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BUTTERFLIES OF GLACIER NATIONAL PARK, MONTANADIANE DEBINSKI¹*Department of Biology, Montana State University,
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ABSTRACT As part of a biodiversity inventory and monitoring project, I sampled butterfly species diversity during three summers in Glacier National Park, Montana. The species lists assembled are compared with two historic species lists in order to identify trends in species richness. The addition of nine new species to the earlier inventories resulted in a total of 97 butterfly taxa in the park. However, of the species reported previously, one has not been sighted since 1935 and another since 1950. Notes regarding species habitat preferences are included.

Key words: Biodiversity, Species diversity, Butterflies, Lepidoptera, Glacier National Park.

In 1987, I initiated a 3-yr project to establish an inventory and monitoring program for biodiversity of birds and butterflies (Debinski, 1991). As part of this project, butterfly species diversity was sampled throughout a range of habitat types in Glacier National Park, Montana. The data gathered were compared with two earlier species lists—one compiled by John Garth in 1955 (pers. comm.) and a second compiled by Steve Kohler (1980)—to identify trends in species richness.

Glacier National Park lies at the northwestern edge of Montana and is one of the most pristine national parks in the U.S. The large variety of habitats in the Park are in part the result of the Park's position relative to the continental divide, which bisects it in a north-south direction. Elevations of

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sites in Glacier National Park range between 1097 and 3048 m. The west side of the park is a temperate rainforest with stands of cedar-hemlock (*Thuja plicata*-*Tsuga heterophylla*), spruce-fir (*Picea engelmannii*-*Pseudotsuga menziesii*), and lodgepole pine (*Pinus contorta*). The east side is drier and windier and is characterized by aspen (*Populus tremuloides*) parklands and sagebrush (*Artemisia tridentata*) meadows. Habitat types include alpine meadows, bogs, rocky ridges, riparian corridors, low-elevation meadows, ponderosa pine stands, and forests dominated by lodgepole pine, spruce-fir, and cedar-hemlock.

MATERIALS AND METHODS

CENSUS SITES

During 1987, 58 sites were sampled with the objective of censusing extensively throughout the park. The sites were selected more on the basis of their position in the topographic and elevational gradients in Glacier National Park than by their habitat type. Temperature and moisture gradients, quite independent of habitat types defined by vegetation, are often of primary importance in determining the distribution and local abundance of many terrestrial plant and animal taxa (Whittaker, 1952; Terborgh, 1970; Brussard, 1985). Several methods of site categorization were considered (e.g., Elton and Miller, 1954; Southwood et al., 1979; Bunce and Shaw, 1973). The technique used consisted of (1) marking the location of each site on a 7.5-min United States Geological Survey (USGS) topographic map, (2) recording the elevation, slope, and exposure of the site, and (3) briefly categorizing the habitat type of the site (e.g., xeric meadow, riparian, lodgepole pine forest). On the basis of these data, each site was plotted on a two-dimensional graph representing the available "ecological space" in Glacier National Park where ecological space is defined graphically with elevation as the ordinate and moisture conditions (ranging from hydric to xeric on the flats and based on aspect, slope, and exposure on mountainsides) as the abscissa. Additional sites then were chosen to sample the full range of combined topographic and elevational conditions in the Park.

The 1987 sites varied in both size and shape. Those that were inaccessible by road, could be visited only once. Temporal replication was necessary because of phenological differences among butterflies; for example, some species emerge early in the summer, whereas others emerge in late summer. To increase the number of temporal replicates, I sampled only 24 sites in 1988 and 1989; this was the maximum number that could be visited at least twice during the summer. Thus, each site was surveyed more intensively, but the Park, as a whole, was sampled less extensively.

Nonetheless, the 24 sites selected are representative of the range of geographic and environmental variation within the Park (Fig. 1). Each of the 1988–89 sampling sites was 1 square kilometer as defined by Universal Transverse Mercator coordinates on USGS topographic maps. Field experience in 1987 indicated that sampling sites must be at least this size to represent the range of small-scale patchiness and microhabitats adequately.

Although standard community-sampling procedures call for use of sampling sites that are homogeneous in structure and composition (Gauch, 1982), I chose to maximize sampling of habitat diversity in the 1988–89

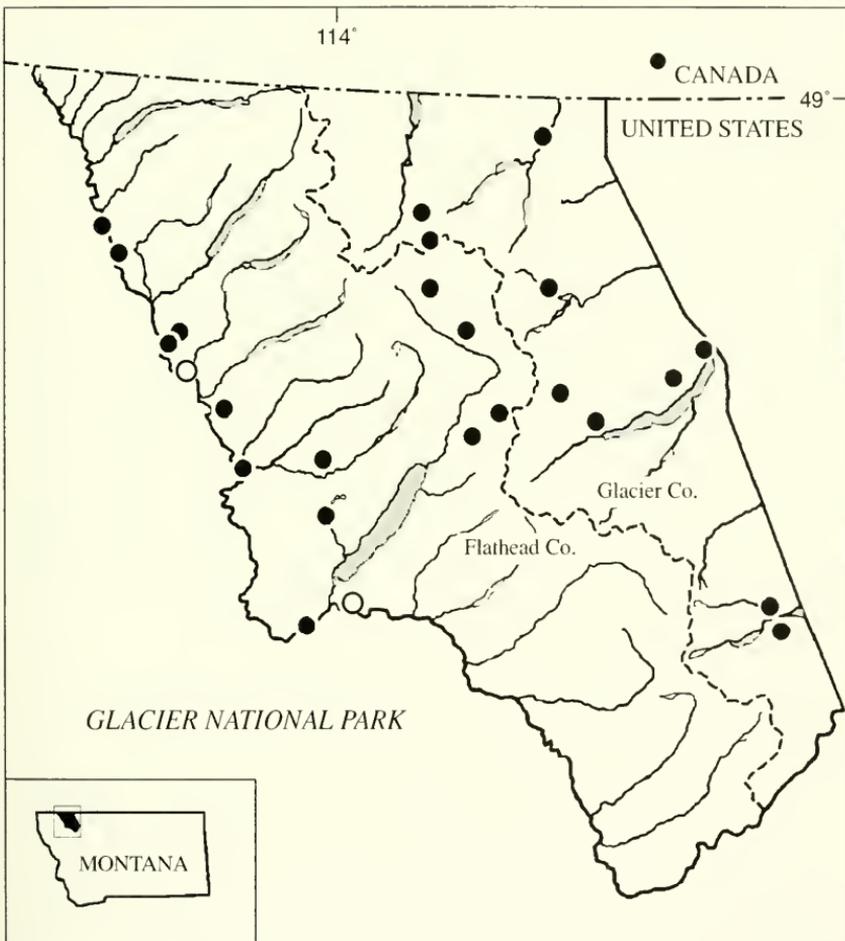


Fig. 1. Glacier National Park biodiversity sites for butterflies in 1988 and 1989. Open circles represent sites surveyed during only one year, whereas closed circles represent sites surveyed during both 1988 and 1989. See Debinski (1991) for detailed descriptions and names of sites.

sites for two reasons. First, this study was designed to inventory species occurrences across a very large area; thus, site homogeneity was ignored to maximize broadscale coverage. Second, because I observed in 1987 that species diversity was much higher along ecotones, I included ecotones in many of the sites. Nevertheless, broad habitat-type characterizations were still possible at each site.

This particular design resulted in a certain bias. Vegetational types or ecological space defined by position on the topographic-elevational gradient were not sampled in direct proportion to their frequency of occurrence in Glacier National Park. Instead, some of the rarer habitats were over-represented as I attempted to sample rare species and to increase coverage of ecological space along temperature and moisture gradients. The primary disadvantage of this approach is in statistical analysis of the data; the perceived rarity of a species may not be indicative of its true rarity in Glacier National Park.

SAMPLING

Butterflies were censused in three separate 50 × 50-m subplots in each site by netting for 20 min and releasing. Subplots were chosen to represent as much of the variation included within the larger plot as possible. The sampling periods were established empirically by plotting the number of species recorded against time. The average time at which the species-effort curve flattened out (i.e., no more species added) was considered to be the optimal sampling time in each subplot. Presence-absence data were recorded rather than abundance values, because collection of abundance data is so time-consuming that the number of samples would have been reduced dramatically. Also, species richness (*S*) is the simplest, most practical, and most objective measure of species diversity (Peet, 1974).

SPECIES RICHNESS THROUGH TIME

Earlier species lists were compared with the results of this study to determine whether species diversity had changed over time. The primary species list was that of Kohler (1980), which is based on data compiled from university collections at Montana State University and the University of Montana, private collections, the Glacier National Park collection, records from natural history museums, and a review of the published literature. John S. Garth, a Glacier National Park naturalist, also compiled species lists of butterflies during the summers of 1935, 1949, and 1950. The nomenclature used in the Appendix is standardized using Scott (1986). Because the data on species diversity were recorded as presence or absence, the significance of changes in species occurrences over time was tested by the use of simple contingency tables and *G*-tests (Sokal and Rohlf, 1981).

RESULTS

SPECIES RICHNESS THROUGH TIME

Fifty-six of the 89 butterfly species historically known to occur in the park were found during the 1 July–9 September 1987 censusing (Appendix). Because field work did not begin until 30 June in 1987, several of the early species are not represented. Earlier censusing (beginning 1 June) in 1988 and 1989 resulted in slight increases in the numbers of species sighted (69 and 65, respectively). Two species (*Lyceana hyllus* and *Nymphalis californica*) absent from both the Kohler and Garth lists were found in 1987; four additional species (*Callophrys sheridanii*, *Vanessa carye annabella*, *Satyrrium saepium* and *Neophasia menapia*) were found in 1988, and three more species were found in 1989 (*Callophrys polios*, *Speyeria aphrodite* and *Danaus plexippus*). Due to taxonomic changes, some taxa previously recognized as species are now recognized as subspecies. Thus, the total number of taxa observed during the 3-yr censusing was 84 and the new taxa total for the Park is 97. Habitat preferences as observed in this research are noted in Appendix I. Species dependent upon rare habitats (e.g., *Euphydryas gillettii* or *Colias nastes*) may be over-represented in this database because of my over-representation of rare habitats.

On comparing the results of this study with the Garth and Kohler records, I noted that all but three of the species on Kohler's list had been sighted within the last decade and most had been seen within the past few years. *Colias pelidne* and *Everes comyntas* had not been sighted since 1935 and *Papilio bairdii* had not been observed since 1950. *Polygonia comma* and *Papilio glaucus* are included on Kohler's list, but are eastern species. Because *P. comma* probably is a misidentification, it was removed from the list. *Papilio canadensis* previously was considered to be a subspecies of *P. glaucus*. *Colias alexandra* is quite scarce in western Montana; most records of this taxon are *C. occidentalis columbiensis* (Steve Kohler, pers. comm.).

MONITORING

Application of a *G*-test to the 1988 and 1989 butterfly data revealed several statistically significant differences (Appendix). There were significant changes in the occurrence of 24 of the 97 taxa between 1988 and 1989; 15 species increased in abundance in 1988 and nine in 1989.

DISCUSSION

SPECIES RICHNESS THROUGH TIME

Approximately 86% of the previously recorded butterflies were observed during the 3 yr of sampling and the total number of species observed

increased each year. Two butterfly species were added to the Park lists in 1987, four in 1988, and three in 1989. Unfortunately, a comparison between the number of species found using the more extensive sampling scheme of 1987 relative to that of the more intensive design of 1988 and 1989 was not possible. Several factors confounded this comparison. For example, sampling in 1987 started 3 wk later than it did during the next 2 yr, so several of the early-emerging species were missed. In addition, some of the biennial species will be missed during any one year.

Lycaena hyllus was found in 1987, but not seen again. *Nymphalis californica* was found in both 1987 and 1988. *Callophrys sheridanii* and *Satyrrium saepium*, *Vanessa carye annabella*, and *Neophasia menapia* were found in 1988, but not in 1989. In 1989, I identified *Callophrys polios*, *Speyeria aphrodite*, and *Danaus plexippus* as new listings for the park. The sitings of *Lycaena hyllus*, *Callophrys sheridanii*, and *Danaus plexipus* can be considered as small range expansions (one county) relative to Ferris and Brown (1981), but the remainder of the species is known to exist in at least one of the two counties in which Glacier National Park resides.

As noted above, three species have not been sighted for many years. *Colias pelidne* occurs in Montana, Idaho, Wyoming, and Oregon (Ferris and Brown, 1980). Given that this species occurs in the two counties (Glacier and Flathead) that comprise Glacier National Park, it should occur in the Park. Although *Papilio bairdii* occurs in many Rocky Mountain states, it is not known to occur outside the park in either Flathead or Glacier counties. *Everes comyntas* is an eastern species that does not occur in Montana. Prior to 1964, authors associated the Montana subspecies *Everes amyntula albrighti* Clench 1944, with *E. comyntas*. *Everes amyntula albrighti* is common in Glacier National Park and surely is the taxon which Garth referred to as *E. comyntas*. *Papilio bairdii* probably is limited in the park owing to the limited occurrence of its foodplant, *Artemisia dracunculus*. Both the plant and the butterfly are found in drier, lower elevation habitats; the butterfly probably strays into the park on occasion from areas in Montana such as western Flathead County, and Sanders, Lake, Missoula, and Ravalli counties.

Other species of concern are those with specific habitat requirements. For example, *Colias nastes* is an arctic species and Glacier National Park may be at the southernmost limit of its range. Because *Colias nastes* occurs only at high elevations within the park, loss of such habitats might reduce the total range of this species. Successional habitats are also important to monitor. Species such as *Euphydryas gillettii* depend on wet meadows where this species deposits eggs on the host plant, *Lonicera involucrata*. These types of meadows are often in the early stages of succession. If large trees begin to encroach, blocking the sun, the habitat may no longer be

suitable for the host plant on which the larvae of *E. gillettii* depend. Management that would preserve the meadow and prevent succession may be called for in this case.

MONITORING

There were significant changes in the occurrences of 24 of the butterfly species found between 1988 and 1989. However, butterfly populations normally fluctuate in size (Scott, 1986); thus, these changes may not be ecologically significant. Nonetheless, 15 species were found in more sites in 1988 than in 1989 and nine were found in more sites in 1989 than in 1988. Three of these species are biennial (*Vanessa cardui*, *Nymphalis vaualbum*, and *N. californica*); thus, one would expect marked fluctuations in their occurrences from year to year. The putative changes in occurrence of *Papilio glaucus rutulus* and *Plebejus icariodes* may be attributed to misidentification during 1987 and 1988. The reasons for changes in the others are unknown.

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APPENDIX

Annual species occurrences and habitat preferences of butterflies in Glacier National Park in the years 1987-1989. Presence-absence data are reported as frequency of presence for a total number of annual samples. The number of annual samples (left of solidus) and the number of sites sampled (right of solidus) are indicated in parentheses beneath each year. Each site was censused more than once, but not all sites were censused with an equal number of samples. An asterisk (*) denotes significant changes in occurrence between 1988 and 1989 at $P < 0.05$ using a G -test. A = Alpine, HM = hydric meadow, MM = mesic meadow, R = Riparian T = transition between low elevation and alpine, W = Woodland, XM = xeric meadow. Note: Most taxa are listed by genus and species. Those taxa that are listed by subspecies have undergone taxonomic revisions since Kohler's (1980) list.

Species	Number of samples in which species occurred			Habitat type & year observed ¹
	1987 (90/58)	1988 (161/24)	1989 (167/24)	
<i>Parnassius clodius</i> American apollo	1	1	0	A
<i>Paruassius phoebus</i> * Small apollo	18	33	17	A
<i>Papilio machaon bairdii</i> Artemisia swallowtail	0	0	0	Garth (1950)
<i>Papilio zelicaon</i> * Western swallowtail	0	5	22	MM, A
<i>Papilio canadensis</i> Tiger swallowtail	0	1	5	MM, R
<i>Papilio glaucus rutulus</i> * Tiger swallowtail	3	17	53	A, MM
<i>Papilio multicaudata</i> Two-tailed tiger swallowtail	0	0	0	—
<i>Papilio eurymedon</i> * Pallid tiger swallowtail	0	6	24	MM, XM
<i>Pieris protodice</i> Checkered white	2	0	0	A, MM

APPENDIX CONTINUED

Species	Number of samples in which species occurred			Habitat type & year observed ¹
	1987 (90/58)	1988 (161/24)	1989 (167/24)	
<i>Pieris callidice occidentalis</i> Peak white	12	38	44	A, MM
<i>Pieris napi</i> Sharp-veined white	4	15	20	A
<i>Pieris rapae</i> Cabbage butterfly (small white)	4	12	6	MM, A
<i>Colias meadii</i> Alpine orange	3	5	2	A
<i>Colias eurytheme</i> * Orange sulfur (alfalfa butterfly)	27	6	52	MM, A
<i>Colias philodice</i> * Common sulfur	10	7	46	MM
<i>Colias interior</i> * Pink-edged sulfur	20	40	27	MM
<i>Colias occidentalis</i> Golden sulfur	3	0	0	XM, A
<i>Colias pelidne</i> Blueberry sulfur	0	0	0	—
<i>Colias nastes</i> Arctic green sulfur	1	3	1	A
<i>Neophasia menapia</i> Pine white	0	2	0	1988: W
<i>Anthocharis sara</i> Western orange tip	0	3	3	T
<i>Euchloe ausonia ausonides</i> Dappled marble	0	8	13	MM, T
<i>Harkenclenus titus</i> Coral hairstreak	2	1	4	T
<i>Satyrium sylvinus</i> Western willow hairstreak	0	0	0	—
<i>Satyrium saepium</i> Buckthorn hairstreak	0	1	0	1988: A, W
<i>Callophrys sheridanii</i> Little green hairstreak	0	4	0	1988: T
<i>Callophrys polios</i> Hoary elfin	0	0	1	1989: A
<i>Callophrys augustus</i> Brown elfin	0	0	1	T
<i>Callophrys mossii</i> Stonecrop elfin	0	0	1	XM, A

APPENDIX CONTINUED

Species	Number of samples in which species occurred			Habitat type & year observed ¹
	1987 (90/58)	1988 (161/24)	1989 (167/24)	
<i>Callophrys eryphon</i> *	0	6	23	MM, XM
Western pine elfin				
<i>Callophrys spinetorum</i>	0	0	1	HM
Blue mistletoe hairstreak				
<i>Lyceana phlaeas</i>	0	1	1	MM, R
Small copper				
<i>Lyceana eupreus</i>	2	3	0	A
Lustrous copper				
<i>Lycaena xanthoides</i>	0	0	0	—
Gray copper				
<i>Lycaena heteronea</i>	7	12	12	A, XM
Blue copper				
<i>Lycaena helloides</i>	5	2	1	A
Purplish copper				
<i>Lyceana dorcas</i>	2	0	0	HM, A
Cinquefoil copper				
<i>Lyceana mariposa</i> *	15	16	3	XM
Forest copper				
<i>Lyceana hyllus</i>	2	0	0	1987: XM
Bronze copper				
<i>Epidemia nivalis</i>	6	3	1	A
Lilac-edged copper				
<i>Plebejus idas "argyrognomon"</i> *	28	46	15	MM, XM
Northern blue				
<i>Plebejus saepiolus</i>	16	32	36	MM
Greenish clover blue				
<i>Plebejus icariodes</i> *	2	2	29	MM, XM
Lupine blue				
<i>Plebejus acmon</i> *	4	7	0	XM, A
Silver-studded blue				
<i>Plebejus glandon</i>	0	11	5	T, A
Primrose blue				
<i>Everes amyntula</i>	3	5	3	MM
Western tailed blue				
<i>Euphilotes enoptes ancilla</i>	0	1	0	T
Dotted blue				
<i>Glaucopsyche lygdamus</i>	0	0	4	MM, XM
Silvery blue				
<i>Glaucopsyche piasus</i>	0	1	0	A, T
Arrowhead blue				

APPENDIX CONTINUED

Species	Number of samples in which species occurred			Habitat type & year observed ¹
	1987 (90/58)	1988 (161/24)	1989 (167/24)	
<i>Celastrina argiolus ladon</i> Spring azure	0	3	1	MM
<i>Limenitis arthemis</i> White admiral	0	0	3	MM
<i>Limenitis weidemeyerii</i> Western admiral	2	3	0	MM
<i>Limenitis lorquini</i> * Orange-tip admiral	11	15	2	XM
<i>Vanessa atalanta</i> Red admiral	2	1	2	R
<i>Vanessa cardui</i> * Painted lady	0	20	1	MM
<i>Vanessa carye annabella</i> Western painted lady	0	4	0	1988: A
<i>Nymphalis vau-album</i> * Comma tortoise shell	6	8	1	MM, W
<i>Nymphalis milberti</i> Fire-rim tortoise shell	23	36	26	MM, A
<i>Nymphalis antiopa</i> Mourning cloak	8	14	11	XM, MM
<i>Nymphalis californica</i> * Western tortoise shell	15	7	0	1987: A
<i>Polygonia gracilis zephyrus</i> Hoary comma	1	4	3	MM, T
<i>Polygonia satyrus</i> Golden angelwing	6	7	3	MM
<i>Polygonia faunus</i> * Green comma	15	19	10	MM, XM, A
<i>Chlosyne gabbii damoetas</i> Pearly checkerspot	1	0	0	A
<i>Chlosyne palla</i> Creamy checkerspot	6	12	16	XM, MM
<i>Phyciodes tharos</i> Pearl crescent	13	24	32	XM, MM
<i>Phyciodes campestris</i> * Field crescent	42	0	43	MM, A
<i>Phyciodes mylitta</i> Thistle crescent	0	0	0	—
<i>Euphydryas gillettii</i> Yellowstone checkerspot	3	3	9	MM, W

APPENDIX CONTINUED

Species	Number of samples in which species occurred			Habitat type & year observed ¹
	1987 (90/58)	1988 (161/24)	1989 (167/24)	
<i>Euphydryas chalcedona colon</i> Western checkerspot	0	0	0	—
<i>Euphydryas chalcedona anicia</i> Western checkerspot	28	30	26	XM, MM, A
<i>Euphydryas editha</i> Ridge checkerspot	3	4	9	A
<i>Boloria selene</i> Silver meadow fritillary	6	6	12	MM
<i>Boloria epithore</i> Western meadow fritillary	6	15	18	MM, A
<i>Boloria alberta</i> Alberta alpine fritillary	2	0	0	A
<i>Boloria astarte</i> Arctic ridge fritillary	0	0	1	A
<i>Boloria titania</i> * Purple bog fritillary	6	13	4	HM
<i>Speyeria coronis</i> Coronis fritillary	0	0	0	Garth (1935)
<i>Speyeria edwardsii</i> Green fritillary	1	0	0	MM
<i>Speyeria zerene</i> * Zerene fritillary	7	15	1	XM
<i>Speyeria callippe</i> Callippe fritillary	0	0	0	—
<i>Speyeria egleis</i> Great basin fritillary	0	2	3	HM, A
<i>Speyeria atlantis</i> * Atlantis fritillary	31	36	20	XM, MM
<i>Speyeria hydaspe</i> * Lavender fritillary	13	12	4	A
<i>Speyeria mormonia</i> * Mormon fritillary	19	64	17	A, XM, MM
<i>Speyeria cybele</i> Great spangled fritillary	1	0	1	XM
<i>Speyeria aphrodite</i> Aphrodite fritillary	0	0	3	1989: MM
<i>Coenonympha tullia ampelos</i> Ringlet	0	0	0	—
<i>Coenonympha tullia inornata</i> Ringlet	6	25	34	XM, MM

APPENDIX CONTINUED

Species	Number of samples in which species occurred			Habitat type & year observed ¹
	1987 (90/58)	1988 (161/24)	1989 (167/24)	
<i>Cercyonis pegala</i> Wood nymph	8	5	12	XM
<i>Cercyonis oetus</i> Small wood nymph	26	43	38	XM
<i>Oeneis uhleri</i> Rocky mountain arctic	0	2	0	A
<i>Oeneis chryxus</i> * Brown arctic	0	7	18	T, A
<i>Oeneis alberta</i> Prairie arctic	0	0	0	—
<i>Oeneis melissa</i> Mottled arctic	0	0	0	—
<i>Erebia epipsodea</i> Common alpine	4	25	40	XM
<i>Danaus plexippus</i> Monarch	0	0	0	1989: MM

¹The year observed by Garth is noted for historically known species not seen since 1950 or 1935. The first year observed is noted for species added to the park list as a result of this survey.



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