REVIEW

Function of Habitat Heterogeneity for the Biodiversity and Demography of Population in Small Mammal Community

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소척추동물군집에서 개체군 변동과
생물다양성 유지를 위한 서식지 이질성의 기능

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ABSTRACT

The central theme of habitat heterogeneity is to provide animals with habitat complexity or structural diversity and to allow resource partitioning among individuals. In turn, this leads to population stability because prey can escape more easily with more hiding places causing less population fluctuation. Species diversity is characterized due to more potential niches both horizontally and vertically. Empirically, in homogeneous habitats population was less abundant, reproduction and survival were lower, spacing behavior, competition and dispersal were higher than in heterogeneous habitats. The results imply that diversity and conservation of species can be maintained through providing heterogeneous habitats.

Key words: Demography, Habitat heterogeneity, Small mammals, Spacing behavior, Species diversity

THEORETICAL REVIEWS OF HABITAT HETEROGENEITY

The importance of habitat heterogeneity is widely acknowledged for birds (MacArthur *et al.* 1962, Ulfstrand 1975, Roth 1976), lizards (Pianka 1967, Schoener and Schoener 1971), and small mammals (Ostfeld and Klosterman 1986, Bondrup-Nielsen 1987). However, habitat heterogeneity can have various meanings to ecologists. It is difficult to measure the suitability for vertebrates of different habitat types. What factors make a habitat optimal and what criteria should we use to determine optimality are not agreed upon (Hansson

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1977, Alibhai and Gipps 1985). Nonetheless, several theories suggest that habitat hetero-geneity leads to population stability. Population stability can be achieved if population density is less fluctuated (i.e., non-cyclic), and when habitat that supports superior demo-graphic performance (e.g., high density, survivorship, reproductive rate) is adjacent to habitat supporting inferior demographic performance (Stenseth 1980).

The idea of habitat variation has been further developed in modeling (Hansson 1977, Anderson 1980). Anderson (1980) speculated on the effects of habitat quality on vole populations by describing three different habitat types: survival, colonization and tra-versable. He described survival habitats as persistently favorable place and occur in well-dispersed patches. He predicted that populations inhabiting them have high repro-ductive success, and infrequent extinctions in a local scale. Colonization habitats are more extensive, generally occur near survival habitats, and their conditions can vary over time. Anderson (1980) predicted that vole populations within colonization habitats will have widely varying reproductive success, life expectancy, and density and are subject to exhibit frequent extinctions. However, recolonization usually occurs within a short time period by excess individuals immigrating from survival habitats. Traversable habitats are crossed by voles but are not used as permanent territories or home ranges. A similar idea of habitat variation has different notations (Hansson 1977) (Table 1).

In the environmental settings of habitat heterogeneity, stability can be achieved in a population with unequal resource partitioning among individuals, as shown in a math-ematical model (Lomnicki 1980, Ostfeld 1992). A further consequence of unequal resource partitioning and a heterogeneous environment are the regulation of population density by emigration, which may result into lower population density, higher food density and even higher stability than without emigration (Lomnicki 1980). Roff (1974, 1975) suggested that the variance in environmental fluctuations leads to stability in a heterogeneous en-vironment. In his model, stability can be achieved through dispersal. Hestbeck (1982) ex-tended Roff's ideas and suggested that population stability can be achieved if there is a gradient of qualities of habitat from and into which animals could disperse. All the vacant spaces in the optimal habitat are filled first with the population being regulated by

Table 1. Different notations of habitat classification by Anderson (1980) and Hansson (1977)

Anderson (1980)		Hansson (1977)
Survival	Most favorable, High and constant density, High reproductive success, Not much extinction, Well-dispersed patches	Donor Hahitat
Colonization	Low densities, Low emigration, Varying reproductive success, Frequent extinction, High immigration rate, High density fluctuation	Reception Habitat
Traversable	Not permanent	Transition Habitat

spacing behavior. Surplus individuals then disperse into a suboptimal habitat until all vacant spaces in there are filled. Once this has been achieved, groups in a suboptimal habitat will 'fence' the central population and inhibit further emigration. This phenomena will cause an increase in population density which is regulated by resource exhaustion. Hestbeck (1982) model considers the role of habitat heterogeneity explicitly.

There are some evidences that the homogeneous nature of the habitat contributes to the ten-year cycles in the snowshoe hare (*Lepus americanus*), where populations in more discontinuous habitats fail to exhibit cycles (Hestbeck 1982). Stenseth (1980) demonstrated that increased structural complexity of habitat leads to increased population stability. His hypothesis is based on predator-prey relationship described by Lotka-Volterra model. Prey can escape more easily in a heterogeneous habitat providing them with more hiding places, theoretically causing less population fluctuations. Three outcomes would result. First, enrichment of a habitat patch may stabilize the predator-prey interaction. Secondly, predator efficiency may destabilize the interaction and result in greater density variation of the prey. This suggests that predator efficiency will be reduced due to the increased ability of prey to escape from predators in heterogeneous habitats. This reduction of efficiency would result in greater stability. Lastly, the stability can be achieved by providing more refuges, thus reducing fluctuations in spatially heterogeneous habitats. However, Rosenzweig and Abramsky (1980) predicted that if greater cover corresponds to higher primary productivity, populations are predicted to be less stable in these sites in the plant-grazer model. If greater cover corresponds to increased prey refuges, then populations are predicted to be more stable.

The size and configuration (distribution) of a patch become important as these may affect the performance of small mammal populations (Hansson 1977, Anderson 1980, Bondrup-Nielsen 1985). The division of space into various local habitats and hostile areas was termed "macroheterogeneity" by Lomnicki (1988). For a population responding to macroheterogeneity, patch size must be smaller than the mean dispersal distance of the population (Bondrup-Nielsen 1987), otherwise the patch will be effectively homogeneous for most individuals. Habitat distribution refers to the proximity of habitat patches - either contiguous or separated by unsuitable areas. The success of individuals in colonizing patches may depend on proximity of the patches. Local habitats are those areas an individual is likely to visit in its daily wanderings. These habitats are also expected to be heterogeneous and this is called "microheterogeneity" by Lomnicki (1988).

HABITAT HETEROGENEITY LEADS TO SPECIES DIVERSITY

Many have found that species diversity is related to habitat complexity (MacArthur and MacArthur 1961, MacArthur and Pianka 1966, Rosenzweig and Winakur 1969, Cody 1975, Terborgh 1977). The term 'complexity' and 'heterogeneity' have been used exchangeably since MacArthur and MacArthur (1961) demonstrated a positive associ-

ation between bird species diversity and foliage height diversity: species diversity increases with increasing habitat complexity. It is reasoned that highly complex habitats offer more potential niches than structurally simpler habitats (Klopfer and MacArthur 1960). Levins (1976) also demonstrated that increasing complexity of habitats results to increase in species diversity of animal communities inhabiting there by providing greater niches in a given space. In small mammal communities, Rosenzweig and Winakur (1969) showed that structural heterogeneity of the environment leads to increased species diversity of small mammal community in desert. August (1983), however, separated the meaning of complexity and heterogeneity. He defined complexity as vertical variation in habitat physiognomy and heterogeneity as horizontal variation in habitat form. He suggested the total number of mammal species is positively correlated with habitat complexity but not correlated with habitat heterogeneity. He argued that abiotic factors such as the degree of flooding play an important role in patterns of small mammal distribution and abundance.

The idea of separation of niches does not always reflect a direct measurement of species diversity. There are animals that are very specific in niches, but others are insensitive to niche separation. Even though complexity of habitat favors greater niches in a given unit species diversity always does not follow. Furthermore, if there are species with overlapping niches, the chance of increasing competition among species may result in. Interspecific competition would drive away less competitive species from the habitat and local extinction may follow. Lastly, habitat elements that signify heterogeneity of habitat (e.g., physical or biological) may be very subjective depending on the purpose of study and researchers. The critical habitat elements to be responsible for species diversity may be difficult to identify.

HABITAT HETEROGENEITY: EMPIRICAL STDUIES

Density

Density seems to be the most conspicuously comparable population reaction associated with habitat heterogeneity. Population density often depends on the variation in habitat quality. Lindroth and Batzli (1984) observed a higher density of voles in prairie habitat than in bluegrass habitat due to better quality food. Similarly, Bondrup-Nielsen (1987) demonstrated that the greater the degree of habitat heterogeneity, the greater the likelihood that a vole population will show stability in density. In his study, habitat heterogeneity was measured by the variation in habitat quality between deciduous and coniferous habitats.

Variation in habitat quality includes measures of physical characteristics of habitat (e. g., soil moisture). Bank voles (*Clethrionomys glareolus*) aggregated more in damp habitat than in dry habitat (Mazurkiewicz 1981). *Microtus pennsylvanicus* density also decreased along with woody gradients and increased along with herbaceous gradients due to habitat

favorability in humidity (Adler 1987). The difference of high density population of *C. gapperi* between lowland swamp and upland in Connecticut indicated that density was limited to the available water and soil moisture (Miller and Getz 1972). Voles were restricted to low swamps where the free water was available at or near the surface.

Several studies have shown that cover plays an important role in changes of population density. The general composition of grassland small mammal communities is determined primarily by structural attributes of habitat. Cornely *et al.* (1981) observed densities of montane voles (*M. montanus*), deermice (*Peromyscus maniculatus*) and vagrant shrews (*Sorex vagrans*) were reduced by removal of cover by burning or haying whereas density in non-use areas remained constantly high. Miller and Getz (1972) suggested that population abundance of *C. gapperi* in forested areas was higher than in non-forested or clear-cut areas because of debris cover. A similar study showed that vole-density (*M. ochrogaster*) was higher in an ungrazed area than in a grazed area due to differences in available vegetation cover (Birney *et al.* 1976). Small mammal communities in tallgrass (*Andropogon gerardi, Panicum virgatum*) and montane grassland (*Festuca idahoensis, Agropyron subsecundum*) appeared to be more affected by reduction in vegetative cover by grazing pressure from domestic livestock than do small mammals in shortgrass (*Bouteloua gracilis, Buchloe dactyloides*) and bunchgrass (*Agropyron spicatum, Stipa comata*) grasslands (Grant *et al.* 1982). The tallgrass and montane ungrazed sites had a significantly higher standing crop of above-ground net primary production than did the shortgrass and bunchgrass sites, thus representing high population abundance. However, if the increased cover represented increased primary production, then population fluctuation could be less stable (Rosenzweig and Abramsky 1980). M'Closkey (1976) found that artificial shrubs constructed with diverse branch angles over the horizontal plane and equal number of branches at the different angles were used more intensively than shrubs lacking these characteristics by *P. leucopus*.

Geuse (1985) showed that bank voles preferred wooded areas showing limited sub-areas of dense ground-level cover of live or dead material. Unfavorable habitats were places bare of litter (beach-grove) or young plantation. Voles used wooded areas of dense cover as a refuge from predation. Bank voles showed stable territories when compared with wood mice (*Apodemus sylvaticus*). Wood mice were frequently found in habitats of bare litter or young plantation. Microhabitat heterogeneity influenced population density more than it did other demographic characteristics in study of *M. pennsylvanicus* (Adler 1987). Many authors point out that habitat heterogeneity should be evaluated more in density issues than any other demographic characteristics.

Spacing behavior

Spacing behavior has been widely implicated as a key factor in regulating the demography of small mammals (Krebs *et al.* 1969, Boonstra and Rodd 1983). Home range size is one of the most commonly used measurement, and appears to be the most conspicuous

phenomena in habitat heterogeneity studies (Bowers and Smith 1979, Bondrup-Nielsen 1986, 1987, Mazurkiewicz 1986, Ostfeld and Klosterman 1986, Szacki 1987). Bondrup-Nielsen (1987) showed that home range size of *C. gapperi* was smaller in grids with a high degree of habitat variation than in grids with low variation. This pattern did not differ between years. Bondrup-Nielsen (1986) concluded home range size was primarily controlled by habitat types. Van Horne (1981) failed to find a difference in home range size of *P. maniculatus* between habitat types in cutover areas. Ostfeld and Klosterman (1986) demonstrated that the degree of home range overlap had been shown to be more flexible for female *M. californicus* in denser, presumably superior patches. *C. glareolus* used a smaller space and reached greater local density in a habitat with clustered distribution of undergrowth than in habitat with random distribution (Mazurkiewicz 1986). As shown in other studies, the home range was larger in the random habitat than in the clustered one, reflecting the variation of quality habitat.

Habitat heterogeneity leads to a difference in habitat use by the sex. Bowers and Smith (1979) proposed that in desert communities female deer mice inhabited the more favorable and moist microhabitats than males resulting in smaller home range size. Biased female sex-ratios often occur in high quality habitats. It was found that the female-sex bias happened when vole density was high. This suggested that males gave way to females to secure a female's territory in an optimal place when resources were patchy so they could increase their reproductive effort and survival of young (Bowers and Smith 1979, Martell and Fuller 1979, Van Horne 1982, Ostfeld *et al.* 1985, Ostfeld and Klosterman 1986). Densely distributed patches (clustered habitat) showed female-biased sex differences causing a difference in spacing behavior, persistence and individual productivity compared to sparsely distributed patches (Bujalska 1973, Ostfeld and Klosterman 1986). In their study, spacing behavior of females, but not males, was responsive to habitat quality, being somewhat relaxed where resources were rich. In these areas males had a higher frequency of wounding, which implied that intrasexual aggressiveness was more pronounced.

Dispersal and movement

Whenever populations increase, the animals invade areas with very little cover and food (e.g., orchards, which were never used in summer) (Hansson 1977). Adler (1987) found a greater variability of demographic structure in high density habitats due to seasonal dispersal of young or subordinate individuals in *M. pennsylvanicus* populations which were forced into adjacent habitats in response to intraspecific competition. Changes in demographic structure due to variation in habitat quality were also noticed. Adler *et al.* (1984) demonstrated that *P. leucopus* in woodland and grassland habitats were similar in terms of sex ratios and reproductive condition, but grassland mice were smaller and had a lower multiple capture rate, presumably because the latter were predominantly dispersing mice and that grassland functioned as a dispersal sink.

Demography

Males usually were more influenced by habitat. They showed lower survivorship in homogeneous habitats (Cockburn and Lidicker 1983, Ostfeld *et al.* 1985, Ostfeld and Klosterman 1986). The lower rate of residing in an area for males may be a result of stress, dispersal or increased susceptibility to predators arising from frequent intrasexual fighting in *M. californicus* (Ostfeld and Klosterman 1986). Ostfeld *et al.* (1985) showed that for males probability of persistence was lower and constant across all seasons while for females it varied markedly in response to seasonal (wet vs. dry) variation depending on resource quality. High habitat quality (high % cover of the perennial grass *Elymus triticoides*) was characterized by longer average persistence and higher rates of juvenile recruitment than low habitat quality (*Conium maculatum* and annual grasses). Voles (*M. californicus*) in native perennial grass also performed better. Female dispersion was more restricted than that of males and there was a higher probability of survival during summer, the hardest time in central California, compared to habitats without perennials (Cockburn and Lidicker 1983).

The earlier onset of reproduction and breeding at a younger age in the experimental woodlot (with supplemental-feeding) was observed (Hansen and Batzli 1978). The experimental woodlot had higher densities and better survival of nestling mice in autumn and winter than in a woodlot without feeding. Hansson (1974) suggested that reforested areas, with a much lower primary production than the undisturbed forest, showed the higher proportion of juvenile age class leading to increased fluctuation in population density. Van Horne (1982) showed that *M. longicaudus* population was higher in a 7~10 year-old clear-cut area than in a 23~26 year-old clear-cut area. The latter showed low overwinter survival and a low growth rate of adults and juveniles because of low nitrogen content in the shrub species. However, Petticrew and Sadleir (1974) indicated that populations of *P. maniculatus* on a recently logged area were similar in numbers, survival and recruitment to those in mature forest.

Survival and reproduction of *M. californicus* were correlated with residency in patches of grassland dominated by the native perennial grass, *Elymus triticoides* (Cockburn and Lidicker 1983). Animals in quality habitat showed the ability to maintain better survival and reproductive performance than those in annual grasses (*Bromus* spp. and *Lolium multiflorum*). *Psedomys fumeus* living in a preferred microhabitat with high quality food sources (fungal sporocarps and seeds) showed high breeding success and were less affected by the spring decline, whereas those living in non-preferred microhabitat were severely affected by the decline and showed high level of fighting during the decline period (Cockburn 1981).

The comparison of quality of habitat is an important consideration when one examines the habitat heterogeneity. Population abundance is the most conspicuous, however, density may not be sufficient to judge the quality of habitat. Other demographic parameters

(e.g., age structure, residency, reproductive rate, survivorship, home range size) should be supplemented. For example, abundant population but low in proportion of adults can be observed in suboptimal habitat leading to increased fluctuation in density. The highly heterogeneous habitats may permit young to escape from density-dependent suppression of reproduction in optimal habitats by dispersing into suboptimal habitats resulting in high proportion of adult population.

CONCLUSIONS

Most studies on habitat heterogeneity have compared population abundance among sites or several habitats. The results may be misleading because the results may be just a simple 'chance event' and does not reflect the causation and effect on the function of the habitat. The simple correlation studies of species presence and absence are descriptive and lack functional understanding of changes in animal populations. Furthermore, majority of studies fail to identify critical habitat elements which influence the survival and reproduction of species in a local community.

The critical habitat elements (yet to be known) control environmental differences (e.g., structural diversity, foods, etc.) and allow testing the effects of different habitat types on animal population. We, therefore, have to identify what can be the most influential habitat element to achieve a successful management towards biodiversity and conservation of species.

요 약

이질적 서식지는 동물에게 구조적으로 복잡한 서식지와 개체군 상호간의 다양한 생태적 지위에 따른 분리된 자원을 공급한다. 소척추동물과 포식자의 관계에서 동질화된 서식지는 소척추동물의 생태적 지위를 단일화시켰으며, 숨을 곳의 급격한 감소로 인해 소척추동물의 군집 밀도를 큰 규모로 변동시킨다. 동질화된 서식지는 또한 서식지 구조의 복잡성을 사라지게 함으로써 종의 다양성이 감소된다는 연구결과를 검토하였다. 실험적연구에서 동질화된 서식지는 소척추동물의 서식밀도와 안정성의 감소, 세력권의 증가로 인한 종간경쟁, 분산의 증가로 특징지워졌다. 따라서 서식지의 이질성 유지는 종의 다양성과 보존의 기능을 높여주는데 기여함을 알게 되었다.

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