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Short Communication

Longevity minimalists: life table studies of two species of northern Michigan adult mayflies

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Abstract

Life table studies were conducted on both sexes of newly emerged subimagoes of the mayfly species, *Hexagenia limbata* ($n = 4472$) and *Ephemera simulans* ($n = 1254$), which have two- and one-year life cycles, respectively. The expectation of life at emergence for *H. limbata* was approximately 2.6 days for both sexes with the last individual (a female) dying on day 8. Expectation of life for *E. simulans* was 1.6 and 2.0 days for males and females, respectively, with the last individuals (both sexes) dying on day 3. The results reveal that mortality does not occur in one large step in this group of rapidly senescing organisms. Rather deaths are spread over several days when the adult mayflies are maintained under laboratory conditions.

Keywords: Life span; Aging; Age-specific mortality; Rapid senescence; Ephemeroptera; *Hexagenia limbata*; *Ephemera simulans*

1. Introduction

Because of the brief duration of the adult stage, mayflies (Insecta: Ephemeroptera) are frequently characterized in the biodemography (Carey, 2001) and gerontology (Finch, 1990) literature as the quintessence of a short-lived organism with the life span of adults usually reported as 1–2 days. Despite the general importance of understanding the actuarial patterns in short-lived organisms such as adult mayflies, virtually no life table studies have ever been conducted on any ephemeropteran species. Therefore I initiated life table studies on two species of adult mayflies endemic to northern Michigan with the following goals: (1) to construct complete life tables for each species in the laboratory; and (2) to answer the question posed by Finch (1990) 'Do mortality rates in mayflies accelerate progressively or increase in one huge step?"

2. Methods

2.1. Background

The order Ephemeroptera consists of 227 genera (Edmunds, 1988) found worldwide about ponds, lakes, and streams (Allan and Flecker, 1989). The immature stages are referred to as nymphs and live in or on the aquatic substrate feeding on algae and other micro-flora (Day, 1968). After 1–3 years of development, depending on the species, fully grown nymphs come to the water surface, molt, and the

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Table 1
Sex-specific life tables (x denotes age in days, N_x denotes number alive at age x; l_x is the proportion of the original cohort alive at age x, $l_x = N_x/N_0$; p_x and q_x denote the fraction alive at age x that survive from x to $x + 1$ and that die in the interval x to $x + 1$, respectively, $p_x = l_{x+1}/l_x$ and $q_x = 1 - p_x$; d_x denotes the fraction of the original cohort that dies in the interval x to $x + 1$, $d_x = l_x - l_{x+1}$; e_x denotes expectation of life defined as the number of days remaining to an individual age x, $e_x = 0.5 + (l_{x+1} + l_{x+2} + \cdots + l_\omega)/l_x$ where ω denotes the last possible age (Carey, 2001.) for the mayfly, *H. limbata*, collected June 29, 1993 at the University of Michigan Biological Station, Pellston, Michigan

x	Males						Females					
	N_x	l_x	p_x	q_x	d_x	e_x	N_x	l_x	p_x	q_x	d_x	e_x
0	2180	1.000	0.921	0.079	0.079	2.59	2292	1.000	0.918	0.082	0.082	2.61
1	2007	0.921	0.729	0.271	0.250	1.77	2105	0.918	0.696	0.304	0.279	1.80
2	1463	0.671	0.470	0.530	0.356	1.24	1466	0.640	0.510	0.490	0.314	1.37
3	688	0.316	0.419	0.581	0.183	1.07	747	0.326	0.461	0.539	0.176	1.20
4	288	0.132	0.306	0.694	0.092	0.86	344	0.150	0.395	0.605	0.091	1.03
5	88	0.040	0.136	0.864	0.035	0.68	136	0.059	0.294	0.706	0.042	0.84
6	12	0.006	0.333	0.667	0.004	0.83	40	0.017	0.125	0.875	0.015	0.65
7	4	0.002	0.000	1.000	0.002	0.50	5	0.002	0.200	0.800	0.002	0.70
8	0	0.000			0.000		1	0.000	0.000	1.000	0.000	0.50
9							0					

winged form flies a short distance to the shore where they alight on the vegetation. This insect, which is usually dull in appearance, is called a subimago. It molts again in the next 24 h to become the easily recognized smooth and shining adult. Adults have vestigial mouthparts and thus do not feed. Mating takes place in the early evening when a female enters a male swarm and is seized by one of its members. Each species has characteristic egg-laying habits ranging from laying eggs on the surface of the water to attaching eggs to vegetation or stones in the water.

2.2. Empirical

The mayfly life table studies were conducted on two different species at the University of Michigan Biological Station (UMBS) situated on Douglas Lake near Pellston. Newly emerged subimagoes were collected from the sides of buildings near lights on a single evening of a major emergence, caged in 8 l styrofoam containers with screened tops, placed on a table near windows in the main boathouse, and maintained at ambient temperature (recorded at UMBS weather station). Virtually, all individuals molted into the adult stage within 24 h after which time they rested quietly on the sides of the container until they died. Each morning at 08:00, the dead individuals were removed from the cages and placed in alcohol for sorting by sex and counting at a later time.

Separate mayfly species were studied during each of two years (Lyman, 1955). (1) *Hexagenia limbata* (Serville), a species with a two-year life cycle (Burks, 1953; Hunt, 1953) was studied in 1993. An initial cohort of 2180 males and 2292 females (total of 4472 individuals) was collected on June 29, 1993 and monitored daily until the last individual died 8 days later (July 7). The eight-day averages for the minimum and maximum ambient temperatures were 15.3°C (range = 10.0–21.1) and 27.0°C (range = 21.1–33.9), respectively. (2) *Ephemera simulans* (Walker), a species with a one-year life cycle (Burks, 1953; McCafferty, 1983) was studied in 1994. An initial cohort of 501 males and 753 females (total of 1254 individuals) was collected on July 7, 1994 and monitored daily until the last individual died 3 days later (July 10). The four-day averages for the minimum and maximum ambient temperatures were 16.7°C (range = 11.7–19.4) and 24.3°C (range = 20.6–27.2), respectively. Selected specimens for each species were shipped to mayfly biologist and taxonomist Dr G.F. Edmunds, for identification.

3. Results

The life tables for each species of mayfly by sex are given in Tables 1 and 2. Several aspects of these

Table 2
Sex-specific life tables for the mayfly, *E. simulans*, collected July 7, 1994 at the University of Michigan Biological Station, Pellston, Michigan

x	Males						Females					
	N_x	l_x	p_x	q_x	d_x	e_x	N_x	l_x	p_x	q_x	d_x	e_x
0	501	1.000	0.916	0.084	0.084	1.56	753	1.000	0.918	0.082	0.082	1.97
1	459	0.916	0.150	0.850	0.778	0.66	691	0.918	0.544	0.456	0.418	1.10
2	69	0.138	0.058	0.942	0.130	0.56	376	0.499	0.104	0.896	0.448	0.60
3	4	0.008	0.000	1.000	0.008	0.50	39	0.052	0.000	1.000	0.052	0.50
4	0	0.000			0.000	0.00	0	0.000			0.000	

life tables merit comment. First, mayfly adults are indeed short-lived with life expectancies at adult emergence ranging from slightly over 1.5 days in male *E. similans* (Table 1) to 2.6 days in female *H. limbata* (Table 2). The life expectancies given in Tables 1 and 2 were determined in the laboratory and therefore are probably slightly higher than the life expectancies of these species in the wild. This is not only due to the increased hazards of inclement weather and predation, but because females die in the act of reproducing (i.e. abdomens burst when they land on the lake surface). Second, the highest one-day probability of survival for both species was in the interval from 0 to 1 day with the values of p_0 exceeding 0.90 in both species and sexes. This suggests that both species of mayfly likely evolved a one-day timetable for mating and reproduction. This is consistent with the basic biology of mayflies — a large cohort of mayfly subimagoes emerges at dusk, molts over the next 24 h and then swarm, mate, oviposit and die the following evening. Third, mortality rates in both species increased rapidly and monotonically with age with no evidence of slowing at 'older' ages. Mortality in both species was less than 10% on from days 0 to 1 but from days 2 to 3 increased to around 50% in *H. limbata* (Table 1) and around 90% in *E. similans* (Table 2). Fourth, although mortality rates increased rapidly, a few individuals of the larger species, *H. limbata* (Table 1) lived a week or more and some individuals of the smaller species, *E. similans* (Table 2) lived for slightly over 3 days. The high rates and the inexorable increase in mortality make it unlikely that the use of higher initial numbers of individuals would have changed the 'record' life span by over a day or two.

4. Discussion

The current life table study reveals that the simultaneous emergence of mayflies is not matched by their simultaneous death if the adults are maintained under laboratory conditions. Depending on species, a substantial fraction of the cohort is capable of living for several days and for the larger mayfly species such as *H. limbata*, the total deaths are distributed over 7–8 days. Therefore, the results of these life table studies on mayflies provide a baseline for comparative studies of other rapidly senescing species. Subsequent studies on other species may reveal whether the type of mortality pattern exhibited by mayflies is general to the rapid senescence type of life history (Finch, 1990) or specific to mayflies.

Understanding the life history strategy of short-lived species, such as mayflies, will provide insights into the more general aspects of selection for life span. That is, the results may shed light on the question "what factors favor the evolution of abbreviated life spans?" Some insights into this question are possible from examination of mayfly life histories. Requirements for species with extremely short life spans may include: (i) synchronous emergence to concentrate adults so that the likelihood of finding a mate is maximized; (ii) the inability to feed due to their vestigial mouthparts which preempts the need for individuals to spend time foraging for food; and (iii) a 'general' nymphal habitat (i.e. nearby lake or stream) which requires that females fly only a short distance to deposit their eggs.

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