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Additive and non-additive effects from a larger spatial scale determine small-scale densities in a web spider *Neriene brongersmai*

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Abstract We examined 15 populations of *Neriene brongersmai*, a common sheet-web spider inhabiting cedar forest floor, to find out how density at a small spatial scale (patch level) is determined by processes operating at this scale as well as those from a larger spatial scale (population level). Here we focus on two types of large-scale effects that may influence small-scale density: an additive effect that changes the density at patch level; and a non-additive effect that changes the relationship between the density and its limiting factor at the patch level. ANCOVA showed that patch-level density of this spider was positively correlated with web-site availability at this level, but the density with a given amount of web-site differed among populations (cedar forests), indicating the existence of an additive large-scale effect. Multiple regression analysis showed that web-site availability at a population level explained the additive large-scale effect well, but prey availability and forest size did not. It seemed likely that increased web-site availability may have reduced the mortality of spiders while moving to a new web-site, and hence increased population density. A non-additive large-scale effect was also revealed: i.e. the relationship between density and web-site availability at the patch level tended to be stronger in populations with a greater additive large-scale effect. Higher intraspecific competition for web-sites in these populations appeared to have strengthened this relationship.

Keywords Density dependence · Emergent property · Limiting factor · Linyphiid spider · Multiple spatial scale · Population dynamics

Introduction

Ecologists now recognize that mechanisms determining the abundance of organisms vary with spatial scale (Levin 1992; Wellnitz et al. 2001; Fuhlendorf et al. 2002). However, it has been less well appreciated that the abundance at a focal spatial scale is determined by factors not only at this scale, but also from larger spatial scales. For example, the abundance of organisms in a patch with a given size varies depending on the structure of surrounding landscapes through the change in immigration rate (Hanski and Thomas 1994; Hanski 1999), and the impact of predators on organism abundance is modified by abiotic factors such as rainfall (Chalcraft and Andrews 1999) and wave forces (Menge and Olson 1990; Menge et al. 2002) that operate at a larger spatial scale. Because these large-scale processes enhance or lower the density at small spatial scales, integration of processes operating at different spatial scales and identification of the underlying mechanisms are essential for making population and community ecology more predictive.

One important point that has received little attention is that a large-scale effect might influence the relationship between abundance and its limiting factor at a small scale in a non-additive way (Thrush et al. 2000). For example, the regression slope between patch size and an organism's abundance may differ among landscapes, resulting in an interaction between landscape and patch size. Nevertheless, few studies have evaluated the additive and non-additive large-scale effects separately, or identified their mechanisms.

Neriene brongersmai, a sheet-web spider inhabiting the forest floor, appears to be well suited for examining the role of large-scale effects in determining the abundance at smaller scales. First, previous studies have indicated that the density of web spiders is often limited by the availability of web-sites (Schaefer 1978; Riechert 1981; Uetz 1991; Wise 1993; Samu et al. 1996), particularly at the patch level, which provides an a priori

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hypothesis for explaining densities at this level. Second, this species almost exclusively inhabits the floor of Japanese cedar (*Cryptomeria japonica*) forests (see Materials and methods), so that a continuous area of cedar forest can be regarded as the unit of a population of this species. This provides an opportunity to examine multiple populations, which may enable us to identify population-level (larger-scale) effects influencing patch-level (smaller-scale) density.

In this paper, we hypothesized that, at the patch level, web-site availability limits density. This relationship was examined using a log-log scale, because (1) dimensionality that determines this relationship was unknown and (2) demographic factors, including survivorship, usually act in an additive way at a logarithmic scale. For detecting population-level effects that may influence patch-level density, we focused on the difference in the y -intercept of the regression equations, as well as on the difference in the regression slopes, which are defined and hereafter referred to as additive and non-additive effects, respectively. The presence of an additive effect means that overall patch-level density for a range of web-site availabilities differs among populations, and that of a non-additive effect implies that the effect of increasing web-site availability at patch-level density varies among populations. These two effects are not mutually exclusive because both effects could exist in a given range of web-site availabilities. We also focused on the difference in absolute deviation from the regression line among populations, and defined it as another non-additive effect, because it represents the strength of web-site limitation on patch-level density.

We investigated 15 *N. brongersmai* populations to find out how patch-level density is affected by factors operating at this level as well as at the population level. Specifically, we examined the following three specific questions (Fig. 1): (1) is density at a patch limited by the availability of web-site at the patch level? (2) is patch-level density affected by processes operating at the population level (i.e., additive effect and non-additive effect from larger spatial scale)? (3) what causes these population-level effects?

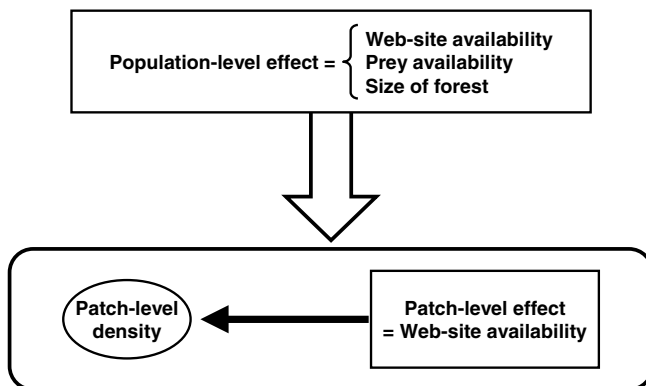


Fig. 1 The hypothetical processes determining patch-level density of *N. brongersmai*

Here we focus on three variables that may lead to the population-level effect: web-site availability, prey availability, and size of cedar forest (Fig. 1), because both web-site availability (Schaefer 1978; Riechert 1981; Uetz 1991; Wise 1993; Samu et al. 1996) and prey availability (Wise 1975; Spiller 1984) are known to limit spider populations, and forest size represents habitat size that possibly affects various population characteristics (Miyashita et al. 1998).

Materials and methods

Natural history of *N. brongersmai*

N. brongersmai is a common linyphiid web-builder inhabiting the litter surface in forest understorey, with female body length about 8 mm. This species has an annual life cycle. After hibernating as a sub-adult stage, adults emerge from April to May. Spiderlings of the following generation begin to emerge in June and juveniles hibernate around November. *N. brongersmai* builds a sheet web with a barrier constructed on the complex structured litter surface about 3 cm above the ground. The main prey are Diptera, Collembola and juvenile crickets (unpublished data).

Study sites and designs

The study was conducted in the Boso Peninsula located in Chiba Prefecture, central Japan (35°N, 140°E). It has an annual precipitation of 2,000–2,400 mm, with monthly temperatures in midwinter and midsummer of about 4°C and 25°C, respectively (The Tokyo University Forests 2000). The vegetation is characterized by evergreen broadleaved forests (e.g. *Machilus thunbergii*, *Castanopsis sieboldii* and *Lithocarpus edulis*) and plantations of conifers (*Cryptomeria japonica* and *Chamaecyparis obtusa*).

Population-level survey

We selected 15 continuous cedar forests (*C. japonica*) varying the forest size and amount of litter. The mean forest age was 43 ± 15.3 years (\pm SD) and the mean distance between adjacent forests that were studied was 718 ± 833 m (\pm SD). Field research was conducted at the juvenile stage (August 2002) and the adult stage (May 2003). We regarded a continuous cedar forest as the unit of a population because of the following reasons. First, the spider is very abundant in the cedar forest, but rarely found in other habitats; the adult density (per 70×70 cm²) was 2.4 in the cedar forest and 0.3 in other types of forests. Second, immigration rate (number/14 days/0.25 m²) was 10.3 in the cedar forests while only 0.6 in broadleaved forests located 100 m apart (unpublished data), suggesting that the spider seldom moves between cedar forests.

We focused on size of cedar forest, web-site availability and prey availability as possible factors causing population-level effects. The size of each forest was measured from aerial photographs taken in 2000. Web-site availability was estimated from the height of the cedar litter, because preliminary observations showed that this spider constructs its web on the litter with a rough structure. We measured the height of the cedar litter at 240 points selected randomly in an area with high spider density in each forest. The mean value averaged over all points was used as an estimate of web-site availability at the population level.

To estimate prey availability in each forest, we used two types of measurements: insect biomass captured by traps and adult body size of females. The advantage of using spider body size is that it reflects cumulative prey availability over a long timescale, and it is usually not affected by spider density due to the lack of exploitative competition (Wise 1983; Miyashita 1992). We established ten sticky traps (May 2003; adult stage) in the area where litter height was measured, left them for 6 days, and measured body length of arthropods captured in the traps. Body mass of arthropod was calculated by $(\text{mass}) = 0.0305 \times (\text{body length})^{2.62}$ (Rogers et al. 1976). We also measured body length (cephalothorax length) of 15 adult female spiders in each forest from photos taken with a digital camera in May 2003.

Patch-level survey

In the area where litter height and prey availability were measured in each forest, we established 15 patches with varying amount of litter. These patches were selected so that the mean web-site availability within a patch became similar among populations (ANOVA; juvenile: $F_{[14,208]} = 1.35$, $P = 0.179$; adult: $F_{[14,209]} = 0.68$, $P = 0.794$). It appeared that this selection enabled us to detect population-level effect more effectively. The size of patch was defined as $50 \times 50 \text{ cm}^2$ at the juvenile stage and $70 \times 70 \text{ cm}^2$ at the adult stage, which were determined by mean web diameter (juvenile: 7.4 cm [$n = 196$]; adult: 17.2 cm [$n = 187$]), assuming that a spider with its web potentially interacts with a few individuals around it. Notice that the patches defined here were not isolated from each other by any physical boundaries. In each patch, we counted all spiders and measured the height of litter at ten randomly selected points. The mean litter height averaged over ten points was used as an estimate of web-site availability at the patch level.

Data analysis

Firstly, we performed ANCOVA using patch-level density as a dependent variable, “population” as a factor, and web-site availability at the patch level as a covariate. Both density and web-site availability were transformed to $[\ln(x + 1)]$ in order to meet a power law (see Introduction).

Because we detected a significant additive population-level effect (see Results), a stepwise multiple regression was performed to identify population-level factors: the three independent variables were (1) size of cedar forest (log-transformed); (2) web-site availability; and (3) prey availability, and the dependent variable was “additive population-level effect”. Here, we defined additive population-level effect as the mean patch-level density in a population adjusted by web-site availability at the patch level [modified after Miyashita (1999)],

$$\frac{1}{15} \sum_{i=1}^{15} [\ln(N_i + 1) - a \ln(W_i + 1)] \quad (1)$$

where N_i is the density at patch i , W_i is web-site availability at patch i , and a is the slope of regression between $\ln(N_i + 1)$ and $\ln(W_i + 1)$ common to all populations. This value is equivalent to a y -intercept in each population.

For the indices of prey availability, mean body size of females in a population was also used for the juveniles, because it reflects cumulative prey availability. For the adult, first principal component combining female body size and arthropod biomass captured by the sticky trap was used because these two parameters correlated positively ($r = 0.51$, $F_{[1,13]} = 4.53$, $P = 0.053$).

To test whether the larger-scale effect changes the strength of the relationship between web-site availability and density at the patch level, we performed ANOVA using absolute deviation from the regression line as a dependent variable and “population” as a factor (Levene’s test; Schultz 1985). Because we detected a marginally significant difference (see Results), we additionally performed multiple regression analysis; the dependent variable was mean absolute deviation in a population, and the independent variables were size of cedar forest (log-transformed), web-site availability, and prey availability at the population level. We also examined the relationship between mean absolute deviation and additive population-level effect by simple linear regression analysis, because we have an a priori hypothesis that the effect of a limiting factor becomes stronger with increasing population density (e.g. Whittaker 1971; Elliot 1987).

Because absolute deviation is likely to be small in populations with low density due to larger random fluctuations in the log-transformed number of individuals, we adjusted it using the following simulation. First, we calculated the mean density of all patches in each population, and assumed that the density at a patch is determined by a value derived randomly from a Poisson distribution with the mean value. For each value sampled, we calculated the absolute value of $[\ln(\text{sampled value} + 1) - \ln(\text{mean value} + 1)]$. We repeated this procedure 1,000 times, averaged these absolute deviations (AD') and obtained adjusted absolute deviation $[AD_{(\text{adj})}]$ using the following formula,

$$AD_{(\text{adj})} = AD - (AD' - AD'_{\text{max}}) \quad (2)$$

where AD was absolute deviation from the regression line obtained from actual data, and AD'_{\max} represents AD' obtained from the population with the highest mean density.

Results

ANCOVA showed that the interaction between population and web-site availability at the patch level was not significant at either the juvenile or the adult stage (Fig. 2; juvenile: $F_{[14,193]} = 1.58$, $P = 0.088$; adult: $F_{[14,194]} = 1.06$, $P = 0.393$), indicating that the slopes of the regressions between web-site availability and density at patch level did not differ among populations. The common regression slope, being 1.01 and 0.97 in juvenile and adult, respectively, was significant at both stages (juvenile: $F_{[1,207]} = 73.57$, $P < 0.0001$; adult: $F_{[1,208]} = 70.56$, $P < 0.0001$), implying that there was a significant positive relationship between density and web-site availability at the patch level. ANCOVA also showed that the patch-level density adjusted by the covariate differed significantly among populations (juvenile: $F_{[14,207]} = 13.27$, $P < 0.0001$; adult: $F_{[14,208]} = 11.93$, $P < 0.0001$), indicating the presence of an additive population-level effect on patch-level density.

A stepwise multiple regression showed that web-site availability at the population level alone positively correlated with the population-level effect at both stages (Fig. 3; juvenile: $r = 0.44$, $F_{[1,13]} = 9.56$, $P = 0.009$; adult: $r = 0.23$, $F_{[1,13]} = 6.81$, $P = 0.022$).

Adjusted absolute deviation tended to differ among populations at the juvenile stage ($F_{[14,208]} = 1.66$, $P = 0.065$) but not at the adult ($F_{[14,209]} = 0.80$, $P = 0.670$). This means that there appeared to be a non-additive effect at the juvenile stage. Multiple regression analysis revealed that none of the population-level parameters explained variations in the absolute deviations. However, we found a marginally significant negative relationship between the absolute deviation and additive population-level effect at the juvenile stage (Fig. 4; $r = -0.50$, $F_{[1,13]} = 4.43$, $P = 0.055$). This indicates that the relationship between density and web-site availability at the patch level appeared to be strengthened by the greater additive effect at the juvenile stage.

Discussion

We found that patch-level web-site availability appeared to be a determinant for patch-level density, because it was correlated positively at both juvenile and adult stages. We also demonstrated a population-level effect that determines patch-level density in an additive way. If this is the case, what causes the additive population-level effect, and how does it affect patch-level density?

Additive population-level effect increased with increasing web-site availability at the population level (Fig. 3), but it showed no relationship with prey avail-

ability index. Since adult female body size, which was used as a measure of prey availability, is known to correlate with fecundity of spiders (Miyashita 1986; Wise 1993; Miyashita 1999), difference in reproductive rate is unlikely to cause the population-level effect. Accordingly, the population-level effect should be attributed to the difference in mortality rate associated with web-site availability at the population level.

The difference in mortality rate among populations associated with web-site availability may be caused by the mortality risk, presumably due to predation, during movement when spiders are seeking new web sites. Lubin et al. (1993) showed that in a widow spider, *Latrodectus revivensis*, the probability of surviving 2 days was 0.98 on its web, whereas only 0.59 during movement to new web sites, demonstrating the higher mortality risk while moving. Web spiders often relocate their webs in response to local variation in food supply (Olive 1982; Vollrath 1985; Gillespie and Caraco 1987; Tanaka 1989) or disturbance such as web destruction by wind, rain, or litter fall (Hodge 1987; Leclerc 1991). Thus, mortality risk associated with movement is likely to be higher in populations with low web-site availability because the distance between the places of web-abandonment and web-establishment may be longer. On the other hand, it appears that the higher population density associated with higher web-site availability increases the likelihood of movement as a result of intraspecific competition (e.g., Riechert 1981). Therefore, frequency of movement may be higher in populations with higher web-site availability but the distance during a movement is longer in populations with lower web-site availability. If the mortality rate due to the risk during one movement exceeds the mortality rate due to movement frequency, the overall mortality rate will be higher in populations with lower web-site availability. We hypothesize that the density became higher in populations with more web-site availability by this mechanism.

It is worth noting that factors operating at the patch and population levels were the same, i.e., web-site availability, which affected patch-level density separately. The population-level effect shown here appears to be an emergent property, i.e., the whole is greater than the sum of the parts (Kauffman 1995), because patch-level density can be anticipated by the patch-level web-site availability plus population-level web-site availability. As noted earlier, the emergent property could have arisen from the alteration in the mortality rate at the time of web relocation that probably occurred at a between-patch level. This concept is basically identical with that of metapopulation in that habitat fragmentation increases mortality rate during movement among patches, which disproportionately decreases metapopulation size and hence patch-level density compared to those expected from the total habitat size (e.g., Hanski 1999). However, in our system, there are no physical boundaries among "patches." This means that, even in seemingly homogenous environments, the abundance of organisms can be determined by emergent processes. It

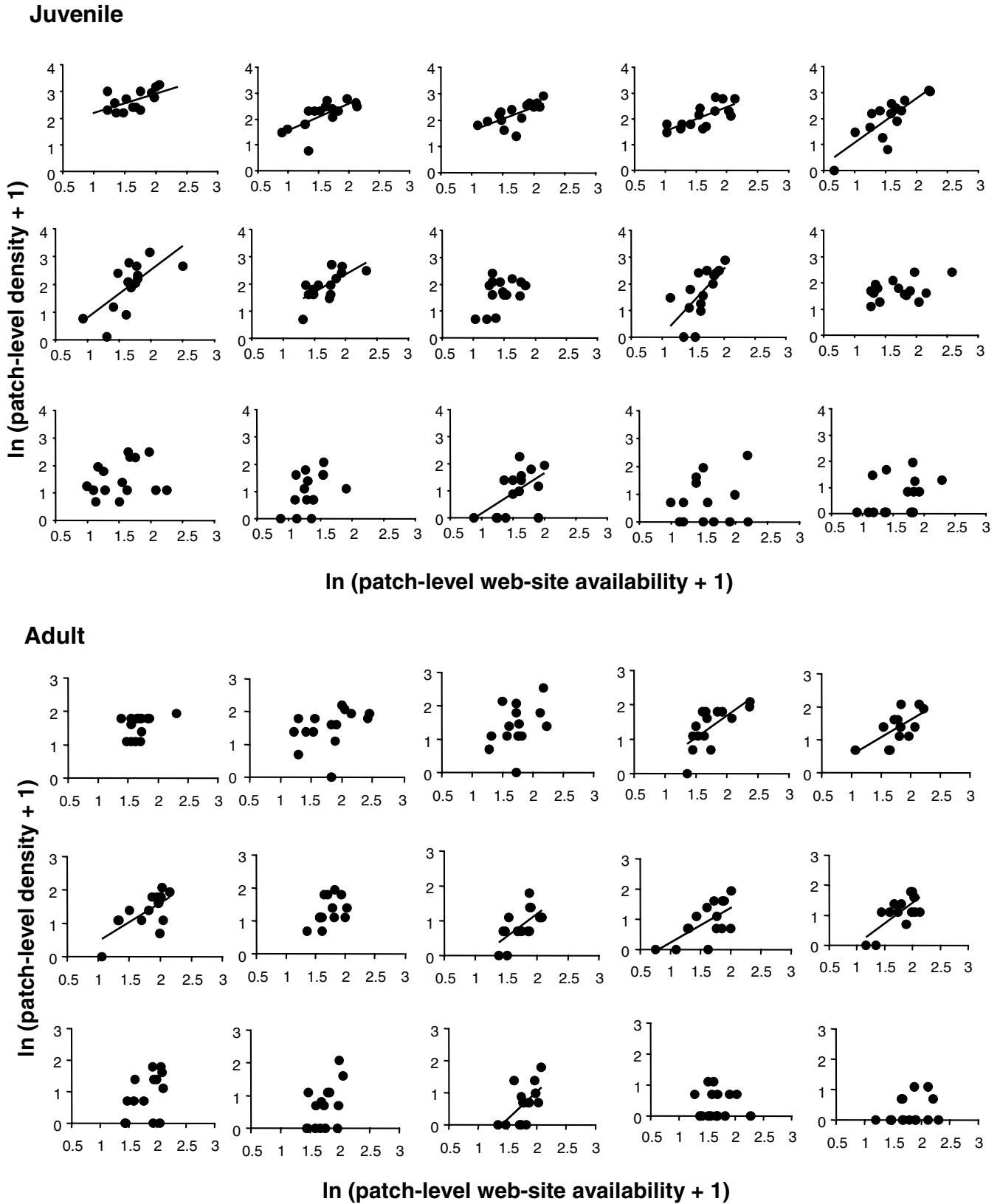


Fig. 2 The relationship between density and web-site availability at the patch level in each population at the juvenile and adult stages. The graphs are ordered from the population with the highest patch-level density (*upper left*) to the population with the lowest density (*lower right*)

should be borne in mind that this process can be identified only when considering multiple spatial scales.

We also found weak evidence for a non-additive larger-scale effect, i.e., absolute deviation from the

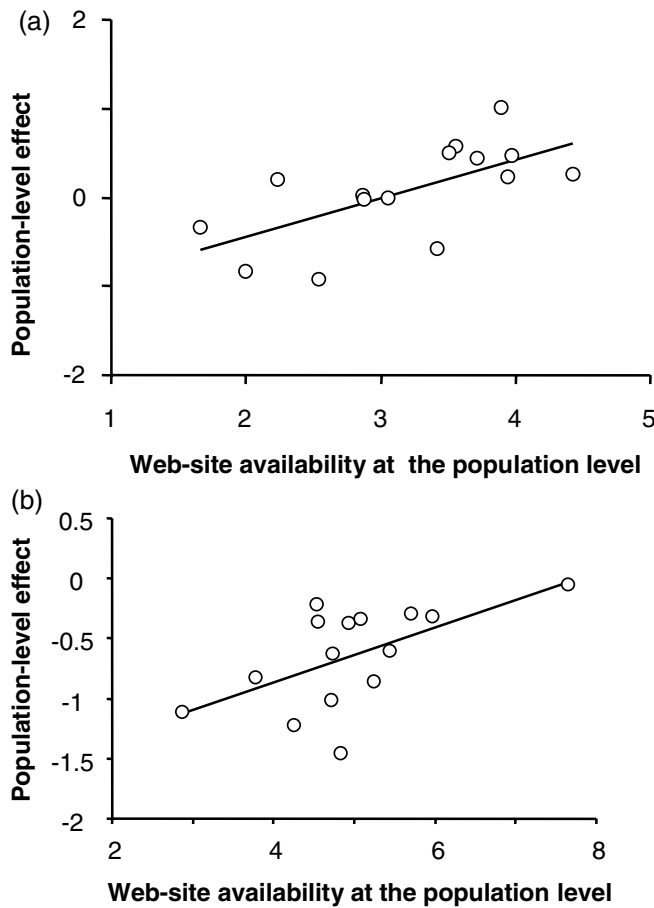


Fig. 3a, b The relationship between additive population-level effect (see text) and web-site availability at the population level at the juvenile (a) and adult (b) stages. Each point represents one population

regression line between density and web-site availability at the patch level decreased with an increasing additive population-level effect (Fig. 4). This is likely to have happened because increasing overall density led to saturation of density with respect to web-site at the patch level, and hence caused a stronger relationship between density and web-site availability at the patch level. This may be equivalent to Haldene's (1956) description that changes in population density are largely due to density-dependent factors in favorable areas, and density-independent factors in unfavorable areas, which has also been demonstrated in natural populations (e.g., Whittaker 1971; Elliott 1987). At the adult stage, however, we detected no larger-scale effects influencing the strength of the patch-level effect. Since the population density was lower in this stage, density dependence appeared to be weaker.

This study has tried to evaluate both additive and non-additive effects of the larger spatial scale, but one type of non-additive effect, i.e., the interaction between large-scale and small-scale effects, was not detected. This effect could be acting in other systems. For example, if prey abundance changes competitive interactions for a web site, and prey abundance differs between popula-

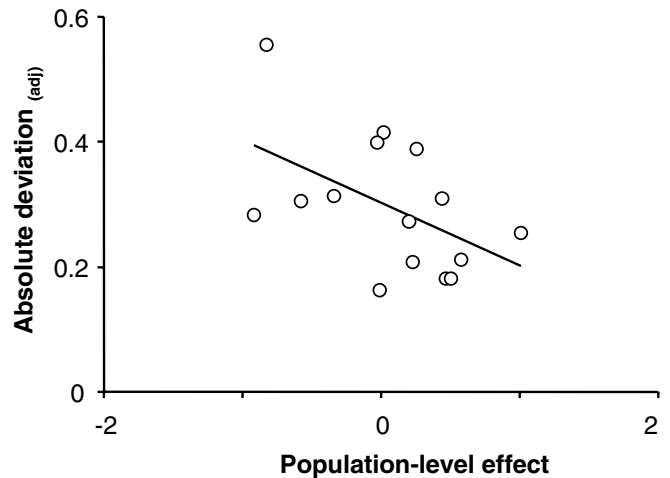


Fig. 4 The relationship between adjusted absolute deviation from the regression line (see text) and additive population-level effect at the juvenile stage. Each point represents one population

tions, the regression slope between density and web-site availability at the patch level could also be different. Considering additive and non-additive processes and identifying the underlying mechanisms seems to be an effective way for generalizing how the abundance of organisms is determined in nature.

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