Growth and dispersal of larvae of the checkerspot butterfly Euphydryas editha

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We investigated growth and dispersal of postdiapause Euphydryas editha larvae in a serpentine soil-based grassland, using groups of individually marked and weighed larvae. Larval weight gain was highly correlated with insolation at ground level which is determined by slope exposure and date. Maximum dispersal distances were in excess of 10 m d^{-1}; dispersal greater than 5 m d^{-1} resulted in depressed growth rates during the period of dispersal. Larvae which disperse such distances can transfer from cool to warm slopes and can pupate up to two weeks sooner than larvae remaining on cool slopes, even after paying the time and metabolic costs of dispersal. We discuss the implications of larval dispersal on individual fitness and population persistence.

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Introduction

The importance of adult dispersal in Lepidoptera has long been appreciated as a major factor in their population biology (see Ehrlich 1984 for review). Dispersal of the larval stage, in contrast, has been less thoroughly investigated. Most studies of larval dispersal have concentrated on the ability of larvae to find host plants (Dethier 1959, Douwes 1968, Jones 1977, Cain et al. 1985). Larval movements in this context are of obvious importance.

Larval movements also occur in association with thermoregulatory behavior. Postdiapause Euphydryas larvae are behavioral thermoregulators; they raise body temperature (T_b) and maximize growth rate by basking in sunlight (Porter 1982, Weiss et al. 1987). Larval T_b is commonly 10–12°C above ambient temperature (T_a), but may reach 19°C over T_a. Fastest growth occurs at T_b of 30–35°C (Porter 1982). Achievable T_b is greatly reduced by shading and low T_a, hence low insolation levels can restrict larval growth even when direct sunlight is available. The growth of Euphydryas larvae, therefore, is constrained by local microclimatic conditions which vary with slope exposure and time of year (Dobkin et al. 1987, Weiss et al. 1987), and can be "adjusted" by dispersal between slopes.

The rate and timing of larval development (and the duration of the pupal stage) determine the timing of adult flight, which in turn is thought to be a key determinant of successful reproduction in Euphydryas editha. To successfully enter diapause, larvae must reach the fourth instar before their annual host plants senesce. As such, the relationship between the adult flight period and the onset of larval host plant senescence largely determines prediapause survival rates and population size in the following year (Singer 1972, Ehrlich et al. 1975, Singer and Ehrlich 1979).

In this study we discuss how topography, microclimate, and larval dispersal and growth interact in a population of Euphydryas editha bayensis (Lepidoptera: Nymphalidae). By combining larval mark-recapture techniques, growth measurements, and a computer simulation of clear sky insolation levels, we investigated how larval dispersal from one slope to another can affect development time. Specifically, we asked how growth rates and movements vary with insolation and how these factors can determine timing of pupation and adult flight. Finally, we used this information to infer how the topographic heterogeneity of a habitat can determine population persistence.

Tab. 1. Growth and dispersal of last (sixth) instar larvae. Dates are start and stop of individual experiments. Fractional days are included in calculations of per day values. 95% confidence interval based on t-test. Exp. A * dispersal distances lumped for last and penultimate instar larvae. ---- denotes complex topography and rainy weather that made isolation calculations in feasible.

Exp.	Dates	Slope	Growth		Dispersal		N	Insolation $(kWh\,m^{-2}\,d^{-1})$
			$mg\,d^{-1}$ (mean) (S.D.)	95% CI	$m\,d^{-1}$ (mean) (S.D.)	range (min–max)		
A	9–12 Jan	SE 13°	30.1 8.5	35.8– 24.4	0.76* 0.13	0.20– 1.30	11	3.50
A	9–12 Jan	N 11°	15.5 6.9	21.3– 9.8	2.29* 1.00	0.60– 4.90	8	2.02
B	19–23 Jan	SE 13°	26.2 6.8	28.8– 23.4	1.60 0.58	0.73– 3.17	36	3.67
B	19-23 Jan	N 11°	14.3 5.6	16.7– 11.9	· 1.17 0.40	0.67– 2.63	24	2.17
C	19–23 Jan	N 5°	9.9 4.1	13.0– 6.7	6.24 4.79	0.70– 12.50	9	2.56
E	24–28 Jan	FLAT	20.3 7.4	23.0– 17.6	2.50 1.02	1.17– 5.55	33	3.25
G	7–9 Feb	N 22°	10.5 4.7	12.2– 8.7	2.54 1.72	0.20– 8.40	31	1.75
H	7–9 Feb	RIDGE	10.3 6.0	13.5– 7.1	6.44 2.59	2.91– 11.95	16	----
I	10–13 Feb	SE 10°	16.1 5.0	17.6– 14.6	0.43 0.20	0.12– 1.10	46	----
J	21–23 Feb	SE 10°	44.0 12.6	48.1– 40.0	0.52 0.32	0.12– 1.25	39	4.95
L	4–14 Mar	SE 13° N 11°	26.0 4.2	28.2– 23.8	0.45 0.14	0.16– 0.59	16	----
M	6–14 Mar	SE 13° N 11°	18.0 5.0	22.3– 14.5	0.57 0.53	0.14– 1.94	9	----
N	18–20 Mar	SE 13°	43.7 13.3	49.6– 37.9	1.10 0.46	0.31– 2.19	22	6.35
N	18–20 Mar	N 11°	43.4 9.7	50.3– 36.5	0.93 0.49	0.17– 1.81	10	5.05

Materials and methods

We conducted this study in a large (>2000 ha) habitat near Morgan Hill, Santa Clara County, California, densely populated by *Euphydryas editha bayensis*. The site has a wide variety of slopes that range up to 40° and face all compass directions. Larval densities exceeded one per m² on cool north-facing slopes, where the larval host plants *Plantago erecta*, *Orthocarpus purpurascens* and *O. densiflorus* undergo senescence later in spring than on warmer slopes. The entire site has been grazed by cattle for decades. Postdiapause larvae feed and bask among short vegetation in the grassland habitat. Collecting and monitoring individual larvae was greatly facilitated by this lack of vegetational complexity.

Postdiapause larvae collected from the field were refrigerated at 5–10°C until they were taken to the laboratory. We then individually marked and weighed larvae following the procedures of White and Singer (1987). We subsequently released the larvae in large groups at selected points and recovered them several days later. We marked the location of each recovered individual with a flag, measured dispersal distance and direction from the release point, and re-weighed the larvae upon

return to the lab. Molting larvae were excluded from analysis.

We used two assumptions in calculating development times of female larvae: first, that growth rates are constant throughout the instar under consideration, and second, that females pupate at 400 mg, as seen in laboratory experiments (unpubl. data). These assumptions allowed us to estimate the effects of dispersal on development rates.

We determined exposure and slope using a compass and clinometer, and calculated theoretical clear sky insolation values with a program run on an Apple II computer, as described by Weiss et al. (1987). All statistical procedures followed those of Sokal and Rohlf (1981).

Results

Tabs 1 and 2 summarize the results of 12 separate releases of larvae. Larval growth varied with exposure, slope, and time of year. For example, on 9 January, larvae were released at the base of a "V" shaped gully formed by a N 11° and a SE 13° slope (Experiment A). Last (sixth) instar larvae which moved to the SE slope grew at 30.1 mg d⁻¹, while those which moved to the N

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Tab. 2. Growth and dispersal of penultimate (fifth) instar larvae.

Exp.	Dates	Slope	Growth		Dispersal		N	Insolation (kWh m^{-2} d^{-1})
			mg d^{-1} (mean) (S.D.)	95% CI	m d^{-1} (mean) (S.D.)	range (min– max)		
A	9–12 Jan	SE 13°	13.1 4.4	14.8– 11.4	0.76* 0.13	0.20– 1.30	35	3.50
A	9–12 Jan	N 11°	7.6 2.6	8.9– 6.3	2.29* 1.00	0.60– 4.90	18	2.02
B	19–23 Jan	SE 13°	13.2 4.2	16.2– 10.2	1.29 0.40	0.73– 1.87	10	3.67
B	19–23 Jan	N 11°	7.2 1.9	8.6– 5.8	0.80 0.30	0.43– 1.63	10	2.17
C	19–23 Jan	N 5°	5.8 2.5	8.1– 3.5	3.52 2.26	0.13– 9.22	7	2.56
D	19–23 Jan	NE 17°	8.8 2.9	10.1– 7.5	0.36 0.23	0.02– 0.74	21	2.10

slope grew at 15.5 mg d^{-1}. A release at the same spot on 19 January (Exp. B) gave similar results. On 18 March, larvae released at the same spot grew at 43.4 mg d^{-1} on both slopes (Exp. N).

Larval growth rates were directly related to ground level insolation (Fig. 1). Growth rates level off at high insolation values at which larvae maintain high T_b. Larvae in the penultimate (fifth) instar gained weight at half the rate of last instar larvae under the same conditions (Tabs 1 and 2, Exp. A and B). This relation presumably holds true for all insolation levels.
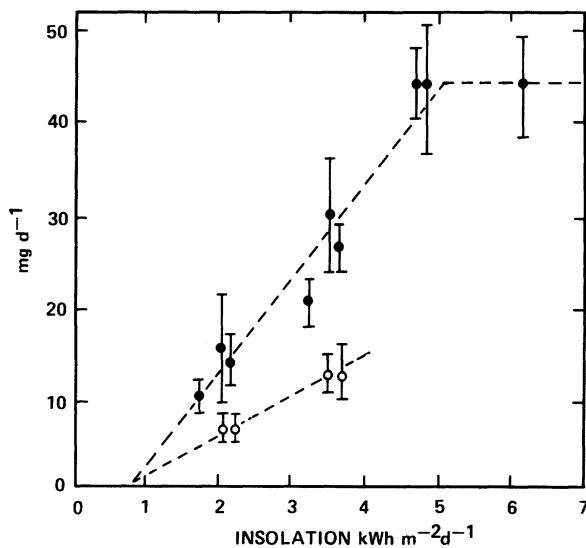

Fig. 1. Larval growth versus insolation. Insolation is calculated for clear skies, and includes both direct and indirect radiation striking the ground. Error bars are 95% confidence intervals (t-test). Closed circles are last instar larvae, open circles are penultimate instar. Dashed lines are calculated regression lines. Regression line for penultimate instar Y = 3.8X − 0.53, r = 0.99; for last instar excluding the highest insolation value, Y = 9.9X − 7.2, r = 0.97. Note the plateau of growth rate above 5.0 kWh m^{-2} d^{-1}

We found no evidence of allometric scaling within each instar, i.e. 100 mg larvae gained as much weight per day as 200 mg larvae.

Cloudy and rainy weather conditions apparently suppressed larval growth. Releases of larvae on the same SE 10° slope on 10–13 and 21–23 February (Exp. I and J) produced mean growth rates of 16.1 and 44.0 mg d^{-1} respectively. Because Exp. I coincided with the onset of an extended period of rainy weather on 11 February, these larvae experienced only one clear day. If all growth in Exp. I is assumed to have taken place on that one clear day, then the mean growth rates of the two groups were similar (40 vs. 44 mg d^{-1}). Larvae released on 4 and 6 March (Exp. L and M) grew at mean rates of 24.1 and 17.1 mg d^{-1}, over 10 and 7 d, respectively. When rainy days are discounted, growth rates were over 40 mg d^{-1}, indistinguishable from clear day growth rates in other samples under similar insolation levels.

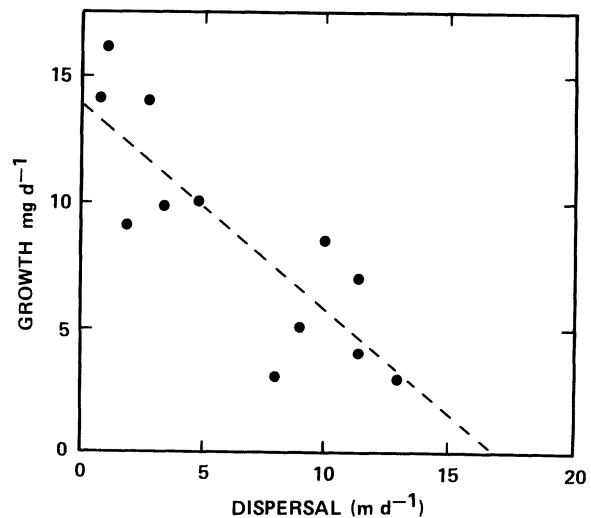The variance in growth rates among individual larvae

Fig. 2. Growth vs dispersal distance. Regression line is Y = −0.84 + 14.12, R = −0.84.
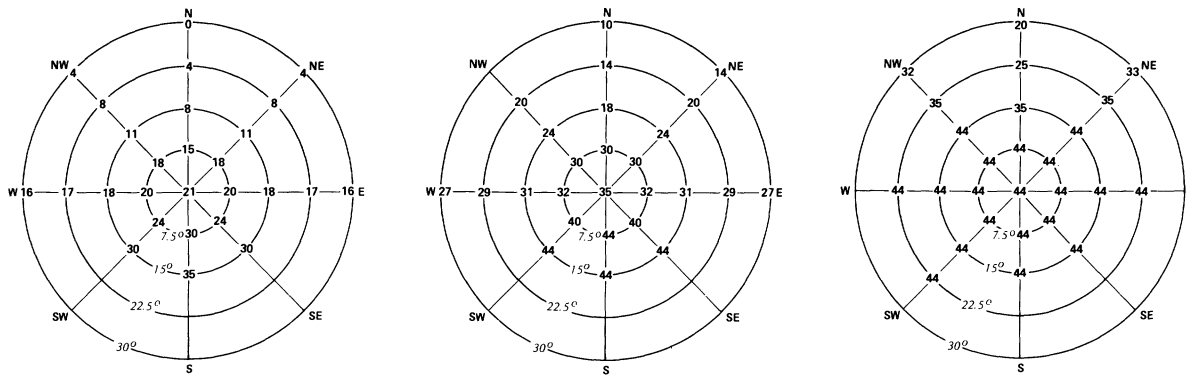
Fig. 3. Calculated last instar larval growth rates by slope and exposure in mg d^{-1} for, left) 21 January, middle) 21 February, and right) 21 March. Compass direction is indicated on circle perimeter, tilt in degrees is indicated along the radius. Growth rates are shown for every 45° in compass direction and 7.5° in tilt.

under the same conditions can be ecologically significant. For example, in the 21–23 February release (Exp. J), four larvae grew more than 60 mg d^{-1}. These larvae would pupate 2.5 d earlier than average larvae (gaining 44 mg d^{-1}), and 5 d earlier than the slowest larvae (gaining 30 mg d^{-1}), assuming they are female larvae. Or, females could reach heavier weights before pupation which might result in higher fecundity.

Last instar larvae can disperse over 10 m d^{-1} (Tab. 1) and larvae appeared to disperse farther on cooler slopes. For example, in Exp. A, larvae on the cool slope dispersed three times as far as those on the warm slope (Tab. 1). Factors other than slope exposure, such as host plant density and quality, certainly can contribute to movement. When and where exposures were warm and host plants were of high quality larvae moved less than 1 m d^{-1}. The longer movements were sufficient for larvae to transfer among microclimates over a wide range of topographic land forms.

Dispersal involved a trade-off with growth, particularly at distances greater than 5 m d^{-1}. Fig. 2 is based on Exp. C, which was the only experiment with sufficient numbers of long distance dispersers (>5 m d^{-1}) from which to draw conclusions. Yet, despite the long dispersal distances, no larvae were found in this experiment to reach significantly different slope exposures.

We did not find unambiguous directionality in group larval movements in most cases. In the case of a release on a rounded ridgetop (Exp. H), we subsequently found larvae on both the cool and warm sides of the ridge. Larvae have a slight tendency to move uphill on north-facing slopes; much of this movement can be ascribed to larvae seeking the sunny exposure on bunch-grasses and rocks to bask. This is the likely explanation for the greater dispersal distances on the N 11° side of the gully than on the SE 13° side in Exp. A and B. Larvae tend to aggregate in warm areas, simply because they stop dispersing when thermal conditions are suitable. This may explain why large concentrations of last instar larvae often are found on the crests of ridges.

We explore the many effects of dispersal from one slope to another at various times in the season in Fig. 3. This polar coordinate plot can be viewed as a truncated sphere. We calculated last instar growth rates for clear days using the empirical relationship in Fig. 1 and insolation calculated for 21 January, 21 February, and 21 March. The figures can be linearly interpolated over exposure, tilt and time with minimal loss of accuracy. (Penultimate instar growth can be obtained by dividing the last instar growth by two.)

Larvae also disperse widely in search of pupation sites and the length of the pupal stage will depend on the slope chosen (White 1986, Weiss et al. 1987). In late February and early March 1986, fresh pupae placed on a SE 13° slope eclosed after 15.1 ±2.5 d, n = 31; pupae on a N 11° slope eclosed after 23.7 ±3.2 d, n = 12, (t = 9.31, P<<.001), a difference of 8.6 d.

Discussion

An adult female *Euphydryas editha bayensis* emerges, is quickly mated, and faces a mosaic of rapidly drying oviposition host plants in its grassland habitat. While the female cannot discriminate between plants that will remain edible and those which will soon senesce she will enhance the chances of her offspring surviving by laying her egg masses on cool, moist slopes where the senescence of host plants is most delayed. Therein lies a paradox of sorts. While cool slopes confer increased chances for prediapause larvae to reach diapause successfully, cool slopes also subject postdiapause larvae to decreased winter insolation, which delays termination of diapause and results in subsequent slow growth rates. A female eclosing late from a cool slope in the next generation will face a higher proportion of senescent hosts and a reduced likelihood of her offspring reaching diapause.

A crucial determinant of fitness for individual postdiapause larvae then is to grow, pupate, and eclose as an adult as quickly as possible. Larval dispersal, as shown here, can have a major impact on eclosion date. We can calculate the potential influence of larval dispersal on
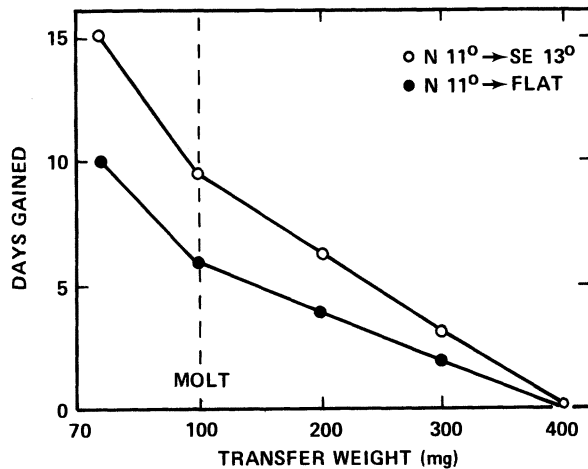
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Fig. 4. Estimated decrease in development time in larval stage for two potential transfers.

growth using the data presented here, extended to the moment of adult eclosion. As an illustration, we can view the hypothetical fate of a larva on the north-facing side of the gully formed by adjoining N 11° and SE 13° slopes; the site used in Exp. A, B, L, M, and N.

Fig. 4 shows the expected decrease in development time for larvae of different weights transferring from the cooler slope to the warm slope in mid-January. The earlier the transfer takes place, the greater the decrease in development time to pupation. A larva transferring at the beginning of its penultimate instar at 20 mg would pupate 15 d earlier. Transferring from the cool to the warm slope at the beginning of the last instar at 100 mg would result in pupation 9.5 d earlier. The difference in the duration of pupation between the slopes is an additional 8.6 d. Thus, larvae transferring to the warmer slope could emerge as adults more than three weeks earlier than those remaining on the cooler slope. (The development time decrease for a similar transfer from a N 11° slope to a flat area is also shown.)

Reductions in growth rates during dispersing are easily compensated for when larvae reach warmer slopes. For instance, in January a hypothetical last instar larva weighing 100 mg dispersing 20 m in two days from a N 11° slope to a SE 13° slope (over a rounded ridgetop) can increase its growth rate from 15 mg d⁻¹ to 30 mg d⁻¹. By staying on the cooler slope, it reaches pupation size in 20 d. By dispersing, it loses some portion of two days growth, but then completes development in only 10 d. Total development time decreases by about 8 d.

Larval movements in many directions will result in growth gains, but transfers in certain directions, particularly from the coolest slopes to warmer slopes have the greatest impact. Larvae transferring in January will realize proportionately greater growth rate increases over short distances than larvae transferring in March. But,

larvae transferring during March from the coolest slopes need not reach the warmest exposures to maximize growth rates, since even comparatively "cool" slopes as those from N 6° to N 11° produce high growth rates.

Decreases in development times can be significant in terms of individual fitness. At Jasper Ridge area H in 1969, for example, oviposition on 22 March would have resulted in an estimated 27% of egg masses hatching into dry environments, with complete mortality. Oviposition just one week later would have resulted in 71% of egg masses hatching into dry environments (Singer 1971). At Morgan Hill in 1985, a female eclosing one week earlier than average from a given slope could oviposit on slightly warmer slopes, and still have offspring survive to diapause size on the warmer slopes (Weiss et al. 1987).

The lack of strong directionality in dispersal does not suggest that movement is not adaptive. The complex topography of this site, with its numerous ridges, gullies, and spurs creates opportunities for dispersal in many directions to lead larvae into warmer environments. Uphill movement on steep north-facing slopes will generally lead to a decrease in the tilt angle, up to a flat crest. On steep slopes, warmer environments are found downward where the slope levels out or forms sharp gullies with opposing slopes. On spur ridges pointed north and in saddles lateral movement to the east or west from north-facing areas will lead to warmer exposures. In some cases, of course, dispersal will lead larvae into cooler areas. Still, the net effect of larval movements is an accumulation of late instar larvae in warmer areas, where they stop dispersing.

The greatest natural threats to *Euphydryas editha* populations inhabiting serpentine-based grasslands are drought years in which pressures on development time intensify. Host plants senesce rapidly under drought conditions, but this is partially compensated for by clear weather allowing faster larval growth and earlier adult flight. Nonetheless, the two year California drought from 1976–77 greatly depressed *Euphydryas editha bayensis* population sizes and forced several colonies to extinction (Singer and Ehrlich 1979, Ehrlich et al. 1980). During the first drought spring, the only prediapause survival came from egg masses deposited on cool slopes by early flying females which had developed on warm slopes. The probable lack of postdiapause larvae on warmer slopes during the next winter resulted in a later flight season, out of phase with early host plant senescence during the second drought spring. Larval dispersal from cool to warm slopes can partially ameliorate this situation by speeding postdiapause larval development and increasing the chance of at least some females eclosing and ovipositing in a favorable phase relationship with host plants.

Years of sustained rainfall can also reduce *Euphydryas editha* populations. Postdiapause larval development may be delayed substantially when growth is restricted to the few days between successive storms. As

in drought years, a poor phase relationship results, with adult flight delayed past plant senescence (Dobkin et al. 1987).

In years of either drought or deluge when macroclimatic conditions threaten to decouple the tight phase relationship between *Euphydryas editha* and its larval host plants, topographically diverse areas take on immense value. Ridgelines and shallow "V"-shaped gullies, where cool slopes are directly adjacent to warm slopes, allow larval dispersal of just tens of meters to greatly speed development. Indeed, dispersing larvae may produce the only adults which emerge in satisfactory phase with their host plants in some years.

This study has important implications for the conservation of this species, which is restricted to serpentine soil-based grasslands in the San Francisco Bay Area (Ehrlich and Murphy 1987, Murphy and Ehrlich 1980, 1987). It sheds light on the often confounding roles of habitat area and habitat heterogeneity in determining local species richness. Area and heterogeneity, of course, often are highly correlated and a strong species-area relationship has been found for invertebrates which have resource requirements that can be met in exceedingly small habitat areas (Murphy and Wilcox 1986a, Wilcox et al. 1986). Our findings for *Euphydryas editha* indicate heterogeneity, rather than habitat area per se, may be the crucial physical determinant of habitat quality for this species. This is consistent with the observation that some dense populations, in large topographically homogeneous habitat areas, went extinct or nearly so in the drought of the mid-1970s, while some less dense populations, in small heterogeneous areas, persisted.

We suggest that the selection and design of reserves for lower trophic level, small-bodied organisms, such as *Euphydryas editha bayensis* and the other herbivorous insects, should maximize habitat heterogeneity. While large habitat areas often will be logical targets for reserves, smaller, highly heterogeneous habitats in some cases may be as attractive or more so, should choices among potential reserves exist (Murphy and Wilcox 1986b). Similarly, if habitats are to be fragmented, areas with high local habitat heterogeneity should receive top priority for preservation. This study also underscores the need for detailed natural history investigations of all possible life stages where conservation efforts target specific species.

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