

PATTERNS OF SEASONAL ACTIVITY AND
HOST-PARASITE RELATIONSHIPS FOR
FLEAS ASSOCIATED WITH
RICHARDSON'S GROUND SQUIRRELS,
SPERMOPHILUS RICHARDSONII, IN SOUTHERN
MANITOBA, CANADA

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of

Graduate Studies

The University of Manitoba

by

Leslie Robbin Lindsay

In Partial Fulfilment of the

Requirements for the Degree

of

Masters of Science

Department of Entomology

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BY

LESLIE ROBBIN LINDSAY

A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
of the degree of

MASTER OF SCIENCE

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ABSTRACT

The host-parasite relationships between several flea species and their host, Richardson's ground squirrel, Spermophilus richardsonii (Sabine), were evaluated at three localities in Manitoba during a three year study. Ground squirrels captured near Darlingford, Manitoba were infested with Neopsylla inopina (Rothschild), Opisocrostitis bruneri (Baker), Oropsylla rupestris (Jordan) and Rhadinopsylla fraterna (Baker). Opisocrostitis bruneri was the only one of these species infesting squirrels at the two sites near Winnipeg, Manitoba (designated Perimeter and St. Norbert).

Adult ground squirrels emerged during late March and early April, males approximately seven days before females. Juveniles first appeared above ground in late May and early June. Adult male squirrels immersed to hibernate from mid-June to early July; adult females from late July to mid-August; female juveniles before male juveniles. The last juveniles were captured in early September to mid-October.

At Darlingford, 268 individual squirrels were captured 2308 times during 1987-1989. At the two sites near Winnipeg, 184 individuals were captured 1689 times during the same period. Juvenile squirrels constituted 64.7% to 92.9% of the total captures and were the most frequently

recaptured stage in 1987 and 1988.

At Darlingford, 1,446 N. inopina, 4,657 O. bruneri, 12,506 O. rupestris and 379 R. fraterna were taken from S. richardsonii during 1987-1989. At the two sites near Winnipeg, 6,212 O. bruneri were collected from squirrels during the same period. Female fleas were usually collected more often than males for all flea species and the observed biweekly sex ratio (M/F) generally favoured females for all flea species.

With the exception of two weeks in April, N. inopina was present on less than 50% of the squirrels. There was one peak in observed mean intensity in April during 1988 and 1989. There were two peaks of prevalence and mean intensity for O. bruneri during May and August at Darlingford and near Winnipeg. During early April, early July and September there were peaks in the prevalence and mean intensity of O. rupestris. The prevalence of R. fraterna adults on Richardson's ground squirrels was generally below 10% and squirrels were rarely infested with more than one or two R. fraterna adults, except during early April and from mid-August to the end of the trapping season.

Nulliparous N. inopina predominated only during April and early May, when the majority of teneral individuals were also collected. Immatures and nulliparous O. bruneri adults predominated throughout April and May. At all sites, the

majority of teneral O. bruneri were taken from squirrels in July. Nulliparous O. rupestris females predominated in early June and occurred sporadically throughout the season. Parous females were numerous during most trapping intervals. Teneral O. rupestris adults were collected in large numbers in August (1987) and June (1988). Nulliparous R. fraterna were abundant only in April of 1988 and 1989 and teneral R. fraterna adults were collected only during April in 1989. The percentage of mated females varied over the season and was usually directly correlated with per cent parity for all flea species. Parous, mated females from all species were collected from squirrels throughout the entire season. Egg development in the different flea species was therefore not dependent on the estrous cycle of female S. richardsonii.

The seasonal activity of O. bruneri adults was not markedly different when this species shared its host with several other flea species compared to when O. bruneri was the only flea species infesting the squirrels.

Chapter I
INTRODUCTION

Several different flea species are associated with Spermophilus richardsonii (Sabine) (Richardson's ground squirrel) in Canada and the United States. Oropsylla rupestris (Jordan) is the most common flea of the Richardson's ground squirrel (Jellison 1947). While O. rupestris has been removed from a variety of other scuirid spp. and certain other mammalian hosts (i.e. Mustela, Canis and Lepus spp.) (Smit 1983), it has rarely been recorded outside the range of the Richardson's ground squirrel (Holland 1949, 1985) (Figs. 1,2). Opisocrostis bruneri (Baker) is found on Richardson's ground squirrels throughout most of the host's geographic distribution (Fig. 3). This flea species is also associated with the thirteen-lined and Franklin's ground squirrel (S. tridecemlineatus (Mitchill) and S. franklinii (Sabine), respectively) (Holland 1985; Smit 1983). Opisocrostis bruneri occurs within the range of these three species and where host distributions overlap, O. bruneri infests all three (Holland 1944). Neopsylla inopina (Rothschild) has been recorded from Richardson's ground squirrels in Alberta, Saskatchewan (Holland 1985), Manitoba

Figure 1. Geographic distribution of Spermophilus richardsonii (adapted from Hall 1981).

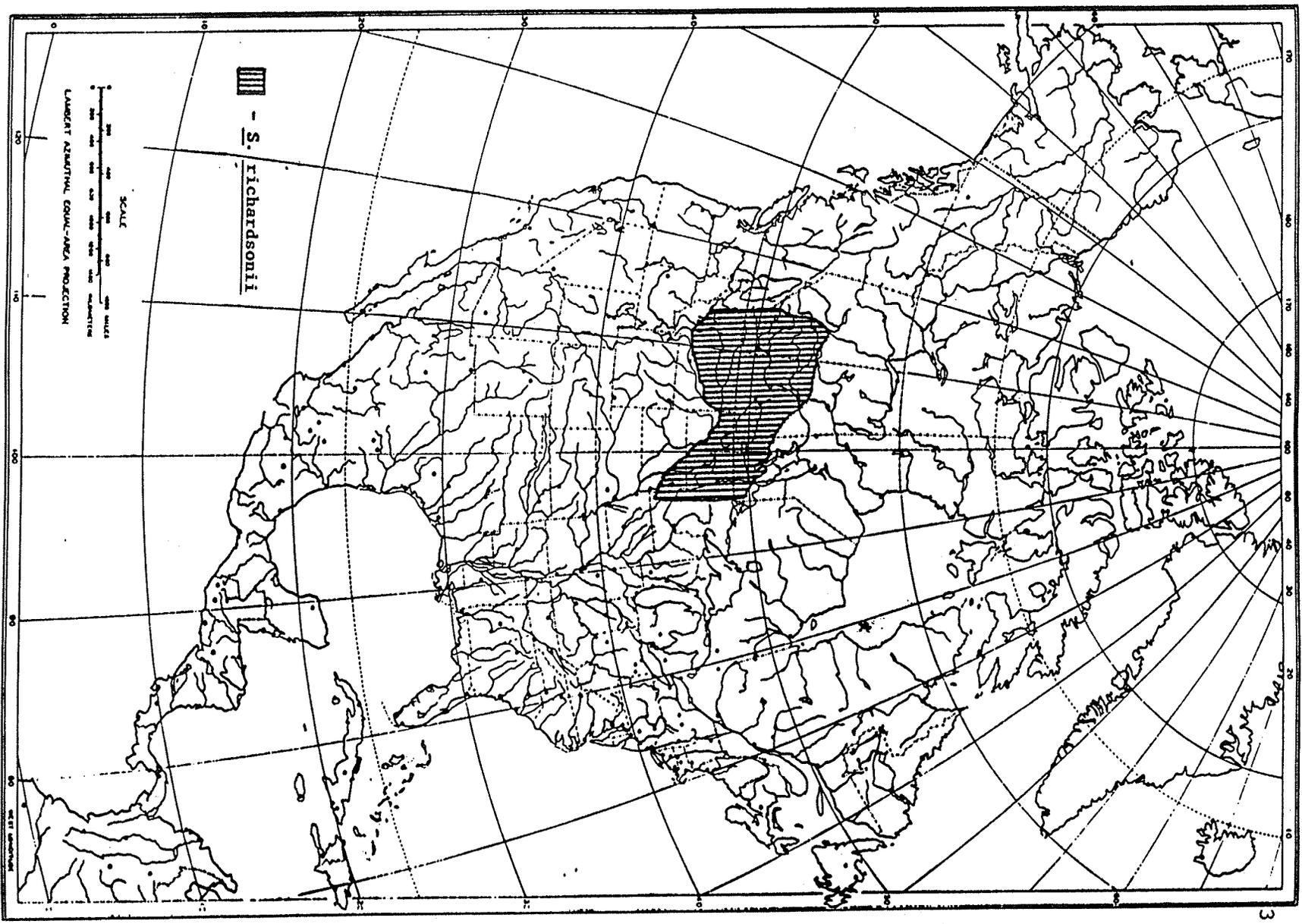


Figure 2. Geographic distribution of Oropsylla rupestris and its primary host, Spermophilus richardsonii (Adapted from Hall 1981, Holland 1985, Smit 1983).

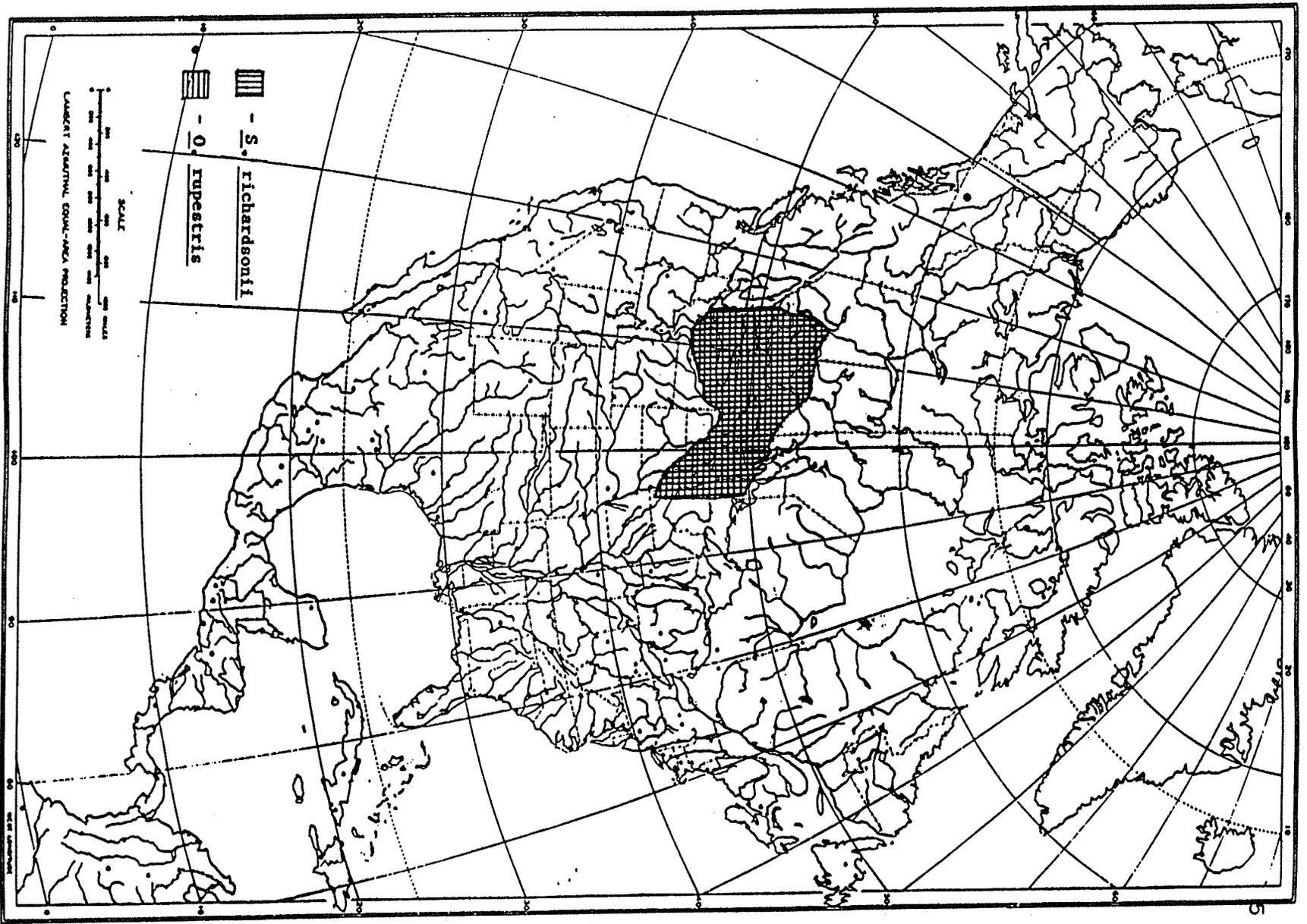
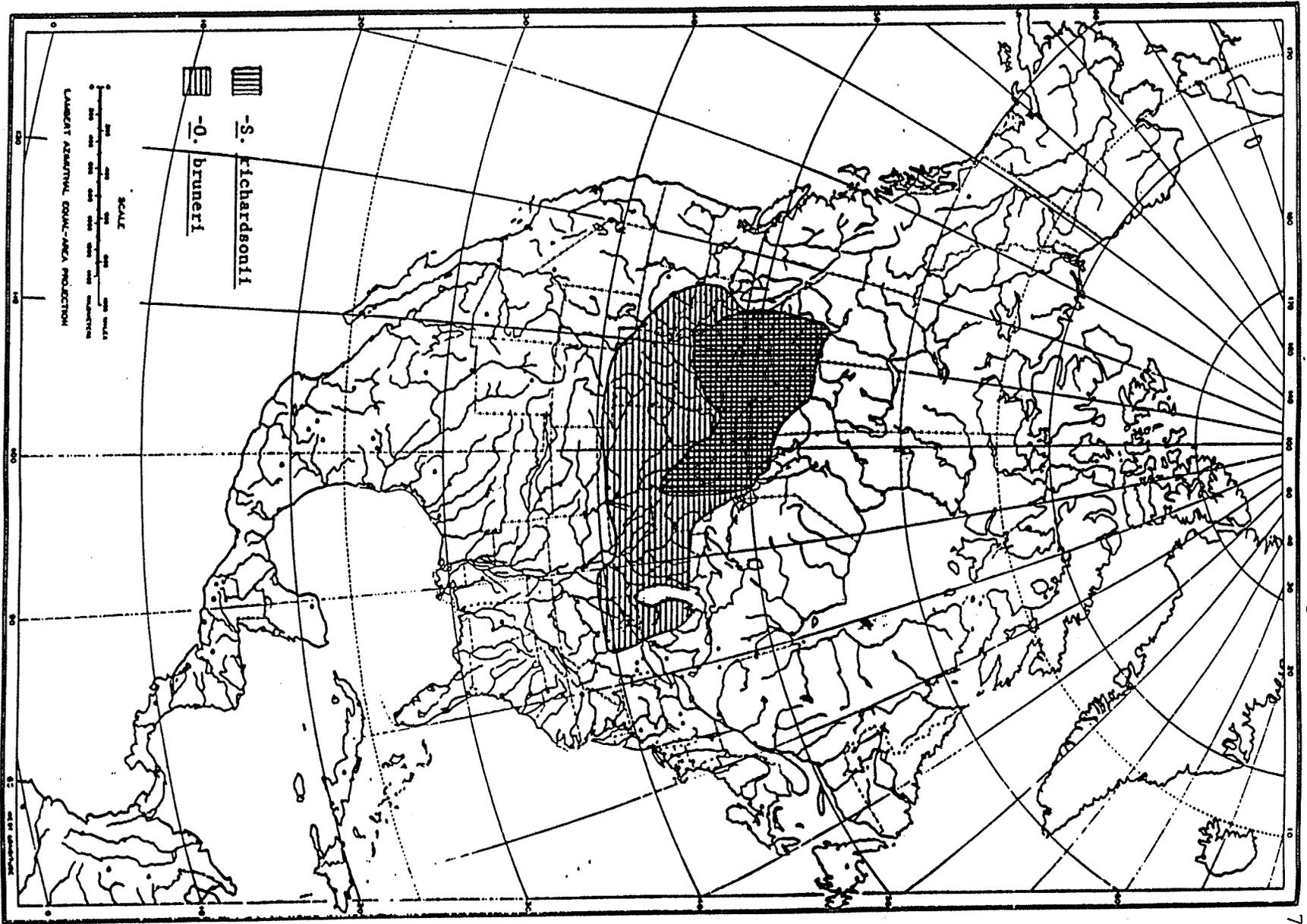


Figure 3. Geographic distribution of Opisocrostitis
bruneri and the host, Spermophilus
richardsonii (Adapted from Hall 1981, Holland
1981, Perdue 1980).



(Galloway and Christie unpublished) and Montana (Hubbard 1947). This species has been recorded from a variety of host species but is considered primarily associated with S. richardsonii (Holland 1985). Richardson's ground squirrels in Montana, Alberta, Saskatchewan and Manitoba are occasionally infested with Rhadinopsylla fraterna (Baker) (Galloway and Christie unpublished; Holland 1949; Hubbard 1947). This species has been collected from several rodent hosts but S. richardsonii is considered its primary host (Holland 1985). At certain localities, Richardson's ground squirrel can be concurrently infested with each of these flea species (Hilton and Mahrt 1971; Galloway and Christie unpublished).

Richardson's ground squirrels form colonies within a common habitat, though all members of the colony have their own burrows (Armitage 1981). Adult and yearling males emerge from hibernation in breeding condition in late March to early April in Saskatchewan (Michener 1984a). The monoestrous females emerge 7-10 days after males and most females are mated within a week (Michener 1985). Gestation is typically 22.5 days and parturition occurs 25-27 days after female emergence (Michener 1980b). Juvenile emergence occurs during the last week of May or early June in Saskatchewan (Michener 1974). Adult males generally immerge to hibernation in the first half of July followed by

nonreproductive and reproductive females, respectively (Michener 1984a). Juvenile females enter hibernation before juvenile males (Michener 1981). Above ground activity ceases during September or October in Saskatchewan (Michener 1974). The annual cycle of Spermophilus richardsonii has not been examined in Manitoba since the early 1900's (Seton 1909).

Five seasonal activity studies have been performed on O. bruneri from thirteen-lined, Richardson's and Franklin's ground squirrels. Hendricks (1967) reported the mean intensity (number of fleas/infested host) of O. bruneri adults collected from S. tridecemlineatus. The highest intensity of adult O. bruneri occurred during October and June. Kinzel and Larson (1973) examined the geographic distribution and relative abundance of O. bruneri and Thrassis bacchi bacchi (Rothschild) infesting S. tridecemlineatus in North Dakota. Regional differences in the abundance of these two species were attributed to geographic and climatic variation. Baesler (1975) collected O. bruneri from Richardson's ground squirrels in North Dakota. Peak numbers of O. bruneri adults were correlated with seasonal changes in rainfall. In each of these studies, the authors suggested that changes in flea activity were dependent on abiotic conditions. However, the data from each of these studies was collected from a number

of different locations, during different periods of the season. Variation in sampling locations may have confounded conclusions concerning flea seasonal activity and the proximate factors controlling flea activity.

Burachynsky and Galloway (1980) and Reichardt (1989) examined the seasonal changes in mean intensity and prevalence of O. bruneri adults on S. franklinii from a single sampling location near Birds Hill Park, Manitoba. Two peaks in observed mean intensity of O. bruneri occurred in May and early September, respectively. During June and July, juvenile emergence resulted in a depression of the number of adult O. bruneri/host.

Reichardt (1989) investigated the dependence of O. bruneri oogenesis on the estrous cycle of S. franklinii. Since the first peak of adult O. bruneri occurred during the breeding season of S. franklinii and was followed by a single peak later in the season, it was hypothesized that O. bruneri ovarian development was initiated by the levels of reproductive hormones of female hosts. Examples of this type of reproductive interdependence have been documented for the fleas, Spilopsyllus cuniculi Dale and Cediopsylla simplex (Baker) from various lagomorph hosts (Rothschild and Ford 1973). Reichardt (1989) also speculated that since O. bruneri is found almost exclusively on S. franklinii that "the high degree of association may have resulted in the

dependence of reproductive cues from S. franklinii to initiate reproduction in O. bruneri".

Ovarian development of S. cuniculi and C. simplex adults is initiated by the levels of circulating estrogen and prolactin in the pregnant female rabbit host, Oryctolagus cuniculus (L.) and Sylvilagus floridanus (Allen) (Rothschild and Ford 1973). Flea oogenesis or mating does not commence until females have fed on doe rabbits which are in latter stages of gestation. Fleas mate and females begin to deposit eggs in the nest of the host only after parturition. Maximum egg deposition occurs 7-10 days post partum. Thereafter, female fleas cease egg development and oogenesis does not occur until fleas are exposed to high levels of host reproductive hormone (Mead-Briggs 1964). This relationship is generally interpreted as a highly developed host-parasite association. Future generations of adult fleas are ensured a food source, since the eggs are deposited within nests occupied by the developing rabbit kittens.

The distribution of the fleas from Richardson's ground squirrels is not uniform in Manitoba (Galloway and Christie unpublished). Squirrels from southwestern regions of the province are routinely infested with up to seven flea species of ground squirrel fleas, including N. inopina, O. bruneri, O. rupestris and R. fraterna. At localities east

of the Manitoba escarpment, however, O. bruneri is generally the only species found on S. richardsonii (Galloway and Christie unpublished).

Several questions concerning the seasonal and reproductive activity of the fleas of Richardson's ground squirrel need to be addressed. (1) Although the seasonal activity of O. bruneri on S. franklinii has been determined, the seasonal activity O. bruneri (and all other flea species) from S. richardsonii has not been investigated. Richardson's ground squirrels emerge earlier in spring and enter hibernation later in the fall than Franklin's ground squirrels. Social interaction among Franklin's ground squirrels is not extensive compared to Richardson's ground squirrel (Michener 1984a). Thus differences in host life histories may result in changes in O. bruneri seasonal activity when this flea infests these two ecologically different squirrel species. (2) Spermophilus richardsonii may be infested with only O. bruneri, or simultaneously with one or more other flea species in addition to O. bruneri. Seasonal activity of O. bruneri may be altered when the host is shared with other flea species. (3) Oogenesis in O. bruneri is not dependent on the reproductive hormones of S. franklinii (Reichardt 1989). This does not preclude the possibility that reproductive activity of the various flea species infesting S. richardsonii is stimulated

by the hormones of this host.

The principle objectives of this study were: to determine the seasonal dynamics of S. richardsonii and its various flea species, establish the gonotrophic age structure of female flea populations, and determine the host-parasite relationships among populations of fleas on S. richardsonii. This information will be used to establish whether seasonal activity of O. bruneri differs when this flea species shares the host with the three other flea species and to determine whether ovarian development of any of the fleas from S. richardsonii is stimulated by the estrous cycle of the host.

Chapter II

REVIEW OF THE PERTINENT LITERATURE

RICHARDSON'S GROUND SQUIRREL

Description

Richardson's ground squirrels are about 30 cm long when fully grown, with short legs, armed with long, slightly curved claws and a stubby tail about a third of the body length (Banfield 1974). Small interval cheek pouches and short, broad ears are evident. Its skull is sturdy and rounded with a short rostrum, zygomatic arches spread posteriorly and the supraoccipital processes are prominent (Hall and Kelson 1959; Hall 1981).

The short pelage is drab or smoky grey dorsally deepening to yellowish on the cheeks, shoulders, flanks and thighs with the underparts and feet grey or buff (Wooding 1982). The crown is cinnamon brown; the rump is dappled with brownish transverse bars (Banfield 1974). The completely haired tail has an indistinct submarginal black band on top and its underside is clay-coloured (Hall 1981).

Richardson's ground squirrels have one annual moult. Hansen (1954) described the moult patterns of all species of Spermophilus as "diffuse type", in which no distinct moult line exists during the course of hair replacement. The

timing of the annual moult is unresolved. Moulting may occur during the summer (Banfield 1974; Wooding 1982; Woods 1980) or spring (Jones et al. 1983).

Distribution

Richardson's ground squirrels are common mammals of the prairies and open flatlands of Canada and north-central United States (Woods 1980). The species was originally described from specimens collected at Carlton house (Prince Albert), Saskatchewan in 1820 (Seton 1909). Since then S. richardsonii has been recorded from the following locations (Figure 1): CANADA - in Alberta, throughout the plains from the Montana border (in the south, west to the foothills) north as far as Battle Creek Valley, beyond the North Saskatchewan River to about 55° 10'N. West of Edmonton to the east end of Wabama Lake and southwest to about Rocky Mountain House, Caroline, Morley and Northeastern Waterton Park (Soper 1964; Banfield 1974; Hall 1981); in Saskatchewan, found north to Prince Albert National Park, southeast to about the latitude of Touchwood Hills (Hall 1981); in Manitoba, maximum numbers in the southwest grasslands, diminished populations eastward to about the longitude of La Broqueri (96° 27'W), with scattered colonies in the Emerson Area (Soper 1961). Occurs sparingly in the Interlake District and west of Lake Manitoba, and colonies have been established as far north as Lunder (Soper 1961;

Hall 1981). UNITED STATES - in Minnesota, squirrels are restricted to the western region of the state occurring no further east than the longitude of Fergus Falls (Hall 1981; Hazard 1982); occurs throughout most of North Dakota except south and west of the Missouri river (Jones et al. 1983); in South Dakota, restricted to the northeastern regions (Hall 1981); in Montana, prevalent throughout north and central regions (Jones et al. 1983), southwest to about Three Forks and Livingston, northwest to about longitude of Birch Creek and Toston (Hall 1981). In southwestern Montana populations of S. richardsonii overlap with S. elegans (Sabine).

Hybridization is rare with little genetic exchange between the groups (Jones et al. 1983).

Life History

The annual cycle of Richardson's ground squirrels is composed of a predictable sequence of events: vernal emergence from hibernation, breeding, gestation, lactation, juvenile emergence, prehibernatory fattening, autumnal immergence and hibernation until the subsequent spring (Michener 1984a).

Squirrel activity begins each year with emergence from hibernation. The timing of vernal emergence is correlated with latitude, altitude, aspect, snow cover, snow depth (Michener 1984a), air temperature (Michener 1977b) and soil temperature (Michener 1979c; Wade 1950). Richardson's

ground squirrels express lability in emergence dates, resuming above ground activity earlier in warm years and later in cooler ones (Michener 1977b, 1985). Adult males (yearlings or older) generally appear above ground 1-2 weeks before adult females (Clark 1970; Michener 1984c; Schmutz et al. 1979; Sheppard 1972). Although, there is some temporal overlap in emergence schedules, the mean (median) dates of emergence for males are significantly earlier than that of females (Michener 1983b). Michener (1983b) reported that the mean dates of adult male emergence, over a five year period in Alberta, varied from 21 February to 13 March. In Saskatchewan, adult males emerge in late March (Michener 1974) while adult males resume above ground activity in late March to early April in Manitoba (this study). Adult females have a more synchronous pattern of emergence than males especially if poor weather conditions prevail in the spring (Davis and Murie 1985). Females generally emerge from hibernation over a 7-23 day period with the majority of females re-entering the active population within two weeks (Michener 1979c, 1980b). The percentage of females not yet emerged when the last male has emerged can range from 27-89% (Michener 1983b). Differential interyear survival results in a female biased sex ratio early in the spring (Michener 1977a). Adult females emerge in early March to mid April in Alberta (Michener 1979c, 1985); early April in Saskatchewan

(Michener 1974); during or before early April in Manitoba (this study).

Like most obligate hibernators, the breeding season for Richardson's ground squirrels begins shortly after emergence from hibernation (Michener 1984a). A latency period of 3-5 days between emergence and conception is typical for adult females (Michener 1985). Male and female squirrels are reproductively mature as yearlings (Michener 1983b). All females, yearling or older breed (Michener 1980a) and the estrous cycle lasts about three days with roughly five days between cycles (Michener 1983b). Typically females are inseminated during their first cycle (Michener 1980b). Mating has rarely been observed in the field (Quanstrom 1971; Davis 1982) and is believed to occur most frequently underground (Michener 1977a), in the late afternoon (Michener 1984b). Females can mate more than once despite the presence of copulatory plugs (Michener 1984b). There is only one litter produced per year (Jones et al. 1983).

The gestation period is between 22-23 days (Michener 1985). Michener (1980b) considered 22.5 days to be the best estimate of conception to parturition. Parturition occurs most often in the late afternoon and most females give birth 25-27 days after emergence from hibernation (Michener 1985). Litter size ranges from 1-14 (Denniston 1957; Michener 1983a; Nellis 1969; Sheppard 1972) and the average mass at

birth is 6.5 g. (Michener 1989b). Lactation lasts for 26-33 days. Juveniles begin to emerge from the natal burrow approximately four weeks post partum (Michener 1980a, 1985). Juveniles appear above ground on average 56.5 days after their mothers' emerged from hibernation (Michener 1985). Timing of juvenile emergence is directly related to the timing of female emergence from hibernation (Michener 1977a) therefore, yearly variation in juvenile emergence dates exists. Juveniles emerge as early as the first week of May in Alberta (Michener 1985); during the last week of May and the first week of June in Saskatchewan (Michener 1974) and Manitoba (this study). Juvenile emergence results in a dramatic increase in squirrel density (Yeaton 1972) however, population density declines shortly thereafter with the immergence of adults (Michener 1983a).

Immergence patterns for adult squirrels are similar to that for emergence. Adult males enter hibernation before adult females. In Alberta, males disappear from the active population in late June to early July (Michener 1979c); in Saskatchewan, by the first half of July (Michener 1974); in Manitoba, adult male above ground activity stopped in mid June to early July (this study). Adult females enter hibernation at different times depending on their reproductive success and body weight recovery. Females that did not produce a litter or which lost their young before

they were weaned entered hibernation before females which produced and weaned litters (Michener 1978). In Alberta, adult female immergence begins in late July and most females are no longer active after August. Inclement weather may delay entry into hibernation such that adult females may remain above ground as late as September (Michener 1979c). Michener (1974) found that adult females were rarely present after July in Saskatchewan. Adult females were not collected after mid August in Manitoba (this study).

Juveniles remain active for several weeks following the entry into hibernation of the adult cohort. Unlike adults, male juveniles enter hibernation after females and may compose 100% of the active population during September and October (Michener 1989a; this study). Similar patterns of juvenile emergence have been reported for Richardson's ground squirrels in Saskatchewan (Michener 1974).

Due to the asynchronous emergence and immergence schedules for the various age classes, each age class is active and in hibernation for variable amounts of the year. Estimates of the duration of activity and hibernation phases for adult males are hampered by small sample size. Michener (1977b, 1979c) estimated that this age class is active for about 90 days and may spend from 225 to 250 days in hibernation each year. Adult females are active for an average of 117 days and hibernation lasts 234 to 258 days

(Michener 1979c). Comparable amounts of time are spent above ground and in hibernation by yearlings (Michener 1984a). Juveniles spend more time above ground than any other age group (females 138 days, males 147 days) and must attain adult size before entry into hibernation (Michener 1983b). Both juvenile sexes are 17-20 weeks old at the time of immergence (Michener 1977b).

Hibernation has been defined as the period from immergence to emergence (Davis 1976). Torpidity or adaptive hypothermia is a physiological state characterized by certain conditions including decreased heart beat, lower rates of respiration and depressed body temperature (McFarland et al. 1979). Photoperiod (Dolman 1983), low ambient temperatures, decreased food availability, decreased food consumption and fat accumulation are considered important cues for squirrel immergence (Davis 1976; Fagerstone 1988; Michener 1977a, 1984b). Michener (1984a) suggested that squirrels immerge as soon as fat reserves are sufficient to enable survival through hibernation. Continued activity only occurs when the costs of remaining active (predator avoidance, maintenance of body fat reserves and meeting dietary requirements) are less than entering hibernation. A special nest or chamber called the hibernaculum is occupied during the hibernation phase. The hibernaculum is usually deeper in the soil than other nests

(up to 2 meters below the surface) and the entrances to the nest proper may be sealed for several meters (Brown and Roy 1943; Davis 1976). Since the areas where adult females spend greater than 80% of their time change 2-4 weeks before hibernation, the hibernacula are not usually located near the natal burrow (Michener 1979a).

Torpor cycles in the Richardson's ground squirrel are composed of several phases: entry into torpor, deep torpor, arousal and inter-torpor homeothermy (Wang 1978). Each episode or bout of torpor is the period when body temperature is minimal and stable. The duration of the bouts of torpor demonstrate a marked seasonal succession (Wang 1979). Bouts are usually of short duration in the fall (2-7 days), gradually increase in duration as winter progresses and then shorten again as spring approaches. Geiser and Kenagy (1988) demonstrated that the duration of torpor bouts was influenced by ambient temperature in Spermophilus lateralis (Say). Richardson's ground squirrels may spend as much as 98% of their time in torpor during the colder months (December and January) (Wang 1978). The duration of inter-torpor homeothermy ranges from 5 to 25 hours during the torpor season (Wang 1979). Terminal arousal ends the last bout of torpor before emergence (Davis 1976), but the relationship between terminal arousal and emergence has not been determined. Because squirrel

emergence (particularly females) is more synchronized in years when spring conditions occur later than usual it has been suggested that animals are aroused but may not emerge until weather conditions are suitable (Michener 1984a). Frequent arousals from torpor in spring, any one of which can result in terminal arousal if suitable conditions prevail, is one hypothesis which may account for the annual pattern of ground squirrel emergence (Michener 1977b).

Richardson's ground squirrels have yearly variation in interyear survival of the different age classes (Michener 1979a, 1989a; Michener and Michener 1971; Michener and Michener 1977; Schmutz et al. 1979). Determination of squirrel survival is confounded by age and sex differences in site fidelity and dispersal. Despite these biases, estimates of survival, based on squirrel recaptures in successive years, generally favour adults over juveniles and females over males (Michener and Michener 1977; Michener 1979b). Occasionally juvenile survival may exceed that of adults (Schmutz et al. 1979; this study). Lower interyear survival (and residency) of males results in sex ratios biased towards females. Regardless of the calendar year, geographic location, size of study area and population density, the sex ratio among adult Richardson's ground squirrels is female biased (Michener 1979a, 1983b; Michener and Michener 1971; Schmutz et al. 1979; Sheppard 1972).

Female biased sex ratios are a consequence of sexual differences in interyear residency that occurs in each year of life. The sex ratios among juveniles, with one exception (Michener 1980a), approximate 1:1 (Nellis 1969; Michener 1979a; Sheppard 1972). However, sexual differences in survival are evident following the first season of squirrel activity (Michener 1989a). Lower interyear survival for males has been attributed to mortality incurred during dispersal (Schmutz et al. 1979), earlier emergence (Michener and Michener 1977) and overwintering mortality (Michener and Michener 1971). Adult females rarely disperse, with major losses from this cohort occurring over winter (Michener 1979b). An additional factor which amplifies the discrepancies between interyear survival and sex ratios among adult squirrels is the sexual differences in squirrel longevity. The maximum recorded lifespan of males is four years while females can live for up to six years (Michener 1989a).

Behaviour

Within the North American Marmotini (Ammospermophilus, Cynomys, Marmota, Spermophilus) (Moore 1961), social groupings range from solitary dwellers (Marmota monax (L.), Spermophilus franklinii Sabine) to species forming multi-harem coterie (Cynomys ludovicianus (Ord), M. olympus L.) (Armitage 1981). The social behaviour of Richardson's

ground squirrels has been defined as one in which members form colonies in favourable habitats, but all members of the colony live individually (Armitage 1981). Michener (1983a) has classified the sociality of S. richardsonii as single-family female kin clusters. The grade of sociality assigned to this species is low (sociality index of two on a scale of 1-5 by Michener 1983a and Armitage 1981), thus social interactions between conspecifics are not extensive compared to some other ground squirrel species.

Opportunities for social interaction among the various age classes in Richardson's ground squirrels are governed by the degree of seasonal coincidence of activity. The overlap in active periods of adult squirrels is extensive. Juveniles, on the other hand, are generally out of contact with adults for extended periods during the summer. The percentage of above ground activity of female juveniles which coincidences with adult males and females is roughly 33% and 52%, respectively. Male juveniles spend a smaller proportion of their first year in the presence of adults, with 23% and 36% of their entire above ground activity coinciding with that of adult males and females (Michener 1984a).

The examination of sociality among Richardson's ground squirrels has involved the determination of age class home range size and evaluation of interactions between the

different age classes (Michener 1979b; Quanstrom 1971; Yeaton 1972). Within each age class, seasonal variations in home range size and behaviour have been recognized. Adult males establish home ranges before the emergence of females. The home ranges of males increase in size during the breeding season with each male's home range generally overlapping the ranges of 5-16 estrous females and several other males (Michener 1979b, 1983b). Males do not establish an exclusive range during the breeding season, but males will actively expel male intruders from their core area (area where 80% of activity occurs) (Davis and Murie 1985). Defense of well defined areas by males during the breeding season has also been reported by Michener (1983b) and Yeaton (1972). Throughout the breeding season males sustain injuries to their backs, hips and face, which probably result from male-male interactions (Michener 1983b) and/or from rejection by inseminated females (Michener 1979a). Males rarely show fidelity to a particular burrow, taking refuge in any burrow and frequently entering burrows known to be used by females (Michener 1983b). Near the end of the breeding season, male home ranges decrease in size and male movements are less extensive due to the lack of receptive females, changing male hormonal status and aggressiveness of pregnant females (Michener 1979b; Michener 1972). Once the young of the year begin to appear above ground, male home

ranges increase in size until several weeks prior to hibernation when home range sizes again decrease (Michener 1979a).

Adult females make only small scale changes in the location of their ranges among and within years (Michener 1979a, 1979b; Yeaton 1972). Home range fidelity is well developed when females are yearlings (Michener and Michener 1973). Female home ranges remain relatively unchanged throughout the breeding season and until litters are weaned. After juvenile emergence, the home range of adult females increases until a few weeks before hibernation when activity is limited to the area where hibernation will occur (Michener 1979a). Females are more aggressive towards other females and males during pregnancy and lactation. Following juvenile emergence, there is a trend towards tolerance, with fewer agonistic interactions between adults (Yeaton 1972). This may be a function of the decrease in home range size prior to hibernation during which the number of encounters between adults is restricted (Michener 1979a).

The home range sizes and interactions with conspecifics for juveniles also change seasonally. During the first month of above ground activity, juveniles remain in close spatial proximity to family members. Thereafter, juveniles become increasingly independent of the family unit, establishing their own spatially distinct core areas

(Michener 1981). Juvenile home ranges can double in size during the first 6 weeks of above ground activity (Michener 1981). For several weeks after emergence, juveniles interact amicably with all family members. Within 8 weeks of emergence juveniles are behaviourally indistinguishable from adults. They establish their own core areas, have fewer interactions with kin, and interact aggressively to trespassing young and adults (Michener and Sheppard 1972). Squirrels are able to distinguish between familial and non-familial members and contacts between mothers and daughters are more frequently neutral or cohesive than ones involving mothers and sons (Michener and Michener 1973; Michener and Sheppard 1972). Female juveniles show greater fidelity to the natal area and daughters often remain on or near their mother's range throughout their lives (Michener and Michener 1977). Male juveniles have a greater tendency to disperse from the natal area (Michener and Michener 1977). Adult females may reject (not aggressively) their own male young while interacting neutrally or cohesively with female young, increasing the tendency for males to leave the natal area (Michener and Sheppard 1972).

Males are the main dispersers among Richardson's ground squirrels (Holekamp 1984). The exact age at which males disperse is controversial. Males have been reported to disperse as juveniles (Michener 1979b, 1981; Quanstrom 1971;

Schmutz et al. 1979; Yeaton 1972), as yearlings during their first spring (Michener and Michener 1973, 1977), or both juveniles and yearlings may disperse (Holekamp 1984; Michener 1983a). Although dispersal is commonly an annual event, it does not always occur. Michener (1979b) determined that dispersal is minimal when female populations are small or when reproductive success is low. Density-dependent constraints on juvenile male dispersal may be reflected in the ability of these squirrels to appropriate a portion of their mother's range when they are 9-12 weeks of age (Michener 1981). Michener and Michener (1973) traced dispersal in yearling males and found that distance moved was greatest for males whose mother had survived relative to ones whose mothers had not. Aggression between mothers and their sons is not believed to be the cause of dispersal (Michener and Michener 1973; Michener and Sheppard 1972; Yeaton 1972). The ultimate cause of dispersal remains unresolved for Richardson's ground squirrels (Michener 1983a). One obvious result of male dispersal and female sedentary behaviour is an avoidance of inbreeding (Michener 1984a). Potential advantages of differential dispersal by males includes promotion of outbreeding, reproduction by females in a familiar area, location by males of more mates, reduction of intrasexual competition for males and avoidance of intraspecific aggression (Michener 1983a).

Richardson's ground squirrels are strictly diurnal animals (Quanstrom 1971; Wooding 1982). Daily activity patterns are dependent on the prevailing weather conditions with squirrels preferring to remain underground during periods of intense heat and rain (Banfield 1974; Clark 1970; Woods 1980). Daily activity changes seasonally with squirrels out late in the day in spring, morning and afternoons in early summer and mostly in the morning in late summer (Clark 1970; Quanstrom 1971). The activities performed while above ground also change seasonally. During spring and early summer, social and solitary behaviours account for a relatively large percentage of above ground activity. Several weeks before the hibernation phase all age groups spend most of their time feeding (Michener 1981). It has been estimated that >80% of the above ground activity is dedicated to feeding 6 weeks prior to hibernation (Michener 1979a). The amount of time spent above ground decreases as animals begin to enter the hibernation phase. Animals may only be active every 3-5 days, early in the hibernation season when bouts of torpor are of short duration (Fagerstone 1988; Quanstrom 1971; Wang 1978).

Richardson's ground squirrels are omnivorous, feeding on many varieties of plant and animal matter. The roots, leaves and stems of native grasses and forbs such as sage, bindweed, pigweed, wild sunflowers and onions are often

consumed. Domestic crops including oats, wheat and flax are utilized by Richardson's ground squirrels (Banfield 1974). It has long been known that these squirrels store materials within their burrows (Seton 1909) yet it remains to be proven whether winter stores of grain are consumed during the winter or in the subsequent spring (Banfield 1974). Crickets, grasshoppers and caterpillars are readily consumed by Richardson's ground squirrels (Wooding 1982). Cannibalism of dead or torpid conspecifics is well documented for this species (Banfield 1974; Jones et al. 1983; Sheppard and Swanson 1976; Woods 1980).

Parasites of the Richardson's ground squirrel

McLeod (1933) examined the external and internal parasites of three members of the genus Spermophilus including Richardson's ground squirrel. Five external parasites were recovered: a tick, Dermacentor variabilis (Say), a flea, Opisocrostitis bruneri, a louse, Linognathoides montanus (Osborne), and two mite spp., Liponyssus occidentalis (Ewing) and L. montanus (Ewing). Two nematode species, Spirura infundibuformis (McLeod) and Warrenicus bifurcatus (Sleggs), and two cestodes, Hymenolepis citelli (McLeod) and Prochoanotaenia spermophili (McLeod) were recovered from the digestive tract of Spermophilus richardsonii.

Brown and Roy (1943) reported that Richardson's ground

squirrels in Alberta were infested with the flea species Opisocrostitis labis (Jordan and Rothschild), O. tuberculatus (Baker), O. rupestris, and Hystrihopsylla dippiei (Rothschild) and the tick, Dermacentor andersoni Stiles. The nematodes, Filaria sp., Spirura sp. and Physaloptera sp. infected the squirrel digestive tracts and the eggs of Capillaria sp. were prevalent within the livers of several ground squirrels. Holland (1944) collected N. inopina, O. bruneri, O. labis, O. tuberculatus, O. rupestris, R. fraterna and Thrassis bacchi (Roths.) from S. richardsonii in Alberta and Saskatchewan. Four tick species, D. andersoni, Haemaphysalis leporis-palustris (Packard), Ixodes kingi Bishopp and I. sculptus Neumann, are common on ground squirrels throughout Alberta, Saskatchewan (Gregson 1956) and D. variabilis have been recorded from squirrels in Manitoba (T.D. Galloway pers. comm.).

Hilton and Mahrt (1971) examined the ectoparasites of three species of Spermophilus and removed the following flea species from S. richardsonii: N. inopina, O. labis, O. tuberculatus, Oropsylla idahoensis (Baker), O. rupestris and R. fraterna. Opisocrostitis bruneri, a flea commonly found on the Richardson's ground squirrel (Holland 1985; this study), was removed only from Spermophilus franklinii. Several weeks after squirrel emergence large numbers of fleas were collected (not identified to species) but intensity of

infestation declined to one or two fleas/animal from June to August. Two sucking lice, Enderleinellus suturalis (Osborne) and Neohaematopinus laeviusculus (Grube), and a tick, Dermacentor andersoni, were also removed from Spermophilus richardsonii.

Sixteen flea species were collected from Richardson's ground squirrels in Montana (Jellison et al. 1943). Woods and Larson (1970) collected O. bruneri in North Dakota from a variety of hosts including S. richardsonii and in South Dakota Thrassis bacchi infests Richardson's ground squirrels (Easton 1982).

FLEAS OF THE RICHARSON'S GROUND SQUIRREL

Description

Several characters readily distinguish the four flea species associated with S. richardsonii in the present study. Neopsylla inopina is the sole Nearctic representative of the subfamily Neopsyllinae and like all members of this subfamily the genal ctenidia are composed of two spines which cross over one another. Neopsylla inopina is the smallest of the four species collected, eyes are absent and pleural arches are poorly developed (Holland 1985; Hopkins and Rothschild 1962). Opisocrostis bruneri is a medium to large flea with well developed eyes; genal ctenidia are absent and setae are present on the first

abdominal tergum. Females have 2 antesensilial setae and setae on the first abdominal terga (Holland 1985).

Oropsylla rupestris shares several characters with O. bruneri. They have large well pigmented eyes, no genal ctenidia, but females have 3 antesensilial setae, and the setae on the first abdominal terga are absent (Smit 1983). The ctenidia of Rhadinopsylla fraterna are composed of five strong spines. Pronotal ctenidia are composed of 24 spines and like N. inopina eyes are vestigial (Holland 1985). Full descriptions of the flea species associated with Richardson's ground squirrel are given by Holland (1985), Perdue (1980) and Hopkins and Rothschild (1962).

Distribution

Holland (1985) considered N. inopina to be a parasite of Richardson's ground squirrel of the plains of Alberta and Saskatchewan. He did not report any Manitoba records of this flea from S. richardsonii although, it can occur upon this host throughout its active season in some localities (Galloway and Christie unpublished; this study). Neopsylla inopina has also been recorded from S. columbianus (Ord) in British Columbia (Holland 1985). Neopsylla inopina has been recorded in North Dakota (Baesler 1975; Larson and Peterson 1969), Montana (Hubbard 1947), Oregon, Idaho, Wyoming, Utah and Colorado, mostly from Spermophilus spp. (Hopkins and Rothschild 1962). Occasionally, N. inopina is collected

from long-tailed weasels, Mustela frenata (Lichtenstein), and several cricetid rodent species (Holland 1985; Jellison et al. 1943).

Opisocrostis bruneri is a flea of Franklin's ground squirrel (Holland 1985; Perdue 1980; Smit 1983) although it has been collected from western Alberta, southern Saskatchewan, Montana, Idaho, Wyoming, Colorado, Ohio and Michigan, all of which are outside the range of S. franklinii. Opisocrostis bruneri is common on Spermophilus richardsonii (Figure 2) and Spermophilus tridecemlineatus (Jellison 1947; Perdue 1980). The distribution of O. bruneri is within the range of these ground squirrel species and where host ranges overlap all three species can harbour this flea (Holland 1944). Opisocrostis bruneri has been reported from a wide variety of other hosts including S. columbianus, S. mexicanus (Erxleben), Glaucomys volans (L.), Sylvilagus floridanus, Canis familiaris (L.), Sciurus niger (L.), Marmota monax (L.) (Perdue 1980), and various vole and mouse species (Galloway and Christie unpublished). This flea is probably less host specific than originally suggested by Holland (1949).

Oropsylla rupestris is common throughout the range of the Richardson's ground squirrel (Figure 3) (Holland 1985). It rarely occurs outside the range of this host but has been recorded as far south as Colorado and Yukon Territory in the

north (Holland 1985; Smit 1983). Records of this flea from hosts other than Richardson's ground squirrel include S. tridecemlineatus (Kinzel and Larson 1973), M. flaviventris (Audubon and Bachman), C. columbianus (Jellison 1945) and predator species such as Mustela spp. (Jellison 1945; Smit 1983).

The distribution of Rhadinopsylla fraterna in Canada is limited to Alberta (Hopkins and Rothschild 1962), Saskatchewan (Holland 1985) and Manitoba (Galloway and Christie unpublished). Rhadinopsylla fraterna has also been recorded from Montana, Wyoming, Colorado (Hopkins and Rothschild 1962), North Dakota (Kinzel and Larson 1973) and New Mexico (Haas et al. 1973). The Richardson's ground squirrel is believed to be the usual host of this flea (Holland 1944) with casual associates including Mustela spp., Clethrionomys, Peromyscus, Microtus, Lagurus, spp. (Haas et al. 1973; Holland 1985; Woods and Larson 1971), Neotoma cinerea (Ord), S. columbianus and Cynomys leucurus (Merriam) (Hopkins and Rothschild 1962).

Related Research

Hendricks (1967) examined the seasonal activity of O. bruneri on thirteen-lined ground squirrels in Indiana. The highest mean intensity and prevalence of infestation occurred in October. Flea burdens were low (<2 fleas/infested animal) during all other months, except June.

Hendricks suggested that macroenvironmental factors may influence the presence of O. bruneri on this host with fleas tending to congregate on squirrels during the cooler months. Whitaker (1972) also examined the ectoparasites of thirteen-lined ground squirrels in Indiana and found that O. bruneri was the only flea species present. One hundred and twenty-three squirrels had an overall prevalence of infestation of 25% with an average of 0.49 fleas/animal. Seasonal changes in flea activity were not reported even though, animals were collected from April to October.

Opisocrostitis bruneri has been recovered from the den of the red fox (Vulpes L.) in Wisconsin (Haas 1970). The occurrence of O. bruneri within the den probably resulted from the abandonment of a prey species (S. tridecemlineatus or S. floridanus). The fate of fleas which abandoned their host was not known.

Seasonal changes in flea abundance and geographic distribution have been reported for O. bruneri and T. b. bacchi infesting S. tridecemlineatus in North Dakota (Kinzel and Larson 1973). A east-west transect of the state was performed and O. bruneri predominated on squirrels in the eastern portions of the state. Opisocrostitis bruneri was replaced by T. b. bacchi as the prevalent flea species in western regions of the state. It was suggested that geographical and climatic factors are responsible for

partitioning these flea species into these specific regional localities. However, no consideration was given to the impact of seasonal changes in flea abundance. Since the study was performed from April to September, flea abundance may have changed during the course of sampling thereby confounding the results. Baesler (1975) examined the biweekly infestation of Richardson's ground squirrels in Grand Forks county, North Dakota. He suggested that peaks of O. bruneri activity occur 2-4 weeks after substantial rainfall. A correlation with O. bruneri or any other flea species activity and precipitation was not observed during the present study. Baesler also collected N. inopina from these hosts and found that this species disappeared in July and remained scarce until September. A similar pattern of seasonal activity was observed for this species on Richardson's ground squirrels in southwestern Manitoba.

Burachynsky and Galloway (1980) sampled thirteen and Franklin's ground squirrels near Winnipeg, Manitoba and reported that peaks in adult O. bruneri activity occurred in May and July. Reichardt (1989) sampled S. franklinii at the same location and found that squirrels were most heavily infested with O. bruneri during May and late August or September. Based on trends in host infestation and evaluation of the reproductive status of female fleas O. bruneri has at least two generations per year and flea

reproduction is not correlated with the estrous cycle of the host (Reichardt 1989).

Plague and the fleas of Richardson's ground squirrel

Sylvatic plague may cycle between Richardson's ground squirrels and its fleas. Plague-infected Richardson's ground squirrels have been collected from several counties in North Dakota (Prince 1943) and Yersinia pestis (Lehmann and Neumann), the causative agent of plague, has been isolated from squirrel tissues in Alberta (Gibbons and Humphries 1941). Eskey and Haas (1940) were the first to report experimental transmission of the plague bacillus by O. rupestris. Opisocrostis bruneri adults collected in Potter county, North Dakota, transmitted plague to healthy guinea pigs after feeding on plague positive animals (Prince 1943). Thus O. rupestris and O. bruneri are both potential vectors of sylvatic plague, though neither of the species has been established as a natural vector to man or ground squirrels (Traub 1983). Neopsylla inopina and R. fraterna became infected when fed on plague positive guinea pigs (Eskey and Haas 1940), but are not considered plague vectors (Holland 1944).

The transfer of sylvatic plague by either O. rupestris or O. bruneri into an urban cycle depends on S. richardsonii maintaining close contact to populated areas. The urban cycle starts when infected fleas are transferred to

uninfected Rattus spp. Richardson's ground squirrels typically inhabit open grasslands areas, throughout the prairies of central North America (Woods 1980). While squirrels are generally more numerous in rural areas, suitable habitats within urban communities are often colonized. Contact between Rattus and Richardson's ground squirrels may be frequent, especially in areas of common use such as grain elevators or grainaries. These behavioural traits greatly enhance opportunities for the transfer of fleas between infected Richardson's ground squirrels and commensal rodents.

Chapter III

MATERIALS AND METHODS

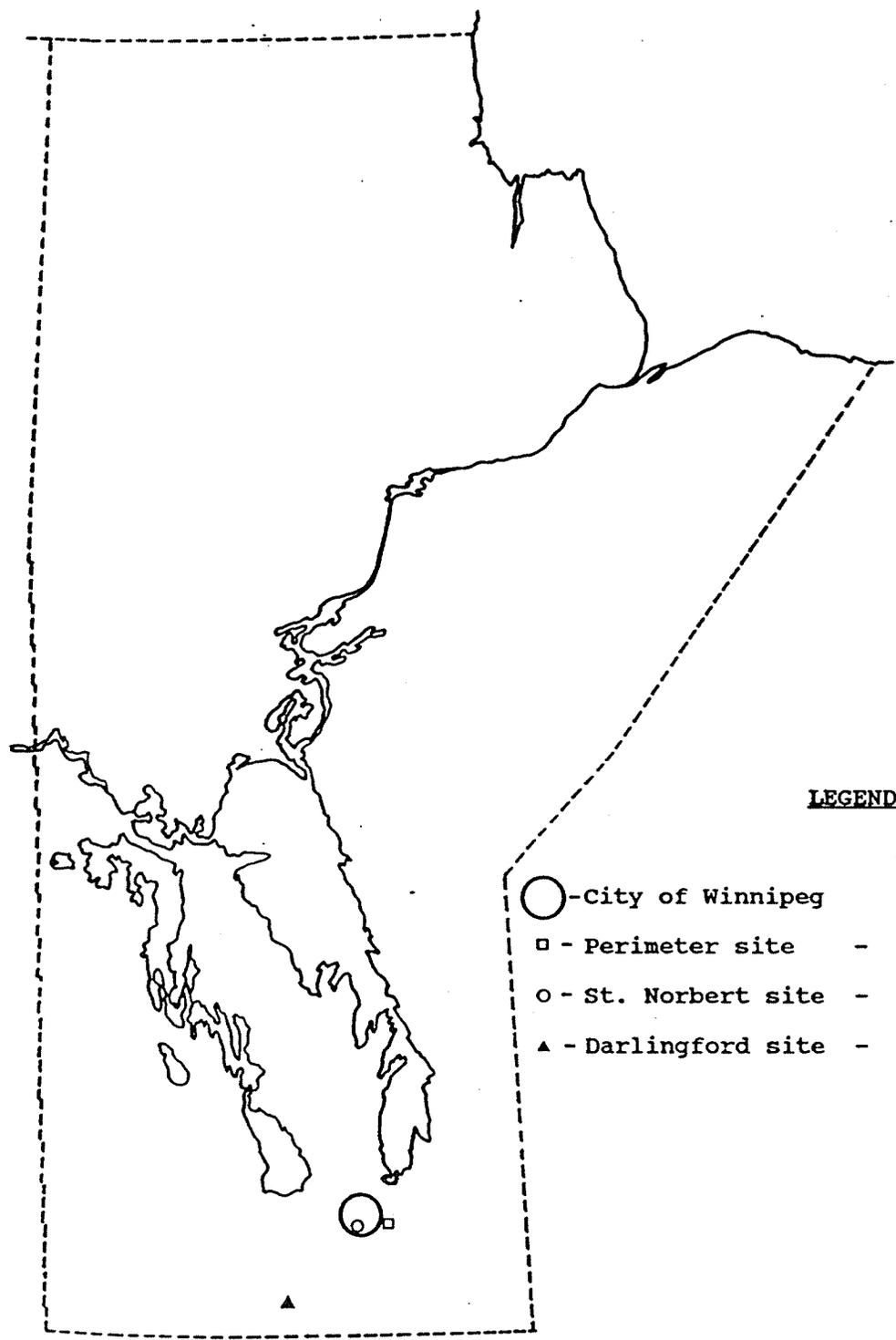
Description of the study sites

Squirrels were examined from three different study sites within Manitoba (Figure 4). Two sites within and near Winnipeg, Manitoba (49° 53' N, 97° 09' W) were established to examine the seasonal activity of O. bruneri on Richardson's ground squirrel. These two sites are referred to as the Perimeter site (sampled in 1987) and the St. Norbert site (sampled in 1988 and 1989).

The Perimeter site was a three hectare pasture located within the rural municipality of Springfield one km southeast of Winnipeg. The elevation of this site was approximately 232 m above sea level (Atlas of Manitoba). The soils are classified as Osborne clay series which is poorly drained Rego Hume Gleysol soil, developed on moderately to strongly calcareous, fine textured lacustrine and alluvial deposits (Michalayna et al. 1975). Runoff is negligible to very slow and permeability is very slow. Unfortunately, at the request of the property owner, squirrel trapping was discontinued at the Perimeter site after the first summer.

A comparable study area was established within the

Figure 4. Location of study sites in Manitoba, Canada and the respective occurrence of Neopsylla inopina, Opisocrostis bruneri, Oropsylla rupestris and Rhadinopsylla fraterna on Spermophilus richardsonii.



municipality of St. Norbert (a subdivision of the City of Winnipeg). The St. Norbert site was a 3.75 hectare pasture located approximately 10 km from the Perimeter site. The elevation of this site was comparable to the Perimeter site. The soil is classified as moderately to well drained Orthic Dark grey soils developed on moderately calcareous, fine textured lacustrine and alluvial deposits (Michalayna et al. 1975).

The third site was located roughly 1.5 km southeast of Darlingford, Manitoba (49° 12' N, 96° 27' W) approximately 120 km southwest of the other sites. Squirrels collected at the Darlingford site were infested with N. inopina, O. rupestris, R. fraterna, and O. bruneri. This site was a five hectare pasture located within the Pembina Hills (elevation 458 m above sea level). Ellis (1938) described the soil in the Darlingford area as Darlingford clay loams with soil of black-earth type, developed on high lime boulder till, with small amounts of shale. The soil is well drained and the texture is a clay loam.

All sites were typical pasture lands covered almost exclusively by grasses; several other plant species, including Canada Thistle (Cirsium arvense (L.)), dandelion (Taraxacum spp.), silverleaf (Psoralea argophylla Pursh) and pasture sage (Artemisia frigida Willd.) were scattered throughout the study plots. All of the sites were bordered

by domestic crops and livestock were pastured on each site during all years of the study.

Trapping regime

All squirrels were trapped using nineteen 13 cm x 13 cm x 40 cm and eight 15 cm x 15 cm x 48 cm wire live-traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin, model nos. 202 and 203, respectively). All traps were set during each trapping date except early and late in the season when the number of active squirrels was small. Trapping was performed for a minimum of six hours per day unless weather conditions were unsuitable for squirrel activity. Each trap was baited with a mixture of rolled oats and peanut butter. One trap was placed at or near the entrance to burrows where squirrels were active above ground or which were known to be in use.

Squirrels were collected weekly at all sites. During 1987, the Darlingford site was trapped on Mondays and Tuesdays; the Perimeter site was sampled on at least two alternative days/week. During 1988, squirrels at the Darlingford site were trapped on Tuesdays and Thursdays for most of the season while at St. Norbert squirrels were collected on Monday, Wednesday and Friday. Trapping was less extensive near the end of the each field season, though animals were trapped at each site at least one day/week throughout the study. In 1989, squirrels were trapped only

one day/week. The duration of the trapping season and the total number of trapping dates/year varied between years and sites (Table 1).

Traps were monitored on average every twenty minutes, with animals rarely remaining in the field for more than 30 minutes. Traps had to be examined frequently, especially on exceptionally hot days when captured animals were subject to heat stress. Each captured animal was taken from the field and when necessary, placed in a cool shaded area before it was examined. Animals were typically captive for less than one hour, except during June when large numbers of animals were trapped simultaneously. After examination, each animal was returned to the location where it was trapped. Trapping was intensive enough during 1987 and 1988 that all resident animals within each study area were captured. During 1987, individual animals were occasionally trapped more than once per trapping date. As a rule, at least one hour elapsed between the original capture and the second examination. Examination of same day recaptures was discontinued after 1987. Of the 2262 captures in 1988, 12 animals were inadvertently examined twice on the same day.

Handling of squirrels and ectoparasites

All squirrels were weighed using an Ohaus spring scale (± 15 grams) (Ohaus Scale Corp., Florham Park, New Jersey). Location of capture, sex and reproductive condition of each

Table 1. Trapping schedule, total number of trapping dates and total S. richardsonii captures at the Darlingford, Perimeter and St. Norbert sites, 1987-1989.

<u>Site</u>	<u>Trapping intervals</u>	<u># of trapping dates</u>	<u>Total captures</u>
<u>1987</u>			
Darlingford	14 May - 17 October	37	811
Perimeter	12 June - 3 September	39	756
<u>1988</u>			
Darlingford	01 April - 01 October	48	1381
St. Norbert	11 April - 17 October	77	881
<u>1989</u>			
Darlingford	12 April - 16 May	05	116
St. Norbert	11 April - 18 May	05	52
Total captures:			
	Darlingford -	2308	
	St. Norbert -	933	
	Perimeter -	756	
	All sites -	3997	

animal were recorded. All animals were tagged with # 1 self-piercing monel metal eartags (National Band and Tag Co., Newport, Kentucky) and in 1988 and 1989 animals were also given unique dye-marks (Lady Clairol® Natural Black Hair Dye). Each animal was placed within a glass jar and anaesthetized with ethyl ether. Once unconscious, each animal was thoroughly brushed with a toothbrush and/or a flea comb over an white enamel tray.

The fleas from each host were sealed within vials (16 X 65 mm) or plastic cryovials (12 X 38 mm) and placed on ice for transfer to the laboratory. Vials were stored in the laboratory at $-15^{\circ}\text{C} \pm 1 \text{ C}$. until fleas could be examined. Fleas were held in storage for less than four months. Losses due to freeze-drying of fleas were minimal ($<<1 \%$) and these fleas were excluded from the age-determination analysis. All fleas were identified to species and sex. The number of external flea associates was also assessed. All fleas collected in 1988 and 1989 were dissected to determine the gonotrophic age of females (Appendix A) and to establish the incidence of internal parasites or external associates in both males and females (Appendix B). Sub-samples of each flea species were dissected in 1987 and 85% of all collected specimens dissected. Fleas which were not dissected were retained as voucher specimens and deposited in the J.B. Wallis Museum of Entomology (Department of

Entomology, University of Manitoba). Mean intensity and prevalence of infestation, as defined by Margolis et al. (1982), were determined for each flea species. Data were analyzed in two week periods. X^2 was used to analyze differences in observed biweekly flea sex ratios. Reinfestation data were analyzed using a two sample sign test. In all statistical analyses, $p < 0.05$ was accepted as the level of significance.

Gonotrophic age categories

Most flea species have panoistic ovarioles (Rothschild et al. 1986), each of which is comprised of a terminal filament, germarium, vitellarium and pedicel (Mead-Briggs 1962). The number of ovarioles per ovary is variable both between and within species (Reichardt 1989; this study). The reproductive age of female fleas can be determined by examining the irreversible changes that occur within the reproductive tract during each gonotrophic cycle (Tyndale-Biscoe 1984). Reproductive age has also been assessed by examining the level of development of the largest proximal oocyte (Klein 1966; Mead-Briggs 1962; Reichardt 1989). Most flea species possess the yellow body type of follicular relic as defined by Tyndale-Biscoe (1984). Yellow bodies¹

¹ Yellow bodies are a misnomer for most species which have this type of follicular relic. Follicular relics were yellow only in Rhadinopsylla fraterna; in all other flea species examined the relics were light brown to black.

(remnants of follicular epithelia) accumulate within the calyx region of each ovariole which has produced a mature oocyte. These follicular relics do not associate with the intima and therefore, it is impossible, based on follicular relics alone, to differentiate uniparous from multiparous females. The only age groups which can be separated with certainty are parous (uniparous or older) and nulliparous females, based on the presence or absence of follicular relics, respectively.

Considering these limitations, the following gonotrophic age categories were established based on the largest proximal oocyte and the presence or absence of follicular relics: **immatures** - all oocytes small, largest proximal and its penultimate oocyte approximately equal in size; little differentiation of proximal oocytes, no yolk deposition, follicular epithelium may or may not be present, follicular relics absent; **nulliparous** - largest proximal oocyte at least twice as large as penultimate oocyte, yolk deposition evident and follicular epithelium present, follicular relics absent; **parous** - follicles at various stages of development, follicular relics present.

Presence or absence of spermatozoa within the spermatheca was recorded for each female flea dissected. Rupturing the spermatheca during the dissection exposed the long and conspicuous spermatozoa. Teneral fleas were

recorded based on the cuticle colour. Teneral individuals were varying shades of yellow to golden and had not developed the characteristic puce colour of sclerotized fleas.

Chapter IV

RESULTS

Mammal captures

General

Adult² emergence patterns could only be estimated for 1988. Adults resumed above ground activity during the last week in March at the Darlingford site (Table 2). Activity was established by observation only and trapping commenced three days after the first ground squirrels were seen above ground. During the first day of trapping, only adult male squirrels were collected. Several other (approximately eight) animals were above ground but could not be trapped. Some of these squirrels may have been females since on the next trapping date two females were collected. Since males were collected in much greater numbers relative to females during the first week of April male emergence probably occurred in late March and female emergence commenced during the first week of April. Squirrels were not active at the St. Norbert site before 4 April (the site was examined for squirrel activity and many burrows were still sealed with snow and/or ice). Trapping began at this site on 11 April

²Unless specified any reference to adult squirrels includes animals yearling or older

Table 2. Emergence and immergence schedules for adult S. richardsonii at the Darlingford, Perimeter and St. Norbert sites, 1987-1988.

<u>Site</u>	<u>Year</u>	<u>Emergence dates*</u>	<u>Immergence dates**</u>
Darlingford - 1987			
	Female	-----	19 August
	Male	-----	08 July
Darlingford - 1988			
	Female	01 April	16 August
	Male	25 March	16 June
Perimeter - 1987			
	Female	-----	20 July
	Male	-----	27 June
St. Norbert - 1988			
	Female	04 April	23 July
	Male	04 April	02 July

* - Emergence dates are based on observations only (no trapping data available). Trapping began 3-7 days after squirrels commenced aboveground activity.

** - Immergence dates are when last adult trapped.

by which time both adult males and females were above ground. Adult emergence had occurred during the first and second weeks of April. At both sites, immediately following emergence, squirrels were very active with males ranging freely over much of the study areas. Home ranges gradually decreased in size after several weeks with adults confining their activities to specific regions of the study plots.

All male squirrels collected during the first several trapping intervals had descended testes. Several males still had descended testes on 27 April at the Darlingford site. By 3 May the testes of all captured males had ascended. Males at St. Norbert had a similar pattern of reproductive activity; the last male with descended testes was captured on 6 May. Female reproductive activity was not directly assessed. Evidence of parturition (e.g. blood on fur or significant weight loss) was observed for several females. One individual collected at the Darlingford site on 3 May, 1988 had a two inch cord extending from her vagina. This was undoubtedly a remnant of the reproductive tract and this squirrel probably gave birth several hours (minutes?) before her capture. Based on these observations and the duration from parturition to juvenile emergence (Michener 1985), most females had given birth by the first week of May. Most females displayed evidence of lactation (e.g. extended nipples) during May at all sites during each

year. Nipples regressed in the majority of females during the first week of June.

Juvenile emergence was reasonably synchronous both between years and sites (Table 2). Juveniles commenced above ground activity during the last week of May in 1987 and 1988 at Darlingford, and in 1989 juveniles were observed during the third week of May. In 1988, juveniles appeared above ground 7-10 days later at the St. Norbert site, consistent with the later emergence of adults at this location.

Immergence schedules were consistent with the patterns described by Michener (1984a). Adult males disappeared before adult females followed by juvenile females and males (Tables 2 and 3). The last active adult males at the Darlingford site were captured on 08 July in 1987 and 16 June in 1988. Adult female activity extended into late July and August. The last adult female was captured at Darlingford on 19 August in 1987 and 16 August in 1988. In 1988, yearling females entered hibernation after older adults (2 years or older). Adult immergence patterns were similar for both the Perimeter and St. Norbert sites with the last adult male active during late June and early July. Adult females disappeared by the third week in July. Juvenile males were always the last age group to enter hibernation. Immergence dates based on the last squirrel

Table 3. Emergence and immergence schedules for juvenile S. richardsonii at the Darlingford, Perimeter and St. Norbert sites, 1987-1988.

<u>Site</u>	<u>Year</u>	<u>Emergence dates*</u>	<u>Immergence dates**</u>
Darlingford - 1987			
	Female	29 May	23 September
	Male	02 June	15 October
Darlingford - 1988			
	Female	24 May	10 September
	Male	24 May	25 September
Perimeter - 1987			
	Female	-----	27 August
	Male	-----	03 September
St. Norbert - 1988			
	Female	01 June	03 September
	Male	01 June	15 October

* - Emergence is date first juvenile seen aboveground.

** - Immergence is the date when last squirrel captured.

active ranged from 27 August to 23 September for females and from 03 September to 15 October for males. Regardless, of the date of emergence the weight of squirrels at the time of their disappearance was always close to or in excess of 400 g.

Darlingford

One hundred and thirty individuals contributed to 811 captures made during the 37 trapping dates at the Darlingford site in 1987 (Tables 4 and 5). Adults accounted for 15.3% of all captures, while juveniles were responsible for the remaining 84.7% of the captures. The maximum number of captures/individual was 29 with an average recapture rate of 6.2 captures/squirrel. There was a marked bias towards females both in number of individuals and captures (64.6% of the individuals were females; 65% of all captures). The sex ratio of male to female squirrels was 1:25 for adults and 1:1.3 for juveniles. Based on total captures, the greatest number of squirrels was active during June (Figure 5A).

Fifty squirrels were captured more than once per trap date and seven of the fifty animals were collected three times during one trapping date. The total number of same day recaptures was 117 (average of 2.3 same day recaptures per recaptured squirrel). Roughly four times more juveniles than adults were captured (104 juveniles vs. 26 adults).

One hundred and sixty-eight individuals contributed

Table 4. Distribution of individual S. richardsoni captures by age and sex of the host at the Darlingford, Perimeter and St. Norbert sites, 1987-1989.

<u>Site</u>	<u>Total # of individuals</u>	<u>Adult</u>		<u>Juvenile</u>	
		<u>Male</u>	<u>Female</u>	<u>Male</u>	<u>Female</u>
1987					
Darlingford	130	01	25	45	59
Perimeter	76	01	08	34	33
1988					
Darlingford	168*	11	30	65	62
St. Norbert	100	07	12	49	32
1989					
Darlingford	35**	07	28	--	--
St. Norbert	21***	05	16	--	--
Total different squirrels:		Darlingford - 268			
		Perimeter - 76			
		St. Norbert - 108			
		All sites - 452			

* - 30/168 squirrels from 1987.

** - 33/35 squirrels from 1988 (24/35) and 1987 (9/35).

*** - 13/21 squirrels from 1988.

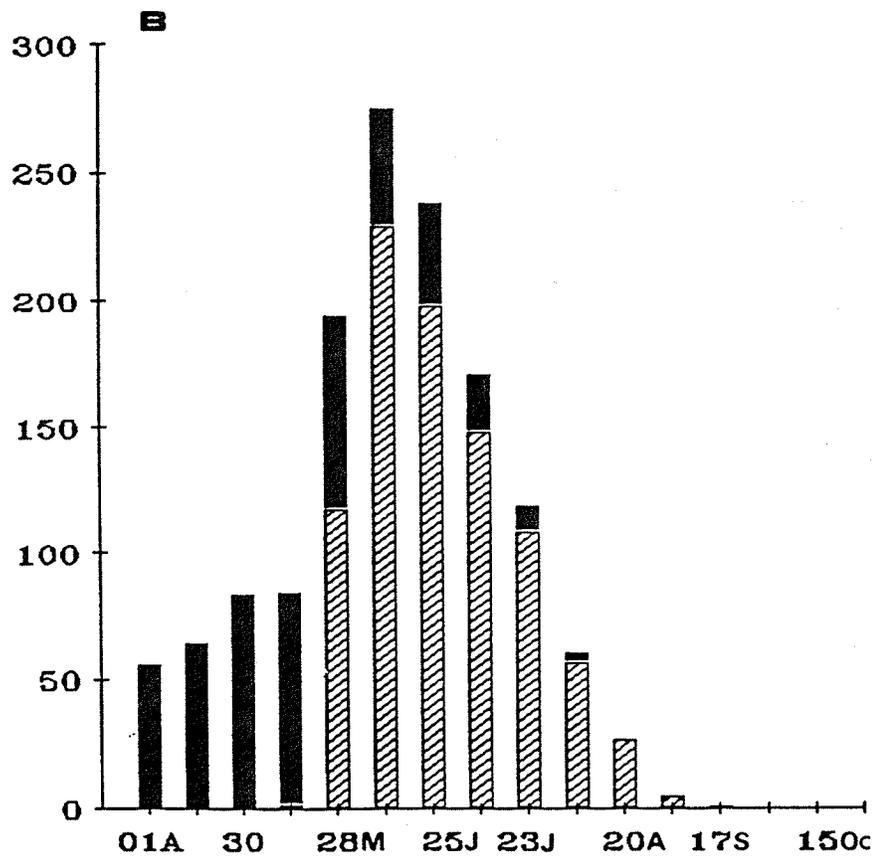
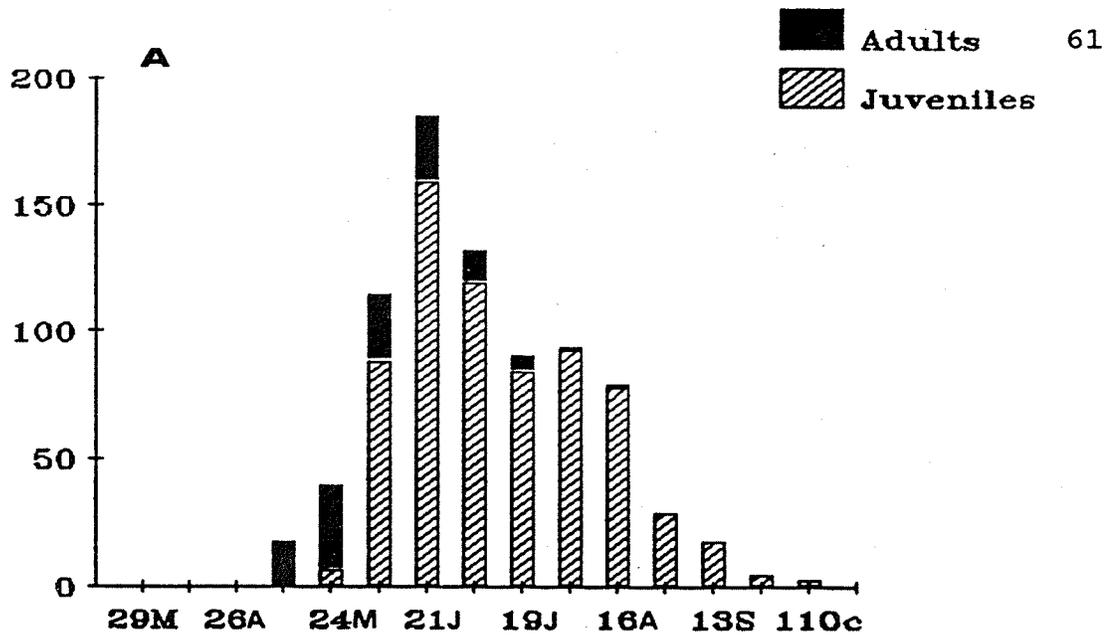
Table 5. Distribution of S. richardsonii captures by age and sex of the host at the Darlingford Perimeter and St. Norbert sites, 1987-1989.

<u>Site</u>	<u>Year</u>	<u>Adult</u>		<u>Total Adults</u>	<u>Juvenile</u>		<u>Total Juven.</u>
		<u>Female</u>	<u>Male</u>		<u>Female</u>	<u>Male</u>	
Darlingford							
	1987	117	07	124	410	277	687
	1988	445	42	487	464	430	894
	1989	95	21	116	---	---	----*
	Total	657	70	727	874	657	1581
Perimeter							
	1987	50	03	53	518	185	703
St. Norbert							
	1988	172	66	238	293	350	643
	1989	39	13	52	---	---	----*
	Total	211	79	290	293	350	643

* - Trapping was discontinued in 1989 before juveniles appeared aboveground.

Figure 5. Seasonal distribution of biweekly captures of Spermophilus richardsonii at the Darlingford site, 1987-1988.

- A. Biweekly total adult and juvenile Spermophilus richardsonii captures, 1987.
(Trapping commenced 14 May, 1987)
- B. Biweekly total adult and juvenile Spermophilus richardsonii captures, 1988.
(Trapping commenced 01 April, 1988)



1381 captures over 48 trapping dates during 1988 (Tables 4 and 5). Thirty of these animals were captured as adults (n=4, females only) and juveniles (n=26, 19 females and 7 males) the previous year. Adult males accounted for 3.0% of all captures, adult females 32.2% and juvenile males and females 31.2% and 33.6% respectively. The maximum number of captures/individual was 34 with an average recapture rate of 8.2 captures per animal. Adult females were three times as numerous as adult males and juvenile males were slightly more numerous than juvenile females. The sex ratio for the entire squirrel population favoured females over males (0.81 male/female). Interyear survival for 1987 - 1988 was 0% for adult males, 19% for adult females, and 16.3% and 33.3% for male and female juveniles respectively. Squirrel population density was highest in June (Figure 5B), declining thereafter primarily because of, immergence of adults and larger juveniles, squirrel dispersal and/or mortality.

The trapping period was limited in 1989. Thirty-five different animals were captured 116 times during the five trapping dates in 1989. Only adults were present on the plots. Females, as in the two previous years, were more numerous and were trapped more frequently than males. The ratio of male to female squirrels was 1:4 during the spring of 1989. Interyear survival for adults was 0% for males and 25% for females. The percentage of yearlings which survived

over winter was 16.7% for males and 36.8% for females; juvenile survival was 7.8% and 31.1% for males and females, respectively.

Perimeter

Seventy-six individuals were captured 756 times during 39 trapping days at this site in 1987 (Table 4). Adults accounted for 7.0% of all captures and juveniles were responsible for the remaining 93.0% of the total captures (Table 5). The maximum number of captures/individual was 30 (average recapture rate = 9.9). Thirty-five squirrels were captured more than once per trapping date accounting for 106 captures. Squirrels were not captured more than twice per trapping date. Adult squirrels were outnumbered by juveniles (11.8% of all individual were adults, 88.2% juveniles). The adult sex ratio was female-biased, while the juvenile sex ratio was approximately 1:1 (34 males and 33 females). Female juveniles were the most frequently captured age class (68.5% of the total captures). Seasonal changes in squirrel density were similar at the Darlingford and the Perimeter site (Figure 6A). Squirrel activity ceased much earlier at this site relative to the Darlingford site.

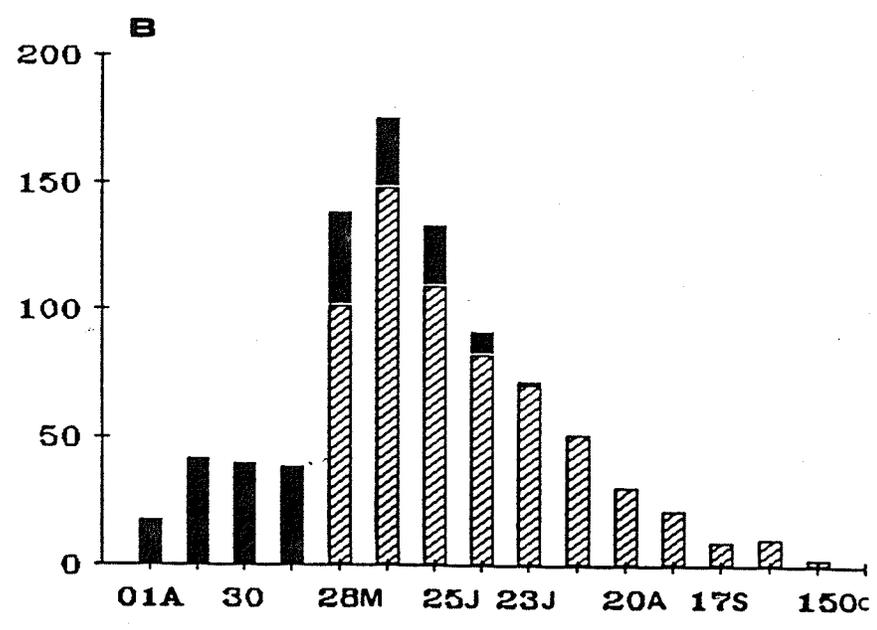
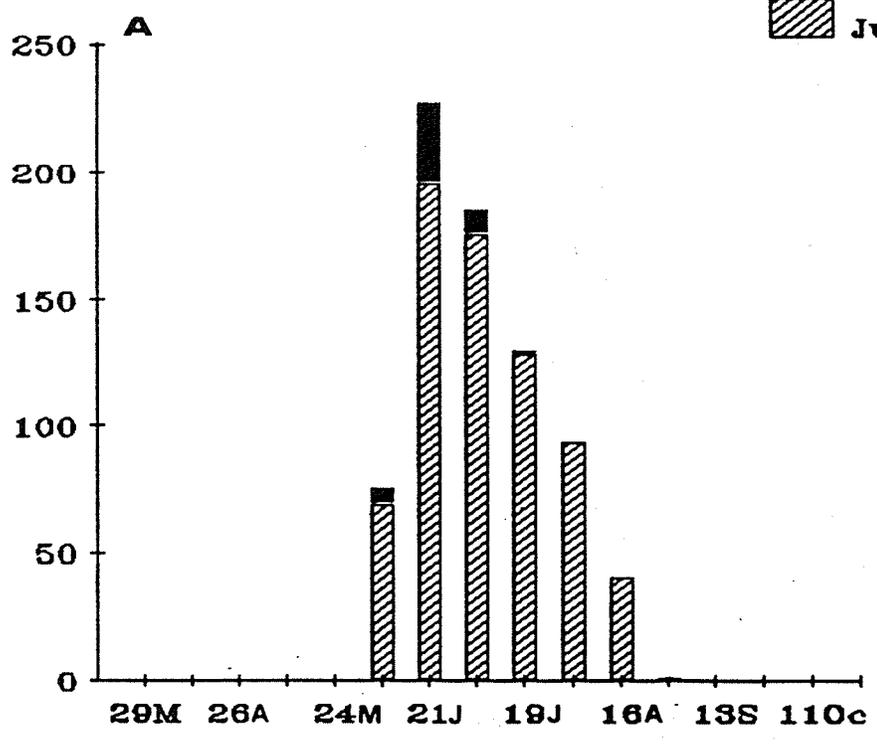
St. Norbert

During 1988, 100 individual squirrels accounted for 881 captures on 77 trapping dates (Tables 4 and 5). The adult

Figure 6. Seasonal distribution of biweekly captures of Spermophilus richardsonii at the Perimeter and St. Norbert sites.

- A. Biweekly total adult and juvenile Spermophilus richardsonii captures, 1987.
(Trapping commenced 12 June, 1987)
- B. Biweekly total adult and juvenile Spermophilus richardsonii captures, 1988.
(Trapping commenced 11 April, 1988)

Adults
Juveniles



population was comprised of 7 adult males and 12 adult females. Juveniles accounted for 81% of all individuals within the squirrel population (49% male and 32% female). The juveniles were male-biased (60.1% male). Juvenile squirrels accounted for more captures than adults (73% vs 27%) and male juveniles were captured more frequently than females. The largest number of captures/individual was for a male juvenile (n=47) and the average recapture rate was 8.8 captures/animal. Seasonal changes in squirrel densities were similar to the patterns observed at the Darlingford and Perimeter sites during 1987 and 1988 (Figure 6B).

Twenty-one squirrels (five males and sixteen females) were captured during the spring of 1989 at the St. Norbert site. These animals accounted for 52 captures. Female adults were more abundant than males. A female-biased adult sex ratio of 1:3 was observed. Interyear survival has 9.1% for adult males and 10% for adult females. Approximately 6% of juvenile males and 18.75% of juvenile females were trapped as yearlings in 1989.

Fleas removed from *S. richardsonii*

Darlingford

Nineteen thousand and sixty-five fleas (ten species) were removed from the 2,308 squirrels captured at Darlingford during 1987 to 1989 (Table 6). During 1987, 6,781 fleas (nine species) were collected from the 811

Table 6. Summary of flea species, total number (N) and observed sex distribution of fleas removed from S. richardsonii at the Darlingford, Perimeter and St. Norbert sites, 1987-1989.

<u>Year</u>	<u>Flea species</u>	<u>N</u>	<u>Males</u>	<u>Females</u>
Darlingford				
1987	<u>Aetheca wagneri</u>	19	06	13
	<u>Ctenophthalmus psuedargytes</u>	03	03	00
	<u>Foxella ignota</u>	02	01	01
	<u>Megabothris asio megacolpus</u>	08	06	02
	<u>Neopsylla inopina</u>	129	51	78
	<u>Opisocrostris bruneri</u>	2054	897	1157
	<u>Oropsylla rupestris</u>	4438	2029	2409
	<u>Pulex irritans</u>	03	01	02
	<u>Rhadinopsylla fraterna</u>	125	55	70
1988	<u>A. wagneri</u>	25	09	16
	<u>C. psuedargytes</u>	02	01	01
	<u>Epitedia wenmanni</u>	02	00	02
	<u>M. a. megacolpus</u>	10	00	10
	<u>N. inopina</u>	983	413	570
	<u>O. bruneri</u>	2473	1130	1343
	<u>O. rupestris</u>	7841	3403	4438
	<u>P. irritans</u>	02	02	00
	<u>R. fraterna</u>	169	64	105
1989	<u>M. a. megacolpus</u>	01	01	00
	<u>N. inopina</u>	334	166	168
	<u>O. bruneri</u>	130	75	55
	<u>O. rupestris</u>	227	96	131
	<u>R. fraterna</u>	85	33	52
Perimeter				
1987	<u>A. wagneri</u>	01	01	00
	<u>O. bruneri</u>	3495	1263	2232
St. Norbert				
1988	<u>A. wagneri</u>	02	01	01
	<u>E. wenmanni</u>	03	01	02
	<u>M. a. megacolpus</u>	02	02	00
	<u>O. bruneri</u>	2504	998	1506
1989	<u>A. wagneri</u>	05	01	04
	<u>O. bruneri</u>	213	107	106

squirrel captures. Of this total, 65.4% of the fleas were O. rupestris, 30.3% O. bruneri, and 1.9% and 1.8% N. inopina and R. fraterna, respectively. The 1,381 squirrel captures during 1988 yielded 11,507 fleas (nine different species) All of the prevalent flea species collected in 1987 were present in larger numbers than in the previous year.

Oropsylla rupestris was again the dominant flea species accounting for approximately 68% of all fleas taken from S. richardsonii. The next most numerous flea species were O. bruneri (21.5%), followed by N. inopina (8.5%) and R. fraterna (1.5%). Five flea species infested Richardson's ground squirrels during the spring of 1989. Neopsylla inopina was the most abundant species collected, followed by O. rupestris, O. bruneri, and R. fraterna. Since trapping was restricted to the spring of 1989, fleas were removed only from adult squirrels. The number of N. inopina, O. bruneri, O. rupestris, and R. fraterna collected each year will be examined separately.

Neopsylla inopina

One hundred and twenty-nine fleas of this species (51 males, 78 females) were collected from ground squirrels in 1987. The overall flea sex ratio (M/F) was 0.65; male fleas comprising 39.3% and females 60.7% of the collection (Table 8). Adult female squirrels carried about 35% of all N. inopina collected. Male and female juveniles were infested

Table 7. Numbers of Neopsylla inopina, Opisocrostitis bruneri, Oropsylla rupestris, and Rhadinopsylla fraterna removed from the different age and sex categories of S. richardsonii at the Darlingford site, 1987-1989. (See Table 5 also, page 59)

<u>Flea species</u>	<u>Squirrel age and sex</u>			
	<u>Adult</u>		<u>Juvenile</u>	
	<u>Female</u>	<u>Male</u>	<u>Female</u>	<u>Male</u>
1987				
<u>Neopsylla inopina</u>	46	01	42	40
<u>Opisocrostris bruneri</u>	123	00	904	1027
<u>Oropsylla rupestris</u>	742	45	1771	1880
<u>Rhadinopsylla fraterna</u>	04	00	32	89
Total -	915	46	2749	3036
1988				
<u>N. inopina</u>	445	227	139	172
<u>O. bruneri</u>	802	46	818	807
<u>O. rupestris</u>	1894	219	2616	3112
<u>R. fraterna</u>	18	53	40	58
Total -	3158	545	3612	4149
1989				
<u>N. inopina</u>	237	97	---	---
<u>O. bruneri</u>	109	21	---	---
<u>O. rupestris</u>	164	63	---	---
<u>R. fraterna</u>	71	14	---	---
Total -	571	194	---	---

with similar proportions of N. inopina (31% from males and 32.6% from females) and the lone male adult squirrel collected during 1987 had only one male N. inopina (Table 7).

Nine hundred and eighty-three (413 males, 570 females) N. inopina were collected during 1988. The observed (M/F) sex ratio was 0.72 (Table 8) with male fleas more prevalent than in 1987. Except during the first trapping interval, female N. inopina were always more numerous than males and during the two week period starting 14 May and 25 June, the ratio of male/female fleas was significantly biased towards females ($X^2=3.84$, d.f.1, $p<0.05$). Unlike 1987, adult squirrels, including males carried most of the N. inopina (Table 7). Juveniles accounted for slightly more than 30% of all specimens collected with male juveniles carrying 17.5% and females 14.1% of the N. inopina burden.

Three hundred and thirty-four N. inopina were collected from the 116 squirrel captures in 1989. The (M/F) flea sex ratio was approximately 1:1 (Table 8). Greater than 81% of the squirrel captures in 1989 were females (Table 5) and these animals carried 71% of the N. inopina collected (Table 7). Male squirrels were captured less frequently and the remaining 29% of the N. inopina collected were removed from these adult squirrels (Table 7).

Table 8. Observed sex ratios (M/F) and numbers (N) of Neopsylla inopina removed from S. richardsonii at Darlingford, Manitoba, 1987-1989.

1987			1988		
Period starting	N	M/F	Period starting	N	M/F
29 March	--	-----*	01 April	217	1.01
12 April	--	-----*	16	99	0.98
26	--	-----*	30	119	0.75
10 May	10	2.30	14 May	100	0.55**
24	27	0.69	28	107	0.59
07 June	14	1.00	11 June	115	0.80
21	30	0.58	25	115	0.44**
05 July	18	0.38	09 July	44	0.62
19	01	0.00	23	18	0.80
02 August	19	0.46	06 August	40	0.67
16	06	2.00	20	09	0.50
30	03	0.00	03 Sept.	00	-----
13 Sept.	01	0.00	17	00	-----
27	00	-----	01 Oct.	--	-----@
11 Oct.	00	-----	15	--	-----@
Total	129	0.65		983	0.72

1989		
Period starting	N	M/F
01 April	57	1.10
15	173	0.96
29	96	0.96
13 May	08	1.00
Total	334	0.99

- * - Squirrels were not trapped during these weeks.
 ** - Significantly female-biased sex ratios
 ($X^2=3.84$, d.f.1, $p<0.05$, all others $p>0.05$).
 @ - No squirrels active during these weeks.

Opisocrostitis bruneri

A total of 2,054 (897 males, 1,157 females) O. bruneri were removed from the 811 captures during 1987. The observed (M/F) sex ratio for O. bruneri was 0.78 (Table 9). Flea sex ratios were significantly different from 1:1 during the two week periods starting 24 May (male-biased) and from 21 June to 02 August (female-biased) ($X^2=3.84$, d.f.1, $p<0.05$). Adult females carried 6.0%, juvenile females 44.0% and juvenile males 50% of all fleas of this species (Table 7). The adult male collected during 1987 was not infested with O. bruneri.

During 1988, 2,473 (1,130 males, 1,343 females) O. bruneri were collected from S. richardsonii. The flea sex ratio was 0.84 with a greater proportion of males collected during 1988 than in 1987. Observed sex ratios were not significantly different from 1:1 during any of the trapping intervals (Table 9) ($X^2=3.84$, d.f.1, $p<0.05$). The number of O. bruneri collected in 1988 was comparable to 1987 despite 570 additional captures in 1988. As in 1987, O. bruneri was rarely collected from adult male squirrels (1.9% of all O. bruneri) (Table 7). Approximately equal numbers of O. bruneri were taken from adult females, juvenile females and males.

Squirrels were infested with 130 O. bruneri in 1989. Male fleas were more abundant than females however, these

Table 9. Observed sex ratios (M/F) and numbers (N) of Opisocrostitis bruneri removed from S. richardsonii at Darlingford, Manitoba, 1987-1989.

1987			1988		
Period starting	N	M/F	Period starting	N	M/F
29 March	--	-----*	01 April	51	0.76
12 April	--	-----*	16	52	1.00
26	--	-----*	30	152	0.77
10 May	12	1.00	14 May	211	0.85
24	21	3.20**	28	248	0.84
07 June	46	1.42	11 June	158	0.95
21	86	0.43**	25	247	0.83
05 July	258	0.50**	09 July	413	0.75
19	355	0.83**	23	320	0.73
02 August	419	0.81	06 August	301	0.88
16	392	0.90	20	264	1.06
30	163	0.77	03 Sept.	40	0.90
13 Sept.	175	0.86	17	16	1.28
27	65	0.55	01 Oct.	--	-----@
11 Oct.	62	0.72	15	--	-----@
Total	2054	0.78		2473	0.84

1989		
Period starting	N	M/F
01 April	13	3.30
15	16	0.78
29	57	1.19
13 May	44	1.59
Total	130	1.36

- * - Squirrels were not trapped during these weeks.
 ** - Sex ratios significantly different from unity ($X^2=3.84$, d.f.1, $p<0.05$, all others $p>0.05$).
 @ - No squirrels active during these weeks.

differences were not significant for any of the trapping intervals (Table 9). More fleas were taken from female (83.8% of all O. bruneri) than male squirrels (Table 7), however, female squirrels were also captured four times as frequently as males.

Oropsylla rupestris

A total of 4,438 (2,029 males, 2,409 females) specimens of this species were collected during 1987. The overall flea sex ratio was female-biased and significantly more female than male O. rupestris were collected between 24 May to 05 July (Table 10). Adult squirrels accounted for fewer than 18% of the specimens collected (16.7% and 1.0% of all O. rupestris collected were taken from adult females and males, respectively). Examination of juvenile males and females yielded 42.4% and 39.9% of the O. rupestris collected (Table 7).

A total of 7,841 (3,403 males, 4438 females) O. rupestris were removed from Richardson's ground squirrels during 1988. A female-biased flea sex ratio was again observed and these biases were significant during the sampling intervals of 01 April, 28 May, 11 and 25 June, 09 July (Table 10). The largest number of O. rupestris adults were removed from juvenile squirrels (73% of the collection). Male juveniles accounted for 39.7% and females 33.4% of O. rupestris collected (Table 7). Adult females

Table 10. Observed sex ratios (M/F) and numbers (N) of Oropsylla rupestris removed from S. richardsonii at Darlingford, Manitoba, 1987-1989.

1987			1988		
Period starting	N	M/F	Period starting	N	M/F
29 March	--	-----*	01 April	280	0.65**
12 April	--	-----*	16	109	0.88
26	--	-----*	30	69	0.64
10 May	03	0.00	14 May	253	0.67
24	111	0.48**	28	405	0.61**
07 June	247	0.45**	11 June	1431	0.56**
21	906	0.74**	25	2527	0.80**
05 July	1137	0.87	09 July	1489	0.85**
19	627	1.12	23	679	0.94
02 August	608	0.94	06 August	363	0.89
16	334	1.09	20	246	1.10
30	458	0.94	03 Sept.	50	1.08
13 Sept.	146	0.95	17	09	0.50
27	91	0.63	01 Oct.	--	-----@
11 Oct.	104	0.55**	15	--	-----@
Total	4438	0.84		7841	0.77

1989		
Period starting	N	M/F
01 April	94	0.84
15	78	0.56**
29	39	0.86
13 May	16	0.78
Total	227	0.73

- * - Squirrels were not trapped during these weeks.
 ** - Significantly female-biased sex ratios
 ($X^2=3.84$, d.f.1, $p<0.05$, all other $p>0.05$).
 @ - No squirrels active during these weeks.

carried approximately 25% of the O. rupestris while males were responsible for only 2.8% of the collection.

During 1989, squirrels at the Darlingford site carried 227 (96 male, 131 female) O. rupestris. Female O. rupestris were more abundant than males during each sampling interval, but the sex ratios were only significantly different for the period starting 15 April (Table 10). More female than male squirrels were captured (81.9% vs 18.1%) and females carried 72.2% of O. rupestris collected (Table 7).

Rhadinopsylla fraterna

One hundred and twenty-five specimens (55 males, 70 females) were removed during examination of squirrels in 1987. The observed (M/F) flea sex ratio was 0.78 (Table 11). As with O. bruneri, this species was not found on the single male adult squirrel and the percentage of R. fraterna collected from adult females was also small (3.2% of all specimens). The largest number of R. fraterna was taken from juveniles. Males carried 71.2%, and females 25.6% of all specimens of this species collected during 1987 (Table 7).

One hundred and sixty-nine (64 males, 105 females) R. fraterna were collected during 1988. A greater proportion of these fleas were females than in 1987 (Table 11). The largest number of R. fraterna were collected from juvenile males (n=58) and adult males (n=53). Rhadinopsylla fraterna

Table 11. Observed sex ratios (M/F) and numbers (N) of Rhadinopsylla fraterna removed from S. richardsonii at Darlingford, Manitoba, 1987-1989.

1987			1988		
Period starting	N	M/F	Period starting	N	M/F
29 March	--	-----*	01 April	57	0.90
12 April	--	-----*	16	07	0.17
26	--	-----*	30	00	-----
10 May	00	-----	14 May	01	0.00
24	01	-----	28	04	3.00
07 June	05	0.25	11 June	04	1.00
21	01	0.00	25	06	0.20
05 July	00	-----	09 July	07	0.17
19	03	2.00	23	04	0.33
02 August	07	0.75	06 August	09	0.50
16	19	0.90	20	63	0.58
30	09	0.12	03 Sept.	07	0.40
13 Sept.	36	0.89	17	00	-----
27	19	0.90	01 Oct.	--	-----@
11 Oct.	25	0.78	15	--	-----@
Total	125	0.78		169	0.61

1989		
Period starting	N	M/F
01 April	30	0.67
15	45	0.61
29	08	1.00
13 May	02	-----
Total	85	0.63

* - Squirrels were not trapped during these weeks.

@ - No squirrels were active during these weeks.

occurred less frequently on female squirrels. Juvenile females accounted for 23.7% and adult females 10.6% of the R. fraterna collected during 1988 (Table 7).

A total of 85 (33 male, 52 female) R. fraterna were collected in 1989. The sex ratio showed a female bias (Table 11). Eighty-three per cent of the R. fraterna collected were removed from female squirrels; females were also captured four times as frequently as male squirrels.

Perimeter

Opisocrostis bruneri

The fleas infesting Richardson's ground squirrel at the Perimeter site were almost exclusively O. bruneri (i.e. 99.97% of 3496 fleas, Table 6). Female fleas were more frequently collected than males (1,263 males and 2,232 females). The observed flea sex ratio was female-biased and these differences were significant for the trapping intervals from 21 June to 16 August (Table 12). Female juveniles accounted for the greatest percentage of O. bruneri collected (71.1% of the entire collection). Male juveniles carried 25.2%, adult females 3.3% and adult males <1.0% of the O. bruneri collected at this site (Table 13).

St. Norbert

Opisocrostis bruneri

During 1988, 2,511 fleas, representing four species, were taken from the 881 squirrel captures. Greater than 99%

Table 12. Observed sex ratios (M/F) and numbers (N) of Opisocrostitis bruneri removed from S. richardsonii at the Perimeter site (1987) and St. Norbert site (1988-1989).

1987			1988		
Period starting	N	M/F	Period starting	N	M/F
29 March	--	-----*	01 April	13	1.17
12 April	--	-----*	16	26	0.73
26	--	-----*	30	61	1.10
10 May	--	-----*	14 May	38	1.00
24	--	-----*	28	85	1.50
07 June	54	1.16	11 June	121	1.47
21	156	0.28**	25	136	0.37**
05 July	699	0.46**	09 July	453	0.32**
19	960	0.52**	23	557	0.73**
02 August	1131	0.62**	06 August	366	0.72**
16	482	0.81	20	232	0.71
30	13	0.63	03 Sept.	215	0.85
13 Sept.	--	-----@	17	90	0.61
27	--	-----@	01 Oct.	85	0.54
11 Oct.	--	-----@	15	26	0.73
Total	3495	0.57		2504	0.66

1989		
Period starting	N	M/F
01 April	01	----
15	19	1.37
29	91	0.98
13 May	102	0.96
Total	213	1.01

- * - Squirrels were not trapped during these weeks.
 ** - Significantly female-biased sex ratios
 ($X^2=3.84$, d.f. 1, $p<0.05$, all others $p>0.05$).
 @ - No squirrels active during these weeks.

of all fleas collected from Richardson's ground squirrels at the St. Norbert site were O. bruneri (Table 6). A total of 2,504 (998 males, 1,506 females) O. bruneri were found during 1988. The observed flea sex ratio of O. bruneri adults was female-biased. There were significantly more female O. bruneri than males collected from 25 June to 20 August (Table 12). Juvenile males carried the largest number of O. bruneri (55.3%) followed by juvenile females (32.5%) and adult females (9.5%) (Table 13). Adult males were responsible for only 2.7% of all O. bruneri collected.

Fifty-two squirrel captures in 1989 yielded 218 fleas (two species). Opisocrostis bruneri was the dominant flea species accounting for 97.7% (n=213) of the collection. The flea sex ratio was approximately 1:1 (107 male, 106 female). The largest percentage of squirrel captures (75%) and number of fleas (85.9% of all O. bruneri) were removed from female squirrels (Table 13).

Flea infestation parameters

Seasonal activity of the various flea species associated with Richardson's ground squirrels was determined by examining changes in the mean intensity and prevalence of infestation. At the Darlingford site, N. inopina, O. bruneri, O. rupestris, and R. fraterna were the only species for which sample sizes were sufficient to allow estimates of seasonal activity. These four flea species are also the

Table 13. Numbers of Opisocrostitis bruneri removed from the two age classes and sexes of S. richardsonii at the Perimeter and St. Norbert sites in 1987-1989.

	<u>Squirrel age and sex</u>			
	<u>Adult</u>		<u>Juvenile</u>	
	<u>Female</u>	<u>Male</u>	<u>Female</u>	<u>Male</u>
Perimeter				
<u>1987</u>	116	12	2485	882
St. Norbert				
<u>1988</u>	238	68	813	1385
<u>1989</u>	183	30	---	---

only true ground squirrel fleas.

Seasonal changes in the infestation parameters for 1987 were similar to patterns observed in 1988 for all flea species. While the magnitude of mean intensity and prevalence were slightly different between years, the temporal distribution of flea species was maintained. The primary function of trapping in 1989 was to determine if N. inopina and R. fraterna were active early in the season as in 1988.

Darlingford

Neopsylla inopina

The prevalence of N. inopina on squirrels was less than 30% throughout 1987 (Figure 7A). The highest observed mean intensity and prevalence of this species occurred within the first month of trapping (15 May - 12 June). Adult squirrels were the only age group active at this time and as a result adults had higher prevalence and intensity of infestation than juveniles. Throughout the remainder of the season, the prevalence of N. inopina dropped to roughly 10% and squirrels rarely carried more than one or two specimens. Neopsylla inopina was not present on Richardson's ground squirrels after 25 September, though squirrels were active until 17 October.

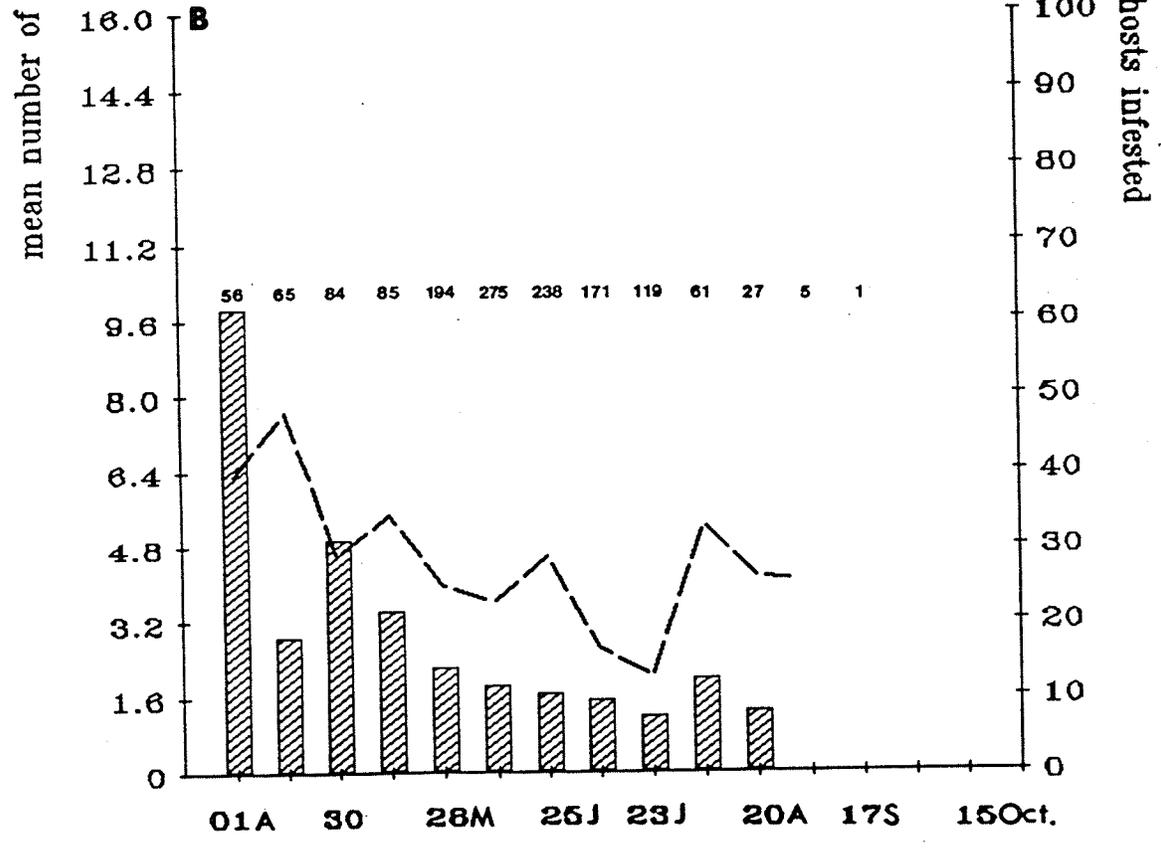
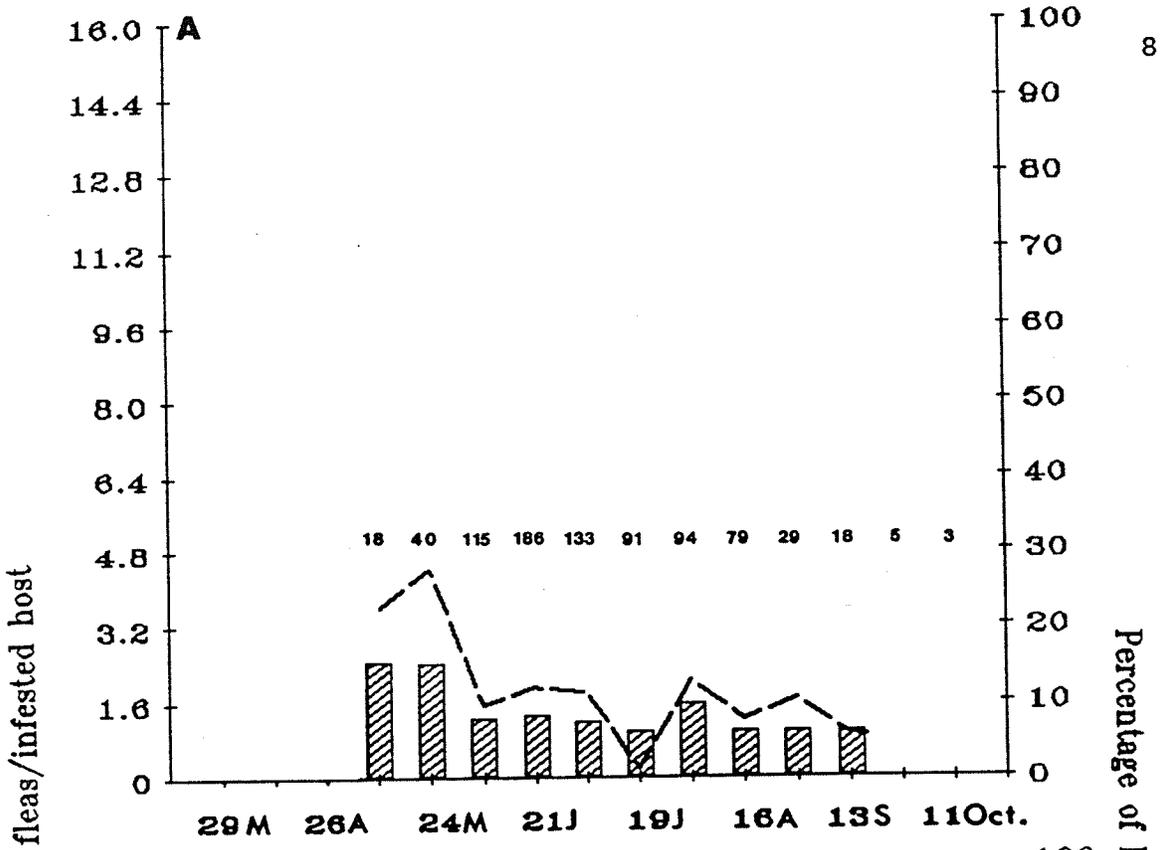
The observed mean intensity of N. inopina infestation was highest during the first month of squirrel above ground

Figure 7. Seasonal variation in the infestation parameters for Neopsylla inopina removed from Spermophilus richardsonii at the Darlingford site, 1987-1988.

A. Biweekly mean intensity (histogram) and prevalence (line) of N. inopina adults removed from S. richardsonii, 1987.
(Biweekly interval, 29 March-11 October)

B. Biweekly mean intensity (histogram) and prevalence (line) of N. inopina adults removed from S. richardsonii, 1988.
(Biweekly interval, 01 April-15 October)

Numbers are biweekly total squirrel captures.



activity in 1988 (Figure 7B). Thereafter, the number of N. inopina/infested squirrel decreased and remained at relatively low levels for the remainder of 1988. Neopsylla inopina was not collected from ground squirrels after 03 September, though squirrels were active until 25 September. The proportion of squirrels infested with N. inopina reached a seasonal high of roughly 50% during mid April and fluctuated between 15% - 30% throughout the summer and fall.

The observed mean intensity and prevalence of N. inopina adults from ground squirrels was highest during the first two trapping intervals in 1989 (Table 14). The number of N. inopina/infested host and the percentage of hosts infested decreased during early May. This pattern is similar to that observed in 1988.

Opisocrostitis bruneri

The observed prevalence of O. bruneri adults on Richardson's ground squirrels changed seasonally (Figure 8A). During the first six weeks of trapping in 1987, prevalence dropped from 50% to less than 25%. Prevalence of infestation increased progressively throughout the remainder of the season, levelling off at roughly 90% by early August. The number of O. bruneri/infested squirrel was low from 10 May - 21 June, and thereafter, the intensity increased progressively. Mean intensity increased as the number of squirrels within the population decreased. Prevalence and

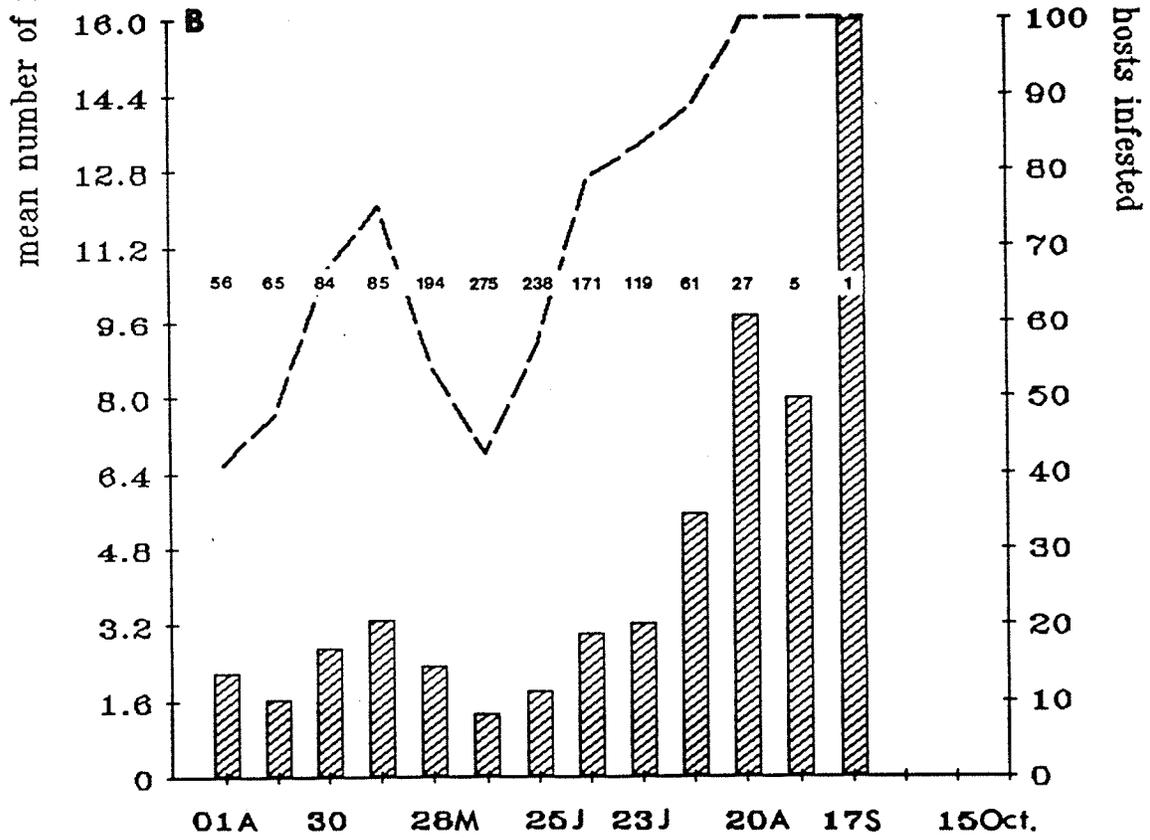
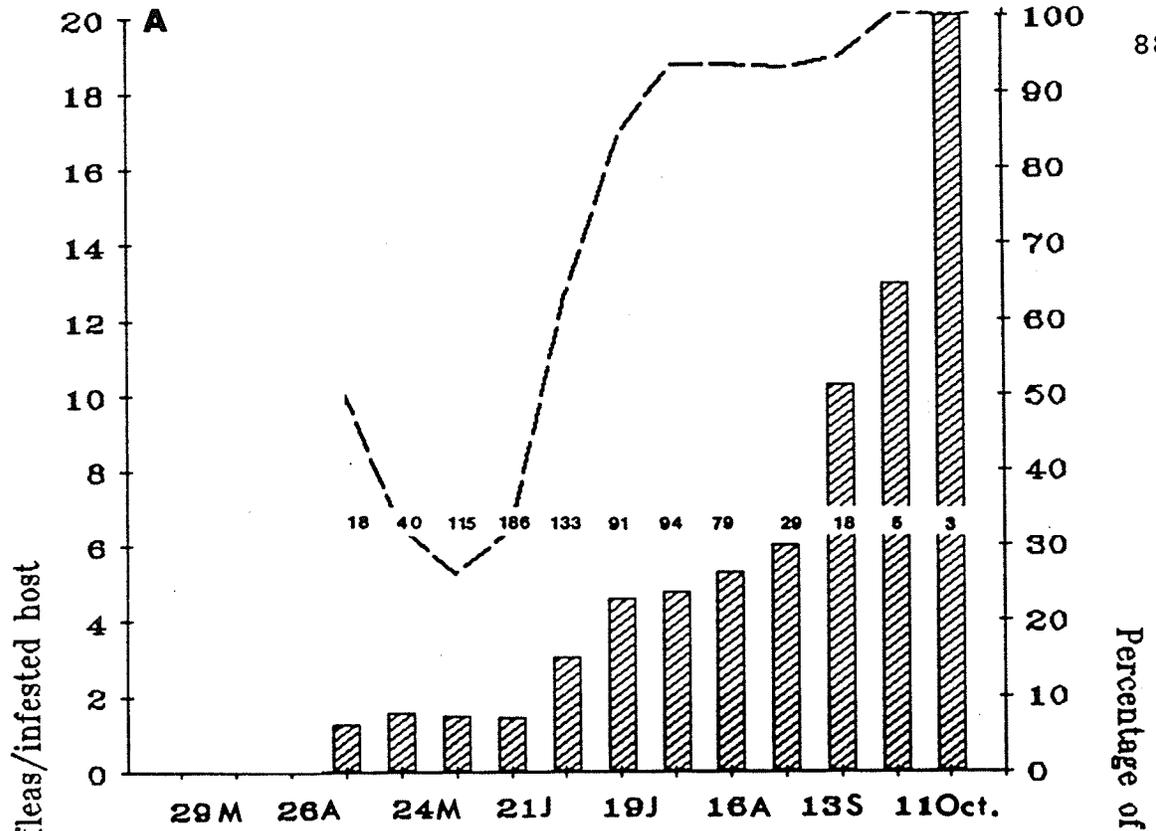
Table 14. Observed prevalence and mean intensity of Neopsylla inopina, Opisocrostis bruneri, Oropsylla rupestris and Rhadinopsylla fraterna adults on S. richardsonii at the Darlingford and St. Norbert sites, 1989.

<u>Flea species</u>	<u>Period starting</u>	<u>Total host captures</u>	<u>Mean intensity</u>	<u>Prevalence (%)</u>
Darlingford				
<u>N. inopina</u>				
	01 April	17	5.2	64.7
	15	29	6.9	86.2
	29	47	3.8	53.2
	13 May	23	2.7	13.0
<u>O. bruneri</u>				
	01 April	17	2.2	35.3
	15	29	2.0	27.6
	29	47	1.8	65.9
	13 May	23	2.3	82.6
<u>O. rupestris</u>				
	01 April	17	5.9	94.1
	15	29	3.5	75.9
	29	47	1.4	36.2
	13 May	23	2.3	30.4
<u>R. fraterna</u>				
	01 April	17	5.0	35.2
	15	29	5.0	31.0
	29	47	1.6	10.6
	13 May	23	2.0	4.3
St. Norbert				
<u>O. bruneri</u>				
	01 April	04	1.0	25.0
	15	18	3.2	33.3
	29	19	6.1	78.9
	13 May	11	11.3	81.8

Figure 8. Seasonal variation in the infestation parameters for Opisocrostitis bruneri removed from Spermophilus richardsonii at the Darlingford site, 1987-1988.

- A. Biweekly mean intensity (histogram) and prevalence (line) of O. bruneri adults removed from S. richardsonii, 1987.
(Biweekly interval, 29 March-11 October)
- B. Biweekly mean intensity (histogram) and prevalence (line) of O. bruneri adults removed from S. richardsonii, 1988.
(Biweekly interval, 01 April-15 October)

Numbers are biweekly total squirrel captures.



intensity of infestation were highest for juvenile squirrels. The maximum intensity of infestation occurred during mid October, however, only three animals were sampled at this time.

The observed mean intensity was generally less than three O. bruneri/infested squirrel during April, May, June and July of 1988 (Figure 8B). Intensity did increase slightly during late May. When juvenile emergence commenced the mean number of O. bruneri/infested animal decreased. The intensity of O. bruneri infestation reached a peak in late August. Prevalence of infestation increased gradually after adult emergence and peaked during the bi-weekly period of 14 May. The percentage of squirrels infested with O. bruneri declined to approximately 40% following the emergence of juveniles. Prevalence began to increase near the end of June and reached 100% by late August.

The observed mean intensity of O. bruneri infestation of Richardson's ground squirrel remained at about two fleas/infested host, during the spring of 1989 (Table 14). The prevalence of this flea increased to a maximum of 82.6% during the last trapping interval.

Oropsylla rupestris

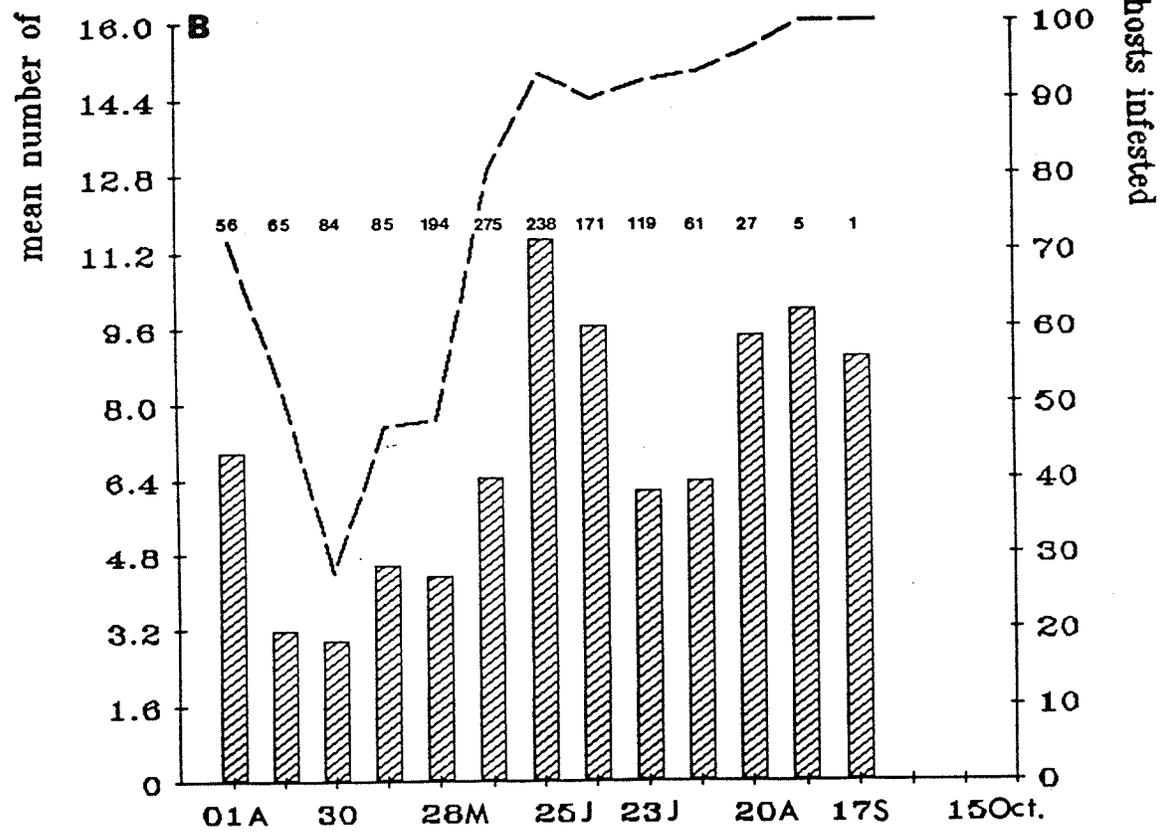
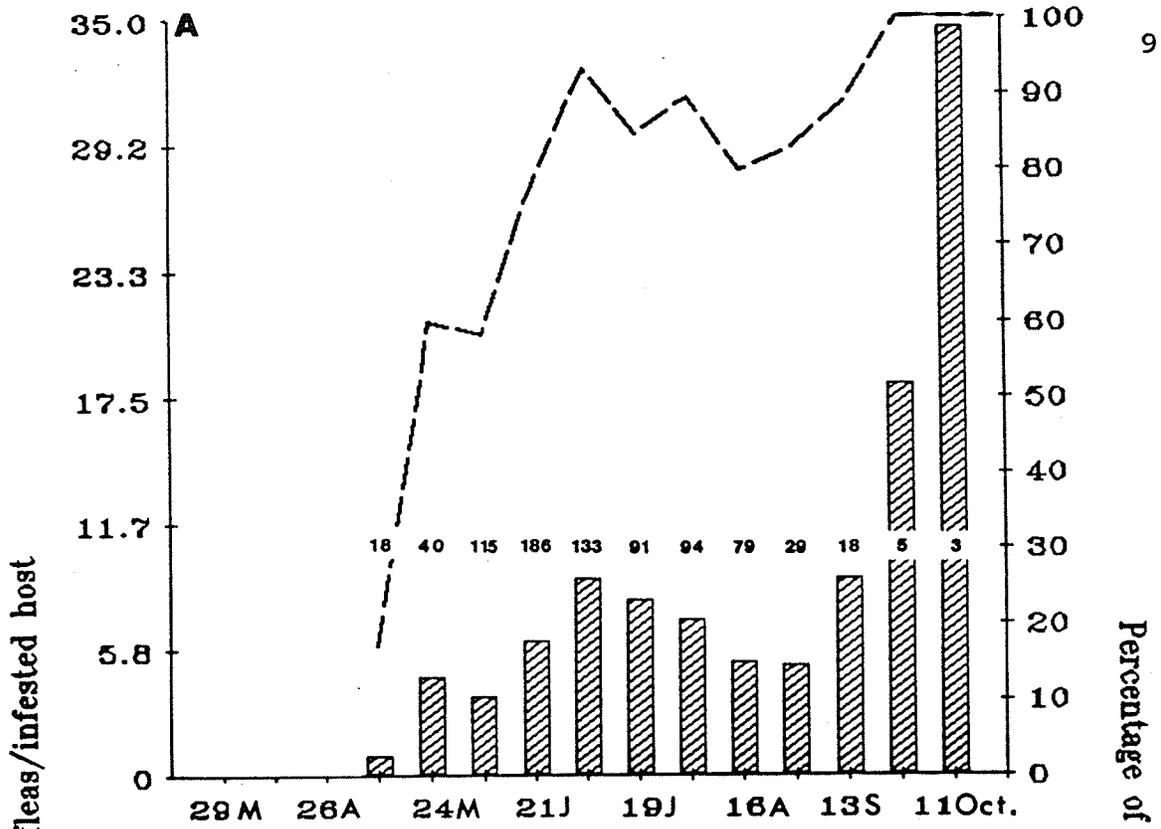
Squirrels carried more O. rupestris than any other flea species. In 1987, two peaks in observed mean intensity of O. rupestris adults occurred in early July and late

Figure 9. Seasonal variation in the infestation parameters for Oropsylla rupestris removed from Spermophilus richardsonii at the Darlingford site, 1987-1988.

A. Biweekly mean intensity (histogram) and prevalence (line) of O. rupestris adults removed from S. richardsonii, 1987.
(Biweekly interval, 29 March-11 October)

B. Biweekly mean intensity (histogram) and prevalence (line) of O. rupestris adults removed from S. richardsonii, 1988.
(Biweekly interval, 01 April-15 October)

Numbers are biweekly total squirrel captures.



September, respectively (Figure 9A). All age classes of squirrels were active in July and the squirrel population had reached its peak during the previous two week period. Mean intensity of O. rupestris decreased after the July peak but increased again late in the season. The observed prevalence of infestation increased early in the season and peaked two weeks before the peak in mean intensity. Prevalence fluctuated at roughly 90% for the remainder of the season increasing to 100% late in September.

The infestation of Richardson's ground squirrels by O. rupestris adults during 1988 followed the same general pattern as in 1987. The summer peak in mean intensity occurred during 25 June - 09 July (Figure 9B). The peaks in mean intensity for this species during 1987 and 1988 overlapped at the end of June. Mean intensity of O. rupestris was above six fleas/infested host immediately after adult emergence but decreased to a seasonal low during mid April and early May. Mean intensity of infestation steadily increased during juvenile emergence to reach its peak in late June. The number of O. rupestris/infested squirrel declined following this peak but increased in early September. The percentage of squirrels infested with O. rupestris decreased from 01 April to 14 May but rapidly increased to near 100% by 25 June. The observed prevalence of infestation remained high until squirrel activity ceased

in late September.

In 1989, large numbers of O. rupestris were collected from the majority of squirrels during the first trapping interval (94.1% of all hosts infested). Thereafter, mean intensity and prevalence of O. rupestris adults gradually decreased (Table 14).

Rhadinopsylla fraterna

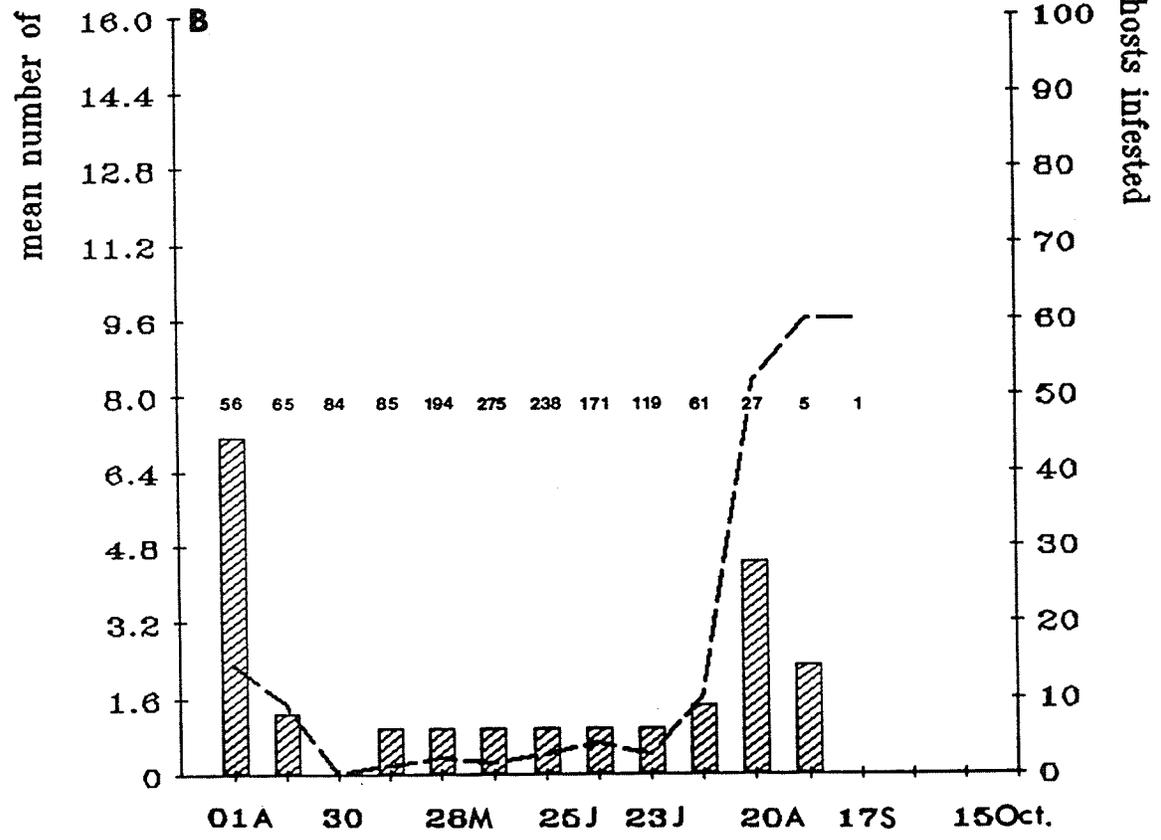
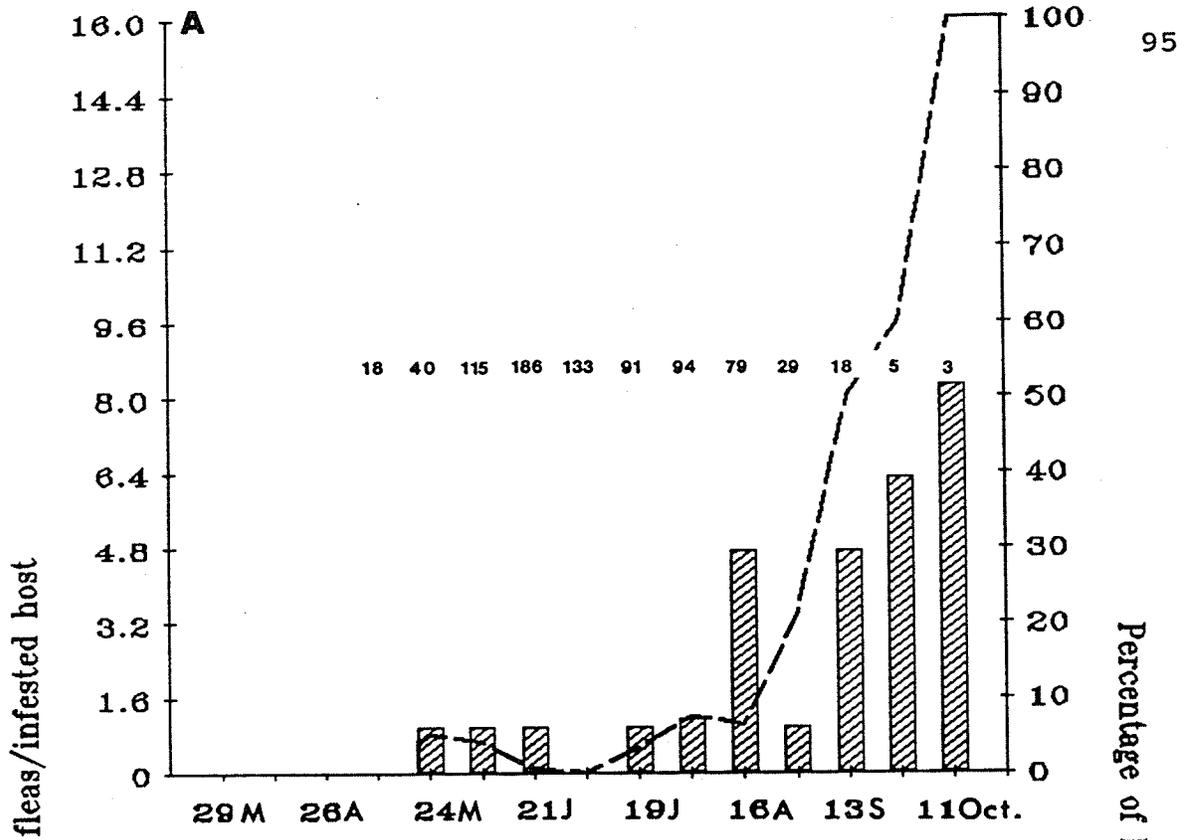
This flea species was most prevalent during the later stages of the squirrel circannual cycle during 1987. Low levels of mean intensity and prevalence of R. fraterna adults were observed throughout the summer. Observed mean intensity of infestation was never greater than one before mid August. During late August and early September both mean intensity and prevalence of R. fraterna infestation increased substantially (Figure 10A).

Two peaks in adult R. fraterna were observed during 1988 (Figure 10B). The first peak occurred during the first two weeks of trapping at Darlingford. Greater than seven R. fraterna/infested host were collected during this period and observed mean intensity and prevalence declined dramatically within the next two week period. Prevalence and mean intensity of R. fraterna adults remained at very low levels until early August when the second peak of R. fraterna activity occurred. Squirrels were not infested with R. fraterna after 10 September.

Figure 10. Seasonal variation in the infestation parameters for Rhadinopsylla fraterna removed from Spermophilus richardsonii at the Darlingford site, 1987-1988.

- A. Biweekly mean intensity (histogram) and prevalence (line) of R. fraterna adults removed from S. richardsonii, 1987.
(Biweekly interval, 29 March-11 October)
- B. Biweekly mean intensity (histogram) and prevalence (line) of R. fraterna adults removed from S. richardsonii, 1988.
(Biweekly interval, 01 April-15 October)

Numbers are biweekly total squirrel captures.



Rhadinopsylla fraterna infested approximately 35% of all squirrels captured during the first trapping interval in 1989 (Table 14). The percentage of squirrels infested with this flea slowly declined until less than 5% of the squirrels were infested. Mean intensity of R. fraterna adults was relatively high through early April but decreased during the following weeks.

Perimeter

Opisocrostis bruneri

Fleas removed from Richardson's ground squirrels at the Perimeter site had similar patterns of seasonal activity, based on changes in mean intensity and prevalence, as the O. bruneri population at Darlingford. Mean intensity of infestation increased after 21 June, peaking in mid August (Figure 11A). Juvenile squirrels had the highest intensities of infestation. During 1987, the number of O. bruneri per infested host was similar for squirrels at the Darlingford and Perimeter sites. The prevalence of O. bruneri increased through June and July, with the majority of squirrels infested by early August.

St. Norbert

Opisocrostis bruneri

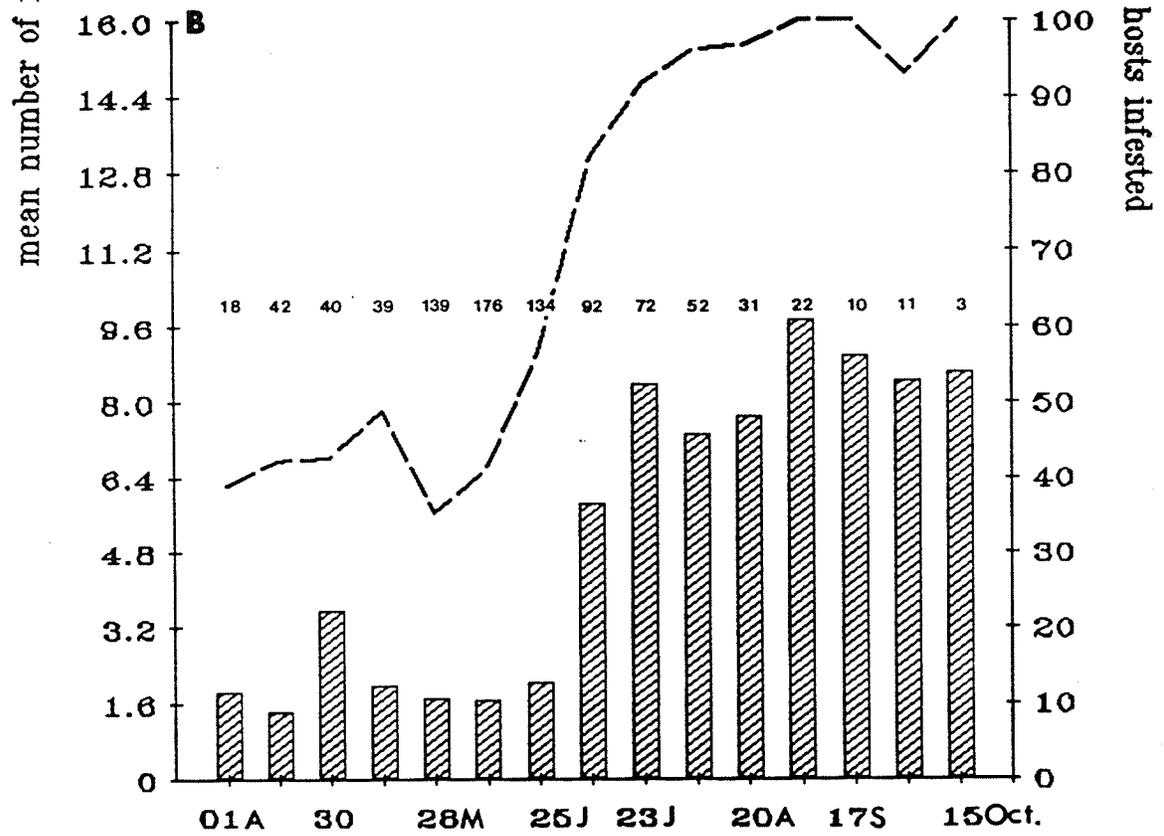
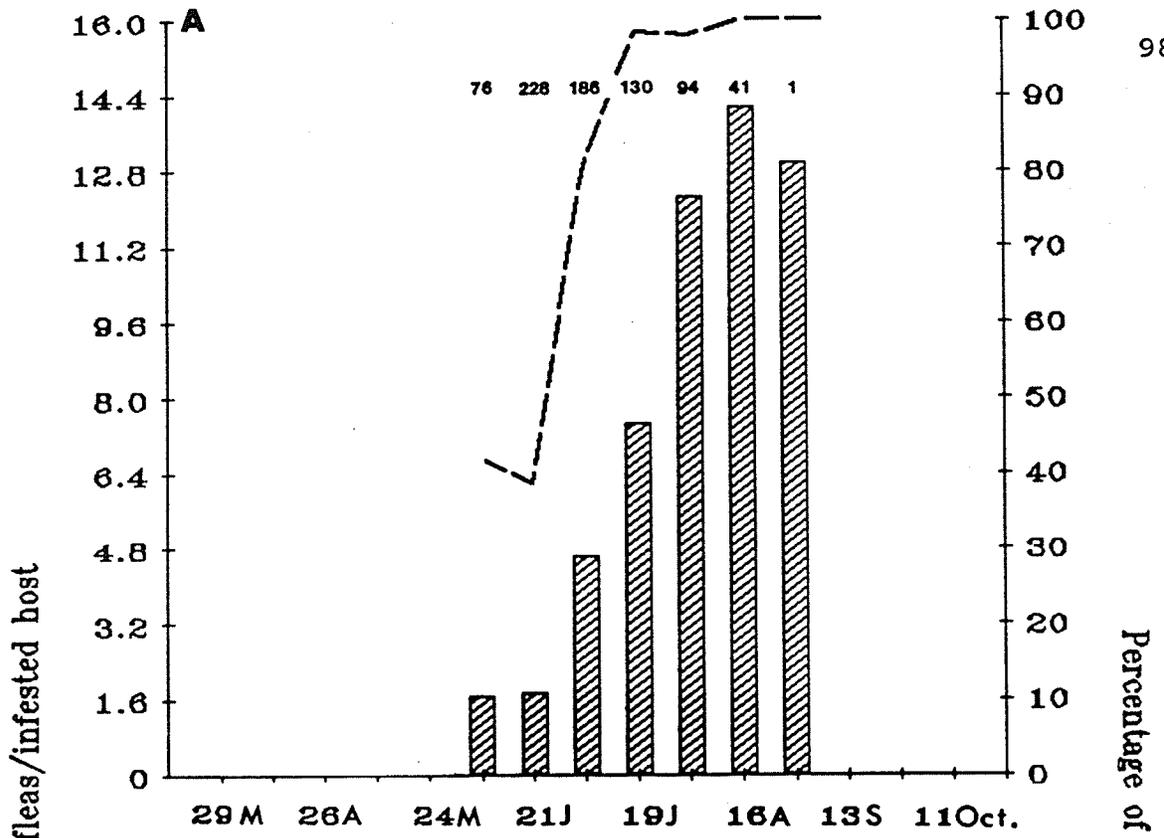
The pattern of seasonal activity for O. bruneri at St. Norbert in 1988 was similar to the pattern observed at the Darlingford site during the same year. The observed mean

Figure 11. Seasonal variation in the infestation parameters for Opisocrostis bruneri removed from Spermophilus richardsonii at the Perimeter (1987) and St. Norbert (1988) sites.

A. Biweekly mean intensity (histogram) and prevalence (line) of O. bruneri adults removed from S. richardsonii, 1987. (Biweekly interval, 29 March-11 October)

B. Biweekly mean intensity (histogram) and prevalence (line) of O. bruneri adults removed from S. richardsonii, 1988. (Biweekly interval, 01 April-15 October)

Numbers are biweekly total squirrel captures.



intensity of O. bruneri adults was low during the first month with a slight peak in activity in early May (Figure 11B). The number of O. bruneri/infested hosts remained low throughout the period of juvenile emergence. The mean intensity of O. bruneri adults began to increase in early June and a peak was observed in early September (period starting 03 September). Mean intensity of infestation remained at roughly nine O. bruneri/infested host for the remainder of the trapping periods. However, from late July to October the number of animals active on the site declined. Less than 50% of squirrels at the St. Norbert site were infested with O. bruneri during the first 12 weeks of trapping. Prevalence dropped dramatically to the seasonal low of 35.2% during the period of 28 May. Juvenile squirrels emerged from their natal burrows within this period. The percentage of squirrels infested gradually increased following juvenile emergence and by 23 July approximately 90% of all hosts were infested. Prevalence of O. bruneri infestation remained high for the remainder of 1988.

The observed mean intensity of O. bruneri adults on squirrels at the St. Norbert site was high during the spring of 1989. The number of O. bruneri/infested hosts increased during each two week period and reached a peak of 11.3 O. bruneri/infested squirrel (Table 14). Prevalence of

infestation also increased as trapping progressed. A similar increase in mean intensity and prevalence was noted for O. bruneri at the Darlingford and St. Norbert sites in 1988 however, the magnitude of these peaks was smaller than those observed in 1989.

Daily reinfestation - 1987

Regardless of the flea species, squirrels carried heavier flea burdens when first captured than at subsequent captures during the same day (Two sample sign test $p(X \geq 58)$ $\alpha = 0.05$). Squirrels which were not infested during either capture or which carried fewer fleas upon recapture comprised the largest percentage of all infestation ratings for all flea species removed from same day recaptures (Table 15). Reinfestation of squirrels by O. bruneri and O. rupestris was unpredictable whereas, the majority of recaptured squirrels were not reinfested by N. inopina or R. fraterna. At the Perimeter site, roughly one third of the recaptured squirrels carried the same or greater O. bruneri burdens than when they were initially captured. Squirrels at Darlingford had similar patterns of reinfestation by O. bruneri (28.1% of recaptures infested with as many or more O. bruneri). Oropsylla rupestris was recovered from 31.9% of the recaptures at the same or greater intensity than the initial capture. Squirrels were much more likely to be infested with O. rupestris. During 1987, only five

Table 15. Reinfestation rating for Neopsylla inopina, Opisocrostis bruneri, Oropsylla rupestris, and Rhadinopsylla fraterna removed from same day recaptures of S. richardsonii at the Perimeter (N=106) and Darlingford (N=110) sites, 1987.

Site	Flea species	Flea infestation rating					N	%
		(00)	(0+)	(++)	(+-)	(=)		
Darlingford								
	<u>N. inopina</u>	92.0	8.0	0.0	10.0	0.0	N	%
		83.6	5.5	0.0	9.1	0.0	%	
	<u>O. bruneri</u>	22.0	7.0	13.0	57.0	11.0	N	%
		20.0	6.4	11.8	52.8	10.0	%	
	<u>O. rupestris</u>	5.0	12.0	18.0	70.0	5.0	N	%
		4.5	10.9	16.4	63.6	4.5	%	
	<u>R. fraterna</u>	101.0	2.0	2.0	5.0	0.0	N	%
		91.8	1.8	1.8	4.5	0.0	%	
Perimeter								
	<u>O. bruneri</u>	9.0	11.0	19.0	60.0	8.0	N	%
		8.5	10.4	17.0	56.6	7.5	%	

Flea infestation rating

- (00) - no fleas recovered during initial capture or upon recapture.
- (0+) - squirrels uninfested upon first capture but had one or more fleas when recaptured.
- (++) - squirrels infested at first and subsequent captures and carried more fleas upon recapture.
- (+-) - squirrels infested at first capture but carried fewer fleas upon recapture.
- (=) - squirrel infested with the same number of fleas at first and subsequent captures.
- N - number of same day recaptures.
- % - per cent of the total same day recaptures.

squirrels were uninfested by this species at both the initial capture and subsequent recapture. Fleas carried by the recaptured squirrels reflected the relative abundance of the various flea species. Only 12% of all recaptured squirrels were infested with N. inopina and R. fraterna.

While the majority of same day recaptures carried fewer fleas than upon their initial capture, the probability of squirrels becoming reinfested was not impaired by the removal of fleas. Many of the same day recaptures ranked as (+-) were infested upon recapture. However, the intensity of infestation was lower than when these animals were initially captured. Squirrels at the Perimeter site which carried fewer fleas upon recapture were uninfested only 18.3% of the time. Similarly, squirrels at the Darlingford site which carried fewer O. bruneri upon recapture were infested 60% of the time. Oropsylla rupestris was absent from recaptures 25.7% of the time. For all recaptures rated as (+-) in 1987, on average 63.7% of the recaptured animals were infested with the same flea species which had been removed earlier that day. In addition, approximately 21% of all recaptured squirrels had infestations which were at least equal to the intensity for their original capture.

Flea reproductive parameters

Of the 25,290 fleas collected during this study, 23,759 individuals were dissected. The gonotrophic age and the per

cent mated were assessed for 13,345 females. The majority of these fleas were O. rupestris (6,416) and O. bruneri (5,893). Neopsylla inopina and R. fraterna females were less abundant (813 and 223 individuals respectively).

Darlingford

Neopsylla inopina

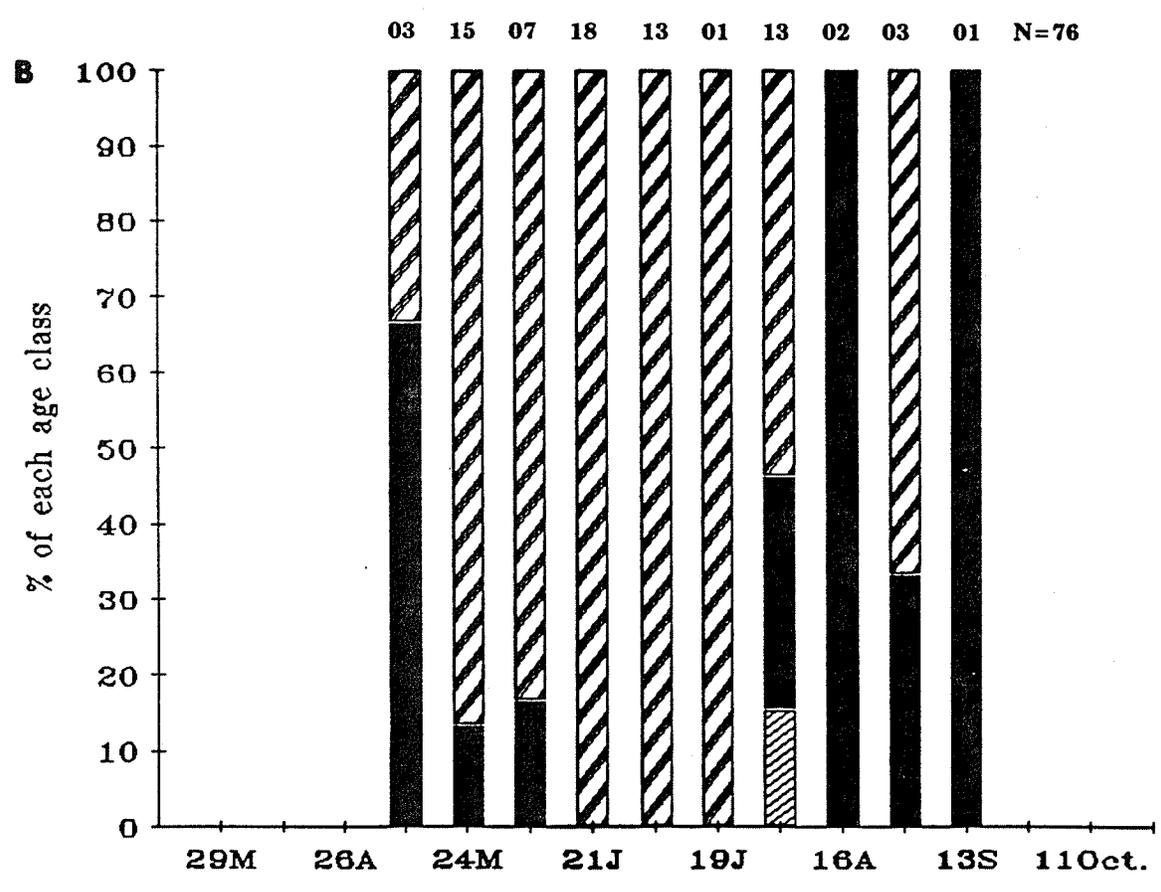
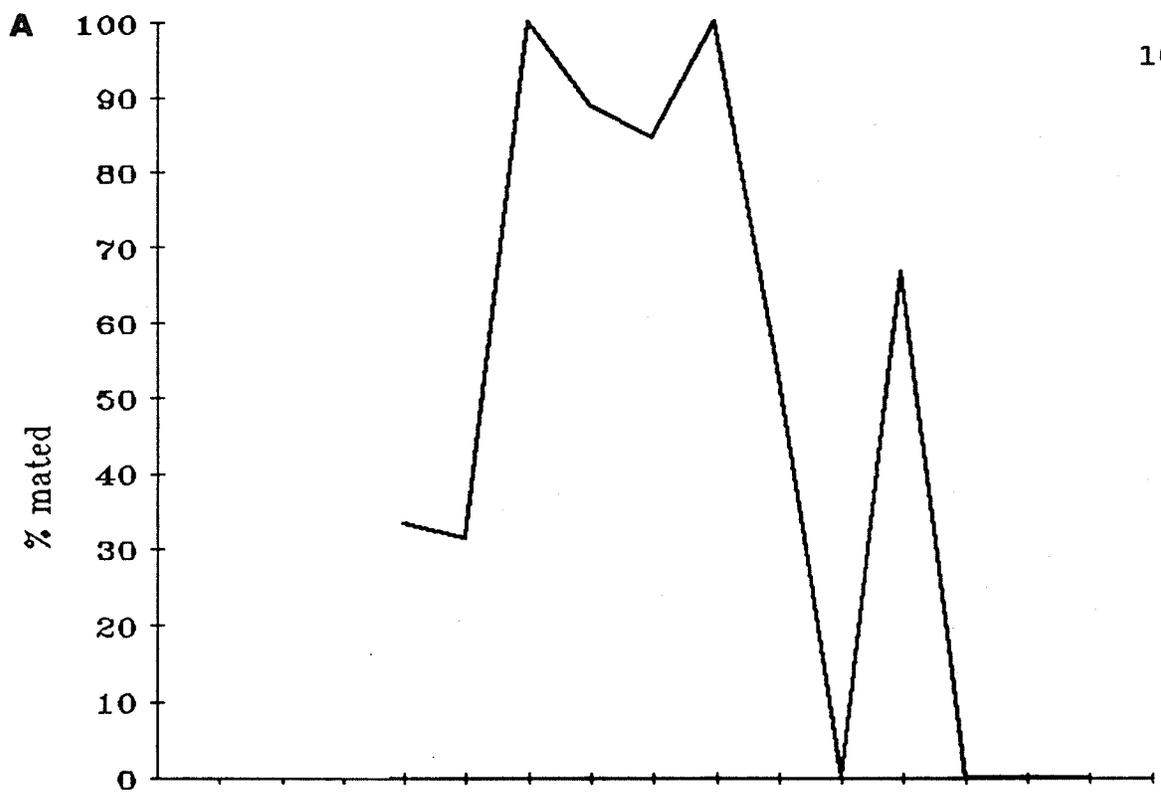
The gonotrophic age of 76 N. inopina females was determined in 1987. Two females were freeze-dried and retained as voucher specimens. Adult females and juvenile males carried 34.4% and 39.3% of the parous N. inopina, respectively. Juvenile males were infested with 46.6% of the nonparous N. inopina in 1987. Most female N. inopina were collected during May and June and during these months the majority of females were parous (90.2% of the 51 females) (Figure 12). Eighty per cent of parous females had spermatozoa within their spermathecae and the percentage of mated females was high throughout May and June.

All five hundred and seventy female N. inopina collected at the Darlingford site in 1988 were dissected. Adult squirrels carried 65.2% of all N. inopina females collected (45% from female and 20.2% male). Forty-eight per cent of all parous N. inopina females were removed from adult female squirrels. Male and female adults carried 82.9% of the 217 non-parous N. inopina removed in 1988. In April, few parous fleas were removed from adult Richardson's

Figure 12. Reproductive parameters for female Neopsylla inopina removed from Spermophilus richardsonii at the Darlingford site, 1987.

- A. Biweekly percentage of mated N. inopina females removed from S. richardsonii.
- B. Percentage of biweekly collection of N. inopina ranked as immature, nulliparous and parous.
(Numbers above histograms are females dissected/interval, N=total number of females dissected).

 parous
 nulliparous
 immatures



ground squirrels. As the season progressed, the proportion of parous females increased to a maximum during the period of 28 May (Figure 13). During early June and July, immature and nulliparous females began to increase in proportion to parous females. The percentage of parous females fluctuated from 55% to roughly 90% during the remainder of the season. Teneral fleas occurred infrequently (N=9). The majority of these individuals were found early in the season (Table 16). The highest percentage of females were mated during the period of 28 May when the seasonal high in per cent parity was observed. Through June, July and August however, the percentage of mated females increased at a time when per cent parity was decreasing.

One hundred and sixty-eight female N. inopina were collected in 1989 and all females except for one freeze-dried specimen were dissected. Non-parous females predominated the N. inopina collections in 1989 (Table 17). Greater than 64% of all females collected were either immatures or nulliparous. Parous females were taken each week; the weekly range in per cent parous was 25.9% to 75%.
Opisocrostis bruneri

During 1987, a sub-sample of 1,071 female O. bruneri was dissected. Fleas that were not dissected (80 females not included in the sub-sample; six freeze-dried fleas) were used as voucher specimens. Greater than 79% of all O.

Figure 13. Reproductive parameters for female Neopsylla inopina removed from Spermophilus richardsonii at the Darlingford site, 1988.

- A. Biweekly percentage of mated N. inopina females removed from S. richardsonii.
- B. Percentage of biweekly collection of N. inopina ranked as immature, nulliparous and parous.
(Numbers above histograms are females dissected/interval, N=total number of females dissected).

 parous
 nulliparous
 immatures

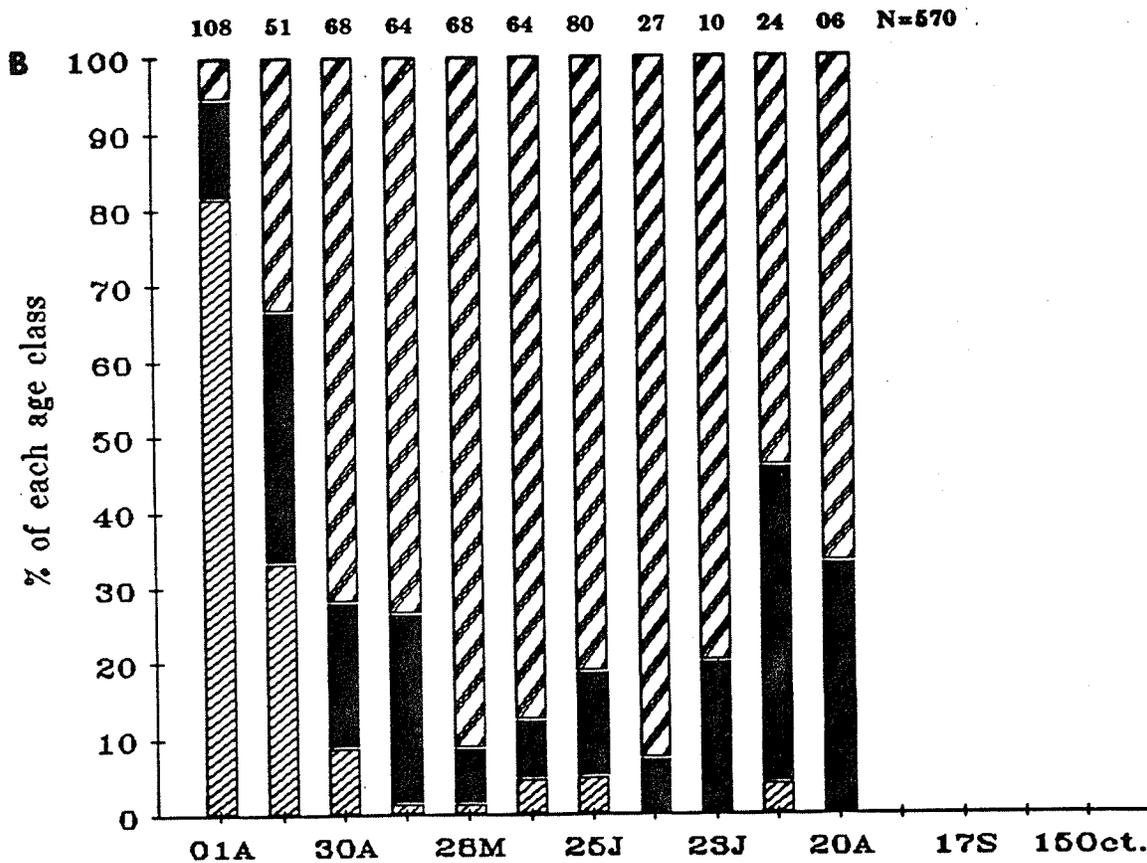
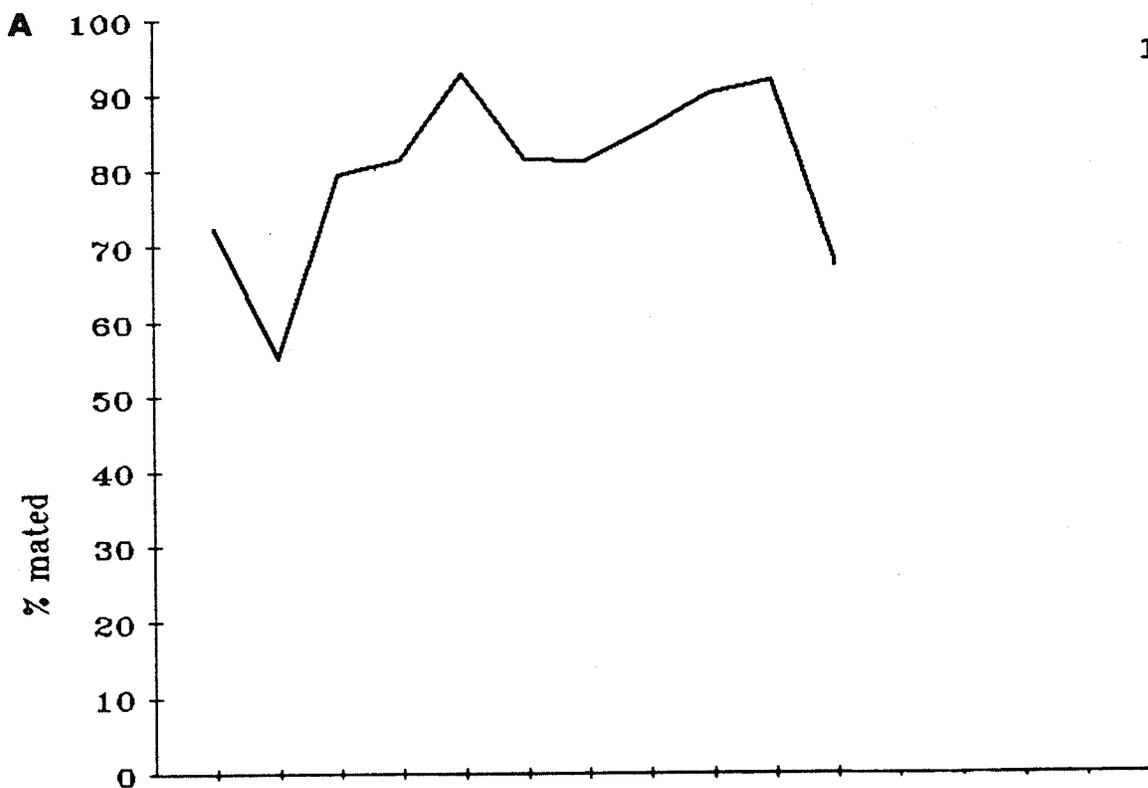


Table 16. Month of maximum abundance of teneral Neopsylla inopina, Opisocrostis bruneri, Oropsylla rupestris and Rhadinopsylla fraterna adults on S. richardsonii at the Darlingford, Perimeter and St. Norbert sites, 1987-1988.

<u>Site</u>	<u>Year</u>	<u>Flea Species</u>	<u>Total Teneral</u>	<u>Month of Maximum Collection (N)</u>
Darlingford	1987	<u>N. inopina</u>	00	-----
		<u>O. bruneri</u>	08	July (04)
		<u>O. rupestris</u>	96	Aug (53)
		<u>R. fraterna</u>	02	-----
	1988	<u>N. inopina</u>	09	April (04)
		<u>O. bruneri</u>	43	July (19)
		<u>O. rupestris</u>	298	June (103)
		<u>R. fraterna</u>	00	-----
Perimeter	1987	<u>O. bruneri</u>	41	July (21)
St. Norbert	1988	<u>O. bruneri</u>	47	July (20)

Table 17. Reproductive status (%) and the total numbers of Neopysylla inopina, Opisocrostis bruneri, Oropsylla rupestris, and Rhadinopsylla fraterna removed from S. richardsonii at the Darlingford and St. Norbert sites, 1989.

<u>Site</u>	<u>Flea species</u>	<u>N</u>	<u>Reproductive Status (%)</u>		
			<u>Immatures</u>	<u>Nullipars</u>	<u>Parous</u>
Darlingford	<u>N. inopina</u>	167	5.4	58.7	35.9
	<u>O. bruneri</u>	55	5.5	45.5	49.0
	<u>O. rupestris</u>	131	5.3	27.5	67.2
	<u>R. fraterna</u>	51	23.5	21.6	54.9
St. Norbert	<u>O. bruneri</u>	106	17.0	50.0	33.0

bruneri females were collected during July and August. Juvenile squirrels carried 94.6% of the O. bruneri females removed in 1987 which included 94.8% of parous and 92.9% of non-parous O. bruneri. The per cent parity of female O. bruneri was high throughout the season except for the first collection interval (Figure 14). From 05 July to 16 August the proportion of nulliparous and immature females increased from less than 8% to slightly less than 16%. Fifty per cent of the teneral individuals collected in 1987 were removed during July (Table 16). The per cent of mated females increased through May and June and remained at about 90% throughout July and August. The proportion of females with spermatozoa in their spermathecae was lower during September and October.

One thousand three hundred and forty-three female O. bruneri were dissected in 1988. Female O. bruneri were removed in about equal proportions from adult female, male and female juvenile squirrels. Each of these squirrel cohorts carried approximately 33% of all parous and non-parous O. bruneri. During early April, most females were removed from adult female squirrels and >80% of these fleas had yet to produce eggs (Figure 15). The proportion of parous females increased during the first 12 weeks of squirrel collection reaching a seasonal maximum of 87% during the period of 11 June. The percentage of parous

Figure 14. Reproductive parameters for female Opisocrostitis bruneri removed from Spermophilus richardsonii at the Darlingford site, 1987.

- A. Biweekly percentage of mated O. bruneri females removed from S. richardsonii.
- B. Percentage of biweekly collection of O. bruneri ranked as immature, nulliparous and parous.
(Numbers above histograms are females dissected/interval, N=total number of females dissected).

 parous
 nulliparous
 immatures

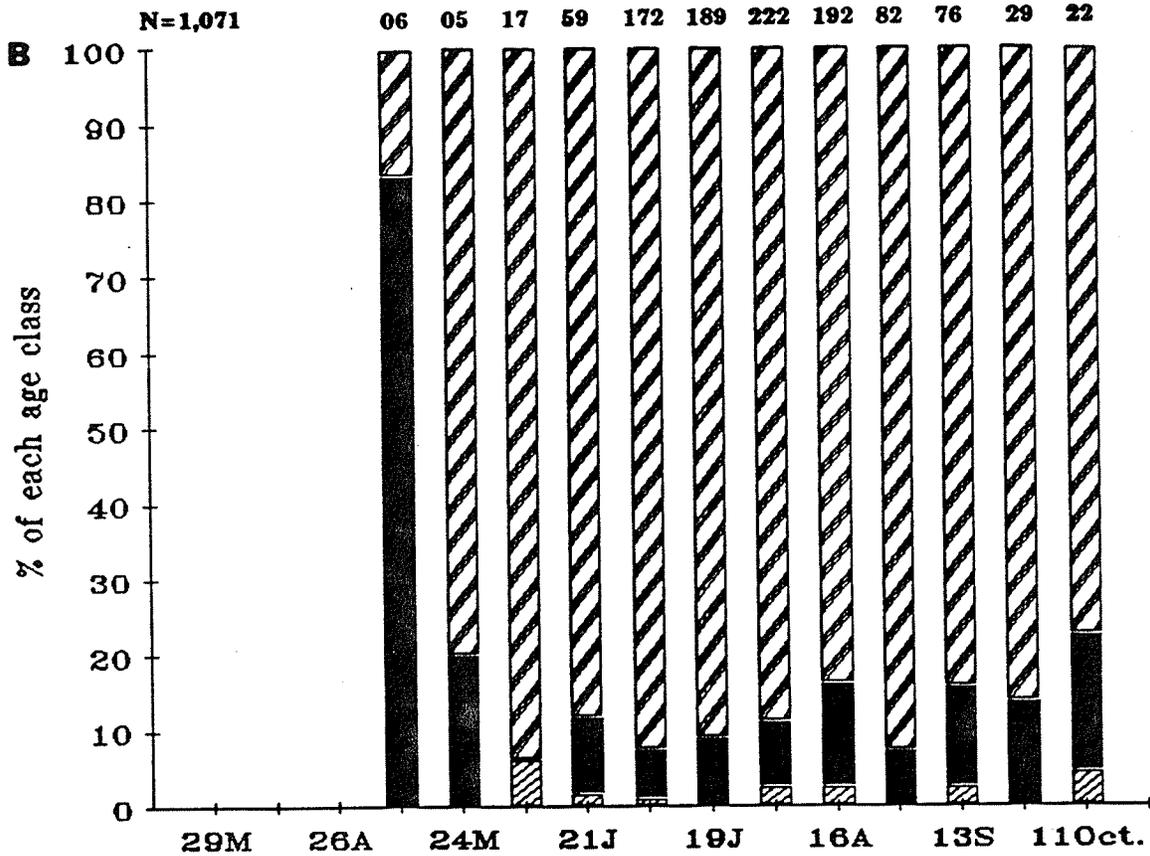
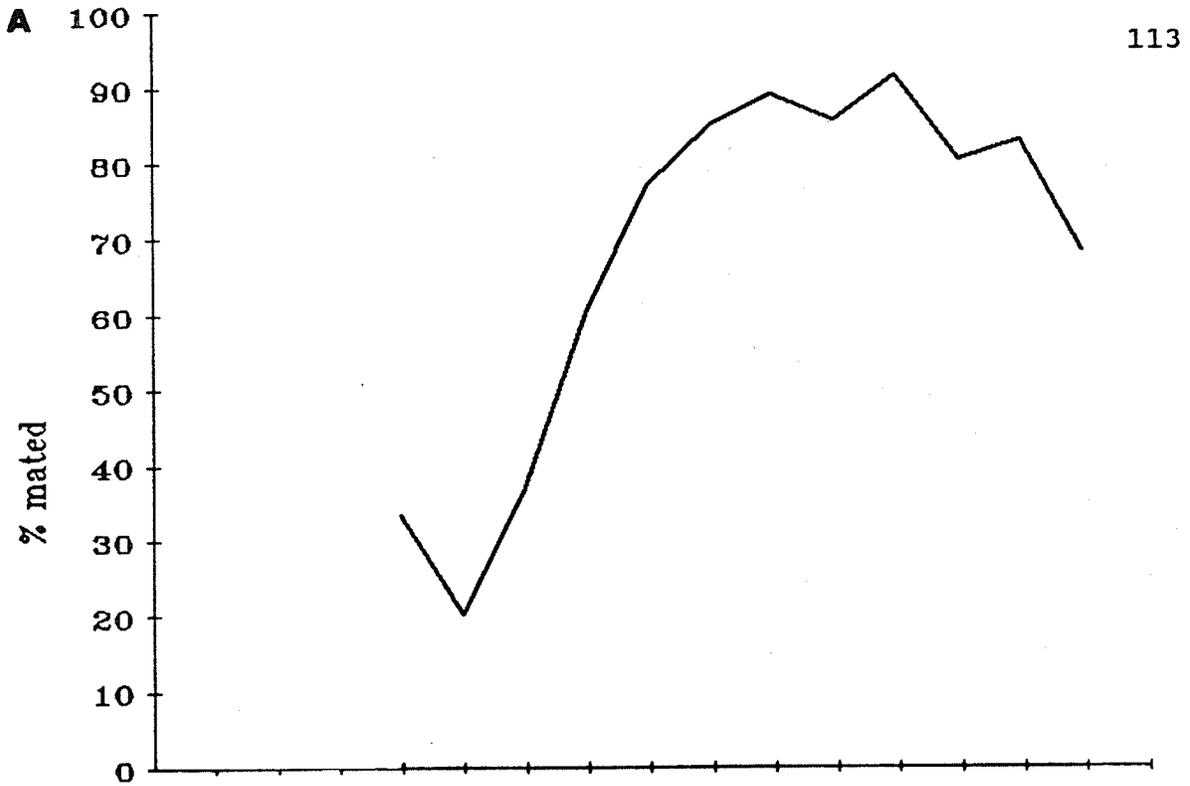
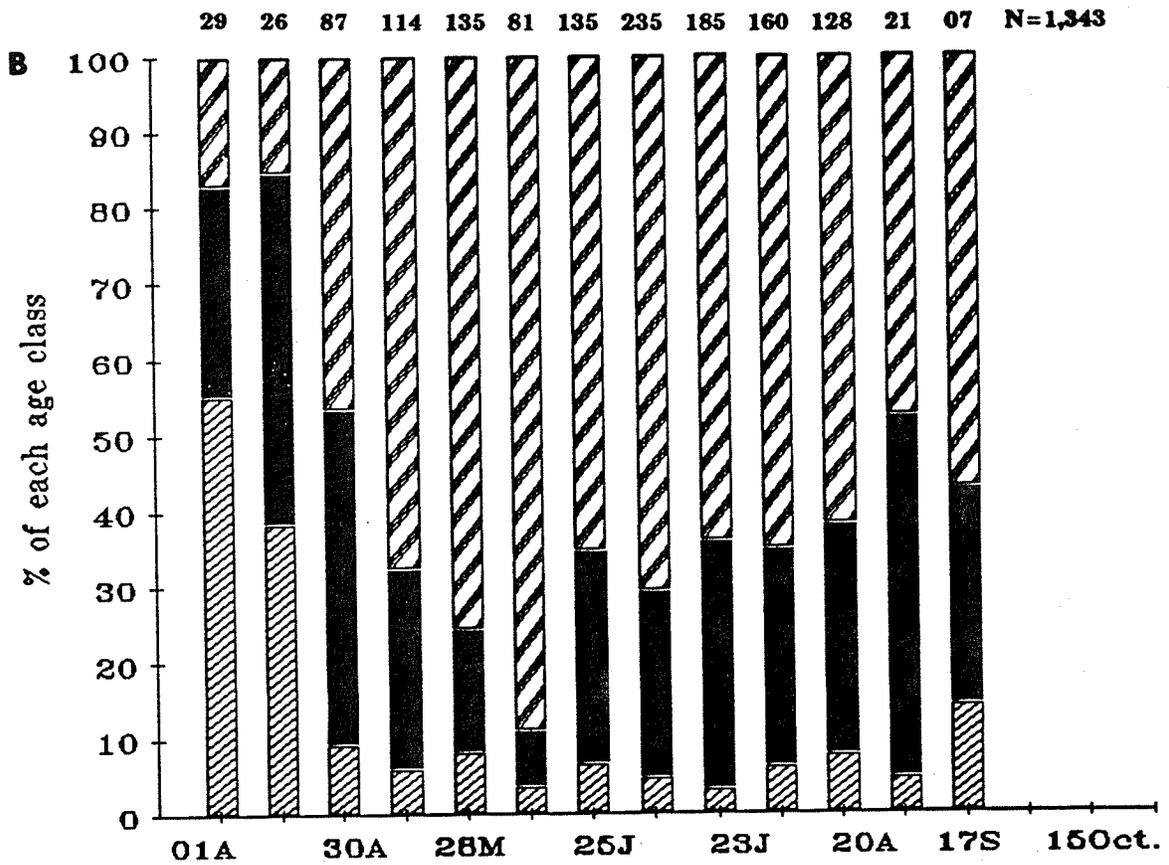
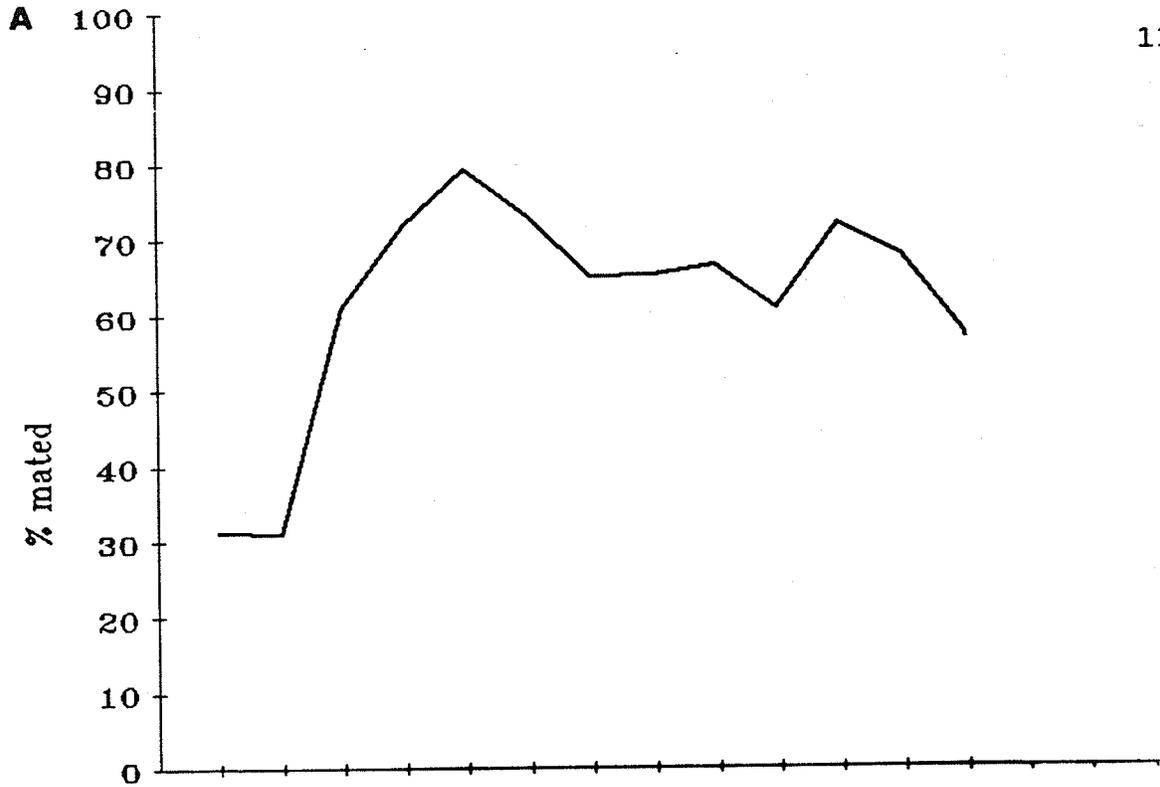


Figure 15. Reproductive parameters for female Opisocrostitis bruneri removed from Spermophilus richardsonii at the Darlingford site, 1988.

- A. Biweekly percentage of mated O. bruneri females removed from S. richardsonii.
- B. Percentage of biweekly collection of O. bruneri ranked as immature, nulliparous and parous.
(Numbers above histograms are females dissected/interval, N=total number of females dissected).

 parous
 nulliparous
 immatures



females gradually decreased during late June and a greater proportion of nulliparous and immatures were collected. Teneral were most abundant in July (Table 16). The percent of mated females increased during the first ten weeks of squirrel collection, then decreased sharply during the month of June. The percentage of mated females fluctuated at approximately 65% for the remainder of the season.

Fifty-five O. bruneri females were dissected in 1989. Immatures and nulliparous females accounted for approximately half of the females collected (Table 17). Parous females comprised from 0% to 70% of the weekly collections.

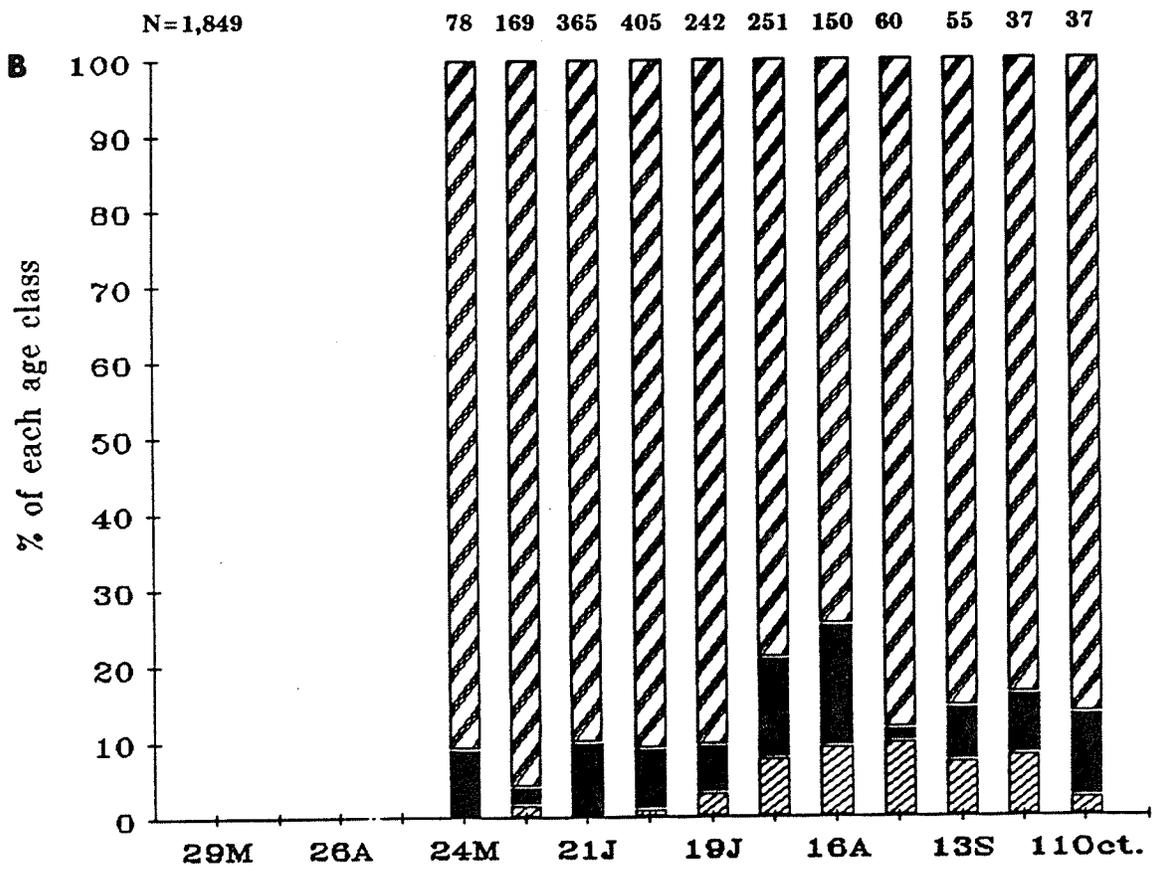
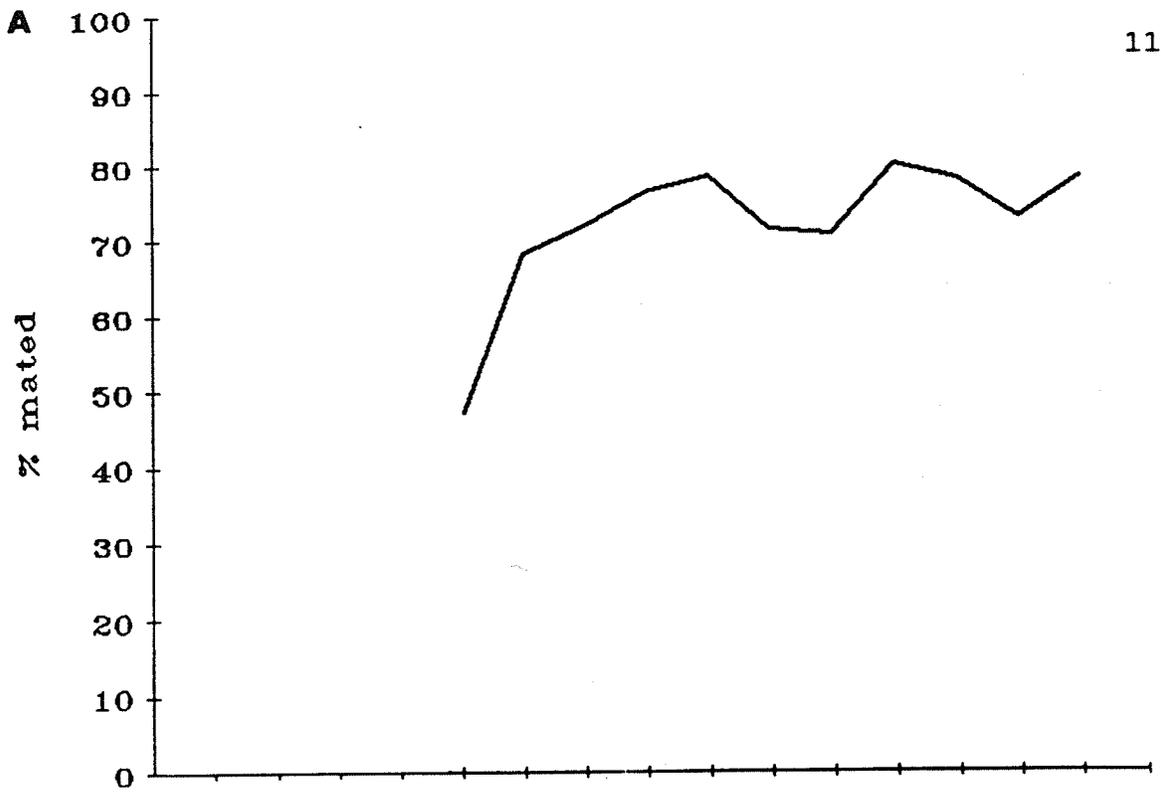
Oropsylla rupestris

Of the 2,409 female O. rupestris collected in 1987, 1,849 were dissected to determine gonotrophic age. Five hundred and sixty-three females were not included in the age analysis (547 voucher and 13 freeze-dried specimens). The majority of females were collected during late June, July and early August (68% of all female O. rupestris). Greater than 80% of all O. rupestris females were collected from juvenile squirrels. Seventy-nine per cent of parous and >90% of non-parous O. rupestris were removed from juveniles. The percentage of parous females exceeded 75% throughout 1987 (Figure 16). An increase in the percentage of non-parous females occurred during late July and early August.

Figure 16. Reproductive parameters for female Oropsylla rupestris removed from Spermophilus richardsonii at the Darlingford site, 1987.

- A. Biweekly percentage of mated O. rupestris females removed from S. richardsonii.
- B. Percentage of biweekly collection of O. rupestris ranked as immature, nulliparous and parous.
(Numbers above histograms are females dissected/interval, N=total number of females dissected).

 parous
 nulliparous
 immatures



Ninety-six teneral individuals were collected in 1987 and 55% of these were found in August (Table 16). The percentage of mated females increased through May and early June, remaining at roughly 75% for the remainder of the season.

Four thousand four hundred and thirty-six O. rupestris females were dissected in 1988 (two freeze-dried females were retained as voucher specimens). Females were abundant during all months of the study particularly in June and July. Juvenile squirrels carried 71.2% of all O. rupestris females collected in 1988. Approximately 67% of the parous and greater than 75% of non-parous O. rupestris were removed from juveniles. Adult females carried about 30% of parous and 20% of the non-parous O. rupestris. During the first six weeks of 1988, greater than 70% of the O. rupestris females were parous (Figure 17). During the period of 14 May to 28 May, per cent parity increased to a seasonal maximum of 87%. From 11 June to 09 July the percentage of parous females decreased. The largest number of teneral individuals was collected during this period (Table 16). From early July to the end of August per cent parity fluctuated, but non-parous female fleas were approximately as abundant as parous females. The percentage of parous females increased during September; only 30 females were collected at this time. The percentage of mated females was

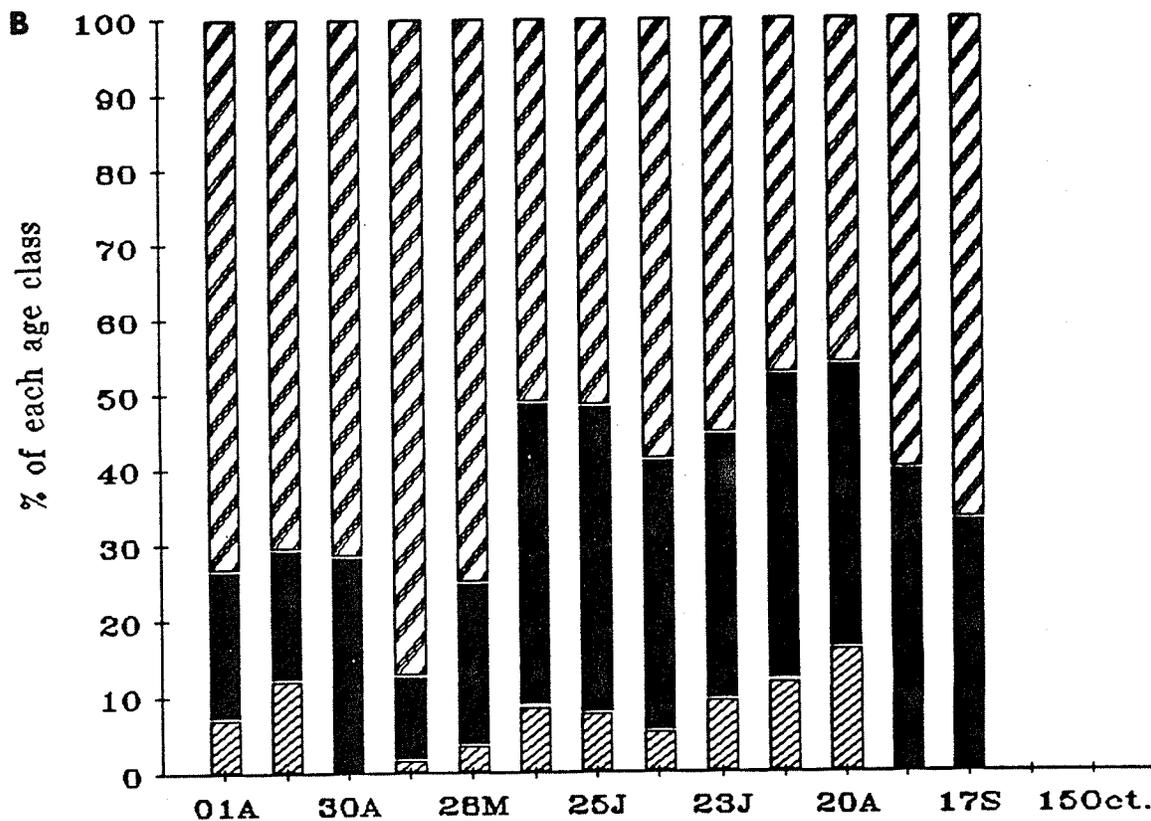
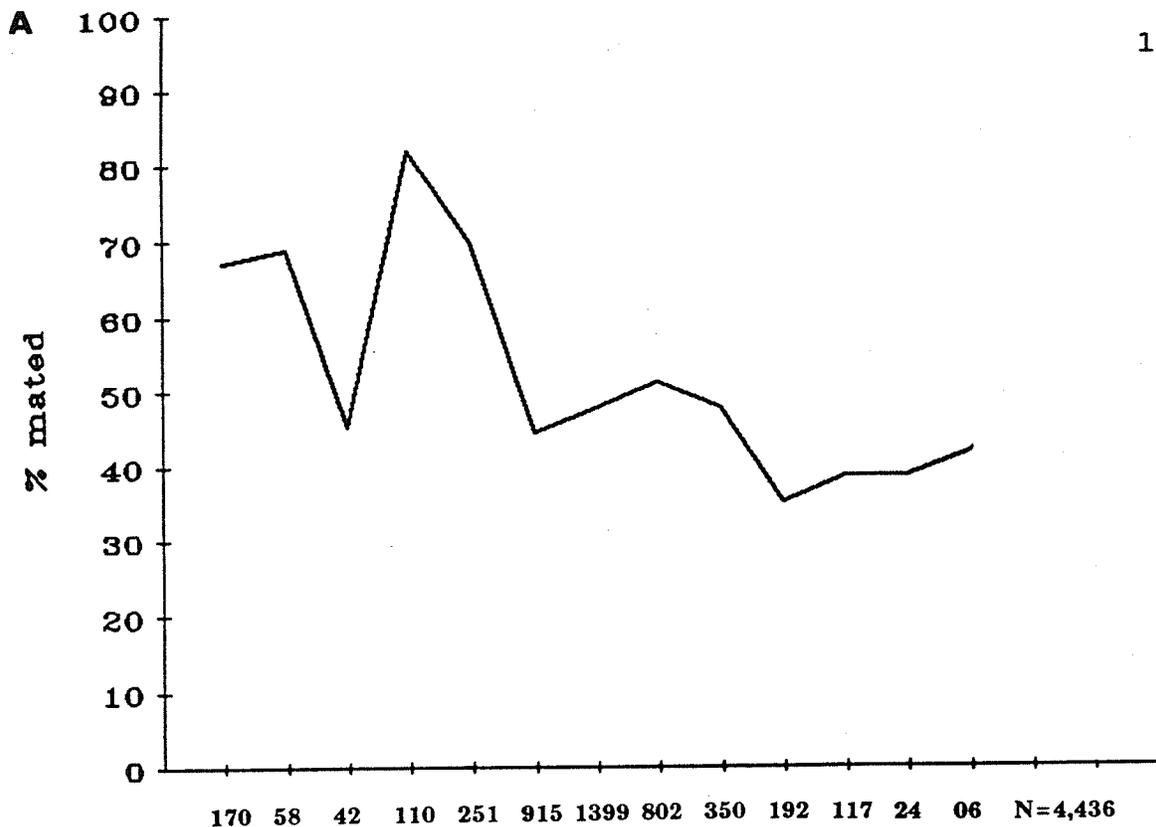
Figure 17. Reproductive parameters for female Oropsylla rupestris removed from Spermophilus richardsonii at the Darlingford site, 1988.

A. Biweekly percentage of mated O. rupestris females removed from S. richardsonii.

B. Percentage of biweekly collection of O. rupestris ranked as immature, nulliparous and parous.

(Numbers above histograms are females dissected/interval, N=total number of females dissected).

 parous
 nulliparous
 immatures



correlated with high per cent parity. The peak in mated females occurred at the same time as the seasonal high in the proportion of parous females. The proportion of mated females decreased and remained at roughly 50% for the duration of the season.

Approximately one third of the 131 female Oropsylla rupestris collected at Darlingford during 1989 were immatures or nullipars (Table 17). The majority of females collected were already producing eggs and the weekly per cent parity was never less than 58.8% and as high as 81.8%.
Rhadinopsylla fraterna

Only 70 female R. fraterna were collected during 1987, three of which were freeze-dried. The majority of females (86.6%) were collected from juvenile male squirrels during mid August to October (Figure 18). Ninety-one per cent of the females taken during this interval were parous. The percentage of mated females was high during this period relative to earlier collection dates.

One hundred and five female R. fraterna were dissected during 1988. Male juveniles carried the largest percentage (36.2%) of R. fraterna females collected. Male and female juveniles were infested with >63% of parous and 50% of the non-parous R. fraterna. During early April and late August, more than 70% of the female R. fraterna were parous, but immature and nulliparous females were also collected (Figure

Figure 18. Reproductive parameters for female Rhadinopsylla fraterna removed from Spermophilus richardsonii at the Darlingford site, 1987.

A. Biweekly percentage of mated R. fraterna females removed from S. richardsonii.

B. Percentage of biweekly collection of R. fraterna ranked as immature, nulliparous and parous.
(Numbers above histograms are females dissected/interval, N=total number of females dissected).

 parous
 nulliparous
 immatures

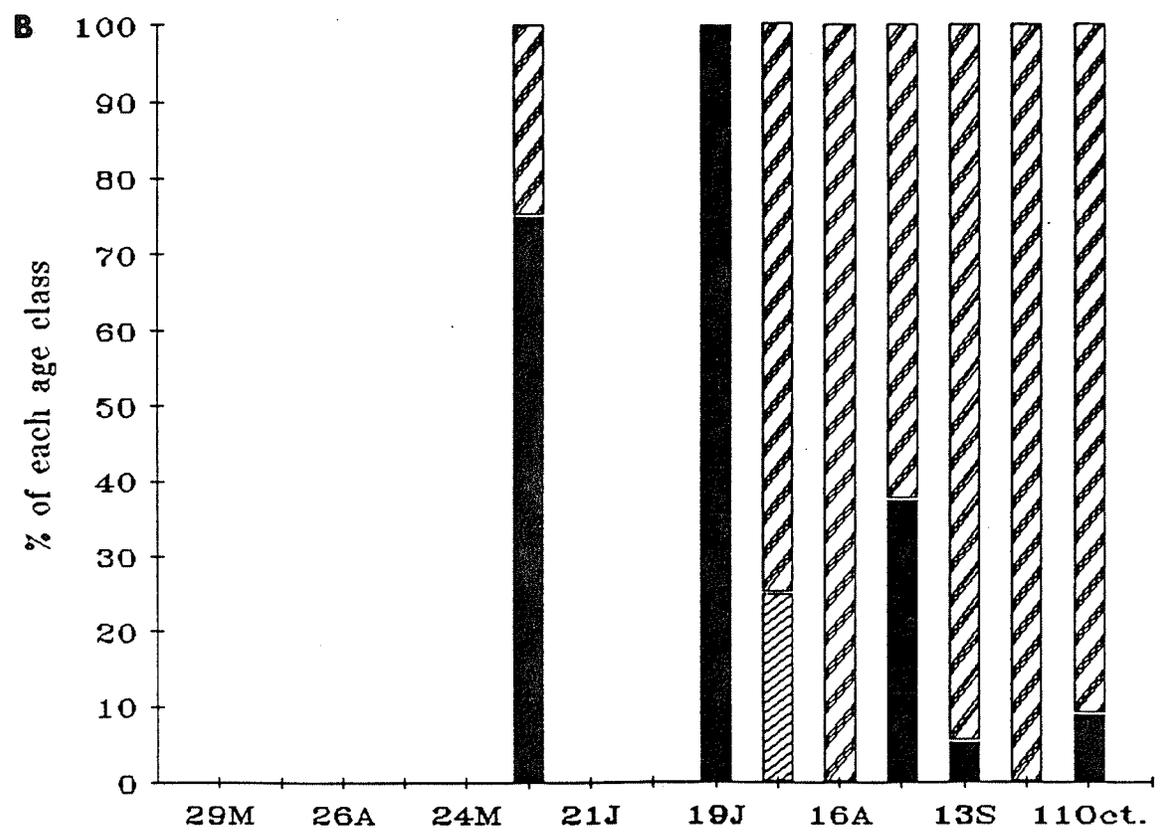
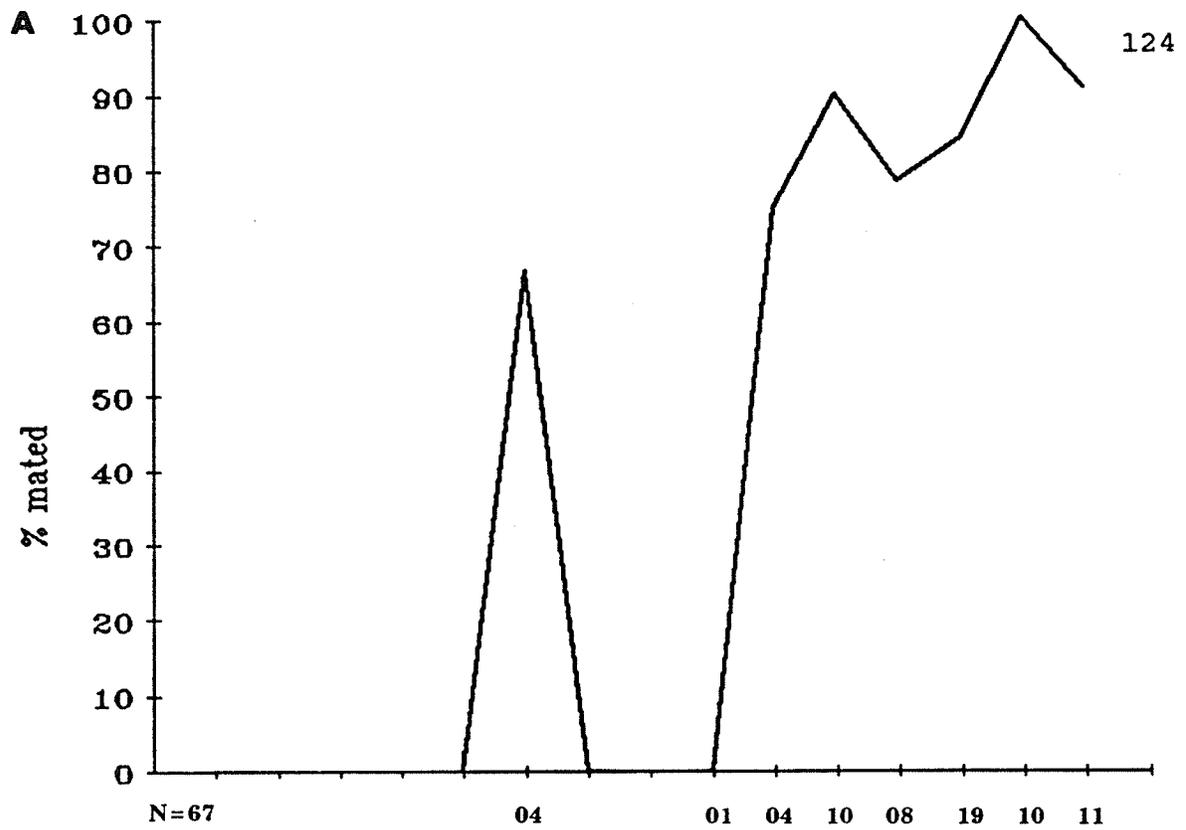
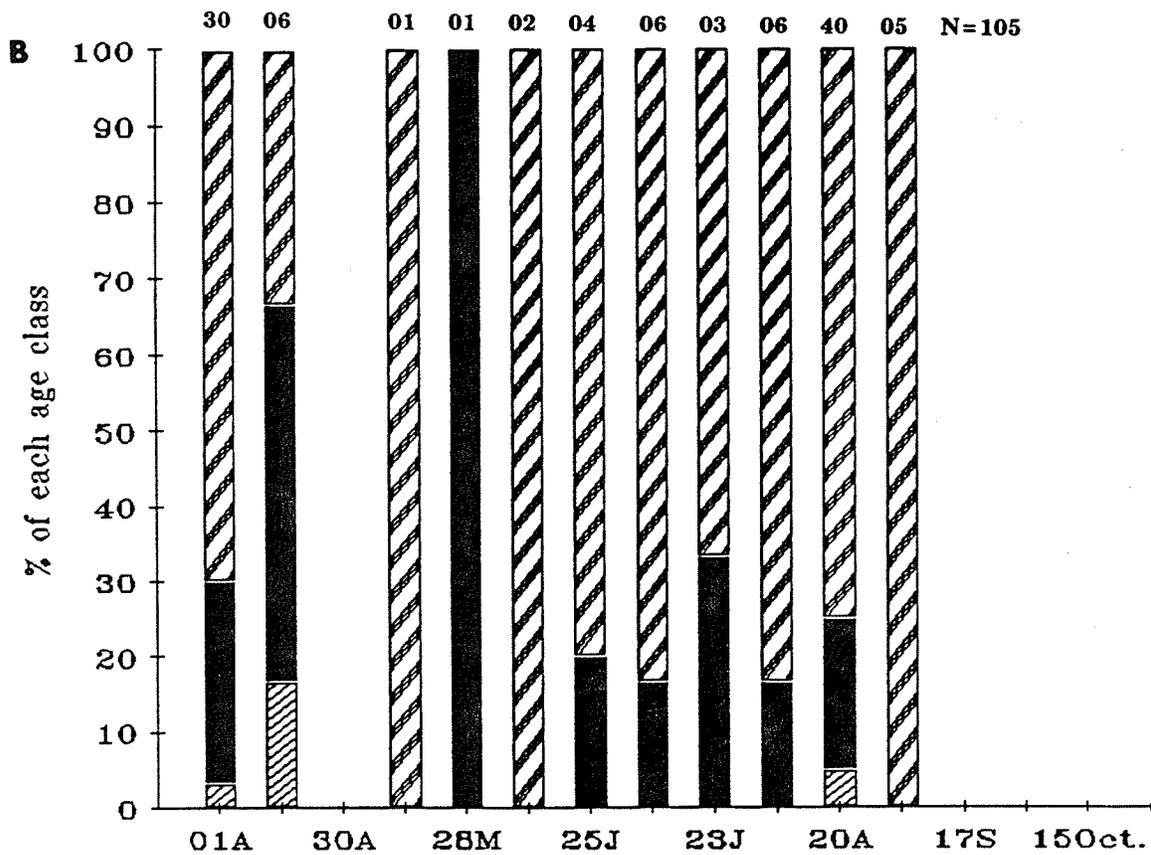
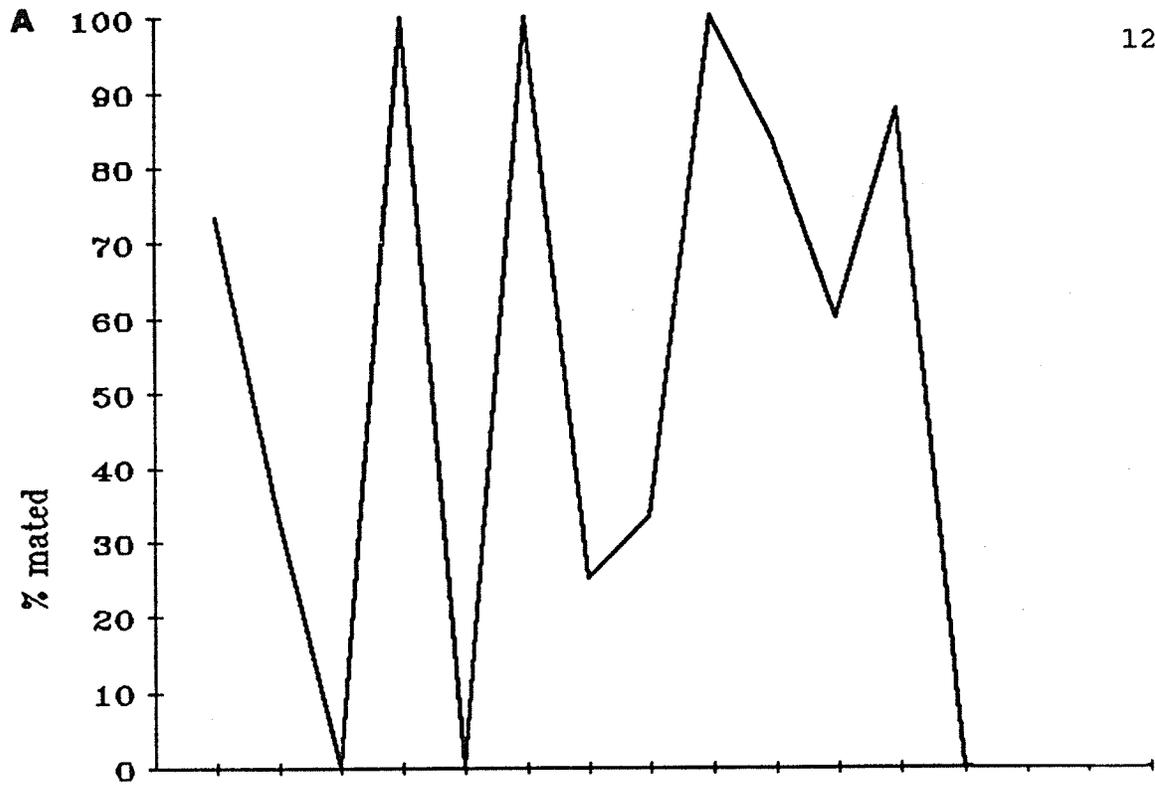


Figure 19. Reproductive parameters for female Rhadinopsylla fraterna removed from Spermophilus richardsonii at the Darlingford site, 1988.

A. Biweekly percentage of mated R. fraterna females removed from S. richardsonii.

B. Percentage of biweekly collection of R. fraterna ranked as immature, nulliparous and parous.
(Numbers above histograms are females dissected/interval, N=total number of females dissected).

 parous
 nulliparous
 immatures



19). Female R. fraterna were scarce throughout the summer months and comparisons of the proportion of parous to non-parous females is meaningless. Due to the small sample size, the percentage of mated females fluctuated radically during the season. During periods of the season when more than 25 specimens of this species were collected, 60% to 75% of the females were mated.

Approximately 45% of the 51 female R. fraterna collected in 1989 were non-parous (Table 17). Parous females were absent during some sampling intervals and accounted for 100% of the collection in others. As in the previous year, R. fraterna adults were abundant during the first collection interval.

Perimeter

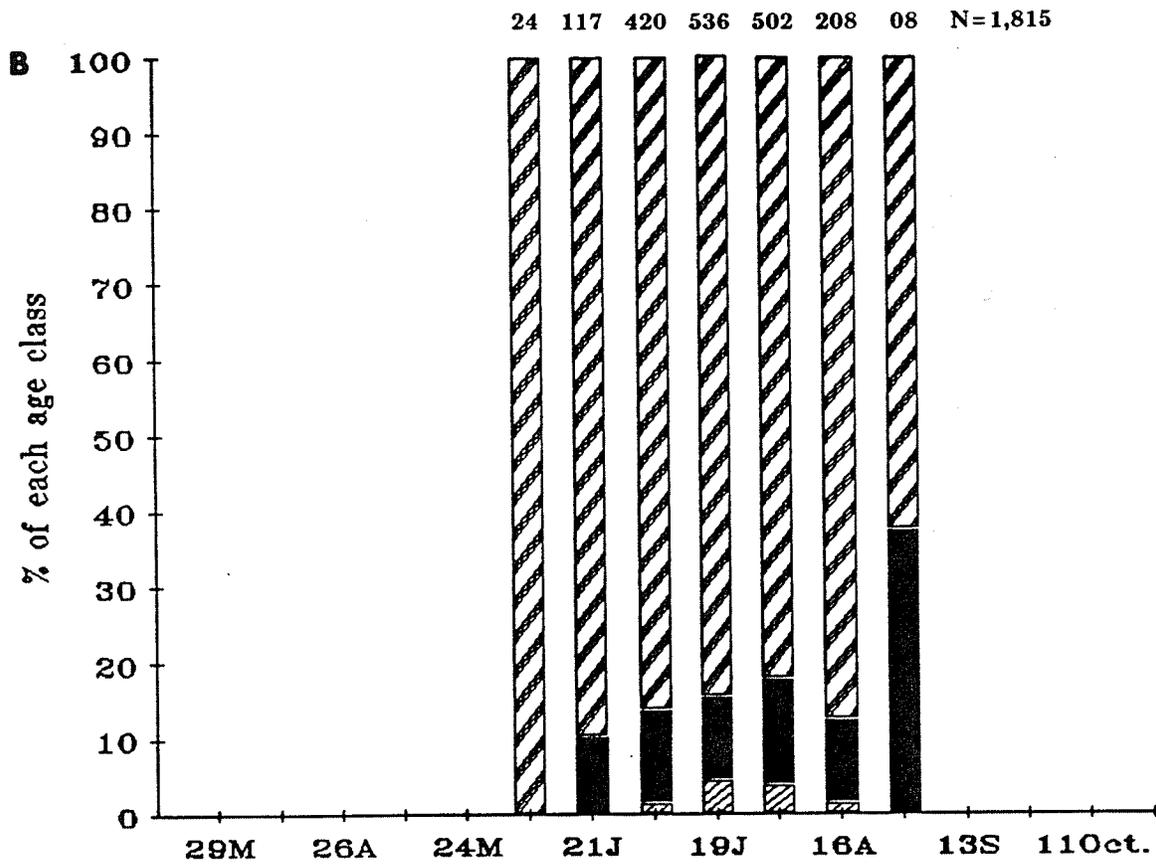
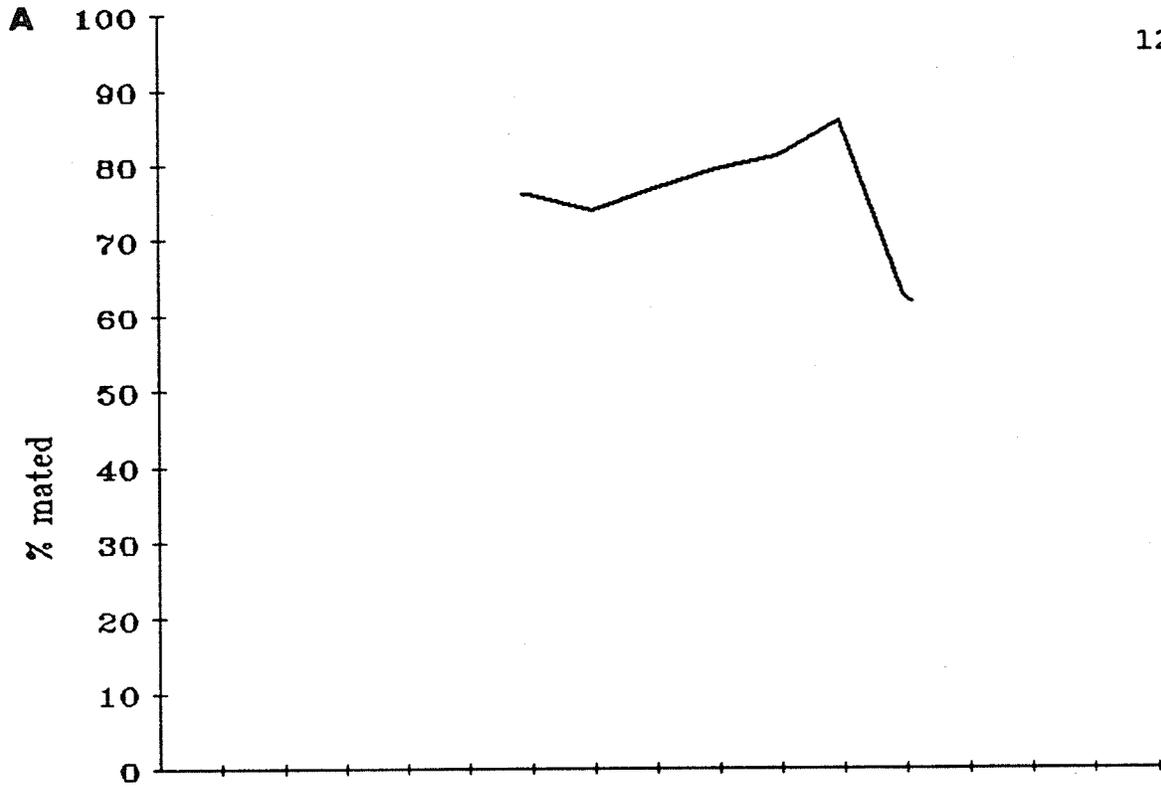
Opisocrostis bruneri

Two thousand two hundred and thirty-two female O. bruneri were removed from Richardson's ground squirrels at the Perimeter site during 1987. Eighteen hundred and fifteen females were dissected (388 females were not included in the samples and 29 specimens were freeze-dried). More than 50% of the female O. bruneri were collected from early July to the end August (80% of all O. bruneri collected during two month period). More than 70% of the O. bruneri females were removed from female juveniles and these animals carried 75.3% of non-parous and 69.7% of parous O.

Figure 20. Reproductive parameters for female Opisocrostitis bruneri removed from Spermophilus richardsonii at the Perimeter site, 1987.

- A. Biweekly percentage of mated O. bruneri females removed from S. richardsonii.
- B. Percentage of biweekly collection of O. bruneri ranked as immature, nulliparous and parous.
(Numbers above histograms are females dissected/interval, N=total number of females dissected).

 parous
 nulliparous
 immatures



bruneri. The percentage of parous females remained high throughout the season and with the exception of the last trapping period was never less than 82%. The percentage of non-parous O. bruneri increased during the period from 05 July to 16 August (Figure 20). Ninety-four per cent of the immature females (N=53) were taken during this period. Teneral fleas were most prevalent during this period of decreased parity (Table 16). The percentage of mated females remained high throughout the season and rarely dropped below 75%.

St. Norbert

Opisocrostis bruneri

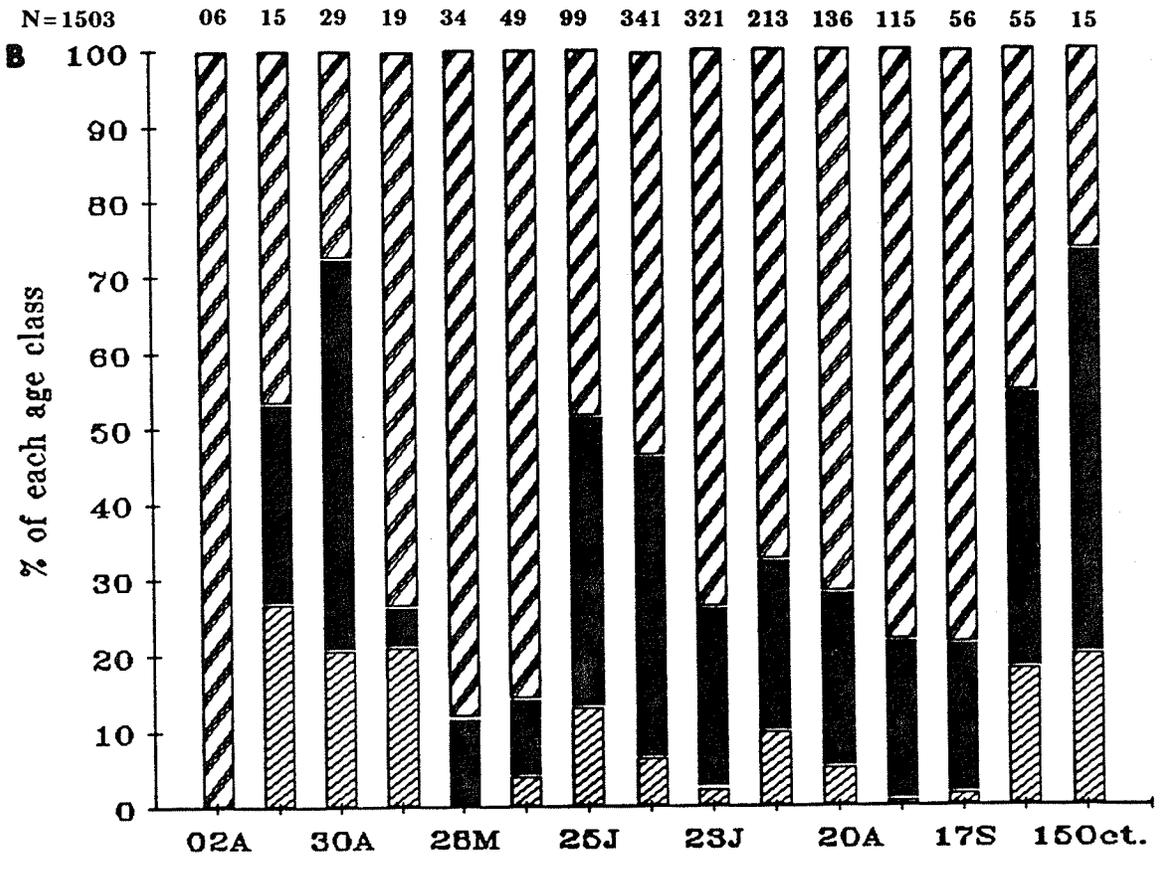
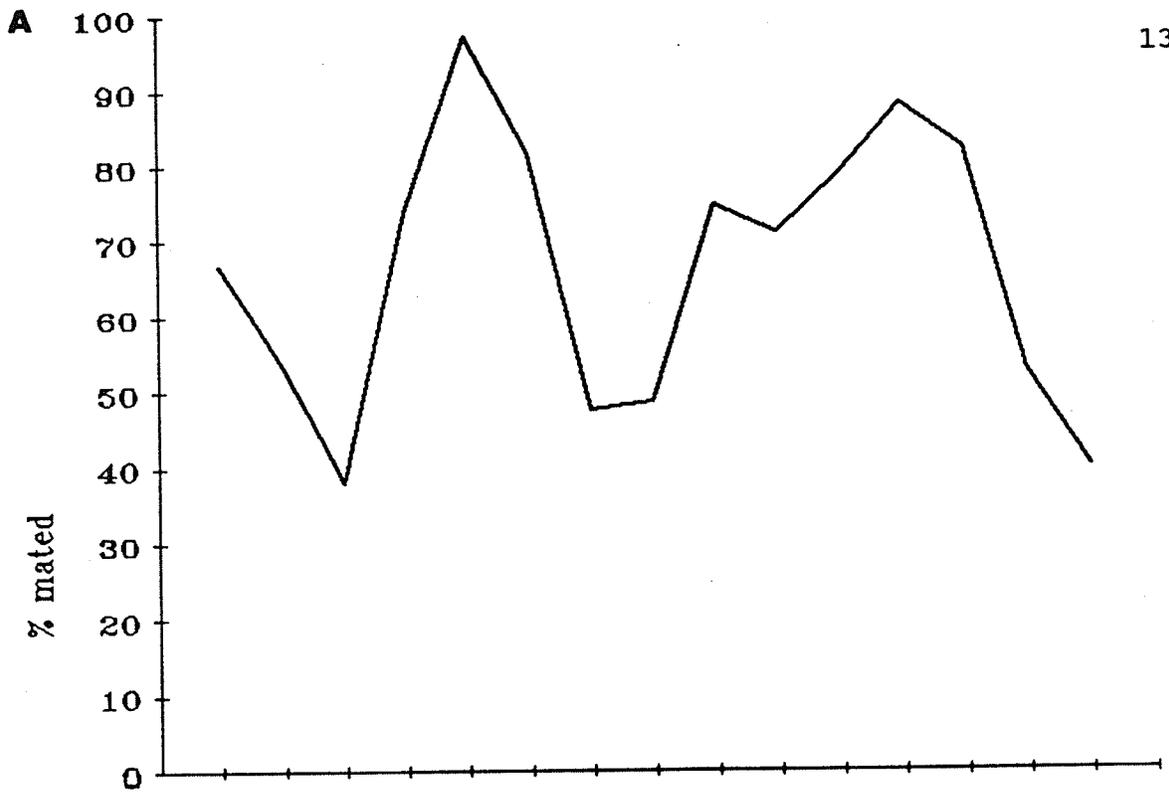
The gonotrophic age of 1,503 female O. bruneri was assessed at St. Norbert in 1988. Juvenile squirrels carried 87.9% of all O. bruneri females. Greater than 90% of parous and 83% of non-parous O. bruneri were removed from juveniles. With the exception of the first collection period, most females were nulliparous or immature during April (Figure 21). Through May and early June, the percentage of parous females increased. The proportion of parous females decreased dramatically near the end of June and early July. During this period the largest number of teneral individuals was collected (Table 16). The percentage of parous females gradually increased until late September. During the last month of flea collection,

Figure 21. Reproductive parameters for female Opisocrostitis bruneri removed from Spermophilus richardsonii at the St. Norbert site, 1988.

- A. Biweekly percentage of mated O. bruneri females removed from S. richardsonii.
- B. Percentage of biweekly collection of O. bruneri ranked as immature, nulliparous and parous.

(Numbers above histograms are females dissected/interval, N=total number of females dissected).

 parous
 nulliparous
 immatures



relatively few parous females were collected however, the number of females collected at this time was small (N=70). The percentage of mated females peaked twice during the season. Both of these peaks in the percentage of mated females occurred when large proportions of the females were parous.

Nulliparous females were the most prevalent gonotrophic age class of *O. bruneri* removed from Richardson's ground squirrels at St. Norbert in 1989. Of the 106 females taken during 1989 one third were parous (Table 17). The parous component of the samples was never greater than 48% and during the first two weeks of sampling no parous females were collected (N=8). The percentage of parous females gradually increased through late April and early May.

Chapter V

DISCUSSION

Squirrel circannual cycle in relation to flea activity

Richardson's ground squirrels in Manitoba had predictable circannual cycles of activity. Activity began each year in late March or early April with the emergence of adult squirrels. The breeding season commenced shortly after female emergence and parturition occurred during early May. Juveniles first appeared aboveground in late May or early June. By mid June adult males had begun to enter hibernation and the majority of adult females had entered hibernation by late July and early August. The cycle was completed in September or October with the immergence of juveniles. The changes in host population density and individual squirrel behaviour which occur during this seasonal cycle may have a profound impact on flea activity and/or the infestation indices used to express flea activity. During the breeding season, prior to and during juvenile emergence, following immergence of adults, and late in the season when few juveniles are still active, the density of the host population and/or the behaviour of individual squirrels may influence the observed patterns of flea activity.

The breeding season may be an important time for dispersal of fleas within ground squirrel colonies. Adult male squirrels ranged freely over the study plots prior to and during the breeding season, presumably in search of estrous females. Michener (1983b) reported that males will investigate burrows in search of receptive females. This behaviour was not directly observed but probably occurred since males were captured near burrows known to be occupied by females. Because of the increased home range size and the investigation of many different burrows during the breeding season, males are likely to contact fleas. This may be an important mechanism enabling fleas from abandoned nests to become established in occupied nests. In addition, it may also serve to distribute fleas throughout an entire colony, since fleas could be picked up in one burrow or nest and dropped off in another. Fleas may also transfer between hosts during copulation. Rothschild and Ford (1973) observed transfer of S. cuniculi between rabbit hosts during copulation and social grooming. Thus the breeding season is probably an important vehicle for circulating fleas among individual squirrels and the colony as a whole. Surprisingly, during the breeding season, the intensity of O. bruneri infestation was low relative to the other three flea species. Therefore, dispersal of O. bruneri is probably minimal during the breeding season.

The changes in host population density which occur following parturition and juvenile emergence may influence flea infestation parameters. For all flea species, with the exception of O. rupestris, dramatic declines in the prevalence and mean intensity of infestation were observed during this interval. At all sites, the number of captures increased two to four fold during the first month in which juveniles appeared aboveground. Decreases in the expected values of mean intensity and prevalence could be explained by a dilution of the flea populations by the increase in the number of available hosts. Reichardt (1989) observed a similar decline in the mean intensity and prevalence of O. bruneri on S. franklinii at the time of juvenile emergence.

The largest number of squirrel captures at each site occurred during June in each year. By July, however, the number of captures had dropped by greater than 50% primarily because of immergence of adults. This decrease in the number of potential hosts available to the fleas may have affected the infestation indices. The mean intensity and prevalence of O. bruneri and O. rupestris on S. richardsonii increased during July. Examination of ovarian age structure verified that the increases were due to flea recruitment. Therefore, without supplemental gonotrophic age assessments, the estimates of mean intensity and prevalence were confounded by changes in host population density.

During the months of August and September, when relatively few animals were still active on the plots, the negative influence of host density on the reliability of infestation indices for expressing flea activity was apparent. Small sample sizes confounded the interpretation of changes in ovarian age structure and mean intensity and prevalence of infestation. Thus the limitations of infestation indices for describing flea seasonal activity are exaggerated as the density of the host population declines.

Specific periods of the circannual cycle, such as hibernation are methodologically difficult to examine under field conditions. However, this phase of squirrel life history may have a dramatic affect on flea activity. Richardson's ground squirrels spend a large proportion of their lives in hibernation. It is reasonable to expect that the fleas from a hibernating host would be adapted to cope with this feature of the host's life cycle. During the first month of hibernation the torpor cycles are of short duration, however, squirrels spent greater than 90% of their time during the preceding months in torpor (Wang 1979). Fleas may be active, early in the hibernation cycle, when squirrels are arousing frequently from bouts of deep torpor. This is especially true for fleas infesting adult squirrels which enter hibernation as early as mid June. However, once

ambient temperatures decline and the duration of the bouts of torpor increase, fleas probably either die or are quiescent for the duration of squirrel hibernation. Thus like their mammalian host, the fleas of Richardson's ground squirrel are probably inactive during most of the cold months.

Specific characteristics of Richardson's ground squirrel biology may, though not directly related to the circannual cycle, have an influence on flea activity. The semi-social life style of this rodent may make it more susceptible to flea infestation. For example, social interaction with conspecifics may provide opportunities for the transfer of fleas. Site fidelity expressed by most female squirrels, the stability of established squirrel colonies and the relative stability of squirrel population size may also enhance the opportunities for the establishment of flea species. These specific characteristics of the host's biology in combination with the predictable cycle of squirrel seasonal activity may have lessened the selection pressure imposed on fleas of S. richardsonii to develop complex mechanisms (like host stimuli for reproduction) to ensure that future generations will have hosts to feed upon.

Flea seasonal dynamics

Neopsylla inopina

Seasonal peaks in observed mean intensity and prevalence of N. inopina infestation on Richardson's ground squirrels occurred during April in 1988 and 1989. Trapping did not commence until May in 1987 and the spring peak in N. inopina activity was probably missed in this year. The intensity and prevalence of N. inopina on ground squirrels during the summer of 1987 were similar to patterns observed in 1988. A large percentage of the females collected during April and May of 1988 and 1989 were non-parous. Neopsylla inopina populations were probably aging during these months because the percentage of parous females increased from April to the end of May, concurrent with a drop in observed mean intensity and prevalence.

Seasonal variation in N. inopina sex ratios did not help to clarify the seasonal activity of this flea species. Marshall (1981b) suggested that seasonal changes in the proportion of male and female fleas removed from their host could be used to indicate periods of flea reproduction or recruitment of new individuals into the population. In general, fleas which are seasonal breeders tend to have corresponding seasonal variation in the ratio of males to females. Upon emergence from the pupal stage, the sex ratio of most flea species is 1:1 (Edney 1945; Marshall 1981b;

Wade and Georgi 1988). Seasonal variation in sex ratios can therefore, be attributed to differences in longevity of the sexes. Males are generally smaller and more active than females, and thus are more likely to be separated from the host, and less likely to withstand adverse conditions of nutrient and climate (Marshall 1981a). Provided flea emergence is synchronous, as fleas within a cohort age, females will become relatively more abundant because males are shorter-lived (Marshall 1981b). Shifts in sex ratios towards a male bias after populations have been strongly female biased have been used as evidence for emergence of a new generation of fleas (Bibikova and Zhovtyi 1980; Reichardt 1989).

Early during the 1988 season, N. inopina sex ratios were near 1:1. By 14 May females were more abundant than males. The proportion of males within the samples did increase after collections were significantly female biased but the sex ratios fluctuated dramatically for the remainder of the season. Sex ratios for N. inopina as a result did not provide strong evidence for emergence of new generations. Yearly variation in biweekly sex ratios of N. inopina adults was apparent. In 1987, too few N. inopina were collected to properly assess whether biweekly sex ratios were significantly different from unity.

Neopsylla inopina was rarely collected from ground

squirrels in large numbers relative to O. rupestris or O. bruneri. It is possible that this species has a greater affinity for the host's nest rather than its body. Because only hosts were sampled, the proportion of time spent on the host's body by the different age classes and sexes of the various flea species and the probability of sampling each age class, sex and species of flea were assumed to be equal. The validity of this assumption remains to be tested since direct evidence of microhabitat affinities of the different ages, sexes and species of fleas is unavailable. Based on morphological characters (lack of eyes and small size) Holland (1944) considered this species to be a nest associate. Ninety-five per cent of Neopsylla setosa Wagner, a related Palaearctic species, occurred within the nest of the suslik (Citellus pygmaeus Pall.), and less than 2.5% of the fleas collected were removed from the host's body (Mironov et al. 1963). Therefore, the possibility exists that the low levels of seasonal intensity and prevalence for this species are due to its microhabitat affinity.

Baesler (1975) collected N. inopina from S. richardsonii in North Dakota from April to September. He reported that this flea was present on the squirrels early in the season but disappeared by July and remained scarce until September. Although, the number of fleas or hosts collected/month were not specified, it is likely that the

majority of the 130 N. inopina collected were removed during the first month or two of the study. Richardson's ground squirrels collected shortly after emergence in Alberta are also heavily infested with N. inopina, however, during the summer months this species is rarely collected (T.D. Galloway, pers. comm.). Susliks in the U.S.S.R. carry the greatest number of Neopsylla setosa/host during March and April and activity during the summer months is limited (Bruchanova and Surkova 1970). It is possible that the seasonal activity of N. inopina may be restricted to the early phases of the squirrels circannual cycle because of the competitive interaction with other flea species. During April and early May, squirrels carry fewer O. rupestris and O. bruneri than in mid-summer and fall, respectively. N. inopina may be competitively excluded from infesting Richardson's ground squirrels by these two numerically dominant flea species during the summer and fall months.

Opisocrostitis bruneri

Patterns of O. bruneri seasonal activity were not markedly different at the Darlingford, St. Norbert or Perimeter sites. Prevalence of infestation increased during April and May in 1988 and 1989 at the Darlingford and St. Norbert sites. With the exception of Darlingford 1989, mean intensity of O. bruneri infestation also increased during these months. Opisocrostitis bruneri populations are probably

expanding or a new cohort is emerging at this time, based on the high percentage of non-parous females collected and increasing infestation indices. Mean intensity and prevalence of O. bruneri infestation began to decline each year at about the time of parturition. Opisocrostis bruneri populations may have been diluted by the increase in available hosts. The seasonal low in mean intensity and prevalence of O. bruneri coincided with the period of juvenile emergence.

Following juvenile emergence, mean intensity and prevalence of infestation gradually increased. During all years and at all sites, increases in mean intensity and prevalence of O. bruneri infestation occurred as the number of available hosts was decreasing. Seasonal peaks in prevalence and mean intensity of infestation occurred during August, September or October. Few animals were active during the last trapping intervals. Estimates of infestation indices are not particularly meaningful when the number of hosts within the population is low since intensities of infestation were also probably exaggerated by the size of the host samples. Heavy O. bruneri burdens very late in the season, when few squirrels were active (<10 animals), probably reflected squirrel rather than flea activity. Once adults and heavier juveniles have entered hibernation, the remaining juveniles were not restricted

from entering the home ranges or burrows of other squirrels. The large numbers of O. bruneri on late emerging juveniles may have resulted because of this behaviour. Recruitment of O. bruneri, based on the presence of immature and nulliparous females, did occur in September and October, though O. bruneri populations were likely stable at this time. These newly emerged fleas were either late emerging individuals from the previous cohort or early emerging ones of the next cohort.

The ratios of female to male O. bruneri were roughly 1:1 early in the season (1988 and 1989, all sites). At each site, the ratio of male to female O. bruneri was lowest during late June or early July. During the weeks preceding the seasonal low in O. bruneri males, the proportion of males collected relative to females increased. A shift in the sex ratio towards a male bias may represent emergence of a new generation of O. bruneri. Reichardt (1989) observed a similar but more pronounced increase in the number of male relative to female O. bruneri on Franklin's ground squirrels during July. Sex ratios were not significantly different from 1:1 at the Darlingford site in 1988. The difference in ratio of males to females approached statistical significance during the period of 23 July, after which males outnumbered females. Male survival may have been unusually high or female survival uncharacteristically low during 1988

thus resulting in the lack of a sex ratio bias during the summer of 1988. The usefulness of sex ratios as a supplement for examining flea seasonal activity should not be over-emphasized. The credibility of seasonal changes in sex ratios depends on the accuracy of assumptions concerning the behaviour of flea sexes, sex ratios at emergence, and the amount of time spent on the host by the respective sexes. These various assumptions have not been verified for any of the flea species associated with Richardson's ground squirrels (or any other host species). As with flea microhabitat affinities, it must be assumed that each sex and age of the different flea species is equally likely to be sampled. It is possible that seasonal changes in the sex ratios reflect changes within the population structure of fleas. The assumptions should be thoroughly tested under laboratory conditions for each flea species before the value of sex ratios as a measure of population activity can be directly assessed.

Similar patterns of mean intensity and prevalence were observed for O. bruneri on S. franklinii (Reichardt 1989). Franklin's ground squirrels were heavily infested shortly after emergence (late April and early May), flea burdens were low following juvenile emergence but increased again during late August and early September. Hendricks (1967) collected O. bruneri from S. tridecemlineatus in Indiana and

reported that infestation indices peaked during October. Mean intensity and prevalence of infestation were low during all other months except June, when another increase in mean intensity was observed. Prevalence and mean intensity dropped during July when juveniles were first captured.

Estimates of seasonal activity for O. bruneri, based on only mean intensity and prevalence, are confounded by changes in host density. The number of O. bruneri/host was closely related to host density. When host densities were relatively constant (April and May) slight increases in prevalence and intensity were noted. Juvenile emergence corresponded with low mean intensity and prevalence of O. bruneri on squirrels. Increases in mean intensity and prevalence coincided with hibernation of adults and larger juveniles. Hendricks (1967) could not evaluate the impact that decreases in the number of available hosts may have had on infestation indices (prior to hibernation) because hosts were sampled from several locations and the fleas were pooled for the estimates of prevalence and mean intensity. Therefore, it is probable that the number of hosts collected was not representative of the number of hosts active within a single squirrel population. Thus when using mean intensity and prevalence to estimate the seasonal activity of O. bruneri, it is difficult to determine how changes in host density affect the observed patterns of flea activity.

Samples from host nest contents might clarify whether flea populations are actually increasing or whether fleas are congregating on the few remaining squirrel hosts.

Oropsylla rupestris

Mean intensity and prevalence of O. rupestris infestation reached a seasonal high during late June and early July in 1987 and 1988. Increases in mean intensity and prevalence later in the season, as for O. bruneri, may have been exaggerated by the decrease in available hosts. Recruitment must have been extensive during June and July because mean intensity and prevalence increased, despite a several-fold increase in the number of available hosts. Prior to the summer peak in mean intensity, larger numbers of immature and nulliparous females were collected, especially during 1988. Also, the largest number of teneral individuals was taken from squirrels in June of 1988. Sex ratios for O. rupestris were significantly female-biased during early June, but thereafter, males made a greater contribution to the collections. Provided the assumptions about changes in sex ratios are correct for O. rupestris, these observations support the hypothesis that a new generation of O. rupestris entered the population during late June and early July. Fleas from this summer generation probably continued to emerge throughout the remainder of the year. It is also possible that at least one generation of

O. rupestris were produced by the summer cohort.

There are no published records of the seasonal activity of any Nearctic species of Oropsylla. The seasonal activity of several related Palaearctic species has been described (Darskaya 1970). The majority of these species infest marmots but several are recorded from Spermophilus species (Smit 1983). It is reasonable to expect that Palaearctic hosts, exposed to climatic conditions equivalent to the prairies and sharing specific life history traits with S. richardsonii will be infested with fleas which have patterns of seasonal activity similar to O. rupestris. The suslik (C. pygmaeus) is a ground-dwelling rodent common throughout the southwestern U.S.S.R.. It occurs within the Soviet Socialist Republics of Kazakhstan, Ukraine, northeastern Caucasus and Russian S.F.S.R. (Honzak et al. 1974). The climate in these areas is described in the Rand-McNally New International atlas as "semiarid mid-latitude, light precipitation (25-50 cm. mean annual), warm to hot summers, cool to cold winters". Susliks have similar seasonal cycles of activity to the Richardson's ground squirrel. Susliks are obligate hibernators. Vernal emergence occurs in March. Breeding commences promptly after emergence and juveniles emerge during April and May. A dispersal phase follows juvenile emergence and older individuals begin to prepare for hibernation from early to late June (Mironov et al.

1963). Susliks are infested with a number of flea species however, Citellophilus tesquorum Wagner is most similar to O. rupestris in terms of seasonal activity. Both of these flea species occur on their hosts in highest numbers during the summer and infestation indices steadily increase from March to August. Increases in infestation indices of C. tesquorum occur during early May and June when the number of available hosts is increasing due to juvenile emergence (Mironov et al. 1963). The similarities between these two flea species may be coincidental. However, the paucity of seasonal activity data for Nearctic Oropsylla species warrants such comparisons.

Rhadinopsylla fraterna

Relatively few R. fraterna were removed from Richardson's ground squirrels compared to the other flea species. Mean intensity and prevalence of R. fraterna infestation were highest during spring and fall. Unlike O. rupestris and O. bruneri, the increases in R. fraterna late in the season when only a few hosts are active probably represented increased flea activity. Oropsylla rupestris and O. bruneri were both collected during the summer months in relatively high numbers, R. fraterna on the other hand, was extremely scarce during the summer months. Thus, when hosts are infested at noticeable levels of intensity and prevalence these may be periods when R. fraterna activity

has increased or is increasing. The presence of nulliparous and immature females, and teneral R. fraterna during spring and fall sampling intervals only is evidence that populations of this species may be expanding. Seasonal activity is difficult to interpret when the overall intensity and prevalence of infestation and the number of fleas collected from hosts is small. The low infestation indices for this species could be due to several factors. Holland (1944) suggested that R. fraterna is a nest associate which spends much less time on the host's body than the other flea species common to this host. The reduced pleural arches and absence of eyes in adult R. fraterna support this hypothesis. Therefore, as with N. inopina the possibility of low host affinity cannot be overlooked. These two species may also require fewer blood meals or less time to imbibe blood than the other species, thus decreasing the time spent on the host's body. It is also possible that R. fraterna has lower fecundity or higher mortality than the other flea species and therefore has a lower capacity for population increase. Rhadinopsylla fraterna may also be prevented from establishing large populations in association with Richardson's ground squirrels because of competitive interaction with the other flea species.

Removal effect

The possible effect of flea removal was not directly assessed during this study. The only evidence available from this study, against this sampling bias is the observations on daily reinfestation. Removal of O. rupestris or O. bruneri did not effect the subsequent reinfestation of the host on the same day (or seasonally). It is implied that there were always more fleas of these species available to replace captured fleas. Reichardt (1989) and Burachynsky and Galloway (1980) collected O. bruneri from Franklin's ground squirrels for five years at a single location within Bird's Hill Park area of Manitoba. No significant alterations in the patterns of mean intensity or prevalence were observed from year to year. Reichardt (1989) sampled O. bruneri only three times on one plot from May to September and found that patterns of mean intensity and prevalence were similar to those obtained from weekly squirrel collections on other plots. Thus intensive removal of O. bruneri does not affect the patterns of seasonal activity on S. franklinii. It is assumed that this is true for all flea species infesting S. richardsonii. Mironov et al. (1963) estimated that fewer than 10% of the fleas present within the host's environment (nest, entrances, or host's body) are upon the host at any given time. Therefore, it is possible that a substantial number of fleas

can be removed from infested hosts before there is any impact on the overall flea population.

Multiple flea species infestations

Seasonal peaks of activity for the four flea species infesting Richardson's ground squirrels occurred at different times during the host's circannual cycle. With the exception of O. bruneri and R. fraterna, peaks of high mean intensity and prevalence did not overlap for the different flea species. Temporal variation in the timing of maximum flea activity has been reported in other host-flea associations in which several flea species share a common host. Peak seasonal activity (number of fleas/host) for Diamanus montanus (Baker) and Hoplopsyllus anomalus (Baker) on California ground squirrels occurs during the winter and summer months, respectively (Holdenreid et al. 1951; Longanecker and Burroughs 1952; Ryckman 1971; Ryckman et al. 1954; Stewart and Evans 1941). Similar temporal separation of peak activity has been observed for Thrassis bacchi gladiolis (Jordan) and H. anomalus infesting antelope ground squirrels (Parker 1958), and for Epitedia faceta (Rothschild), Conorhinopsylla stanfordi Stewart, Opisodasys pseudarctomys (Baker) and Orchopeas howardii (Baker) from the nests of the southern flying squirrel (Benton and Day 1980; Day and Benton 1980).

Several selection pressures may be responsible for the

separation of peak activity of the fleas infesting Richardson's ground squirrels. It is possible that all four species were preadapted for life in the Richardson's ground squirrel ectoparasite community. That is, all of the species had the life cycles now in evidence regardless of the presence of the other three species. The seasonal activity of *O. bruneri* was not markedly different when it shared the host with the other three species compared to when it was the only flea species infesting ground squirrels. However, it is reasonable to hypothesize that these species have at least coevolved life history strategies as the result of interspecific competition. Adult fleas compete for blood of the host (Day and Benton 1980) and larvae may compete for space and resources in the nest of a host (Marshall 1981a), and flea seasonal activity patterns which place the least pressure on the host are favoured by natural selection. If the four flea species associated with Richardson's ground squirrels occurred on the host at maximum intensities at the same time, the host may respond by increased grooming, or nest abandonment or there might be decreased larval survival due to overcrowding. These factors may act as significant selective pressures favouring the temporal separation of flea species.

Benton and Day (1980) suggested that "when fleas share

a common host, some modification in behaviour, life cycle or spatial distribution must be made in order to maximize the success of each species and minimize competition for whatever resources may limit the number of ectoparasites." There are two ways that fleas can exploit a common host with minimal impact on each other. Fleas can avoid interaction with other species by either temporal or spatial separation. Spatial separation occurs when fleas preferentially infest specific regions of the host's body or infest only certain hosts or nests within a host population. Temporal separation occurs when the life cycles of different flea species vary such that adults and/or larvae of each species are dominant at different times of the year. The mechanisms which govern temporal separation can include differences in the response of fleas to specific environmental factors and/or differences in overwintering strategies.

Certain flea species tend to occupy specific regions of the host's body (Allan 1956; Haas and Dicke 1959; Horak 1982). Partitioning the host in this manner ensures that competition among adult fleas is minimal. Fleas may also partition a population of hosts so that certain nests or locations within the host's habitat are occupied by specific flea species but not others (Layne 1963). It is unlikely that spatial separation is prominent for fleas of the Richardson's ground squirrels. Although the technique for

flea removal was not designed to determine the spatial distribution of fleas on the host's body, fleas from all four species were more abundant on the posterior regions of the host's body. Also, the different flea species were not restricted to specific burrows or locations within the study area. The fleas removed from a host are assumed to infest the burrow where the animal was trapped. If this assumption is correct then fleas from each of the four species were distributed throughout the entire study site.

Seasonal patterns of flea activity are undoubtedly influenced by environmental parameters such as temperature and humidity (Marshall 1981a). The growth of flea populations is influenced by the developmental thresholds for each parameter. For example, D. montanus appears on Californian ground squirrels during the cool, moist months and is rarely found on the host when burrow temperatures exceed 10°C (Longanecker and Burroughs 1952). Fleas sharing a common host may be temporally separated because environmental conditions at certain times of the year are suitable (or optimal) for growth and development of certain flea species and inhibitory for others. Variation in the seasonal activity of flea species sharing a common host have been attributed to differential responses to ambient air temperature (Holdenreid et al. 1951; Layne 1963; Mitchell 1971; Rumreich and Koepke 1945), rainfall (Olson 1969), soil

temperature (Haas 1965; Holdenreid et al. 1951; Schwan 1986), and both temperature and relative humidity (Amin 1966; Flux 1972; Longanecker and Burroughs 1952; Parker 1958; Ryckman 1971; Ryckman et al. 1954; Stark and Miles 1962; Yeh and Davis 1950). In most instances, it is assumed that the observed patterns of flea activity are partly or completely a result of the influence of specific environmental factors. The influence of environmental parameters on flea activity should not be over-emphasized however, since factors such as host density may simultaneously affect the patterns of flea infestation observed.

Temporal separation of the various flea species infesting Richardson's ground squirrels was probably due to species-specific differences in temperature and relative humidity requirements and life histories. Temporal separation may also have resulted from interspecific competition among the four flea species. It is likely that each flea species has different temperature and humidity requirements for optimum growth and development and these environmental parameters probably fluctuate during the season. For example, burrow temperatures should increase substantially during early May when the young of the year are born. Seasonal variation in these environmental parameters may favour the survival and reproduction of one

or more flea species over the others. Differences in overwintering strategies and generation times could also have an influence on the temporal distribution of flea species. The relative influence that each of these factors may have on the temporal separation of flea species could not be determined during the present study. However, it is probable that temporal separation results from the combined affect of these factors.

The principle weakness of field studies for interpretation of temporal separation in fleas is that the methods do not yield sufficient information concerning the underlying causes of seasonal variation in flea activity. Field studies can be used to determine whether flea species are temporally and/or spatially separated when several species infest a common host however, the reasons for the separation usually cannot be resolved. In order to determine the ultimate causes of temporal separation the proximate factors which activate reproductive behaviour and regulate timing of different life stages must be determined. Proximate factors must include the effects of all relevant environmental parameters. Detailed knowledge of the life cycles of each flea species is obviously needed.

Unfortunately, very little is known about the life cycles of any of the fleas infesting Richardson's ground squirrels. Laboratory studies (or equivalent methods) aimed

at determining the influence of specific environmental parameters (e.g. temperature) and life history attributes must be applied to these species before the reasons for temporal separation will be fully understood.

Flea life histories

One of my original hypotheses was that ovarian development in Richardson's ground squirrel fleas was stimulated by circulating reproductive hormones within S. richardsonii. Reichardt (1989) concluded that oogenesis of O. bruneri was not initiated by the reproductive hormones of S. franklinii. Since Richardson's ground squirrels in Manitoba were known to harbour O. bruneri (Galloway and Christie unpublished; McLeod 1933) and several other flea species including O. rupestris, N. inopina and R. fraterna (Galloway and Christie unpublished) the dependence of these flea species on the estrous cycle of S. richardsonii to initiate oogenesis was assessed. The ovarian age structure of fleas was also examined with the intent that knowledge concerning flea population age structure would be useful for understanding the dynamics of seasonal changes in flea intensity and prevalence.

If any of the flea species were dependent on levels of circulating reproductive hormones in S. richardsonii to initiate oogenesis, as occurs in S. cuniculi-rabbit reproductive cycle, then the following would be observed: 1)

only one generation of each flea/species would be produced each year; 2) flea ovarian development would commence only during late April and early May when female ground squirrels are entering the latter stages of pregnancy; 3) regardless of flea species, females with mature ovarioles would be collected only during parturition of S. richardsonii (early May); 4) mating and egg deposition by flea spp. would be maximal one week post partum and would not recommence until the following year; 5) females would remain non-reproductive for the duration of the season (i.e. immature and nulliparous females only).

Fleas of each species would also be expected to alter host-seeking behaviour such that most fleas would occur almost exclusively on pregnant female squirrels. Prior to parturition, female S. richardsonii would harbour the highest proportion of female fleas, as observed with S. cuniculi (Rothschild and Ford 1973). Following the birth of young squirrels, flea infestation parameters for male and female squirrels would reestablish to levels characteristic of pre-reproductive activity.

Neopsylla inopina

The first adult squirrels to emerge from hibernation were infested with newly emerged (non-parous) N. inopina. Neopsylla inopina probably overwinter as non-reproductive (teneral) adults, and/or adults or pupae within cocoons.

Flea emergence may be initiated by mechanical disturbance such as extensive movement by the aroused host. This type of stimulus is common for many mammalian fleas (Cotton 1970; Edney 1945; Marshall 1981a). Flea emergence may also be stimulated by an increase in temperature. Humphries (1969) reported that a rise in temperature rather than the actual level of temperature caused the emergence of Ceratophyllus styx jordani Smit. The stimulus for emergence of all of the fleas of Richardson's ground squirrels is undoubtedly one or a combination of these factors. Regardless of flea species, the age of fleas collected from the first emerging hosts at the time of emergence was unknown. The duration of time that elapses between terminal arousal and emergence of the host was also unknown. It is proposed that the flea emergence coincided with terminal arousal of the host. If hosts are active before appearing aboveground, it is possible that fleas begin feeding and egg development prior to host emergence.

Throughout April, the proportion of parous N. inopina females increased and by early June the majority of females had commenced egg-laying. Parous and non-parous N. inopina females were removed from squirrels during late April and early May and N. inopina did not selectively infest female squirrels. Parous N. inopina were collected from Richardson's ground squirrels several months post partum and

the majority of these females had mated. Non-reproductive females were scarce in collections after the end of July. Reproductively active, mated female N. inopina occurred on Richardson's ground squirrel throughout the season.

The life cycle of N. inopina probably began each year with emergence of adults. Flea emergence was likely extended over several weeks since not all hosts resume activity at the same time and immatures and teneral fleas were predominate in April. Most females produced eggs during April since the percentage of parous females increased during this month. The percentage of parous females remained high throughout the remainder of the season. Bruchanova and Surkov (1970) reported similar high percentages of nulliparous female N. setosa in suslik nests immediately following host emergence, when by June, 100% parity was observed. During the summer months, the eggs produced by N. inopina develop into larvae within the nests of adult squirrels, but adults may not emerge until the following year. This observation is supported by the rapid decline in the number of fleas collected following juvenile emergence. If the adults emerged from the eggs produced during April and May, a second peak in mean intensity or prevalence of N. inopina and an increase in the percentage of immature and nulliparous females should have been observed. The numbers of adult N. setosa on the body of the

suslik and within its nest also dropped to very low levels by August (Bruchanova and Surkov 1970). The immature and nulliparous females collected late in the season could be females which overwintered in the late larval, or pupal stages and therefore, took longer to reach the adult stage than spring emerging N. inopina. These recently emerged fleas might represent a small or partial second generation of N. inopina. Alternatively, these non-parous N. inopina may have spent most of the summer in unused nests or burrows and were picked up later in the season when juveniles entered these abandoned burrow systems.

Opisocrostis bruneri

At the time of squirrel emergence the majority of female O. bruneri were non-parous. An exception to this pattern was observed in 1988, when the six female O. bruneri collected from the newly emerged hosts were parous. It is possible that some squirrels were active underground long enough before vernal emergence for fleas to commence egg development. During the week of parturition, female squirrels did not on average carry more O. bruneri than males and a large percentage of the female fleas were reproductively active. Shortly after parturition (early May), most O. bruneri were parous and during most years the majority of females had sperm within their spermathecae. Per cent mated was more closely related to the level of

parity rather than the reproductive cycle of the host. Parous and non-parous females were removed from squirrels throughout the remainder of the season.

Adult O. bruneri probably overwinter as teneral adults, or adults and/or pupae within cocoons. Most newly emerged females commenced egg laying during April and as a result per cent parity increased. Eggs deposited with the host's nest emerged as adults in mid to late June. The influx of non-parous females and a shift in sex ratios towards a greater per cent male support the hypothesis of emergence of a new generation of O. bruneri. The duration from squirrel emergence to the production of a new generation is 80-90 days. Cotton (1970) reported that Ctenophthalmus nobilis (Rothschild) requires 58-70 days at 14°C to develop from egg to adult. Duration of the life cycle was directly related to temperature. At Morden, Manitoba the Darlingford loam soil temperature at depths of 150 cm ranges from 5°C in April to 10°C in June (Krpan 1982). The presence of juvenile squirrels in the nest would tend to increase burrow temperatures. Provided these estimates are indicative of the duration of flea development and environmental conditions within the host's nest, there would be sufficient time for the summer generation to complete development to adulthood.

The summer generation probably entered the population

over a period of several weeks with mating and egg development commencing immediately after flea emergence. Eggs produced by the summer generation could either emerge as adults and commence production of a second summer generation or arrest development in the overwintering stage (*i.e.* teneral adult or pupae within cocoons). In the latter case, development would be completed in the following spring. It is not known whether eggs laid by the second summer generation *O. bruneri* females, during September or October, would be capable of completing development to the overwintering stage before hosts became torpid or before ambient temperatures fell below the developmental threshold. Thus the non-parous females collected later in the season are either late emerging females from the first summer generation, or individuals of the second summer.

Opisocrostitis bruneri has similar life history patterns when it infests Franklin's ground squirrels (Reichardt 1989).

Oropsylla rupestris

At the time of squirrel emergence, the majority of *O. rupestris* females were parous. During the weeks prior to parturition, an increase in per cent parity was observed, though females on average carried fewer *O. rupestris* fleas than males. Following parturition in 1987, the majority of females were parous and had mated. However, in 1988, the frequency of parous and mated *O. rupestris* females

fluctuated after young of the year were born.

During the first month of squirrel activity, a larger proportion of female O. rupestris had begun laying eggs than either N. inopina or O. bruneri. During April and early May of 1988 and 1989, the majority of O. rupestris females were parous. Female O. rupestris may overwinter as mated nullipars which are capable of egg production as soon as the host emerges. The other flea species may require several days (weeks) to complete emergence, sclerotization and insemination thus lengthening the time required to develop their first egg batch. Eggs deposited in the host's nest in the spring develop to the adult stage in early June. Increases in the percentage of male O. rupestris, teneral individuals and non-parous females at this time are evidence for the emergence of a summer generation. During this same period, mean intensity and prevalence of O. rupestris infestation were increasing. The summer generation of O. rupestris adults commences mating and egg-laying. These eggs may complete development to form a second summer generation. The influx of immatures in late August may be due to emergence of adults of the second summer generation or late emerging first summer generation adults. Eggs deposited by the second summer generation of O. rupestris probably developed to the adult stage and become inactive at the time of host emergence. Richardson's ground squirrels

are active as early as February and can remain active until December in Alberta (Michener 1983b). Squirrels are infested with O. rupestris at both the beginning and the end of the annual cycle (T.D. Galloway, pers. comm.) and therefore, more than two summer generations may develop in localities where the host's active season is longer than in Manitoba.

Many Soviet authors report that N. setosa and Oropsylla silantiewi Wagner are capable of activity and reproduction while the host is hibernating (Bibikova and Zhovtyi 1972; Darskaya 1970; Darskaya et al. 1962; Mjalkovskaja and Bruchanova 1972; Zhovtyi 1972). The appearance of parous O. rupestris on newly emerged Richardson's ground squirrels may be evidence for this characteristic in O. rupestris. A small proportion of parous O. rupestris may be able to survive during hibernation of the host, however, ovarian development is probably minimal. Survival must be greater for individuals that remain within cocoons over winter or which emerge but have limited activity, than for reproductively active females. Reproduction is a metabolically demanding process (Chapman 1982) and it is difficult to accept that females are capable of extensive egg production at a time when the host's body and environmental conditions are so inhospitable. Squirrels spend more than 90% of their time during August to February

in deep torpor and body temperatures generally drop to about 4°C (Wang 1978). Under these conditions, fleas would be inactive. Without blood feeding, oogenesis would cease. At the time of host emergence, metamorphic and reproductive development in O. rupestris is likely more advanced compared to the other flea species, though blood feeding and oogenesis prior to host terminal arousal is improbable.

Rhadinopsylla fraterna

The small number of R. fraterna collected from Richardson's ground squirrels confounds interpretation of changes in ovarian age structure. Dramatic fluctuations in percentage of mated or egg-laying females were, in most instances, an artifact of small sample sizes. Despite these limitations, it is possible to establish whether oogenesis is stimulated by hormones from S. richardsonii and to speculate on the possible life history patterns of R. fraterna.

It is unlikely that oogenesis of R. fraterna is initiated by the estrous cycle of Richardson's ground squirrels. Prior to parturition, approximately equal numbers of R. fraterna were parous and non-parous. During the latter stage of squirrel pregnancy, R. fraterna was not present in large enough numbers to evaluate whether males or females were differentially infested with this flea. In addition, reproductive and non-reproducing R. fraterna were

present on Richardson's ground squirrels throughout the season. Thus host reproductive hormones did not stimulate ovarian development in R. fraterna.

It is hypothesized that the overwintering generation of R. fraterna emerges at the time of host emergence. Egg-laying is initiated at this time and by early May the observed mean intensity dropped dramatically, primarily due to adult mortality. Larval development proceeds through June, July and August. Late in the season, the first summer generation of R. fraterna may complete development to the adult, or development may be arrested in the later larval stages or pupal stage until the following year. Development to the adult stage during September or October may depend on environment parameters such as temperature. For example, if R. fraterna reach the pupal stage before or after some critical temperature threshold is reached, fleas emerge as adults or remain quiescent until the following year, respectively. Emergence of a the first summer generation would explain the increase in observed mean intensity and prevalence which started in late August. Newly emerged adults would produce eggs which may contribute to the overwintering generation. The small numbers of adult R. fraterna emerging during May through June may from overwintered pupae.

The summer generation of R. fraterna may mature to

adulthood during late July and August. This generation lays eggs and the flea development proceeds slowly during winter and is completed just prior to host emergence. It is also possible that the eggs produced by the summer generation reach the pupal or adult overwintering phase before host activity ceases. These latter two hypotheses are less tenable than the former, but each hypothesis requires testing.

When modelled after the S. cuniculi-rabbit reproductive system, none of the species infesting Richardson's ground squirrel have reproductive strategies which are stimulated by host reproduction. Mating and ovarian development in all flea species were independent of the host's estrous cycle. Flea reproduction may be influenced by the hormone levels of S. richardsonii, but any such influences are much more subtle than the interdependence observed between S. cuniculi or C. simplex and their lagomorph hosts.

While oogenesis in the flea species associated with Richardson's ground squirrels was not initiated by the presence of reproductive hormones, flea life histories were closely associated with the host's circannual cycle of activity. It is possible to propose certain generalizations about the life histories of the fleas of the Richardson's ground squirrel. During host hibernation, all life cycle stages are dormant, or if not, activity is limited and

ovarian development is minimal. Flea arousal is initiated at or slightly before the time of host emergence. Mating, feeding and oogenesis commence immediately after fleas are aroused. Fleas produce eggs throughout the summer and depending on flea species, production of a number of adult generations may be possible each season. When hosts first enter hibernation, flea activity and oogenesis decrease dramatically. Flea activity probably ceases entirely when hosts are in deep torpor for extended periods of time. Thus most flea species are active whenever the host is active and peaks in flea activity may be closely related with periods of changing host density and dispersal rather than during the reproductive cycle. With the exception of reproductive activity during winter, the proposed annual cycle of S. richardsonii fleas is very similar to the patterns proposed by Zhovtyi (1972) for the fleas of hibernating rodents in the Soviet Union.

Several unresolved characteristics of host and flea biology confounded the estimates of flea life cycles. The length of time required to develop from egg to adult and the duration of the various ovarian age categories are not known for any of the fleas associated with the Richardson's ground squirrel. Attempts to determine these intervals by rearing fleas on captive squirrels and by excavating squirrel burrows were unsuccessful. Another confounding influence on

estimates of flea life cycles was that the duration of the interval from terminal arousal to host emergence was unknown. Traps were set as early in the season as possible. However, it was not known how long the host or its fleas had been active before appearing aboveground. Egg-laying fleas removed from the first squirrel captures of the year made it difficult to establish the most probable overwintering stage for the different flea species. Clearly, laboratory examination of flea life histories is required to supplement data obtained by field techniques.

Establishing laboratory colonies of hosts and fleas, despite the reported failure of such a system in this study, can be successful (Hilton 1972). Equipment failures did not permit proper evaluation of the viability of this technique for rearing ground squirrels and their fleas. The development of artificial nest systems as described by Ryba et. al. (1980) may serve as an alternative for detailed examination of flea life histories parameters. Such a system can be monitored year round and if successful, could be used to determine overwintering strategies and per cent survival for all flea life cycle stages, frequency of egg production, mating and feeding during host hibernation, as well as to evaluate the proximate factors which may be responsible for differences in the patterns of seasonal activity of the various flea species.

CONCLUSIONS

1. The annual cycle of S. richardsonii activity in Manitoba commenced each year with adult emergence. Juveniles emerged during the last week of May to the first week of June. Emergence schedules were adult male before adult females > juvenile female > juvenile males. Yearling females entered hibernation after older females (\geq two year old). Squirrel populations were female biased at all sites and females generally had greater interyear survival than males. During the weeks that preceded parturition, mated, egg-laying fleas from each flea species were removed from Richardson's ground squirrels. However, egg production continued throughout the remainder of the season. Thus oogenesis in N. inopina, O. bruneri, O. rupestris and R. fraterna was not controlled by the hormone levels of female S. richardsonii.
2. Neopsylla inopina completes a single generation per year in Manitoba. Emergence of adult N. inopina during early April coincided with a discrete peak in mean

intensity and prevalence. During April, an influx of nulliparous females and teneral N. inopina adults provided evidence that a teneral generation of adult N. inopina was emerging. There was no summer generation of adults based on the low levels of intensity of adult N. inopina following the spring peak.

3. Opisocrostitis bruneri completed two generations during each year. The presence of large proportions of newly emerged fleas corresponded with increases in prevalence and mean intensity of O. bruneri adults during early May and August - early September. Emergence of a summer generation of O. bruneri adults is also supported by the occurrence of a large number of teneral fleas during July and by the shift from strongly female biased O. bruneri collections to more uniform representation of the two sexes.
4. Oropsylla rupestris completes at least two generations each year on Richardson's ground squirrels in Manitoba. Emergence of O. rupestris adults coincided with peaks in mean intensity and prevalence during early April and late June. Female O. rupestris which overwintered as

mated, unfed nullipars may have been responsible for the peak in mean intensity in April. An influx of nulliparous O. rupestris adults during early June was from the summer generation and resulted in the observed seasonal peak of intensity in late June. A second summer generation of adults may have emerged during late August based on the presence of a large numbers of teneral O. rupestris adults in 1987 and an increase in the proportion of nulliparous and immature O. rupestris adults.

5. Rhadinopsylla fraterna probably completes two generations each year in Manitoba. The overwintering generation started development in April and the eggs produced by this generation began to develop to produce the summer generation in late June and July. The summer generation may commence egg production, or enter developmental arrest until the following year. The observed spring and fall peaks in mean intensity of R. fraterna adults probably resulted from emergence of overwintering adult fleas following host emergence, and the emergence of the summer generation of adults late in the summer, respectively.

6. Peaks in mean intensity and prevalence of O. bruneri adults on Richardson's ground squirrel occurred in early May and late August - September at all sites. Thus the seasonal activity of O. bruneri was not affected by the presence of N. inopina, O. rupestris or R. fraterna.
7. The lowest levels of mean intensity and prevalence for O. bruneri on S. richardsonii occurred during the period of juvenile emergence. The emergence of juvenile squirrels in the summer resulted in a reduction in O. bruneri intensity on S. richardsonii from June to early August.
8. Although the overwintering stage for each flea species could not be determined directly, it is probable that O. rupestris overwinters in a more advanced reproductive condition than any of the other flea species. The proportion of parous O. rupestris females was generally much higher than the other three species during the first trapping periods. Neopsylla inopina, O. bruneri, and R. fraterna likely overwinter as teneral adults or pupae within cocoons. A portion of

the O. rupestris population may be capable of overwintering as quiescent, unfed nullipars. The life cycles of these flea species must be examined under controlled conditions before definitive statements can be made concerning their overall life histories.

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APPENDIX A

Dissection TechniquePreparation for dissection

Each flea was placed on a glass slide. Fleas were immersed in several drops of physiological saline to prevent dessication of reproductive organs. Dissections and examination of the exterior of fleas for mites were performed using a Wild dissecting microscope.

Dissection procedure

The dissection procedure was similar for male and female fleas. The exoskeleton joining the metathorax and the first abdominal segment was ripped by holding tergum VIII and gently pulling anteriorly on the metathorax. The midgut generally remained attached to the thorax and was examined for gregarines. Dorsal sclerites of the abdomen were removed by pulling tergum VII anteriorly while holding tergum VIII stationary. Flea reproductive tracts were completely exposed when sternum VI or VII was pulled anteriorly. The discarded exoskeleton and haemocoel contents were examined for external associates and internal parasites. Ovarioles and spermatheca were cleaned of any fat body or extraneous tissue and placed under a coverslip. Additional physiological saline was placed under the

coverslip to prevent rupturing of ovarioles. Ovarioles and spermatheca were examined using a Wild phase contrast microscope. Development of the ovarioles was recorded, and then pressure was applied to the coverslip so that the contents of the spermatheca were exposed.

APPENDIX B

Flea Associates and ParasitesFlea associates

Neopsylla inopina, Opisocrostis bruneri, Oropsylla rupestris and Rhadinopsylla fraterna were occasionally infested with two different types of mites. The hypopal stage of the uropodid mite, genus Trichouropoda were attached to the exoskeleton of fleas via a stalk. The occurrence of phoretic mites attaching via a stalk to flea integuments has been reported by others (e.g. Schwan and Corwin 1987). Anoeetid mites, genus Psyllanoetus were found under the tergal and sternal sclerites of each of the four flea species. The presence of either mite did not influence the reproductive or blood-feeding activity of any of the flea species.

Flea parasites

Allantonematid nematodes were removed from the haemocoel of less than one per cent of adult O. bruneri and O. rupestris. Two Aetheca wagneri (Baker) were also infested with these nematodes. Usually one to eight adult nematodes and 50-200 L1 to L3 larval stages were present within the haemocoel of infested fleas. Except for one female O. bruneri, fleas infested with these nematodes never

had fully developed ovaries or testes and in most cases, reproductive tracts were undeveloped or absent.

Allantonematid nematodes have been taken from the flea haemocoel of several genera of fleas (Launay and Deunff 1984; Poinar and Nelson 1973; Linardi et al. 1981). The effects of allantonematid infections on their host's reproductive activity can be negligible (Linardi et al. 1981) or inhibitory. For example, Poinar and Nelson (1973) reported that the reproductive organs of Monopsyllus (=Aetheca) wagneri, M. ciliatus protinus (Baker) and Diamanus montanus infested with nematodes were normal while a male Catallagia sculleni rutherfordi (Augustson) was partly castrated. Launay and Deunff (1984) reported that infection with nematodes inhibited reproduction in S. cuniculi.

Gregarine cysts were routinely removed from the midgut of O. bruneri and O. rupestris. Megabothris asio megacolpus (n=2) was the only other species in which gregarines were found. The prevalence of gregarine infestation ranged from less than 1 per cent (O. rupestris) to 15.3 per cent (O. bruneri, St. Norbert 1988). Reichardt (1989) found gregarine cysts in the midguts of O. bruneri from S. franklinii.