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# Movement and Demography of At-Risk Butterflies: Building Blocks for Conservation

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demography, behavior, dispersal, conservation, restoration, insect, butterfly

## Abstract

The number of insect species at risk of population decline and extinction is increasing rapidly. Yet we know almost nothing about the ecology of these species, except for at-risk butterflies. A growing body of literature shows how butterfly vital rates, including demography and movement, are essential for guiding conservation and recovery. History has shown us that without these data, conservation decisions often weaken, rather than enhance, population viability. This is especially true in changing landscapes. We review knowledge of vital rates across all at-risk butterflies. We have information on movement for 17 of 283 butterfly species and information on demography for 19 species. We find that habitat-specific movement behavior is key to understanding how to connect populations, and habitat-specific demography is central to managing habitats. Methods and analyses worked out for butterflies can provide a scaffold around which to build studies for the conservation of other at-risk insects.



## INTRODUCTION

Amid growing evidence of the long-term, ongoing, global decline of insects (29, 103), a fundamental question is, What can be done to reverse declines and recover populations? This question is particularly relevant for insects that are threatened with extinction. Yet we know next to nothing about the population ecology of most at-risk insect species (**Table 1**). There is a lone exception: at-risk butterflies found on national or governmental lists but not listed by the International Union for Conservation of Nature (IUCN). We review the fundamental biological knowledge needed to understand causes of decline and provide conduits for recovery, the mechanisms of demography and behavior. Our review draws on the significant knowledge accumulated for at-risk butterflies and provides a model for how to conserve other insects. Which strategy or combination of strategies are sufficient to reverse population trajectories—from declining to increasing populations—depends on species biology within a landscape context.

For butterfly and other insect species, there is a critical need, more than ever before, to assess status of at-risk populations and identify clear pathways for recovery. Butterfly populations are in decline around the world; in a review of all long-term data sets for Lepidoptera, Dirzo et al. (29) found a 40% decline in the last 40 years. Early documentation of butterfly declines was often limited to narrow endemics with closed populations or to flashy species that were the target of zealous butterfly collectors (15, 36, 66, 96). Today, formerly widespread and abundant butterfly species have joined these taxa, with rapidly dwindling population sizes (1, 69, 77, 95, 99).

To assess population status, scientists have two primary approaches. First, if long-term data on population abundance exist, time series analysis can be used to make inference about population parameters and extinction risk (83, 92). Unfortunately, outside of one well-established effort, the United Kingdom Butterfly Monitoring Scheme (27), such data rarely exist for at-risk butterfly taxa. Instead, we have >25-year time series for only a few well-known butterfly taxa, such as the monarch, *Danaus plexippus* (73, 77; but see 19). Second, demographic rates throughout the life cycle can be used to predict population growth rates and extinction risk. This is a common approach for vertebrates and plants (e.g., matrix population models) (63). In this review, we assess how often we have such knowledge for at-risk butterflies, with extensions across listed insect species.

**Table 1** Population ecology of insects listed as critically endangered or endangered on the International Union for Conservation of Nature Red List<sup>a</sup>

Order	Critically endangered <sup>b</sup>	Endangered <sup>b</sup>	Dispersal <sup>c</sup>	Demography <sup>c</sup>	Population size <sup>c</sup>
Coleoptera	49	110	1	4	7
Hymenoptera	12	18	1	0	4
Lepidoptera	11	48	0	0	3
Odonata	62	109	0	0	2
Orthoptera	110	157	0	0	2
Other	29	16	0	0	1
Total	273	458	2	4	19

<sup>a</sup>We reviewed 731 species (273 critically endangered and 458 endangered), primarily in the Coleoptera, Hymenoptera, Lepidoptera, Odonata, and Orthoptera. For nearly all species, we identified papers primarily reporting the description or the collection location of the species.

<sup>b</sup>Columns indicate number of species that are critically endangered and endangered.

<sup>c</sup>Columns indicate number of species with at least one published reference in the Web of Science on dispersal behavior, demography, and/or population size.



Ultimately, we seek to recover declining populations across their range. Diverse conservation strategies are in use to recover butterfly taxa (56, 66, 86, 111). Key to understanding population decline and recovery is knowledge of species biology, including demography and dispersal, in a landscape context (54). Restoration of butterfly species often hinges on restoring spatial population structure (i.e., the metapopulation—a spatially structured population that is spread across multiple spatially distinct subpopulations or patches) (31). Strategies to restore a functionally connected population draw on multiple conservation approaches, with emphasis on enhancing habitat quality within resource patches in concert with size and spatial arrangement of habitat across the landscape (59). The effectiveness of these recovery strategies depends on functional habitat quality (i.e., female fecundity and survival of immature and adult stages) and successful movement within and between patches. The latter is critical because butterfly population dynamics are often highly variable, and long-term metapopulation persistence relies on recolonization following within-patch extinction (42).

Restoring at-risk insect species also hinges on understanding the factors that allow populations to persist. Disturbances, such as fire or flooding, are often essential to restore habitat for at-risk butterfly populations (40). Here, the positive indirect effects of disturbances on habitat quality are often time delayed and must outweigh the negative direct effects of the disturbance itself (40, 53, 96, 109). Nonetheless, incorrect assumptions about a butterfly's life history and the importance of disturbance to that species has led to extinction of at least one butterfly species (96). To understand how to use disturbance to restore or enhance habitat for an at-risk butterfly, it is essential to estimate vital rates across the annual life cycle and across successional habitat stages. These vital rates include demographic costs (e.g., lower immature survival) and benefits (e.g., higher female fecundity) and either assumptions about movement (82, 84) or explicit measurement of movement behavior in response to disturbance (108). That is, we need to assess the net effects of disturbance on a butterfly population to provide a quantitative guide to the long-term effect of the disturbance on population dynamics. This analysis leads to guidelines for managers, who can then decide when, where, and how much disturbance is helpful in a given context (84). Ecologists are recognizing the important role of disturbance in managing butterfly populations (65). To manage at-risk species, however, there is an additional first step. Recovery of at-risk butterfly species requires understanding the underlying mechanisms of demography and dispersal before disturbance is implemented.

In this review, we examine the degree to which we broadly understand demography and movement behavior of at-risk butterflies. Butterfly ecologists have increasingly become aware of the importance of measuring demographic and dispersal rates throughout the life cycle (33, 76). Collectively, we consider demography and movement behavior as vital rates because together these factors influence whether a population will shrink, persist, or expand within current and potential landscapes. A key finding of our review is that there are few butterfly taxa for which we have estimates of vital rates throughout the life cycle in a natural setting and that estimates of vital rates for other insect taxa are even sparser. However, for a few taxa, we have these estimates, and they are the basis for rules of thumb to set recovery criteria and to guide conservation planning (13, 86, 108).

We demonstrate that collecting these data is not technologically challenging or expensive but does require commitment to focused studies structured with clear hypotheses and methodologies. Gaining estimates of these vital rates sometimes requires recognizing that acquiring critical information about population ecology of at-risk species to inform long-term recovery may come with the short-term cost of losing a few individuals. Combining these approaches with careful and practical application in the field is contributing to recovery for some species, holds the promise to contribute to recovery for a diversity of butterfly species, and could be broadly applied across other at-risk insect taxa (3, 31, 58, 86).

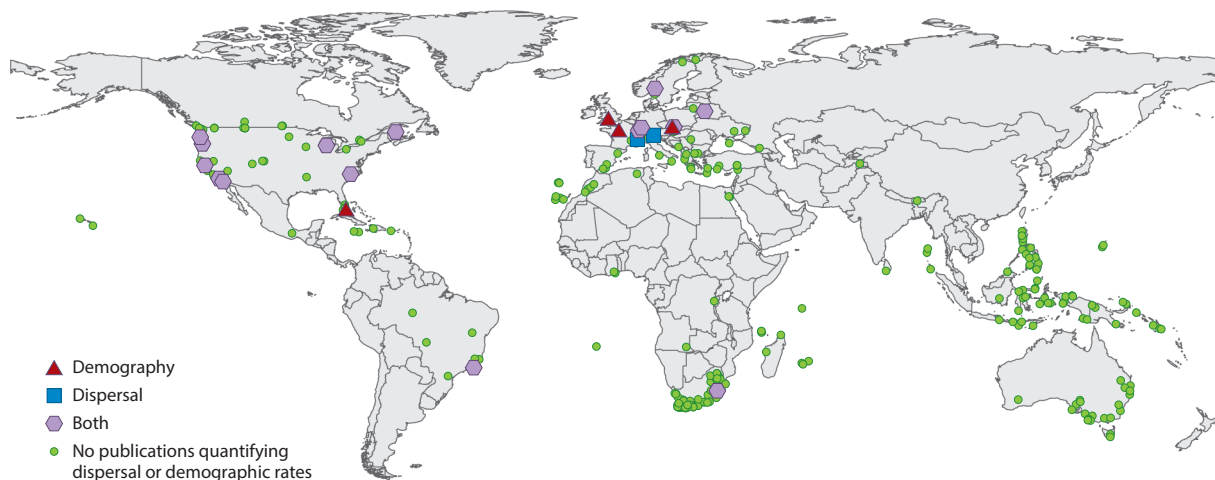


## MOVEMENT AND DEMOGRAPHY OF AT-RISK BUTTERFLIES

We review demography and dispersal of at-risk butterflies and moths found on six lists: the IUCN Red List [under the categories of critically endangered, endangered, and vulnerable (47)], European Red List [critically endangered, endangered, and vulnerable (100)], U.S. Fish and Wildlife Service (USFWS) list of Endangered Species list [endangered and threatened (98)], Canadian List of Wildlife Species at Risk under the Species at Risk Act [endangered and threatened (38)], Southern African Butterfly Conservation Assessment [critical (61)], and Australian Butterfly Action Plan (79). For this set, we searched the Institute for Scientific Information's Web of Science for all studies based on Latin names and on common and Latin names for North American species. We conducted a similar review for all IUCN Red List insects considered critically endangered or endangered but found virtually no relevant studies (Table 1).

Limiting our review to species with formal endangered/threatened/imperiled designation inherently excludes species that are at risk because of their rapid rate of decline and not yet listed (e.g. monarchs) or are regionally rare. To address this limitation, we also review all studies in which authors indicate the focal species are at risk in the region of interest and with species-specific population biology in the *Journal of Insect Conservation* (*JICO*) over the last five years (2013–2017). This latter survey represents a cross-section of what scientists and researchers consider as at-risk butterflies and moths beyond international and regional lists of protected species. For taxonomic consistency, we considered species at the full species level, even if the butterfly is listed at the subspecies level.

We identified 283 species in our list of at-risk species (Supplemental Text 1, Figure 1). Of these, 27 species were listed as critically endangered, 99 species were listed as endangered, 148 as vulnerable or threatened, and the remainder in other categories (“candidates” on the USFWS Endangered Species list or “regionally extinct” on the European Red List). For ease of writing,



**Figure 1**

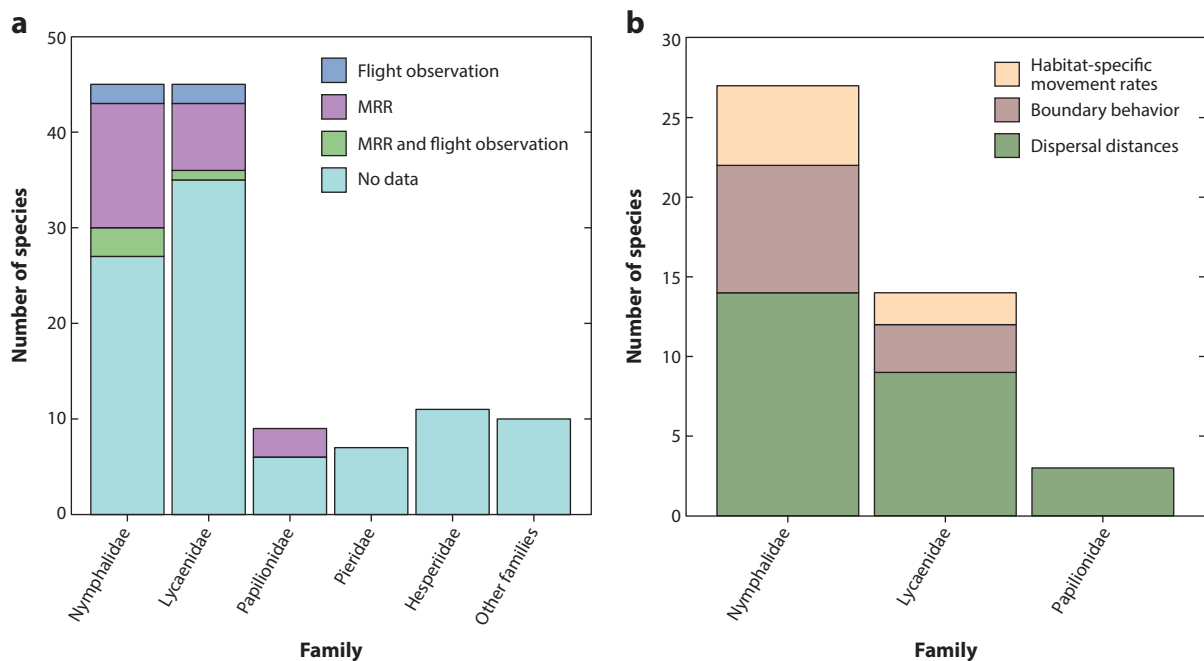
Map of 283 butterfly species on six lists: International Union for Conservation of Nature and European Red Lists, U.S. Fish and Wildlife Service Endangered Species List, Canadian List of Wildlife Species at Risk under the Species at Risk Act, Southern African Butterfly Conservation Assessment, and Australian Butterfly Action Plan. Green circles are species with no published literature in the Institute for Scientific Information's Web of Science; red triangles are species with demographic studies; blue squares are species with dispersal studies, and purple hexagons are species with both demographic and dispersal studies in the published literature. Points are roughly centroids of range distribution for species with no data. For species with published studies, points are located in regions with the greatest numbers of published studies. Only studies with estimates of dispersal or demographic rates from wild populations are included.

we include the few moth species as at-risk butterflies. Of these at-risk species, 76 had at least one published study in the Web of Science, 32 had one published study, 23 had two to six studies, and 21 had seven or more. Of butterfly species, these include 29 Lycaenidae, 19 Nymphalidae, 8 Papilionidae, 7 Hesperidae, 5 Pieridae, and 2 Riodinidae. There were 6 moth species. Only 6 species had fifty or more studies in the Web of Science as of November 2017 (**Supplemental Text 1**).

In the additional subset of papers in the last five years of *JICO* (2103–2017), the studies include 26 species from our initial list and 51 additional species considered at risk within the region of interest by the study authors. We use the combined set of 127 species in our review (**Supplemental Text 2**).

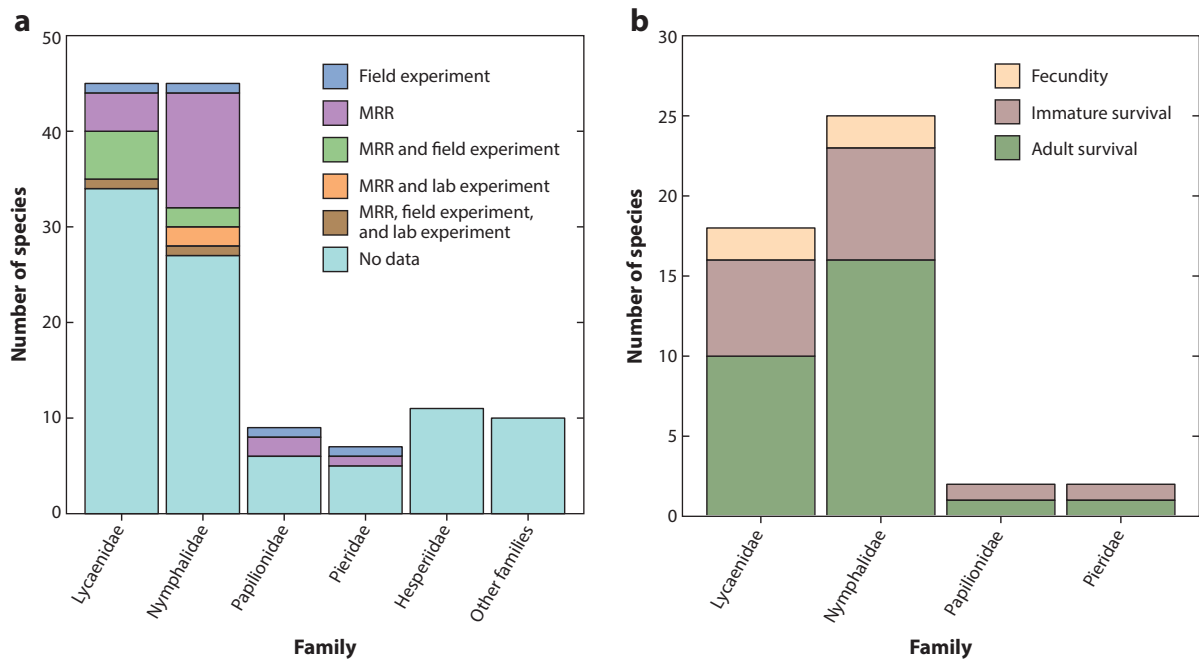
For each study that included butterfly population ecology, we categorized papers with information on movement and demography. For nonmigratory and nonterritorial butterflies, movement and dispersal are analogous; for clarity, we use the term movement to describe adult butterfly flight behavior, which is the mechanism for dispersal. We noted method(s) by which movement data were collected, especially if studies had habitat-specific measures of movement rates (i.e., diffusion, move length, turning angle, and/or net squared displacement) and boundary behaviors. We also noted whether studies had overall measures of landscape connectivity (e.g., maximum dispersal distance or estimates of parameters in dispersal kernels). We noted method(s) by which demographic data were collected and whether studies had habitat and/or stage-specific measures of survival or fecundity.

We found 31 species—13 of which were only in the *JICO* subset—had data in published literature on species-specific movement behavior (**Figure 2**). Similarly, we found 34 species—14



**Figure 2**

Dispersal data for at-risk butterflies, including listed species in **Figure 1** and regionally at-risk species included in articles in the *Journal of Insect Conservation* from 2013 to 2017. (a) Methods of collecting dispersal data, including mark-release-recapture (MRR), flight observation, and a combination of these and (b) types of data collected, including habitat-specific movement rates, boundary behavior, and dispersal distance as estimated in MRR or virtual migration studies.



**Figure 3**

Demography data for at-risk butterflies, including listed species in **Figure 1** and regionally at-risk species included in articles in the *Journal of Insect Conservation* from 2013 to 2017. (a) Methods of collecting demographic data, including mark-release-recapture (MRR), field experiments, lab experiments, and a combination of these, and (b) types of data collected, including adult survival, immature survival, and fecundity. Note that demographic data from lab experiments are included only if the species also has demographic data collected from populations in the wild.

of which were only in the *JICO* subset—with demographic information (**Figure 3**). For both dispersal and demography, species were largely in the families Lycaenidae and Nymphalidae.

### Movement

Many butterflies move more or less continuously throughout their lives; fewer have discrete dispersal phases associated with territory establishment or migratory phases (though notable exceptions exist). The ways butterflies move across the landscape determine how long butterflies spend in their natal habitat patch, as well as realized dispersal among habitat patches. Both of these parameters (residence time in natal patches and dispersal among patches) are important for population viability and for designing conservation strategies to promote/restore population connectivity.

**Mark-release-recapture studies.** Of the studies that are part of our systematic review, most of the ones that assess butterfly movement and dispersal use mark-release-recapture (MRR) methods (used for 23 of the 31 noted species). For the rest of the species, four were studied through flight observations and four were studied through both MRR and flight observations (**Figure 2**). MRR is perhaps the oldest and simplest method to study butterfly dispersal (30). These studies are useful in estimating maximum realized distance traveled and connectivity between patches within an existing network. Three limitations arise because MRR studies provide information on the location and date of capture (or resight) but not the direct path or timing of the butterfly. First,



one cannot estimate rate of movement (e.g., diffusion rate) within specific habitat types (e.g., high-quality habitat versus low-quality habitat). Second, one cannot assess the most important landscape attribute that impedes movement, behavior at boundaries. Third, behavior at boundaries and habitat-specific movement rates are confounded (52). For example, if butterflies are rarely resighted beyond the boundary, scientists may conclude that the species is highly sedentary. However, a species with high within-habitat movement rates and a tendency not to cross boundaries (e.g., forest boundary) is also unlikely to leave a patch. Thus inference from MRR data may lead to the conclusion that a butterfly is sedentary (i.e., low within-habitat diffusion rates) when, in fact, the impermeability of the boundary limits dispersal. These differences lead to strikingly different recommendations for restoration or metapopulation design. A truly sedentary butterfly may need closely spaced stepping-stone patches or a continuous corridor to promote connectivity. A butterfly limited by boundary preference/avoidance might thrive given a conservation plan that reduces structural boundaries and promotes sufficient habitat scattered across the landscape.

Newer modeling approaches allow some of these limitations to be overcome. In one novel modification of MRR methods, researchers adjust their methods to estimate habitat-specific movement rates and boundary behavior (71). Essential to this approach is collecting field data to quantify recapture rates in all major land cover types the butterflies might encounter rather than just known resource patches. Recent work on *Parnassius mnemosyne* indicates the success of this modeling approach and resulting conservation actions. The species expanded its range from a translocated site through a forested landscape as predicted by the model (78). Virtual migration models (VMM) are a related technique that are simpler, less powerful, and more widely used than the case study above. In brief, the VMM is a multistate mark-recapture model adapted to fit survival and dispersal parameters with inference from patch size and isolation across the network based on assumptions about inferences from mortality while moving within and between patches (41). Multistate mark-recapture models are a general method for estimating survival and realized movement rates among habitat patches using MRR data (23). To date, 17 butterfly studies have used VMM. These studies primarily focus on three well-developed species complexes: *Boloria (Proclossiana) eunomia* (62, 72, 80, 81); often co-occurring checkerspot species *Euphydryas aurinia*, *Euphydryas maturna*, *Melitaea athalia*, *Melitaea phoebe*, and/or *Melitaea diamina* (18, 21, 34, 104, 106); and often co-occurring *Pbengaris* species (*P. nausithous* and *P. teleius*) (10, 45, 67, 68) as well as *Parnassius smintheus* (57), *Parnassius mnemosyne*, (102), *Coenonympha hero* (20), and *Iolana iolas* (75). A common thread that emerges from these studies is that when dispersal parameters are measured for the same species in different landscapes, the estimates are notably different among landscapes (34, 81). Eight of the VMM studies either directly compare dispersal biology for at least one species in multiple networks or quantitatively compare findings in the focal network to other studies that document the same species in another network (10, 18, 21, 34, 62, 68, 80, 81). Fric et al. (34) conclude in a similar manner across these studies, that “dispersal distances critically depend on the habitat patchwork configuration and/or composition of the separating matrix” (p. 350). In addition, a key limitation to understanding effects of current patch configuration in VMM is its failure to account for behavioral responses at habitat boundaries (80, 112, 113).

**Habitat-specific movement and boundary behavior.** In general, a key limitation of MRR is that dispersal rates are estimated for static landscapes under a particular set of conditions. Because conservation strategies need to plan for butterflies encountering landscape characteristics new to them, parameter estimates from static landscapes can be problematic and not predictive of butterfly movement and dispersal through a novel landscape.

In contrast, a combination of habitat-specific movement rates and behavior at boundaries allows inference in a dynamic landscape and produces general recommendations (e.g., minimum



critical patch size) (13, 25). Habitat-specific movement parameters can be combined with demographic information in spatially explicit individual-based models to simulate population dynamics within a given landscape (44, 46, 59, 78). In both cases, the assumption is that if we understand only patterns of movement (e.g., from MRR), we cannot extrapolate beyond the range of observations. However, if we understand the mechanisms, we can explore what might happen in new situations.

We found only seven species with estimates of habitat-specific movement behaviors (**Figure 2, Supplemental Text 2**). Sei (90) quantified flight behavior of *Coenonympha nipisiquit* near dense and sparse patches of host plants, and she observed greater turning angles in areas with a higher density of host plants. This behavior is consistent with lower movement (diffusion) rates near high-quality habitat. Such behavior leads to concentrated movement in areas with high-quality habitat and can also lead to higher population densities (89). Other species had similar responses: slower movement rates in high-quality habitat and much faster movement rates in low-quality habitat (82, 87, 94).

We found 11 species within our review of formally listed species and recent *JICO* publications with estimates of boundary behavior (**Supplemental Text 2**). Six of these are *Erebia* species from a single study in which Polic et al. (74) set up experimental plots and quantified the proportion of butterflies crossing to an adjacent experimental plot on the same side of or across a large road. They found that butterflies were less likely to cross the road than fly to the adjacent plot. In these studies, forests limit, but do not halt, butterfly movement (52, 87). In addition, attraction to host-plant patches is strong, suggesting that conservation actions aimed at increasing residence time could focus on either increasing available host-plant habitat or creating structural barriers to limit movement out of the patch. This can lead to a suite of flexible options for constructing conservation strategies that may depend on available land, habitat resources, and restoration efficiency. Roads may reduce, but are not a barrier to, butterfly movement (74, 114).

Many past studies have assessed butterfly mobility on a per-species basis, as a single parameter averaged across the landscape. For example, Viljura & Teder (101) used estimates of mobility from a European butterfly atlas as a basis for analysis of presence/absence of butterfly species in forested areas in Estonia. They were surprised when sedentary species were found on isolated parcels of forest. We suggest an alternative view in which dispersal is not a species-specific trait but rather a response to environmental context, which has important implications for conservation planning. In this example, by assuming dispersal traits are species invariant, Viljura and Teder conclude that dispersal limitation does not influence these butterfly populations. However, this conclusion might be redirected or reversed when movement varies within patches, at boundaries, and in the matrix. This change in how we view movement could transform approaches to conservation.

## Demography

Demography refers to estimating survival, growth, and reproduction of individual animals. Combined, these demographic rates provide estimates of whether a population is increasing or declining in a given patch and allows for assessment of how a population responds to a specific conservation action. Linking demographic rates and population dynamics to management actions is critical to designing conservation strategies that result in growing butterfly populations. Understanding these rates throughout the life cycle of a species is also important because vital rates of different life stages can respond to environmental variation in different directions.

**Adult survival.** As with dispersal, the most common method used to estimate demographic rates has been MRR techniques (used for 30 of the 34 species in **Figure 3**). This is especially true





for species on the European Red List, for which all 8 listed species with known demographic rates used MRR to quantify at least one vital rate. In contrast to efforts in Europe, MRR was used to quantify rates for only 5 of 8 North American species for which there are demographic data. Of species with demographic data that were not collected with MRR methods, all are North American. This points to a cultural difference between European and North American approaches to method selection; apparently, North Americans are more risk averse to marking (64). We have found that these methods do not harm populations of at-risk species (13, 70), and the knowledge benefits outweigh harm to individuals or habitat. Moreover, our experiences suggest that MRR studies with adult butterflies, in combination with experimental methods to estimate vital rates for other life stages, provide a means to use rigorous methods to estimate vital rates while limiting impact to habitat and focal species (3, 13, 43, 85).

We identified 28 butterfly species, with estimates of adult daily survival, of which 17 are listed as at-risk butterflies, and 11 are recent *JICO* studies that describe the focal species as an at-risk butterfly in the region of interest. Bubova and colleagues (16) reviewed 50 European butterfly species and, on the basis of the estimate life span, which is interchangeable with calculations of adult daily survival, determined that “endangered” and “vulnerable” European butterfly species had shorter life spans than those that are “near threatened” or of “least concern” (16). With standard MRR methods, daily survivorship is actually apparent survival (i.e., the probability that individuals remain alive and in the study area). Multistate mark-recapture models (including VMM) at least partly account for this by separating the probabilities of daily survival from emigration to other patches within the study area, though emigration outside the study area would still be included with mortality. Thus, most applications of VMM estimate daily within-habitat survival ( $\varphi_p$ ).

**Immature survival.** Compared to estimates of adult survival, estimates of immature (egg and/or larval) survival have been collected for half as many species (16 species; **Supplemental Text 2**). Studies in which researchers estimate larval survival are more focused on mechanistic responses to habitat quality than those of adult daily survival. For example, *Pbengaris alcon* larvae were more likely to survive to the fourth instar if eggs were deposited on larger flower buds and on apical flower buds (2), *Coenonympha nipisiquit* were less likely to survive in habitats with lower host-plant stem density (91), *Euphydryas editha* larval groups were less likely to survive to the third instar in clearings with higher rates of host-plant senescence (11), and larval survival of *Lopinga achine* was higher at the edges of forest glades than in full sun (8). In addition, researchers were more likely to quantify larval survival than other vital rates in response to conservation actions (107).

**Fecundity.** We identified only three at-risk species with quantitative estimates of per capita fecundity in a natural setting (**Supplemental Text 2**). However, estimates of potential maximum fecundity in the laboratory are available in books and in reports because rearing Lepidoptera is a favorite pastime of many professional and amateur lepidopterists (48). Such estimates set the maximum potential eggs per female. Realized fecundity in field settings can be estimated by modifying study designs to include specific additional data collection. In our review, it was common for studies to assess egg density as part of either an assessment of oviposition preference or an assessment of habitat association with density of immature stages. If researchers systematically evaluated the abundance of host plants, this would lead to eggs per host plant  $\times$  host plant per area  $\times$  total area = total number of eggs. Then number of eggs divided by number of females in the population naturally leads to per capita rates for eggs per female. Adding this step to many studies would transform the data from estimated habitat association or preference to estimated habitat-specific fecundity. Alternatively, Cushman and colleagues (26) have devised methods to



associate realized fecundity with biomass in the laboratory and translated this to field conditions. Yet another approach, albeit a data intensive one, is to model female movement and egg laying on a real landscape to estimate realized fecundity (112, 113). Such approaches would provide a much-needed assessment of the relationship between maximum potential fecundity, as measured in a laboratory setting, to realized fecundity in the wild.

## RESPONSES OF VITAL RATES TO CONSERVATION ACTIONS

To construct effective conservation plans, we need to know how vital rates respond to changes in habitat quality and to conservation actions. For example, we need to know the value of high-quality habitat (e.g., host plants/m<sup>2</sup>) for increasing reproductive value for a focal species in comparison to alternatives (e.g., increasing patch size). Similarly, how much is the short-term cost of a restoration action (e.g., burning) relative to a long-term gain? All these metrics rely on estimates of habitat-specific vital rates and are at the crux of our ability to do efficient and effective conservation planning.

### Movement

Strikingly few studies of at-risk butterflies measure movement rates or boundary behavior in response to conservation actions. Dennis et al. (28) and others have written extensively on the importance of habitat quality in achieving butterfly conservation success—often stressing that for butterfly conservation, resource needs far outweigh the importance of patch size and spatial arrangement of habitat. We find extremely sparse data on how conservation efforts that change habitat quality or structure (e.g., through burning) might influence butterfly dispersal behavior. A few notable exceptions are studies of the response of *Plebejus icarioides* to fire-based management (108), response of *Neonympha mitchellii* to restoration flooding (43), and response of *Boloria eunomia* to grazing (4). In general, we observe that at-risk butterflies in high-quality habitats have slower movement rates (14, 87), a pattern observed in many butterfly species (49, 52, 113). We expect faster movement rates in nonhabitat (matrix) and low-quality habitat and slower movement rates in high-quality habitat. This provides a useful metric by which to assess how a butterfly perceives habitat quality as it declines in response to anthropogenic stressors or increases in response to restoration actions.

### Demography

Given clear interest in using conservation actions to influence at-risk butterfly populations, surprisingly few studies of at-risk butterflies measure adult or immature survival or fecundity in response to habitat quality, disturbance, or management efforts. Studies with a focus on mechanistic responses to conservation actions most often measured larval survival either directly in response to a management event or assessed a metric directly related to larval survival in the wild. For example, Kajzer-Bonk et al. (51) measured larval survival of *Phengaris nausithous* and *Phengaris teleius* in response to flooding and found that larval survival in inundated nests of their *Myrmica* host ant was low while survival in noninundated nests was high. Survival of *Coenonympha tullia* was also lower in flooded areas (50). Some studies document that larval survival is low at the time of disturbance but increased in the year(s) that follow. Warchola et al. (107) found that larval survival of *Plebejus icarioides* is low in the year of a management burn and high in the year after the burn, when ant tending is more common, and Henry (43) discovered that larval *Neonympha mitchellii*



have higher larval survival in vegetation present in restoration areas that were flooded and logged a few years previously than in control areas without flood-influenced vegetation.

Unfortunately, studies designed to assess the effects of disturbance or management actions often have designs that are insufficient to estimate vital rates. For example, Goffart and colleagues (35) set up an experimental study to assess the effects of mowing on *Lycaena helle* and *Boloria eunomia*. They observe that fewer adults emerge from mowed strips than control strips. Similarly, two studies on *Danaus plexippus* suggest a demographic response to disturbance. Baum & Sharber (6) note that well-timed fire increased egg density in late summer, and Fischer and colleagues (32) note a similar response to well-timed mowing. However, because the number of individuals and eggs per adult butterfly before mowing or fire are unknown, per capita rates cannot be assessed. Finally, another design flaw in some studies is assuming that a similar species serves as a suitable surrogate in measuring the demographic or behavioral response to disturbance (43, 44). Such flaws can have significant implications for misdirection in taking conservation actions (43). Without quantitative estimates, we cannot integrate a management effect into the assessment of an action's impact on projection of the full life cycle of the butterfly. Thus, for at-risk butterflies and beyond, data on how conservation efforts or changes in habitat quality might influence butterfly population dynamics are extremely sparse.

### Vital Rates Throughout the Life Cycle

Vital rates are a common currency for assessing effects of global change on population trends. Radchuk and colleagues (76) combined experimental work in the laboratory and in natural settings to measure the response of vital rates to changing temperatures. They showed that warmer temperatures positively influence many life stages of *Boloria eunomia* while they negatively influence overwinter survival. Together, the net effect of these factors is reduced population viability (76). Similarly, the influence of nonnative host-plant species in the diet of specialist butterflies can be evaluated only by estimating demographic rates throughout the life cycle (12). Only three at-risk species to date have published estimates of vital rates throughout the life cycle (*Euphydryas editha*, *Plebejus icarioides*, and *Plebejus melissa*). All three of these species are on the USFWS Endangered Species list, which requires the use of quantitative recovery criteria. These criteria can contribute to research on at-risk species. Collectively, the integration of habitat quality into studies of butterfly demography and dispersal offers great promise to develop conservation approaches for butterflies and other at-risk taxa.

### VITAL RATES AND THE VIABILITY OF POPULATIONS AND SPECIES

Population viability analyses (PVAs) provide integrated projections of the fate of at-risk butterfly populations. A great challenge is to incorporate vital rates to increase their rigor and their value to assess the relative effectiveness of conservation alternatives. In vertebrates and plants, such analyses often rely on stage-based estimates of vital rates (i.e., stage-specific estimates of fecundity and survivorship) (63). In contrast, PVAs for most at-risk butterflies rely on inference from time-series analysis. In some cases, short time series (<10 years) over multiple sites have been used to set recovery criteria (88). With sufficient data in the presence of a disturbance history, time series of butterfly populations as a function of time since disturbance can shed light on the influence of disturbance on population viability (58). One problem with monitoring is that programs are often initiated after declines have already been noticed. One case study solved this problem by using state-space models to integrate sparser historical data with more systematic recent data and



estimate the population trend over more than 30 years (83). Long time series and/or time series that co-occur with disturbance or with desired management are rare. We see an increasing need to predict the viability of butterfly populations based on short time series or novel conditions such as those presented by climate change.

Approaches that integrate habitat-specific movement and boundary preference into PVAs have great promise to predict butterfly population viability, given current and potential landscapes. For example, Brown et al. (13) use movement behavior in concert with estimates of vital rates through the life cycle to estimate minimum area requirements for *Euphydryas phaeton*. The authors observe that the butterfly has very limited diffusion rates within habitat patches, and individuals rarely leave habitat patches. As a result, the butterfly has very high potential population growth rate, and a relatively small area (<1.5 hectare) can support a population with a high likelihood of persistence. In addition, experimental studies to measure vital rates in response to disturbance can provide a mechanism to estimate population viability for a population over a short time period (<4 years of data) (108). Movement and demography are the building blocks for PVA to evaluate conservation strategies in dynamic landscapes. Because vital rates are based on mechanistic understanding of butterfly biology, approaches that incorporate these cornerstones can move beyond explaining patterns in static landscapes and consider alternatives for potential recovery of at-risk populations in changing landscapes (44).

## CONCLUDING THOUGHTS AND EXTENSIONS ACROSS AT-RISK INSECTS

Conservation of at-risk butterflies depends on reorientation of research approaches toward demography and behavior. There is a long history in butterfly ecology and natural history of describing habitat with reference to the presence of adults, eggs, or larvae. These studies are often an essential first step in understanding the autecology of at-risk butterflies (105). However, these studies do not directly translate into use of this information to inform effective conservation strategies because they are not conducted in a manner that can lead to estimates of vital rates. The ecological notions of source-sink dynamics and ecological traps stem from the challenge that for many conservation-dependent taxa, animals may use or select habitats that are not optimal for performance (5, 110). Such dynamics have been observed in multiple butterfly populations [e.g., *Phengaris nausithous*, *Phengaris teleius* (97), and *Lycaena xanthoides* (93)]. Thus, assessment of habitat association or preference in the absence of performance measures (i.e., demographic rates) is often insufficient to develop effective conservation strategies.

Estimation of vital rates throughout the life cycle are the building blocks for developing conservation actions in the face of continual threats to population, habitats, and landscapes. To date, vital rates have been measured for a fraction of at-risk butterfly species.

Beyond butterflies, the decline of at-risk insects is alarming (29, 69, 103). Although it could be argued that we need better information about the demography and behavior of at-risk butterflies, there are almost no data for any other at-risk insect (**Table 1**). One exemplar is the critically endangered American burying beetle, *Nicrophorus americanus*, with data on demography and dispersal estimated primarily from MRR studies (7, 24, 55, 60). Another species with some related information is the critically endangered *Bombus affinis*, for which there are MRR studies (9) and long-term distribution records of foraging workers (17, 22, 37, 39). Even for this relatively well-studied species, we lack knowledge of vital rates of reproductive queens and colonies. Studies of demography and dispersal of at-risk insects need to be expanded, and research on at-risk butterflies provides a model for those efforts.



### SUMMARY POINTS

1. Reversing worldwide declines of insect populations is a paramount challenge for our generation.
2. We have sparse knowledge about the biology of at-risk butterflies and even scarcer knowledge about declining species within other insect orders.
3. Estimation of vital rates throughout the life cycle are the building blocks for developing conservation actions in the face of continual threats to population, habitats, and landscapes.
4. In the absence of such data, conservation decisions are often incorrect or detrimental to at-risk species.
5. Conservation of at-risk insects depends on reorientation of research approaches toward demography and dispersal behavior throughout the life cycle.
6. Which conservation actions are sufficient to reverse declining population trends depends on species biology within potential future landscape contexts.
7. For species for which data now exist, the use of research tools dependent on butterfly movement and demography in the context of habitat-enhancing disturbance is leading to recovery of at-risk butterfly species.

### FUTURE ISSUES

1. We anticipate that insect populations will continue to encounter nonanalog (heretofore unobserved) environmental conditions, in concert with the diversity of anthropogenic landscape and climate changes.
2. By understanding vital rates, including movement, throughout the life cycle, we can potentially reverse population declines and restore insect populations.
3. New research will benefit from a commitment to estimating vital rates in 'natural' settings and, when possible, estimating vital rates in the context of experimental changes in habitat that mimic potential changes due to disturbance, restoration, and enhancement.
4. Expanding the scope of research to measure vital rates across at-risk insects is imperative.

### DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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