

Prairie dog engineering indirectly affects beetle movement behavior

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Abstract

Previous studies have shown that landscape structure influences animal movement and population structure. In this study, we show an indirect interaction between beetles and prairie dogs due to prairie dog ecosystem engineering. Gunnison's prairie dog (*Cynomys gunnisoni* Hollister) towns have more bare ground and are structurally less complex than adjacent unmodified grasslands. This results in bare ground facilitating beetle movement. Differences in landscape structure between prairie dog towns and unmodified grasslands had a significant effect on the movement of the darkling beetle, *Eleodes hispilabris* Say. Beetle movement tended to be more linear (pathway fractal dimension approached 1) on prairie dog habitats and more sinuous on adjacent grasslands. Beetle velocity was 44% greater and net displacement 63% farther on the prairie dog habitat. These differences were also evident at fine scales when beetles moved between grass and bare ground patches regardless of habitat. Beetles moved 2.3 times faster and displaced 3.0 times farther after making this microhabitat transition. Beetles avoided grass and selected bare ground for movement 12–22% more than the percent of bare ground on the landscape. Since beetles exhibited directed movements and grasslands inhibit movement, it might be expected that beetles would accumulate in this habitat upon encounter. However, beetles were approximately twice as abundant on prairie dog towns as on adjacent grasslands. A difference in beetle movement behavior, between prairie dog towns and grasslands, suggests that prairie dog towns are an important component of this desert grassland landscape for these beetles.

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1. Introduction

The study of animal movement patterns provides important insights into the behavioral ecology of an organism and may reveal how an animal interacts with the landscape. Both empirical and theoretical work has examined the attributes of animal movement and population distributions (e.g. Kareiva, 1983; Dicke and Burrough, 1988; Turchin, 1991; Crist and Wiens, 1995). Much of the work exploring the interaction between landscape structure and movement has been done with several species of darkling beetles (Tenebrionidae: Slobodchikoff and Doyen, 1977; Wiens and Milne, 1989; Crist et al., 1992; Johnson et al., 1992; Wiens et al., 1997).

By studying movement pathways, we might functionally connect organisms to the landscape, thus moving “towards a behavioral ecology of ecological landscapes” (Lima and Zollner, 1996). Movement should be important to organisms because movement attributes (e.g. pathway pattern, velocity, and net distance traveled) coupled with landscape structure can determine spatial population structure, can influence encounter rates with resources, mates, and predators, and can influence dispersal (Turchin, 1991; Crist and Wiens, 1995; With and Crist, 1995, 1996; McIntyre and Wiens, 1999b). The effects of individual movement can have consequences at the level of individual fitness as well as at the population level and can help explain community composition and habitat selection.

In the arid and semi-arid grasslands of western North America, prairie dog activities significantly influence landscape structure by reducing grass cover and altering the spatial pattern of grass and bare ground (Bangert and Slobodchikoff, 2000). Gunnison’s prairie dog (*Cynomys gunnisoni* Hollister) towns and the grasslands surrounding these towns have abundant populations of *Eleodes hispilabris* Say (Tenebrionidae), a large, black, flightless beetle that walks on the ground surface and feeds on detritus. In this paper, we address the general question: is beetle movement behavior correlated with landscape structure? The following predictions on beetle movement were guided by percolation theory (Gardner et al., 1989) and empirical work on darkling beetles (Wiens and Milne, 1989; Crist et al., 1992). We predicted that on habitats modified by the activities of prairie dogs: (1) beetle pathways will be more linear; (2) beetle velocities will be greater; (3) beetle net (i.e. straight-line) displacements will be farther per unit time than on adjacent unmodified grassland landscapes. We also predicted that *E. hispilabris* should choose bare ground more often than bare ground availability. If bare ground is the factor facilitating beetle movement, then velocity, displacement, and the ratio of displacement to path length should increase when beetles make the transition from grass to bare ground patches. Finally, because prairie dog habitats have large areas of bare ground, we predicted that beetles would be more abundant on this habitat type relative to the adjacent grasslands.

2. Materials and methods

2.1. Study sites and organisms

This work was conducted on the high desert grasslands (1600–1750 m) at Petrified Forest National Park, Arizona, USA. Petrified Forest has an average annual

precipitation of 24.4 cm (range 8.6–40.1) and average high temperatures ranging from 0.8°C in January to 23.5°C in July. Precipitation has a single peak in July and August due to the summer south-west monsoon. The vegetation in the Park is characterized as shrub-steppe dominated by large shrubs and grasses (Kierstead, 1981).

Gunnison's prairie dog (*C. gunnisoni*) is a medium sized (675–1350 g) ground squirrel in the family Sciuridae. This species is found on the Colorado Plateau extending across four states in North America: Arizona, Colorado, New Mexico, and Utah (Fitzgerald et al., 1994; Goodwin, 1995). Gunnison's prairie dogs are colonial and social animals (Slobodchikoff, 1984, pp. 227–251; Hoffmeister, 1986; Fitzgerald et al., 1994). Prairie dogs modify the surface of the landscape through grazing activities and digging for seeds (Shalaway and Slobodchikoff, 1988), which increases the patchiness of grasses and shrubs on prairie dog colonies (Bangert and Slobodchikoff, 2000).

Beetles in the genus *Eleodes* are conspicuous animals of the dry grasslands in western North America and make a considerable contribution to both the richness and abundance of arthropod communities (Crawford, 1981, 1991, pp. 89–112; Hawkins and Nicoletto, 1992; Bangert and Slobodchikoff, unpublished data). *E. hispilabris* is a generalist detritivore (Rogers et al., 1988). Because these beetles are flightless, they are particularly constrained to interact with landscape structure. Therefore, this is a good model species in which to study the relationship between landscape structure and movement behavior in naturally manipulated landscapes. In the second week of July 1996, we measured 12 pathways of *E. hispilabris* that were located opportunistically on one prairie dog town and five beetles on the adjacent grassland habitat between 0600 and 0800 MST. This is during the time of *E. hispilabris*' preferred activity period (Slobodchikoff, 1983; Whicker and Tracy, 1987). After a beetle was located, we waited 5 min for the beetle to habituate to our presence and then began marking the beetle's pathway. When these beetles are disturbed, they stop and adopt an aposomatic defensive headstand posture (Slobodchikoff, 1987). We feel that we were not influencing beetle movement because no beetles exhibited this behavior (see Johnson et al., 1992).

In 1998, a different prairie dog town and grassland site were used to increase the generality of our findings. Paired *t*-tests were planned a priori for the 1998 pathway trials in order to reduce the variance between beetles and to introduce an experimental component into this study. Beetles were collected at least 2 weeks prior to the tracking trials and maintained on rolled oats and water ad libitum. Beetles were randomly selected and assigned to either the prairie dog or grassland habitat for their initial pathway. Following this, the same beetles were then tracked on the other habitat within 1 week of the first tracking. For tracking, beetles were placed under an opaque cover for 5 min to reduce stress from handling and then released. The first few movements tend to be short and slow in released beetles so we waited 30 s before the initial marking of the pathway (Crist et al., 1992).

Beetle locations were marked with numbered toothpicks every 5 s for a maximum of 100 time steps, resulting in a maximum time of 8 min 20 s per pathway. We waited for the beetle to move to the next location before placing the marker at the previous

location to avoid disturbing or herding the animal (Johnson et al., 1992). Timing stopped as long as the beetle was stationary for any reason, because we were specifically interested in movement and not other activities such as foraging. Some pathways were terminated before the allotted 100 time steps if the beetle entered a prairie dog burrow or ceased movement for > 5 min. Beetle locations were measured to the nearest 0.5 cm by establishing a Cartesian coordinate grid over each pathway so the pathway fractal dimension, velocity, turn angles, and net displacement could be calculated (analytical methods follow Wiens and Milne, 1989; Crist et al., 1992; Johnson et al., 1992). Cover at each beetle location was recorded to assess beetle microhabitat selection between bare ground and grass.

For fine scale analysis of movement we used adjacent path segments of equal size on bare ground and grass to test if movement attributes per unit time changed as the beetle moved from grass to bare ground. Only one pair of segments was used from a beetle path and the data were analysed with paired *t*-tests. The ratio of displacement to segment length was used as a surrogate for linearity because the fractal dimension could not be calculated for these short pathway segments. Displacement to segment length ratios closer to unity is an indication of more linear movements.

We analysed beetle turning behavior with circular statistics (Batschelet, 1981) to assess whether habitat structure influenced beetle movement parameters. We tested for the independence of successive turns within a pathway with a runs test since successive measurements are obtained from a single individual (Cain, 1989). Beetle turn angles were not different between habitats and beetles did not exhibit patterns of successive right-hand or left-hand turns between habitats. As a general result, beetles exhibited directed movements in both habitat types. Consequently, we can analyse other attributes of their movement behavior (e.g. path structure, beetle velocity, and net displacement) as a function of habitat structure rather than a function of intrinsic beetle behavior.

Fractal methods facilitate the quantification of movement pathways by describing the complexity or tortuosity of a pathway which is neither a straight line (Euclidean exponent of 1) nor plane filling like the path traced out by a Brownian particle (Euclidean exponent of 2). Sinuous pathways have a fractional exponent *D*, where $1 < D < 2$ (Mandelbrot, 1983; Dicke and Burrough, 1988; Sugihara and May, 1990). For example, the length of a sinuous line is dependent on the length of the measurement scale and cannot easily be described with Euclidean geometry. The fractal dimension of beetle pathways were extracted using the dividers method (Dicke and Burrough, 1988; Sugihara and May, 1990) where the apparent length of the pathway was measured using “rulers” of varying size giving length as

$$L(\delta) = k\delta^{1-D},$$

where *L* is the apparent length measured with ruler length δ , *k* is a constant, and *D* is the fractal dimension, i.e. the scaling exponent of the pathway. $1 - D$ is the slope of the log–log plot of path length versus ruler length and linear regression was used to extract this slope. If the pathway is fractal, r^2 will be close to unity (Wiens and Milne, 1989). In these analyses r^2 ranged from 0.8991 to 0.9904 for all 33 paths indicating a

strong relationship between pathway length and measurement scale over the range of time steps (1, 2, 4, 8, 16, 32, 64, and 100) in this study.

We calculated beetle velocity as the total distance traveled measured with the smallest ruler length, divided by the total number of seconds to give velocity as cm/s. Velocity was calculated the same way in both years and was not scaled to the pathway with the shortest number of time steps. *t*-Tests were used to analyse differences in velocity between habitat types within year.

Net displacement measures how far an animal moves in a straight line. It is a function of pathway tortuosity, velocity, and is scale dependent. To standardize comparisons, we scaled displacement to the shortest path within each year and used *t*-tests to quantify differences between habitats for each year.

Microhabitat selection measures beetle preference for bare ground or grass within a habitat type. We recorded cover type for each beetle location to assess microhabitat selection for grass and bare ground, i.e. the beetle was either on bare ground or in a clump of grass. We performed binomial tests for each beetle to determine selection for these two cover types and we adjusted probabilities for the proportion of the two cover types at each site. For graphical purposes, we pooled all beetle locations by habitat within year and the overall binomial test reported. The overall test was not different from the individual tests. Analysis of microhabitat selection on the 1998 prairie dog town was not performed because the plot was 100% bare ground, thus, no choice was available.

Finally, we quantified beetle relative abundance as an estimate for habitat selection between prairie dog towns and grasslands with chi-square tests. We conducted pitfall trapping in 1996–1998 on the study sites where beetles were tracked. There were 50 pitfall traps per habitat type randomly located over one hectare. Over the 3 years of population sampling, habitats were sampled simultaneously, for a total of 1286 trap days. One visual survey was conducted for 5 days on the 1996 tracking sites. Beetles were always marked so individuals would not be counted twice. A combined probability test (Sokal and Rohlf, 1995) was used for the four surveys of beetle abundance.

3. Results

3.1. Beetle movement

The landscape structure at the sites where beetles were tracked was significantly different between the habitat types. Grassland habitats were more complex and bare ground patch size was more variable (Bangert and Slobodchikoff, 2000). The structure of beetle pathways was different in different habitats in both years (Fig. 1). Pathway structure described by the fractal dimension, *D*, was higher, i.e. more sinuous, on grassland habitats and relatively linear on prairie dog towns (*D* closer to unity), although these differences were not statistically significant (1996: $p = 0.06$, power = 0.33, 1998: $p = 0.13$, power = 0.63).

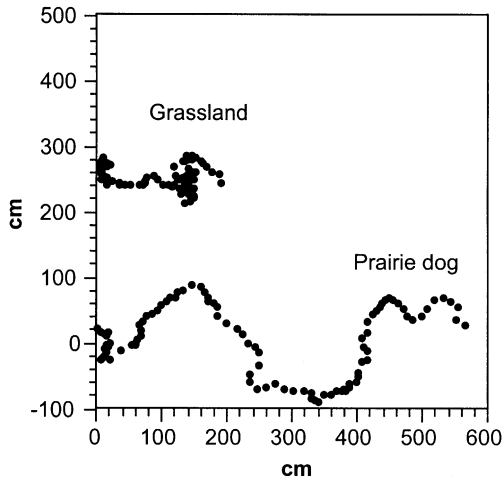


Fig. 1. Representative beetle pathways on the 1996 grassland (upper path), and prairie dog town. Both paths were marked over an 8 min 20 s time period.

In both years, beetle velocities were significantly greater on prairie dog habitats compared to grassland habitats (1996: $N = 17$, $t = 2.19$, $p = 0.023$; 1998: $N = 8$, paired $t = 2.83$, $p < 0.02$; Fig. 2a). There was a strong positive relationship between mean landscape structure and mean beetle velocity; beetles moved faster as landscape fractal dimension increased and the habitat became less complex ($r^2 = 0.9919$, $F_{1,2} = 244$, $p = 0.004$, Fig. 3b).

When beetle pathways are linear and velocities higher, beetle mean displacement should be greater. In both years, beetles exhibited significantly greater mean displacements on prairie dog towns (1996: $N = 17$, $t = 1.76$, $p < 0.05$; 1998: $N = 8$, paired $t = 2.19$, $p < 0.03$; Fig. 2b). There was a strong positive relationship between mean landscape structure and mean beetle displacement; beetles displaced farther as landscape fractal dimension increased and the habitat became less complex ($r^2 = 0.9803$, $F_{1,2} = 99.5$, $p = 0.01$, Fig. 3b).

Beetle movement at finer scales changed significantly, when beetles made a microhabitat transition from a grass patch to a bare ground patch. Beetle velocity ($N = 8$, paired $t = 4.08$, $p = 0.002$), net displacement ($N = 5$, paired $t = 4.44$, $p = 0.004$), and displacement to total path length ratio ($N = 5$, paired $t = 2.37$, $p = 0.03$) each exhibited a significant increase when beetles made this microhabitat transition (Fig. 4). This indicates that the landscape attributes of bare ground and grass are the factors facilitating or inhibiting beetle movement.

3.2. Microhabitat selection and beetle abundance

Because less complex habitats facilitate beetle movement, and bare ground is a major component of simple landscapes, bare ground should be important to these animals. In all habitats, *E. hispilabris* chose bare ground significantly more often

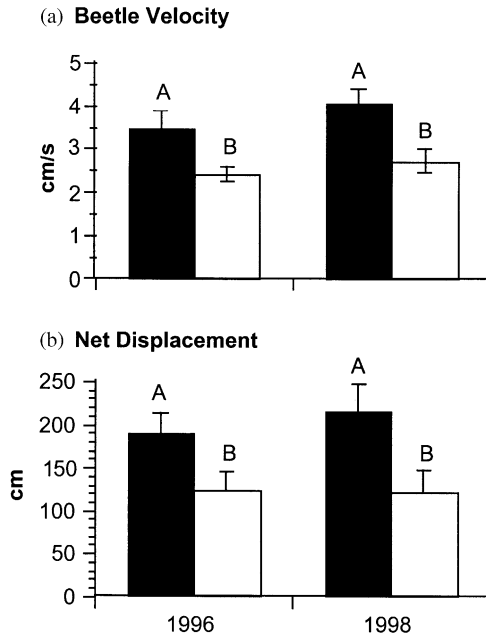


Fig. 2. Beetle movement attributes. Error bars are ± 1 S.E. of the mean and letters above the bars indicate significant differences. Black bars represent prairie dog habitat.

than the proportion of bare ground in that habitat (binomial test, $N = 33$, all $p < 0.000$; Fig. 5).

If simple landscape structure and higher proportions of bare ground are important to these beetles we should find more beetles on the prairie dog landscapes. In four different surveys for *E. hispilabris*, there were significantly more beetles found on the prairie dog habitats than the adjacent grassland habitats where beetles were tracked (combined probabilities test $\chi^2 \approx 28.4$, df. = 8, $p < 0.001$; Fig. 6). In the visual survey, the area surveyed in the grassland was 1.67 times greater than the area surveyed on the prairie dog town, and yet there were nearly two times as many beetles encountered on the prairie dog habitat (goodness of fit $\chi^2 \approx 19.2$, df. = 1, $p = 0.0001$). This indicates that the pitfall data did not overestimate beetles on the prairie dog habitat. Since beetle movement is directed and they move significantly faster across the prairie dog town, when beetles encounter grassland habitats, they might be expected to be retained in that habitat type. Our results are the opposite of this expectation.

4. Discussion

All but one of our predictions was met for beetle movement and population distribution. Habitats modified by prairie dogs had a significant impact on beetle

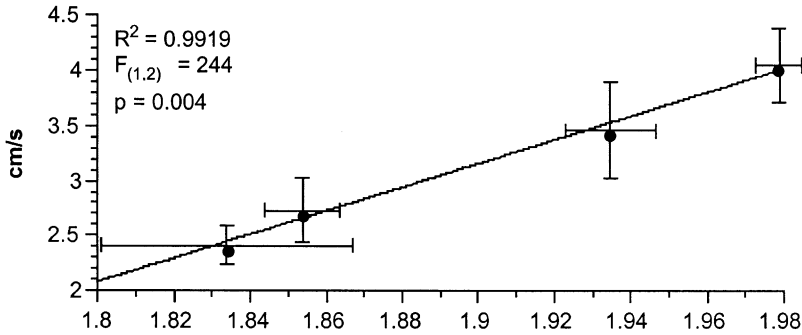
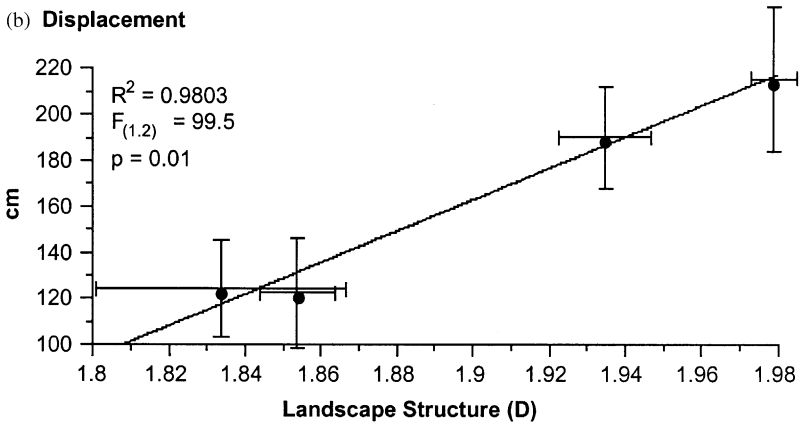
(a) **Velocity**(b) **Displacement**

Fig. 3. Mean beetle movement attributes correlated with landscape structure. Error bars are ± 1 S.E. of the mean.

movement behavior and distribution. Beetle movement was facilitated on the less complex prairie dog towns, was inhibited on the complex grasslands, and beetles were more abundant on landscapes modified by prairie dogs. Moreover, the observational results were similar to the experimental results. As landscapes became simpler in structure, beetle movement became more linear, velocity increased, and beetles moved farther. The same patterns were evident at fine scales when beetles made transitions from grass to bare ground, independent of the habitat they were on. These three movement parameters may have fitness consequences for these beetles since movement may influence beetle encounter rates with food resources (McIntyre and Wiens, 1999a), mates, microsite refugia (e.g. prairie dog burrows; unpublished data), and predators. Previous studies have shown that landscape structure influences animal movement (e.g. McIntyre and Wiens, 1999a; With et al., 1999); however, this is the first study to show that landscape structure modified by an ecosystem engineer resulted in an indirect interaction that affects beetle behavior.

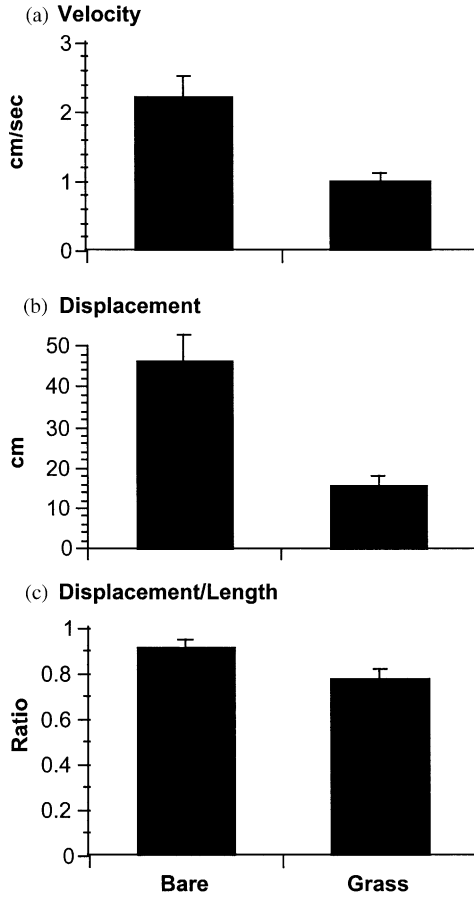


Fig. 4. Microhabitat transitions and beetle movement attributes when the beetle moved from a grass patch to bare ground. Error bars are ± 1 S.E. of the mean. Black bars represent prairie dog habitat.

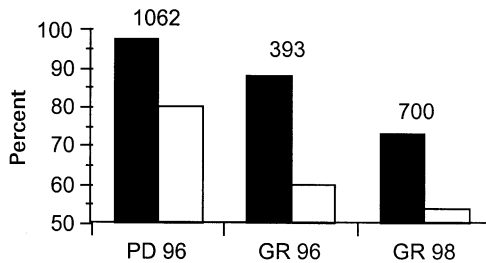


Fig. 5. Beetle microhabitat selection for bare ground over grass when moving versus the availability of bare ground. All binomial test $p < 0.000$. No tests were done on the 1998 prairie dog town because the entire area was 100% bare ground, thus no choice was available on this plot. Numbers above bars are the total number of beetle locations on that habitat. Black bars represent bare ground use and white bars represent bare ground availability. PD = prairie dog, GR = grassland, and numbers = year.

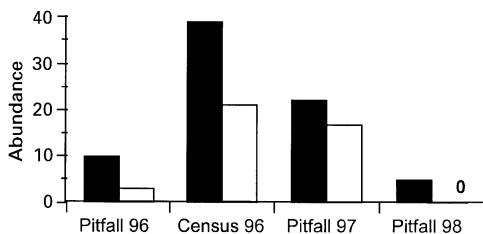


Fig. 6. Beetle macrohabitat selection for prairie dog towns compared to grassland habitats with a combined probabilities $p = 0.001$. Black bars represent prairie dog habitat.

Landscape structure may interact with resource distribution. It is possible that food on prairie dog towns might exhibit a clumped distribution on a landscape surface with more open areas and more isolated clumps of grass. Other studies have found that particles of detritus and seeds tend to gather in depressions and around clumps of vegetation due to the physics of particle transport (Reichman, 1984; Price and Reichman, 1987). On the other hand, food resources may have a more even distribution on the grassland habitat with less bare ground and its subsequent influence on particle transport. If the grassland habitat is difficult to negotiate, resources may become functionally unavailable regardless of distribution, resulting in habitat selection for bare ground and more open landscapes that facilitate movement, that is, the prairie dog habitat. Resources can also be augmented by the digging activities of prairie dogs, opening up patches of detritus and seeds that the beetles can utilize.

Additionally, the prairie dogs may provide microrefugia to the beetles. The beetles operate within a relatively narrow temperature range (Slobodchikoff, 1983). Once this temperature range is exceeded, the water balance of the beetles is seriously affected, and the beetles can die from water stress. The burrows of prairie dogs may provide an equitable environment where the beetles can ameliorate the consequences of water stress suffered through foraging on the surface of the ground (e.g. Schmidt-Nielson and Schmidt-Nielson, 1950). Thus, prairie dog modified habitats may offer a suite of resources that potentially can increase the beetles' fitness.

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