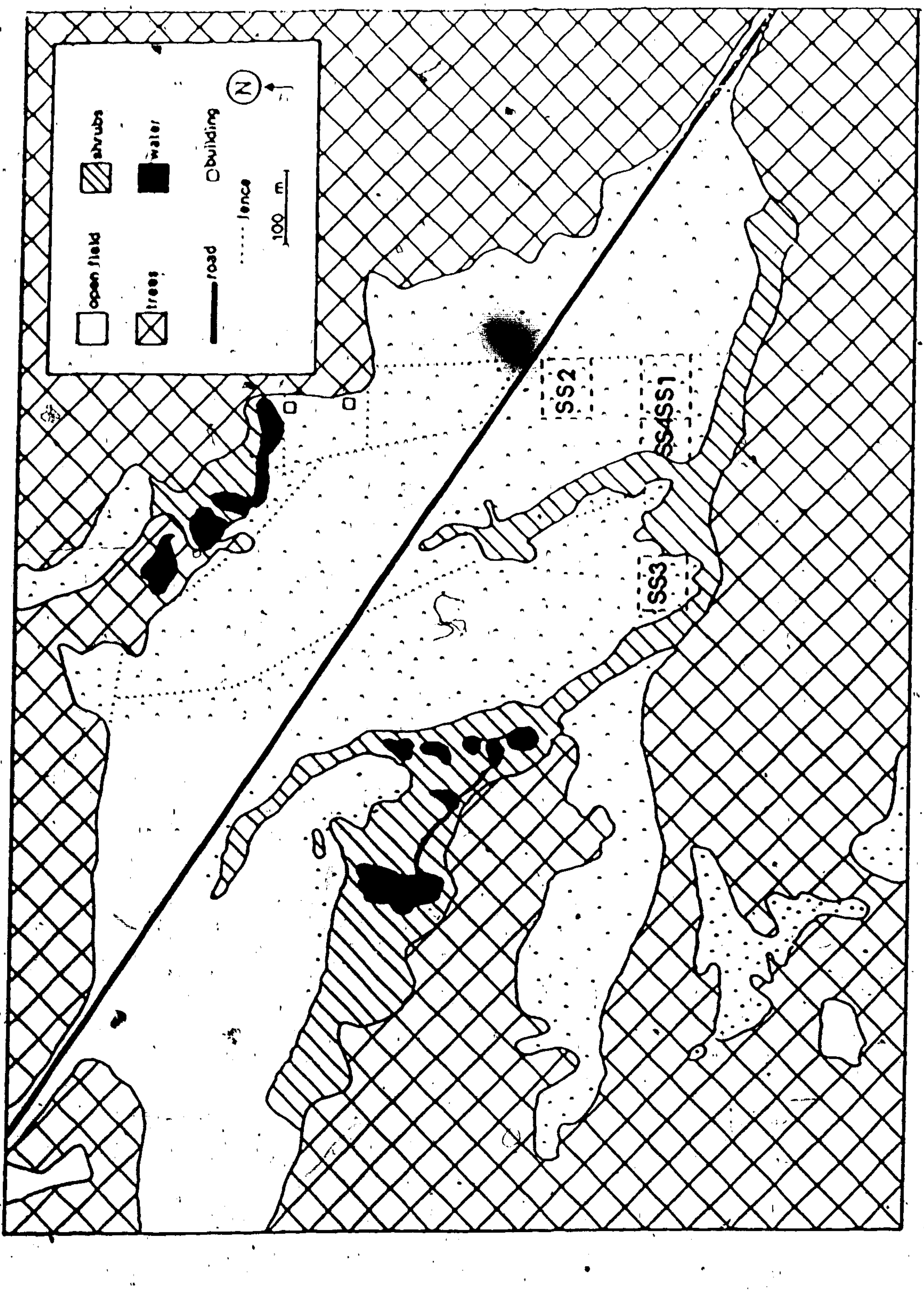

open field
trees
road
fence
100 m
shrubs
water
building
N
SS2
SS4
SS1
SS3

Fig. 1.2 - Postdispersal locations of yearlings that emigrated from study sites. Yearlings numbered 1-18 dispersed from Site 1; Dispersers from Sites 2, 3, and 4 are numbered as 20's, 30's and 40's, respectively. Circled numbers represent yearlings that dispersed to areas where they were not known to make previous excursions.

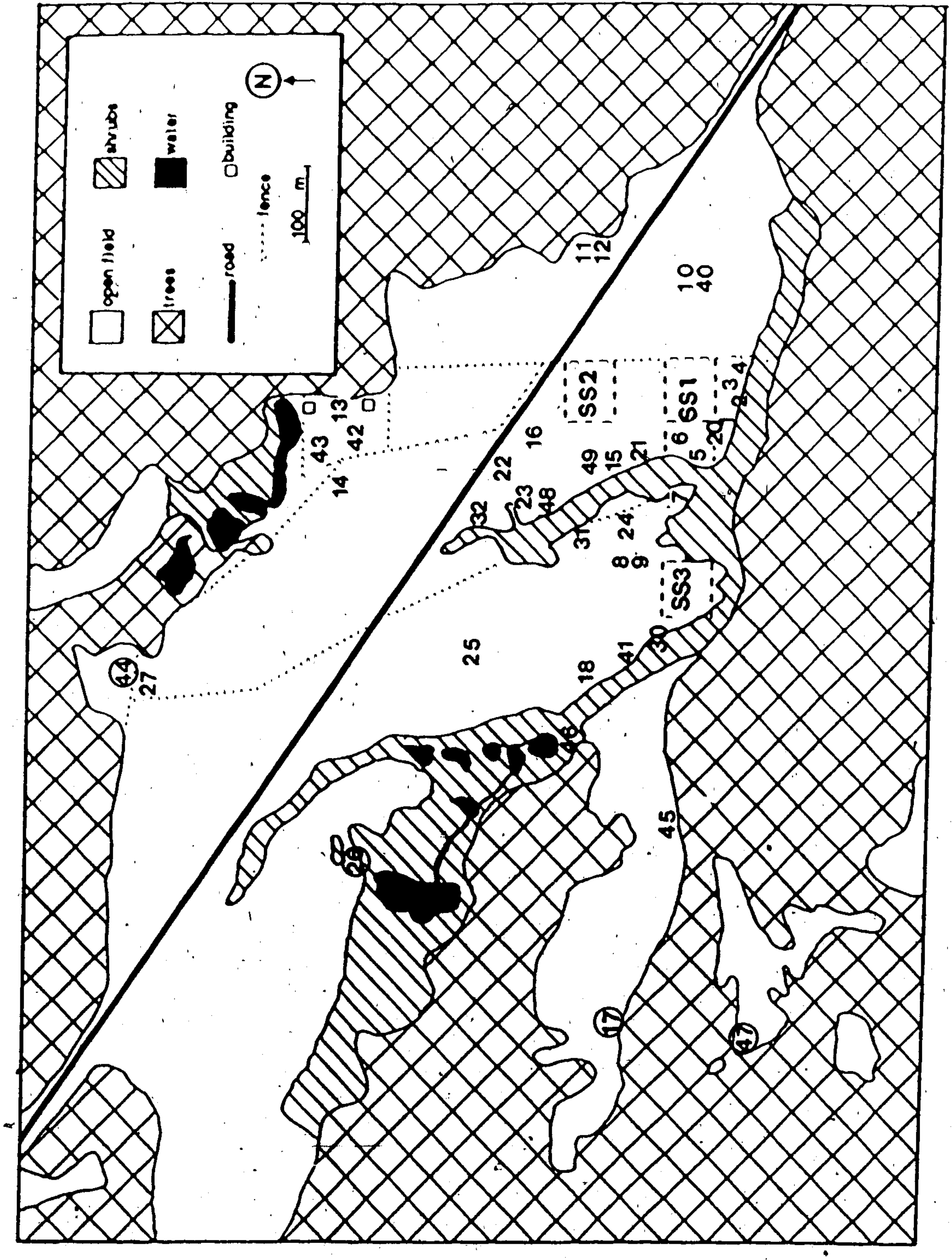

open field
trees
road
shrubs
water
building
fence
100 m
N
11
12
10
40
SS2
SS1
3
4
2
20
6
5
13
42
43
14
16
22
49
15
21
32
23
48
7
31
24
8
9
SS3
25
18
41
30
44
27
46
45
26
17
47

Fig. 1.3 - Composite survivorship curve of three cohorts of yearlings, from 100% survival at spring emergence through subsequent seasons. Dispersers and nondispersers are represented by closed circles and open squares, respectively. Numbers are sample sizes for each period and vary according to the number of cohorts available (Table 1.2). The symbols "S" and "F" refer to spring and fall seasons.

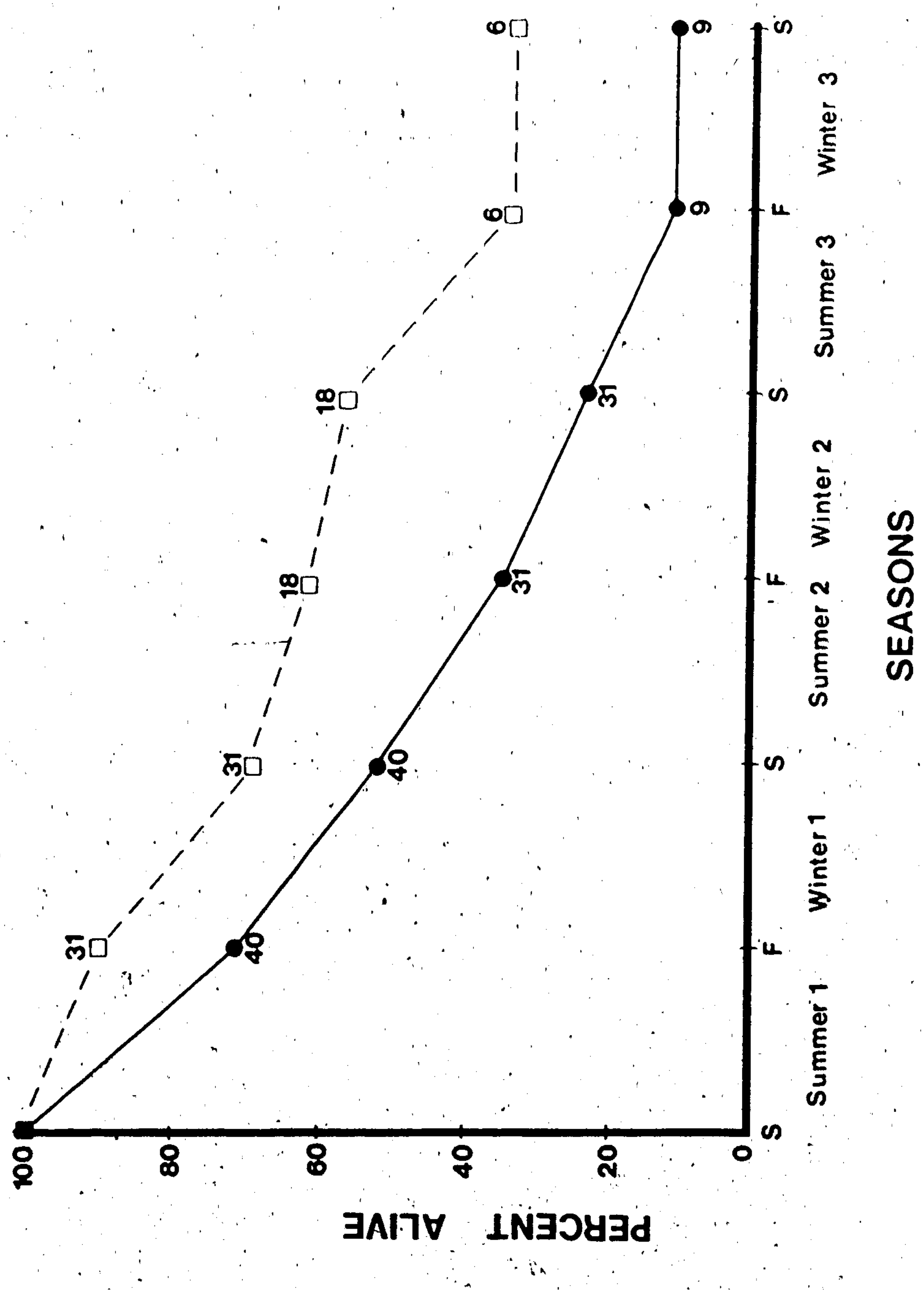

PERCENT ALIVE
100
80
60
40
20
0
S
F
S
F
S
F
S
Summer 1
Winter 1
Summer 2
Winter 2
Summer 3
Winter 3
SEASONS
40
40
31
31
9
9
31
31
18
18
6
6

Fig. 1.4 - Composite survivorship curve of yearlings grouped by dispersal status and gender. Dispersers are represented by closed symbols (circles, males; squares, females). Nondispersers are represented by open symbols. Other symbols are the same as in Figure 1.3.

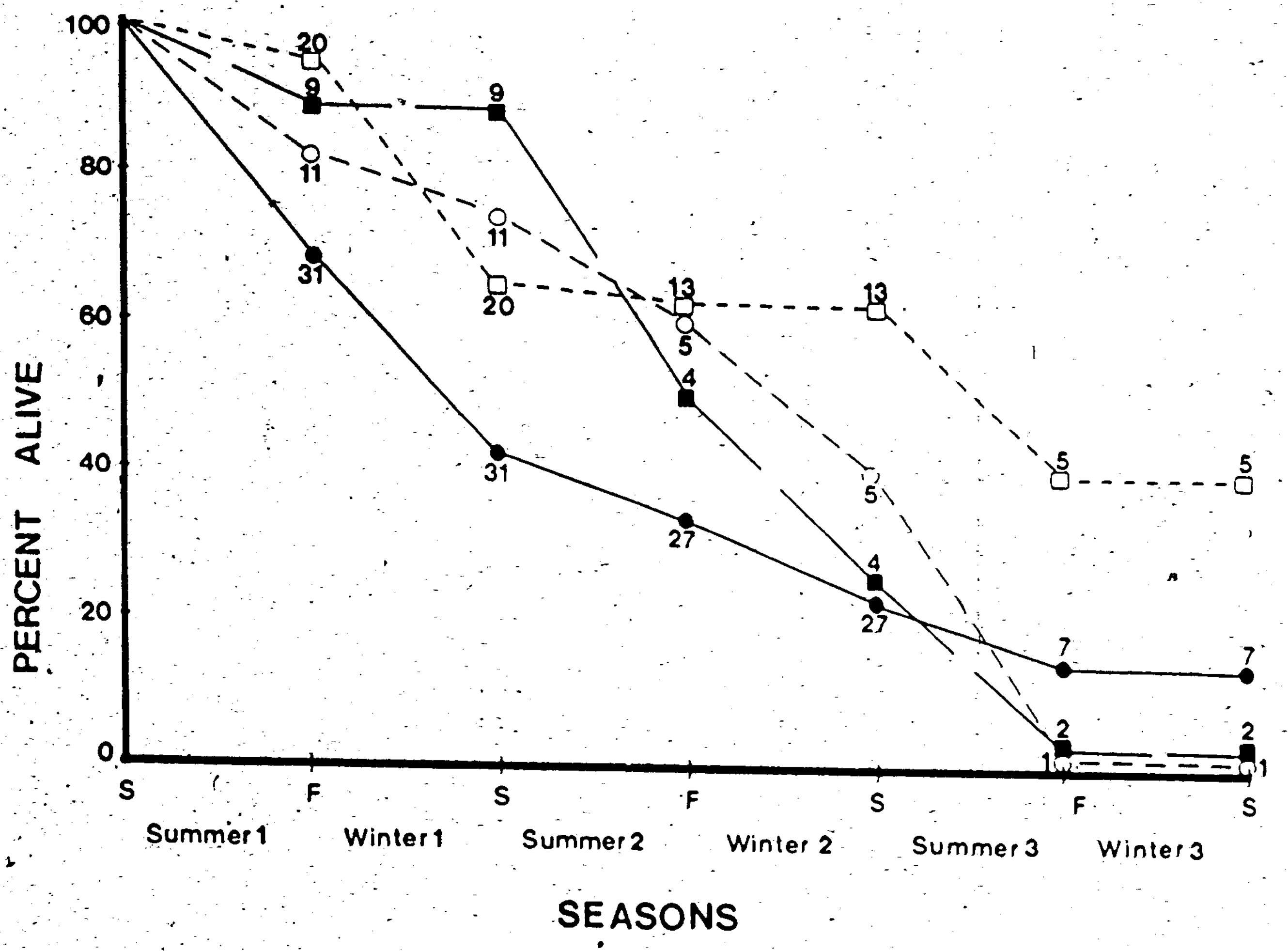

PERCENT ALIVE
100
80
60
40
20
0
S
F
S
F
S
F
S
Summer 1
Winter 1
Summer 2
Winter 2
Summer 3
Winter 3
SEASONS
20
9
11
31
9
11
20
31
13
5
4
27
13
5
4
27
5
2
1
7
5
2
1
7

Fig. 1.5 - The distribution of dispersal distances for yearlings that left their natal home ranges. Arrows represent median dispersal distances for males (open bars) and females (stippled bars).

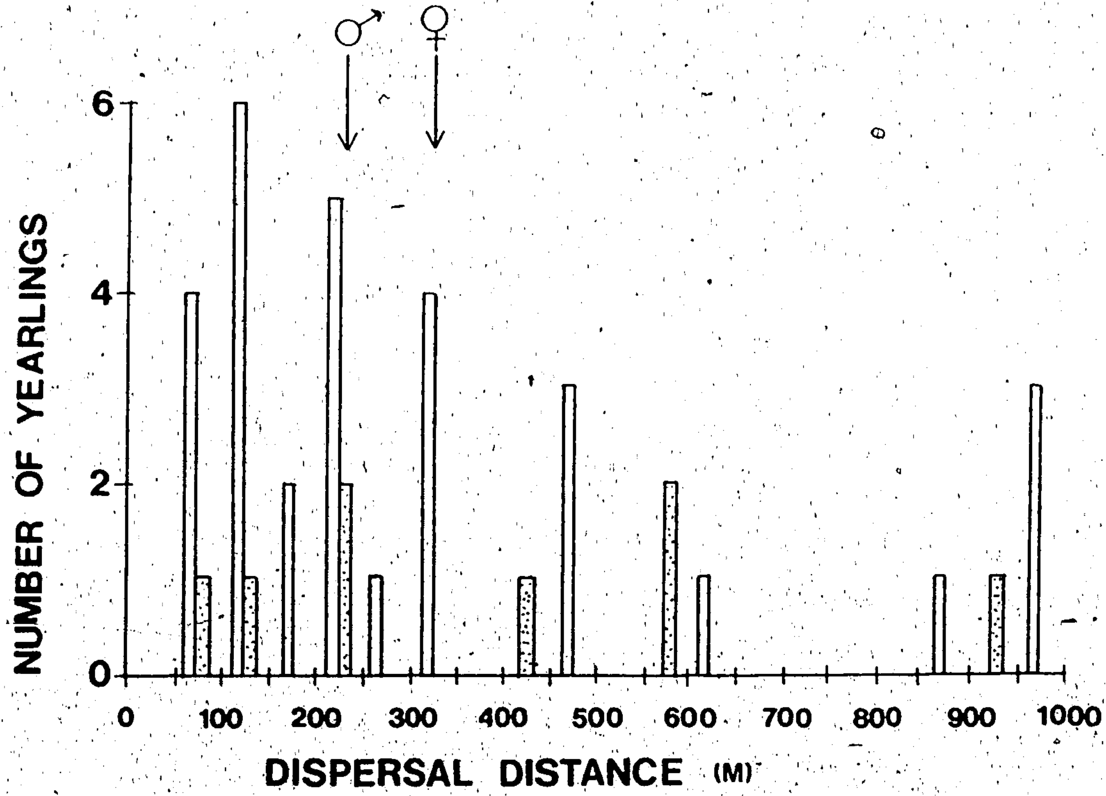

♂
♀
NUMBER OF YEARLINGS
0
2
4
6
0
100
200
300
400
500
600
700
800
900
1000
DISPERSAL DISTANCE (M)

Fig. 1.6 - Two competition models applied to the postdispersal distribution of all yearlings. Equation 1 is Murray's (1967) model, $p_n=t(1-t)^n$. Equation 2 is Waser's (1985) model, $p_n=(1-(1-t)^{6n})(1-t)^{1+3n^2-3n}$. The histogram represents the observed distribution of dispersal distances. See text for further explanation of models.

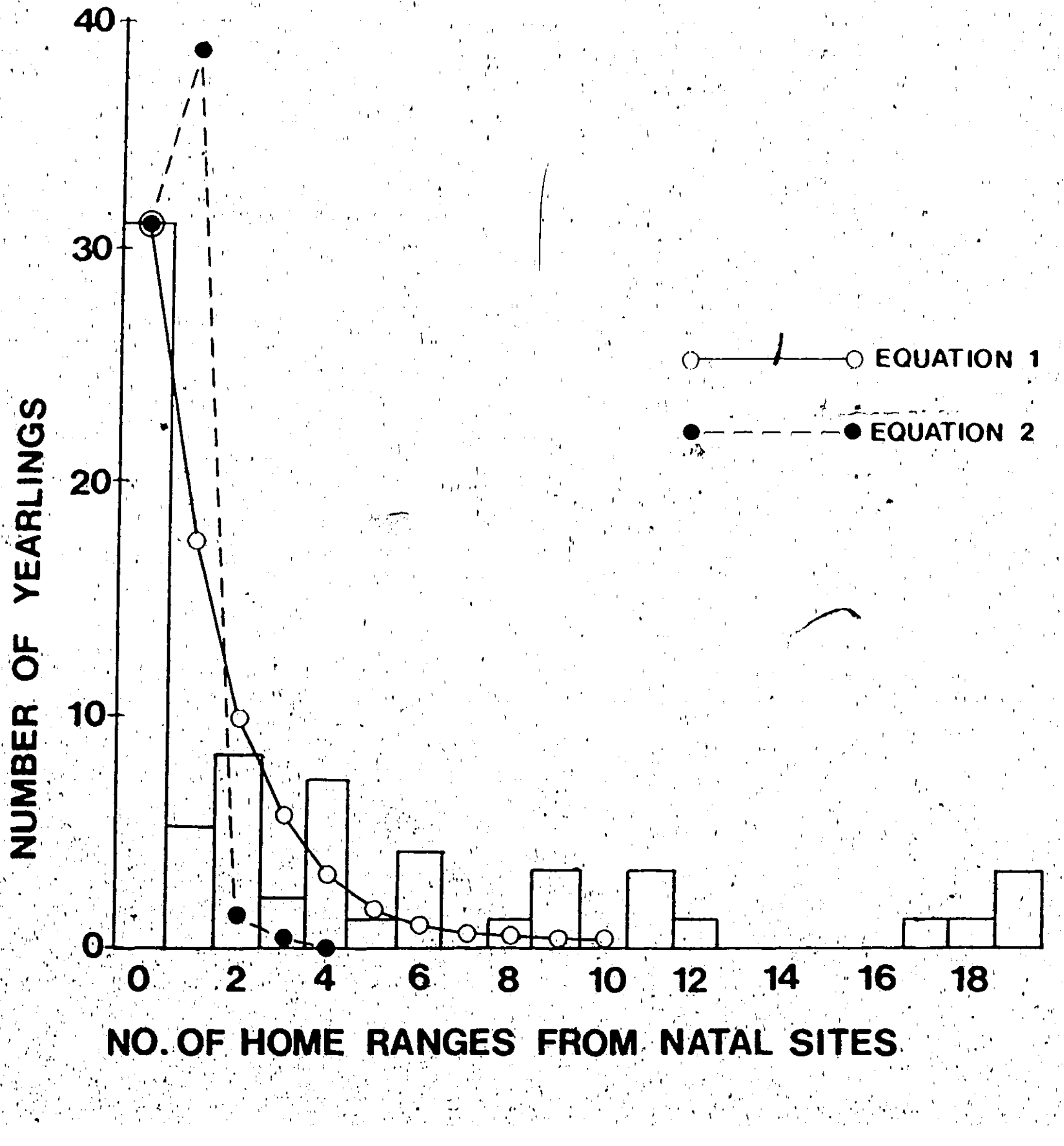
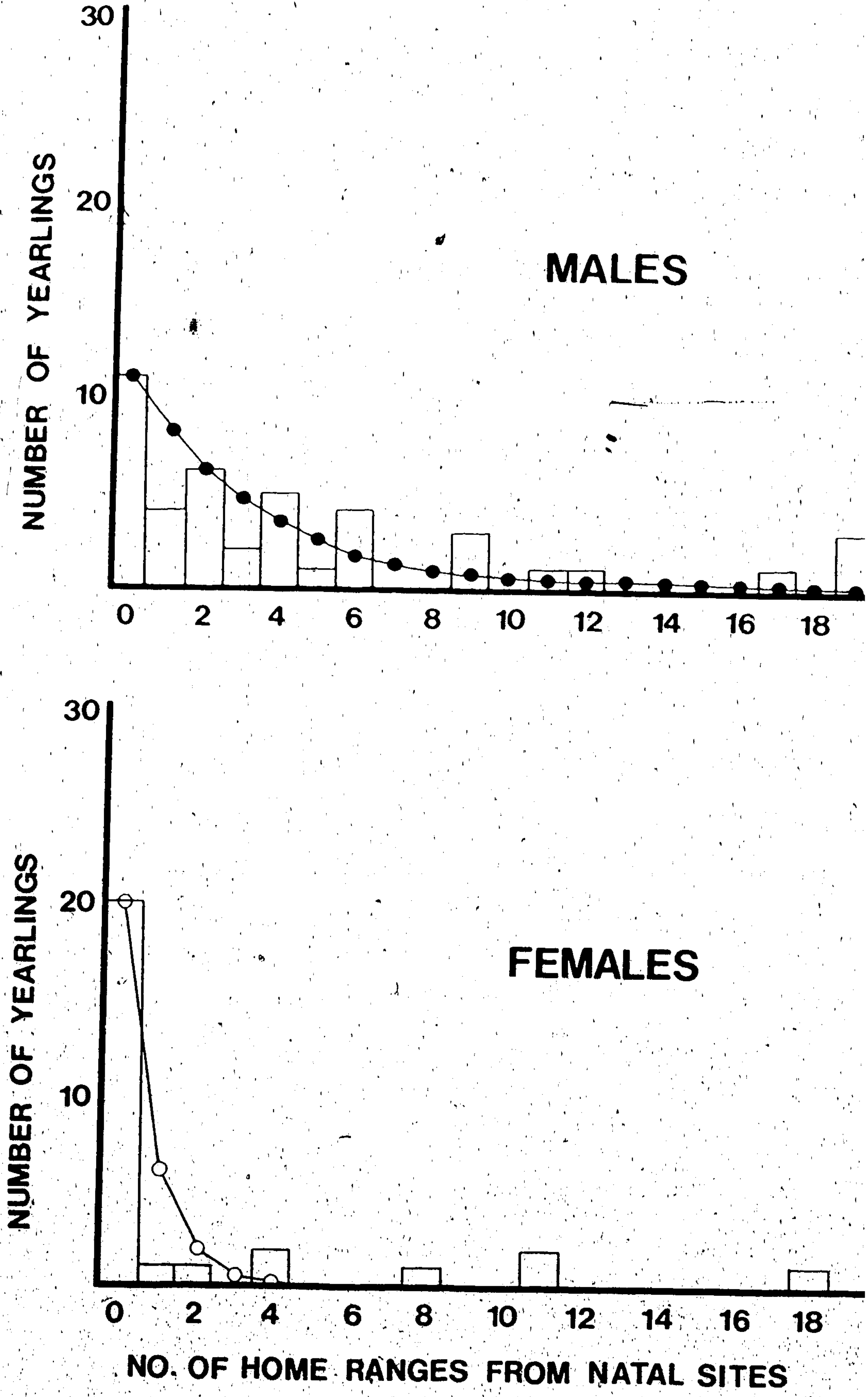

NUMBER OF YEARLINGS
40
30
20
10
0
0
2
4
6
8
10
12
14
16
18
NO. OF HOME RANGES FROM NATAL SITES
EQUATION 1
EQUATION 2

Fig. 1.7 - Murray's (1967) competition model applied to the postdispersal distribution of male and female yearlings separately. Histograms represent the observed distributions of dispersal distances.


MALES
FEMALES
NUMBER OF YEARLINGS
30
20
10
0
2
4
6
8
10
12
14
16
18
NO. OF HOME RANGES FROM NATAL SITES

III. Paper 2 - DOES BODY WEIGHT TRIGGER DISPERSAL OF YEARLING COLUMBIAN GROUND SQUIRRELS?

A. ABSTRACT

Weekly weights of yearling Columbian ground squirrels (Spermophilus columbianus) were collected in conjunction with a 3-year telemetric and observational study of dispersal. Yearlings gained weight slowly in the interval surrounding juvenile emergence, apparently because maternal aggression and adult female territoriality resulted in increased social pressure. Male dispersers were no heavier than nondispersers at the time of emigration, but dispersers were as much as 100 g heavier by fall; the additional weight likely reflected escape from social pressure and competition for food, and represents a potential benefit for dispersing males. Female nondispersers were heavier than dispersers at the time of emigration, supporting female competition as a factor influencing their dispersal; female dispersers lost the benefits of philopatry and still weighed no more than nondispersers at the end of the season, suggesting that little advantage accrues to female dispersers. These findings are generally in agreement with empirical ground squirrel studies but do not support predictions stemming from behavioural hypotheses concerning proximate causes of male dispersal.

B. INTRODUCTION

The small mammal literature offers many opportunities for speculation concerning the relationship between body weight and dispersal. Lidicker (1975) suggested that emigrants from high density populations ("saturation dispersers") were juveniles, social outcasts, and those in poor condition; the Social Subordination Hypothesis (Christian 1970), and the Genetic-Behavioural Hypothesis (Chitty 1967, Krebs 1978), also describe dispersers as social subordinates (i.e. probably lightweight animals). In contrast, the Social Cohesion Hypothesis (Bekoff 1977) predicts that dominant and subordinate individuals (probably heaviest and lightest) are most likely to disperse. In most studies of species smaller than ground squirrels, dispersers were found to be lighter than residents - however, indirect methods such as disappearance from sites, or appearance on removal plots, were typically used to identify "dispersers" (Gaines and McClenaghan 1980). Most ground squirrel studies have found no significant differences in weights between animals remaining on study sites and those that disappeared (Slade and Balph 1974, Dunford 1977, Pfeifer 1980, 1982), but these authors were unable to differentiate between dispersal and mortality *in situ*.

Holekamp (1984a, b, 1986) used a combination of observation, trapping, and telemetry to study dispersal of Belding's ground squirrels (Spermophilus beldingi) in more detail than previous researchers had. She reported that male juveniles that dispersed were heavier than those that had not yet dispersed, and proposed that emigration was triggered by attainment of a critical body weight ("the Ontogenetic Switch Hypothesis"). A number of predictions can be made from her hypothesis: 1) Dispersers should be heavier than nondispersers at the time of emigration. 2) There should be evidence of a critical weight threshold, i.e. a plot of dispersal weights versus dispersal dates should approximate a horizontal line. 3) Heavy dispersers should emigrate before lighter dispersers, i.e. a plot of weights of dispersers determined on a standard pre-emigration date versus their dispersal dates should result in a line with negative slope.

Further points could be clarified through study of weights associated with dispersers and nondispersers. Do males and females have the same weight trends, or are there differences related to sex-biased dispersal tendencies? Do weights of emigrants decline, perhaps through energetic costs of dispersal and relocation in marginal habitat - or do their weights increase in response to escape from social pressure and competition for food? If weight differences exist between dispersers and nondispersers, does this imply that one group must remain exposed to above-ground danger for a longer period in the fall in order to amass sufficient weight for hibernation?

This report examines relationships between body weight and dispersal of yearling Columbian ground squirrels (S.

columbianus). Special attention is focussed on predictions and implications of the Ontogenetic Switch Hypothesis as it applies to *S. columbianus* - a species in which dispersal occurs primarily in the yearling age-class, rather than in the juvenile age-class as is the case with most ground squirrels (Holekamp 1984a).

C. METHODS

Four study sites, each approximately one hectare in area, were established in grazed meadow on a ranch 10 km southwest of Chain Lakes Provincial Park in southwestern Alberta (50 06' N, 114 33' W, elevation 1400 m). During May-August 1982, Columbian ground squirrel populations of Sites 1 and 4 were trapped and observed, and yearlings of both sexes were radio-collared and tracked using handheld antennas and receivers. The field season was divided into 10-day periods aligned so that the first day of juvenile emergence ("Juvday") was always Day 50, the beginning of the fifth period. In this way, observation dates and periods were attuned to the phasing of the annual cycle. During April-August 1983, Sites 1, 3 and 4 served as reference areas as described above; adult female ground squirrels on Site 2 were sedated twice daily with acepromazine maleate as part of a behavioural experiment aimed at investigating the effects of aggression on dispersal (Paper 3). During April-August 1984, Site 2 became a reference area, adult females on Site 1 were sedated, and adult females on Site 3 were temporarily sterilized with ethynylestradiol 3-methyl ether ("Mestranol") to block pregnancy and postpartum aggression. Further details of vegetation and terrain, radio-telemetry, behavioural observation and experimental design have been described elsewhere (Papers 1 and 3).

Throughout all summers, ground squirrels were captured in National live-traps (15X15X50-cm), examined for wounds and reproductive condition, weighed to the nearest 5 g using a Pesola spring scale, eartagged with serially numbered metal tags, and given unique body marks with hair dye (Lady Clairol blue-black). An attempt was made to weigh all yearlings at least weekly. Only weights of animals that could be classified as dispersers or nondispersers were analyzed, thus disappearance was not used to infer dispersal. "Dispersers" (31 males, 8 females) were those animals that left their natal home ranges and established themselves in new home ranges; a yearling became a disperser on the day (evening) it ceased returning to spend the night in its natal area, provided that it was subsequently found to be alive elsewhere. "Nondispersers" (12 males, 22 females) continued to live and sleep near their natal burrows (Paper 1).

A general description of weight versus time was afforded by determining the mean weight of each individual per 10-day observation period and grouping the means according to sex and dispersal status; this facilitated comparisons with behavioural data collected during the same intervals (Paper 3). Weights of yearlings were compared more precisely by assigning a number of standard dates and interpolating weight values for those dates from individual growth curves (Fig. 2.1). The standard dates, and rationales for using them, are as follows:

1) Day of initial juvenile emergence ("Juvday") - the first appearance of juvenile litters was highly synchronous across the study sites and took place on 21, 14, and 10 June during the years 1982-4, respectively. This event was a recognizable stage of the ground squirrel reproductive cycle, marked the beginning of a new behavioural phase associated with the above-ground presence of juveniles, and was close to the beginning of the dispersal period.

2) Day of dispersal - dispersal dates of individuals were known, and weight values for those days were interpolated from growth charts of dispersers.

3) Maximum weight - the peak weight of each yearling that survived until fall, and the date associated with its maximum weight, were recorded. If a yearling had the same maximum weight on two or more occasions, the earliest date was used.

Weights associated with standard dates, and the dates on which dispersal and maximum weights occurred, were normally distributed and of suitable variance for parametric statistical procedures. Mean growth curves were compared using Kolmogorov-Smirnov nonparametric tests (Nie 1983).

D. RESULTS

Individual weight-versus-time or "growth" curves of the 73 yearlings were similar to the example shown (Fig. 2.1). Individuals gained weight through most of the season but typically experienced a reduced rate of increase, or a loss, during one or more of Periods 4 to 6. Fifty-two yearlings were captured at least weekly during this interval, making it possible to determine whether these animals showed a levelling or decline between weighings taken five to seven days apart. Sixty-seven percent (14/21) of male dispersers, 62% (5/8) of male nondispersers, 86% (6/7) of female dispersers and 94% (15/16) of female nondispersers failed to gain weight for intervals of 5 to 18 days; differences among the four groups were not significant (G=5.64, P=0.13), but females were more likely than males to experience a pause in their growth curves (G=3.68, P=0.05). Yearlings that did not show a levelling or decline of weight were dispersers that emigrated before Day 47 (4/4), yearlings from the edge of forest (4/5), male nondispersers with no sisters or pregnant mothers (2/5), and yearlings from the 1984 Mestranol treatment on Site 4 (2/4). Most individuals again showed a weight loss in Period 10 before hibernation.

Mean growth curves summarize the weight increments of dispersers and nondispersers of both sexes (Figs. 2.2 and 2.3). Male dispersers did not differ in weight from male nondispersers before Juvday (K-S Z=0.483, P=0.97); thereafter male emigrants gained significantly more weight

(Z=1.789, P=0.003). Female nondispersers tended to be heavier than female dispersers before Juvday although the trend is not statistically significant (Z=1.186, P=0.12), possibly because weight differences were not apparent in Week 1 following emergence from hibernation; after Juvday, weight differences between the two groups diminished (Z=1.00, P=0.27). Males and females were relatively similar in weight before Juvday (Z=1.106, P=0.17); females gained at a lower rate than males during Period 5, accounting largely for the divergence of male and female weight curves after Period 4 (Z=2.427, P<0.001).

Comparisons Among Males on Standard Dates

Weights of male yearlings on Juvday did not differ among sites (F=0.94, P=0.43) although there were highly significant differences among years (F=6.38, P=0.004); in 1982, yearlings were approximately 50 g lighter than in 1983 or 1984 at the time of juvenile emergence (Table 2.1). Maximum weights were similar among sites (F=0.74, P=0.54), but yearly differences approached significance (F=2.72, P=0.08) because the 1983 dispersers gained more weight during the summer than 1982 and 1984 dispersers (Table 2.2). Maximum weights of nondispersers were relatively consistent among sites and years. Dispersers and nondispersers did not differ in weight on Juvday (t=0.2, P=0.82); however, dispersers that survived to the end of their yearling summers were significantly heavier than surviving nondispersers (t=3.1, P=0.004).

Weights of emigrants at the time of dispersal ranged from 385 g to 620 g (Table 2.3), and differed among sites (F=3.20, P=0.04) and years (F=5.39, P=0.01). Dispersal dates ranged from Day 42 (8 days before juvenile emergence) to Day 89 (39 days after juvenile emergence) with a mean dispersal date of Day 59 ± 2 and a median of Day 57. Dispersal dates were similar among years (F=0.10, P=0.91), but differences among sites approached significance (F=2.46, P=0.08).

A plot of dispersal weights versus dispersal dates (Fig. 2.4) appears to indicate a positive linear trend when all data are included (n=30, r=0.57, P=0.001, Y=2.8X + 301). This relationship is greatly affected by two late dispersers from a sedation site, and one exceptional individual that shifted its home range very late (July 21) during Summer 1983. No trend is apparent during the interval of Day 42 to Day 69 when all other yearlings dispersed (n=27, r=0.14, P=0.44). When all dispersers from sedation sites are excluded and the exceptionally late disperser is considered an outlier, there is no linear relationship between dispersal weight and dispersal date (n=21, r=0.17, P=0.45).

In order to determine whether heavy dispersers tended to emigrate before lighter ones, weights of dispersers on a common day (Juvday) were correlated with departure dates (Fig. 2.5). The result (r=0.41, P=0.02, Y=-1.5X + 527) suggests a linear relationship with low correlation and a negative slope, but the trend is influenced by late departures of the three individuals described previously. For all dispersers except these three, a linear relationship with higher correlation and a stronger negative slope is indicated ($r=0.57$, $P=0.001$, $Y=-3.34X + 630$). Excluding all dispersers from sedation sites and the exceptionally late disperser from 1983 improves the correlation and results in a negative slope ($r=0.63$, $P=0.001$, $Y=-3.6X + 643$). When yearlings are viewed as groups defined by site and year, early dispersers were heavy animals in four groups, early dispersers were relatively light animals in two groups, and weights of early and late dispersers were similar in two groups.

The dates on which maximum weights were achieved (Table 2.4) did not differ among sites ($F=0.21$, $P=0.89$) or years ($F=0.91$, $P=0.41$), or between dispersers and nondispersers ($F=0.32$, $P=0.57$). Male yearlings attained their maximum weights at 40 days, 43 days and 39 days after juvenile emergence during the years 1982-4 respectively (42 days ± 1 after Juvday).

Comparisons Among Females on Standard Dates

Weights of female yearlings on Juvday did not differ among sites ($F=1.48$, $P=0.24$) although there were highly significant differences among years ($F=9.58$, $P=0.001$) owing largely to the 1983 yearlings which were approximately 55 g heavier than 1982 and 1984 yearlings (Table 2.5). Juvday weights of female yearlings were approximately 15 g less than those of their male counterparts (Table 2.1) for the first two summers, but in 1984 were smaller by approximately 75 g; that summer corresponded to 42% (5/12) dispersal of yearling females compared to 14% and 18% female dispersal during 1982 and 1983, respectively. Maximum female weights were similar among sites (F=1.62, P=0.21), but differed among years (F=3.84, P=0.04) (Table 2.6). Yearling females that dispersed were 34 g lighter on Juvday than nondispersers (t=-1.9, P=0.07); in 5 of 6 litters containing more than one yearling female, the heaviest sister remained whereas the lighter sister(s) dispersed. Maximum weights achieved by 7 dispersers were 31 g lighter on average than those of 21 nondispersers, but the difference was not significant (t=-1.5, P=0.15).

Dispersal weights of female emigrants ranged from 320 g to 460 g. Average dispersal weights of Site 1 females were 375 g (n=1), 445 ±15 g (n=2), and 350 ± 15 g (n=4) during 1982-4; the single 1984 Site 4 disperser weighed 360 g. Dispersal weights differed among years (F=9.37, P=0.02) but not among sites (F=0.86, P=0.78), although statistical tests based on the small number of female dispersers should be viewed cautiously. Departure dates for dispersers ranged from Day 45 (5 days before juvenile emergence) to Day 60 (the Site 4 female was the latest disperser); the mean and median dispersal date was Day 52. Differences in dispersal dates were not significant among years (F=1.58, P=0.29), but approached significance among sites (F=5.17, P=0.06).

Dispersal weights and dates were not related (r=0.07, P=0.44), nor were dispersal dates correlated with Juvday weights (r=0.25, P=0.27).

The dates on which females reached their maximum weights (Table 2.7) did not differ among years (F=0.72, P=0.50) or sites (F=0.60, P=0.62), or between dispersers and nondispersers (F=0.51, P=0.48). Female yearlings attained their maximum weights 42 days ± 2 after the date of juvenile emergence, the same time male yearlings did so.

E. DISCUSSION

The Midseason pause in Yearling Growth Curves

Yearlings gained weight at relatively slow rates in Periods 4 to 6. Data from a 7-year study by Boag and Murie (1981) illustrate a similar trend using larger sample sizes but less precise time intervals (Fig. 2.6). They reported that yearlings gained weight slowly in the three-week period associated with juvenile emergence; adult males continued to gain weight at unchecked rates, whereas female weights reflected their midseason costs of reproduction and territorial defence (Festa-Bianchet and Boag 1982).

I suspect that the slowing of mean yearling weight gains was largely a result of aggressive pressures faced by yearlings in the weeks surrounding juvenile emergence. At that time adult females were actively defending their territories against other ground squirrels, including their own yearlings; female yearlings were competing with their siblings to gain control of a burrow between adult female territories; yearlings encountered high rates of chases, and typically responded by spending less time on study sites (Paper 3). Some energetic costs were likely incurred by yearlings making excursions and digging at distant burrows, but the greatest costs appear to have been associated with study sites. Female nondispersers were the only group to show a reduction in mean weights (Fig. 2.3), and female yearlings were more likely than males to experience a levelling or decline in their individual weight curves; this may have been related to energetic expenditures by females while competing to remain philopatric (Paper 3). Males, the predominant dispersers, were less likely to show individual weight pauses, and yearlings that emigrated before Day 47 (3 males, 1 female) continued to gain weight throughout Periods 4 to 6. Other yearlings that gained weight were those exposed to relatively little social pressure. Yearlings that lived on the edge of forest had relatively few neighbours and had the option of avoiding conspecifics by retreating into forest habitat; males with nonpregnant mothers and no sisters experienced relatively little aggression within their natal home ranges and were able to remain philopatric; yearlings on the mestranol site encountered low rates of aggression, but two males lost weight in Period 6 when they left their sister in possession of the natal burrow and renovated burrow systems in adjacent home ranges (Papers 1 and 3). Maternal aggression and territoriality made it difficult for most yearlings to avoid harrassment while on study sites (Paper 3), resulting in interrupted weight gains and perhaps providing yearlings with increased motivation to disperse.

Do Yearlings That Attain a Critical Weight Become Dispersers?

The Ontogenetic Switch Hypothesis proposes the existence of a sex-linked mechanism causing dispersal and associated behaviours to occur in male S. beldingi when they attain some minimal body weight or store some minimal amount of energy as fat (Holekamp 1986:371). Neither Holekamp nor I have any data describing fat storage. Holekamp (1986:372) found that all male S. beldingi dispersed and suggested that "the ontogenetic threshold in males occurs at a body mass of 125-175 g". In this study, 28% (12/43) of male S. columbianus remained philopatric throughout their yearling summers, providing a "nondisperser" class for comparison. There were no significant differences between body weights of dispersers and nondispersers when compared on Juvday (Day 50). Some nondispersers were clearly heavy animals; in 1982, the single nondisperser was only 5 g short of matching the heaviest disperser and at 425 g was approximately 30 g heavier than the mean weight of dispersers for 1982. Apparently, there was no threshold weight that determined the dispersal status of male yearling S. columbianus.

Slade and Balph (1974:997) found no significant difference in the weights of juvenile S. armatus leaving the natal area and those remaining, with the exception of runts that seldom left the vicinity of their natal burrow. Juvenile S. tereticaudus that eventually "dispersed" (disappeared) were heavier than those that did not, but the difference was less than 3 g and was not significant (Dunford 1977:1260-1262). Pfeifer (1980:119, 129) found that juvenile S. elegans that disappeared from her study populations were approximately 20 g lighter in weight than philopatric juveniles; again, the difference was not significant. These studies compared predispersal weights of animals that eventually disappeared (dispersed or died) with weights of animals that survived and remained philopatric. If dispersers were heavier than nondispersers as suggested by the Ontogenetic Switch Hypothesis, then the disappearing class of each of the above studies must have contained a complement of lighter-than-normal animals that died *in situ*; otherwise the disappearing group would have outweighed the philopatric group. This does not seem likely, particularly in the case of Pfeifer (1980). The differences that Holekamp (1984b) reported stemmed from comparing **postdispersal weights of emigrants with animals that had not yet dispersed.** I support her finding that ground squirrels can achieve increased body weight once they have dispersed; **she did not, however, demonstrate weight differences before dispersal which might be interpreted as determining dispersal status.** Holekamp (1986) admitted that factors other than weight might influence dispersal since she observed dispersers whose weights were identical to those of animals that had not yet dispersed.

Holekamp (1984b, 1986) was not specific about how the Ontogenetic Switch Hypothesis applied to weights of female S. beldingi. Since her hypothesis described a "sex-linked mechanism" involving males, the implication appears to be that the same body weight arguments are not appropriate for females. On the other hand, she speculated about whether the increased dispersal rate of females treated with testosterone propionate was a result of hormonal effects on body weight (Holekamp et al. 1984:478). In fact, there were no significant differences in mean weights of her TP-treated (84 g) and untreated (83.7 g) females.

In this study, female yearlings that dispersed were 34 g lighter than nondispersers when compared on Juvday. The year of peak female dispersal was the year with the lowest Juvday weights of females (Table 2.5), although yearling males did not exhibit a similar reduction of Juvday weights. Female dispersers were lighter than their nondispersing sisters within 5 of 6 litters containing two or more females. These facts seem to support Pfeifer (1980, 1982) who found that disappearing female S. elegans were 23 g lighter than "homebody" females and who concluded that competition among young females was the driving force behind their dispersal. Elsewhere I have argued that the high rate of female dispersal appeared to result from competition within multi-female litters which were particularly common in 1984 (Paper 3). Perhaps energetic costs of female competition were reflected in body weights, as suggested by the reduced weights of females in 1984 when males exhibited no similar loss.

Do Dispersers Emigrate Upon Reaching a Critical Weight?

If body weight is the sole or primary criterion triggering departure among dispersers, one would expect dispersal weights to be relatively consistent since dispersers would simply attain their critical weight requirements and then emigrate. Dispersers should be able to reach their critical weights sooner in years of favourable growth (as indicated by high Juvday weights), which would result in differences of dispersal dates among years. Given that Juvday weights were similar for all sites, one would expect dispersal weights and dates to be similar for all sites. The above scenario was not supported by the present study. Male yearlings dispersed at a wide range of weights rather than at a recognizable critical value. Dispersal weights varied among years, as did Juvday weights and maximum weights, in response to climatic factors such as early (1983-4) or late (1982) springs, but the mean dates on which yearlings dispersed did not vary significantly among years; this may indicate that dispersal dates were more closely tied to the reproductive events used to align years (Juvday) than to yearling weight gains that were taking place. Weights determined on Juvday and at the time of maximum weight gain were consistent among sites, but dispersal weights were not. Apparently, some factor other than an "ontogenetic switch" caused yearlings from different sites to disperse at different weights.

As a second approach to the problem, I plotted dispersal weights against dispersal dates (Fig. 2.4). If dispersers departed upon reaching a particular threshold weight, the plot should yield a scatter of points along a horizontal line since a series of dispersal dates would be correlated with essentially the same dispersal weight; presumably dispersers would leave at any point in the season after attaining sufficient weight. If dispersers left at random throughout the season, one would predict a scatter around a positively sloped line that described the growth rate of yearling ground squirrels. If dispersers were induced to leave within a short interval, particularly Periods 4 to 6 when many individuals were not gaining weight, a concentrated pattern of relatively random dispersal weights would result.

The correlation of dispersal weight versus dispersal date for males did not result in a horizontal line (Fig. 2.4). Male yearlings exhibited a wide range of dispersal weights, and most left during Periods 4 to 6 when rates of aggression were high on study sites. The latest dispersers in this group were from Site 4 which contained a shaded hillside where reproduction and peaks of aggression were later than on the other sites. Elsewhere I have elaborated on the role of maternal aggression and adult female territoriality as a factor that appears to synchronize the timing of yearling dispersal (Paper 3). The three dispersers leaving after Day 79 were heavy because they emigrated late in the season when yearlings were approaching their maximum weights (Fig. 2.1). Two of them were from a plot where sedation of adult females was associated with delayed dispersal of all male yearlings. The third late disperser had no living mother or sisters, and remained on its natal area until fall when it emigrated leaving a brother in possession of the natal burrow (Paper 3). In short, it seems unlikely that the timing of male dispersal was caused by reaching a critical weight as suggested by the Ontogenetic Switch Hypothesis. On the contrary, the observed weights apparently resulted from the timing of yearling dispersal.

Dispersal weights and dates of female yearlings showed little evidence of a weight threshold. All females left within a 15-day interval in Periods 4 and 5 despite wide-ranging weight differences. Most left between Days 51 and 55, immediately following the emergence of juveniles.

Do Heavy Dispersers Tend to Leave Before Lighter Dispersers?

When male dispersers from all sites and years are compared, it appears that dispersers that were heaviest on Juvday tended to emigrate first (Fig. 2.5). A number of factors complicate interpretation of these results. The cycle of spring emergence, juvenile emergence and yearling dispersal was delayed on the shaded hillside comprising much of Site 4 (Papers 1 and 3). Some of these animals were out of phase with the other study animals by as much as 10 days, resulting in delayed dispersal dates and light Juvday weights. Did light Juvday weights cause late dispersal or were the two factors correlated through the action of an additional factor such as a delayed annual cycle? In the case of Site 4, the latter appears to be true. Sites 2 and 3 tended to have intermediate dispersal dates. Juvenile emergence commenced on the same day on all sites each year, but little attention was paid to how quickly juvenile emergence was completed on individual sites; the possibility remains that Sites 2 and 3 were at an intermediate phasing between Sites 1 and 4 despite the attempt to align reproductive events using "Juvday". In addition, four dispersers from Site 1 that emigrated before Day 47 did not experience the decreased weight gains associated with remaining on study sites; their relatively heavy Juvday weights may have been partly the result of early departure allowing them to avoid the social pressure experienced by other yearlings. When dispersers are subdivided into groups according to sites and years, in only half the groups were early dispersers heavy individuals. Thus I suspect that the trend across all sites combined, whereby dispersers that were heaviest on Juvday tended to emigrate first, may have been influenced by extrinsic local factors. It is possible that juveniles from early litters were relatively large yearlings at a given point in the following season (this was true of yearlings from Sites 1-3 compared to yearlings from Site 4 where reproduction was known to be delayed). If their mothers gave birth to early litters again and began to exclude former litters from their natal burrows (Paper 3), heavy yearlings would tend to emigrate sooner without weight being a direct cause of their departure.

A comparison between dispersers emigrating from Holekamp's two study sites does not appear to support the Ontogenetic Switch Hypothesis: males from her LVC site were significantly more likely to disperse at a younger age than males from her HMH site, yet LVC males were significantly lighter than HMH males (Holekamp 1984:23-25). This suggests that extrinsic factors that differed between the two sites, such as elevation and timing of the reproductive cycle (Holekamp 1984:22), may have had a large impact on the timing of dispersal. It is possible that the LVC males were lighter in weight simply <u>because</u> they dispersed earlier than HMH males.

Body Weight and Hypotheses Concerning Dispersal

I concur with most ground squirrel researchers to date in reporting no significant differences between weights of male dispersers and nondispersers at the time of emigration (Slade and Balph 1974, Dunford 1977, Pfeifer 1980, 1982). These findings do not support behavioural hypotheses from which one might expect dispersers to be lighter (Christian 1970, Lidicker 1975, Krebs 1978), heavier (Holekamp 1984a, b, 1986), or heavier and lighter (Bekoff 1977) than other potential dispersers that remained philopatric. They are consistent with observations implicating maternal aggression and yearling competition as proximate causes of Columbian ground squirrel dispersal (Paper 3). Male yearlings emigrated if their pregnant mother or a yearling sister survived to occupy the natal home range. Since dispersal was dependent on familial circumstances rather than on physical or behavioural attributes of the males themselves, it is not surprising that there were no systematic weight differences between dispersers and nondispersers at the time of emigration. Female yearlings competed aggressively to remain philopatric, and all females that dispersed were from multi-female litters (Paper 3); that is consistent with observations that females typically experienced individual weight losses during periods characterized by having most aggressive interactions, and that female nondispersers were heavier than those that emigrated. The existence of lightweight female dispersers suggests that the hypotheses of Christian (1970), Lidicker (1975) and Krebs (1978) may be appropriate for female ground squirrels. As Gaines and McCleneghan (1980) pointed out, the three hypotheses overlap broadly and include a common theme that dispersers are social subordinates.

I agree with Holekamp (1984a, b, 1986) that dispersers can gain extra weight once they emigrate, apparently because they disperse to locations where there is little social pressure and competition for food (Paper 1). Holekamp (1986: 382) thought that she could "predict" an animal's dispersal status based on a combination of weight and other factors such as gender, age, litter size and population density; I believe that the weight portion of her model contributed descriptive rather than predictive power since no weight differences emerged until her juveniles were 9 weeks old, when early dispersers had been living away from natal areas for as much as two weeks. There is little doubt that gender has a powerful influence on dispersal tendencies of birds and mammals (Greenwood 1980, Holekamp et al. 1984, Liberg and von Schantz 1985). Elsewhere, I have elaborated on the role that factors such as gender, litter composition, and population density may play as cues to Columbian ground squirrel dispersal (Paper 3).

Holekamp (1986:385) suggested that natal dispersal "might be so taxing energetically that it does not occur until some critical body mass threshold". However, neither Holekamp nor I found any significant weight losses associated with dispersal. In both studies, male dispersers gained more weight than nondispersers soon after emigrating (Holekamp 1984: Fig. 4, present study: Fig. 2.1); as mentioned earlier, midseason weight losses recorded in the present study appeared to be associated with remaining on study sites. I found that male dispersers gained significantly more weight than nondispersers by the end of the season; Holekamp (1984: Fig. 4) reported the same for S. beldingi although her final sample, based on only two dispersers and three nondispersers, suggested that the weight advantage was lost before hibernation (but see Holekamp 1986: Fig. 5). Differential weight gain provided yearling male Columbian ground squirrels with a trade-off situation: while it was slightly more dangerous to disperse

(Paper 1), those that emigrated were as much as 100 g heavier than nondispersers by fall. Additional size and weight might be an advantage in terms of recruiting successfully from edge locations into established ground squirrel populations (Murie and Harris 1984). Heavy individuals may be physiologically capable of breeding sooner (Morton and Gallup 1975, Holekamp 1984b) which would also increase their potential for reproductive success.

Advantages accruing to female dispersal are not clear: emigrants lose benefits of philopatry, such as familiar burrows and the presence of kin, that could increase female reproductive success (Sherman 1977, 1981, Greenwood 1980, Waser and Jones 1983), and still gain no weight advantage over nondispersers. This lack of alternative benefits may explain why females compete aggressively to remain philopatric (Paper 3).

Dispersers and nondispersers of both sexes attained maximum weights at the same time and hibernated soon after, i.e. no group remained at risk longer in order to continue gaining weight. Maximum weights of nondispersers were relatively consistent among years and sites, probably because study sites offered similar feeding opportunities. The variability among maximum weights of dispersers was likely related to their settling in pockets of edge habitat which had different vegetation, microclimate and ground squirrel density from that occurring on study sites (Paper 1).

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Table 2.1 - Mean weights (grams ±SE) of male yearlings on 'Juvday', the date of initial juvenile emergence. Sample sizes are given in parentheses.

Group	Site				Year			All
	1	2	3	4	1982	1983	1984	
Dispersers	443±13 (11)	454±9 (9)	450±15 (3)	421±17 (8)	* 396±11 (7)	457±7 (18)	449±13 (6)	441±7 (31)
Nondispersers	437±20 (3)	425±5 (2)	446±25 (6)	415 (1)	425 (1)	433±16 (6)	446±25 (5)	438±13 (12)
All	441±11 (14)	449±8 (11)	447±16 (9)	421±15 (9)	** 399±10 (8)	451±7 (24)	448±13 (11)	440±6 (43)

* Weights of dispersers differed significantly among years (ANOVA, $P<0.05$).

** Weights of male yearlings differed significantly among years (ANOVA, $P=0.004$).

Table 2.2 - Mean maximum weights (grams ± SE) attained by male Columbian ground squirrels within their yearling summer. Sample sizes are given in parentheses.

Group	Site				Year			All
	1	2	3	4	1982	1983	1984	
Dispersers	616±25 (9)	630±25 (6)	640±10 (2)	572±20 (8)	* 558±17 (6)	630±17 (16)	585±22 (3)	607±13 (25)
Nondispersers	555±30 (3)	555±15 (2)	550±24 (4)	550 (1)	525 (1)	555±19 (6)	557±9 (3)	552±12 (10)
All	600±21 (12)	611±22 (8)	580±24 (6)	570±18 (9)	+ 554±15 (7)	609±15 (22)	571±12 (6)	592±11 (35)

* Weights of dispersers differed significantly among years (ANOVA, $P<0.05$).

\+ Differences in weights of male yearlings approached significance among years (ANOVA, $P=0.08$).

Table 2.3 - Mean dispersal weights (grams ±SE) and mean dispersal dates (relative to Day 50, "Juvday") for male yearlings leaving study sites during 1982-4. Dates are in bold type. Sample size in parentheses.

Year	Site 1	Site 2	Site3	Site 4	•All sites +
1982	416±11 **54±4** (4)			437±23 **67±1** (3)	425±11 **59±10** (7)
1983	476±10 **48±2** (5)	513±29 **66±6** (6)	537±72 **64±12** (2)	465±15 **61±2** (4)	494±14 **60±3** (17)
1984	422±7 **60±5** (2)	463±17 **55±2** (3)	- - (0)	500 **58** (1)	456±14 **57±2** (6)
•All years	445±11 **52±2** (11)	497±21 **62±4** (9)	537±72 **64±12** (2)	459±13 **63±2** (8)	470±10 **59±2** (30)

• Dispersal weights differed among years and sites ($P<0.05$).

+ Differences in dispersal dates among sites approached significance ($P<0.10$).

Table 2.4 - Mean dates (± SE) on which male yearlings attained their maximum weights (Day 50 = the day of juvenile emergence). Sample sizes are given in parentheses.

	Site				Year			
Group	1	2	3	4	1982	1983	1984	All
Dispersers	92±3 (9)	94±4 (6)	93±8 (2)	91±3 (8)	90±4 (6)	93±2 (16)	91±6 (3)	92±2 (25)
Nondispersers	98±5 (3)	85 (2)	89±2 (4)	85 (1)	88 (1)	93±3 (6)	86±1 (3)	90±2 (10)
All	93±3 (12)	92±3 (8)	91±8 (6)	91±3 (9)	90±3 (7)	93±2 (22)	89±3 (6)	92±1 (35)

Table 2.5 - Mean weights (grams ±SE) of female yearlings on 'Juvday', the date of initial juvenile emergence. Sample sizes are given in parentheses.

Group	Site				Year			All
	1	2	3	4	1982	1983	1984	
Dispersers	381±19 (7)	- (0)	- (0)	325 (1)	* 390 (1)	445±15 (2)	343±11 (5)	374±18 (8)
Nondispersers	405±10 (9)	452±7 (2)	416±37 (4)	395±10 (7)	* 381±6 (6)	434±14 (9)	398±13 (7)	408±9 (22)
All	395±10 (16)	452±8 (2)	416±37 (4)	386±12 (8)	** 382±5 (7)	436±12 (11)	375±12 (12)	399±8 (30)

* Weights of dispersers and nondispersersers differed significantly among years (ANOVA, P<0.05).

** Weights of female yearlings differed significantly among years (ANOVA, P<0.01).

Table 2.6 - Mean maximum weights (grams ±SE) attained by female Columbian ground squirrels within their yearling summer. Sample sizes are given in parentheses.

Group	Site				Year			
	1	2	3	4	1982	1983	1984	All
Dispersers	498±23 (6)	- (0)	- (0)	465 (1)	* 515 (1)	595 (1)	469±13 (5)	494±20 (7)
Nondispersers	524±10 (9)	557±17 (2)	536±11 (4)	506±12 (6)	** 493±10 (6)	535±9 (9)	540±8 (6)	525±7 (21)
All	514±11 (15)	557±17 (2)	536±11 (4)	500±12 (7)	* 496±9 (7)	541±10 (10)	508±13 (11)	517±7 (28)

* Weights of all yearlings, and of dispersers alone, differed significantly among years (ANOVA, $P<0.05$).

** Weights of nondispersers differed significantly among years (ANOVA, $P<0.01$).

Table 2.7 - Mean dates (±SE) on which female yearlings attained their maximum weights relative to Day 50, the day of initial juvenile emergence. Sample sizes are given in parentheses.

Group	Site				Year			
	1	2	3	4	1982	1983	1984	All
Dispersers	90±2 (6)	- (0)	- (0)	86 (1)	85 (1)	87 (1)	91±3 (5)	90±2 (7)
Nondispersers	92±4 (9)	93±7 (2)	87±1 (4)	95±3 (6)	93±2 (6)	95±4 (9)	88±2 (6)	92±2 (21)
All	92±2 (15)	93±7 (2)	87±1 (4)	94±3 (7)	92±2 (7)	94±4 (10)	90±2 (11)	92±1 (28)

Fig. 2.1. A sample growth curve typical of individual yearling Columbian ground squirrels. Yearling weights were compared on: 1) the day of initial juvenile emergence ("Juvday"); 2) dispersal dates of emigrants; and 3) when individuals achieved their maximum weight within the yearling summer. The solid vertical line represents a fixed date (Juvday was always assigned Day 50), whereas the other weights and dates depended on attributes of individual yearlings.

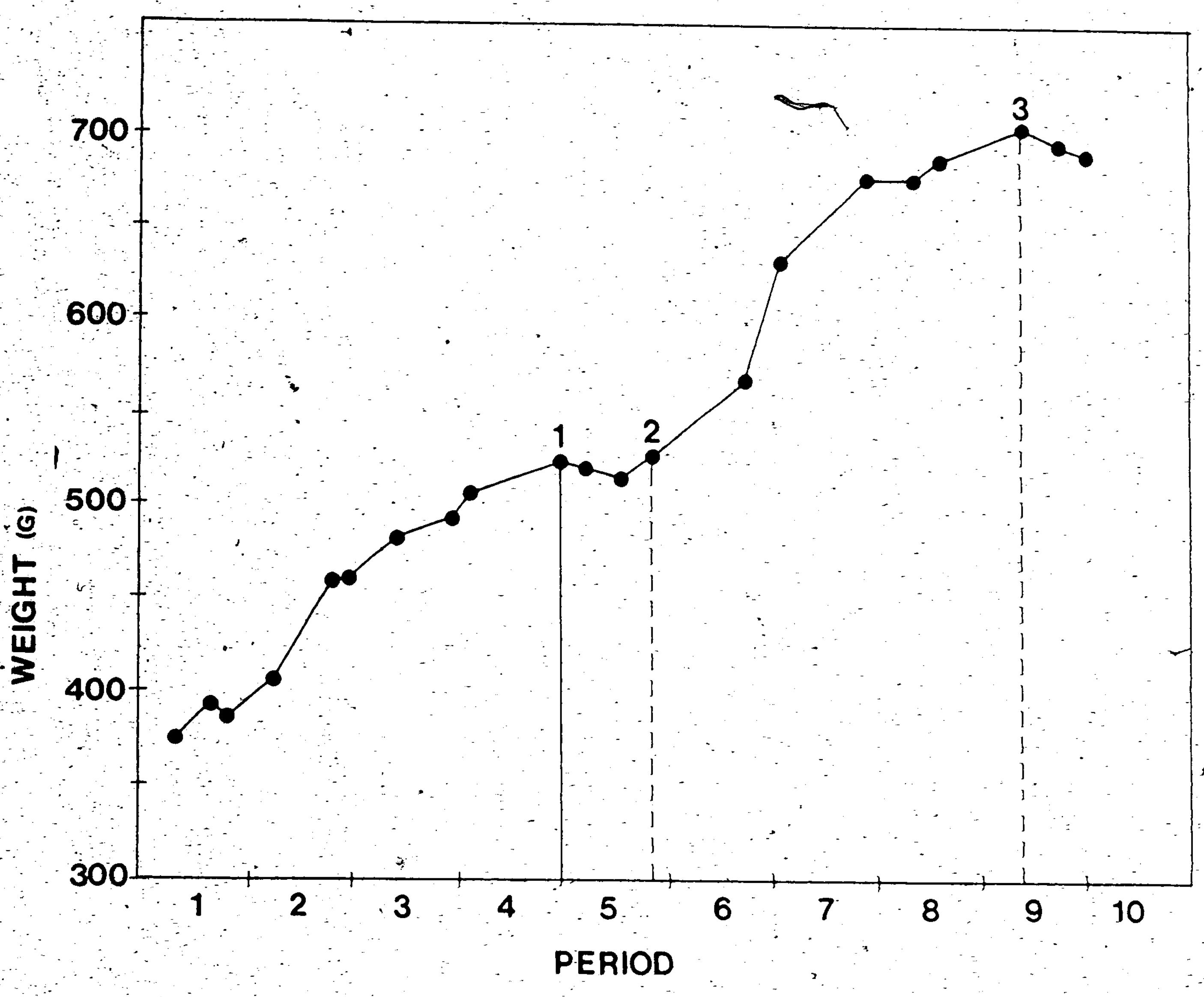
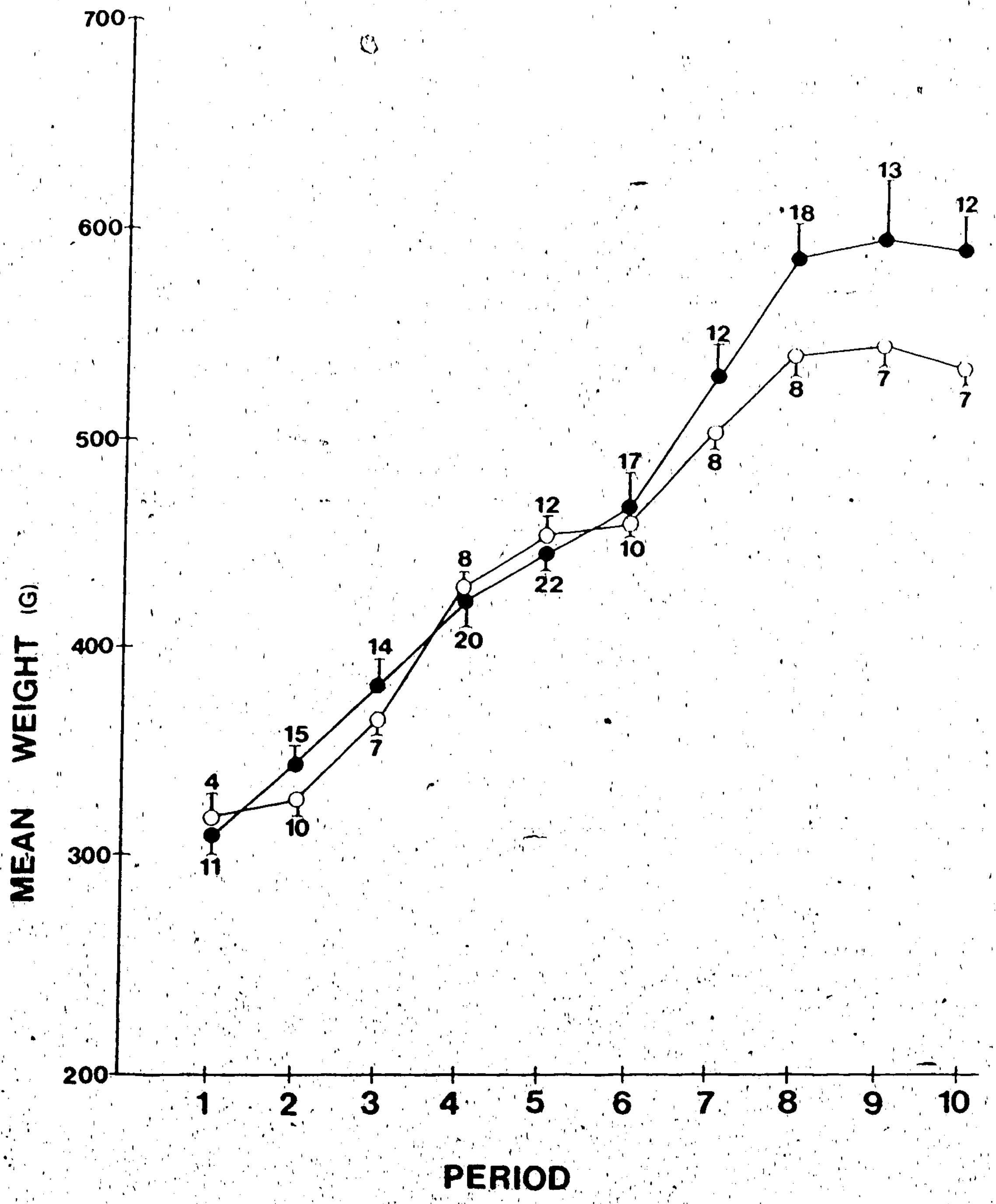

WEIGHT (G)
700
600
500
400
300
PERIOD
1
2
3
4
5
6
7
8
9
10
1
2
3

Fig. 2.2 - Mean body weights of male dispersers and nondispersers for each 10-day period during the yearling summer. Vertical bars represent standard errors and numbers represent sample sizes for dispersers (solid circles) and nondispersers (open circles).


MEAN WEIGHT (G)
700
600
500
400
300
200
PERIOD
1
2
3
4
5
6
7
8
9
10
4
11
15
10
14
7
8
20
12
22
17
10
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8
18
8
13
7
12
7

Fig. 2.3 - Mean body weights of female dispersers and nondispersers for each 10-day period during the yearling summer. Symbols are as described in Figure 2.2.

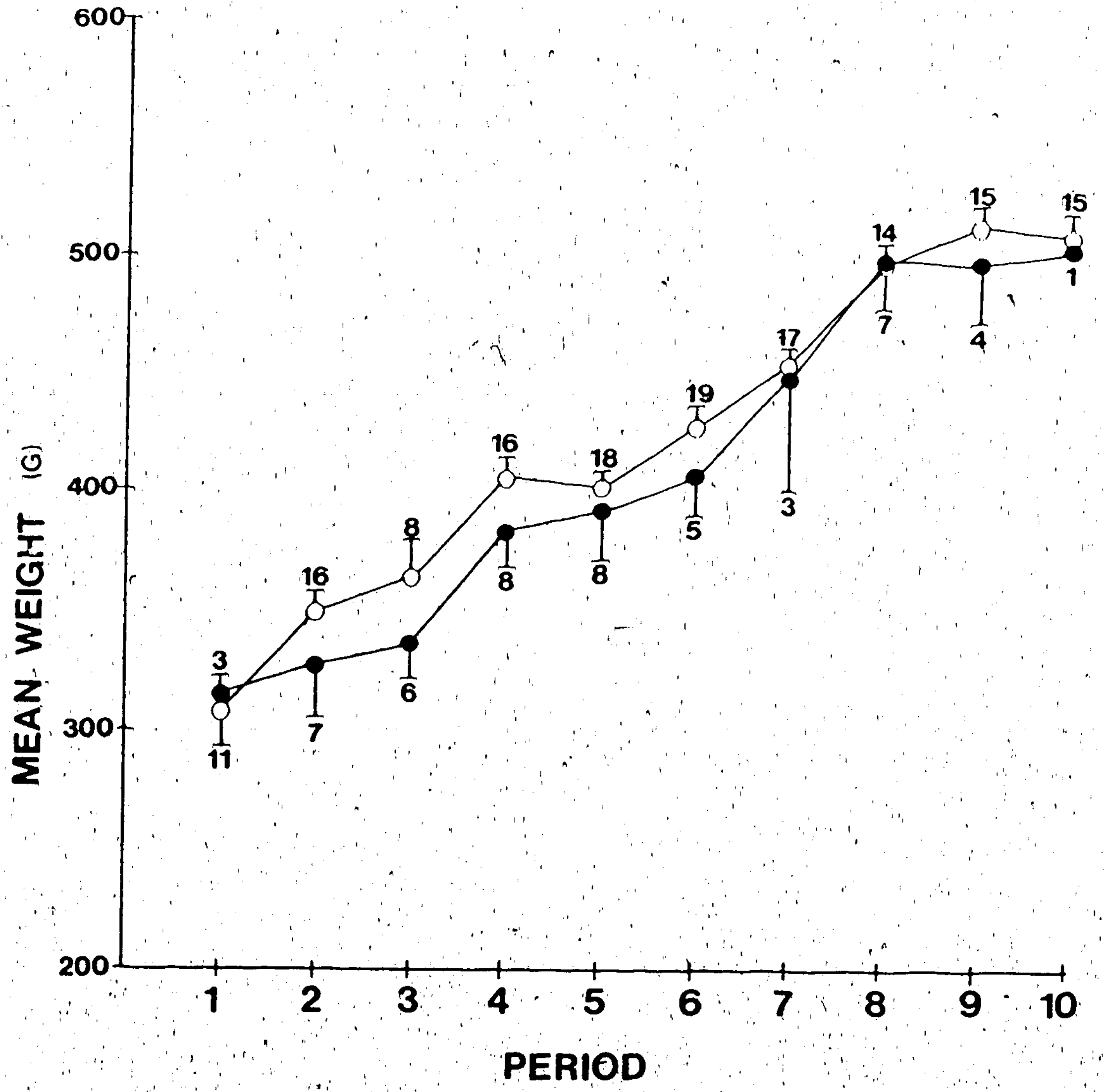

MEAN WEIGHT (G)
600
500
400
300
200
PERIOD
1
2
3
4
5
6
7
8
9
10
3
11
16
7
8
6
16
8
18
8
19
5
17
3
14
7
15
4
15
1

Fig. 2.4A Dispersal weights of male yearlings versus their dispersal day relative to initial juvenile emergence (Day 50). Symbols indicate yearlings from Site 1 (triangle), Site 2 (circle), Site 3 (square) and Site 4 (X); solid symbols represent yearlings from sedation treatments.

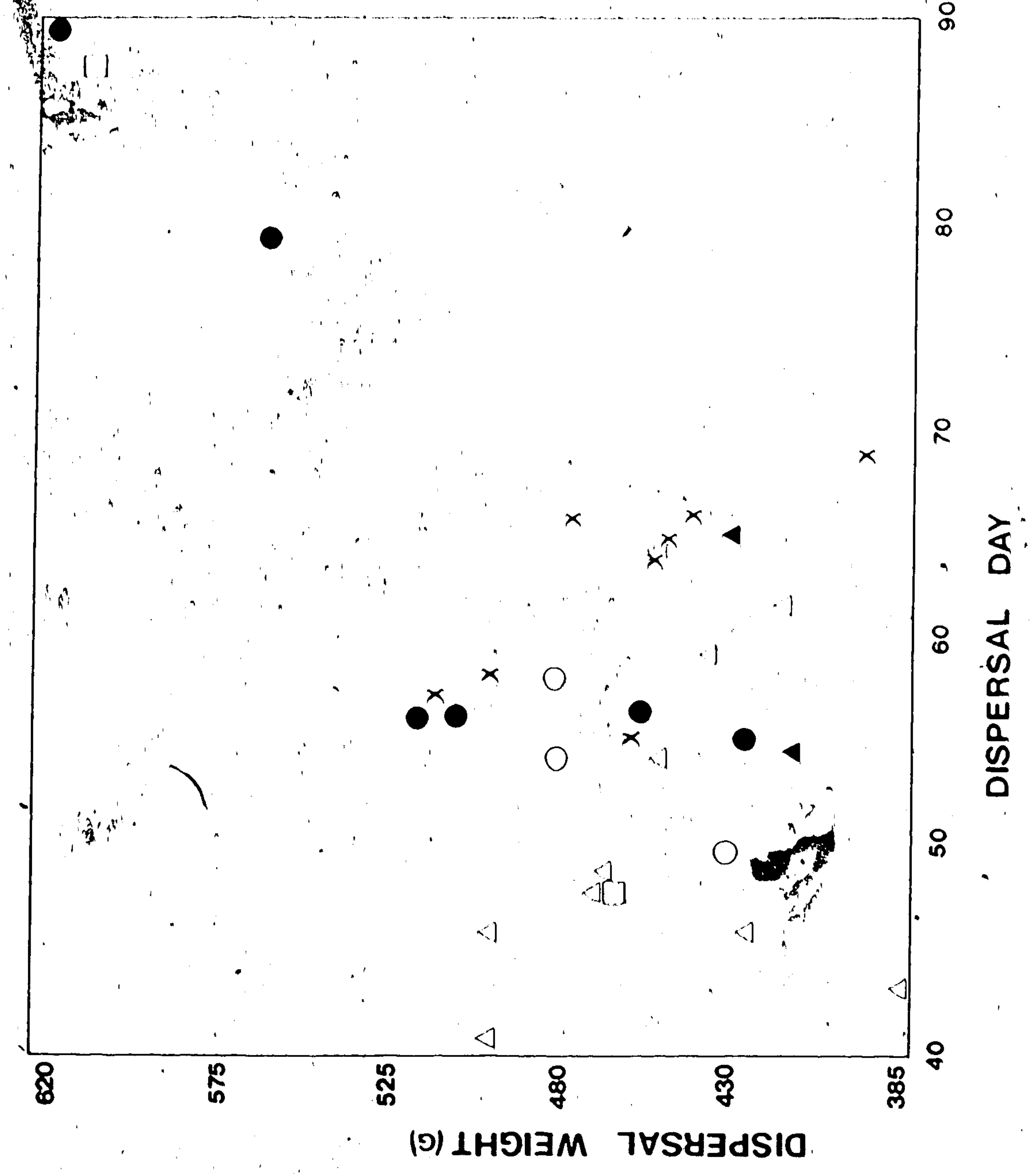

DISPERSAL WEIGHT (G)
620
575
525
480
430
385
DISPERSAL DAY
40
50
60
70
80
90

Fig. 2.5 - Weights of male dispersers on Juvday versus their dispersal days. Symbols as in Figure 2.4.

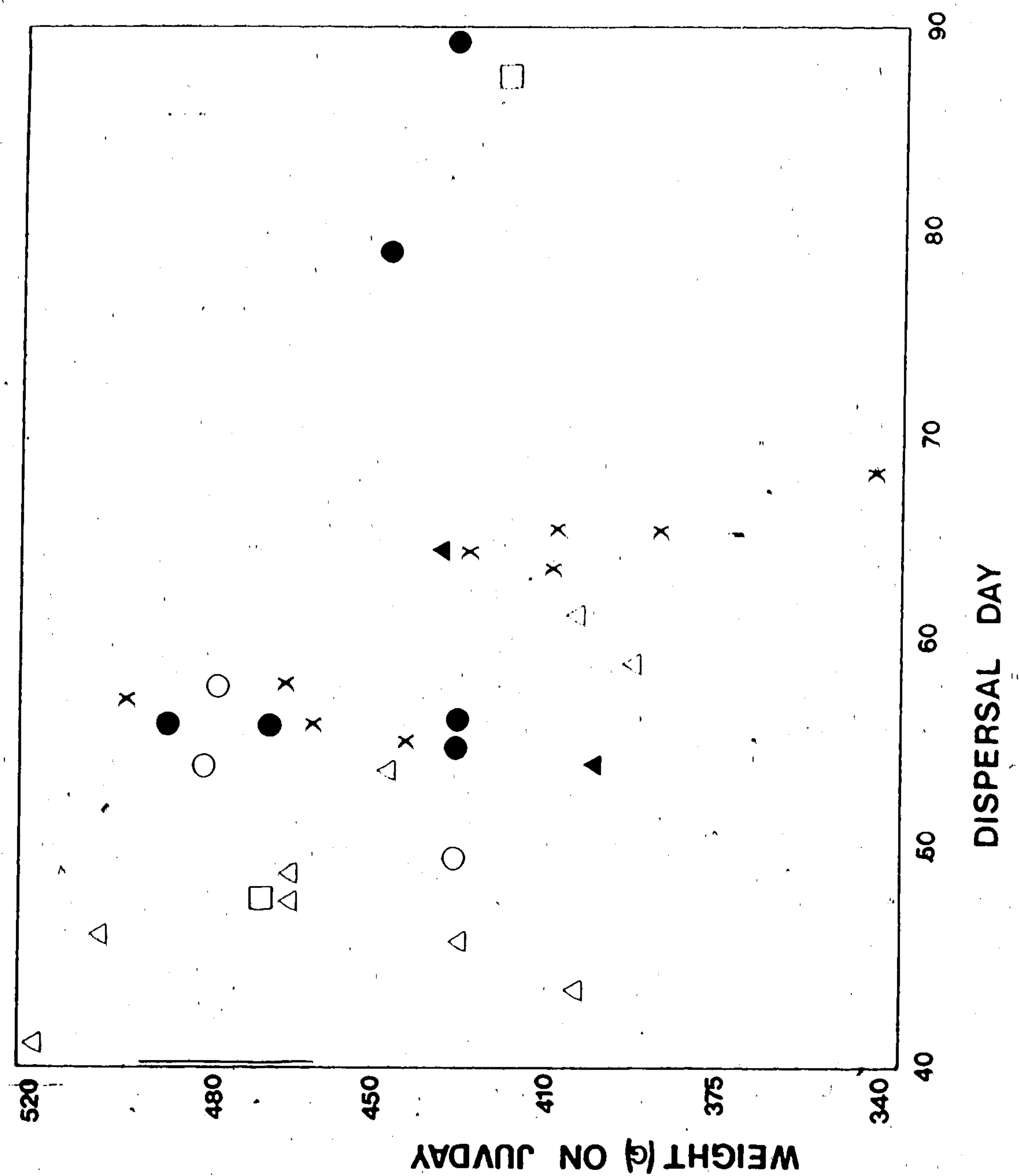
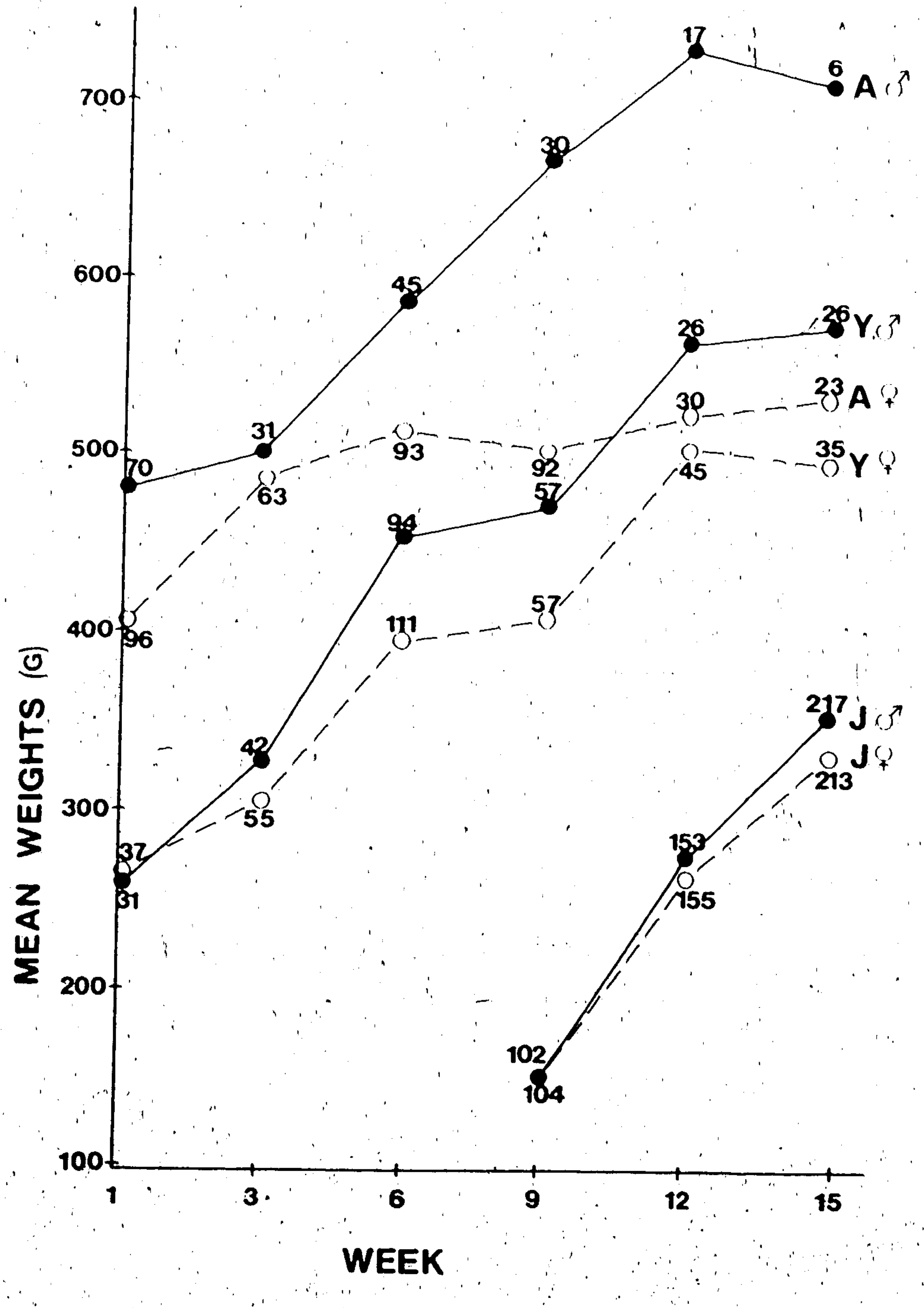

WEIGHT (g) ON JUVDAY
520
480
450
410
375
340
DISPERSAL DAY
40
50
60
70
80
90

Fig. 2.6 - Mean weights of Columbian ground squirrels over a 15-week summer, adapted from Boag and Murie (1981:Table 3). Symbols A, Y and J represent adults, yearlings and juveniles; Numbers are sample sizes from a 7-year study. Juveniles initially emerged at a weight of about 100 g (pers. comm., J.O. Murie).


MEAN WEIGHTS (G)
WEEK
700
600
500
400
300
200
100
1
3
6
9
12
15
A ♂
Y ♂
A ♀
Y ♀
J ♂
J ♀
70
31
45
30
17
6
96
63
93
92
30
23
31
42
94
57
26
26
37
55
111
57
45
35
102
104
153
155
217
213

IV. Paper 3 - PROXIMATE CAUSES OF DISPERSAL IN COLUMBIAN GROUND SQUIRRELS

A. ABSTRACT

The role of aggression as a proximate factor influencing dispersal of yearling Columbian ground squirrels (Spermophilus columbianus) was assessed during 1982-4 using a combination of chemosterilants, sedatives, radio-telemetry, behavioural observation, and trapping. Dispersing yearlings from each of seven reference plots typically emigrated during a two-week interval closely associated with maternal aggression and emergence of juvenile litters on that area; the reproductive cycle (birth of litters, maternal aggression, emergence of litters) was relatively late on three of the reference plots, and yearling dispersal there was correspondingly delayed. Dispersers left significantly later from two plots on which adult females were sedated with acepromazine maleate ("Atravet"). Sterilizing adult females with ethynylestradiol 3-methyl ether ("Mestranol") resulted in low levels of aggression (few chases), and no yearlings dispersed. The Mestranol treatment, and an adults-removed treatment, were applied in 1985 without behavioural observation - again, no yearlings dispersed. It appeared that adult female territoriality associated with maternal aggression and defence of new litters created a social pressure influencing yearlings to leave their natal home ranges. The matter of

which yearlings dispersed seemed to be determined by circumstances within each maternal home range: females dispersed only if they were outcompeted by aggressive sisters; males dispersed unless they encountered little aggression from close female kin (i.e. no sisters alive and the mother was dead or not pregnant). The consequences of Columbian ground squirrels responding to aggression as a proximate cue are considered in view of current dispersal theory.

B. INTRODUCTION

Most species of ground squirrels (Tribe Marmotini, Genus Spermophilus) disperse as juveniles, at the end of their first summer (Holekamp 1984a). Columbian ground squirrels (S. columbianus) disperse as juveniles from Washington farmland (personal communication J. Murie, B. Weddell) but delay dispersal until the yearling summer in the foothills of Alberta (Boag and Murie 1981a). This intraspecific difference may be an adaptation to the constraints of a shorter growing season which does not permit juvenile S. columbianus of higher altitudes and latitudes time to disperse, become established, and gain sufficient weight before obligate hibernation.

A similar pattern exists among species of marmots (Tribe Marmotini, Genus Marmota) when arranged from low to high altitude: woodchucks (M. monax) disperse as juveniles; yellow-bellied marmots (M. flaviventris) typically disperse as yearlings; Olympic marmots (M. olympus) disperse in their third summer of life (Barash 1973). Marmots also display intraspecific differences in dispersal ages: yellow-bellied marmots from low, medium, or high altitude populations have been reported to disperse as juveniles (Webb 1981), yearlings (Armitage and Downhower 1974, Webb 1981), or two-year-olds (Johns and Armitage 1979), respectively. The age at which marmots disperse is thought to be affected by environmental constraints such as length of the growing season, and morphological factors such as the weight of potential dispersers relative to adult body weight (Barash 1973). Most authors agree that in cases of delayed dispersal, adult marmots are amicable or tolerant toward young marmots (Barash 1973, Armitage and Downhower 1974, Downhower and Armitage 1981, Brody and Armitage 1985). Aggression is often cited as the means by which delayed dispersers are finally encouraged to emigrate at an appropriate age or weight (Downhower 1968, Armitage 1974, Downhower and Armitage 1981) although Webb (1981) thought that aggression was only necessary in patchy habitat since high transit difficulty and low desirability of surrounding areas increased the reluctance of young marmots to emigrate.

Aggression has been rejected as a proximate factor affecting dispersal of ground squirrels (Dunford 1977, Holekamp 1984a); however, the delayed dispersal of S. columbianus is similar to that of marmot species and may employ a cue not required by ground squirrels which emigrate as juveniles. Festa-Bianchet and King (1984) reported that the disappearance (dispersal plus mortality) of yearling S. columbianus from a high density site in closed habitat coincided with high levels of adult female aggression directed at yearlings. The purpose of this paper is to establish whether aggression (particularly maternal aggression) acts as a proximate factor prompting dispersal of yearling Columbian ground squirrels living in open habitat. To this end, behavioural observations were made on several populations of S. columbianus living in continuous ground squirrel habitat. Adult females on some sites were observed under natural conditions whereas other adult females were sedated to decrease their aggression, or sterilized to eliminate reproduction and associated maternal aggression. Yearlings were radio-collared so that dispersal could be distinguished from mortality.

C. METHODS

Four study sites, each approximately one hectare in area, were established on a private ranch 10 km southwest of Chain Lakes Provincial Park in southwestern Alberta (50 06' N, 114 33' W, elevation 1400 m). All sites were in open pasture occasionally grazed by horses and cattle. Sites 1 and 2 were in flat terrain with good visibility in all directions; Site 3 was flat but flanked by bushes to the south and east; Site 4 sloped to the west where it abutted a strip of trees and shrubs bordering an intermittent stream.

Further details of vegetation and terrain have been described elsewhere (Paper 1).

During May-August 1982, Columbian ground squirrel populations of Sites 1 and 4 were trapped and observed[1], and yearlings of both sexes were radio-collared and tracked using portable telemetry equipment. During April-August 1983, Sites 1, 3 and 4 served as reference areas as described above; Site 2 was operated in an identical fashion to the other sites except that during 5 to 20 June, adult females were sedated twice daily with acepromazine maleate ("Atravet", at a dosage of 2 mg/kg body weight) to reduce aggression; this treatment was modelled after Wirtz (1970) and Barash (pers. comm.) and was first used with captive ground squirrels under the counsel of Dr. R. McKay[2]. Atravet granules were ground to a fine powder using a mortar and pestle, mixed with peanut butter to form a uniform putty, and shaped into peanut-butter balls of measured volumes. Initially, drugged peanut-butter balls were placed at the burrows of adult females. After a week, some nontarget animals learned to anticipate and steal the balls, so it became necessary to detain target animals in livetraps for approximately 15 minutes until sedatives were delivered and consumed. In Summer 1984, Sites 2 and 4 were reference areas, adult females on Site 1 were sedated during 19 May to 19 July[3] (with up to 6 mg Atravet per kg body weight), and

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[1] Site 4 was not watched by a fulltime observer until 1984.

[2] Director of Bioscience Animal Services, University of Alberta.

adult females on Site 3 were temporarily sterilized by forcefeeding them ethynylestradiol 3-methyl ether (1 mg suspended in 1 ml peanut oil) to block pregnancy and postpartum aggression (Goulet and Sadleir 1974).

Ground squirrels were trapped in National livetraps (15X15X50 cm) baited with peanut butter. Captured animals were examined for wounds and reproductive condition, weighed to the nearest 5 g using a Pesola spring scale, eartagged with serially numbered metal tags, and given unique numbers or letters on their pelage with Lady Clairol blue-black hair dye. All yearlings were further identified by attaching a coloured disc to the eartag in one ear. Most animals were trapped and weighed weekly, including yearlings that had dispersed to distant locations. "Wounds" were recent (not noted previously and not including scars) punctures of the skin on the face, body or tail that appeared to have been rendered by ground squirrel bites; facial wounds were carefully distinguished from cuts occasionally self-induced by naive animals struggling within livetraps.

Study sites were subdivided with rows and columns of coloured surveyors' flags at 10 m intervals, and ground squirrel activities were watched for a total of 1190 hours between early May and early August of 1982-4. Observations were made from atop a 3-m high platform located on each study area. Sites were "scanned" at 15-minute intervals between 0800-1230 hours for presence, locations and behaviours of ground squirrels. As well, all occurrences of agonistic and cohesive interactions (Pfeifer 1982) were described, with top priority given to behaviours involving yearlings. Agonistic interactions included fights, attacks, chases, run-ats, and displacements (Betts 1976). Chases proved to be the most useful index of aggression since fights among adults and yearlings, and attacks on yearlings by adult females, were rare; run-ats often appeared to involve mistakes in identity among interactors, and displacements were too subtle to be uniformly observed throughout each site and by all observers. Cohesive interactions included play, greeting "kisses", and peaceful proximity within 3 m. Aggressive chases among yearlings were distinguishable from play because the former chases were carried out with great intensity, often involved social signals (bushed tails, growls, squeals), and were frequently coupled with other aggressive behaviours (such as attacks or fights) that went beyond the "rough and tumble" of playful yearlings. A complete list of behavioural categories is given in Appendix 3.

Seventy-five yearlings were radio-collared during spring trapping sessions using modified R-collars designed for this study by AVM Instruments (Appendix 1). Radio-collared yearlings were located at least once per afternoon between May and early August, with additional attention given to animals that were making excursions, dispersing, or establishing themselves at postdispersal locations. Data include descriptions of locations, behaviours, dispersal routes, new habitats and burrows, and details of mortality. Yearlings were radio-tracked every evening after 2100 hours to determine their current sleeping burrows. Precise locations of yearlings within burrow systems was accomplished by holding the portable antenna in a vertical position, decreasing the gain to minimum, and carefully sweeping the area in different directions until the source of the signal was pinpointed. On six occasions that radio-collars were retrieved from burrows after predation (n=4) or removal by squirrels (n=2), the collars were found directly beneath the location indicated by telemetry.

"Dispersers" were yearlings that moved to new sleeping burrows beyond their natal home ranges, whereas "nondispersers" continued to live on natal home ranges and sleep within a few metres of their natal burrows. The shortest move accepted as dispersal involved a yearling male that shifted its sleeping burrow from the middle of a flat study site to a hillside location 62 m away, and altered its movement patterns so that it was no longer seen on the site. Other dispersal moves ranged between 93 m and 980 m. "Dispersal date" was the first day (evening) on which an animal stopped using sleeping quarters in its natal area, provided that it was located alive elsewhere (Paper 1).

Each season was divided into ten 10-day intervals aligned so that the first day of juvenile emergence ("Juvday") was always Day 50, the beginning of the fifth interval. In this way, behavioural periods were attuned to the phasing of the annual cycle. Initial juvenile emergence was highly synchronous across the flat meadow comprising Sites 1-3 and the eastern edge of Site 4, but varied among years, commencing on 21, 14, and 10 June in 1982-4. Most of Site 4 was on a shaded hillside where juvenile emergence was delayed by as much as 10 days compared to the adjacent flat meadow.

The daily "attendance" of each yearling was calculated as the number of 15-minute scans during which the yearling was seen divided by the total number of scans that day. Daily rates of interaction between members of different sex and age classes such as chases of yearlings by adult females, were determined by dividing the sum of chases by the observation period in hours. Daily chases per individual yearling were divided by the number of scans in which each individual was present (not the total observation period) to produce an estimate of the aggression experienced by each yearling while on the study site. Daily figures were then grouped according to 10-day intervals, age-classes, and dispersal status, for specific comparisons. In cases of complex interactions such as reversals or multireversals, each chase in the sequence was scored as a separate event. Core areas, and overlaps of core areas, were computed using the Midas Cartograph program which included the 80% of an individual's locations that were closest to its centre of activity; 80% was chosen as the cutoff point since it eliminated excursions and infrequently used areas, and was consistent with other ground squirrel literature (Davis and Murie 1985, Waterman 1986).

Following the intensive study of 1982-4, I was obliged to reduce ground squirrel populations on the private land I had been permitted to use. During 5-11 May 1985, I removed all adults from Site 2 and repeated the Mestranol treatment using adult females of Site 1. In mid-June, I trapped and observed yearlings of Sites 1 and 2 to assess their dispersal status. I returned again during 14-17 July to assess the dispersal status of all study yearlings and to reduce the population further. Skins, skulls and skeletons of approximately 50 former study animals are available at the Provincial Museum in Edmonton. Digestive organs and internal parasites were collected by Pat Carr and Roger Smith of Brandon University.

D. RESULTS

Reproductive Events and Study Periods

Most litters emerged within 10 days following Juvday although precise emergence dates are not known for some litters due to our preoccupation with yearling dispersal activity at that time. Since the beginning of juvenile emergence was always assigned "Day 50", Period 5 encompassed most juvenile emergence on Sites 1-3. Juvenile litters on the flat portion of Site 4 emerged in step with Site 1 litters, but on the sloped and shaded portion of Site 4, newly emerged juveniles were still found well into Period 6. Thus Site 4 provided delayed and extended reproductive phases compared to the other sites.

Backdating from initial juvenile emergence by 23-26 days (Ferron 1984), the first litters could have been born as early as Days 24-27 of this study. In 1983, four pregnant females captured in flat-meadow habitat near Sites 1 and 2 were detained in cages until they gave birth to their litters on Days 32, 33, 34 and 35. Therefore I believe that Period 3 best represents the study interval associated with birth of new litters on Sites 1-3. Litters on the shaded slopes of Site 4 were born somewhat later, mainly during Period 4.

Population Density of Study Sites

Ground squirrels and burrow locations were distributed fairly evenly throughout Sites 1, 3 and 4. On Site 2, ground squirrels concentrated their activities around a horseshoe-shaped belt of burrows with the result that most of their activities were contained within 0.5 hectare. Thus although a one-hectare area was flagged for Site 2, almost all Site 2 data were generated by squirrels interacting at a high local density (Table 3.1). Densities are reported as the number of resident adults and yearlings per hectare after all animals had emerged from hibernation (Appendix 4). The spring density of each site remained essentially unchanged until mid-June (Period 5) when juvenile litters emerged and dispersers departed. Thereafter, densities were adjusted gradually by predation, immigration and winter mortality, leading to the spring density of the following year. There were no broad temporal trends affecting all sites simultaneously: during 1982-4, spring densities increased on Site 1, decreased on Sites 2 and 3, and remained the same on Site 4.

The Timing of Dispersal

All yearling male dispersers emigrated within a period of approximately seven weeks (Fig. 3.1). With the exception of three late dispersers (two from sites on which adult females were sedated), male yearlings emigrated between Days 42-69, a period of less than four weeks. In a given year, the dispersers of any one site typically left within two weeks, at approximately the time of juvenile emergence on that site. Site 1 males usually began dispersing before Juvday except in 1984 when resident adult females were sedated. Similarly, dispersal was delayed on Site 2 when adult females were sedated in 1983; three dispersers left on 21 June (Day 57) when the sedation treatment was interrupted by the temporary presence of some prize bulls. In combination, yearling males from the two sedation treatments left significantly later than those from the same plots during reference years (n=15, T=2.67, P=0.04, T-test contrast). Yearlings from Site 4 (the delayed reproduction site) tended to be late dispersers, although this site was always a reference plot. These animals and the single late disperser of 1983 from Site 1 will be discussed in greater detail in subsequent sections.

Yearling female dispersers emigrated within a period of 15 days (Day 45-60) centred on juvenile emergence. Only on two occasions did more than one female disperse from the same site within a season; of these, the greatest interval between the departure of first and last dispersers was 6 days.

Numbers of Dispersers, Population Density, and Timing of Dispersal

During Summers 1982-4, 74% (31/42) of radio-collared yearling males and 31% (9/29) of radio-collared yearling females dispersed. Four yearlings (3 males, 1 female) that were killed by predators before they could be classified as dispersers or nondispersers were not included in these numbers. Male dispersal from different sites ranged from 60-100% (Table 3.2), with the exception of 1984 Site 3 (the Mestranol treatment) from which no yearlings dispersed. Female dispersal ranged between 0-67% with all dispersing females originating on Sites 1 and 4.

The relationship between population density and the percentage of yearling males dispersing from each site approached significance (r=0.51, P=0.08). On most sites, male dispersal was a rough reflection of trends in population density (Tables 3.1 and 3.2). For example, spring population density on Site 4 remained the same during 1982-4, and 80-100% of the yearling males dispersed each year. Spring density increased throughout 1982-4 on Site 1 and the percentage of yearling males dispersing increased from 80% to 100%, but the middle year (62% dispersal) was lower than would be expected from a direct relationship between density and dispersal. Yearling female dispersal on Site 1 increased in step with population density but this is not significant in view of small sample size (r=0.92, P=0.26, n=3). On Site 4 where spring densities remained stable, either zero or one yearling female dispersed each year.

Timing of dispersal was not a function of population density. There was no significant correlation between mean (r=0.28, p=0.27) or median (r=0.27, p=0.12) dispersal dates and population densities of the seven reference plots (Tables 3.1 and 3.3); the three treatment plots were excluded because dispersal there was artificially prevented (Mestranol plot) or delayed (sedation plots). Probabilities approached significance largely because the delayed reproduction site - from which dispersal was also delayed - had a relatively high density of 30 adults and yearlings per hectare during 1982-4. Mean and median dispersal dates on Site 4 varied by 8 and 7 days, respectively, despite the unchanging spring population density. Mean (and median) dispersal dates for Site 1 female dispersers were Days 45, 52 and 52 during 1982-4 although population density increased steadily during that interval.

Treatment of Juveniles and Yearlings Within Maternal Home Ranges

When juveniles first emerged, they spent much of their time playing and feeding within a few metres of their natal burrows. Mothers were very tolerant of their offspring, but usually discouraged nursing with a shove or avoidance. Gradually, juveniles extended their travels and began to trespass on other home ranges, occasionally eliciting a chase from an adult or yearling. Mothers became less protective of their offspring and wandered off to feed, but they still rushed back to the natal area when their offspring were chased by other adults. Juveniles were thus tolerated and protected within their mother's home range. Late in the season, juveniles were known to make excursions hundreds of metres beyond their natal burrows, but they returned to sleep and hibernate with siblings in or near their natal burrow.

Upon spring emergence, surviving offspring (now yearlings) were still within their mother's home ranges. They sunbathed, fed and played in the vicinity of their natal burrows and were greeted and tolerated by their mothers. Gradually social tensions increased. Mothers broke up yearling play, and yearlings began to be chased by adults whenever they attracted attention to themselves by moving quickly or playing. Spiral chases were seen in which pursued yearlings circled back toward familiar burrows but were not allowed to remain there. Sometimes yearlings zigzagged back and forth, chased away by their mothers and back by other adults. By Period 5, all yearling play had stopped. Dispersers and nondispersers alike made excursions and often spent little time on study sites. Yearlings that were present tended to be in pockets of space between home ranges, watching for and avoiding adults.

There were exceptions to the above. On the 1984 Mestranol Site (no reproduction), adult females continued to tolerate their yearlings in close proximity throughout the season, even greeting and playing with them on occasion. Adult females that did not become pregnant on reference plots (n=2) also remained amicable with their yearlings.

General Levels of Chasing by Adult Ground Squirrels

On every site, adult females chased other adult females, adult males, resident yearlings, and transient yearlings. Numbers of chases directed at these groups are illustrated for the 1984 Site 2 reference plot (Fig. 3.2) but the following statements are true of all sites. Adult females typically chased other adult females most often during Period 4 which corresponded to late lactation. Adult males were not chased to any great extent, although there was usually a slight increase during Period 4. Resident yearlings were chased most often during Period 3 - a time of birth and early lactation. Throughout the summer, but especially in Periods 3 and 4, nonresident yearlings appeared in scans; they were recognizable by their size, lack of body marks, hopping-and-looking gait (Paper 1), and transitory appearance on study sites. Total female chases - the sum of chases directed at yearlings, adult females and adult males - typically peaked during late lactation in Period 4. The following two sections will focus on adult female chases directed at adult females and resident yearlings, since interactions among these groups make up the majority of chases and reflect maternal aggression.

Adult males were most aggressive early in the season, in conjunction with spring breeding. Rates of chases directed at yearlings were low (less than 30% of total chases by adult females) and did not appear to be associated with the midseason departure of yearling dispersers.

Chases Among Adult Females

Chases among Site 1 adult females peaked during Period 4 in 1982 (Fig. 3.3). Site 1 was again a reference treatment the following year, but female/female chases peaked during Period 5. In 1984, when adult females were sedated, there was a depression in rates of chasing during Period 4; the value for Period 6 was inflated by the fact that we missed drugging on Day 65 and levels on that day rose to 4 times normal. Site 1 density increased each year through 1982-4 and may account in part for greater levels of chasing; there was a significant correlation between peak chases on study sites[3] and population densities ($r=0.66$, $P=0.05$, $y=0.08X-0.57$). **Chases per resident** adult female were 0.09, 0.15 and 0.15 (sedated) during the three summers. In 1984, nonresident adults were attracted to the site by the twice-daily presence of peanut butter and may have been partly responsible for increased aggression on Site 1. Although sedated adult females appeared slightly wobbly and lethargic for several hours after being fed drugged peanut butter, they still gave chase to strange animals in their vicinity.

During both years that Site 2 was observed, the peak in chases among adult females occurred in Period 4 (Fig. 3). There were fewer chases per hour when Site 2 was a sedation sit[illegible]n 1983, despite greater population density (Table 3.2). At the height of aggression in Period 4, each adult

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[3] The Mestranol site was excluded because chases were greatly reduced by the treatment.

female was involved in 0.26 chases per hour when sedated compared to 0.59 chases per hour when not sedated.

Adult females of 1983 Site 3 (reference) chased other adult females most often during Period 4 (Fig. 3.4). Levels of chasing were much reduced in 1984 when Site 3 was a mestranol plot, and there was no peak coinciding with lactation. Site 4 (reference) was not watched by a fulltime observer until 1984. Then chasing among adult females peaked during Period 5 in conjunction with the relatively late juvenile emergence there.

Chases of Resident Yearlings by Adult Females

Adult females chased resident yearlings most often during Period 3, although there were exceptions on some sites (Fig. 3.5 and 3.6). When Site 1 was a reference plot during 1982-1983, peak chases of yearlings by adult females took place in Period 3, with higher levels of chasing in the year of higher density. When Site 1 adult females were sedated in 1984, the peak of yearling chases was delayed to Period 4 and the rate of chasing was reduced. Peak chases of Site 2 yearlings occurred during Period 3 in both years (Fig. 3.5). There were more chases per hour on the 1983 sedation plot than on the 1984 reference plot but this is likely associated with greater densities; the correlation of peak chases on study sites (excluding the Mestranol treatment) and population densities approached significance (P=0.13, r=0.49). Peak rates per adult female on Site 2 averaged 0.27 and 0.41 on sedation and reference plots, respectively.

The 1983 Site 3 (reference) yearlings were chased most often during Period 3, and levels declined gradually thereafter (Fig. 3.6). The same site in 1984 (Mestranol treatment) had low levels of chases that declined during Period 3. On the 1984 Site 4 (reference) plot, levels of yearling chases changed gradually, but were highest during Periods 3, 4 and 5.

The number of times that adult females chased various categories of yearlings before Juvday were compared, since after this date an increasing number of yearlings were absent. No significant differences were found between numbers of chases directed at males and females (G=0.125, P=0.72), or at dispersers and nondispersers (G=0.021, P=0.88), as yearlings were cleared from the vicinity of natal burrows.

Attendance, and Chases of Individual Resident Yearlings

Yearling "attendance" during scans, and hourly rates of chases directed toward individual yearlings by adult females, varied seasonally and fluctuations were most pronounced under conditions of high density. Initially, 1984 Site 2 yearlings were observed in approximately 70% of all scans (Fig. 3.7); the remaining time was spent underground or making brief excursions. Beginning with Period 4, there was an increase in hourly rates of adult female chases directed at yearlings on Site 2 and an associated decline in yearling attendance during scans. Dispersers (three males) were seen in only 20% of scans and had disappeared from the site by Period 6 (except for occasional sightings of dispersers returning to "visit" briefly). Nondispersers (two males and one female) also declined in attendance, and appeared in only 20-30% of scans between Periods 5 and 8 although they continued to sleep in close proximity to their natal burrows. By Periods 9 and 10 when levels of chasing were much reduced, nondispersers were seen in approximately 50% of all scans.

In 1983, Site 2 adult females were sedated twice daily. The single nondisperser, yearling female #16, lived in a burrow complex with two adult females and was chased frequently (Fig. 3.8) until she shifted her sleeping burrow slightly; she lowered her daytime attendance until late in the season when levels of chasing diminished, and then resumed onsite activity similiar to that of spring. The five dispersers (males) did not share burrows with adult females and were chased at low levels; they gradually decreased attendance, finally dispersing in Periods 5 to 8.

In 1983, Site 1 was a reference plot of below-average density. The five nondispersers (three females, two males) were chased infrequently and their attendance varied little throughout the season (Fig. 3.9). The five dispersers (three females, two males) were chased more frequently during Periods 5 and 6 because two returned to 'visit' their natal sites, and appeared to be treated as intruders by resident females.

In 1984 when Site 1 was a sedation plot of high density (Fig. 3.10), there were more chases of yearlings than in the previous year, and the peak was delayed compared to adjacent Site 2 (Fig. 3.7). The six dispersers (four females, two males) decreased their attendance and emigrated by the end of Period 6, although one yearling female (#73) continued to visit until Period 9. Both nondispersers (females) decreased their attendance until chases declined in Period 8. The peak of chases and attendance associated with nondispersers in Period 6 was caused by a yearling female that moved to a burrow 630 m away during Period 5 but continued to visit her natal site during Periods 6-8, until she re-established herself in Period 8. Another yearling female made a series of visits back to Site 1 but was chased by adult females and her nondispersing sister, and did not re-establish on her natal site.

Female Defence of Natal Burrows

As females became aggressive during Period 3 (birth of litters) they chased any animals that approached the area of their natal burrows, including their own yearlings. Half of all adult-female chases of yearlings before Juvday were mothers chasing their yearlings (147/303 chases on Sites 1 and 2 during 1983-4); mothers did not chase their male offspring more than females (G=0.002, P=0.96) or their dispersing offspring more than nondispersers (G=1.32, P=0.25). Here I present a detailed example describing an adult female (#77) and her five yearlings (females #2, #9, #73; males #5, #7) on Site 1 in 1984. In Period 2, #77 was tolerant of her yearlings. She allowed them in close proximity, greeted them occasionally, and permitted them to use all burrows. They lounged and played within their mother's core area, slept near their mother's burrow, and explored surrounding areas with little reaction from other ground squirrels (Fig. 3.11A). During this interval, #77 was involved in no chases. In Period 3, #77 chased six adults that approached her natal burrow. These chases were not random but effectively directed intruders away from the vicinity of her new litter. Her yearlings were still tolerated in close proximity until Day 38 when she began to chase them away from the natal burrow. Within the first two days of Period 4, #77 chased her yearlings 11 times; they began to avoid her and changed their home ranges accordingly (Fig. 3.11B). The adult female spent most of her time close to the natal burrow, and was involved in only two chases with other adults. Two juveniles emerged on Day 51. Female #77 expanded her travels to chase her own yearlings 7 times in the first three days, while she chased neighbouring adults 11 times, occasionally being chased herself at the edge of her territory. In Period 6, yearling female #2 was becoming established adjacent to #77's home range, yearlings #5 and #7 were spending much of their time making excursions, #9 had already dispersed and #73 was avoiding both her mother and #2. The mother disputed a border with her daughter (#2) once, chased five adults away, and ran after three juveniles that were not her own. By Period 8, all of #77's yearlings had dispersed except #2; this yearling now stood her ground against all squirrels near her burrow. The mother ran at #2 once and chased four adults (two nonresidents). After Period 8, #77 tolerated other ground squirrels in close proximity.

The above scenario describes a typical pattern of activities that occurred within maternal home ranges, except that the events happened relatively late on Site 1 in 1984 (Figs. 3.3 and 3.5). In general, the core areas of yearlings overlapped a large portion of their mother's core area in Period 2, decreasing in Periods 4 and 5 at the time of peak maternal aggression (Table 3.4). Overlap associated with yearling males (all males with reproductive mothers emigrated), and dispersers of both sexes, remained low in conjunction with their departure by Period 6. Philopatric yearlings overlapped their mother's core areas increasingly in Periods 6 and 7 after juvenile emergence, then overlap declined late in the season as nondispersers became established adjacent to their mother's core area. Overlap may have been partly related to changes in the sizes of core areas used by mothers and yearlings (Table 3.5), but also involved shifts in the regions used by yearlings, as illustrated in Figure 11. A circle of 15-m radius around the natal burrow, approximating the diameter of an adult female's territory (Festa-Bianchet and Boag 1982), contained about 80% of the average mother's locations during Periods 2-4 (Table 3.6). Once juveniles emerged, mothers spent less time close to the natal burrow, expanding their core areas in Periods 5 and 6. In Period 2, yearlings spent about 75% of their time within 15 m of the burrow where nonlittermate siblings would be born; the proportion of locations near the natal burrow declined through Periods 3 to 6, particularly in the case of emigrants. Avoidance of the natal area was usually accomplished by yearlings shifting their core areas into pockets between territorial females, decreasing their onsite attendance, or dispersing, but could also take the form of a home range which overlapped with that of the mother but avoided the defended natal burrow (Fig. 3.12).

Changes in Sleeping Burrow Locations

Since yearlings were radio-collared, it was possible to determine where they slept. Typically yearlings began the season by sleeping within 5-10 m of where they had been born, and in the company of any surviving littermates. From morning-emergence locations, it appeared that yearlings were not sleeping with their mothers, although she permitted them to enter burrows she was using. By the end of Period 3, most yearlings had switched to new burrows close to the periphery of their mother's home range; they were no longer scanned or radio-tracked in the vicinity of burrows used by the mother.

Occasionally, an individual from one yearling group would spend a night sleeping with members of another nearby (nonsibling) group.

Within a yearling burrow system, not all individuals slept in exactly the same location. For instance, #77's yearlings slept together in various combinations but #2 (female) and #5 (male) were always at least 2-5 m from each other regardless of other animals they slept with. A general tendency for yearlings to space themselves within burrow systems began in Period 3 and increased through the season until it became unusual to find two yearlings sleeping close together within a burrow (Table 3.7). Initially, the location and volume of radio signals showed that yearlings were at least several feet underground and 2-5 metres from the nearest opening. In Period 5, when as many as four or five yearlings still shared a burrow, some individuals were noted whose loud radio signals were broadcasting from just beside burrow openings. These individuals soon dispersed and the norm became single yearlings (occasionally two) sleeping well inside burrow systems.

Mothers probably slept with their juvenile litters until they brought them above ground in Period 5. Weaning of litters is thought to approximately coincide with juvenile emergence (Ferron 1984), and it appears from morning-emergence locations that mothers were no longer sleeping with litters after Period 5. Two mothers and their litters were radio-collared in Period 10, 1984. The mothers were found to be sleeping in their early season burrows (as opposed to natal burrows); the juveniles slept with their siblings, either in their natal burrows or in burrows that yearlings had occupied at the beginning of the season.

Mestranol and Removal Treatments of 1985

During 5-11 May 1985, all adults were removed from Site 2 and the Mestranol treatment was replicated on Site 1. Unfortunately, Winter 1984-85 was extremely harsh and only 29% (4/14) and 46% (6/13) of all 1984 juveniles survived to become yearlings on Sites 1 and 2, respectively. Juvenile emergence in populations surrounding Sites 1 and 2 commenced on 17 June, but no juveniles emerged on either site. All yearlings of Site 1 (2 males, 2 females) and Site 2 (2 males, 4 females) were still present on June 23, although they were making excursions into surrounding areas. At the final 14-17 July trapping session, no yearlings had yet emigrated from Sites 1 and 2. Since yearling dispersal would normally have been closely associated with Juvday, these animals were certainly late dispersers; I suspect that they would not have dispersed at all with hibernation approximately three weeks away. Henceforth, I refer to these animals as "1985 nondispersers".

Under What Circumstances Did Yearling Males Not Disperse?

Following the first year on each site, mothers and siblings of yearlings were known. The fact that yearlings of known familial relationship were always found to commence the season sleeping in spring groups of surviving littermates within their mother's home range was used to infer mother/sibling relationships for the 13 males from first-year sites. Based on these assumptions, I have sufficient information to make statements about 10 of the 11 male nondispersers radio-tracked in 1982-4: as yearlings, five had no surviving mothers or sisters; two had a nonpregnant mother and no sisters; three had a sister but no mother. Regardless of assumptions about the two nondispersers from first-year sites, no philopatric males lived within the home range of a pregnant adult female.

All 26 yearling males with a pregnant mother dispersed, even if they had no surviving sisters (n=11). Most of the 7 males with a sister but no mother dispersed: four emigrated as yearlings; one departed but returned to sleep and hibernate near his sister before dispersing permanently the following spring; two brothers on the 1984 Mestranol plot did not disperse but shifted into adjacent home ranges beside their sister. Only one of the six males with no mother or sisters dispersed. This was a case in which two brothers shared a burrow on 1983 Site 3. They remained amicable throughout the summer but after June 26, they began renovating their burrow system and sleeping 12 m apart. On July 21, the lightest brother took up a new residence 62 m away, on a hillside among bushes where he remained until killed by a predator. Since he had completely changed his home range I considered this move to be "dispersal", although it was the shortest distance and latest nondrugged dispersal date recorded (see RESULTS - The Timing of Dispersal).

Among the four yearling males from 1985 Removal and Mestranol treatments, three had no mothers, and one had a nonpregnant mother and no sisters. In July when these animals were trapped and killed by nembutal injection, all were still living near their natal burrows.

Under What Circumstances Did Yearling Females Disperse?

I have sufficient information to describe the spring groups of eight of nine female dispersers: all were from six litters with more than one surviving sister, and except for one litter the mother was alive and reproductive. Three litters included two sisters each, and three litters contained three sisters. Throughout the study, every litter with more than one surviving sister resulted in female dispersal. In five cases, all but one sister dispersed from the natal home range. In the remaining case, two of three females from the same litter were philopatric: after much chasing between mother and daughters, and among sisters, the mother lost her litter before juvenile emergence. Two of the daughters established home ranges budding off the south end of their mother's home range, while the most subordinate daughter (chased 9 and 3 times by her two sisters while only chasing them 1 and 0 times) dispersed.

Yearling Competition

Ninety chases among yearlings were recorded during 1984-86. The 30 females chased other yearlings 59 times, whereas 45 yearling males chased other yearlings 31 times (G=9.83, P=0.002). Forty-two percent (25/59) of chases by yearling females were directed at males and 58% were chases of other females. Yearling males pursued other males in only 29% (9/31) of their chases.

There were 15 spring groups of yearlings, each composed of 2-5 surviving littermates sleeping in the same burrow system within their respective mother's home range. Beyond these 47 animals, the remaining 28 radio-collared yearlings slept alone within their mother's home range. This arrangement meant that there were as many as six animals per maternal home range prior to the emergence of any new litters. As female territories were established, yearlings were partitioned into areas between female territories to compete among themselves for space and burrows.

Twelve yearlings belonged to four all-male groups (range 2-4 yearlings per group). These males engaged in chases with males and females from other litters, but did not chase each other. The two groups within home ranges of reproductive adult females dispersed, although group members remained amicable with each other until disbanding; two pairs of brothers that dispersed to the same areas behaved amicably and sometimes slept together (Paper 1). The mothers of the remaining two groups had disappeared overwinter.

Brothers 1 and 17 retained their mother's home range and remained amicable with each other, although they tended to sleep 3-10 m apart from Period 4 through Period 9. Two brothers from 1983 Site 3 were amicable with each other, but one brother shifted his home range late in the season, as described earlier.

Ten yearlings belonged to four all-female groups. Three groups were harried regularly by adult females and interacted infrequently among themselves, making it difficult to assess dominance/subordinance relationships. All three sisters from one of these groups left the natal area, but the heaviest sister (who had chased her sisters once each without reprisal) returned before the end of the season to establish a home range. In the fourth group, the yearlings were clearly competing among themselves. Starting on Day 35, the three sisters chased each other, fought, scent-marked near their burrow and toothchattered at each other. By the beginning of Period 5, yearling female #55 would flee at the sight of her sisters; she dispersed on Day 55 after a series of excursions starting Day 45. As mentioned earlier, the mother of this group lost her litter before Juvday, and the remaining daughters were both able to remain philopatric although they slept at burrows 6 m apart and at distances of 9 and 14 m from their mother's burrow.

Twenty-five yearlings belonged to seven groups containing both males and females (range 2-5 yearlings). Four of these groups were rarely seen interacting among themselves or with other yearlings, although a female from each group remained a nondisperser. In the other three groups, the female nondisperser was the most dominant yearling. On 1984 Site 1, female #4 gave her brother four unanswered chases and an attack before he dispersed. A female on the 1984 Mestranol plot gave her brothers several chases each before they shifted onto adjacent home ranges. The most dramatic case was seen on 1984 Site 1 (adult females sedated): #77's five offspring exchanged 32 chases and 3 fights, the outcomes of which indicated a linear hierarchy (#2f, #7m, #9f, #5m, #73f). Daughter #2 was most dominant, and remained the sole nondisperser (Appendix 5).

Wound Data

Adult females exhibited some wounds in Period 1 (Fig. 3.13), but numbers of wounds declined in Periods 2-3 when litters were born; wounding then increased to a peak during late lactation and juvenile emergence (Period 5), dropping off rapidly thereafter. Adult males showed a decrease in wounds during Period 3, a time when adult females were nursing newborn litters underground. Numbers of wounds increased during Period 4, but declined during juvenile emergence and remained low for the rest of the season. Yearlings of both sexes were found to have no wounds during Period 1; numbers of wounds increased during Period 2, decreased when adult females were nursing new litters (Period 3), and peaked <u>before</u> juvenile emergence, coinciding with the beginning of the dispersal period. The decline of yearling wounds after Period 4 may have reflected the departure of dispersers from well-populated study regions, in addition to lower levels of wounding that occurred among all animals after Period 5. This decline cannot be attributed to the escape of dispersers from researchers, since yearlings were radio-located and trapped for regular examinations. There were four cases of yearlings (males) receiving wounds <u>after</u> dispersing; all other wounds (46/50) occurred while yearlings were still residing on natal areas, although the possibility remains that some wounding took place during excursions from study sites. Eighty-four percent of all yearling wounds were received in the first 5 periods of the season as opposed to 16% in the last 5 periods. Males received 64% (34/50) of all yearling wounds, but the difference between sexes was not statistically significant (G=1.61, P=0.20).

Seventy-six percent (13/17) of male yearlings that received wounds became emigrants, compared to 72% (18/25) of unwounded males; apparently wounding had no affect on the predisposition of male yearlings to disperse (G=0.001, P=0.98). Fifty-seven percent (4/7) of wounded females dispersed compared to 23% (5/22) of unwounded females, but the difference is not statistically significant (G=1.48, P=0.22) owing to small sample size.

E. DISCUSSION

Reproduction and Dispersal

No yearlings dispersed from two Mestranol plots on which adult females were temporarily sterilized, and males on reference plots were able to remain philopatric if their mother died or did not become pregnant. Presumably, the lack of reproduction in these cases resulted in a lack of cues for dispersal. Possible cues include maternal aggression from adult females, changes in population density related to juvenile emergence, or behavioural avoidance of juveniles by yearlings.

The Mestranol treatment resulted in low levels of adult female aggression (Figs. 3.4 and 3.6). Goulet and Sadlier (1974) used Mestranol on populations of Richardson's ground squirrels (_S. richardsonii_) and reported reduced levels of adult female aggression; their data reveal no dispersal from treated sites, however their cohort of potential dispersers was greatly reduced by the Mestranol treatment since _S. richardsonii_ disperse as juveniles.

There is no reason to believe that yearlings dispersed in response to increased density caused by emerging litters, or to avoid associating with juveniles. Some yearlings emigrated up to eight days before juveniles emerged (Fig. 3.1). Yearlings were dominant to juveniles and sometimes chased them, which resulted in eliciting more aggression from the protective mothers. Furthermore, on the two sites where adult females were sedated, juveniles emerged at normal times but yearling dispersal was delayed and took place over a longer period. This implies that a temporal cue to disperse was associated with adult females, since they were the only animals to receive sedatives. Similarily, the delayed case of dispersal on 1983 Site 3 happened when two brothers, whose mother was dead, moved apart late in the season. Brody and Armitage (1985) reported greatly increased female philopatry and a case of delayed male dispersal after removing adult females from a colony of yellow-bellied marmots. Holmes (1984) found that female hoary marmots (Marmota caligata) in Alaska reproduced every two, three, or four years, depending on food resources. Dispersal occurred whenever adult females reproduced. Two-year-old marmots whose mothers brought a litter above ground dispersed or moved to peripheral locations; those whose mothers did not reproduce remained within their natal colony. Similarly, Johns and Armitage (1979) noted that dispersal of yellow-bellied marmots as yearlings or two-year-olds seemed to be tied to adult female reproduction, which varied in frequency at different elevations.

Site 4 was known to have delayed emergence of juvenile litters compared to the flat meadow, presumably the result of reproductive delays experienced by adult females emerging late on the shaded hillside in spring. I observed iceplugs in some of the hillside burrows after adults had emerged on the flat meadow in spring, but I did not quantify the delay.

Shaw (1925) noted a 10-day difference of emergence dates between Columbian ground squirrel populations on north-east versus south-west slopes, and described how the 10-day difference continued to affect the timing of life history events, such as the reproductive cycle, through the season. The delayed reproductive cycle on Site 4 was associated with a delayed peak of chases by adult females, and delayed yearling dispersal. All of these facts combine to suggest that adult female behaviours associated with reproduction may act to stimulate yearling dispersal.

The Effect of Density on Dispersal

The relationship between population density and male dispersal approached significance, and on each site the percentage of males or females emigrating roughly followed trends in density. I suggest that dispersal is not caused by density *per se*, but that density provides a crude estimate of other factors that are directly relevant to ground squirrel biology. Given that burrow systems are stationary and mainly populated by the same adults from year to year, higher density means that one or both of the following is true. More adults may have survived - leaving fewer vacated burrows to appropriate. More juveniles may have survived to become yearlings. Thus on a given site, depending on the size and composition of spring yearling groups, increased density would generally translate into increased yearling dispersal. Some researchers have noted a relationship between population density and numbers of ground squirrels dispersing (Michener 1979, 1981, Festa-Bianchet 1982) but others disagree (Dobson 1979, Holekamp 1984b). Slade and Balph (1974) removed about half of the adult age-class from a population of Uinta ground squirrels (S. armatus) and found that juvenile dispersal from their study area was sharply reduced; juveniles continued to move out of their mother's burrows at the same rate, but more were able to settle nearby.

Timing of dispersal was not related to the population densities of study sites. Each yearling started within its maternal home range and was shunted to the edge if its mother survived and became pregnant. Increased density meant that this could happen on more maternal home ranges per hectare, but timing was determined by reproductive events unless modified by an experimental treatment or an unusual natural occurrence (e.g. mother not pregnant).

Study Periods and Maternal Aggression

In this study, periods were aligned on a biological event (juvenile emergence) which removed some environmental variation and focussed on the underlying reproductive cycle. Much of the literature is difficult to interpret in terms of maternal aggression because behavioural rates determined on different sites and years were not aligned to reproductive events. This is particularly important in the case of montane species since differences of elevation and aspect among study sites could produce large variations in reproductive phases (Shaw 1925, Moore 1937). It is possible that descriptions of marmot dispersal in alpine habitat taking place over a period of months, of early dispersers weighing more in June than yearlings that disperse later, or of yearlings remaining longer on sites where rates of amicable behaviour were high (e.g. Downhower and Armitage 1981) may contain a degree of variation contributed by phasing of the annual cycle at individual sites. If populations on different study sites vary greatly in reproductive phasing, the overall dispersal period would be extended, animals from some sites would be heavier and disperse sooner when measured against a calendar date, and fluctuating behaviours (e.g. peaks of aggression or amicability) might not be compared on an equal footing. In short, I believe that alignment of data to reproductive events is essential to the study of relationships between maternal aggression and dispersal.

Adult females chased other ground squirrels most frequently from Period 2 (early births) through Period 4 (late lactation). After juvenile emergence and weaning in Period 5, levels of chasing declined (Fig. 3.2). Adult female aggression associated with the interval from parturition to weaning is common throughout the Order Mammalia (Klopfer et al. 1973), and has been particularly well documented in laboratory studies of rodents. "Maternal aggression" as it was termed by Moyer (1968, 1976) has a number of distinctive characteristics including its rapid onset (Beniest-Noirot 1958), the ferocious nature of attacks under laboratory conditions (Gandelman and Svare 1974), and the fact that this aggression can be elicited by the proximity of an individual that normally would not be attacked (Brain 1979). There is also some evidence that submissive postures by recipients of a maternal attack are ignored (King 1963) and that bites are directed at vulnerable body parts more frequently than in other forms of fighting (Ostermeyer 1983). Typically, there are two peaks of maternal aggression: the first appears during early days of pregnancy and declines thereafter; the second and larger peak takes place between parturition and weaning (Green 1978, Ostermeyer 1983). A series of experiments have shown that a combination of circulating (or injected) hormones, and exposure to young (particularly suckling stimulation) result in maximal levels of maternal aggression; levels decline at weaning unless extended by replacing a female's own young with neonate foster young at frequent intervals (Svare 1976).

Despite the inherent differences between laboratory and field studies, a number of useful parallels can be drawn between the maternal aggression of confined rodents and that of wild Columbian ground squirrels. Adult females in this study showed increased levels of chasing in the interval between parturition and juvenile emergence, similar to changes in rates of attacking by lab rodents; this is apparently the free-ranging expression of maternal aggression, involving the same timing and distinctive characteristics (sudden onset, attacking individuals that would normally be tolerated) but without the restriction of movement which leads to ferocious attacks in laboratory situations. Yearling Columbian ground squirrels changed sleeping burrows and no longer used central parts of their previous home ranges after being chased away by their mothers in Period 3. It appeared that behavioural changes in the mothers caused yearlings to be excluded from certain areas, and in particular, from certain burrows. Surveillance of these defended areas showed that juvenile litters later emerged from natal burrows that had been closely guarded by resident mothers. Rates of chasing by adult female ground squirrels declined after Period 5, probably resulting from hormonal changes and the absence of sucking stimulation, as has been demonstrated for laboratory rodents. In this study, most observations took place in the interval from birth of litters through yearling dispersal to fall immergence; Festa-Bianchet and King (1984) started their behavioural study with the spring emergence of adults, and reported a bimodal curve of adult female chases. The first peak was smaller and corresponded with early pregnancy, whereas the larger peak encompassed parturition to weaning. Thus reproductive female Columbian ground squirrels duplicate the timing of maternal aggression reported for laboratory rodents, but in terms of chases rather than attacks.

Site-specific dominance and chasing by free-ranging female rodents has been noted for lactating tree squirrels (Layne 1954, Shorten 1954, Taylor 1966), chipmunks (Broadbooks 1970), marmots (Barash 1973), and ground squirrels (McLean 1984, J. Murie pers. comm.).

The Timing of Peak Chases and Dispersal

Adult females typically chased yearlings most frequently in Periods 3 or 4 (Figs. 3.5 and 3.6) after the majority of juvenile litters were born. This was a transition phase for yearlings since they had been tolerated and permitted to move freely until adult females began to exhibit maternal aggression; the yearlings began to spend more time away from contested areas, thus managing to avoid aggressive females to a greater extent. Peak chases among adult females typically occurred in Period 4 (Figs. 3.3 and 3.4) during late lactation, demonstrating that maternal aggression was still very much in evidence. On the 1984 Mestranol plot where there was no reproduction, few chases occurred. On Site 4 where reproduction was known to be delayed, and on the 1984 Site 1 sedation plot, peak chases of yearlings and adult females were both delayed. I suspect that the Period 6 value for chases among adult females on 1984 Site 1 was artificially high since I was unable to sedate squirrels on Day 65; omitting the day in question would result in a Period 6 value of 0.8 chases per hour, indicating that peak chases occurred in Period 5.

Dispersers emigrated late from the delayed reproduction site each year, and from the Site 1 sedation plot in 1984; peak chases of both yearlings and adult females were delayed on those plots. The 1983 Site 2 sedation plot produced two of the latest dispersers yet had no lags in peak chases of yearlings or adult females; the 1983 Site 1 reference plot had normal dispersal but a delayed peak of chases among adult females. It seems that the timing of peak levels of chasing on each site was not a reliable indicator of the timing of dispersal there. This is not surprising since dispersers came from within individual maternal home ranges where the resident female may have reacted differently than the mean number of chases on the entire area would indicate. As well, each yearling had its own circumstances to contend with, including proximity to aggressive adults, numbers of surviving littermates, and availability of nearby uncontested space. Mean rates of chasing apparently provided only an overview of the general climate of aggression prevailing on different sites.

Conflict of Interest Between Adult Females and Yearlings

Columbian ground squirrels disperse as juveniles at low elevations in Washington, but postpone dispersal to the following summer in the foothills of Alberta. Juvenile Columbian ground squirrels from 1540-m elevation in Alberta had an average weight of 328 g (males) and 318 g (females) at the end of their first summer (Boag and Murie 1981b), whereas juvenile males from 760 m elevation in Washington finish their summer weighing approximately 470 g (B. Weddell, pers. comm.). Juvenile Columbian ground squirrels in the foothills of Alberta may have an active season of only 45-55 days in their first summer (Boag and Murie 1981a, Festa-Bianchet and King 1984); ground squirrels that disperse as juveniles are active for approximately 100 days in their first summer and hibernate at a weight more closely approaching that of adults (Michener 1977, McLean 1981, B. Weddell pers.comm.). The implication is that Columbian ground squirrels from higher altitudes and latitudes may be unable to gain sufficient weight to bear the costs of juvenile dispersal followed by successful hibernation. Indeed, Murie and Boag (1984) have shown that juvenile survival over winter is significantly related to body weight. Yearling dispersal may have been selected for in Alberta as a means of improving the survival of young animals, much as Barash (1973) suggested for marmots that delay dispersal. Johns and Armitage (1979) proposed that the production of new litters by adult female yellow-bellied marmots limited the extent to which their prior litters could delay dispersal; this appears to be the case for yearling Columbian ground squirrels as well, but other factors must be involved for ground squirrels and marmots that disperse within their first summer, since reproduction does not occur again until the following summer.

As a result of delayed dispersal in Alberta, adult female Columbian ground squirrels face a conflict of interest (Trivers 1974) each spring. They have harboured last year's litter as long as possible without jeopardizing the success of this year's litter. Their yearlings did not disperse as juveniles and have been reaping the benefits of philopatry (Waser and Jones 1983). If an adult female now becomes pregnant, it is in her interest to disperse last year's offspring and begin investing in her new litter; her yearlings, however, might find it advantageous to continue sharing her home range. Note that there is no conflict of interest if the adult female is not pregnant.

Dispersal prompted by this arrangement takes place at a time of year tha~~t is fa~~vourable to yearling survival; this is a direct benefit to the dispersing young but also benefits the mother in terms of increasing the success of genotypes to which she is related by 0.5 (Hamilton 1964, Krebs and Davies 1981). Past authors have considered the advantages of dispersal from the viewpoint of parents (Anderson 1980, Liberg and von Schantz 1985), dispersers (Murray 1967, Greenwood 1980, Dobson 1982) or nondispersers (Greenwood 1980, Waser and Jones 1983), but the system of dispersal described here may have advantages for both mothers and offspring. Some authors have argued that it is unlikely that dispersers gain any benefits because most probably die soon after emigration (Lidicker 1975, Schmutz <u>et al.</u> 1979). I found no significant difference in the survival of dispersers and nondispersers within their yearling summer, that members of both groups survived to reproductive age, and that male dispersers achieved a weight advantage over nondispersing males (Papers 1 and 2).

Female Territoriality

During the interval between birth of litters and juvenile emergence (Periods 3 to 5), reproductive female Columbian ground squirrels defended the area around natal burrows against intrusion by other ground squirrels. Female aggression and territoriality associated with reproduction has been reported in several species of ground squirrels (e.g. Slade and Balph 1974, Dunford 1977, Michener 1979, Festa-Bianchet and Boag 1982, McLean 1984), usually at high density. Festa-Bianchet and Boag (1982:1064) implied that high density might be a necessary stimulus to territorial behaviour. I concur with McLean (1984:331) that territorial behaviour is more likely to be noticed by investigators working with high population densities. More animals are apt to encroach upon natal burrow locations in dense populations, resulting in more chases by reproductive adult females. In other words, rates of chasing may be an artifact of population density (more trespassing) and may not imply that maternal aggression and defence of offspring vary on sites of different density. Presumably, all adult females have a vested interest in increasing offspring survival through reduction of infanticide (Michener 1982, Sherman

1982, McLean 1983, Waterman 1984, Brody and Melcher 1985, Wolff 1985). The underlying motivation for these defensive behaviours appears to be reproduction-related hormonal changes and suckling stimulation (discussed earlier), i.e. these stimuli are experienced by individual adult females irrespective of local densities.

Some authors have dismissed the role of aggression and territoriality on the grounds that they saw few chases on their study sites (Yeaton 1972, Dobson 1979). In addition to the effects of density on probabilities of interaction, it is possible that a good deal of aggression is communicated by means other than chases and fights. Lyon et al. (1985) described subtle threats such as piloerection, back-arching and vocalizing that effectively "peripheralized" a captive two-year-old female primate (Callimico goeldii) once her parents gave birth to a new offspring. Columbian ground squirrels have a behavioural repertoire that includes various threatening vocalizations (e.g. growls), toothchattering, tailbushing, displacing and scent marking, as well as unknown subterranean interactions. Kivett (1975) and Festa-Bianchet and Boag (1982) have established that scent marking is related to aggression and territorial behaviour; I have described burrow changes and underground spacing that may be related to aggressive behaviours (present study). Webb (1981) suggested that aggression (attacks, chases and fights) was only necessary to stimulate emigration from patchy habitat where unsuitable surroundings increased the reluctance of potential dispersers to leave; it may be that the most overt forms of aggression only become obvious where young animals are unable to avoid conflict because of surrounding habitat barriers or high population density.

Given that female territoriality has been reported among other species of ground squirrels, the unusual feature of S. columbianus in Alberta is that surviving offspring from the previous year are still in place during their yearling summer to experience a behavioural change in their mother. Thus maternal aggression and associated territoriality appear to have a secondary effect of creating behavioural and spatial pressure timed to the reproductive cycle; the resulting "conflict of interest" between mothers and yearlings is resolved by the dispersal of some or all yearlings from each maternal home range.

Yearling Competition

My results indicated that whether or not yearling males dispersed was dependent on the presence or absence of close female kin within the maternal home range. Similiar tendencies have been noticed by other researchers: young male S. richardsonii (Michener and Michener 1973), S. elegans (Pfeifer 1980, 1982), and S. columbianus (Wiggett pers. comm.) were less likely to disperse if their mothers disappeared (no comments were made regarding sisters). This suggests that males have some flexibility in dispersal behaviour, that there are advantages to be gained by retaining a familiar burrow and home range, and that males would stay except for the presence of female kin.

Within spring groups containing females, yearlings that were able to interact without frequent adult female harassment appeared to be dominated by a yearling female in each case; the dominant female remained philopatric whereas the other yearlings dispersed. It was difficult to assess dominance within spring groups that were regularly harassed by adult females; however, nondispersing sisters were heavier than dispersing sisters within 5 of 6 groups containing more than one female yearling (Paper 2), and heavy females may have had an advantage in competing for dominance. Overall, yearling females were the aggressors in more chases than yearling males. Spring groups of yearling males chased other yearlings but did not chase other members of their group. These observations appear to indicate that although yearling males were generally heavier than yearling females (Paper 2), they were not as aggressive and did not compete with other siblings to be philopatric. The fact that all female dispersers came from spring groups containing two or more females suggests that yearling females were more site-tenacious than yearling males and were unlikely to be dislodged from their natal area unless a sister was present. Pfeifer (1980, 1982) reported that juvenile female Wyoming ground squirrels (S. elegans) interacted more aggressively among themselves than did juvenile males or male/female pairs. She concluded that competition to remain in the natal area and possibly inherit the mother's maternal burrow site was the driving force behind female dispersal. Female Columbian ground squirrels often inherit their mother's home range (Harris and Murie 1984) and there are kin-related advantages to remaining in the vicinity of the natal site (Sherman 1981, Michener 1982, Waser and Jones 1983). Site-tenacity may be a primarily female characteristic that develops during the yearling summer for Albertan S. columbianus and earlier for most other ground squirrels. Michener (1981) found that juvenile Richardson's ground squirrels rapidly acquired the spatial and social patterns characteristic of adults, exhibiting site-dependent dominance on individually distinct core areas at 9-10 weeks of age; by 12 weeks of age, juveniles were behaviourally indistinguishable from adults. She suggested that juvenile dispersal in S. richardsonii was related to a squirrel's inability to appropriate a portion of its mother's home range at 9-12 weeks of age while aggressive behaviours were emerging. Since dispersal is typically male-biased in Richardson's (and all other) ground squirrels, the implication is that females are more likely to develop site-tenacious behaviours; Pfeifer (1980, 1982) argued that females are selected to be site-tenacious in order to gain philopatric reproductive advantages. Species of ground squirrels which disperse as juveniles are known to acquire their behavioural repertoires rapidly (Balph and Stokes

1963, Dunford 1977, Clark 1977) whereas Ferron (1984) has shown that Columbian ground squirrels are relatively delayed in development of agonistic patterns.

Wound Data

Wound data has limitations in terms of identifying the aggressor, and the timing and circumstances under which the wound was received. On the other hand, wounds provide tangible evidence of aggression and are the only information available on aggression that may have occurred underground or after the daily observation periods.

Generally, wound data reinforced information from observational studies. Adult males and females received some early season wounds, probably in association with breeding aggression, but most wounds were observed in Periods 4 and 5, at or shortly following the height of adult female aggression. Yearlings had no wounds in Period 1, a stage when they were tolerated by adult ground squirrels and when their interactions with other yearlings were playful. Wounds in Period 2 may have been related to the birth of litters and changing to new sleeping burrows. The peak of wounding, observed in Period 4, could have resulted from adult female chases during Period 4 and the latter part of Period 3, as well as yearling competition that was apparently taking place above and below ground at that time. Period 4 wounding corresponded with the beginning of yearling dispersal; after dispersers left study sites, they were rarely wounded.

The presence of wounds did not appear to be related to the predisposition of males to disperse, whereas females that received wounds were twice as likely to disperse as females that did not receive wounds. From behavioural observations presented earlier, wounded female dispersers were likely the losers of aggressive competitions with female siblings. This idea is supported by the fact that female dispersers weighed less than female nondispersers (Paper 2).

Ultimate Repercussions of Proximate Aggression

The results of this study indicate a proximate role for aggression in cuing the dispersal of yearling Columbian ground squirrels. Maternal aggression from reproductive females apparently synchronized dispersal by displacing yearlings from areas near natal burrows to spaces between female territories; here yearlings appeared to compete among themselves, as suggested by surface aggression and subterranean spacing behaviour. Yearling males were less site-tenacious than yearling females and dispersed unless they had no mother or sister to compete with; yearling females that dispersed were subordinate individuals from multi-female litters. If maternal aggression was disrupted through disappearance or sedation of the mother, dispersal could still occur through yearling competition but was less synchronous.

Proximate aggression, as described above, may have provided a simple and flexible set of rules by which the actions of mother and offspring were attuned to ultimate forces impinging on them. Maternal home ranges and burrow systems can be viewed as spatial units related to reproduction within ground squirrel colonies; if all yearlings were retained within the maternal home range, the success of subsequent litters would be jeopardized through depletion of resources just as surely as the "fence effect" (Krebs et al. 1969) depleted resources of voles that could not disperse. Some animals must leave, or the inclusive fitness of the mother and her offspring would suffer. In the event of reproduction, maternal aggression from lactating females provided a defended space to improve the survival of vulnerable juvenile litters. When adult females did not become pregnant, this spacing mechanism was not activated and yearlings could remain, depending on interactions among littermates.

Any mechanism that results in dispersal by predominately one sex has the theoretical advantage of avoiding inbreeding among close kin. In this system, female yearlings tended to remain philopatric unless they were outcompeted by a sister; male yearlings tended to disperse unless they had no mother or sister to compete with. The ultimate consequence was that the chance of inbreeding between mothers and sons, or sisters and brothers, was much reduced.

Avoidance of inbreeding might be accomplished whether males or females were the predominant dispersers; for example, birds typically exhibit female-biased dispersal (Greenwood 1980). In the case of ground squirrels, there are several benefits associated with a mechanism that encourages yearling males to relinquish the maternal home range to a surviving mother or sister. One is that females have much to gain through philopatry and little to gain through dispersal. From a female viewpoint, a maternal burrow system and associated home range are essential to reproduction. Dunford (1977) thought that ground squirrels could dig burrows quite easily, but Phillips (1984) has shown that costs of pregnancy delay the onset of the prehibernation weight gain period by approximately 60 days leaving a very narrow safety margin for reproductive females; the additional cost of time and energy incurred by digging new burrows would likely be detrimental to female reproduction and survival. Furthermore, females inheriting a burrow system on or near their natal site have advantages of site familiarity and kin-related cooperation (Sherman 1977, 1981, Waser and Jones 1983) to improve litter survival. Thus females should be selected to remain philopatric, and they compete aggressively to do so (Pfeifer 1980, 1982, this study).

Males have no similar requirement for an elaborate burrow system, attain hibernation weights with comparative ease (Phillips 1984), and are not directly involved in the survival of litters (Sherman 1981). Moreover, there may be some advantages to male dispersal. Ground squirrels are polygynous and a reproductive male has the potential of mating with as many as 11 females (Sherman and Morton 1979). If brothers and fathers fertilize the same females, or if brothers and fathers interfere with each other while competing for matings, they are wasting their inclusive reproductive potential. By dispersing to invest their related genes in different females and more litters, and by not impeding the reproduction of males to which they are closely related, male kin may be able to increase the spread of their genes through the surrounding population. In contrast, whether a female is fertilized by one mate or many (Hanken and Sherman 1981), she produces one litter; presumably, her best strategy is to maximize the survival of that litter through her control over resources and location. Yearling male S. columbianus that emigrated were able to gain more weight than nondispersing males, which could be an advantage in terms of recruiting into the breeding population; dispersing females achieved no comparable weight advantage (Paper 2).

A number of authors have proposed evolutionary hypotheses to explain sex-related differences in dispersal. Greenwood (1980) hypothesized that the predominant occurrence of male philopatry in birds and male-biased dispersal in mammals was a result of differences in mating systems. Birds are typically monogamous and territorial, and under these conditions males should gain advantage by defending resources to attract females; they can best defend resources on familiar ground where kin-related advantages or at least "dear enemy" recognition (Wilson 1975, Jaeger 1981, Murie and Harris 1984) could reduce their costs. Mammals are typically polygynous and defend mates. Since intrasexual competition is more intense among males than females (Trivers 1972), young males may be forced to disperse in order to reproduce, or may gain an advantage by dispersing to encounter more females. Dobson (1982) continued the above theme, but emphasized the importance of competition for mates as a force influencing the dispersal of male mammals from polygynous mating systems. Dobson thought that aggression from territorial males limited the reproductive opportunities of juvenile males and suggested that young males should disperse if they were not dominant enough to procure a part of the natal territory - provided that territories could be found elsewhere. Liberg and von Schantz (1985) also recognized the importance of mating systems but pointed out that the two former arguments were based on individual-selection advantages conferred upon young dispersers and nondispersers. They found it more reasonable to assume that the parents were in a position to evict offspring and proposed the "Oedipus" hypothesis whereby the sex that could cuckold either parent would be driven out by that parent.

The above evolutionary hypotheses have proximate predictions and assumptions that I would like to address in terms of Columbian ground squirrel dispersal. There was no evidence that natal dispersal by yearling males resulted in immediate exposure to more females; most yearlings settled on edges of forest or shrubland where high predation provided empty burrows and a sparse population largely consisting of other yearling males (Paper 1). Yearling males were not expelled by adult males as implied by Competition for Mates, and explicitly required by the Oedipus Hypothesis; dispersers emigrated almost a year prior to adult male territoriality. If competition for mates were the only consideration, it might be advantageous for yearling males to delay dispersal until the following spring in case an adult male should die overwinter. Dispersal appeared to be dependent on the survival of mother and siblings within the natal home range, not on the occurrence of potential territories elsewhere as suggested by Dobson (1982); there was an abundance of low density edge area nearby, but male yearlings remained philopatric if their natal home range was not occupied by their mother or sister. Dobson (1982) did not consider that costs of female reproduction had a bearing on female philopatry although he previously showed resources to be of particular importance to female California ground squirrels, S. beecheyi (Dobson 1979, 1981). Columbian ground squirrel dispersal appears to support several of Greenwood's ideas in that the advantages to philopatric females and dispersing males (discussed earlier) are largely a consequence of the mating system, and result in reduced probabilities of close inbreeding.

A paper of great relevance to discussions of ultimate hypotheses is that of Cockburn et al. (1985). Those authors studied a dasyurid marsupial, Antechinus, that exhibits the male-biased dispersal typical of polygynous and promiscuous mammals, but is unique in having discrete generations of adult males. As such, the Competition for Mates and Oedipus hypotheses appear to be ruled out. The conclusion reached by the authors was that inbreeding avoidance was sufficient explanation for male-biased dispersal. I suggest that the Antechinus findings have similarities to results of the present study, although we differ in interpretation. Cockburn et al. (1985) reported that young males dispersed abruptly, that male dispersal from within litters was often complete, and that juvenile females were highly philopatric. When the mother was alive, all sons dispersed; upon removal of mothers, sons could be philopatric (i.e. mothers had a direct influence on dispersal). In the absence of the mother, one male or female juvenile inherited the home range while all others dispersed or died (i.e. there may be yearling competition). The authors speculated about whether sisters or brothers were dominant based on body size, but provided no behavioural data; male S. columbianus and Antechinus were both larger than their sisters, but females were more dominant and site-tenacious in the case of S.

columbianus. In short, there are differences in the biology of Columbian ground squirrels and Antechinus marsupials, but similarities in dispersal raise the possibility that cues such as adult female aggression and competition among offspring may be involved. I agree that there are likely ultimate advantages to inbreeding avoidance, but this alone would not indicate which sex should be the predominant disperser. I suggest that the benefits to females through philopatric behaviour (familiar resources, presence of kin, proven nesting sites), and advantages gained by males in increasing their inclusive reproductive potential through dispersal, may have both contributed to the evolution of male-biased dispersal in this species.

Recent studies of yellow-bellied marmots and black-tailed prairie dogs bear analogies to Columbian ground squirrel dispersal. Brody and Armitage (1985) found that 6/6 (100%) female yearling marmots and 1/4 (25%) male yearlings remained philopatric in an adults-removed colony until mid-August (the male later dispersed); in contrast, only 1/4 (25%) yearling females and zero (0/1) male yearlings remained on a reference site. They concluded that agonistic interactions between adults and yearlings were not necessary for dispersal to occur, and that the proximate causes of dispersal were not the same for both sexes. Certainly, the absence of adult females had a large effect since 6/6 female yearlings were philopatric whereas only 5/16 had previously remained philopatric on the area during 1964-81. I suggest that maternal aggression in the reference colony may have synchronized dispersal and forced young marmots to compete for space, with the result that only one yearling female remained. The lack of adult females in the experimental colony meant that more yearlings could stay, and the space was then occupied by site-tenacious female yearlings; the late male disperser was similar to some male ground squirrels (sedation plot or no mother) that dispersed late. It is not essential that proximate causes of dispersal differ for males and females, provided that the two sexes react differently, as seems to be the case for Columbian ground squirrels. Garrett and Franklin (1986) proposed that dispersal of yearling black-tailed prairie dogs was primarily innate but that males might be influenced by a lack of related females, whereas female dispersers might be attempting to secure adequate resources for reproduction. They found that most intercolony dispersal occurred within the first two weeks of June and speculated that the timing of dispersal may have evolved to coincide with abundant food and cover, which would likely improve survival during long-distance travel. While accepting the logic of this point, I suspect that favourable conditions for dispersal are not as predictable and time-limited as seems to be implied by a concentrated annual dispersal period in early June. Most Columbian ground squirrel dispersers emigrated within a few weeks in mid-June, yet cover appeared to increase throughout the summer and squirrels continued to gain weight until just before hibernation (Paper 2), indicating that food was still abundant. Intercolony dispersal of yearling prairie dogs occurred at approximately the time of juvenile emergence each year (Garrett and Franklin 1986); I suggest that this emigration may have been linked to the reproductive cycle of adult females, as appears to be the case for at least two species of marmots (Johns and Armitage 1979, Holmes 1984) and Columbian ground squirrels (Festa-Bianchet and King 1984, present study).

In this study, there was no evidence of innate dispersal (Howard 1960) whereby certain individuals emigrated regardless of external factors, and no indication of genetically predetermined dispersers and nondispersers as envisioned by Krebs (1978) and others; dispersal of both sexes appeared to be related to external local cues. It would likely be maladaptive if dispersers were rigidly preprogrammed to abandon uncontested natal sites or to overburden crowded maternal home ranges. The only "behavioural polymorphism" that could be interpreted from this study was the tendency of females to remain philopatric unless ousted, and the predisposition of males to yield to female site-tenacity. Such traits may stem from basic sexual differences in behaviour established hormonally during the neonatal period (Phoenix <u>et al.</u> 1959, Holekamp 1983), and may provide the raw material upon which natural selection operates in shaping dispersal behaviour.

In conclusion, dispersing Columbian ground squirrels appear to respond to simple proximate cues, related to maternal aggression and yearling competition, which reflect the reproductive opportunities available within maternal home ranges. The resulting dispersion of closely related individuals appears to involve male and female dispersal advantages, yearling survival, yearling selection, retention of the maternal burrow among close kin, physical protection of vulnerable juvenile litters, and some adjustment of numbers to the finite resources of a maternal home range; as such, this system may maximize the inclusive fitness of mother and offspring beyond that which selfishly acting individuals would attain if not directed by reliable cues. Presumably, ancestral Columbian ground squirrels that responded to appropriate cues received reproductive advantages, which when passed to progeny and selected through time, resulted in a proximately tuned dispersal system. The ultimate forces behind Columbian ground squirrel dispersal appear to be a balance of not over-exploiting resources while gaining reproductive advantages of female philopatry, realizing male reproductive potential, and decreasing the possibility of mother-son and sister-brother matings.

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Table 3.1 - Spring densities of adult and yearling Columbian ground squirrels per hectare on the four study sites over three years.

	Site			
Year	1	2	3	4
1982	22	-	-	30
1983	25	52	24	30
1984	33	32	21	30

Table 3.2 - Percentage of yearlings dispersing from each site in each year (total yearlings present in parentheses).

	Site							
Year	1		2		3		4	
	M	F	M	F	M	F	M	F
1982	80	17	-		-		100	50
	(5)	(6)					(3)	(2)
1983	62	50	100	0	60	0	80	0
	(8)	(4)	(5)	(2)a	(5)	(1)	(5)	(2)
1984	100	67	60	0	0	0	100	33
	(2)	(6)a	(5)	(1)	(2)	(2)b	(2)	(3)

a Adult females were sedated.
b Adult females were sterilized.

Table 3.3 - Mean and median (parentheses) dispersal dates of yearling male Columbian ground squirrels.

	Site			
Year	1	2	3	4
1982	54 (54)	-	-	67 (66)
1983	49 (49)	68 (57)a	64 (57)	60 (61)
1984	60 (60)a	55 (55)	b	59 (59)

a Adult females were sedated.
b No dispersal from the Mestranol treatment.

Table 3.4 - Percent overlap (±SE) of 80% core areas of yearlings with those of their mothers.* Number of yearlings in parentheses.**

Period	All yearlings	Males	Females	Dispersers	Nondispersers
2	65±5.3 (23)	80±6.8 (10)	53±6.3 (13)	67±7.0 (16)	59±8.0 (7)
3	46±6.4 (23)	34±10.0 (10)	56±7.6 (13)	39±7.6 (16)	61±10.2 (7)
4	21±4.4 (23)	14±4.6 (10)	26±6.5 (13)	20±5.9 (16)	24±5.8 (7)
5	24±6.2 (19)	25±10.0 (8)	24±8.2 (11)	18±7.2 (12)	35±10.7 (7)
6	30±10.6 (11)	1±0.7 (3)	41±12.4 (8)	6±5.4 (4)	44±14.0 (7)
7	72±9.1 (7)	-	72±9.1 (7)	-	72±9.1 (7)
8	39±9.2 (7)	-	39±9.2 (7)	-	39±9.2 (7)
9	0 (7)	-	0 (7)	-	0 (7)
10	28±16.9 (7)	-	28±16.9 (7)	-	28±16.9 (7)

* Core Areas of Tables 3.4 and 3.5 were based on 42.8 ± 2.3 (SE) locations per individual per period during Periods 2-8, but fewer locations were recorded during Periods 9-10 (22.2 ± 2.1), largely because tall grass made observation more difficult after Period 8.

** Study animals of the delayed reproduction site, those of the Mestranol site, and those with core areas on the edge of observation grids, were excluded from Tables 3.4 to 3.6 to avoid introducing temporal or spatial biases.

Table 3.5 - Size of 80% core areas (square metres ±SE) of yearlings and their mothers. Number of ground squirrels in parentheses.

Period	Mothers	All yearlings	Males	Females	Dispersers	Nondispersers
2	487.0±142.1 (10)	406.2±63.4 (23)	533.6±104.1 (10)	279.0±64.5 (13)	401.9±79.7 (16)	422.3±114.7 (7)
3	553.7±132.1 (10)	447.8±59.1 (23)	449.6±78.9 (10)	446.1±89.5 (13)	395.9±58.1 (16)	594.8±144.1 (7)
4	268.0±35.1 (10)	305.4±54.0 (23)	331.5±101.2 (10)	283.6±57.8 (13)	300.6±72.0 (16)	318.2±69.2 (7)
5	419.4±54.8 (10)	296.0±44.2 (19)	331.6±117.2 (8)	260.4±60.7 (11)	288.0±52.4 (12)	313.6±89.7 (7)
6	712.6±140.8 (10)	628.1±101.9 (11)	182.5±137.6 (3)	755.4±84.9 (8)	471.3±263.9 (4)	706.5±83.7 (7)
7	435.0±68.5 (10)	574.7±79.9 (7)	-	574.7±79.9 (7)	-	574.7±79.9 (7)
8	466.2±125.1 (10)	357.8±92.6 (7)	-	357.8±92.6 (7)	-	357.8±92.6 (7)
9	86.9±19.4 (8)	94.0±22.3 (7)	-	94.0±22.3 (7)	-	94.0±22.3 (7)
10	91.8±32.1 (4)	259.0±56.7 (7)	-	259.0±56.7 (7)	-	259.0±56.7 (7)

Table 3:6 - Percentage of locations (±SE) that mothers and their yearlings were seen within a 15-m radius of the juvenile-emergence burrow within the mother's home range. Number of ground squirrels in parentheses.

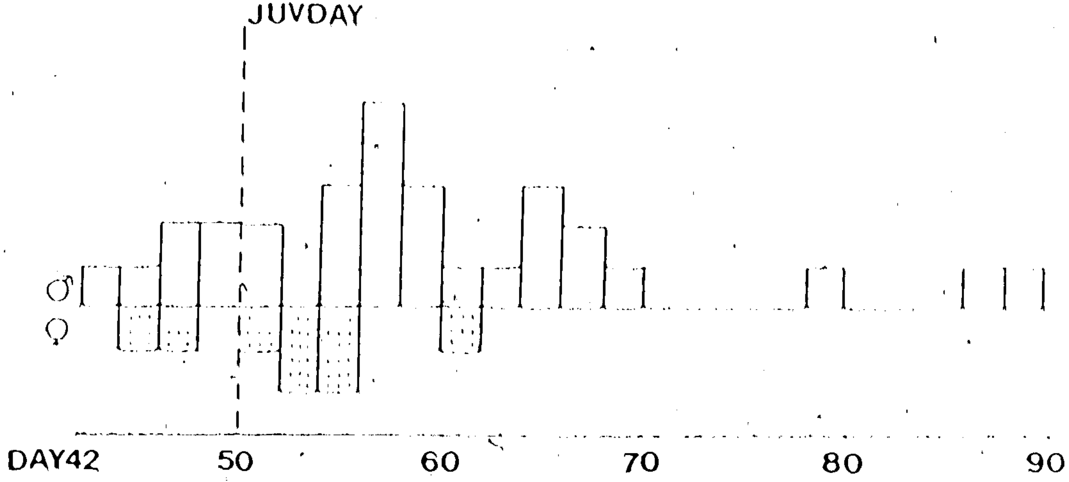
Period	Mothers	All yearlings	Males	Females	Dispersers	Nondispersers
2	78.9±3.6 (10)	73.9±2.4 (23)	74.4±2.8 (10)	73.4±3.9 (13)	75.1±2.2 (16)	70.5±7.1 (7)
3	78.0±2.9 (10)	54.8±4.2 (23)	45.9±7.5 (10)	61.7±4.0 (13)	53.8±5.6 (16)	57.1±5.6 (7)
4	80.5±3.2 (10)	38.3±4.2 (23)	25.7±4.3 (10)	48.0±5.4 (13)	35.1±5.1 (16)	45.6±7.4 (7)
5	73.8±2.9 (10)	38.9±6.0 (19)	29.6±8.0 (8)	47.1±8.3 (11)	34.4±8.1 (12)	49.6±7.2 (7)
6	66.0±3.4 (10)	29.8±7.9 (11)	0.0 (3)	36.4±8.6 (8)	2.7±2.3 (4)	40.0±8.8 (7)
7	63.0±1.4 (10)	66.7±0.6 (7)	-	66.7±0.6 (7)	-	66.7±0.6 (7)
8	63.1±5.9 (10)	57.7±7.3 (7)	-	57.7±7.3 (7)	-	57.7±7.3 (7)
9	68.2±9.9 (8)	21.5±5.9 (7)	-	21.5±5.9 (7)	-	21.5±5.9 (7)
10	69.4±2.7 (4)	47.7±15.9 (7)	-	47.7±15.9 (7)	-	47.7±15.9 (7)

Table 3.7 - Distances between sleeping locations, and numbers of yearlings present, within the 15 spring groups of yearlings. Locations of sleeping burrows were determined using radio-telemetry after 2100 hours (see text).

	Distances (m)		Number per group	
Period	Range	Mean	Range	Mean
2	0-2	0.1	2-5	3.1
3	0-7	0.9	2-5	3.1
4	0-10	1.5	2-5	3.1
5	0-15	2.9	1-5	2.6
6	0-12	5.2	0-3	1.6
7	6-12	8.8	0-3 a	1.2
8	6-12	9.1	0-3 a	1.2
9	1-10	5.6	0-3 a	1.1

a The group from the 1984 Mestranol plot was unusual in that none of the three yearlings (1 female, two males) dispersed. Otherwise, the maximum number of nondispersers from the same spring group was two.

Fig. 3.1 - The timing of dispersal relative to the date of initial juvenile emergence, Day 50. A, All years combined. B, Separated by years and study sites (numbers 1-4). This figure represents 30 male dispersers and 8 female dispersers whose exact day of dispersal was known.


JUVDAY
♂
♀
DAY42
50
60
70
80
90

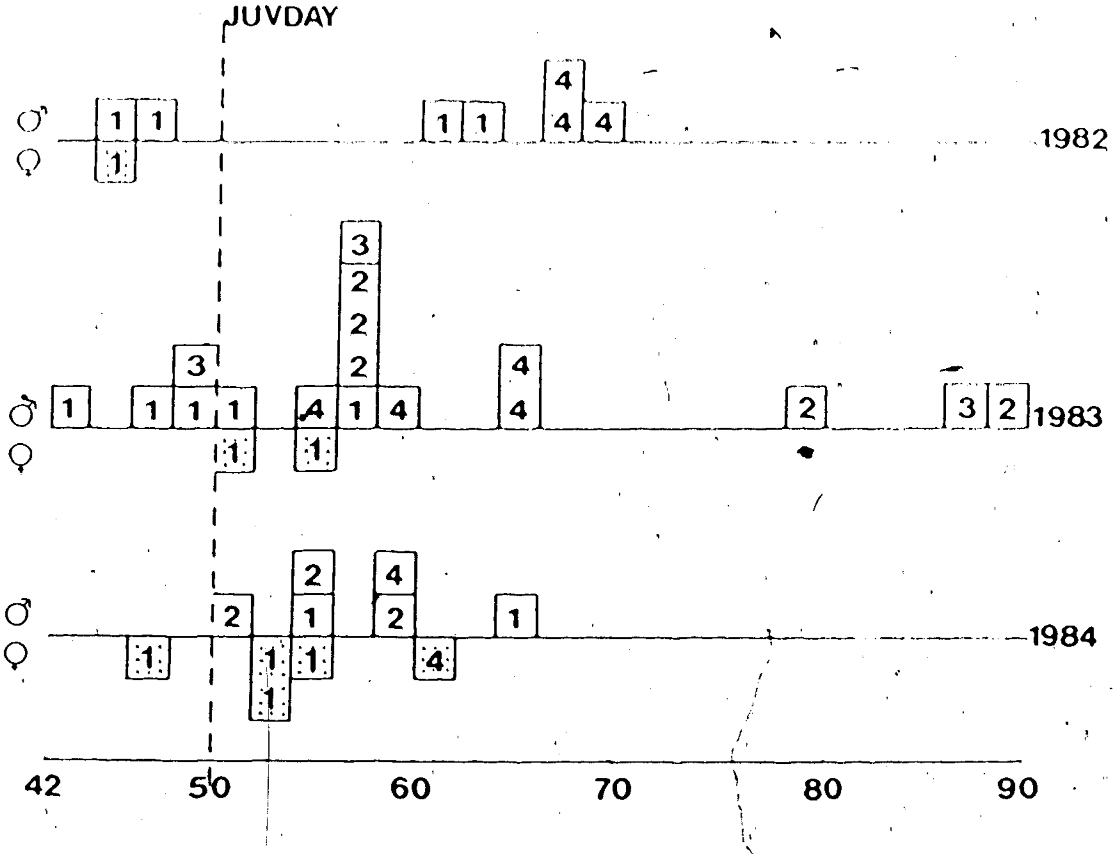

JUVDAY
♂
♀
1 1 4 4 4
1
1982
3 2 2 2 3 4 4
1 1 1 1 4 1 4 2 3 2
1 1
1983
2 4 2 1 2 2 1
1 1 1 1 4
1984
42
50
60
70
80
90

Fig. 3.2 - Frequency of chasing by adult females on Site 2 in 1984.

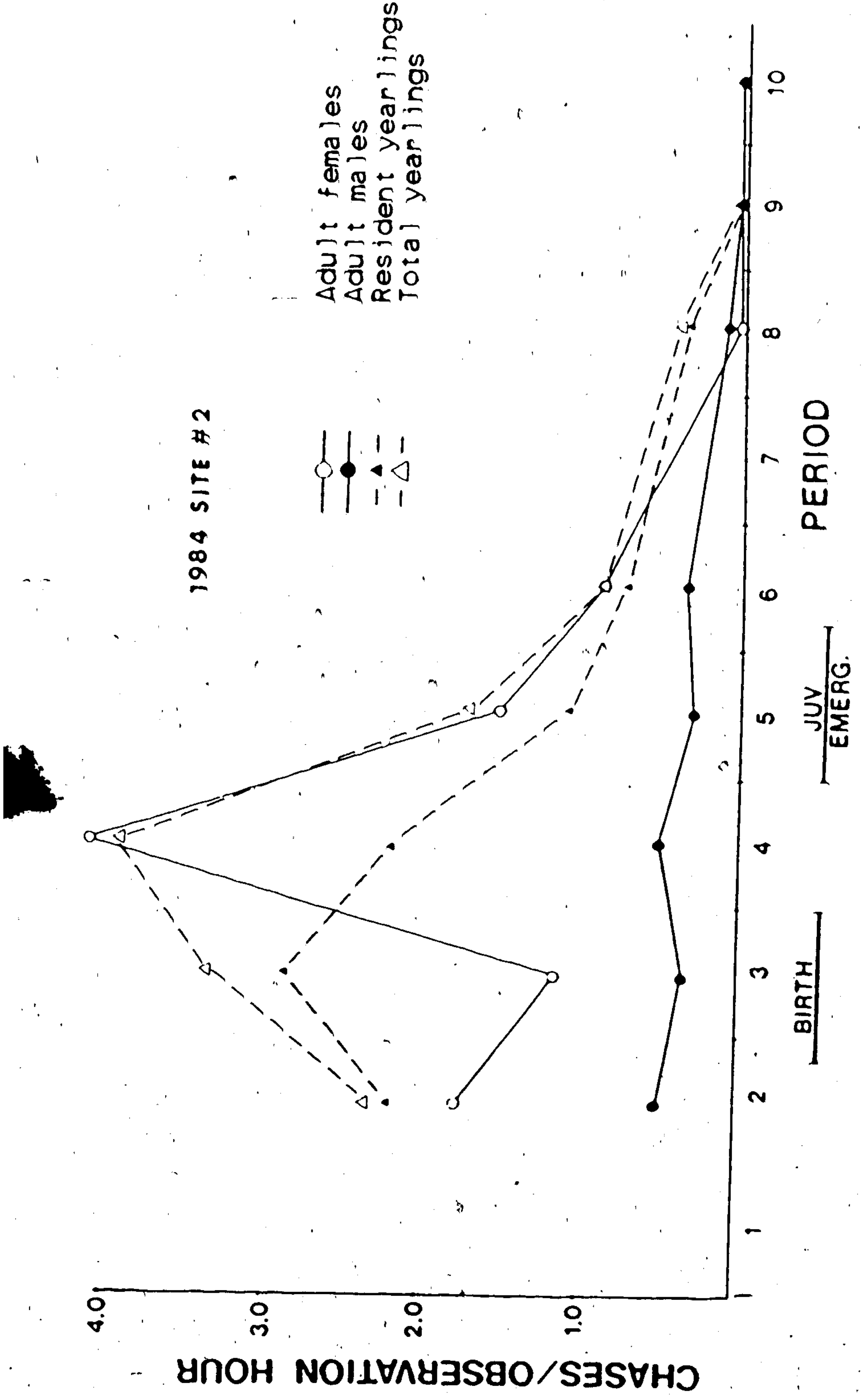

1984 SITE #2
Adult females
Adult males
Resident yearlings
Total yearlings
CHASES/OBSERVATION HOUR
4.0
3.0
2.0
1.0
PERIOD
1
2
3
4
5
6
7
8
9
10
BIRTH
JUV EMERG.

Fig. 3.3 - Chases among adult females on Sites 1 and 2. Reference and sedation treatments are indicated by "R" and "S". Intervals during which adult females were sedated are shown with horizontal lines.

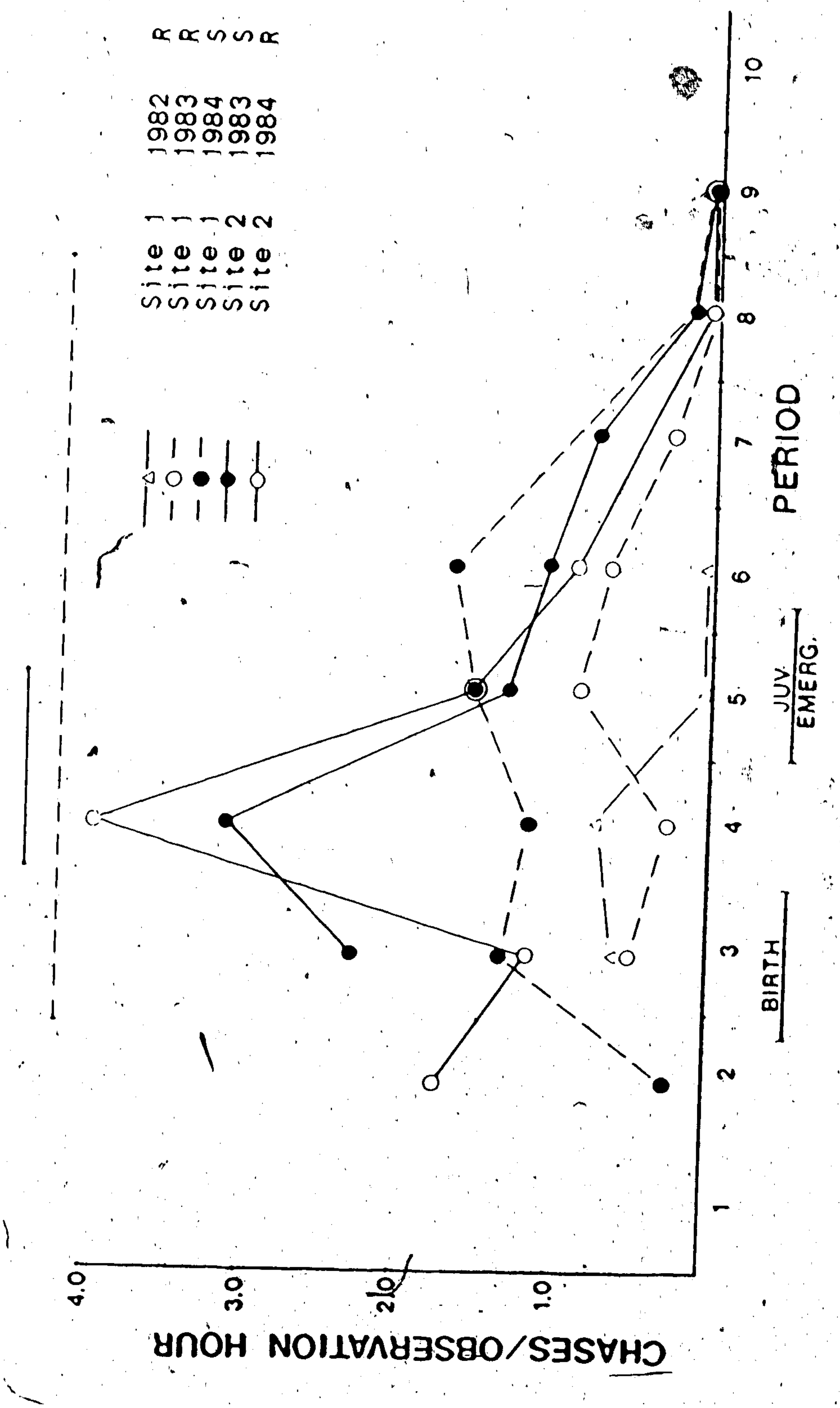

CHASES/OBSERVATION HOUR
4.0
3.0
2.0
1.0
1
2
3
4
5
6
7
8
9
10
PERIOD
BIRTH
JUV.
EMERG.
Site 1 1982 R
Site 1 1983 R
Site 1 1984 S
Site 2 1983 S
Site 2 1984 R

Fig. 3.4 - Chases among adult females on Sites 3 and 4. Reference and Mestranol treatments are indicated by "R" and "M".

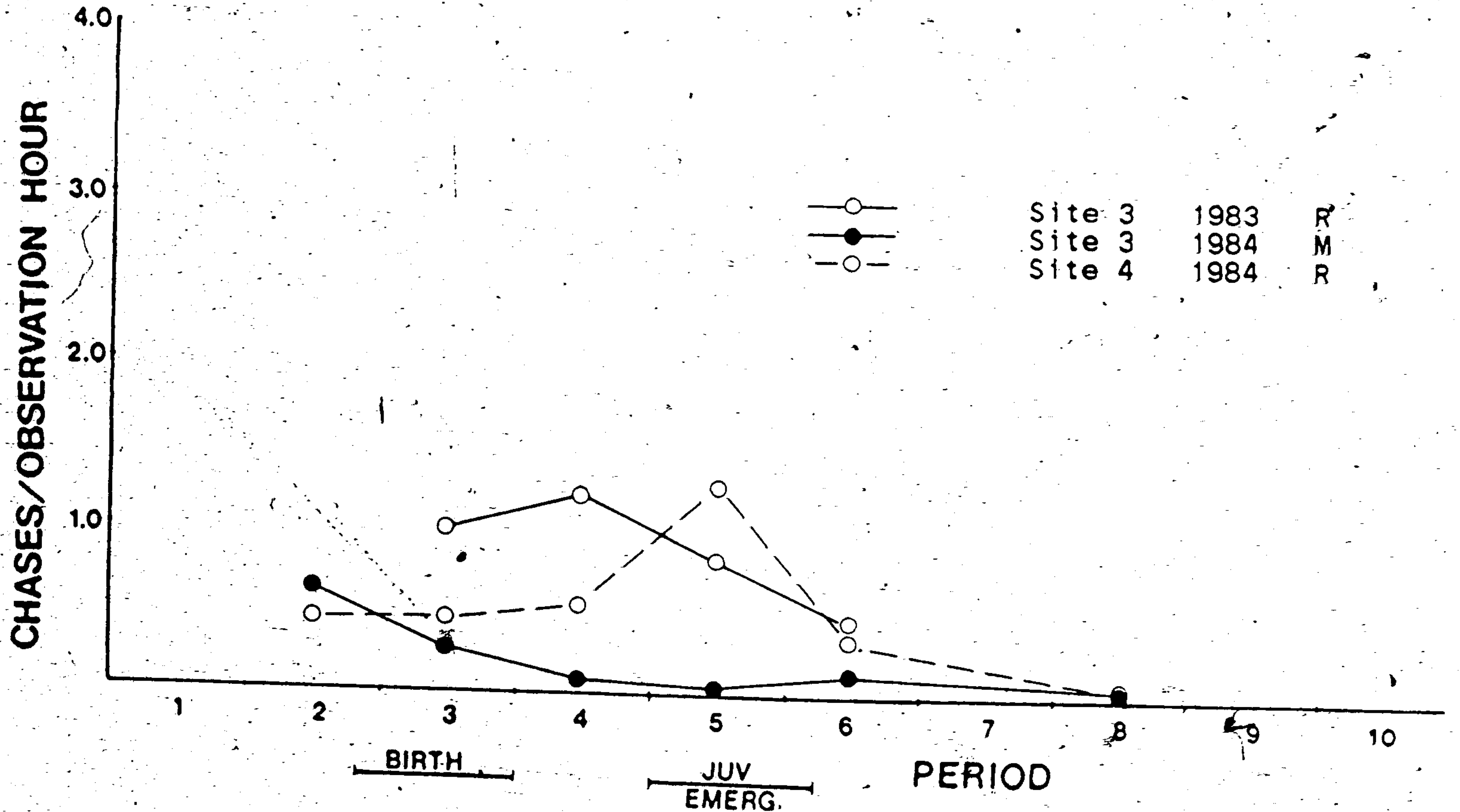

CHASES/OBSERVATION HOUR
4.0
3.0
2.0
1.0
1
2
3
4
5
6
7
8
9
10
PERIOD
BIRTH
JUV
EMERG.
Site 3 1983 R
Site 3 1984 M
Site 4 1984 R

Fig. 3.5 - Chases of resident yearlings by adult females on Sites 1 and 2. Symbols as in Figure 3.3.

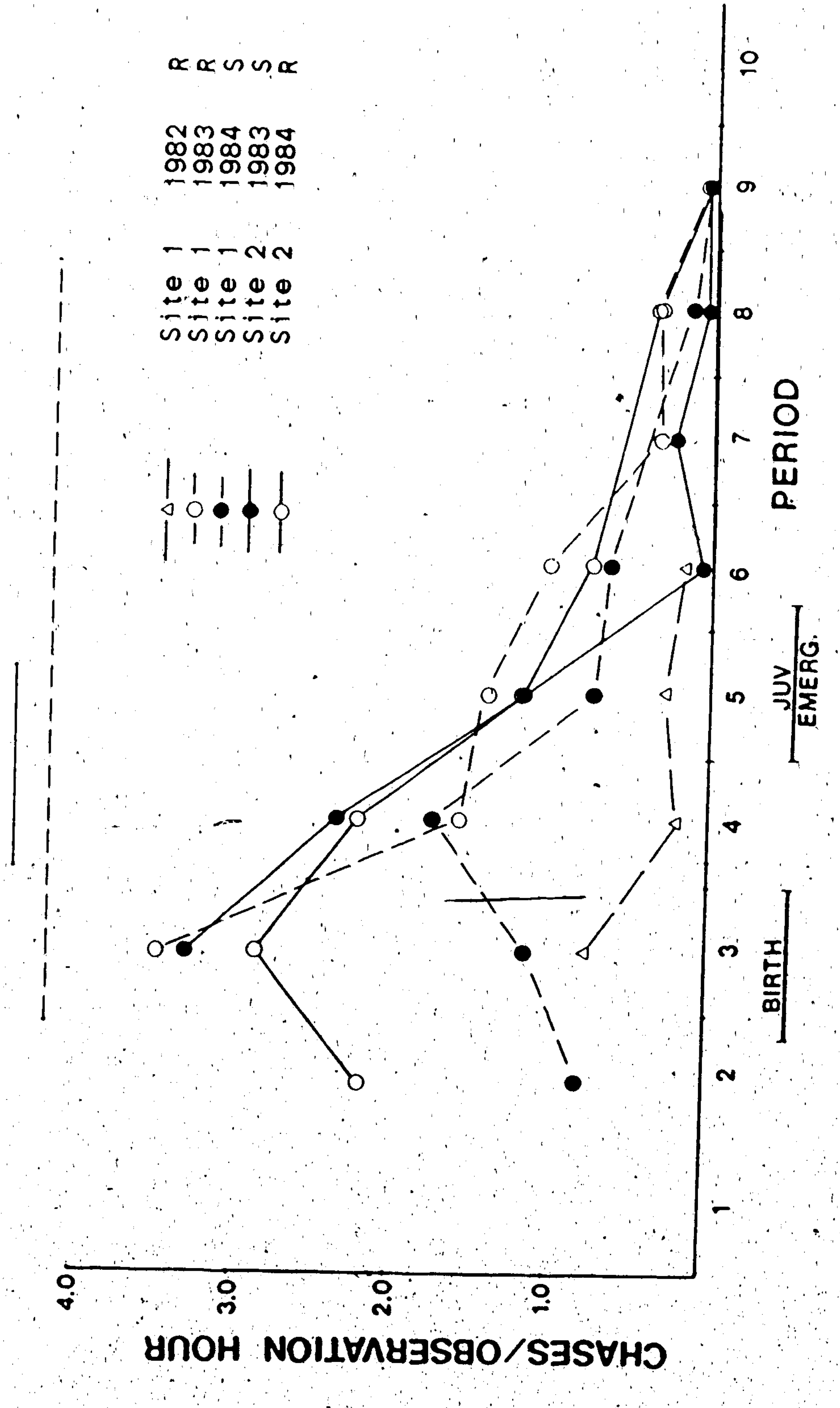

CHASES/OBSERVATION HOUR
4.0
3.0
2.0
1.0
PERIOD
1
2
3
4
5
6
7
8
9
10
BIRTH
JUV EMERG.
Site 1 1982 R
Site 1 1983 R
Site 1 1984 S
Site 2 1983 S
Site 2 1984 R

Fig. 3.6 - Chases of resident yearlings by adult females on Sites 3 and 4. Symbols as in Figure 3.4.

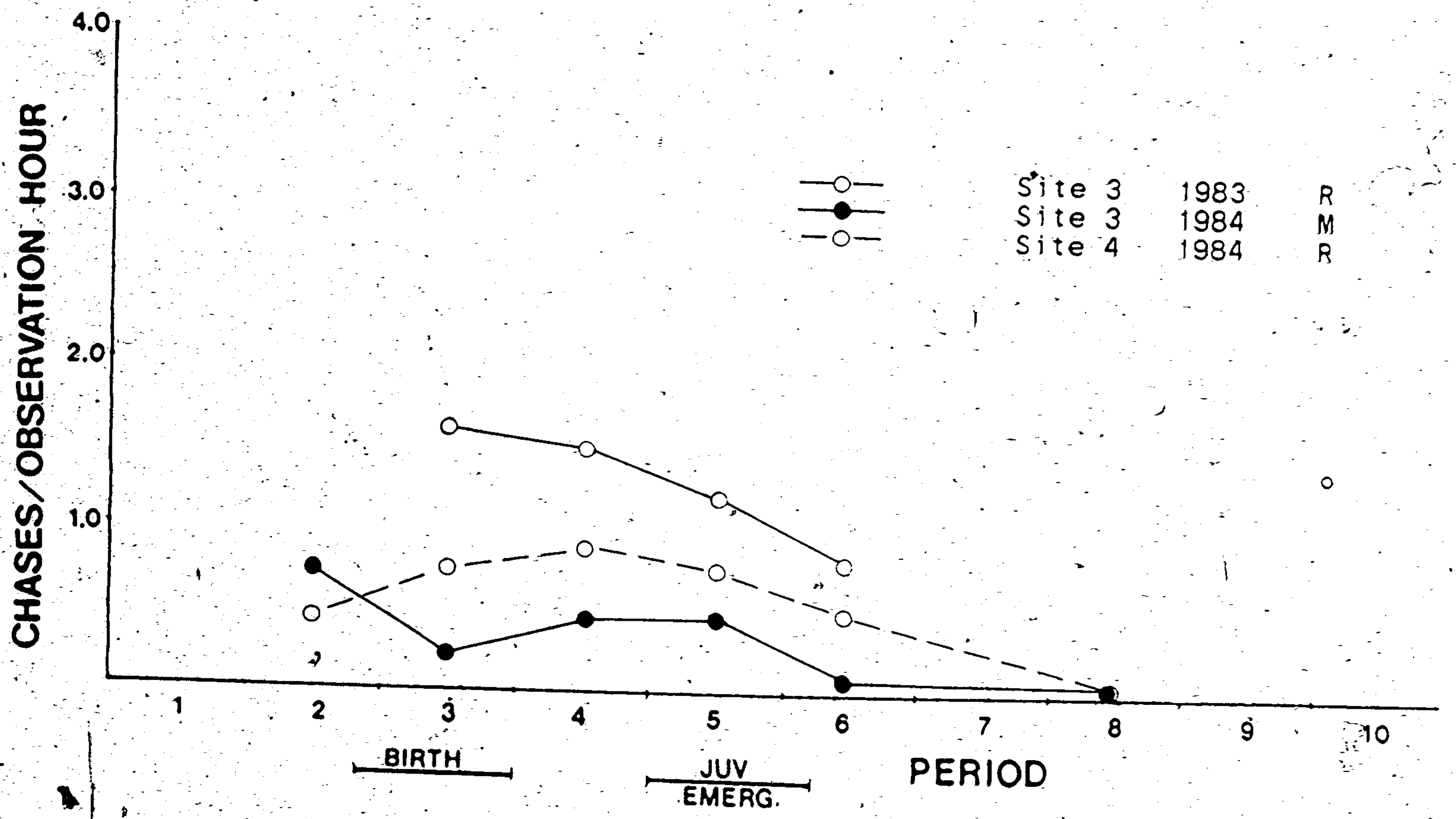

CHASES/OBSERVATION HOUR
4.0
3.0
2.0
1.0
1
2
3
4
5
6
7
8
9
10
PERIOD
BIRTH
JUV
EMERG.
Site 3 1983 R
Site 3 1984 M
Site 4 1984 R

Fig. 3.7 - Chases per hour present, and attendance, of dispersers (D) and nondispersers (N) on 1984 Site 2 (reference plot). Solid lines are rates at which individual yearlings were chased while on the site, grouped according to dispersal status. Broken lines are attendance (scans seen / total scans).

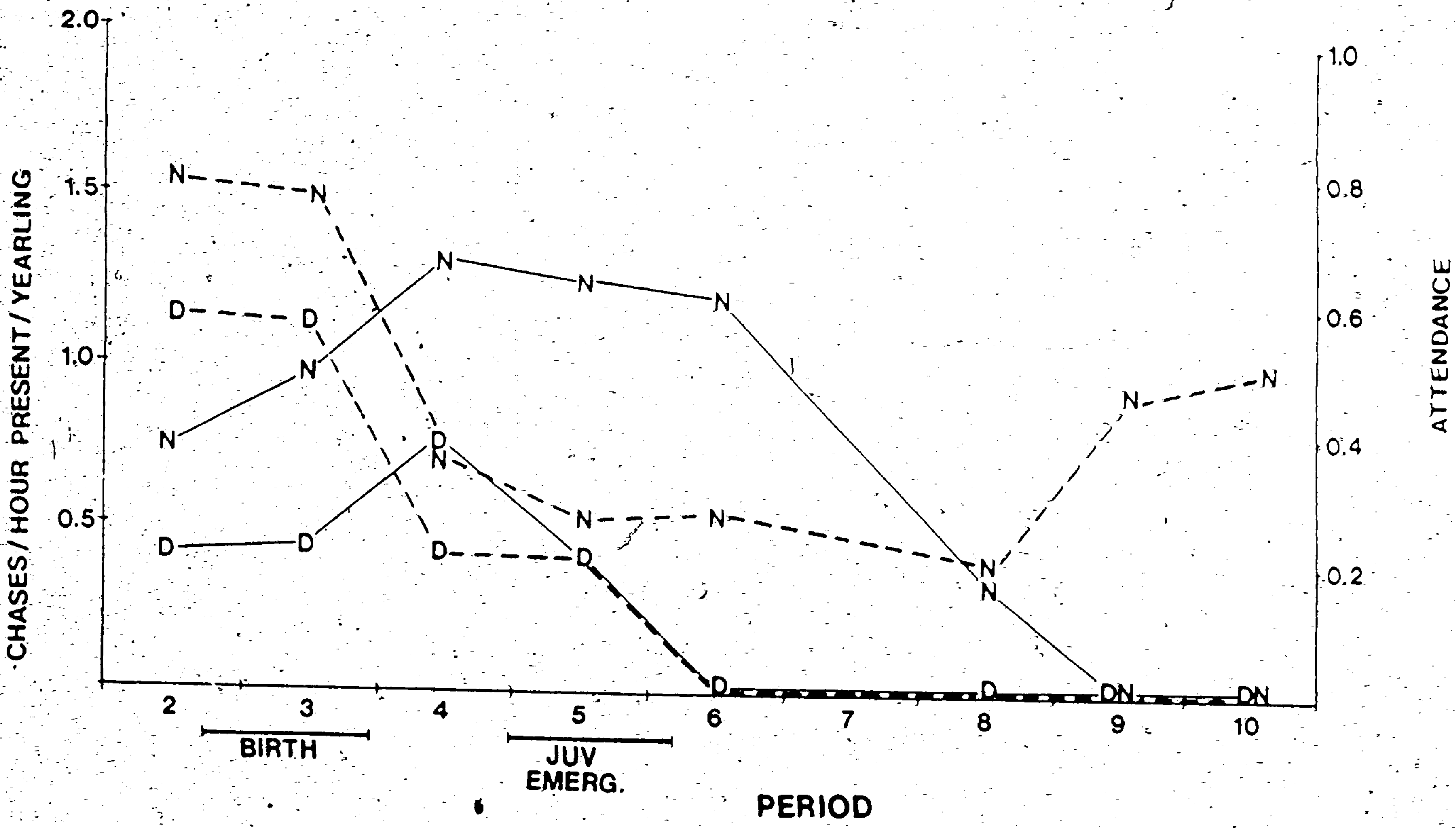

CHASES/HOUR PRESENT/YEARLING
2.0
1.5
1.0
0.5
ATTENDANCE
1.0
0.8
0.6
0.4
0.2
N
D
DN
2
3
4
5
6
7
8
9
10
BIRTH
JUV EMERG.
PERIOD

Fig. 3.8 - Chases per hour present, and attendance, of dispersers and nondispersers on 1983 Site 2 (sedation plot). Symbols as in Figure 3.7.

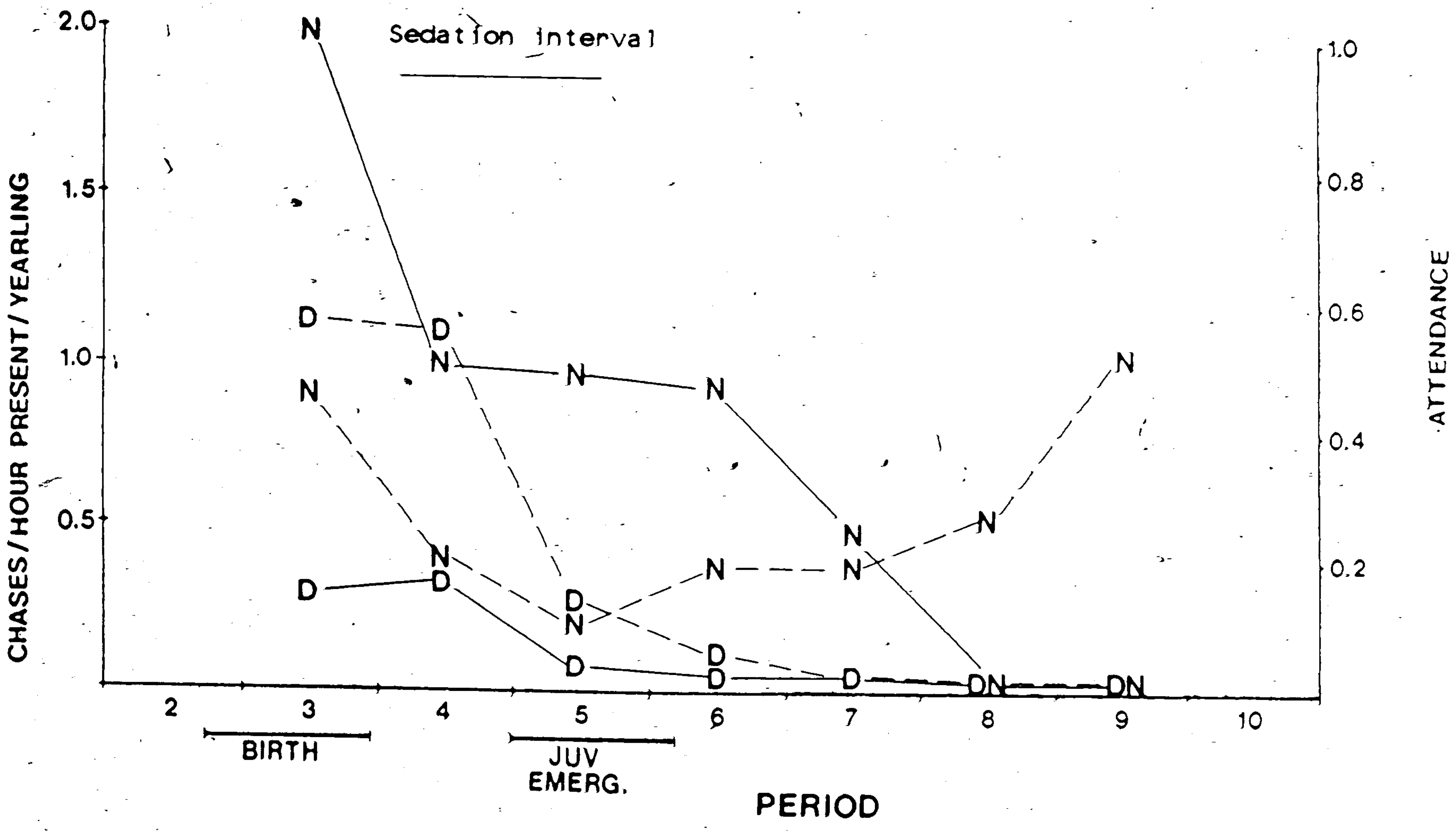

Sedation interval
CHASES/HOUR PRESENT/YEARLING
2.0
1.5
1.0
0.5
ATTENDANCE
1.0
0.8
0.6
0.4
0.2
2
3
4
5
6
7
8
9
10
BIRTH
JUV
EMERG.
PERIOD
N
D
DN

Fig. 3.9 - Chases per hour present, and attendance, of dispersers and nondispersers on 1983 Site 1 (reference plot). Symbols as in Figure 3.7.

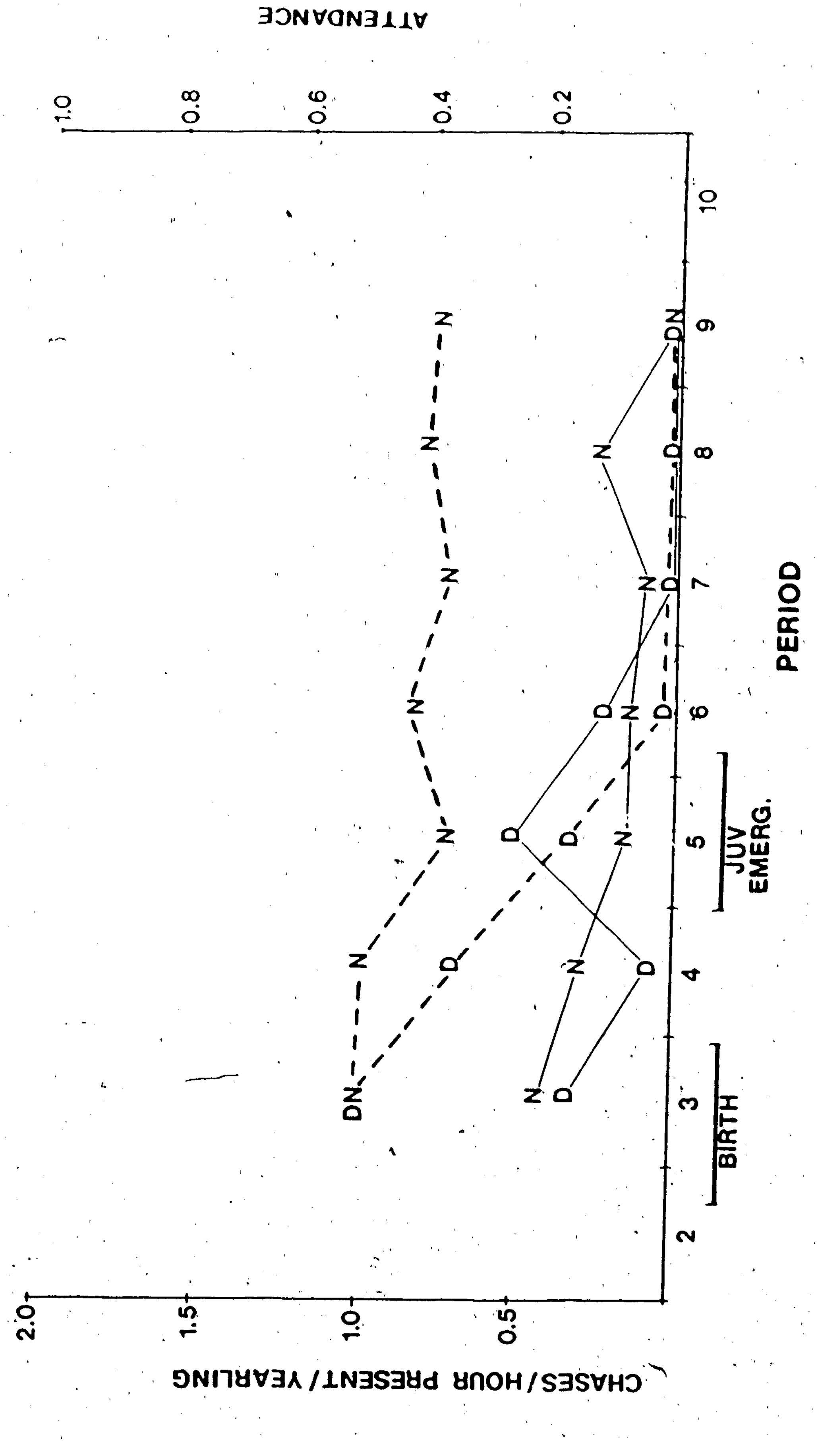

ATTENDANCE
1.0
0.8
0.6
0.4
0.2
CHASES/HOUR PRESENT/YEARLING
2.0
1.5
1.0
0.5
PERIOD
2
3
4
5
6
7
8
9
10
BIRTH
JUV
EMERG.
D
N
DN

Fig. 3.10 - Chases per hour present, and attendance, of dispersers and nondispersers on 1984 Site 1 (sedation plot). Symbols as in Figure 3.7. Horizontal line shows sedation interval.

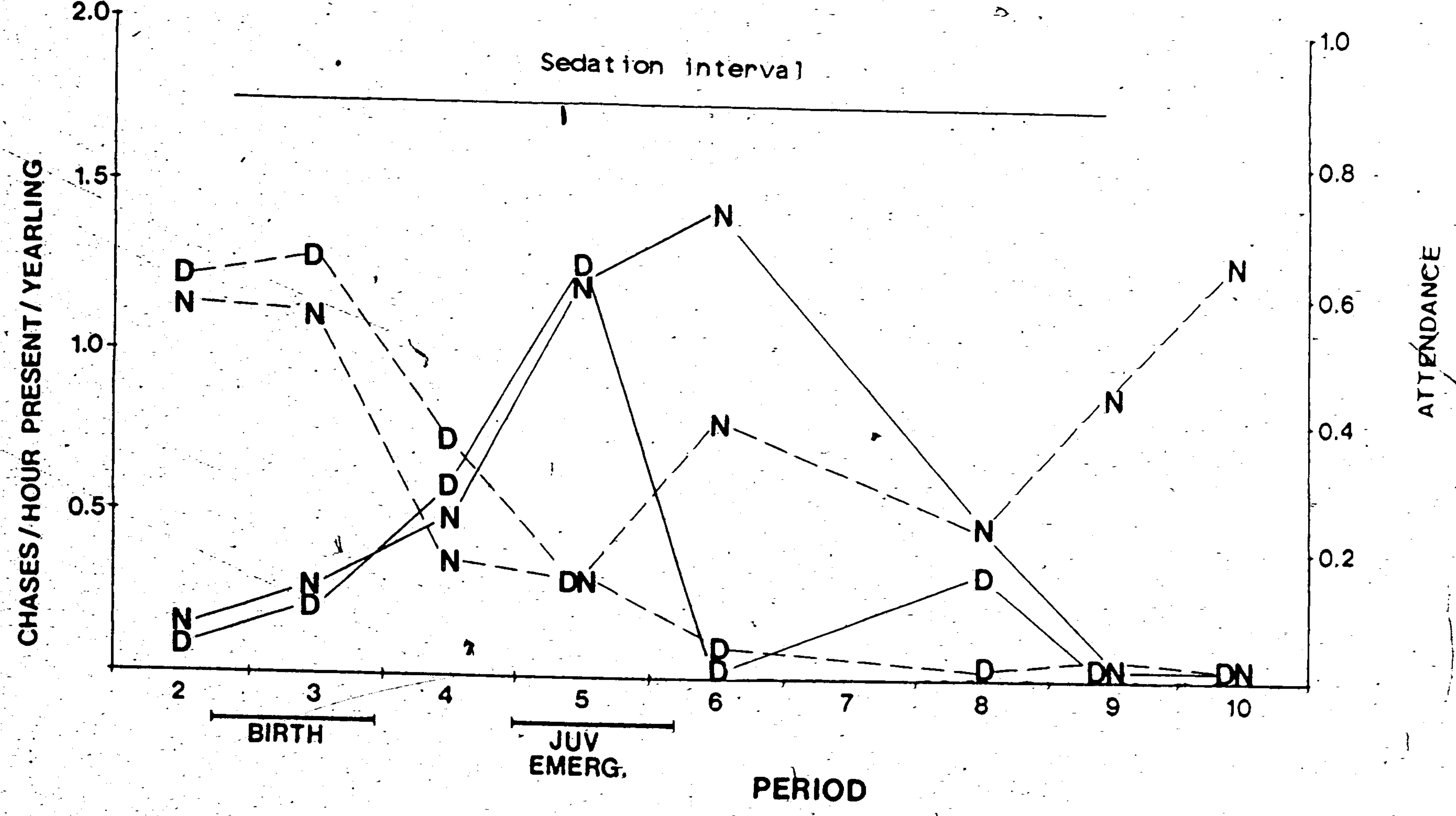
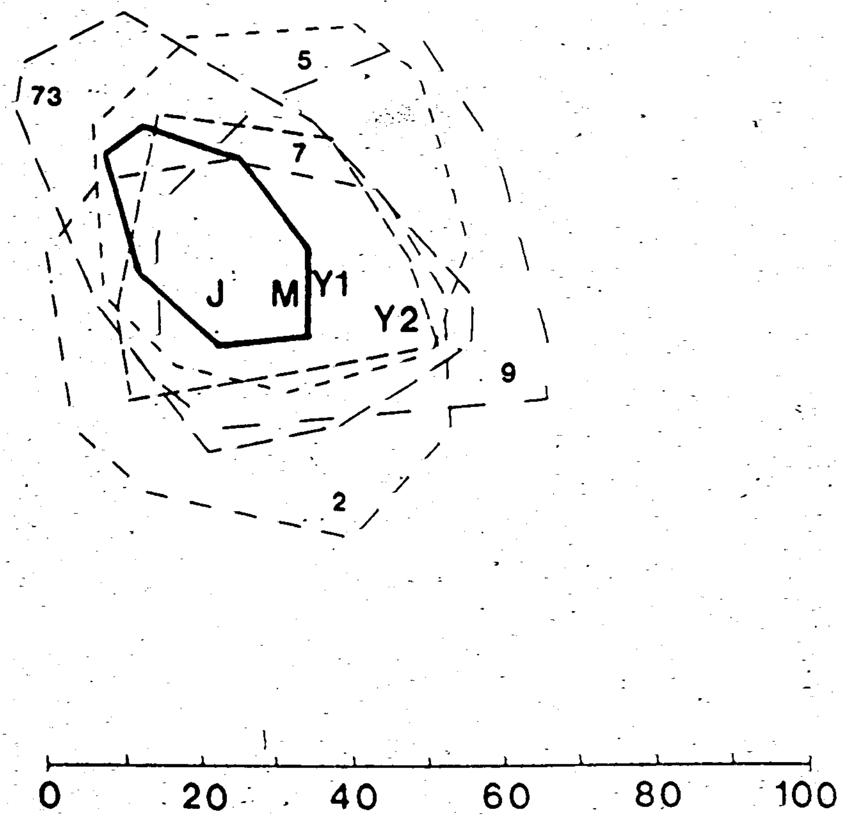
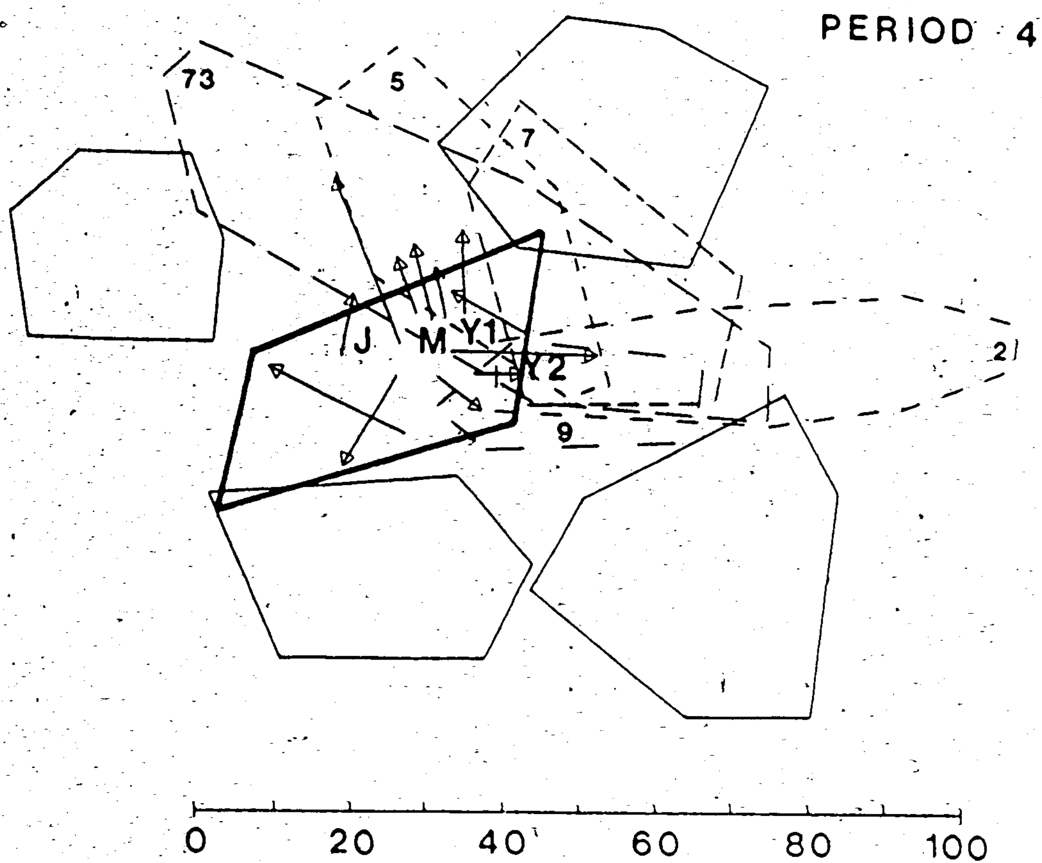

Sedation interval
CHASES/HOUR PRESENT/YEARLING
2.0
1.5
1.0
0.5
ATTENDANCE
1.0
0.8
0.6
0.4
0.2
2
3
4
5
6
7
8
9
10
BIRTH
JUV
EMERG.
PERIOD
D
N
DN

Fig. 3.11 - Home ranges and burrows of adult female #77 and her five yearlings. Burrows are: M, main maternal burrow; J, natal burrow where juveniles first emerged; Y1, burrow where yearlings usually slept before the birth of new litters; Y2, burrow where yearlings slept after the birth of new litters. Home ranges of #77 (thick line) and her numbered yearlings (dashed lines) are shown for three periods: A, Period 2; B, Period 4; C, Period 6. Home ranges of some neighbouring adult females (thin lines) are shown for Period 4. Arrows are chases by adult female #77. Scale in metres.

PERIOD 2





PERIOD 4

PERIOD 6

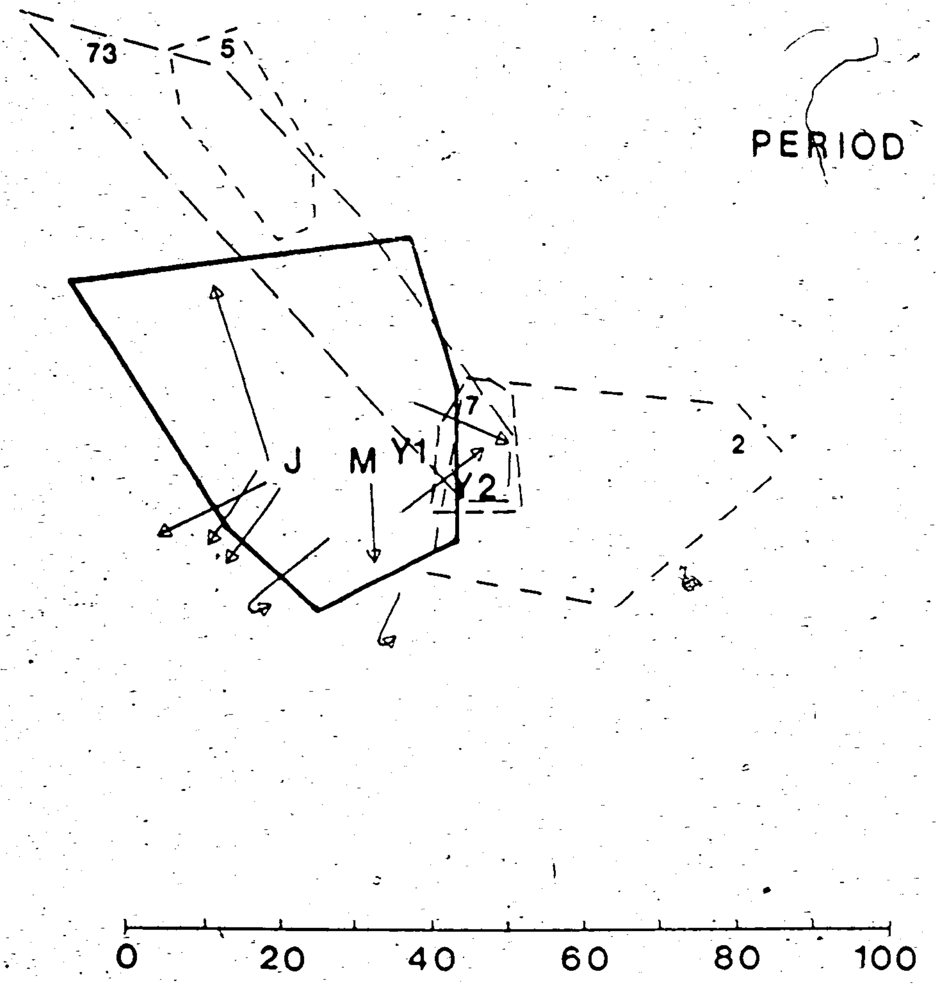


Fig. 3.12 - Example of a yearling overlapping the home range of its mother, but avoiding the defended area where juveniles were located. Yearling female #19 (solid line) maintained much the same home range throughout the summer, but avoided the central part of her mother's home range (heavy dashes) during Periods 3-5. Dots and numbers represent #19's locations during Period 3. Home ranges of surrounding adult females (light dashes) and their juvenile emergence burrows (J) are shown. Scale in metres.

PERIOD 3

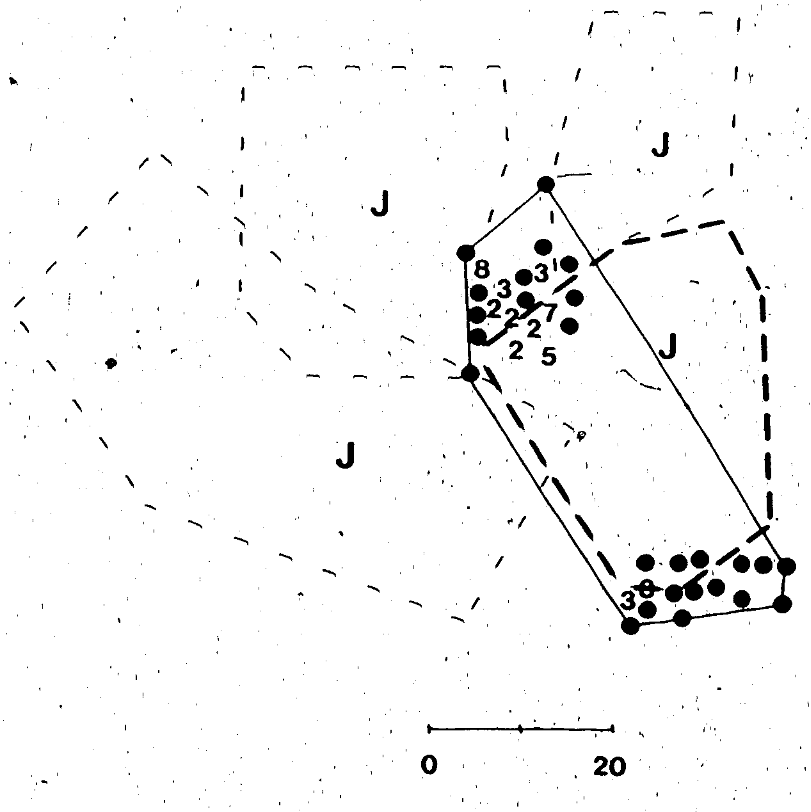
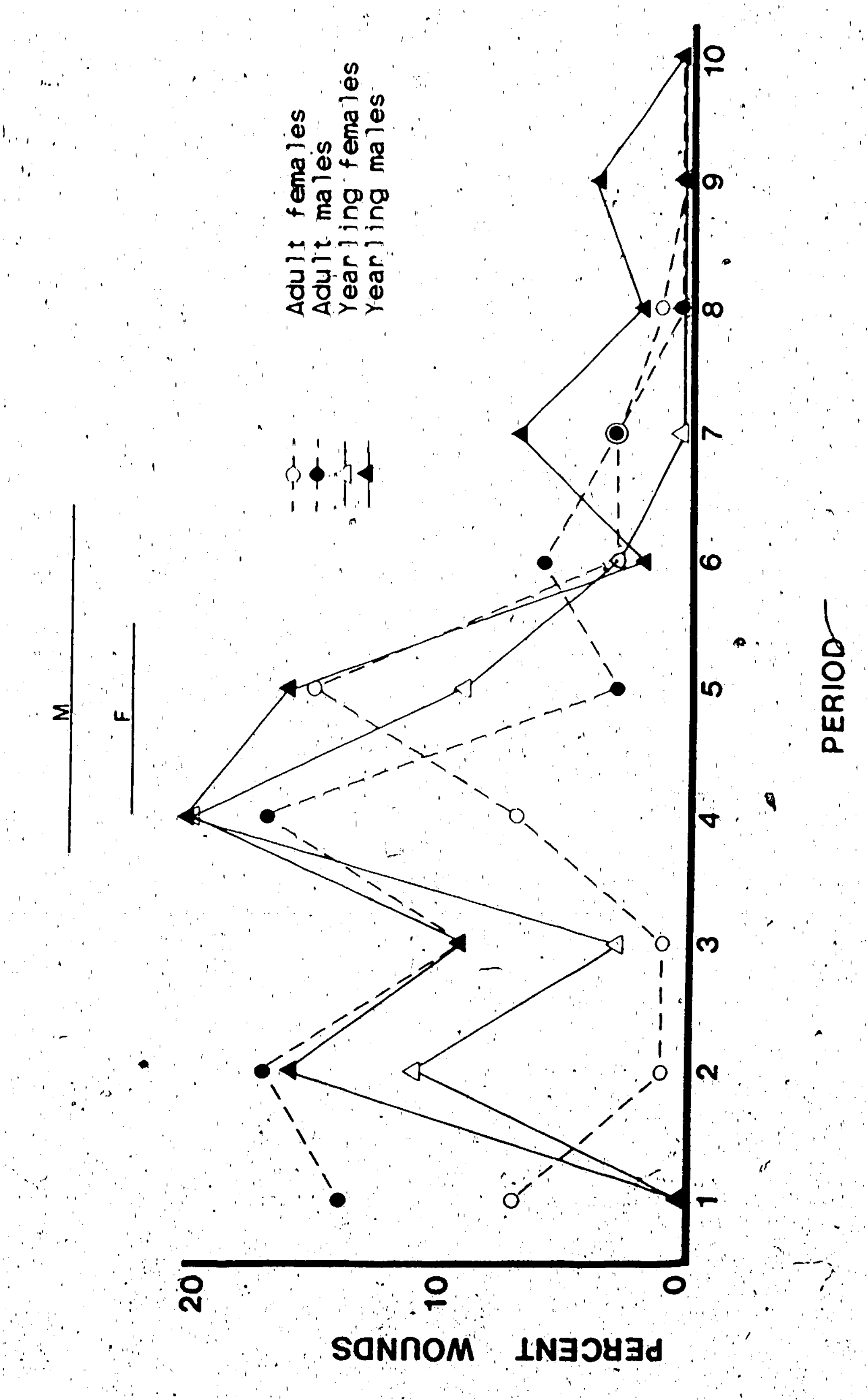


Fig. 3.13 - Seasonal pattern of wounds observed on Columbian ground squirrels from Sites 1-4 in all years. Horizontal lines show the dispersal period for male (M) and female (F) yearlings.


M
F
Adult females
Adult males
Yearling females
Yearling males
PERCENT WOUNDS
20
10
0
1
2
3
4
5
6
7
8
9
10
PERIOD

V. CONCLUDING DISCUSSION

I believe that the aims of this project were fulfilled. Precise details of yearling Columbian ground squirrel dispersal were quantified using known dispersers (i.e. dispersal was distinguished from on-site mortality). The possibility that the mid-June dispersal of yearlings is triggered by attaining a critical weight was explored and rejected. The role of aggression as a proximate factor was investigated and found to operate in two ways: maternal aggression of reproductive adult females appeared to synchronize dispersal of "surplus" yearlings from their natal home ranges; competition among yearlings apparently determined which yearlings remained philopatric. Although different types of data were emphasized in each of the three papers (radio-locations, body weights, and behavioural observations), the results were mutually supportive. For example, competition for space on the natal area in June seemed to be indicated by high rates of chases, defence of space by adult females, aggressive yearling interactions, subterranean spacing of yearling groups, the timing of wounds, the loss of weight by yearlings, and the reasonably close fit of dispersal distances to competition models (Murray 1967, Waser 1985).

In view of the above findings, I suggest that there are several avenues that merit further exploration. Competition among yearling groups should be studied in more detail, particularly on sites where adult females do not interfere with yearling interactions (this may require female removal). Specific details within maternal home ranges - locations of existing and evolving burrow systems, sleeping quarters of radio-collared mothers and offspring through each season, ownership of maternal burrows and home ranges among years, and use of space by any accumulating philopatric kin - should be monitored in a longterm study. Finally, lifetime reproductive prospects of dispersers and nondispersers should be quantified and compared.

This project was limited in scope to one species of ground squirrel that disperses as a yearling in part of its range. However, delayed dispersal is found among a variety of animals including marmots (Barash 1973, Downhower and Armitage 1981, Webb 1981), black-tailed prairie dogs (Garrett et al. 1982), sloths (Sunquist 1986), and primates (Packer 1979, Pusey 1980, Lyon et al. 1985), and attention should be focussed on the role of behavioural cues affecting those species. The possibility that adult aggression may be involved in dispersal of juvenile ground squirrels has been largely dismissed (Holekamp 1984); however, the work of Michener (1981) and Pfeifer (1980, 1982) suggests that juvenile competition and territoriality may be associated with dispersal. A number of papers dealing with species other than ground squirrels have pointed to possible relationships among competition, territoriality and dispersal (Rusch and Reeder 1978, Randall 1984, Whitworth and Southwick 1984), or served to emphasize the role of adult females in spacing behaviour (Savidge 1974, Hansen and Nixon 1984, Graf 1984). I suspect that further developments in these areas will be forthcoming.

There has been much discussion in recent literature about ultimate forces that may underlie dispersal (Greenwood 1980, Moore and Ali 1984, Liberg and von Schantz 1985). Many authors have used deductive reasoning or extrapolations from laboratory work to arrive at their conclusions; few have used field-demonstrated proximate factors as stepping stones to approach their evolutionary arguments. Krebs and Davies (1981) have pointed out that proximate and ultimate factors must be viewed on separate levels, but an understanding of the more tangiable proximate factors may be useful in determining what is reasonable to propose in terms of evolutionary arguments. Based on the results of this study, I suggest that there is no need to envision animals assessing abstract qualities such as relatedness on natal areas before "deciding" to disperse in avoidance of close inbreeding, or in order to settle at suitable distances to achieve optimal inbreeding. Columbian ground squirrels apparently responded to simple proximate rules such as: 1) "move to avoid aggression", which was typically associated with a defensive mother or a competitive sister, and 2) "travel only as far as the first vacant home range" (Paper 1). Animals responding to <u>any</u> <u>cues</u> that eventually resulted in evolutionary benefits would presumably prosper, leaving progeny that would also tend to focus on appropriate proximate cues. The stimulus used as a cue might have no direct relationship to the ultimate advantage achieved. For example, the simple act of delivering, or moving to avoid, an immediate "bite on the butt" might result in increased inclusive fitness for a mother and her offspring because they responded in ways that eventually decreased probabilities of close inbreeding (Pusey 1980, Hoogland 1982, Cockburn et al. 1985), achieved a degree of beneficial inbreeding (Smith 1979, Shields 1983), solved problems of competition for resources (Lidicker 1975, Boutin et al. 1985), or increased their inclusive reproductive potential (this study).

In terms of historical proximate explanations, my conclusions appear to support some features of Christian's (1970,1971) Social Subordination Hypothesis in that yearlings were apparently encouraged to emigrate through aggression and tended to settle in suboptimal areas. Yearling Columbian ground squirrels were not subordinate to juveniles but since mothers protected juveniles, yearlings were most subject to the social pressures in effect and many solved the problem by leaving (Paper #3). Christian proposed that density and adult-male aggression were related to dispersal; I found that density was a crude estimate of a more important variable, the number of offspring sharing the maternal home range, and that adult female aggression apparently played a key role associated with the timing of dispersal. There was no evidence of "innate" dispersers leaving without cause (Howard 1960) or of genetic-behavioural polymorphisms predisposing certain individuals to disperse (Krebs 1978) except in the sense that females tended to be more site-tenacious. A few features of Lidicker's (1975) Presaturation-Saturation Hypothesis seem applicable in that surplus yearlings were not permitted to endanger the finite resources of maternal home ranges (i.e. they might be considered "saturation dispersers" that emigrated in response to pressures associated with new litters); however, Lidicker's ideas are stated in terms of density and carrying capacity, which reveal little of the proximate mechanisms described for Columbian ground squirrels. Bekoff's (1977) Social Cohesion Hypothesis suggests that social interaction prior to emigration is more important than agonistic interaction at the time of dispersal; this hypothesis proposes the existence of social and asocial individuals, and emphasizes the role of avoidance rather than aggression. Yearling Columbian ground squirrels competed aggressively before dispersing (Festa-Bianchet and King 1984:165, this study) whereas earlier interactions had been playful. Some avoidance was seen, but this appeared to be the result of learning from aggressive interactions rather than an indication of asocial individuals. In short, elements of several historical hypotheses seem to apply to Columbian ground squirrel dispersal, but none of the four provided an adequate explanation by itself. I have outlined a proximate explanation that describes the yearling dispersal I observed (Paper #3), and which may have applicability to a number of delayed dispersers including marmots and black-tailed prairie dogs.

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VI. APPENDIX 1 - An Improved Radio-collar For Sciurids

Some sciurid rodents can be difficult to study using telemetry because of their ability to remove radio-collars (L.S. Davis and J.O. Murie, pers. comm.; Madden and Giacalone-Madden, J. Wildl. Manage. 46: 525-527). In 1982, I outfitted 25 yearling Columbian ground squirrels (Spermophilus columbianus) with R-type collars (a loop of wire serves as both the transmitting antenna and neckstrap) manufactured by the AVM Instrument Company of Dublin, California. Within two weeks, more than half of the ground squirrels had lost their radio-collars. Recovery of some collars showed that the wire neckstrap had been bitten through (apparently by another squirrel) or had fatigued where the solid-core wire of the neckstrap enters the dental acrylic surrounding the transmitter and battery. These problems are not normally associated with R-collars; I have used similiar collars on rodents such as the eastern chipmunk (Tamias striatus) and least chipmunk (Eutamias minimus) without such losses.

Rather than risking changes in dispersal dates and hibernation success by surgically implanting and removing internal transmitters at sensitive points in the season, and in order to avoid the increased cost and limited adjustability of collars employing a solid brass band, I modified some R-collars in the following way. The thin solid-core wire neckstrap was replaced with a flexible 20-gauge multistrand wire. Fatigue at the wire-acrylic interface of the transmitter package was prevented by reinforcing the wire with a 1-cm length of 3/16 inch diameter polyolefin heatshrink tubing potted into the transmitter casing. The antenna/neckstrap was then wrapped in coloured PVC tape to minimize wear on the animals' fur, to guard against chewing, and to make visual identification possible. Collars were fastened using three nylon cinches ("cable tie fasteners") rather than with the conventional sleeve of heatshrink tubing; cinches provided better purchase on the supple multistrand wire and permitted frequent changes in order to accommodate collar-size to the rapidly growing yearlings. After testing these collars on captive animals, I had 40 more "modified R-collars" manufactured by the AVM Instrument Company.

The radio-collars performed well in the following two May-August seasons. Only one collar was known to be chewed off by another squirrel; I was aware that the neckstrap was being chewed for several days, but I was unable to capture the animal in time to save the collar. Another four radio-collars were severed during five cases of predation by badgers. Predation by weasels, mink, coyotes and raptors did not damage the radio-collars.

Entire packages including SM1 transmitter, Hg675 battery, and modified neckstrap (minus tape) weighed 8 to 9 g - approximately 2 to 3% of the weight of yearling Columbian ground squirrels. A standing observer with a handheld yagi antenna could receive signals from an aboveground animal at a range of approximately 300 m distance (occasionally up to 600 m); belowground animals could be detected from about 100 m distance. Radio reception of greater than 1 km could be obtained from atop ridges and foothills overlooking surrounding meadows.

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VII. APPENDIX 2 - Predator Assessments

Badger predation - Two cases of mortality were attributed to badger predation because the burrows in question were completely dug up, coincident with the disappearance of the squirrel and loss of radio contact; bits of fur were evident in both cases and a tail was found in one case. A third case also involved massive digging and disappearance of the squirrel, but the collar continued to transmit from below ground until recovered. Several families of badgers lived in the area, and much evidence of badger activity was seen.

A number of above-ground badger attacks were witnessed in which a badger charged at a ground squirrel, trying to overtake the squirrel before it reached its burrow. Two of six such attacks (on unmarked animals) were successful, both in tall grass that provided cover for the badger. When two radio-collared yearlings suddenly disappeared in tall-grass habitat where surface-hunting badgers had been seen for several days previously, badger predation was suspected. The facts that radio contact was lost suddenly in the post-dispersal phase (late July) and that both ground squirrels had been radio-located near their burrows hours earlier supported the idea of predation. Badgers were the only predators known to disrupt radio-transmission by severing collars, and our widespread attempts to receive signals from atop surrounding foothills and ridges weighed against the possibility that the yearlings were carried off by local predators.

Weasels or mink - If predation occurred below ground with no disturbance to the burrow system, I concluded that weasels or mink were responsible. Both mustelids were seen in the area, and weasels were observed investigating ground squirrel burrows on several evenings. Some cases involved intact squirrels with punctured skulls; in other cases, only bits of fur remained. One dead yearling was radio-located in a beaver dam where a protective mink was guarding it.

Raptors - One radio-collared yearling was found dangling in a bush where it had apparently been dropped from above. The carcass was largely intact, but the thorax had been picked open. I drove a Swainson's hawk from a freshly killed ground squirrel later in the summer and noted that the thorax had been picked open in a similar manner.

Coyotes - A number of collars were found under low bushes in the woods, typically with no carcass but with bits of fur in evidence. The collars were relatively unscathed and appeared to have been licked clean. Often a tail, jawbone or stomach were present. I attributed such kills to coyotes because of the circumstances and locations of the remains, and because coyotes had recently been seen stalking ground squirrels in those areas.

VIII. APPENDIX 3 - Behavioural Categories Used to Classify Visual Observations

Single Squirrel Categories

feeding

standing erect (on hind feet)
sitting erect
sitting slouched (curved back)
standing on four legs, head up
standing on four legs, head down
crouched (like a sphinx)
lying down
rolling
stretching

near burrow
on mound or in burrow opening
entering burrow
leaving burrow

self-grooming
cheek-marking
twist-marking
ventral drag

looking
sniffing
scraping
digging
collecting nest material
carrying nest material
disappeared from view
defecating
climbing
running
walking
loping, bounding, hopping

Interaction Categories

cohesive

allogrooming
mounting
playing
kissing
following
approaching
leaning against
sniffing
tolerating within 3 m

agonistic

fighting (two combatants)
attacking (one aggressor)
chasing (chaser and chasee)
running at[1]
displacing[2]
running parallel
standing broadside
jumping back
retreating (rapidly withdrawing without pursuit)

social signals

tail-flick
tail-bush
chirp
growl
squeal
toothchatter
alarm call

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1 - One animal runs at another, resulting in further aggressive acts or no obvious interaction or (rarely) cohesive interactions, depending on the identities of the two squirrels involved.
2 - Animal A approaches Animal B but B slips away, surrendering its previous location to A.

IX. APPENDIX 4 - Demographic Information

Table A1 summarizes adult and yearling populations of study sites, which were used to calculate spring densities (Table 3.2). All sites were flagged as one-hectare grids but the growth of shrub and grass cover on Site 4 limited clear observation to those squirrels living on an area of 0.5 ha. Visibility was excellent on Site 2 but the squirrels there confined most of their activities to an area of 0.5 ha around several clusters of burrows, as mentioned previously. In 1984, only 0.7 ha of Site 1 could be rigorously controlled with sedatives, therefore residents of this area were considered to be the study population.

I suspect that the number of adult males that were truly occupants of study sites was lower than shown below. Adult males ranged over large areas relative to the one-ha grids. Some adult males did not appear to have sleeping burrows on study sites, but they were observed regularly in scans and were thus included.

Table A1 - The number of adult and yearling ground squirrels on each site in May after spring emergence. Adults are in bold type. Symbols "F" and "M" refer to females and males.

Year	Site 1		Site 2		Site 3		Site 4	
	F	M	F	M	F	M	F	M
1982	**8**	**3**	-		-		**5**	**2**
	6	5	-		-		4	4
1983	**6**	**4**	**12**	**3**	**7**	**5**	**5**	**2**
	7	8	3	8	5	7	3	5
1984	**11**	**3**	**7**	**3**	**9**	**7**	**6**	**4**
	6	3	1	5	2	3	3	2

X. APPENDIX 5 - An Example of Dominance Assessment

Dominance within spring groups of yearlings was determined by ranking individuals according to the number of times they chased, or were chased by, other members of their group. This was straightforward in groups of two or three yearlings; in more complex cases, yearlings were arranged in a dominance matrix (Lehner 1979)[3] according to chases given and received. In the example shown (Table A2), dominance decreases from left to right. Yearling female #2 chased all others and was not chased herself, whereas yearling female #73 was chased by all others and initiated no chases. The three fights (2 versus 9, 7 versus 73, and 9 versus 5) were won by the underlined contestants and supported the dominance hierarchy shown by Table A2. After Period 6, the dominant individual (#2) remained and all other group members dispersed.

TABLE A2 - A dominance matrix of five yearlings from the same spring group.

Chasee	Chaser				
	2	7	9	5	73
2	-	0	0	0	0
7	2	-	0	0	0
9	3	2	-	0	0
5	2	2	4	-	0
73	5	3	3	6	-

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[3] - Lehner, P.N. 1979. Handbook of Ethological Methods. Garland STPM Press, New York.