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Population Dynamics and Dispersal in Waterstriders: a Comparative Approach

Todd C. Butler

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ABSTRACT

Population Dynamics and Dispersal in Waterstriders: a Comparative Approach

Todd C. Butler

Population dynamics, phenology, wing morphology and dispersal of pond dwelling waterstriders were studied by means of a mark recapture field study among three permanent and 17 temporary habitats. Populations of *Gerris buenoi* and a species assemblage comprised of *G. comatus*, *G. marginatus* and *G. insperatus* were not self-sustaining as all sites were recolonized by immigration in spring. Data confirm that *G. buenoi* is partially bivoltine at all permanent sites, but the *G. comatus* group may be partially bivoltine at only one of three permanent sites. Phenology is very plastic, with variability depending upon local environmental conditions. Both groups or species were seasonally wing polymorphic. Species within the *G. comatus* group were primarily macropterous, with a maximum of 23% wing reduction in the summer generation, while *G. buenoi* exhibited up to 90% wing reduction.

Dispersal was measured as movement of macropters of *G. buenoi* and the *G. comatus* group among temporary and permanent sites. No difference in dispersal distance was observed. Dispersal was primarily in spring. The

G. comatus group macropters had a higher proportion of dispersers than *G. buenoi* throughout the year. The data concerning dispersal provide support for the hypothesis, based upon a laboratory analysis of flight threshold by Fairbairn and Desranleau (1987), that dispersal capacity of macropters is correlated with the proportion winged in a species. The greater dispersal ability of the *G. comatus* group is also shown by its more frequent occurrence on temporary habitats than *G. buenoi* .

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INTRODUCTION

It is widely believed that all extant pterygote insects evolved from a common, winged ancestor (Gillott 1980, pp 24). Through various selective forces, loss or reduction of wings has occurred among and within various insect species. Wing polymorphisms are commonly observed in Orthopteran, Coleopteran and Hemipteran species of insects (Johnson 1969; Roff 1986; Calabrese 1979; Harrison 1980). For such species, there has been a relaxation of selective pressures for wings to be used in activities such as foraging, mating and escaping predation (Johnson 1969; Calabrese 1979; Harrison 1980; Andersen 1982). It has been suggested that in these species, wing polymorphisms are dispersal polymorphisms (Johnson 1969; Dingle 1972; Andersen 1973, 1982; Vepsalainen 1978; Harrison 1980). The morphs exhibiting wing reduction (collectively termed shortwinged or SW) are usually flightless (Andersen 1982). Thus, it is the macropterous morph (longwinged or LW) that is considered to be the dispersal morph for such species (Brinkhurst 1959; Johnson 1969; Vepsalainen 1971, 1974, 1978; Andersen 1973, 1982; Harrison 1980; Roff 1986).

Among the Gerridae (Hemiptera), wing polymorphisms are quite common and have been extensively studied (Brinkhurst 1959; Guthrie 1959; Vepsalainen 1971, 1974, 1978; Andersen 1973, 1982; Jarvinen 1976; Jarvinen and Vepsalainen 1976; Calabrese 1979; Fairbairn 1985a+b, 1986; Fairbairn and Desranleau 1987). The proportions of the morphs in polymorphic species are greater than could be maintained by chance mutation or pleiotropic effects (Andersen 1973). Therefore, selective advantages must exist for both macropterous and wing-reduced morphs.

The macropterous morph <u>is</u> selected for its dispersal ability. This permits colonization of new habitats, escape from unsuitable or deteriorating habitats, and allelic exchange among local populations (Brinkhurst 1959; Vepsalainen 1971, 1974, 1978; Andersen 1973; Jarvinen and Vepsalainen 1976; Calabrese 1979). The existence of macropters may permit the spatial dispersion of eggs among a series of variably unstable, patchy habitats (Landin and Vepsalainen 1976; Spence 1983). A further advantage of macroptery has been proposed. It is possible that the LW morph can escape possible flooding and freezing during diapause by selecting overwintering sites away from the immediate edges of their aquatic habitats (Vepsalainen 1971; Nummelin and Vepsalainen 1982). Lastly, it is thought that the presence of macropters can result in avoidance of overcrowding (Brinkhurst 1959; Vepsalainen 1971; Andersen 1973). The LW individuals are believed to leave their natal sites shortly after final development of the flight apparatus (Vepsalainen 1971; Andersen 1973). This leaves the SW individuals active on the site. The result is a relatively large overwintering population without overcrowding or depletion of available resources in late summer and fall (Brinkhurst 1959; Vepsalainen 1971, 1974; Andersen 1973).

The advantages of the SW morph are seen in reproduction. There appears to be a difference in egg production between SW and LW females of a species where short-winged females produce more eggs (Zera 1984, 1985; Fairbairn unpubl.). The advantage is also in terms of development time and, more importantly, its influence on subsequent reproduction. SW females appear to reach reproductive maturity faster than LW females (Guthrie 1959; Andersen 1973; Zera 1984, 1985). Andersen (1973) suggests the reproductive advantage of SW over LW occurs only in the first generation of bivoltine species (voltinism refers to the number of generations produced per year). In many bivoltine species, the SW morph is only produced in the first generation (Blatchley 1926; Scudder 1971; Vepsalainen 1971, 1974; Andersen 1973; Calabrese 1974, 1979). The SW females become reproductively mature soon after the imaginal molt, whereas LW females only become mature following diapause (Andersen 1973). Therefore, in bivoltine species, the

SW morph of the first generation quickly matures and produces the second generation. This generally macropterous second generation, along with LW individuals of the first generation, comprises the overwinter population (Vepsalainen 1971; Andersen 1973).

All insects exhibit a teneral period in their development, subsequent to the final molt, when the exoskeleton becomes fully sclerotized and flight and reproductive structures mature (Gillott 1980; Andersen 1982). For winged females, "competition" for available resources between reproductive and flight structures occurs during the teneral period. This phenomenon is termed the "flight-oogenesis syndrome" (Johnson 1969). This phenomenon may be very important in wing polymorphic insects because SW insects display little or no development of flight structures (Johnson 1969; Andersen 1973, 1982; Harrison 1980). Therefore, more energy can be diverted to the production and maturation of reproductive structures, enabling SW females to begin reproduction earlier than macropterous females.

A further indication of the trade-off between flight and reproduction is found in studies of the association between reproductive activity and condition of flight muscles. In wing polymorphic gerrid species, macropters typically undergo flight muscle histolysis before and during reproduction (Brinkhurst 1959;

Andersen 1973; Vepsalainen 1974; Fairbairn and Desranleau 1987). Histolysis of the flight muscles renders the macropters as flightless as the SW individuals. This histolysis associated with reproductive activity indicates the dissociation of dispersal and reproduction in these species.

A final advantage of wing reduction is that it maintains populations on sites which have proven suitable for producing offspring (Brinkhurst 1959).

Given the advantages of both SW and LW morphs, the persistence of wing poly- and dimorphisms can be seen as "a balanced and adaptive strategy for a discontinuous habitat" (Calabrese 1979). Different selective pressures are exerted at various times and under various conditions. The macropterous morph, with its dispersal and colonizational abilities, is favoured in temporary and unstable habitats. The SW morphs, however, are favoured in isolated and/or stable habitats where they can exploit the newly colonized habitat (Vepsalainen 1971, 1974, 1978; Andersen 1973, 1982; Calabrese 1979; Harrison 1980).

It was previously stated that macropters form the dispersing segment of polymorphic species (op. cit.). There is growing evidence that considering all macropters in such species to be dispersers is not correct. Various levels of flight ability and dispersal tendency of macropters have been observed between and within various insect species (Dingle 1965, 1966; Young 1965; Davis 1980, 1984; Fairbairn and Desranleau 1987). The presence of a LW morph in a population does not necessarily mean it is the dispersing morph (Fairbairn 1986). Where macropters are relatively rare, wing morphology may be an essentially neutral characteristic (Honek 1985; Fairbairn 1986). Fairbairn (1986), and Fairbairn and Desranleau (1987) argue that macropterous individuals of a given species can exhibit variable tendencies for flight due to varying behavioural and physiological influences. The hypothesis that Fairbairn and Desranleau (1987) formulated was based upon literature data and field studies of <u>Gerris</u> <u>remigis</u> (Fairbairn 1986). The hypothesis was then tested in the laboratory using tethered flight techniques described by Dingle (1965). They further suggest that the observed variabilities in tendency to fly are intricately dependent upon a suite of associated characteristics. These characteristics are: proportion macropterous, degree of flight muscle histolysis, and reproductive condition.

Based upon the literature reviewed, particularly that of Fairbairn and Desranleau (1987), a general hypothesis can be formulated. As habitat stability decreases, we expect the proportion of macropters to increase, flight muscle histolysis to decrease, and the flight threshold of the macropters of a given species to decrease. If we assume that flight threshold is a valid indicator of dispersal tendency in the field, then the macropters of species with lower flight thresholds should show more dispersal or a higher rate of dispersal than macropters of species with higher flight thresholds.

The purposes of this study are twofold. First, to test the hypothesis that the variations in flight threshold among macropters of different species are indicative of variations in the actual dispersal tendencies of those species. To test this hypothesis, I conducted a field study of the dispersal patterns of five species of gerrids, *Limnoporus dissortis* Drake and Harris, *Gerris buenoi* Kirkaldy, *G. comatus* Drake and Hottes, *G. marginatus* Say and *G. insperatus* Drake and Hottes. Temporal patterns of dispersal were recorded and comparisons made between sexes, wing morphs and species. The results obtained herein can then be compared to the results of flight threshold analysis by Fairbairn and Desranleau (1987) for three of the species. The observed pattern of wing morphology was also recorded for these species.

The second purpose was to describe the phenology and population dynamics of the five species. Much of the information concerning the species included in this study is derived from a series of taxonomic keys and investigations of wing polymorphism and habitat associations (Blatchley 1926; Brooks and Kelton 1967; Cheng and Fernando 1970; Scudder 1971; Calabrese 1974, 1977, 1979; Hilsenhoff 1986). Previous data concerning population dynamics and dispersal come from western North American studies (Maynard 1969; Jamieson 1973; Spence 1981, 1983, 1986; Spence and Scudder 1980; Nummelin et al. 1984). Furthermore, because L. dissortis is difficult to visually separate from its congener L. notabilis , in western Canada, the western studies have examined the ecology of the two species combined. Thus, no reliable data exists concerning the population dynamics and dispersal of L. dissortis alone. Therefore, the detailed data from eastern Canada for these species are both useful and original.

MATERIALS AND METHODS

Study Subjects

The general characteristics of the five species studied are presented in Table 1. Gerris comatus , G. insperatus and G. marginatus have been combined for all analyses as the G. comatus group. This was done because the females of the three species are virtually indistinguishable in the field. Also, the three species have been observed mating in the field and in the laboratory (Fairbairn, unpubl.). Gerris comatus, G. marginatus and G. buenoi are widespread and abundant in southern Quebec. Limnoporus dissortis is widespread but rarer within its range (Brooks and Kelton, 1967). Southern Quebec is towards the northeastern margin of the range for G. insperatus (Cheng and Fernando 1970). Identification of species was made in the laboratory using keys by Blatchley (1926), Brooks and Kelton (1967), Cheng and Fernando (1970), Scudder (1971), Calabrese (1974) and Hilsenhoff (1986).

Study Sites

The study was carried out at Morgan Arboretum, in Ste. Anne de Bellevue, approximtely 35 km west of Montreal, Canada. The arboretum contains a mix of beach-maple forest, coniferous plantations, agricultural fields, and meadows. The study sites were a series of twenty-one permanent, temporary and ephemeral aquatic habitats (Figure 1). See Table 2 for descriptions of the sites. The study was concentrated on sites 1 through 4. Sites 1, 2 and 3 are man-made, permanent ponds up to 2m deep and sustain breeding populations of gerrids. Vegetation surrounding and within the permanent ponds is variable. Site 1 is surrounded by a small meadow, while sites 2 and 3 are surrounded by forest. Site 1 contains a considerable amount of emergent and floating vegetation. Site 2 contains little floating vegetation, but partially submerged willow thickets are very common. Site 3 has virtually no emergent nor floating vegetation. Site 4 is an abandoned quarry that has large numbers of gerrids while standing water is available during the spring. The quarry was examined as a possible source or sink for migrants and to determine whether or not gerrid life history is modified by local environmental conditions. Site 7 was not extensively sampled, but was examined as another possible source or sink for migrants. The remaining sites were either ditches or spring-runoff puddles. The ephemeral puddles, rarely more than 20 centimetres deep, were the first available sites for gerrids in early spring.

Sampling Period and Methods

Sampling was performed from September 3 to September 26 1985; April 1 to October 26 1986; and March 25 to June 2 1987. During these sampling periods each site (except site 7) was sampled once per week, unless the site was dry. Long and short-handled nets were used to capture the waterstriders. A rope with a series of plastic floats was used to "herd" the insects to a position for easier capture. The shore of each site was circled on foot and the emergent and floating vegetation was rustled to force the gerrids onto open water where they were more easily captured. To collect waterstriders from the centre of a site an inflatable rubber raft was also employed. We attempted to collect all extant waterstriders on each visit. At site 7, sampling was less frequent and consisted of censusing for individuals marked at other sites. Captured waterstriders were held in plastic buckets containing water, grass and/or leaves to prevent dessication. Escape was prevented by draping cheesecloth over the mouths of the buckets.

Marking Techniques

Each individual gerrid captured during the 1985 sampling period was given a mark to designate the site upon which it was captured. During the 1986 and the 1987 sampling periods, all newly captured gerrids were individually marked. All marks were made using 'Testor' enamel paint. The individual-marking scheme was modified from that used by Fairbairn (1985a and b) and by Matthey (1976). The marks were a series of "dots" placed on the dorsal and ventral aspects of the prothorax, and on the meso-, and metathoracic legs. Different colours or combinations of colours were used to designate a series of 100 individuals, while the positions of the leg and prothoracic "dots" coded for numbers 1 through 100 of any series. See Figure 2 for positions of marks. During all sampling periods, each individual was marked and released "in situ".

Preliminary laboratory experimentation was conducted to test for effects of the marks on survival and flight ability. Marked and unmarked G. buenoi and G. comatus were placed in holding cages in the laboratory. Daily checks for mortality were performed for a 12 week period in order to ascertain if the marks adversely affected mortality. There was not a significant difference in survival time between marked and unmarked G. buenoi (Table 3). For G. comatus, marked individuals had significantly greater survival time than unmarked individuals (Table 3). Marked and unmarked G. comatus and G. buenoi were also subjected to a flight threshold experiment. The gerrids were attached to a thread with wax and their ability to fly was measured according to criteria outlined by Fairbairn and Desranleau (1987). Marking did not adversely affect the flight ability of either species (Table 3).

During the 1986 sampling period, the following information was recorded for each individual captured:

- mark number
- date
- wing length
- venter colour
- site number
- sex
- cuticular hardness

Cuticular hardness was recorded in the hope that it would provide an indication of whether or not the individual had recently emerged as an adult. It has been reported that newly emerged adult gerrids exhibit a softness of the meso-alinotum, which is located beneath the pronotal lobe (Andersen, 1973). The degree of softness of the general cuticle was observed, and it was hoped that, like the meso-alinotum softness, such a condition would indicate a recent recruit to the adult population. Venter colour was recorded as an indication of post- or prediapause conditions. Andersen (1973) and Spence and Scudder (1980) both reported that the venter of diapause individuals is a darker colour than that of non-diapause individuals. I found that individuals captured in spring, summer and fall exhibited varying amounts of venter pigmentation. Furthermore, wing-reduced individuals exhibited both dark and pale venters, which indicated that venter colour differences were not associated with wing length. Most individuals captured in the earliest weeks of the summer generation (ie. those individuals that had recently emerged as adults) did not exhibit a cuticular softness. Thus, during 1987, venter colour and cuticular hardness were not recorded.

Analytical Methods

The Jolly-Seber (JS) estimates of population size and associated standard error were obtained using a computer program based upon formulae in Southwood (1978). The formula is:

$$\hat{N} = \frac{\hat{M}_i \, n_i}{r_i} \quad ; \quad \hat{M}_i = \frac{a_i \, Z_i}{R_i} + r_i$$

(see Appendix I for descriptions of symbols)

Minimum Number Alive (MNA) is a count of all individuals captured in a given sample plus any previously marked individuals not captured in that sample, but captured subsequently (Hilborn and Krebs 1976). The formula is:

$$N = n_i + z_i$$

As MNA is a direct count, standard errors cannot be included. Both J-S and MNA values are presented because MNA is a consistent estimate of the lowest possible population size. The estimates of trappability were obtained from formulae in Krebs and Boonstra (1984). Population estimates were determined only for sites 1 through 4 because only these sites were intensively sampled and supported breeding populations in both 1986 and 1987. Movements were recorded when an individual was marked in a particular site then subsequently recaptured in a different site.

Ambient temperature at a site was recorded by suspending a thermometer from a tree branch approximately three feet above the ground. The water-surface temperature was obtained by using a thermometer placed horizontally on a styrofoam float. This method measured temperature 1 cm above the water-surface. Water temperature was taken at a depth of 16 cm below the surface.

RESULTS

Part I General Population Ecology

1. Population Dynamics

For L. dissortis, Jolly-Seber estimates were not possible because sample sizes were very low. Table 4 shows the numbers of L. dissortis captured at different sites in 1986 and 1987.

Figure 3 shows the population estimates for G. buenoi at sites 1-4. Populations of G. buenoi at all three permanent sites (sites 1-3) exhibit a suggestion of three separate population peaks in 1986. This pattern is most obvious at site 1. The first peak was in May, the second in July and the third was late August to early September (Figure 3a-c). At site 1 (Figure 3a), the peak in May was the smallest, the peak in July larger, and the peak in August largest. At sites 2 and 3 (Figure 3b and c), the August peak was the smallest. Two contrasting scenarios could account for these observed patterns. First, it is possible that a large August population could compensate for high overwinter mortality, thus permitting continuance of the local population. This idea would suggest that G. buenoi populations at sites 2 and 3 risk extinction during winter. However, recaptures of 1986-marked individuals in the spring of 1987 suggest that even if fall populations are small, some individuals successfully overwinter. Table 5 shows the proportion of successfully overwintered individuals at permanent sites. We see from this data that even when fall populations are small, total extinction does not necessarily occur.

Second, if summer-born imagoes leave the site shortly after maturation to go to overwintering sites, the population does not build up in situ. If this were occurring, then there should be a large number of new recruits at each sampling period, but these individuals would be present at the site for a very short period of time. At sites 2 and 3 for G. buenoi, the total number of new recruits in fall is quite low (Table 6). This indicates that the low fall population estimates at these two sites are probably not a result of rapid loss of newly matured imagoes.

A comparison of fall and spring population sizes suggests that immigrants may comprise a major component of spring populations. Peak spring populations exceed peak fall populations at two of three permanent sites. Furthermore, animals marked in fall at a given site make up a small proportion of those captured in spring at all sites (Table 5). It is, therefore, apparent that spring populations are comprised primarily of new immigrants.

Figure 4 shows the population estimates for the G. comatus group at all sites. For G. comatus group populations at permanent sites (sites 1-3), there were only two peaks. The population estimates thus do not indicate a bivoltine phenology (the presence of two summer generations) as did G. buenoi. These peaks occurred in May and early August (Figure 4a-c). At all permanent sites the JS estimate was larger in May than

July. However, for site 3 (Figure 4c), the MNA values in April were much smaller than the JS estimates. The JS estimates for that period are not very reliable because recapture rates were less than 10%, which created a large positive bias in the population estimate. At permanent sites, G. comatus group populations are not self-sustaining as almost all post-diapause individuals are new immigrants (Table 5). Furthermore, as seen in table 6, the number of new recruits in summer and fall at sites 1 and 2 is low. Once again, this indicates that rapid loss of newly matured imagoes is probably not the cause of the low population sizes observed.

These analyses of population dynamics have been based on both MNA and JS values. The standard errors of the JS estimates are generally quite large and trends indicated by the JS estimates do not always follow those revealed by the MNA estimate (Figure 4c). The apparent inaccuracy and/or imprecision of the JS estimates could be due to either an effect of the sampling interval, or to an inability to collect a large proportion of extant individuals. If there is a rapid turnover in population relative to the sampling interval, there will be a large number of unmarked individuals present at each sampling occasion. This will create an overestimate of population size and an overestimate of the associated standard error. Similarly, a small proportion of marked individuals could result in a population overestimate and large standard error (Southwood 1978, Roff 1973a+b). To determine which of these two possibilites is responsible for the large standard errors observed, the following test was performed. In August 1987, a total of 31 G. buenoi were marked and released in situ at site 3 using the same sampling techniques as the regular mark-recapture work. After 1.5 hours, the site was resampled. A total of 30 G. buenoi were captured, of which 28 were marked and 2 were unmarked. Of the unmarked individuals, one exhibited cuticular softness, which indicated it could have been recently recruited to the population. If one excludes the "new" recruit, the Petersen estimate (Southwood 1978) at that time would be 32.107 individuals. Therefore, one could conclude that, for site 3 at least, a large proportion of the extant population was sampled at each interval. According to Roff (1973b), sampling at such an intensity will produce population estimates that will include the true population value within the associated 95% confidence intervals.

The JS estimates can also be influenced by trappability of the animals. Trappability estimates the proportion of the extant population which is actually captured in each sampling period. The greater the trappability, the more likely a population estimate, +/- two standard errors, will include the true population size. Table 7 shows Jolly trappability and mean maximum trappability estimates for the two Gerris species on sites 1 through 4. The Jolly trappability values appear to be acceptable, as the range of Jolly trappabilities for small mammals listed by Krebs and Boonstra (1984) are from 32 to 98.5%. However, as the formula to calculate Jolly trappability includes the JS population estimate, Jolly trappabilities will underestimate the true trappability if the population estimate is an overestimate of the true population size. It is interesting to note that maximum trappability averages, which are based on Minimum Number Alive, consistently provide values in excess of 70%. This value agrees with the results of the August 1987 recapture experiment.

For both G. buenoi and G. comatus group, the lowest Jolly trappabilities were for site 1 and the highest were for site 3. The differences in trappability among permanent sites for the same species may be due to the physical characteristics of the sites. For example, site 3 has very little floating or emergent vegetation. This factor may permit greater facility in capturing extant individuals. Conversely, site 1 has much more floating and emergent vegetation, which may render that site more difficult to sample.

We have established that sampling intensity is not likely responsible for the JS overestimates and large standard errors. Thus, it is quite probable that the frequency of sampling was not sufficient because the population exhibited rapid turnover. Residence time is a measure of how long an individual is known to be on a given site, and, therefore, could be an indicator of turnover rate in a population. Table 8 shows median residence times by species and site for 1986. Median values were used as a measure of central tendency because residence times are highly positively skewed. As can be seen, the median residence time in most situations is less than 7 days, which is the sampling interval used in this study. This suggests that turnover rate is indeed high, and could thus account for the JS overestimates observed.

Andersen (1973) and Spence and Scudder (1980) suggest that macropters of di- or polymorphic species leave natal sites for overwintering sites shortly after maturation in summer and fall while SW individuals remain on natal site to reproduce. Such an occurrence would be reflected as differences in residence time between the wing morphs. Residence times of LW and SW individuals were compared for G. buenoi and G. comatus group. Only weeks in which both LW and SW individuals were present have been included. For G. buenoi , shortwinged individuals had a significantly longer residence time than longwinged individuals at site 1 (mean difference = -0.270, t= 3.607, df= 8, p< 0.01). At sites 2 and 3, longwinged and shortwinged residence times did not differ significantly, but a similar trend of SW residence time being longer than that of LW was observed (site 2; mean difference = -0.080, t= 0.198, df= 7, p> 0.20: site 3; mean difference = -0.708, t= 0.234, df= 5, p> 0.20).

For G. comatus group, a comparison of residence time between the wing morphs was possible only for one week at site 3. It was found that, although not significant, SW residence time was longer than LW residence time (median residence times: SW = 14.00; LW = 4.67; U= 53, U0.05(1)15,5 = 61, p> 0.10).

These results provide additional support of the previous findings that LW individuals leave for overwintering sites sooner after maturation than SW individuals do (Andersen 1973; Spence and Scudder 1980).

Further analysis of residence time was undertaken to establish whether or not differences between seasons existed for macropterous G. buenoi and G. comatus group. The separation of spring, summer and fall individuals was based upon the pattern of population size. For G. buenoi, spring individuals were all those first captured before June 18, summer individuals were those first captured between June 19 and August 16, and fall individuals were those first captured after August 17. For G. comatus group, the separation date between spring and summer/fall samples was June 18 at all sites. Median residence times of macropterous G. buenoi , grouped by week of first capture, are usually less than seven days, but median values of up to 35 days have been observed (Figure 5a-d). For all permanent sites, residence times differ significantly among spring, summer and fall populations (Kruskal-Wallis tests for all: site 1; $H= 7.314$, $df= 2$, $p< 0.05$: site 2; $H= 39.060$, $df= 2$, $p< 0.001$: site 3; $H= 70.535$, $df= 2$, $p< 0.001$). In all cases, spring residence time was the longest and fall residence time was the shortest.

For G. comatus group, residence times were also quite variable. Like G. buenoi , median residence times of macropters for most weeks were less than seven days, yet medians of up to 16 days were recorded (Figure 6a-d). At site 1, there was not a significant difference in residence time between spring and summer/fall populations ($U= 18560.5$, approximate $t= 0.681$, $p> 0.25$). Residence times were significantly higher in spring than summer at both sites 2 and 3 (site 2; $U= 27435.5$, approx. $t= 3.665$, $p< 0.001$: site 3; $U= 25117.5$, approx. $t= 2.741$, $p< 0.01$).

Weekly medians calculated for L. dissortis would not be meaningful because of exceedingly small sample sizes. Overall median residence times were calculated for various sites during various seasons. At site 1, the median was 0.6 days. At site 2, median residence time was 1.6 in spring, and 0.8 in summer. At site 3, the median was 1.3 days. For site 4 it was 1.2. In 1987, overall median residence time at site 20, an intermittent site, was 14.0 days. See Table 4 for sample sizes for L. dissortis .

2. Phenology

Wing Morphology

The terminology and criteria used for separations of wing morphs are those of Andersen (1982). All L. dissortis individuals captured during this study were fully macropterous (LW). G. comatus group was found to be dimorphic, with macropterous and brachypterous individuals recorded. G. buenoi was observed to be polymorphic, as macropters, brachypters, micropters and apters were all noted. Because apters, micropters and brachypters are functionally flightless, they will be collectively referred to as shortwinged (SW, Andersen 1973).

The SW individuals for G. buenoi were present during early and mid-summer 1986 on all permanent sites. At sites 1 and 2, the maximum proportion of SW individuals was approximately 90% (Figure 7a and b). The maximum proportion of SW _G. buenoi_ at site 3 was 60% (Figure 7c). For all permanent sites, the proportion of SW individuals was greater than the 50% reported (Calabrese 1977).

Shortwinged _G. comatus_ group were observed only in early summer at site 3 (Figure 8). The maximum proportion of SW individuals in any week was 23%, which approaches the 30% reported in the literature (see Table 1). This may be confounded by the inclusion of _G. insperatus_ and _G. marginatus_ within the species assemblage. Both of these species are reported to be fully macropterous (Table 1). However, current research indicates that all species included in the assemblage exhibit wing dimorphisms (Fairbairn, unpubl.).

For both _Gerris_ species, the maximum proportion of SW individuals occurred the first week that SW individuals were captured, then subsequently decreased with time. For _G. comatus_ group, the SW individuals were present from the end of June until early August. The SW _G. buenoi_ were present from the end of June to September.

Voltinism

The literature (Table 1) suggests that the Gerris species in this study are bivoltine and that the Limnoporus species is univoltine. We found no evidence to refute this for G. buenoi and L. dissortis. However, there was little evidence to indicate that G. comatus group was bivoltine.

For G. buenoi on permanent sites, the population estimates (Figure 3a-c) indicate three peaks, each of which may indicate the recruitment of a "generation". The May peak is the overwintered portion of the diapause generation. The July peak represents the peak of recruitment for the summer-born generation which includes SW and LW individuals. As noted previously, summer-born macropters may leave natal sites for overwintering sites shortly after maturation, while SW individuals remain on natal sites and reproduce. Thus, summer-born individuals may include diapause and non-diapause individuals. The August peak represents the peak of recruitment for pre-diapause individuals. Secondary support of bivoltinism for this species is the temporal pattern of wing-reduction. The diapause generation is fully macropterous, while the non-diapause generation is represented primarily by the wing-reduced individuals (Figure 7a-c). The changes in proportion macropterous are temporally synchronous to the summer peaks in the population estimates.

G. comatus group in this study area appears to be partially bivoltine at best. Among the permanent sites, no separate July and August population peaks were observed. The only indication of bivoltinism is the presence of wing-reduced individuals in July at site 3 (Figure 8). Because the SW individuals are present for only five weeks, and they occur only at one site, it would appear that the non-diapause generation is a partial one.

The only indication of voltinism for L. dissortis is derived from the temporal pattern of new captures (Figure 9). There is only a large increase in captures at one time of year, which may correspond to the recruitment of a new generation.

Synchrony of Development

For this study, there are three possible indicators of developmental rate. One factor is the first occurrence of nymphs in the spring and in summer. This factor was difficult to assess for three reasons. First, sampling effort was directed towards adults, thus nymphs were overlooked. Second, the first instar nymphs of all species are rather small and, therefore, difficult to see amongst vegetation (Nummelin et al. 1984). Lastly, it was not possible to differentiate species in the field using nymphs. Since no nymphs were removed from the study sites for laboratory identification, this indicator of developmental rate was not feasible.

The second indicator is to compare the temporal pattern of population peaks. If there are differences in development time among sites, the slower developing populations would reach their maximum size later than the faster developing ones. For _G. buenoi_, the time of peak summer population varied between the first and the last week of July (Figure 3a-c). For _G. comatus_ group, the maximum summer populations varied between the last week of June and the last week of July (Figure 4a-c). The differences among sites are consistent for the two _Gerris_ species; the earliest summer peak populations occurred at site 1 and the latest at site 3. It was observed that the spring population peak for _G. buenoi_ occurred between May 12 and 16 for all sites. This would indicate that the differences among sites of the July peak were not due to delayed colonization and subsequent reproduction at different sites. The spring peaks for _G. comatus_ group occurred between May 12 and June 3. This is a difference of 3 weeks, whereas a difference of 5 weeks between sites for the July population peak was observed. Therefore, at least some of the differences seen for G. comatus group could be due to differential development rate.

The third indicator of temporal synchrony is to compare the temporal pattern of wing-reduction among sites. It was observed that the proportion SW was greatest the first week that SW individuals were recorded. For this study, only G. buenoi exhibited wing-reduction at more than one site. The pattern of wing-reduction for G. buenoi shows the maximum SW proportion varied from June 19 to June 26 among sites (Figure 7a-c). Peak proportion SW for G. comatus group occurred June 19 (Figure 8).

Development rate does appear to differ slightly among sites for both Gerris species. Ambient, water-surface and water temperatures were recorded at each site (Table 9). It is probable that, because nymphs are also surface dwellers, the water-surface temperature is an important factor influencing development time. Water temperature will also have an effect because eggs are laid below the water-surface. Through use of a randomized blocks design ANOVA, it was determined that both water and water-surface temperatures varied significantly among the three permanent sites during 1986 (water; F= 18.129, df=

17,34, p< 0.001: surface; F= 6.592, df= 17,34, p< 0.001). Among ambient, water and water-surface temperatures, the warmest permanent site was site 1 and the coldest was site 3. It was site 1 that exhibited the earliest July population peak for both <u>G. buenoi</u> and the <u>G. comatus</u> group. This suggests that differences in water temperatures among the sites may have a marked effect on development time.

<u>Part II. Dispersal Patterns</u>

<u>1. Direct Assessment</u>

<u>Time of Dispersal</u>

The success of recapturing overwintered waterstriders was very low. Only 13 previously marked <u>G. buenoi</u> were recaptured in spring 1986. Of these, 3 were recaptured in a site different from the one in which they were marked. No marked <u>G. comatus</u> group individuals were recaptured in spring 1986. In spring 1987, only 68 <u>G. buenoi</u> and 4 <u>G. comatus</u> group marked the previous summer and fall were recaptured. Of these, 15 <u>G. buenoi</u> were recaptured in a different site. Thus, there is not sufficient information concerning overwinter dispersal for statistical analysis.

Table 10 shows the number of recorded movements by species and season in 1986 and 1987. For 1986, 75% of all *G. buenoi* dispersals were by post-diapause individuals. For *G. comatus* group, 86.5% of all dispersals were by post-diapause individuals. All *L. dissortis* dispersals were made by post-diapause individuals. Thus, all species appear to move primarily after diapause. It is also seen that there were no differences in number of dispersers between sexes for any species in either 1986 nor 1987.

Distance of Dispersal

Both *G. buenoi* and *G. comatus* group are capable of dispersals exceeding 1 kilometre (Figure 10). The distribution of movement distances did not differ significantly between *G. buenoi* and *G. comatus* group ($\chi^2 = 15.957$, df= 11, $p > 0.10$). The scale of the study did not permit detection of dispersals exceeding 1350 m.

Comparative Dispersal Abilities of the Gerris Species

To make a comparison between the number of *G. buenoi* and *G. comatus* group dispersers, it is necessary to eliminate the bias of unequal sample sizes of the source populations. This is done by calculating an "adjusted" number of G. buenoi dispersers. If macropters of both G. buenoi and G. comatus group disperse at the same rate, one could expect the following to be true:

$$\text{if } p(\text{Gb dispersers}) = p(\text{Gc dispersers})$$

then:

$$\frac{\text{N Gb dispersers}}{\text{total N Gb}} = \frac{\text{N Gc dispersers}}{\text{total N Gc}}$$

and

$$\text{N Gb dispersers} = \frac{\text{N Gc dispersers}}{\text{total N Gc}} \times \text{total N Gb}$$

The value of N Gc dispersers can then be used as an index of the expected number of G. buenoi dispersers if the proportion dispersing is the same in the two species. This adjusted number of dispersers can then be compared statistically to the observed number of G. buenoi dispersing. If there are fewer observed than adjusted Gb dispersers, this indicates that G. comatus group disperses at a greater rate than does G. buenoi. Conversely, if the observed number exceeds the adjusted number of dispersers, then G. buenoi disperses at a greater rate.

Figure 11 shows the adjusted and observed number of G. buenoi dispersers for 1986 and 1987. Comparisons between the observed and adjusted number of G. buenoi dispersers were made using a paired design to eliminate the effect of time. Over the entire 1986 sampling period, the number of G. buenoi dispersers observed was significantly less than the adjusted number (mean difference = -1.267, t = -1.985, df = 20, $p < 0.05$). When spring and summer/fall samples were analysed seperately, it was found both seasons had significant differences between observed and adjusted number of dispersers (spring: mean difference = -2.684, t = -2.714, df = 8, $p < 0.05$; summer: mean difference = -2.031, t = -1.880, df =11, $p < 0.05$) In 1987, the adjusted number of dispersers was significantly greater than the observed number of dispersers (mean difference = -9.895, t = -2.400, df = 5, $p < 0.05$). This means that G. comatus group individuals disperse at a proportionately greater rate than do G. buenoi individuals. Close inspection of Figure 11 reveals an interesting pattern. The observed number of dispersers is greater in spring 1986 and spring 1987. This indicates once again that G. buenoi is dispersing primarily in spring, but less so at other times of the year. Based upon the adjusted number of dispersers, G. comatus group disperses throughout the season, but less so during July and August.

2. Indirect Assessment

Residence Time

Residence time is the duration an individual is known to be present at a site. This variable is influenced by two factors; mortality and dispersal. If mortality among various groupings is constant, then differences in residence time between the groupings could be attributable to differences in dispersal abilities. This method of assessing dispersal has been used for the stream-dwelling waterstrider G. remigis (Fairbairn 1985b, 1986). However, analysis of residence times for the gerrids in this study failed to show any consistent patterns between 1986 and 1987 and revealed no association between residence times and the direct evidence of dispersal. In these species, residence times appear to be influenced primarily by high and variable mortality rates and thus cannot be used to indicate dispersal.

Site Choice

As the temporary sites within the study area are dry for most of the year and do not support breeding populations even in spring, the gerrids found on those sites in spring must be immigrants. Therefore, the species composition of the temporary habitats should reflect the relative dispersal abilities of the component species.

The numbers of G. comatus group and G. buenoi present at temporary and permanent sites were compared for the weeks that temporary habitats were available (Table 11). The number of the two species on sites 1,2,3,4 and all ephemeral sites combined were analysed. It was found that the ratio of the two species was contingent upon site: G. comatus group was more commonly found on temporary sites, while G. buenoi was more commonly found on permanent sites in both years. These findings support the actual recorded movement results (Figure 11). G. comatus group, during the spring dispersal period, is more common on temporary sites than is G. buenoi and can thus be assumed to possess greater dispersal abilities than G. buenoi.

Spring Recapture Success

We have seen that dispersal occurs primarily in spring, and that G. comatus disperses more than G. buenoi. Based on these facts, it is expected that the relative proportions of recaptured, overwintered individuals should differ between the two species. The number of recaptures must be considered as a proportion of the previously marked individuals.

Table 5 shows the number of marked individuals in

1986 and subsequent 1987 recaptures, by site, for *G. buenoi* and *G. comatus* group. Significantly more *G. buenoi* were recaptured than *G. comatus* group (M-W test; $U = 9$, $U_{0.05(1)3,3} = 9$, $p < 0.05$). This supports the hypothesis that *G. comatus* group disperses more frequently than does *G. buenoi*.

DISCUSSION

The results of this study indicate that the dispersal ability of macropte[illegible] associated with the proportion macropterous as p[illegible]ted by Fairbairn and Desranleau (1987). This study suggests that dispersal capacity of macropters as assessed by flight threshold (Fairbairn and Desranleau 1987) reflects dispersal ability under natural conditions. Furthermore, this study presents new information concerning wing morphology, voltinism, and population dynamics of the gerrids present at Morgan Arboretum.

The objective of studying the population dynamics of these species was to describe changes in density that would indicate voltinism and ascertain the productivity of the species over the season. Unbiased estimators of population size are required to accurately track density changes. Mark-recapture methods of population estimation have been used in previous studies of gerrid populations (Brinkhurst 1966; Vepsalainen 1971; Matthey 1976; Zimmermann et al. 1982; Fairbairn 1985a+b, 1986). When a number of consecutive samplings are performed, Southwood (1978) advocates use of the Jolly-Seber method of population estimation. Such a method was used by Fairbairn (1985a+b, 1986) in studies of Gerris remigis . However, J-S estimates are inaccurate if trappability is low and/or turnover in the population is high. Both over- and underestimates could result, creating false trends in population size.

In this study, the J-S estimates are not very accurate, as indicated by the large standard errors. This inaccuracy appears to be due primarily to the rapid turnover rate relative to the sampling interval. Generally, median residence times in the present study were less than 7 days, and frequently less than 3 days. Fairbairn (1985b), whose J-S estimates were considerably more accurate than mine, reports overall median residence times of between 5 and 16 days at different sites for G. remigis . Therefore, in comparing Fairbairn's (1985b) median residence times to those in this study, it is apparent that residence times are noticeably lower in this study. These low median residence times, when combined with the large numbers of new individuals captured in various samples, result in a high turnover rate.

It is because of this inaccuracy in J-S estimates that I also present Minimum Number Alive values. Minimum Number Alive, as the name implies, is a consistent underestimator of the population size. However, it does provide a reliable lower boundary for the estimate of population size and is not likely to give false trends in the population dynamics. Jolly-Seber methods can lead to false trends in the population dynamics. An example of this taken from my results is for G. comatus group at site 3. Here, the first two J-S estimates in 1986 are gross overestimates (based upon MNA as a lower boundary of the population size) with incredibly large standard errors. Because the J-S estimates may be unpredictably biased, while MNA is always a negative bias, MNA values may be more accurate than J-S estimates.

Bivoltinism was observed for G. buenoi at all permanent sites in 1986. The non-diapause generation adults were recruited in late June and early July at all sites. Spence and Scudder (1980) found that non-diapause individuals, as identified by pale venter pigmentation, comprised a partial generation for G. buenoi in British Columbia. Although venter colour was not a reliable indicator of non-diapause individuals in my study, the possiblity that the non-diapause generation was only a partial one cannot be excluded.

Under such a situation, SW individuals would be considered the non-diapause generation and LW individuals the diapause generation, as seen for the European species G. odontogaster (Vepsalainen 1971). The diapause generation adults continued to be recruited until October at all sites.

For G. comatus group, a bivoltine life cycle was recorded at site 3 only. Here, a partial non-diapause generation (SW individuals) was recruited in late June and early July. At site 3, the diapause G. comatus group individuals continued to be recruited until October. At the other two permanent sites, G. comatus group exhibited a univoltine life cycle. Pre-diapause individuals were recruited from late June to late August. Unlike site 3, at sites 1 and 2, G. comatus group individuals were not recruited in September or October. In comparing voltinism among sites for G. comatus group, we can suggest that voltinism has a certain plasticity and is modified by local conditions encountered.

Success of a population can be measured in terms of increasing population size over the season. If a population is to be self-sustaining, a large pre-diapause population should be present to counteract effects of overwinter mortality and emigration. For G. buenoi , only at site 1 did the population become progressively larger from April to September. In other words, at this site, the pre-diapause population was larger than either the non- or the post-diapause population. At site 1, the G. buenoi populations could be self-sustaining. At sites 2 and 3, the pre-diapause populations were the smallest. Because the number of new recruits during this period was relatively low, it is unlikely that these low pre-diapause populations are the result of macropters emigrating to overwinter sites shortly after maturation. Also, as the post-diapause populations are larger than pre-diapause populations, there must be considerable immigration during the October-April period. Thus, for sites 2 and 3, the population is not self-sustaining because new immigrants are necessary to re-establish the species on these sites.

For G. comatus group, only site 3 exhibits a pattern of population sizes where the pre-diapause portion is largest. At sites 1 and 2, pre-diapause populations were smallest. Once again, macropterous emigration to overwinter sites is not believed to greatly influence the apparent size of the pre-diapause populations because numbers of new recruits were especially small at sites 2 and 3 in summer and fall. This suggests that, as for G. buenoi, new immigrants are necessary for re-establishing G. comatus group on some sites after diapause.

A pattern of increasing population sizes over the season appears typical of many other gerrid, as well as non-gerrid populations. In studies of _G. remigis_ in Canada (Matthey 1976; Fairbairn 1985b), _G. buenoi_ , _G. comatus_ , _G. pingreensis_ and _Limnoporus_ spp. in western Canada (Spence and Scudder 1980), _G. lacustris_ in Switzerland (Zimmermann et al. 1982) and _G. najas_ in England (Brinkhurst 1966), pre-diapause populations were larger than post-diapause populations. Furthermore, the same pattern was observed for a lady-beetle population (Hirano 1985) and a whirligig beetle population (Svensson 1985).

The patterns of population size at sites 2 and 3 for _G. buenoi_ and at sites 1 and 2 for _G. comatus_ group indicate that productivity is reduced through the year. As noted earlier, mortality, as indicated by median residence time, appeared to be quite high in this study. I believe that predation is a major cause of mortality for waterstriders at Morgan Arboretum. There is a wide diversity and large number of potential gerrid predators. Frogs of various species are common at all sites throughout the seasons. On a number of occasions, frogs were observed eating gerrids. Gerrids were also seen to be eaten by spiders, by _Notonecta_ spp. and by waterscorpions (Nepidae). Other potential predators include newts, dytiscid and hydrophilid beetles and perhaps insectivorous birds. Spence (1986) found adult and nymphal populations of <u>G. buenoi</u> to be limited primarily by predation. He observed that the predators included notonectids, <u>Aeshna</u> spp., and <u>Dolomedes</u> spiders, while shore-birds and other vertebrates were possible predators. Furthermore, the results of Spence and Scudder (1980) indicate that predation of nymphs is an important factor limiting populations of <u>G. pingreensis</u> , <u>G. buenoi</u> , <u>G. comatus</u> and <u>Limnoporus</u> spp. in British Columbia.

Species success at a given site is probably also influenced by various biotic and abiotic factors in addition to predation. One abiotic factor that can be considered is habitat structure. Although all the gerrids in this study inhabit lentic habitats, finer-grained selection appears to occur for all species. <u>L. dissortis</u> was consistently captured on one permanent pond (site 2) and on ditches (sites 20 and 21). Surprisingly, given that <u>L. dissortis</u> is reported to inhabit temporary habitats (Calabrese 1977, Spence and Scudder 1980; Spence 1981), few captures of this species were made on ephemeral sites. This may be a result of <u>L. dissortis</u> dispersing later in the spring, after ephemeral sites have become dry. Jamieson (1973) and Spence (1983) indicate that <u>Limnoporus</u> exhibits delayed reproduction relative to Gerris species. Such a habit may result in delayed dispersal as well. Nonetheless, it appears that ditches are the common habitat for L. dissortis at Morgan Arboretum.

G. buenoi was very successful at site 1, but less so at other permanent sites. G. buenoi is reported to be associated with habitats containing little open water but much emergent and floating vegetation (Brooks and Kelton 1967; Maynard 1969; Calabrese 1977; Spence 1981, 1983; Hilsenhoff 1986). Site 1 is a small pond with much emergent vegetation compared to the other sites in this study. Site 1 appears to be the most productive G. buenoi habitat among the permanent sites.

G. comatus group was most successful at site 3. This success was in terms of population size as well as occurrence of a partial non-diapause generation. Spence (1981, 1983) and Hilsenhoff (1986) both indicated that G. comatus was associated with larger ponds and lakes with open water. Calabrese (1977) indicated that G. comatus was associated with emergent vegetation (not floating or overhanging), G. marginatus was found in ponds and streams, and that G. insperatus was associated with habitats void of vegetation. Site 3 has little aquatic vegetation of any sort and a large open-water area. This would be favourable to the G. insperatus component of the G. comatus group. Other sites have less open water and, concomitantly, more emergent and floating vegetation. The other sites were definitely not as productive for G. comatus group.

As noted earlier, the patterns of population size indicate that immigration is high for the post-diapause population. Proportions of 1986-marked individuals recaptured in the same site in spring 1987 were between 0.0 and 0.14. This means that spring immigration is very important. For G. buenoi at site 1 and G. comatus group at site 3, spring recapture success was 0.023 and 0.004, respectively. Thus, even if pre-diapause populations are large, post-diapause immigration is an important factor influencing the success of a population at a given site for these species.

These observations indicate that the populations are sustained by considerable spring immigration. Productivity through the season is seriously reduced by high mortality, which seems to be mostly the result of predation. The apparently high rate of post-diapause immigration indicates that these species are ideal for studying relative dispersal abilities of different species and the seasonal patterns of dispersal.

The analysis of dispersal in this study revealed that gerrids in the G. comatus group tend to disperse more than G. buenoi. This advantage is primarily in terms of proportion dispersing rather than distance dispersed. Furthermore, this difference occurred primarily among post-diapause individuals. In fact, over 80% of all dispersal for both species occurred in spring. Unfortunately, sample sizes were too small for *L. dissortis* to be included in the analyses of dispersal.

The occurrence of dispersal primarily in spring as observed in this study is similar to that reported by Landin and Vepsalainen (1977) for several European species. Also, although not quantified, several other authors have suggested dispersal in gerrids to be primarily a post-diapause phenomenon (Brinkhurst 1959; Vepsalainen 1971, 1974; Andersen 1973; Spence 1981, 1983). In a study of dispersal tendency in the laboratory, Fairbairn and Desranleau (1987) determined that pre-diapause, non-reproductive individuals were more likely to fly than post-diapause, reproductive individuals. As Fairbairn and Desranleau did not begin sampling until May for most species (pers. comm.), compared to April 1 as I did, it is possible that post-diapause, non-reproductive individuals were excluded from their study.

Although movements exceeding 1350 metres could not be measured, I believe that I assessed long-distance dispersal. Taylor (1978) used a general equation to describe the density decline of dispersers over distance (Figure 12). In comparing the observed frequency distribution of movement distances by both G. buenoi and G. comatus group (Figure 10) to the theoretical distribution (Figure 12), one can see the observed distribution most closely resembles the asymptotic portion of the theoretical distribution. The asymptote of the theoretical distribution represents long-distance dispersal. Both G. buenoi and G. comatus group had similar movement distance distributions. That the two Gerris species did not differ in dispersal distance is significant because it indicates that variation in flight duration may not be as important a factor in gerrid dispersal as it seems to be for milkweed bugs (Dingle 1965, 1966, 1985).

The difference in dispersal ability between G. buenoi and G. comatus group is seen in two characteristics; the proportion of dispersers and the use of ephemeral habitats. First, because ephemeral habitats are discontinuous in time and space and waterstriders are poor terrestrial locomotors (Bowden 1978a+b), appearance of gerrids on these sites must be due to dispersal by flight. Thus, the fact that G. comatus group was more common on ephemeral sites than G. buenoi implies that G. comatus group has greater dispersal abilities.

Second, as most dispersal occurred during the period that both Gerris species were fully macropterous, the difference in proportion dispersing between the two species reflect differences in the flight capacity of the macropterous morph. Vepsalainen (1971, 1978) developed an argument suggesting that the dispersal capability of a species is based only upon the proportion of macropterous individuals present at the time of dispersal. The results of this study are different because I found that, although in spring all individuals of G. buenoi and G. comatus group are macropterous, there are variations in the dispersal abilities of those individuals as reflected in the difference in proportion dispersing. In other words, not all macropterous individuals are equally capable of dispersal. This supports the general hypothesis that the dispersal ability of the macropterous morph is variable, and in the Gerridae, is correlated with proportion macropterous.

Based upon the hypothesis of a photoperiodic-switch determinant of wing morphology (Vepsalainen 1971, 1974, 1978; Andersen 1973), it is expected that SW individuals will be among the early recruits to the non-diapause population. This was observed for G. buenoi at all permanent sites. However, for G. comatus group, SW individuals were recorded at site 3, but not at the other two permanent sites. The SW G. comatus group individuals at site 3 were all captured in the early portion of the non-diapause generation.

This study has shown that the observed dispersal ability of macropterous Gerrids under natural conditions is correlated with the proportion macropterous within the species, as predicted by Fairbairn and Desranleau (1987). Our results further indicate that the laboratory flight thresholds used by Fairbairn and Desranleau (1987) do reflect dispersal capacity under natural conditions for these species. The differences in dispersal ability of the species studied are not in terms of differences in flight duration, but are in terms of habitat choice and proportion dispersing among macropters in the spring.

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TABLE 1

General Characteristics of the five species of Gerridae in this study. (Modified from Fairbairn and Desranleau 1987)

Species	L. *dissortis*	G. *comatus*	G. *marginatus*	G. *insperatus*	G. *buenoi*
alary morphism	monomorphic macropterous (1,2,5,7)	seasonally dimorphic (2,4,5,7)	monomorphic macropterous (7)	monomorphic macropterous (7)	seasonally polymorphic (7)
% macropterous	100 (7)	70+ (summer) (7)	100 (7)	100 (7)	50 (summer) (7)
phenology	univoltine or partially bivoltine (7)	bivoltine (7,8)	bivoltine (7)	?	bivoltine (7)
preferred habitat	temporary habitats, small ponds, lakes, streams, (1,2,3,6,7,9)	temporary habitats, small ponds, lakes (3,6,7,9)	temporary habitats, small ponds, streams, lakes. (6,7,9)	temporary habitats, small ponds, lakes (6,7,9)	temporary habitats, small ponds, lakes (1,6,8,9)

1. Blatchley (1929); 2. Brooks and Kelton (1967); 3. Cheng and Fernando (1970); 4. Scudder (1971); 5. Calabrese (1974); 6. Calabrese (1977); 7. Calabrese (1979); 8. Spence and Scudder (1980); 9. Hilsenhoff (1986).

TABLE 2

Descriptions of sample sites and total number of G. *buenoi* and G. *comatus* group marked at each site within Morgan Arboretum September 3 1985 to June 7 1987.

Site	Type	N *Gb*	N *Gc* +	Duration * (date observed dry) 1986	1987	Max. Area (m)
1	pond	3760	688	p	p	1650
2	pond	2119	889	p	p	3265
3	pond	716	948	p	p	3190
4	quarry	332	781	27/06	20/06	7385
5	puddle	25	26	23/04	15/04	35
6	puddle	16	35	19/04	15/04	6200
7	pond	4		p	p	19545
8	puddle	39	29	16/05	29/04	15
9	puddle	12	18	23/05	29/04	10
10	puddle	39	31	30/04	15/04	25
11	puddle	48	41	i	i	10
12	puddle	9	15	06/05	16/04	15
13	ditch	5	1	09/06	29/04	5
14	puddle	3	8	16/05	21/04	25
15	puddle	17	22	16/05	21/04	10
16	ditch	104	107	i	i	15
17	puddle	9	16	30/04	21/04	15
18	puddle	13	8	16/05	21/04	45
19	puddle	27	31	30/04	15/04	25
20	ditch			i	14/07	90
21	ditch			i	14/07	75

* p = permanent
i = intermittent
\+ species assemblage

TABLE 3

Preliminary tests of the effect of marking on survival and flight of waterstriders.

	G. buenoi		G. comatus	
	marked	control	marked	control
median survival in days	87	87	79	63
Mann-Whitney test comparing marked and unmarked survival	U= 119.5 n= 20 U crit = 181 p> 0.20		U= 99.5 n= 32 U crit = 77 p< 0.001	
proportion to fly	0.22	0.17	0.25	0.33
	(n=36)		(n=9)	
median flight threshold	10	10	10	10
Mann-Whitney test comparing marked and unmarked flight thresholds	U= 198.5 n= 32 U crit = 236 p> 0.20		U= 11 n= 10 U crit= 19 p> 0.20	

TABLE 4

Total number of *L. dissortis* marked by site.

site	number
1	80
2	236
3	21
4	11
8	1
11	13
16	13
20	55
21	12

TABLE 5

Proportion of individuals recaptured in spring at same permanent sites as last captured in the previous fall. Does not include individuals captured on temporary sites.

		Site 1	Site 2	Site 3
	N in fall	1712	274	50
G. buenoi	recaptured	40	8	7
	proportion	0.023	0.029	0.140
	N in fall	156	170	865
G. comatus	recaptured	0	0	3
	proportion	0.000	0.000	0.004

TABLE 6

Total number of new recruits by season for *G. buenoi* and *G. comatus* group at permanent sites in 1986 only.

Site	Season	G. *buenoi*	G. *comatus* group
1	spring	324	236
	summer	622	142
	fall	1655	13
2	spring	384	283
	summer	664	157
	fall	272	15
3	spring	156	288
	summer	192	541
	fall	50	194

TABLE 7

Jolly and average Maximum Trappabilities for waterstriders at sites 1 to 4, 1986-1987.

		G. *comatus* group			G. *buenoi*			
		Ap-Jn 1986	Jl-Oc 1986	Ap-Jn 1987	Ap-Jn 1986	Jl-Au 1986	Se-Oc 1986	Ap-Jn 1987
Site 1	Jolly Trap.	0.235	0.458	0.367	0.217	0.219	0.366	0.256
	X̄ Max. Trap.	0.843	0.934	0.938	0.829	0.801	0.909	0.951
Site 2	Jolly Trap.	0.380	0.508	0.437	0.340	0.457	0.600	0.328
	X̄ Max. Trap.	0.857	0.934	0.918	0.729	0.930	0.963	0.899
Site 3	Jolly Trap.	0.315	0.720	0.458	0.352	0.490	0.510	0.368
	X̄ Max. Trap.	0.726	0.908	0.778	0.752	0.919	0.823	0.817
Site 4	Jolly Trap.	0.509	-	0.285	0.431	-	-	0.158
	X̄ Max. Trap.	0.910	-	0.902	0.832	-	-	0.955

TABLE 8

Median residence times in days for waterstriders at Morgan Arboretum, 1986. Sample sizes are given in table 6.

	G. buenoi	G. comatus
site 1		
spring	1.2	0.9
summer	0.9	-
fall	0.7	0.8
site 2		
spring	2.4	1.7
summer	0.9	-
fall	2.0	0.8
site 3		
spring	7.3	5.4
summer	1.7	-
fall	1.5	3.0

Table 9

Summary statistics of ambient, water-surface and water temperatures (°C) at primary study sites.

Site		ambient	water-surface	water
1	$\bar{x}$	18.4	18.8	18.5
	s	2.56	2.38	2.38
	n	27	27	27
2	$\bar{x}$	18.1	17.3	17.6
	s	2.62	3.36	2.33
	n	27	27	27
3	$\bar{x}$	17.9	17.2	15.5
	s	2.51	2.33	2.30
	n	27	27	27
4	$\bar{x}$	16.0	16.9	16.9
	s	2.13	2.36	2.34
	n	10	10	10

TABLE 10

Number of dispersers for all species at all sites in 1986 and 1987 at Morgan Arboretum

Generation	*L. dissortis*		*G. buenoi*		*G. comatus*	
	m	f	m	f	m	f
spring 86	4	1	20	19	33	31
summer 86	-	-	1	3	-	-
fall 86	-	-	5	4	5	5
spring 87	2	4	34	26	34	36

comparisons between sexes for number of dispersers

	L.d.	G.b.	G.c.
1986	$\chi^2 = 0.90$	$\chi^2 = 0.00$	$\chi^2 = 0.03$
1987	$\chi^2 = 0.33$	$\chi^2 = 0.53$	$\chi^2 = 0.03$

critical (0.05), df= 1 = 3.841
$p > 0.25$ in all comparisons

Table 11

Total numbers of *G. comatus* and *G. buenoi* newly caught on all sites for weeks that temporary sites supported waterstriders in 1986 and 1987.

	1986						
Site	1	2	3	4	eph.	temporary*	permanent+
Gc	204	180	186	200	387	587	570
Gb	255	317	194	34	109	143	766
p(Gb)	0.556	0.638	0.511	0.145	0.220	0.196	0.573

$\chi^2 = 291.61$ df= 4
$p < 0.001$

$\chi^2 = 288.82$ df= 1
$p < 0.001$

	1987						
Site	1	2	3	4	eph.	temporary*	permanent+
Gc	80	146	210	149	115	264	436
Gb	493	235	140	70	79	149	848
p(Gb)	0.861	0.617	0.400	0.320	0.361	0.361	0.660

$\chi^2 = 320.03$ df= 4
$p < 0.001$

$\chi^2 = 120.73$ df= 1
$p < 0.001$

* site 4 plus ephemeral sites.

\+ sites 1-3.

Figure 1. Map of study area at Morgan Arboretum.

MORGAN ARBORETUM

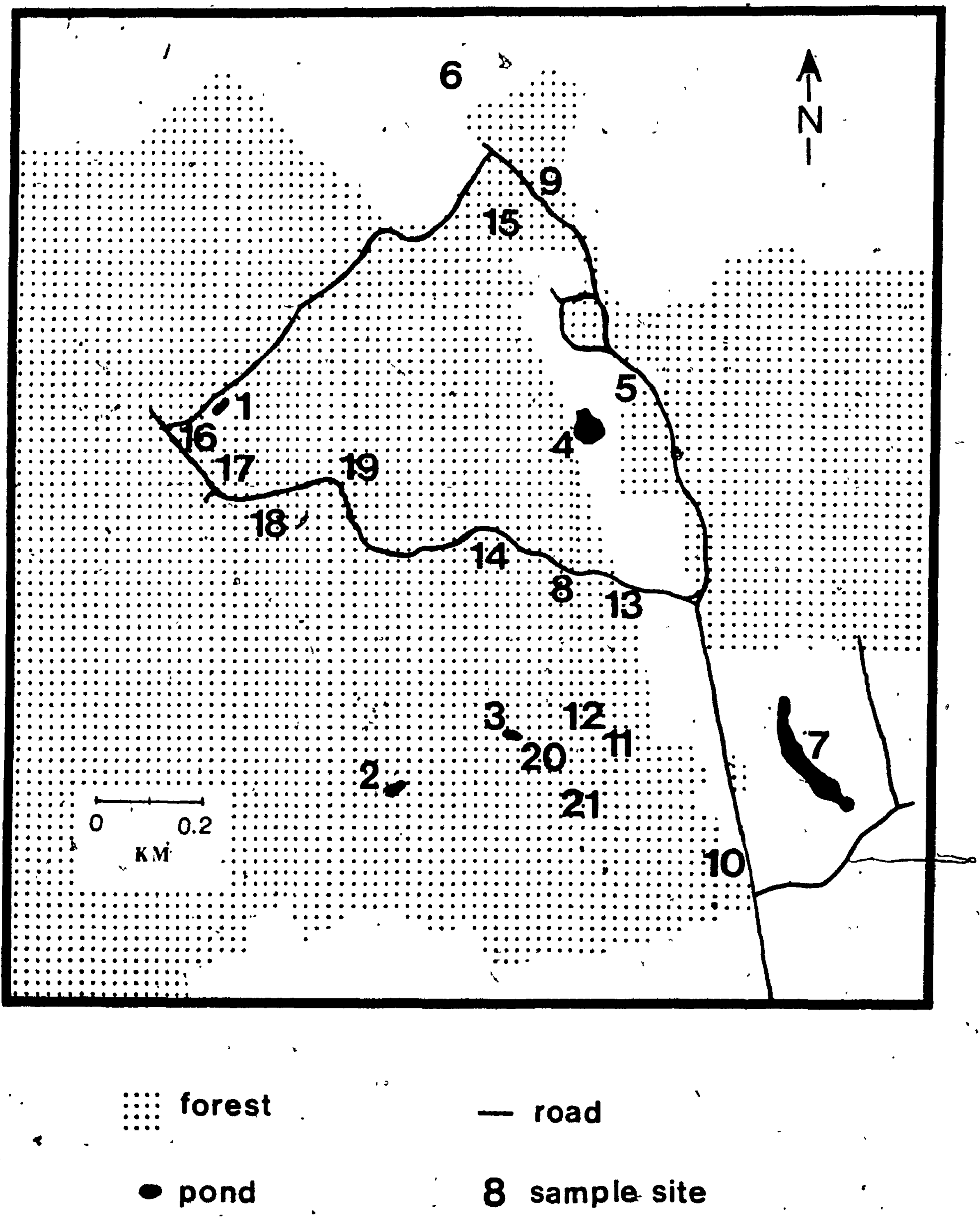
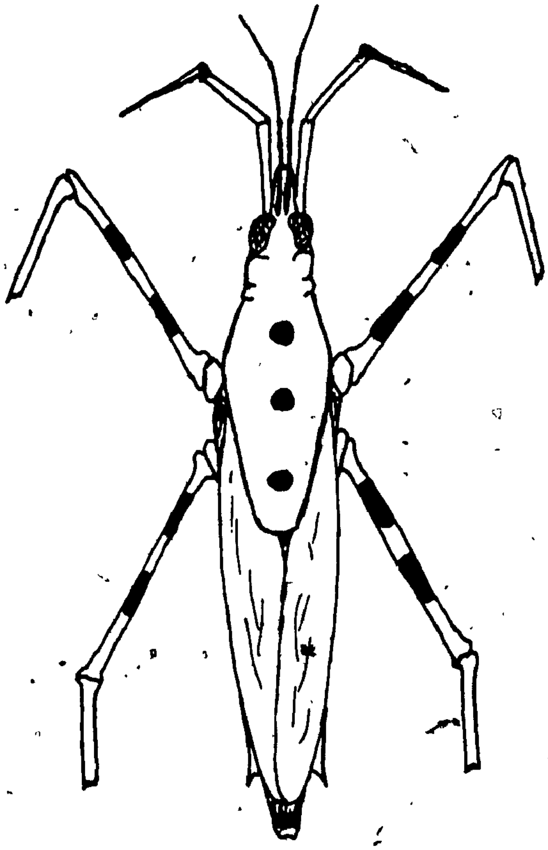
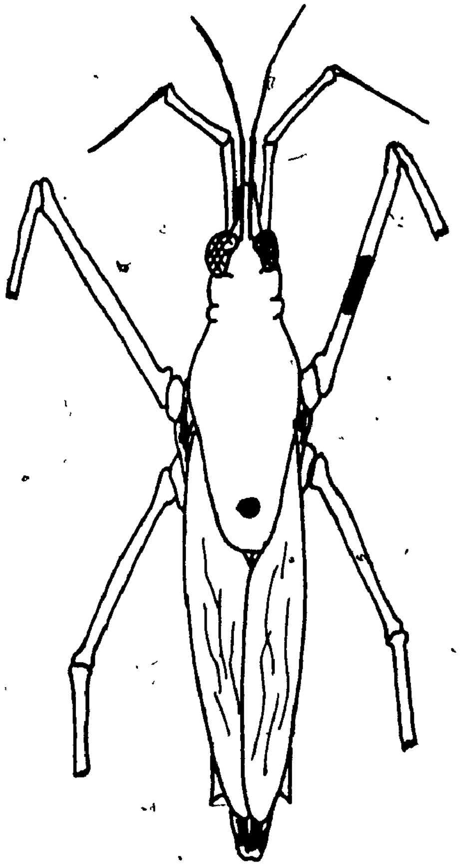


Figure 2. Example of position of marks used on waterstriders.



100



42

Figure 3. Jolly-Seber (+/- S.E.) and Minimum Number Alive estimates for G. buenoi at study area: a) site 1, b) site 2, c) site 3, d) site 4.

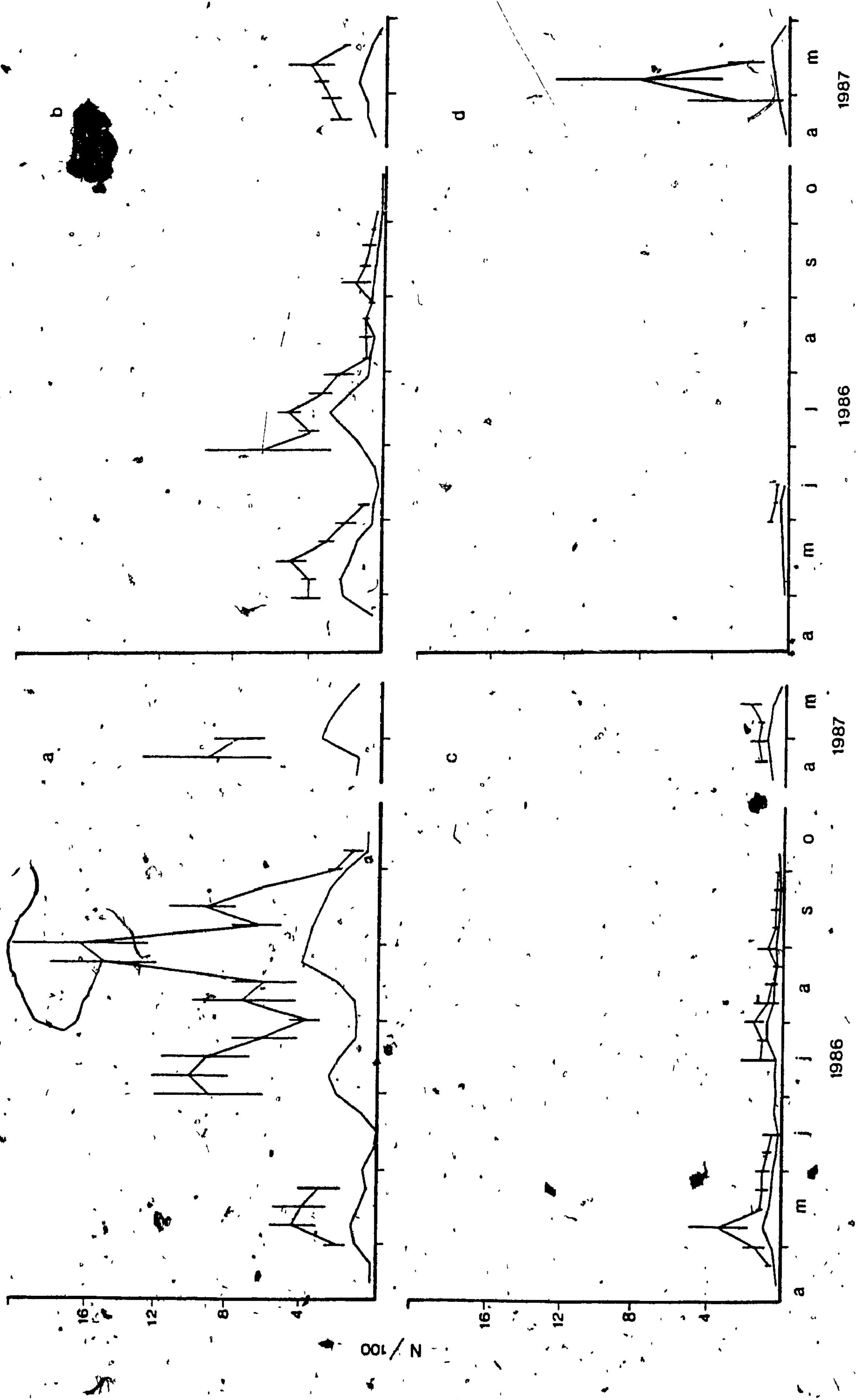

a
b
c
d
N / 100
16
12
8
4
a
m
j
j
a
s
o
a
m
1986
1987

Figure 4. Jolly-Seber (+/- S.E.) and Minimum Number Alive estimates for G. comatus group at study area: a) site 1, b) site 2, c) site 3, d) site 4.

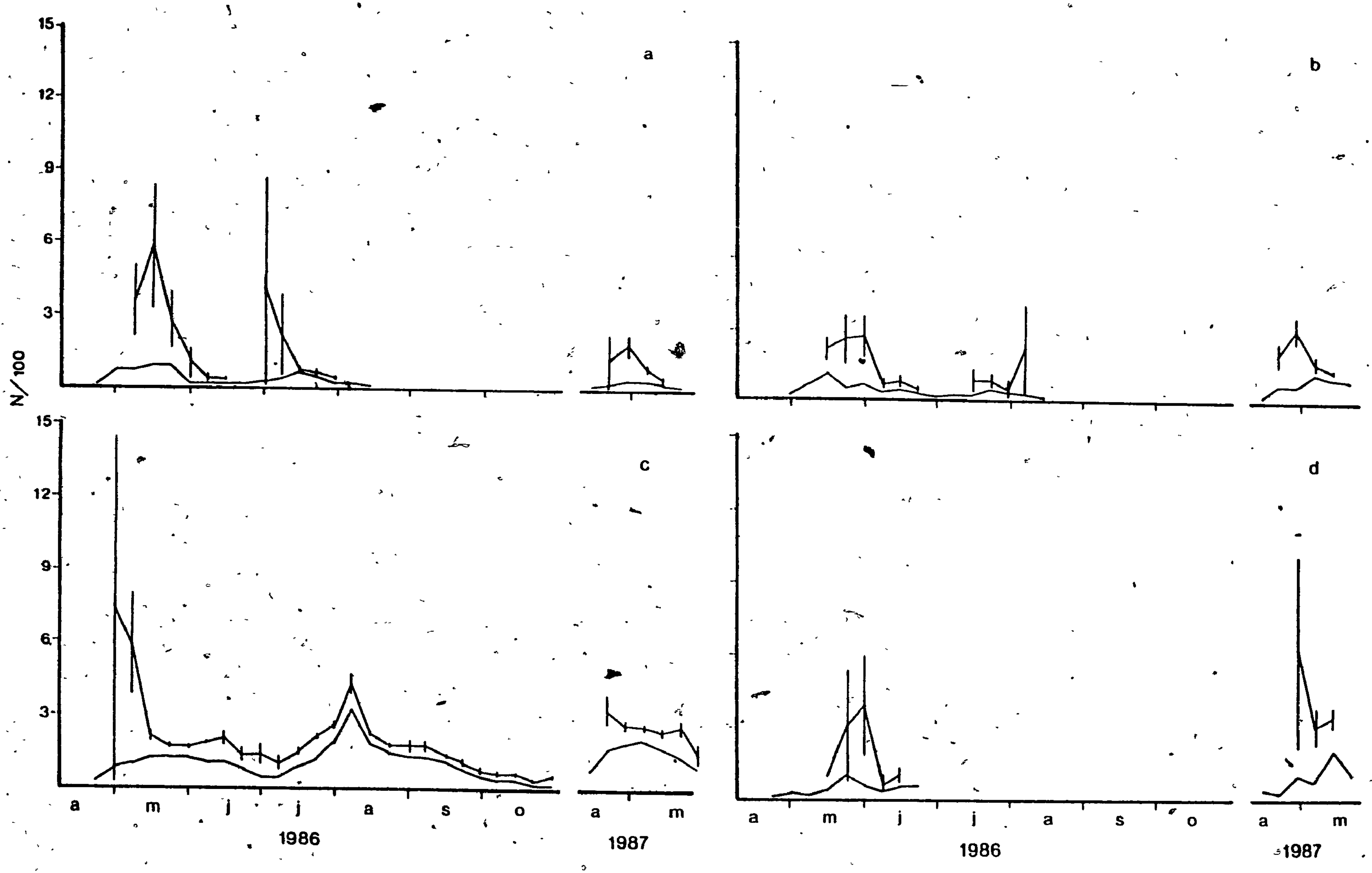

N/100
15
12
9
6
3
a
b
c
d
a
m
j
j
a
s
o
1986
a
m
1987
a
m
j
j
a
s
o
1986
a
m
1987

Figure 5. Median residence times for G. buenoi macropters in 1986 at: a) site 1, b) site 2, c) site 3, d) site 4.

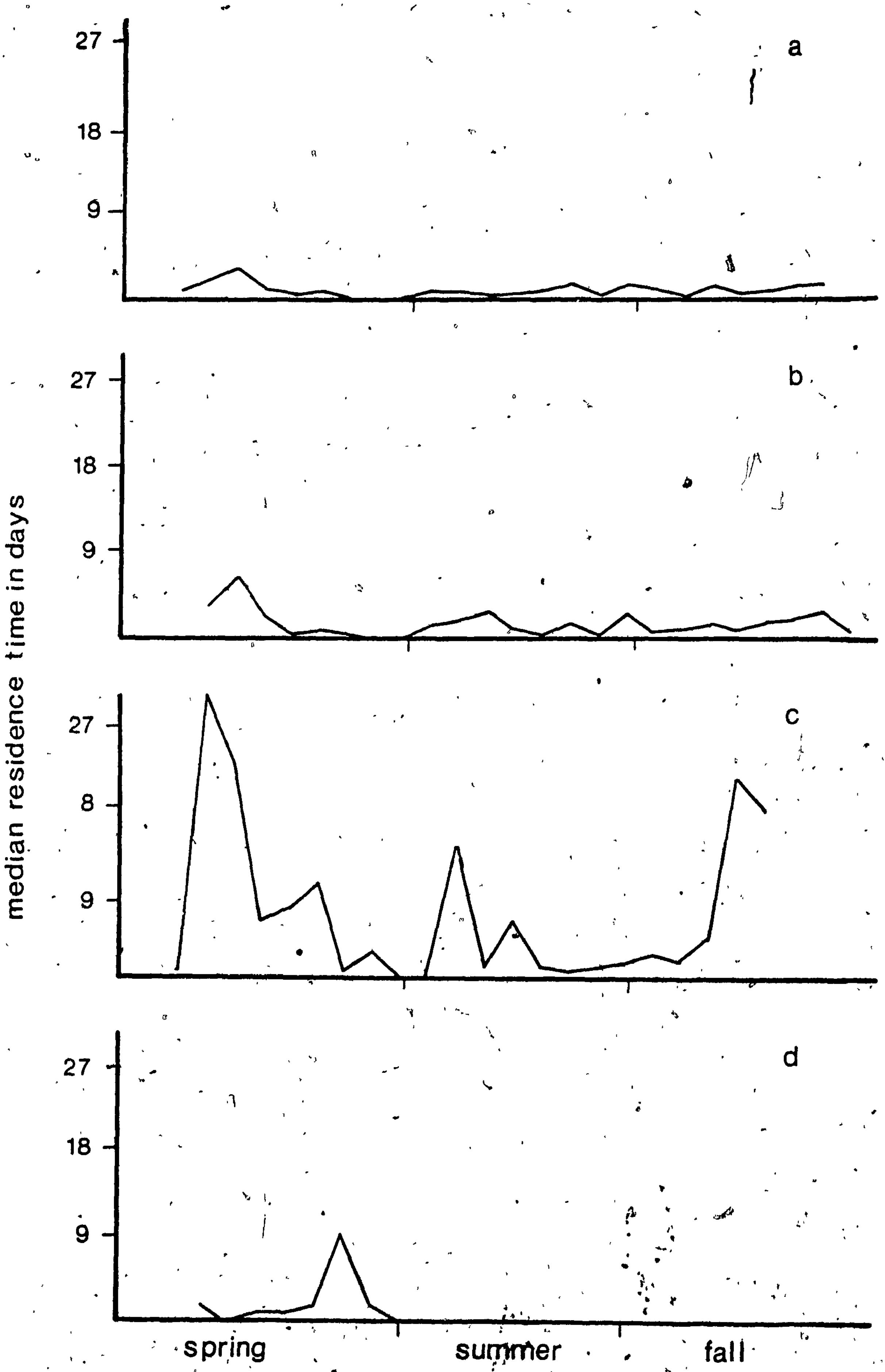

median residence time in days
a
27
18
9
b
27
18
9
c
27
8
9
d
27
18
9
spring
summer
fall

Figure 6. Median residence times for G. *comatus* group macropters in 1986 at: a) site 1, b) site 2, c) site 3, d) site 4.

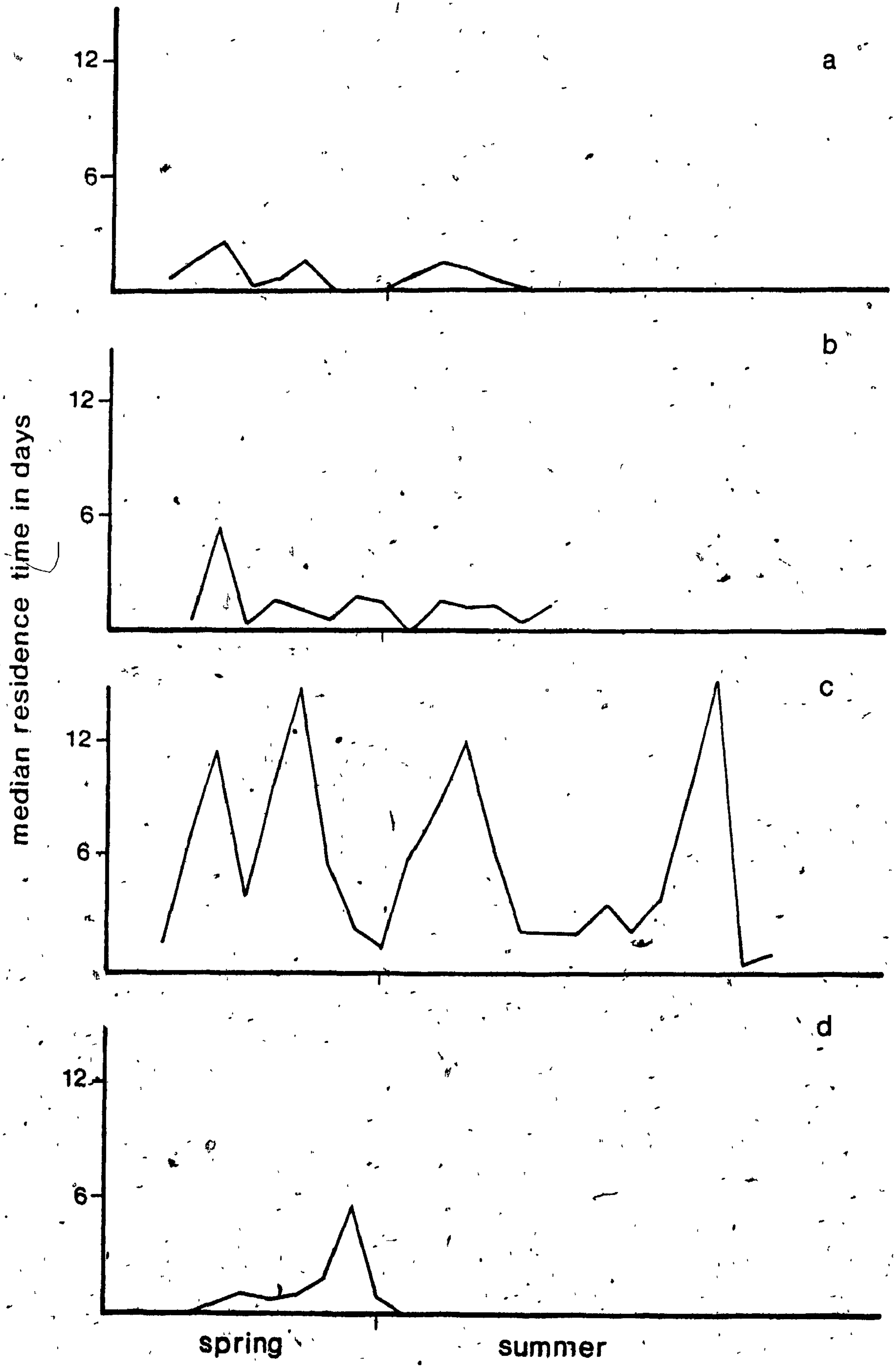

a
12
6
b
12
6
c
12
6
d
12
6
median residence time in days
spring
summer

Figure 7. Proportions of wing reduced G. buenoi by week of first capture in 1986 at: a) site 1, b) site 2, c) site 3.

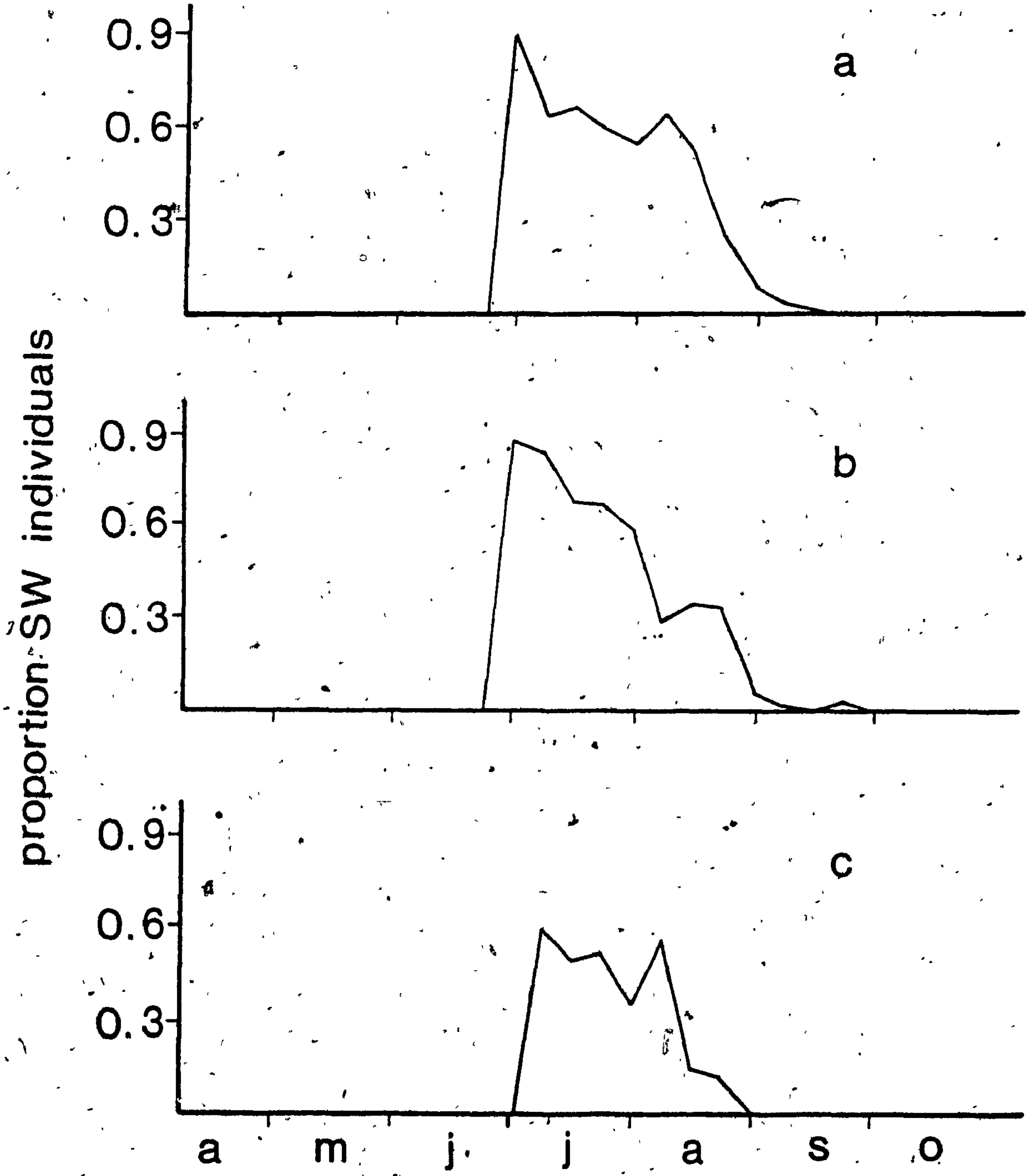

proportion SW individuals
0.9
0.6
0.3
a
0.9
0.6
0.3
b
0.9
0.6
0.3
c
a
m
j
j
a
s
o

Figure 8. Proportion of wing reduced G. <u>comatus</u> group by week of first capture in 1986 at site 3.

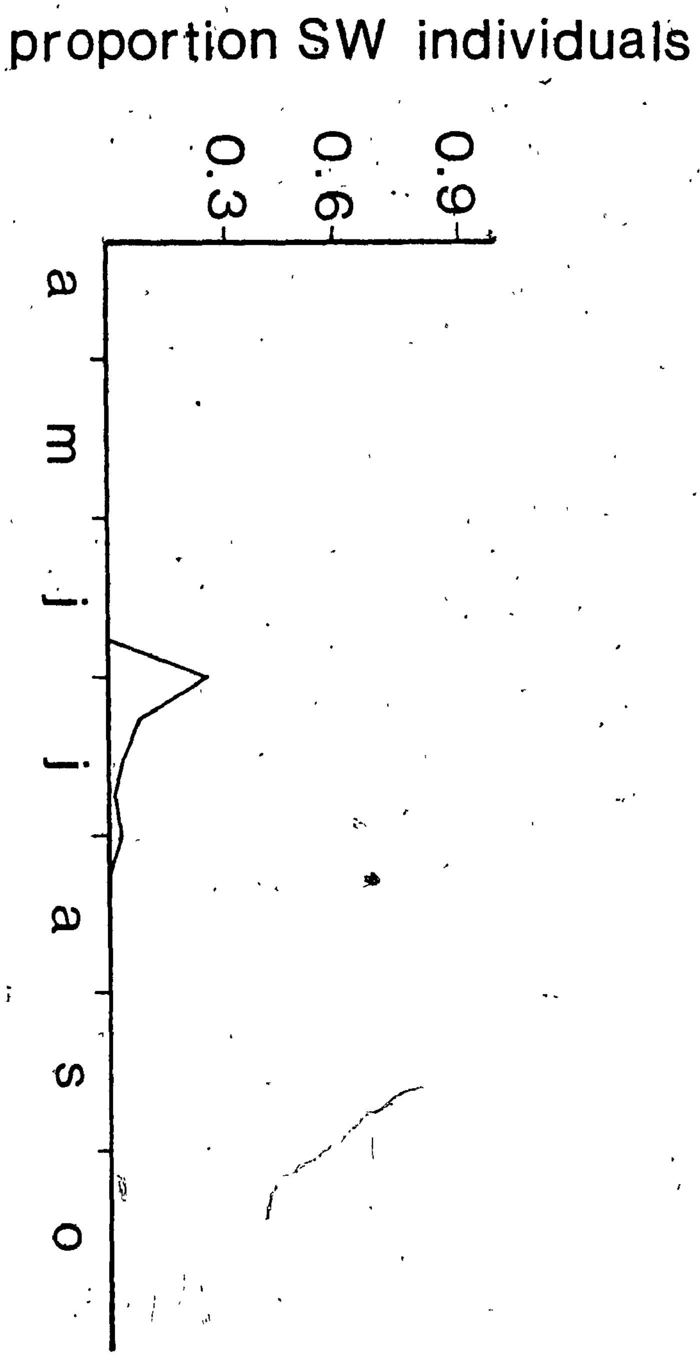

proportion SW individuals
0.9
0.6
0.3
a
m
j
j
a
s
o

Figure 9. Total number of marked L. dissortis by week of first capture at all sites in 1986.

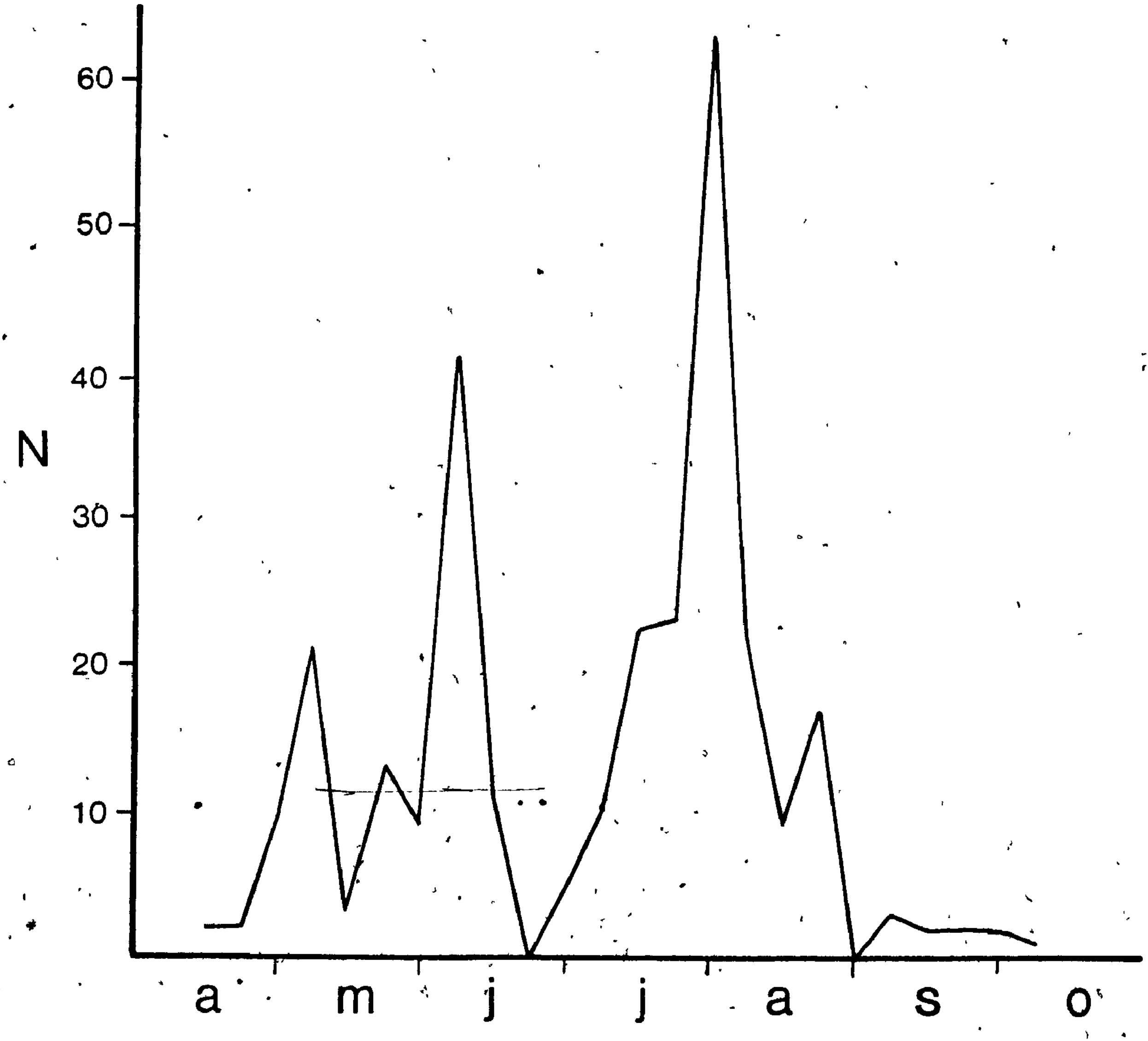

60
50
40
N
30
20
10
a
m
j
j
a
s
o

Figure 10. Relative frequency distribution of dispersal distances for G. _buenoi_ and G. _comatus_ group from September 3 1985 to June 7 1987.

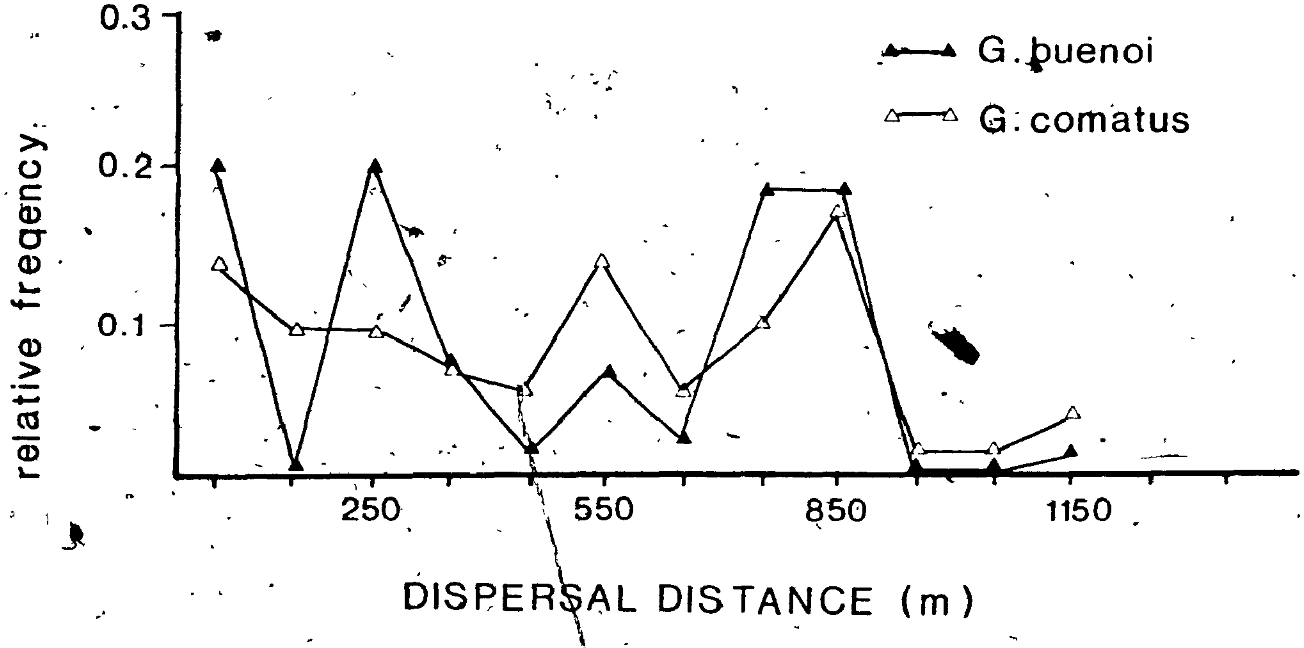

0.3
0.2
0.1
relative freqency
250
550
850
1150
DISPERSAL DISTANCE (m)
G. buenoi
G. comatus

Figure 11. Observed and adjusted number of G. <u>buenoi</u> migrants over all sites within the study area.

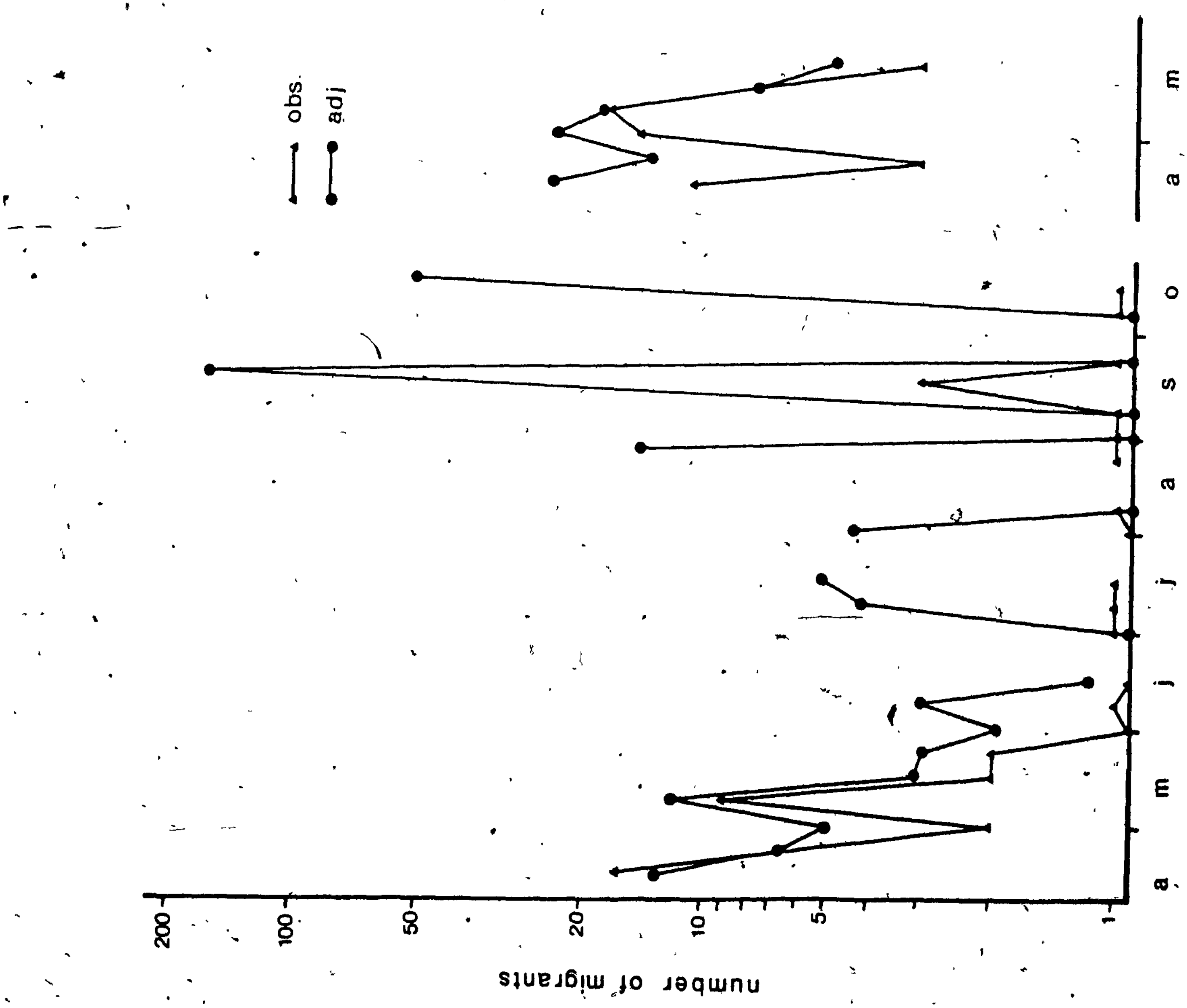
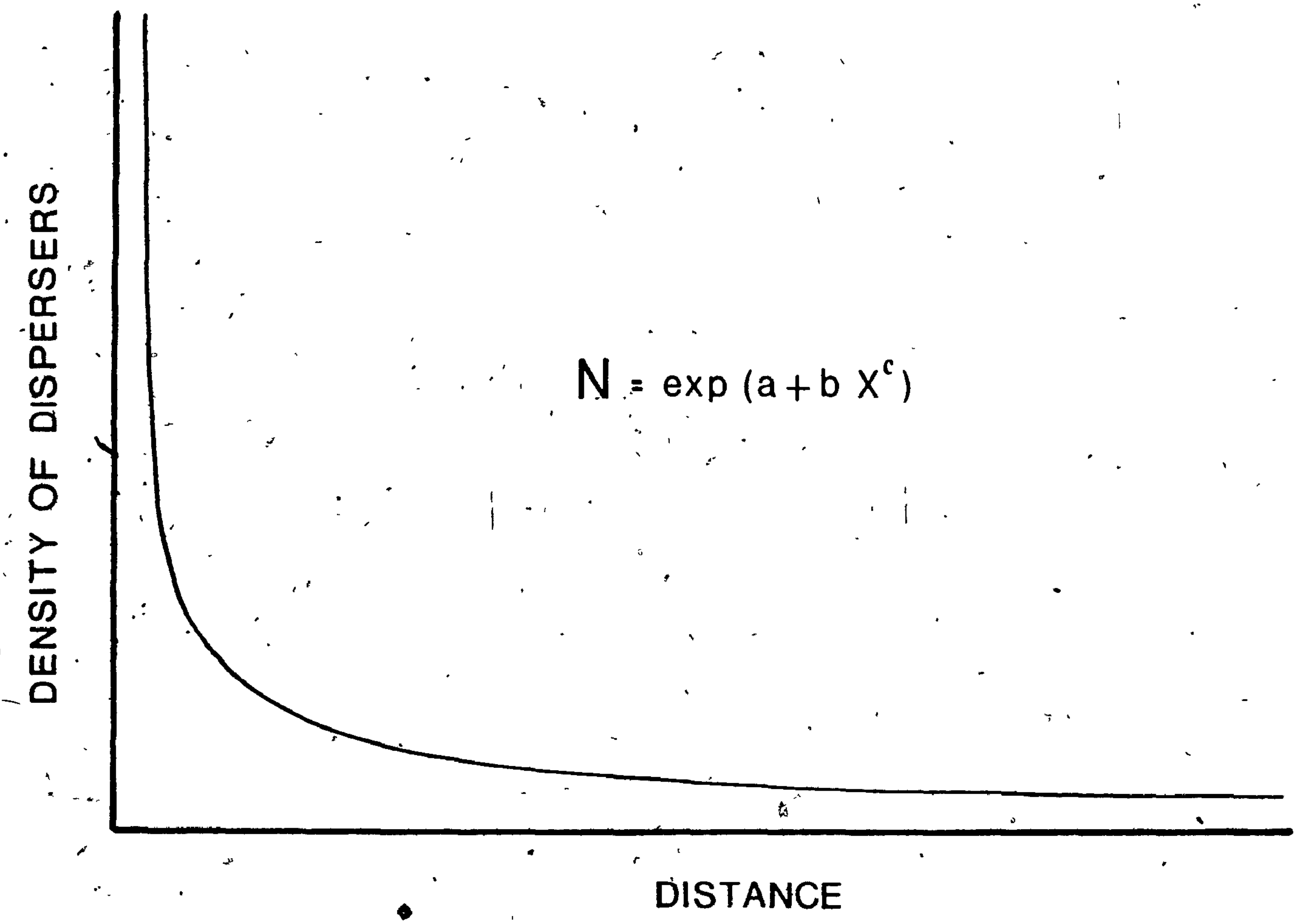

obs.
adj
200
100
50
20
10
5
1
number of migrants
a
m
j
j
a
s
o
1986
a
m
1987

Figure 12. Theoretical distribution and arithmatic model describing density of dispersers away from a central source. Model and graph derived from Taylor (1978).


N = exp (a + b X^c)
DENSITY OF DISPERSERS
DISTANCE

Appendix I

Explanation of formulae used in population estimates.

1. Jolly-Seber population estimate:

$\hat{N}$ = population estimate at time i

n = total number captured at time i

r = total number of marked individuals recaptured at time i
$\hat{M}$ = estimate of the total number of marked animals in the population at time i
a = total number of animals released at time i

R = number of animals released at time i and subsequently recaptured
Z = number of animals released previously, not captured at time i, but subsequently recaptured

2. Minimum Number Alive:

N = population size at time i

n = total number captured at time i

z = number previously marked not captured at time i, but subsequently recaptured