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STRAIGHT TALK ABOUT BUTTERFLY POPULATION BIOLOGY

by Ann Swengel, 1997

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To continue to exist, each butterfly species must occur at least in some places as groups called populations. In populations, the males and females of the species find each other, mate, and successfully reproduce year after year. The size of a butterfly population depends to a great extent on the amount of resources required by the species that are available for the population to use. Some adults of a species may appear in a place where an actual population does not exist because the site is in some way unsuitable for supporting the species consistently over time. (E.g., it might lack adequate amounts of appropriate caterpillar food plants). For such a site to continue recording these stray individuals, the population must continue to exist elsewhere (usually nearby) and the site must remain attractive to the adults to draw them in.

In general, large populations are more likely to persist over time than small populations. Larger populations tend to be more successful at finding mates and surviving unfavorable conditions such as adverse weather. Large populations can decline relatively quickly into small populations, however, under persistent adverse conditions. If a population becomes very small, it may die out. However, several small populations may lie near each other, connected to each other by "dispersal corridors" that the butterfly individuals are able and willing to travel across. If the several small populations actually interact with each other, they

can behave as if they are one larger population. Certain common species may exist in low numbers over large areas. These butterflies depend on their ability to disperse over large areas to find mates and survive adverse conditions.

If a population goes extinct at a site, it can naturally re-establish only if individuals from another population successfully recolonize the site. The population supplying the individuals for recolonization at the extinct site is called the source.

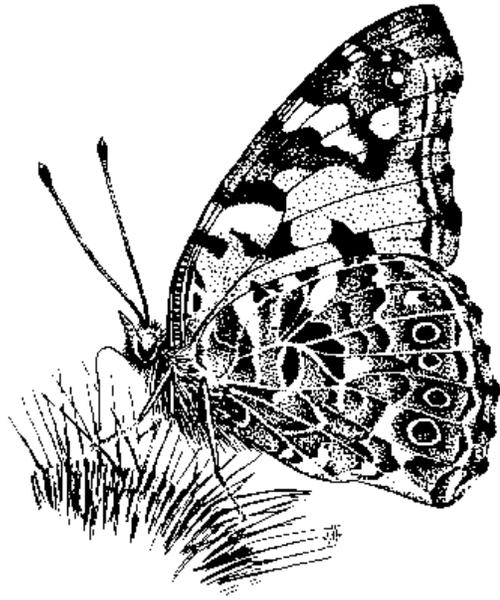
Recolonization is more likely if the source is near the extinct site and is connected to it by short dispersal corridors the butterflies are able and willing to cross. These corridors usually must be about the same vegetational structure (e.g. grassland, scrub, forest) as the habitat the species requires. Dispersal down corridors is more likely if they offer some sort of resource, such as preferred adult food, that lures the individuals in and through them. Successful recolonization is more likely if the source is large. More individuals are likely to disperse out of a large source and find the extinct site. The more individuals dispersing into the extinct site, the larger the new population they might found.

Larger recolonizations are more likely to "take" and persist over time. But if the cause for the extinction of the original population has not been corrected, the newly re-established population is likely to decline and go extinct for the same reason.

Most butterflies at a site are resident in the area yearround. Most individuals of many species appear to stay within a relatively small area called the home range. Despite their ability to fly, most butterflies are unable or unwilling to travel far from this home range. Most climates include times of the year unsuitable for butterfly activity, usually because of cold or drought. Most butterfly species survive such periods not by leaving (migrating out of) the region but by waiting out such periods by going into dormancy (diapause). To maintain the most kinds of species possible at a site, attention should focus on catering to the needs of resident species there. The existence of resident species depends on maintaining populations that are "viable" – able to persist over time. This in turn depends largely on the adequacy of the resources available at that site to support those populations.

By contrast, some butterfly species tend for some of their individuals to wander or "immigrate" into sites from somewhere else.

These individuals may travel great distances and are adaptable to a variety of resources and habitat types. Immigrant individuals may be found in many places where they do not reside yearround. However, the long-term existence of such species still depends on their viability (persistence) in places where they reside yearround. Little can be done to make more immigrants pass through an area and happen to chance upon a particular site. It is possible, however, to make a site more attractive to immigrants once they happen to arrive. This includes a consistently abundant supply of a variety of nectar sources generally attractive to butterflies. A good representation of commonly used caterpillar food plants is also likely to include ones that immigrants can use, especially since these species tend to be flexible in their habitat needs. Of course, nectar and caterpillar food plants are also what resident butterflies need. What makes a site favorable for resident butterflies is likely to appeal



to immigrants, too.

Maintaining butterfly populations already present at a site is easier than trying to establish new populations. Habitat can be deliberately changed to become suitable for different butterflies than currently live in it. Habitat might also be damaged and then restored, becoming suitable again for species once living at the site. In both cases, new butterfly populations might subsequently get established in the habitat either from natural invasion or by deliberate (man-caused) introduction of the butterflies to the site. However, the first result of changing (or damaging and then restoring) the habitat will likely be harm to the butterflies currently living in the habitat. Furthermore, no new populations may actually get established successfully later on. Ecology operates under a form of inertia. It is easier to retain current populations than to create new ones. This is true even for re-establishing a butterfly once living at a site in habitat formerly used by the species and seemingly unchanged since it last lived there. Because of this, all areas and aspects of a site with ecological value to butterflies currently living there should be maintained as much as

possible. Be cautious about "improving" habitat if the process includes destruction of habitat currently useful to butterflies and/or destruction of the butterflies themselves. Habitat can be improved while still retaining the native species already present at the site, but this may not be simple or easy.

Widespread, common butterflies tend to differ from localized, rare butterflies in number of generations per year, mobility, and adaptability to different habitat types.

Abundant species tend to have multiple generations per year that often overlap (i.e. are "homodynamic"). They are also usually capable of relatively high mobility to disperse widely and are adaptable to a wide variety of habitats. By contrast, localized and rare butterflies usually have only one or perhaps two synchronized generations per year. They tend to be more sedentary and particular in their resource and habitat needs. This means that rare butterflies tend to be fussy specialists with narrow habitat requirements while common species are adaptable and wide-ranging generalists.

For a site to approach its full potential of butterfly species, it must support populations not just of the common generalists but also of the rarer specialists appropriate to its habitats.

The easiest butterflies to cater to are the commonest ones, but they are least likely to need special attention because of their flexible requirements. The rarest species are most difficult to satisfy but most need this effort, since they are the easiest to lose from a site because of their low numbers and particular habitat requirements. Moreover, the extinction of a rare species' population is more likely to be permanent than loss of a common species. To get re-established naturally, a source population must be nearby - within dispersal distance of the extinct site. Because of its overall scarcity, such a source

population is less likely to exist for a rare species than a common one. Furthermore, the source population of a rare species must likely be closer to the extinct site for successful re-invasion because of rare species' lower and shorter dispersal tendency.

Also, the source population of a rare species may not be large enough to disperse enough colonizers into the extinct site to have much chance of founding a successful population.

A site must have adequate resources necessary for all life stages of a butterfly species at all times when the butterflies need them every year to support a population of that species. For example, adequate supplies of appropriate larval food must exist every time when hungry larvae need them. Suitable conditions for successful breeding must exist every time when the butterfly life cycle schedules it. A habitat should be suitable and available for a species to survive in it all the time for that species to continue as a resident population there.

Particular plant species are not the only resources required by butterflies. Most caterpillars are exclusively herbivorous, often restricted to a very narrow group of plants. Many



adult butterflies feed mostly or exclusively on flower nectar. But beyond that, butterflies may prefer certain vegetation for roosting cover, hibernation spots, basking locations, and territorial perches. These depend not just on the particular plant species, but on the structure they grow in. In arid climates, sources of moisture may be a critical limiting factor on the location and size of butterfly populations. Butterfly species relate to each other and to the other animal species in their habitat both in competitive and cooperative (mutualistic) relationships. Sometimes one or both of these types of relationships can very strongly affect a butterfly population. Rarely have all the resources a particular butterfly species requires been thoroughly documented. But it has often been found that some critical resource needs, such as vegetational structures or microclimatic conditions, can be seemingly minor yet vital features of a habitat. The way the various plants at a site grow together is called the vegetational structure. It is not just the types of plants at a site that are important to butterflies. Also significant are the vegetational structures these plants form as well as the history at the site that caused these vegetational structures to come into existence.

Resources needed by a butterfly population can vary over space and time. The resources used by the immature life stages may occur in different places in the habitat than resources used by the adult butterflies. The resources for different needs of the adults may also occur in different places. For example, resources for nectaring and roosting may be located in different places while the larval host where the females lay their eggs may occur yet another place. Yet all of these resources must be accessible to the butterflies. They must occur within the home range the species typically flies over and must be connected to each other along dispersal corridors the butterflies are able and willing to fly across.

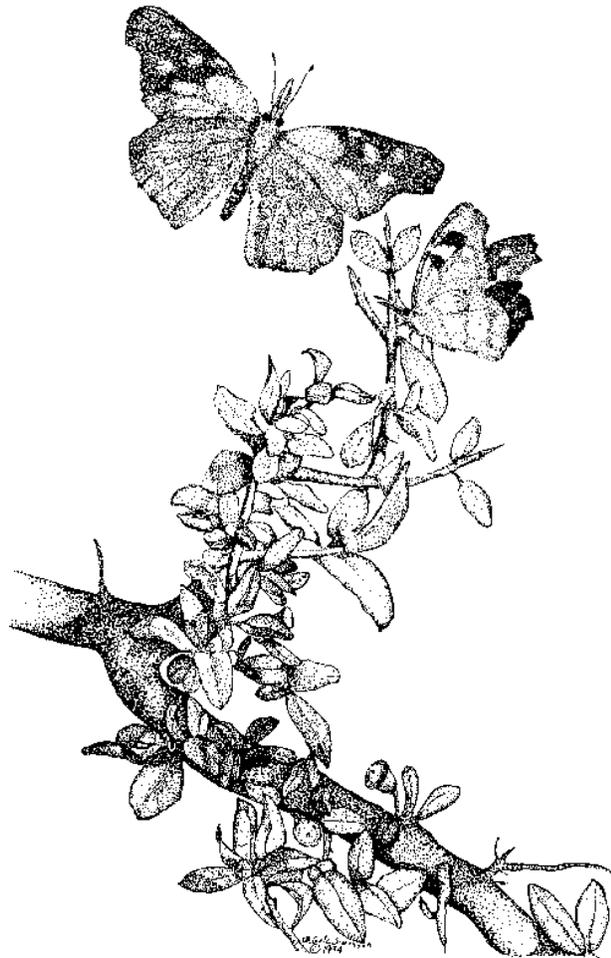


Some resources may be of use only in unusual years. For example, adults may fall back on a certain flower when a preferred nectar source fails to bloom. Different species of larval food plants or different locations where the same food plant grows may be used in certain years depending on growing conditions. These resource variations are buffers in unusual and adverse conditions.

Butterfly species experience a complete turnover of individuals between each generation. Each individual butterfly usually gets only one short time for breeding. It does not get more chances to breed in following years as many plants and animals do. In butterflies with synchronized flight periods, this turnover between generations happens in a very short time, usually over several weeks. That synchronized group of individuals is called a single age class or cohort. If some catastrophic event occurs at the time of that turnover, the next generation will be much reduced or even non-existent. In multivoltine, homodynamic butterflies (species with more than one generation per year, with the timing of those life

cycles desynchronized), breeding events within the population are staggered throughout the year, often nearly continuously throughout the flight period. But each individual within the population still has a rather short time when it breeds.

Butterfly populations tend to fluctuate in abundance. This is true even for resident butterfly populations in a site maintained consistently and suitably for them. Butterfly abundance (as measured within the appropriate flight period) varies over the years for many reasons. Weather conditions in different years can cause particularly favorable or unfavorable conditions for a species by enhancing or disfavoring the resources it needs. Variation in the occurrence of parasites and diseases can also affect butterfly numbers. Because of the short life cycle and complete turnover of individuals between generations, butterflies respond



quickly to these factors. But different species vary greatly in just how much they tend to fluctuate up and down among the years. These fluctuations are different from actual trends (or changes) in population size. The fluctuations represent short-term ups and downs that balance each other out over the long run. The average of these ups and downs corresponds to the population's size and tends to remain stable overall. If most of the fluctuations tend to go up, the population is increasing over time. But if most of the fluctuations tend to go down, the population is declining.

Butterflies lay many eggs but these experience high mortality so that butterfly species may not be capable of rapid or predictable population increases. Some animals (known as K-selected animals) produce few young but provide them with parental care to reduce their mortality. Other animals (known as r-selected) produce many young (usually eggs) that typically experience high mortality because they receive little or no parental care. Butterflies, which are r-selected, normally experience high mortality throughout their life cycle. Scientists typically expect only about 1% of eggs to survive to reproductive maturity. The rest die, usually when something else eats them. This loss to predators is part of the balance of nature. R-selected animals often (but not always) experience larger population fluctuations than K-selected ones. But these fluctuations are usually not controllable or even predictable much in advance - and they can go in either direction, up or down. Although some butterfly populations can show sharp increases as well as decreases, they are usually capable of sharper and faster declines than increases. For a population to persist over time, it must be able to survive and recover from these low points in sufficient numbers that it does not go extinct.

Butterflies are usually not capable of prolonged dormancy during lengthy adverse

conditions. Butterflies usually have an inactive period called diapause in their annual cycle during cold winters or tropical dry seasons. But butterflies do not normally undergo prolonged dormancy lasting more than part of a year. This is unlike many plants that may be dormant for many years, existing only as rootstocks or seeds. Some individuals of some desert species are known to be an exception.

They may apparently remain in diapause for several years during exceptional dry spells.

Butterflies can be very sensitive to changes in their habitat. Combined with a relatively short life cycle, the complete turnover of individuals between each generation causes butterflies to be much more sensitive to changing habitat conditions than many plants and vertebrates.

Many plants are able to survive prolonged adverse conditions in rootstocks and seedbeds. Many animals may be able to wait out the poor conditions or move elsewhere. If conditions subsequently improve, the plants may resprout and the animals return or resume breeding. Unlike these plants and animals, butterfly individuals can't make up for poor conditions one year by waiting for improved breeding conditions another year. Resident butterflies must proceed with their life cycle in that place at that time regardless of conditions. If the habitat declines in suitability for them, the butterfly populations may quickly reflect this by declining and dying out

Caterpillar food plants often restrict the size and location of associated butterfly populations. To persist, butterfly populations require an adequate supply of appropriate food consistently available when the caterpillars need it.

A large population of these food plants is more likely to support associated butterflies than a small one. Small populations of food plant can support only small populations of associated butterflies, if any at all. Scattered pockets of a few plants may each be too small to support populations of

associated butterflies, even though the plant may be widespread in the region and not rare overall.

Caterpillar food plants can be much more common and widespread than associated butterflies. To persist, butterfly populations must be in balance with their food plants. Enough plants must be left over after the caterpillars feed on them so that the plant population can survive and feed the next generations of caterpillars. Furthermore, butterfly species often have more specific resource and habitat requirements than their caterpillar food plants. In fact, these more narrow butterfly requirements make it possible for several butterfly species, or one butterfly species and several other insect species, to share the same food plant. They do this by divvying up different parts or growth forms of the plant to each species, or different regions within the plant's range, or different microhabitats the plant can live in, or different ages of the plant (such as younger vs. older trees), or different times of year when they each feed on the plant. The greater the variety of growth forms, ages, and growing conditions for a certain plant species at a site, the more kinds of butterflies and other insects that plant species might support. In fact most butterflies, including many rare species, feed on common plants. At a particular site, a plant



might happen to be rare, causing the associated butterfly to have a small population there. While there are exceptions to this observation, usually it is not the overall rangewide rarity of a plant that makes an associated butterfly generally rare, but some other factor(s).

Maintaining plants required by butterflies does not guarantee that populations of those butterflies will continue to exist at a site. If a plant species declines, the associated butterfly will probably decline too. If the plant dies out, the butterfly population must also. But if the plant increases, the associated butterflies may not. Other resources the butterflies require may or may not be available in sufficient abundance to support a larger butterfly population. The process used to increase the plant may be compatible or unfavorable for the butterflies. In sum, a site cannot have populations of resident butterflies without having the plants they require in adequate abundance. But a site can have the plants without having the associated butterflies. All the other specific conditions and requirements of the species must also exist at the site.

Preserving habitat does not guarantee that resident butterfly populations will continue to exist at the site. Generally protecting habitat from destruction is certainly necessary, but this alone does not guarantee that the particular resource and habitat requirements of the resident butterfly populations will continue to exist there. After preservation, the needs of resident butterflies may happen to be maintained through naturally occurring ecological processes, efforts on behalf of other species, general ecosystem or landscape conservation, and/or luck. But often, deliberate actions specifically to benefit the butterflies are necessary to ensure that their particular habitat needs are determined and maintained. This need not be in conflict with other habitat goals, but in addition to them.

A greater diversity of habitats usually

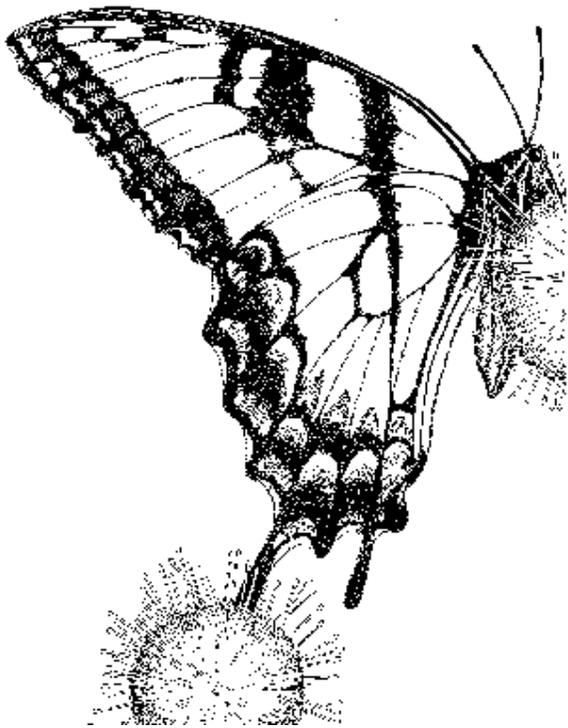
maintains a greater diversity of butterflies. A mix of habitats allows more kinds of species specific to any one habitat to live at the site. Moreover, habitat diversity itself may be a requirement of some species. Some butterflies may prefer the special habitat type that is the "edge" or transition between two habitats. Other species may use different habitats at different stages in their life history - one area may contain the caterpillar food plant but another may contain preferred adult foods. These different habitats must be within comfortable traveling distance of the species. Adult butterflies may roost in one area or habitat in a site while feeding in another.

Maintaining continuity of habitat is more important for maintaining existing butterfly populations than improving the quality or diversity of a habitat. Less degraded and more diverse habitats are certainly favorable for the butterfly populations in that habitat. Actions that enhance habitat quality and diversity should therefore benefit these butterflies. But past experience in butterfly conservation has shown, however, that it is not always obvious how to make a habitat better for a butterfly. The more localized and specialized butterfly species can be very sensitive to subtle changes in the habitat - even ones intended to benefit them eventually. For example, increasing larval food plants is often useful, but not if the growth habit or location or technique used to do so are unsuitable for the butterfly. Thus, the first priority is to insure that the critical resources used by the butterfly population remain continuously available to keep on maintaining the species. Efforts to improve habitat quality and diversity should be additive to that, not in conflict with it.

It is better overall for conservation when a site maintains specialized habitats with their localized and rare butterflies than maintaining a diversity of habitats supporting more but

common butterflies. Consider two hypothetical sites. One might have wetlands, meadows, and forests that grew back after plowed farm fields were abandoned. Of equal size and landscape context, the second site might have only extensive wetlands that have never been drained or altered.

The first site might have as many or even more butterfly species than the second site. But the first site's butterflies may only be the most widespread and common species found throughout that region



in those general habitat types. That's because they all had to find their way into the site after the habitats got re-established. The second site is much more likely to have localized and rare wetland butterflies because the habitat is a larger and higher-quality wetland in consistent existence over the decades as habitat for wetland butterflies. Even though the second site may have fewer butterfly species, it contributes more to the region's overall butterflies because it contains species rarely found elsewhere.

Land use and management choices have a large effect on what butterflies live in a site's

habitats. Of course, we can't do anything now about what happened on a piece of land in the past, important as that has been in causing the site to be the way it is today. But we do have choices about what to do with the land now that will affect its future, including its butterflies. These choices concern how we use and manage the land, or choose not to. The subject of managing butterfly habitat is a large one. But a lesson from the two hypothetical sites in the previous paragraph is this:

We can recognize the greater value of a pristine habitat that has existed consistently and continuously for long periods of time in comparison to the value of having more habitat types, causing the site to have a longer list of resident butterflies.

Draining part of the wetland to plant meadow flowers or forest trees would bring loss to the wetland butterflies, including rare and localized ones, while possibly only gaining widespread, common butterflies. Instead, with a focus on maintaining an intact pristine habitat with rare butterflies, the land owner would seek to maintain the undegraded quality of the wetland. Likewise, such an attitude directed at the first site would seek to enhance the existing habitat types to support as many of the region's butterflies as possible that live in such habitats, in the hope that more of these butterflies will find their way to these habitats and colonize them. These differing strategies, each one specific to the individual characteristics of a site, work toward the same goal: having the most diversity and abundance of butterflies possible given the site's habitat(s).