Journal of Ecology 1998, **86**, 1021–1031

Spatial and temporal variation in population size of *Eichhornia paniculata* in ephemeral habitats: implications for metapopulation dynamics

BRIAN C. HUSBAND* and SPENCER C. H. BARRETT
Department of Botany, University of Toronto, Toronto, Ontario, Canada M5S 3B2

Summary

1 The annual plant *Eichhornia paniculata* occurs in discrete, ephemeral habitats formed by pools, wet ditches and flooded pastures in arid north-eastern Brazil. We conducted a large-scale geographical survey of populations four times over a 7-year period (1982–89) and measured population size, population persistence and patch occupancy. In total, 167 populations were censused.

2 To investigate the importance of local and regional influences on population size, we posed the following specific questions. Are fluctuations in population size independent of their initial size and independent among years? Is persistence uniform among populations of different size and age? Are the proportion of patches occupied related to the density of habitat patches in a region? What are the relations between the size, persistence and density of populations?

3 Population size averaged 86 over the 4-year period with 52% of populations containing less than 100 individuals. Sixty-four per cent of populations persisted from one year to the next, but the rate at which populations became absent from a patch was independent of initial population size and time since the last census. For populations that persisted, there was a significant positive correlation between the initial census number and their size in subsequent years.

4 In 29 transects through different regions of north-eastern Brazil, an average of 21.6% (range 3.8–47.2%) of suitable habitat patches were occupied by *E. paniculata*. The proportion of patches occupied was positively correlated with the density of patches in a region. No populations were found when the density of patches fell below 0.23 patches km^{-1} or 0.18 patches km^{-1} in 1988 and 1989, respectively, indicating the probable existence of a habitat threshold for species persistence within a region. There was no correlation between patch occupancy and either the average number of individuals per population or the probability of persistence in a region. Hence, even when *E. paniculata is* regionally common, it is not necessarily locally abundant.

5 We conclude that the distribution of *E. paniculata* populations in north-eastern Brazil is governed, in part, by metapopulation dynamics.

Keywords: aquatic, environmental stochasticity, metapopulation structure, population size, regional processes

Journal of Ecology (1998) **86**, 1021–1031

Introduction

Most organisms are not distributed uniformly in space, but occur in habitats that are patchily distributed across the landscape (Andrewartha & Birch 1954). In such species, local populations are finite and vulnerable to size fluctuations and extinction due to environmental variation and demographic stochasticity (Richter-Dyn & Goel 1972; Leigh 1981; Schaffer 1981; Ewens *et al.* 1987; Goodman 1987). Under these circumstances, the dynamics and persistence of patchily distributed species may depend on the existence of an array of interconnected populations (metapopulation), which are affected by regional processes such as migration and recolonization (Levins 1969,

---

*Present address: Department of Botany, University of Guelph, Guelph, Ontario, Canada N1G 2W1.

1970; Hanski 1985). An important question concerning patchily distributed organisms in ephemeral habitats is to determine the relation between the dynamics of local populations and their regional distribution. A necessary first step in addressing this question is to obtain detailed census information on the spatial and temporal patterns of variability in population size.

Beginning with the initial work on metapopulations by Levins (1969, 1970), several theoretical models have been developed to study the dynamics of single species in patchy environments and to examine the factors that account for their abundance or rarity (Hastings 1991; Hanski & Gilpin 1991; Hanski 1997). In these models, the geographical structure of populations varies along a continuum of patchiness, from discrete isolated populations to neighbouring patches within a single interbreeding population. In general, the models show that when local conditions within each patch are independent, regional processes may be particularly important in determining species persistence and abundance (Harrison & Taylor 1997). In species that consist of isolated patches with frequent local extinction, populations will occur in only a fraction of available habitats and their distribution can be predicted from knowledge of patch extinction and recolonization rates. Specifically, the more habitat patches there are available in a region, the higher patch occupancy rates are likely to be (Hanski 1985a; Lande 1987).

In species whose patches are less isolated, frequent migration may result in dampened fluctuations in local abundance leading to the long-term persistence of populations. This process has been referred to as the rescue effect and is likely to be prevalent in species with high patch occupancy rates (Brown & Kodric-Brown 1977). Despite the potential importance of interactions between populations for the persistence of species within a region, empirical studies of the regional and local patterns of population dynamics have been few and have primarily involved animal species (reviewed in Eriksson 1996; Hanski 1997; Harrison & Taylor 1997). Empirical studies of plants in a metapopulation context that have considered regional processes are few (see Hanski 1982; Nilsson *et al.* 1982; Carter & Prince 1988; Kadmon & Shmida 1990; Menges 1990) and, as yet, the relation between the density of populations in a region and the demographic characteristics of local populations has not been examined. A major objective of this study is to investigate these issues in an annual aquatic plant of ephemeral habitats.

Eichhornia paniculata (Spreng.) Solms. (Pontederiaceae) occurs in seasonal, aquatic habitats sparsely distributed throughout the arid interior of north-eastern Brazil (Barrett 1985). Only a small fraction of habitats are ever occupied by *E. paniculata* in any given year and population sizes vary widely both spatially and temporally as a result of frequent population bottlenecks (Barrett 1985; Husband & Barrett 1992a,b). In this study, we were interested in documenting the extent of this demographic variability by censusing large numbers of populations over several years. Here we address four specific questions concerning the size and spatial structure of *E. paniculata* populations in north-eastern Brazil: (i) Are fluctuations in population size independent of their census number and among years? (ii) Is persistence uniform among populations of different size and age? (iii) Are the proportion of patches occupied related to the density of habitat patches in a region? (iv) What are the relations between the size, persistence and density of populations?

Materials and methods

NATURAL HISTORY OF *EICHHORNIA PANICULATA*

Eichhornia paniculata is an emergent aquatic that occurs primarily in seasonal pools, ditches, and temporarily inundated pastures in north-eastern Brazil and the Caribbean islands of Jamaica and Cuba (Barrett 1985). In north-eastern Brazil, the species occurs in transient pools that are found along roadsides which traverse the caatinga, a region of thorn scrub and extreme aridity (Friese 1938). The seasonal, aquatic habitats occupied by *E. paniculata* are usually dry throughout most of the year but are replenished with water during the rainy season, which occurs primarily as concentrated but localized showers between March and May (Friese 1938). Rainfall in the caatinga is unevenly distributed both in space and time, and has one of the highest annual coefficients of variation in the world (Nimer 1972). Due to the unpredictable nature of habitats occupied by *E. paniculata*, populations behave primarily as annuals with only a narrow window of time suitable for germination, growth and reproduction. Although dispersal between habitats has not been quantified from direct observations, seed is likely to be transported through the movement of waterfowl and cattle and via flash floods that occur during the rainy season. Further details of the natural history and ecological genetics of *E. paniculata* in north-eastern Brazil can be found in Husband & Barrett (1992a,b, 1993), Barrett *et al.* (1989) and Barrett & Husband (1997).

POPULATION CENSUSES

We surveyed pools, ditches and flooded pastures in north-eastern Brazil in 1982, 1987, 1988 and 1989 in the states of Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe and Bahia. As most *E. paniculata* populations in north-eastern Brazil are associated with disturbed sites and transportation corridors, our surveys were conducted along road transects that were 50–100 m in width and between 29 and 300 km in length. Between 1500 and 4000 km of road were sampled each year. Populations encountered in each survey were censused and their locations recorded so they could be relocated in future surveys. Virtually all (96%) previously sampled populations were relocated each year for subsequent examination. A total of 167 populations were censused during the four surveys (for map see Fig. 1, Barrett & Husband 1997).

POPULATION SIZE

Population size (*N*) was estimated each time a population was sampled. A population comprised all individuals within a habitat patch, which was physically discrete from other pools or related wetland habitats. The estimate of size was based on at least two independent estimates of the number of reproductive individuals present within a patch. If a population contained less than 250 individuals, we censused the entire population. If it exceeded 250 individuals, population size was based on estimates of density and area of habitat. *Eichhornia paniculata* does not reproduce vegetatively and therefore individual genets could be readily distinguished. Most populations comprise a single cohort of plants that germinate and flower synchronously; therefore, a single visit was sufficient for estimating population size, and the number of flowering individuals was a reasonable estimate of the total number of individuals in a population. As in most surveys of plant population size, our definition of a population concerns the above-ground plants and did not include the seed bank. Populations of *E. paniculata* fluctuate dramatically from year-to-year and may often disappear from a site. The absence of populations results from drought, flooding and human disturbance. In this study we report on the presence and absence of populations without implying that absence from a site necessarily results from the complete local extinction of a population (see Discussion).

Since the population size distribution was skewed, the geometric mean was used to describe its central tendency and size distributions were illustrated by assigning populations to size classes based on a $\log_2$ scale. The distribution of population sizes was compared among years using a Kolmogorov–Smirnov two-sample test. In addition, a Spearman's rank correlation was used to determine whether the sizes of individual populations sampled over 1- and 2-year intervals were correlated (Sokal & Rohlf 1981).

POPULATION PERSISTENCE

In each survey, we relocated habitat patches sampled in previous years and determined whether individuals of *E. paniculata* were present. The annual probability of persistence, measured as the proportion of popu-

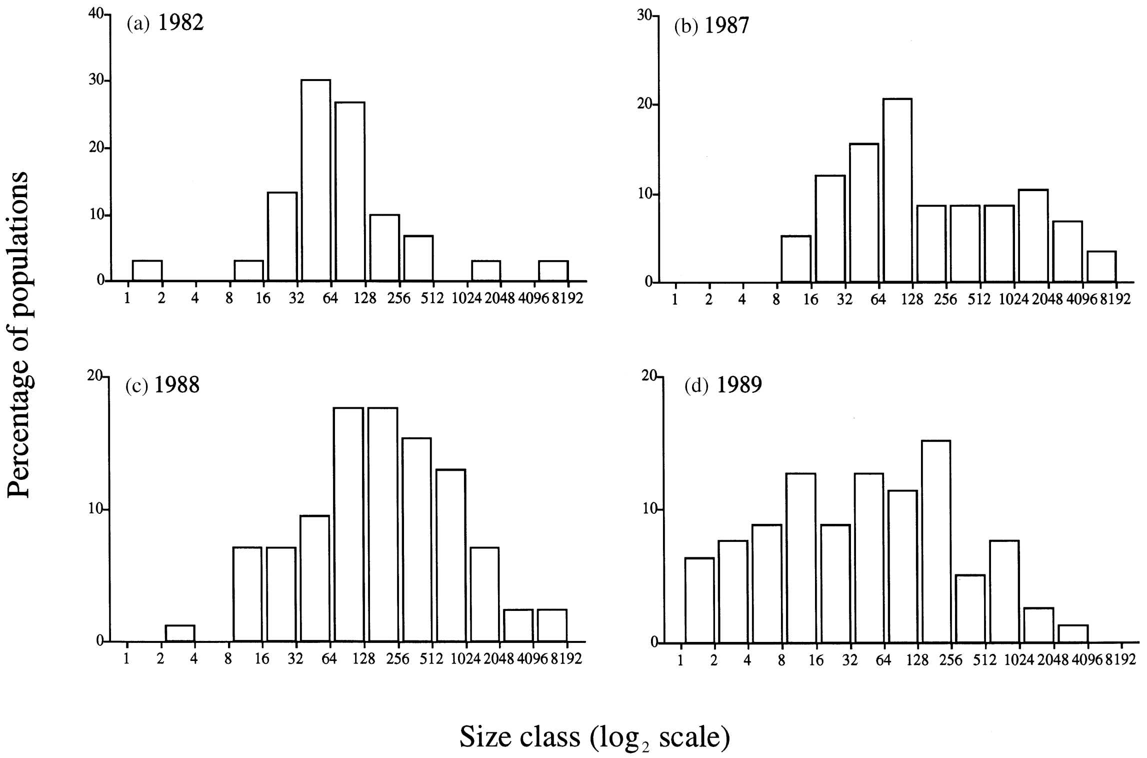

Fig. 1 Population–size distributions for *Eichhornia paniculata* surveyed during 1982–89 in north-eastern Brazil. Population size was measured from at least two independent estimates (or a complete census if the population had less than 250 individuals). Since size distributions are strongly skewed to the right, a $\log_2$ scale was used to normalize data. Only distributions from 1987 and 1989 are significantly different based on a Kolmogorov–Smirnov test ($P < 0.05$) (see Results).

lations present at time t that were still present at time $t+1$, was calculated for each 1-year interval and, averaged for all 1-year intervals combined. The annual probability of persistence between surveys in 1982 and 1987 was determined by solving for p in the formula $p^t = y/x$ where x is the number of sites occupied at time 0 and y represents those remaining after t generations. For this calculation we assumed that populations did not become absent and then reappear within the sampling interval. The value for the 1982–87 period was then included in the calculation of the average rate of persistence, weighted by the number of years it represents.

PATCH DENSITY AND OCCUPANCY

The spatial structure of *Eichhornia paniculata* populations was characterized by the density of populations (number per km of roadway) and the proportion of patches occupied throughout its geographical range in north-east Brazil. Patch occupancy was estimated by censusing occupied and empty habitat patches along roadways in 1989 and 1990. Empty patches were counted if they had the characteristics of a typical *E. paniculata* habitat This was possible to identify only because of the discrete aquatic habitats in which the species occurs. To minimize error in identifying sites we also used criteria such as size of pond (< 50 m diameter), water depth (< 1 m) and presence of indicator species in the following genera (*Heteranthera*, *Sagittaria*, *Hydrocleis*, *Nymphoides*, *Cyperus* and *Scirpus*). In total, we surveyed 720 patches along 1477 km of roadway in 1988 and 1244 patches over 3120 km of roadway in 1989. A second range-wide estimate of patch occupancy, based only on sites in which populations had occurred in the past, was also obtained from the 1988 and 1989 survey data. This second estimate can be viewed as a conservative measure of patch occupancy compared to the one described above, and avoids the potential for misclassification of unsuitable habitats as suitable for *E. paniculata*.

Interpreting estimates of patch occupancy based on a range-wide survey may be misleading because it is unlikely that all suitable patches are equally accessible and uniformly distributed throughout the range. In fact, the distribution of populations in *E. paniculata* consists of several geographically distinct clusters (Husband & Barrett 1995). Genetic analyses have shown that populations within a cluster are genetically more similar than those in different clusters. This pattern is consistent with the idea that most migration occurs within rather than between these regions (Husband & Barrett 1995). To examine regional patterns of patch occupancy, we examined the density of populations and the percentage of patches occupied within each of the 18 and 29 road transects surveyed in 1988 and 1989, respectively. In 1989, 18 of the initial transects were resurveyed, together with a further 11 regions. Because of their geographical and genetic distinctness, we consider each of the transects to represent a naturally occurring region that contains a semi-independent cluster of populations. Using these regions, we examined variation in the density of local populations and the relations between population size and persistence.

Results

POPULATION SIZE

Population size (N) in *E. paniculata* averaged 73.8, 177.2, 173.0 and 39.7 in 1982, 1987, 1988 and 1989, respectively. Mean population size for all surveys combined was 86. Of the populations sampled, 67, 46.5, 35.3 and 67.1% contained fewer than 100 individuals in 1982, 1987, 1988 and 1989, respectively, and 6.7, 20.7, 14.1 and 3.8% of populations contained more than 1000 individuals. Although there were small differences in the geographical area surveyed each year, all pair-wise comparisons of size distributions, with the exception of one, were statistically insignificant (Kolmogorov–Smirnov D, $P > 0.05$, Fig. 1). In the single exception, populations in 1987 were, on average, larger than in 1989 (Kolmogorov–Smirnov $D_{58,79} = 0.302$, $P < 0.05$, Fig. 1).

Individual populations that were censused in the last 3 years varied widely in size between 1987 and 1989 (Fig. 2). In the time interval 1987–88, 17 of 52

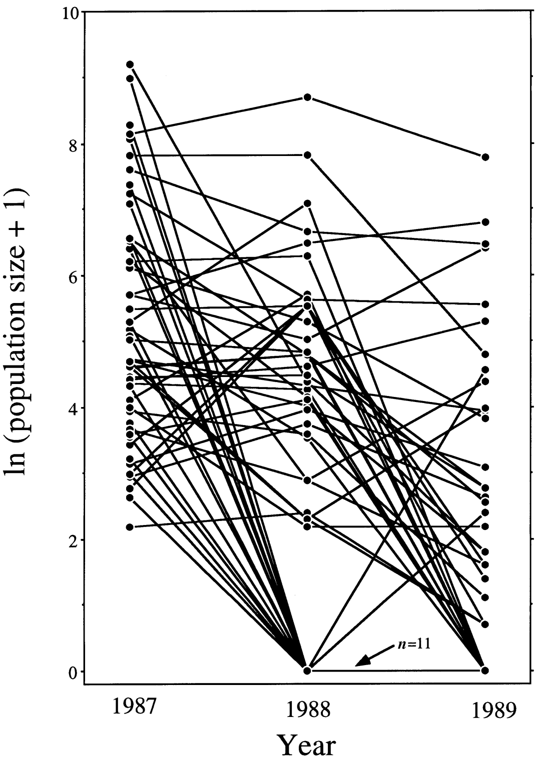

Fig. 2 Fluctuations in population size estimates (N) in 52 populations of *Eichhornia paniculata* monitored from 1987 to 1989 in north-eastern Brazil. Population size in one year was not statistically correlated with size in the next year.

populations increased in size, 34 decreased and one showed no change. From 1988 to 1989, seven populations increased, 15 remained the same and 30 decreased in size. For all populations censused, initial population size was not correlated with size in the next year (1987–88, $r_s = 0.089$, $P > 0.5$, $n = 52$; 1988–89, $r_s = 0.16$, $P > 0.25$, $n = 36$; all 1-year intervals combined, $r_s = 0.15$, $P > 0.15$, $n = 88$). However, if populations that were absent in the second census are removed, all three comparisons reveal a significant association (1987–88, $r_s = 0.43$, $P < 0.01$, $n = 36$; 1988–89, $r_s = 0.49$, $P < 0.05$, $n = 26$; all 1-year intervals combined, $r_s = 0.51$, $P < 0.001$, $n = 62$). Figure 3a illustrates these patterns for combined data for 1987–88 and 1988–89. A significant positive correlation was also found between the magnitude of change in population size, measured as ln population size in year 1 minus ln population size in year 2, and their initial size (Fig. 3b). This indicates that smaller populations were more likely to increase in size whereas larger populations more often decreased.

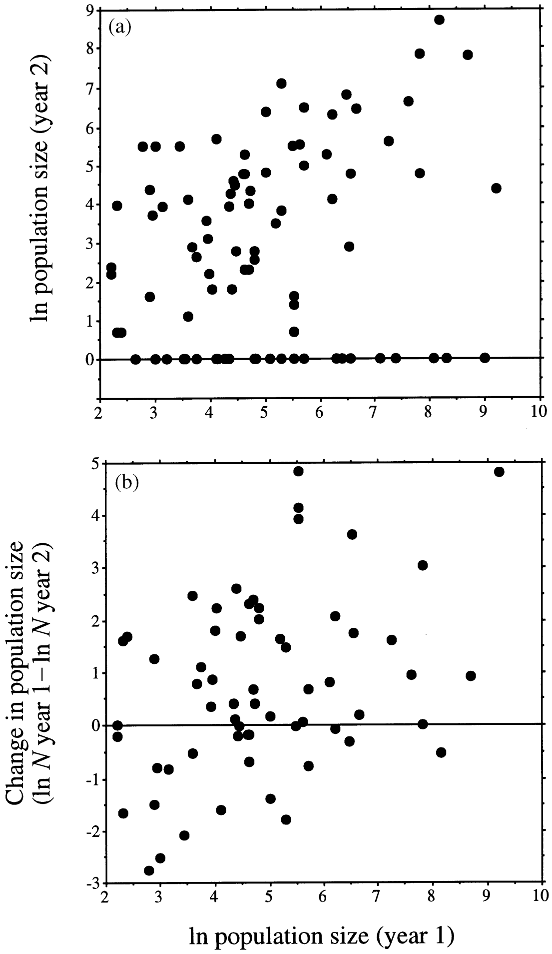

Fig. 3 Yearly changes in population size in *Eichhornia paniculata* in north-eastern Brazil. (a) Relation between ln population size in year 1 and year 2. (b) Relation between ln population size in year 1 and change in population size (ln size year 1 – ln size year 2) excluding populations absent in second year.

POPULATION PERSISTENCE

The probability that a population present one year would appear in the next was 0.66 (range = 0.75–0.53; Table 1). When the estimate was based only on data from 1988 and 1989, which had the largest sample sizes, the probability of persistence was 0.64. Populations that were present in 1987 but absent in 1988 tended to remain absent in 1989. For example, of the 52 populations monitored in 1987, 13 did not appear in 1988. Of these 13, 11 remained unoccupied in 1989 and two populations reappeared. The likelihood that a previously unoccupied patch remained empty was significantly greater than the probability that a previously occupied patch became empty (2 × 2 contingency test, $G = 17.2$, $P < 0.001$).

Whether a population persisted from one year to the next was unrelated to its initial population size. The distribution of sizes (N) for populations observed in 1987 and 1988 that were either present or absent 1 year later are presented in Fig. 4. In both years, the initial sizes of populations persisting were not statistically different from those that became absent (Logistic regression: 1988, Wald chi-square = 1.15, $P > 0.25$p; 1989, Wald chi-square = 0.55, $P > 0.25$). Furthermore, presence or absence of a population was not a function of the time since it was initially sampled. This is illustrated by a population persistence curve which represents the fraction of populations sampled at one point in time that remained present after increasing intervals of time (Fig. 5). For *E. paniculata*, the persistence curve was concave and, after 7 years, 10.3% of the original populations remained. The relation between the log population persistence and time is nearly linear, indicating that the probability of persistence is constant ($P = 0.65$) throughout at least the first 6 years, regardless of population age.

PATCH OCCUPANCY

Surveys of patch occupancy in 1988 and 1989 revealed a total of 207 (28.8%) and 179 (14.4%) patches,

Table 1 Persistence of *Eichhornia paniculata* populations at sites in north-eastern Brazil from 1982 to 1989. Sites throughout the geographical range were surveyed in each of 4 years and populations classified as present or absent. The number of sites differed among years depending on the geographical area surveyed. See Methods for further details

	1982	1987	1988	1989
Populations sampled	30	58	85	79
Sites from previous survey	–	29	52	77
Populations present	–	4	39	41
Populations absent	–	25	13	36
Annual probability of persistence	–	0.67	0.75	0.53

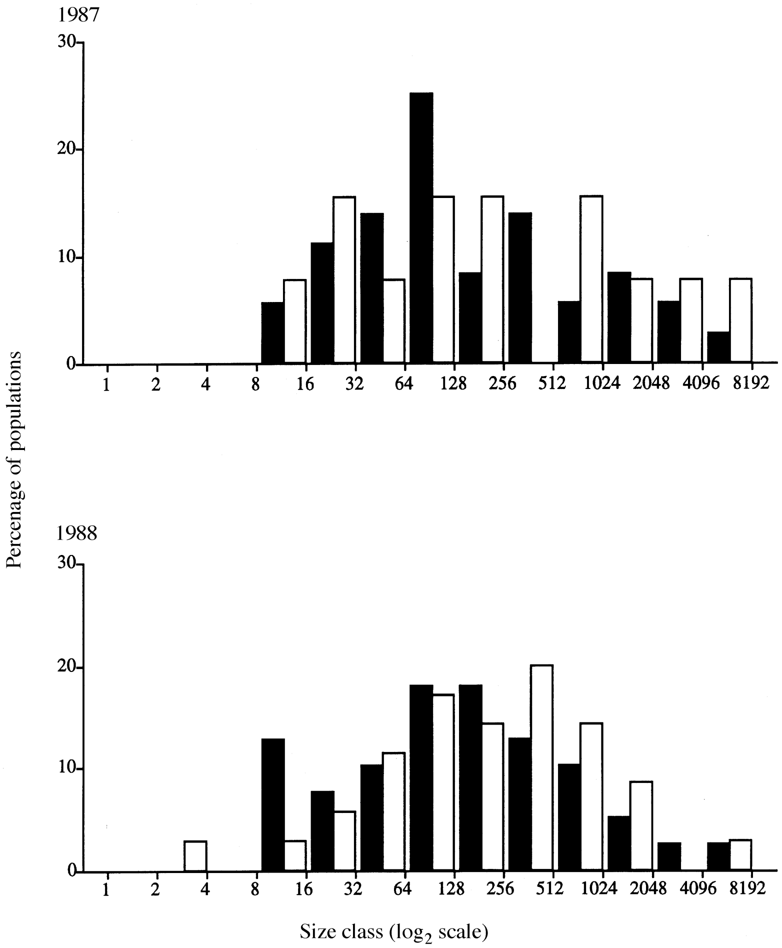

Fig. 4 Distribution of size (*N*) for populations of *Eichhornia paniculata* observed in 1987 and 1988 that were either present (open bars) or absent (filled bars) 1 year later.

respectively (mean = 21.6%), that were occupied by *E. paniculata*. As an independent measure of distribution across the entire range, we determined the proportion of patches that were occupied using only those patches that had been repeatedly visited and in which *E. paniculata* had been observed in the past. The patch occupancy values were 13.3% (4 of 30 previously occupied sites) for 1987, 42.8% (36 occupied of a total 84) in 1988 and 34.4% (45 of 131 sites) in 1989. The mean percentage of patches occupied (30.1) is somewhat higher than the estimate based on putatively suitable patches (mean 21.6).

Among the 29 regional road transects surveyed, the mean density of habitat patches ranged from 0.17 to 1.14 sites km^{-1} (mean = 0.42 sites km^{-1}). The density of sites in transects surveyed in two consecutive years (and with non-zero values) were statistically correlated except for two neighbouring regions (all sites $r_s = 0.172$, $P > 0.05$, $n = 18$; excluding two sites, $r_s = 0.76$, $P < 0.05$, $n = 16$). The density of *E. paniculata* populations among the 29 transects, averaged over 1988 and 1989 where resampled, ranged from 0.01 to 0.34 populations km^{-1} (mean = 0.08 km^{-1}). Patch occupancy ranged from 3.8 to 47.2% (mean = 20.6%). In both years there were transects in which none of the habitat patches were occupied, despite having pools that appeared suitable for establishment ($n = 1$ in 1988, $n = 3$ in 1989)

There was no significant correlation between patch occupancy of *E. paniculata* (number or density of sites occupied) and the average number of individuals per population among transects surveyed in 1988 or 1989 with a minimum of three populations (1988, *N* vs. Number occupied, $r_s = 0.02$, $n = 16$; *N* vs. Number occupied km^{-1}, $r_s = 0.01$, $n = 16$; 1989, *N* vs. Number occupied, $r_s = -0.13$, $n = 23$; *N* vs. Number occupied km^{-1}, $r_p = -0.13$ $n = 23$). Hence, when *E. paniculata* is regionally common, it is not necessarily locally abundant.

The density of local populations of *E. paniculata* was highly correlated with the density of suitable patches among the regions (1988, $r_s = 0.93$, $n = 18$, $P < 0.001$; 1989, $r_s = 0.90$, $n = 29$, $P < 0.001$, Fig. 6). Similarly, the percentage of patches occupied was positively correlated with the density of suitable patches (1988, $r_s = 0.44$, $n = 18$, $P = 0.07$; 1989, $r_s = 0.41$, $n = 29$, $P = 0.05$). The threshold density of sites required for *E. paniculata* to persist was similar in both years examined. No populations occurred when patch densities were less than 0.23 or 0.18 km^{-1} in

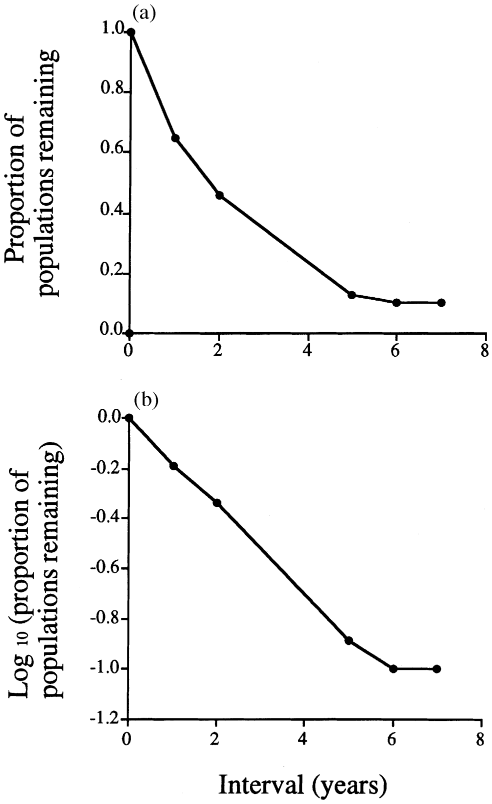

Fig. 5 Population persistence curve for *Eichhornia paniculata* populations sampled over a 7-year period in north-eastern Brazil. Each point represents the proportion of populations remaining after a given sampling interval. The same data, log-transformed, are shown to illustrate the constant rate of decline in population numbers during the sampling period.

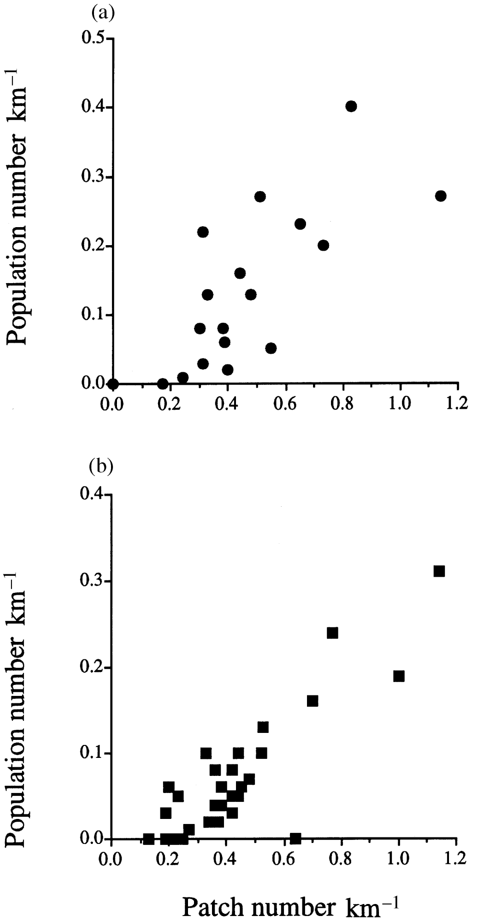

Fig. 6 Observed relation between population density and habitat patch density for *Eichhornia paniculata* among 18 and 29 regions sampled in (a) 1988 and (b) 1989, respectively.

1988 and 1989, respectively. When the 1988 and 1989 values are averaged for each region, the observed threshold level was estimated to be 0.22 sites km^{-1}.

Population persistence varied widely among regional transects. During the 1987–88 time interval, populations became absent in 9 of 14 regions surveyed. In 1988–89, populations became absent in 11 of 21 regions. For both time periods, population persistence ranged from 100 to 0% among regional transects. Persistence within each regional transect, over the 1988–89 period, was not dependent on the density of populations in a region (1988, $r_s = -0.13$, $n = 16$, $P > 0.50$; 1989, $r_s = -0.01$, $n = 21$, $P > 0.95$).

Discussion

The geographical distribution of *Eichhornia paniculata* in north-east Brazil is subdivided among many isolated habitats, which are ephemeral as a result of the unpredictable occurrence and duration of rainfall. Since *E. paniculata* is an aquatic and restricted to seasonal pools and roadside ditches, it is incapable of surviving in the surrounding dry caatinga vegetation. Such discrete spatial structure provides an opportunity to consider the demography of *E. paniculata* populations within a metapopulation context. While metapopulation concepts have broadened considerably since the original idea was formulated by Levins (1969), his model represents a benchmark by which empirical studies can be compared and hence we consider our results for *E. paniculata* within this framework. We begin our discussion by considering the role that environmental stochasticity plays in regulating population size in *E. paniculata* and then examine the importance of regional processes for the local population dynamics of this species. Since seed banks complicate the study of plant metapopulations (Husband & Barrett 1996), we also consider the role of seed dormancy in populations of *E. paniculata.*

POPULATION SIZE AND DISTRIBUTION

Annual censuses of *E. paniculata* indicated that populations contained an average of 86 individuals, and ranged in size from 3 to 10 000. Furthermore, sizes were skewed in distribution, with ≈ 50% of populations containing less than 100 individuals and only 3% over 1000. These demographic characteristics have important genetic and evolutionary consequences because genetic stochasticity (drift) and inbreeding are more likely to occur in small populations. The impact of genetic drift is likely to be stronger than these values indicate, as previous studies have revealed that the genetically effective population size (N_e) is about 10% of the census number (Husband & Barrett 1992a). The genetic effects of small population size and stochasticity in populations of *E. paniculata* have been demonstrated by the strong relation between population size and genetic loci governing isozyme and mating-type diversity (Husband & Barrett 1992b; Barrett & Husband 1997).

Populations of *E. paniculata* in north-east Brazil were separated from one another by 1–30 km, and therefore most recruitment probably involves individuals produced by matings within each population rather than by migration. Previous population genetic analyses indicate that while migration can occur, it is relatively infrequent, with the average population receiving the equivalent of one migrant every 3 years (Husband & Barrett 1995). In many species, the degree of population subdivision is insufficient for local extinction to occur because of recurrent migration (reviewed in Harrison & Taylor 1997). In contrast, populations of *E. paniculata* are significantly isolated from one another and this makes them particularly vulnerable to large size fluctuations and the possibility of local extinction.

Population size in *E. paniculata* in a given patch fluctuated widely from one year to the next. Moreover, size changes were asynchronous, with populations differing in the magnitude and direction of change for any given time interval. These size changes suggest that local dynamics are somewhat independent among populations, and therefore simultaneous extinction of the whole metapopulation through such factors as severe regional drought is extremely unlikely (Hanski 1997). Despite the seemingly random changes in population size, however, changes were not completely unpredictable. In patches occupied for at least two successive censuses, population size was correlated among years. Moreover, the magnitude of the change in population size over a 1-year interval was size-dependent. Large populations tended to decrease in size while, on average, small populations became larger. These patterns suggest that population size is determined, in part, by more deterministic forces. Although population size fluctuates widely and asynchronously among populations, the changes appear to occur within limits imposed by the size of the habitat and density-dependent interactions among individuals.

POPULATION PERSISTENCE

Censuses of 167 populations over a 7-year period indicated that populations of *E. paniculata* do not persist indefinitely, at least not as reproductive individuals. Populations present in one year have a 64% chance of reappearing the next year, with the remainder either becoming extinct or surviving in the seed bank. While we have no quantitative information on the relative importance of seed banks, several lines of evidence indicate that the absence of populations from a site most commonly results from true extinction. First, at many sites disturbance as a result of anthropogenic activity resulted in the loss of suitable habitat for *E. paniculata*. Secondly, preliminary studies in *E. paniculata* indicate that the duration of seed dormancy is limited, with the vast majority of seeds germinating within the first wet cycle provided (Husband 1992). Thirdly, field observations indicated that dormancy played an obvious role in only two patches observed in this study. In both cases, the populations reappeared in large numbers after being absent for a year. In all of the remaining sites, however, once a population was absent it remained so for the duration of the census period, despite in many cases suitable growing conditions. Notwithstanding these observations implicating limited seed dormancy, further empirical investigations into the contribution of dormant seed to metapopulation dynamics in *E. paniculata* are clearly required. This is especially important because seed dormancy is often well developed in plant species that occur in ephemeral habitats (Roberts & Feast 1973; Harper 1977).

How do rates of population loss in *E. paniculata* compare with other organisms in which this parameter has been examined through repeated censuses? Before we discuss this comparison, it is worth noting that most workers have interpreted the absence of a population in a particular location as resulting from extinction. However, because of the ambiguities introduced by seed banks in plants discussed above, we refer to this parameter in *E. paniculata* as the apparent extinction rate of populations. In *E. paniculata*, values for this parameter were high (0.36) compared to other species. Rates of population extinction in orb spiders (mean = 0.022, see Fig. 1 in Schoener & Spiller 1987), ambush bugs (0.033, Mason 1987), milkweed beetle (0.02, McCauley 1989) and the bay checkerspot butterfly (0.04–0.08, Harrison *et al.* 1988) are all considerably lower than for *E. paniculata*. Although our estimate of apparent extinction may be inflated owing to the role of seed dormancy in some populations, we suspect that values in this range may well be a feature of plants in ephemeral environments subject to environmental stochasticity. Studies involving temporal censuses of population size in plants from unpredictable environments are needed to assess this hypothesis (for example, see Menges & Gawler 1986).

The rate of apparent extinction in *E. paniculata* was uniform across populations of all size classes. This is in marked contrast to the prevailing assumption of most theoretical models concerned with metapopulation dynamics (Leigh 1981; Hanski 1985b) as well as empirical observation from animals such as spiders (Toft & Schoener 1983; Schoener & Spiller 1987), birds (Williamson 1981; Jones & Diamond 1976), island lizards (Schoener & Schoener 1983) and ambush bugs (Mason 1987). In these groups, extinction rates are negatively correlated with population size and this pattern has usually been interpreted as resulting from demographic stochasticity. In *E. paniculata*, demographic stochasticity may play less of a role because of the overriding impact of local environmental variation associated with drought, flooding and human disturbance. The size of a population and its demographic and genetic characteristics may be largely irrelevant to survival where catastrophic changes to local environments occur as a result of environmental stochasticity.

REGIONAL INFLUENCES

Populations of *E. paniculata* are geographically isolated, fluctuate in size independently of one another, and persist for only limited periods of time. How can this species persist in the long term under these demographic conditions? Several metapopulation models suggest that for persistence to occur, species rely on migration and recolonization to alleviate the risks of local extinction (Stacey *et al.* 1997). The influence of these regional processes on the size and dynamics of individual populations was examined in *E. paniculata* by testing for a correlation between the density of populations in a region and the size and persistence of local populations. We found no significant association between the degree of isolation of populations (measured as populations km^{-1}) and either their size or probability of persistence, suggesting that the proximity of surrounding populations does not affect local population dynamics or the likelihood of extinction. This result contrasts with genetic studies of these populations, which indicated a relation between the local density of populations in a region and genetic diversity. Such a pattern was interpreted as resulting from higher levels of gene flow in regions with high population density (Barrett & Husband 1997). This comparison highlights the different demographic vs. genetic consequences of migration. While a small number of migrants can have a profound effect on the genetic composition of populations (Wright 1978), the demographic consequences of an equivalent amount of migration may be trivial.

There was a significant positive relation between the percentage of patches occupied and total patch density in *E. paniculata* for 18 (in 1988) and 29 (in 1989) regions in north-eastern Brazil. This association has been reported for only one other species, a butterfly (*Melitaea cinxia*) occurring on the Aland islands in south-western Finland (Hanski *et al.* 1995). Levins (1969) predicted this pattern on the basis that recolonization rates should increase as patch density rises. Assuming that the probability of extinction is constant, increasing the patch density would result in a higher proportion of patches occupied. Moreover, his model predicts that below some threshold density of patches, extinction will exceed recolonization and the species should not persist. This situation may occur in *E. paniculata* because no populations were observed in regional transects with patch densities at or below 0.2 km^{-1} in either 1988 or 1989. The fact that patch occupancy is associated with patch density in *E. paniculata* suggests that regional processes affecting recolonization of unoccupied patches may be an important determinant of the distribution and persistence of this species in north-eastern Brazil.

Hanski (1997) described the classical metapopulation of Levins (1969) as having the following characteristics: (i) a group of isolated populations; (ii) local dynamics of populations independent from one another; (iii) recolonization and migration among populations possible; and (iv) populations with approximately equal probabilities of extinction. As one of the first studies of regional population structure in a plant species, it is important to evaluate *E. paniculata* with respect to each of these criteria. Consistent with the metapopulation model of Levin (1969), populations of *E. paniculata* occur in habitats that are discrete, restricted in size and isolated on the landscape. Local population dynamics also conform to Levins' model (1969) since population size fluctuated randomly in direction. As in most plant species, direct estimates of colonization and migration are not available for *E. paniculata*. However, indirect estimates of gene flow based on genetic markers have demonstrated low levels of migration among populations (Husband & Barrett 1995). Finally, the probability of persistence in *E. paniculata* was independent of initial population size and the time from the first census. Only two of the 30 populations initially observed in 1982 persisted over the 7-year census period. Expressed in these terms, the probability of persisting from one year to the next was random and uniform among populations. Therefore, for each of these four criteria some evidence exists that *E. paniculata* conforms to the classical metapopulation model. While debate continues as to whether such concepts can be applied to all plant species, and whether the Levins' model is appropriate for certain plant life histories (Eriksson 1996; Husband & Barrett 1996), ecological and genetic data from *E. paniculata* suggest that the size and structure of populations of this species in north-eastern Brazil are governed, in part, by metapopulation dynamics.

Acknowledgements

We thank William Cole, Jan Conn, Martin Morgan and Joel Shore for assistance in the field and John Bishop and Mary Ruckelshaus for comments on the manuscript. Research was funded by grants from the Natural Sciences and Engineering Research Council of Canada to B.C.H. and S.C.H.B.

References

Andrewartha, H.G. & Birch, L.C. (1954) *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago.

Barrett, S.C.H. (1985) Floral trimorphism and monomorphism in continental and island populations of *Eichhornia paniculata* (Spreng.) Solms (Pontederiaceae). *Biological Journal of Linnean Society*, **25**, 41–60.

Barrett, S.C.H. & Husband, B.C. (1997) Ecology and genetics of ephemeral plant populations: *Eichhornia paniculata* (Pontederiaceae) in Northeast Brazil. *Journal of Heredity*, **88**, 277–284.

Barrett, S.C.H., Morgan, M.T. & Husband, B.C. (1989) The dissolution of a complex genetic polymorphism: the evolution of self-fertilization in tristylous *Eichhornia paniculata* (Pontederiaceae). *Evolution*, **43**, 1398–1416.

Brown, J.H. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, **58**, 445–449.

Carter, R.N. & Prince, S.D. (1988) Distribution limits from a demographic viewpoint. *Plant Population Ecology* (eds A.J. Davy, M.J. Hutchings, A.R. Watkinson), pp. 165–184. Symposium 28 of the British Ecological Society. Blackwell Scientific Publications, Oxford.

Eriksson, O. (1996) Regional dynamics of plants: a review of evidence for remnant, source–sink and metapopulations. *Oikos*, **77**, 248–258.

Ewens, W.L., Brockwell, P.J., Gani, J.M. & Resnick, S.I. (1987) Minimum viable population size in the presence of catastrophes. *Viable Populations for Conservation* (ed. M.E. Soulé), pp.59–68. Cambridge University Press, Cambridge.

Friese, F.W. (1938) The drought region of northeastern Brazil. *Geographical Review*, **28**, 363–378.

Goodman, D. (1987) The demography of chance extinction. *Viable Populations for Conservation* (ed. M.E. Soulé), pp. 11–34. Cambridge University Press, Cambridge.

Hanski, I. (1982) Distributional ecology of anthropochorous plants in villages surrounded by forest. *Annales Botanici Fennici*, **19**, 1–15.

Hanski, I. (1985a) Colonization of ephemeral habitats. *Ecology of Natural Disturbances and Patch Dynamics* (eds S. T. A. Pickett & S. P. White), pp. Academic Press, Orlando.

Hanski, I. (1985b) Single-species spatial dynamics may contribute to long-term rarity and commonness. *Ecology*, **66**, 335–343.

Hanski, I. (1997) Metapopulation dynamics: from concepts and observations to predictive models. *Metapopulation Biology*: *Ecology*, *Genetics and Evolution* (eds I.A. Hanski & M.E. Gilpin), pp. 69–91. Academic Press, San Diego, USA.

Hanski, I. & Gilpin, M. (1991) Metapopulation dynamics: brief history and conceptual domain. *Metapopulation Dynamics*: *Empirical and Theoretical Investigations* (eds M. Gilpin & I. Hanski), pp. 3–16. Academic Press, London.

Hanski, I., Pakkala, T., Kuussaari, M. & Lei, G. (1995) Metapopulation persistence of an endangered butterfly in a fragmented landscape. *Oikos*, **72**, 21–28.

Harper, J.L. (1977) *Population Biology of Plants*. Academic Press, London.

Harrison, S., Murphy, D.D. & Ehrlich, P.R. (1988) Distribution of the bay checkerspot butterfly, *Euphydryas editha bayensis*: evidence for a metapopulation model. *American Naturalist*, **132**, 360–382.

Harrison, S. & Taylor, A.D. (1997) Empirical evidence for metapopulation dynamics. *Metapopulation Biology*: *Ecology*, *Genetics and Evolution* (eds I. A. Hanski & M. E. Gilpin), pp. 27–42. Academic Press, San Diego, USA.

Hastings, A. (1991) Structured models of metapopulation dynamics. *Metapopulation Dynamics*: *Empirical and Theoretical Investigations* (eds M. Gilpin & I. Hanski), pp. 57–71. Academic Press, London.

Husband, B.C. (1992c) *Stochastic processes and the evolution of self-fertilization in tristylous* Eichhornia paniculata (*Pontederiaceae*). PhD thesis, University of Toronto.

Husband, B.C. & Barrett, S.C.H. (1992a) Effective population size and genetic drift in *Eichhornia paniculata* (Pontederiaceae). *Evolution*, **46**, 1875–1890.

Husband, B.C. & Barrett, S.C.H. (1992b) Genetic drift and the maintenance of the style length polymorphism in tristylous *Eichhornia paniculata*. *Heredity*, **69**, 440–449.

Husband, B.C. & Barrett, S.C.H. (1993) Multiple origins of self-fertilization in tristylous *Eichhornia paniculata* (Pontederiaceae): inferences from style morph and isozyme variation. *Journal of Evolution Biology*, **6**, 591–608.

Husband, B.C. & Barrett, S.C.H. (1995) Estimates of gene flow in *Eichhornia paniculata* (Pontederiaceae): effects of range substructure. *Heredity*, **75**, 549–560.

Husband, B.C. & Barrett, S.C.H. (1996) A metapopulation perspective in plant population biology. *Journal of Ecology*, **84**, 461–469.

Jones, H.L. & Diamond, J.M. (1976) Short-time base studies of turnover in breeding bird populations on the California Channel Islands. *Condor*, **78**, 526–549.

Kadmon, R. & Shmida, A. (1990) Spatiotemporal demographic processes in plant populations – an approach and a case study. *American Naturalist*, **135**, 382–397.

Kareiva, P. (1990) Population dynamics in spatially complex environments: theory and data. *Population Regulation and Dynamics* (eds M. P. Hassell & R. M. May), pp. 53–68. Royal Society, London.

Lande, R. (1987) Extinction thresholds in demographic models of territorial populations. *American Naturalist*, **130**, 624–635.

Leigh, E.G. Jr (1981) The average lifetime of a population in a varying environment. *Journal of Theoretical Biology*, **90**, 213–239.

Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, **15**, 237–240.

Levins, R. (1970) Extinction. *Lectures in Mathematics and Life Sciences*, **2**, 75–107.

Mason, L.G. (1987) Extinction, repopulation and population size in natural populations of Ambushbugs. *American Naturalist*, **129**, 445–447

McCauley, D.E. (1989) Extinction, colonization, and population structure: a study of a milkweed beetle. *American Naturalist*, **134**, 365–376.

Menges, E.S. (1990) Population viability analysis for an endangered plant. *Conservation Biology*, **4**, 41–62.

Menges, E.S. & Gawler, S.C. (1986) Four-year changes in population size of the endemic Furbish's lousewort: implications for endangerment and management. *Natural Areas Journal*, **6**, 6–17.

Nilsson, S.G. & Nilsson, I.N. (1982) Turnover of vascular plant species on small islands in Lake Mdckeln, South Sweden 1976–1980. *Oecologia*, **53**, 128–133.

Nimer, E. (1972) Climatologia de regiio Nordeste do Brasil. *Rev. Bras. Geogr*., **34**, 3–51.

Richter-Dyn, N. & Goel, N.S. (1972) On the extinction of a colonizing species. *Theoretical Population Biology*, **3**, 406–433.

Roberts, H.A. & Feast, P.M. (1973) Emergence and longevity of seeds of annual weeds in cultivated and undisturbed soil. *Journal of Applied Ecology*, **10**, 133–143.

Schoener, T.W. & Schoener, A. (1983) The time to extinction of a colonizing propagule of lizards increases with island area. *Nature*, **302**, 332–334.

Schoener, T.W. & Spiller, D.A. (1987) High population persistence in a system with high turnover. *Nature*, **330**, 474–477.Shaffer, M.L. (1981) Minimum population sizes for species conservation. *BioScience*, **31**, 131–134.

Sokal, R.R. & Rohlf, F.J. (1981) *Biometry*, 2nd edn. W.H. Freeman, San Francisco.

Stacey, P.B., Johnson, V.A. & Taper, M.L. (1997) Migration within metapopulations: the impact upon local population dynamics. *Metapopulation Biology*: *Ecology*, *Genetics and Evolution* (eds I. A. Hanski & M.E. Gilpin), pp. 267–291. Academic Press, San Diego, USA.

Toft, C.A. & Schoener, T.W. (1983) Abundance and diversity of orb spiders on 106 Bahamian islands: biogeography at an intermediate trophic level. *Oikos*, **41**, 411–426.

Williamson, M. (1981) *Island Populations*. Oxford University Press, Oxford.

Wright, S. (1978) *Evolution and the Genetics of Population*, Vol. 4. *Variability Within and Among Natural Populations*. University of Chicago Press, Chicago.

Received 5 February 1998
revision accepted 10 June 1998