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Time Limitation, Egg Limitation, the Cost of Oviposition, and Lifetime Reproduction by an Insect in Nature

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abstract: For more than 80 years, ecologists have debated whether reproduction by female insect herbivores and parasitoids is constrained by the time needed to find hosts (time limitation) or by the finite supply of mature eggs (egg limitation). Here we present the first direct measures of permanent time limitation and egg limitation and their influences on the cost of oviposition and lifetime reproduction for an insect in nature. We studied the gall midge *Rhopalomyia californica*, which neither matures nor resorbs eggs during the adult stage. By sampling females soon after their death and correcting for predation effects, we demonstrate that females lay a large proportion of their total complement of eggs (multiyear mean: 82.9%). The egg supplies of 17.1% of females were completely exhausted, with the remaining 82.9% of females being time limited. As predicted by theory, we estimate that even though egg limitation is a minority condition within the population, egg costs make a substantial contribution (57% of the total) to the cost of oviposition. We conclude that insect life histories evolve to produce a balanced risk of time and egg limitation and, therefore, that both of these constraining factors have important influences on insect oviposition behavior and population dynamics.

Keywords: time limitation, egg limitation, lifetime reproduction, life history, limiting factor, oviposition behavior.

An enduring debate in the study of insect herbivores and parasitoids surrounds the question of whether the realized lifetime reproduction of adult females is constrained by the time available to locate suitable oviposition sites (termed "time limitation" or "host limitation") or by the supply of mature eggs (termed "egg limitation"). This debate reaches back more than 80 years to the first models of host-parasitoid population dynamics, with Thompson (1924) assuming that parasitoid attacks are limited by their egg supply and Lotka (1925) and Nicholson and Bailey (1935) assuming instead that attacks are limited by the time available to search. The distinction between time limitation and egg limitation is crucial for population dynamics, because egg limitation produces much more strongly saturating functional responses than does time limitation (Getz and Mills 1996; Heimpel et al. 2003; Schreiber 2006; Schreiber and Vejdani 2006). Furthermore, time and egg costs together determine the cost of oviposition, which must be balanced against reproductive benefits when insects make reproductive decisions, including host acceptance, clutch size, parental investment, and, in some cases, sex allocation (Godfray 1994; Rosenheim et al. 1996; Rosenheim 1999*a*; Jervis et al. 2008). Thus, resolution of this controversy is critical to insect behavioral and evolutionary ecology as well as to the study of insect population dynamics.

An insect uses its resources most efficiently when it perfectly balances its investment in longevity and searching ability with its investment in egg production so the female dies immediately after laying her last egg on a suitable host. In this case, no resources are "wasted" by maturing eggs that are never laid or in supporting longevity and searching activity that occurs after the egg supply has been permanently exhausted. However, stochastic variability in the environment, including fluctuations in host availability, food availability, weather conditions, and the impact of predators, creates unpredictability in opportunities to mature eggs and in realized reproductive opportunities, making it essentially impossible to achieve this perfectly balanced allocation. The question of what is observed in the absence of this perfect balance has been controversial

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(Rosenheim 1996, 1999*a*; Sevenster et al. 1998; Ellers et al. 2000; Rosenheim et al. 2000; van Baalen 2000; Jervis et al. 2008).

What explains the longevity of this controversy? The time and egg limitation viewpoints became entrenched as behavioral ecologists developed optimality models for oviposition behavior. The first school of workers assumed strict time limitation (Charnov and Skinner 1985; Visser et al. 1992; Godfray 1994). The second school of workers assumed instead that eggs could be limiting (Iwasa et al. 1984; Mangel 1987; Mangel and Heimpel 1998; but see West and Cunningham 2002). Importantly, these different assumptions led to different predictions for behavior (Mangel 1989); time-limited females are predicted to be much less choosy about laying their eggs than are egg-limited females. These diverging predictions led to efforts to model insect life histories to assess whether egg limitation is a plausible outcome of the evolutionary process. These models also yielded conflicting conclusions, with some authors arguing that an evolutionary equilibrium cannot exist without some fraction of the population being egg limited (Rosenheim 1996, 1999*a*; Rosenheim et al. 2000; van Baalen 2000) and others arguing that realistically high levels of stochasticity in reproductive opportunity drive egg limitation to negligibly low levels (Sevenster et al. 1998; Ellers et al. 2000). All the models agree that egg limitation is likely to be a minority condition in most populations. Nevertheless, because the magnitude of egg costs for an egg-limited female is generally much greater than the magnitude of time costs for a time-limited female (with both costs expressed in terms of the amount of future reproduction that is expected to be foregone), egg costs are still predicted to add substantially to the total cost of oviposition (Rosenheim 1999*b*) and thus to shape insect reproductive behavior.

The empirical literature on time limitation versus egg limitation in insects is mixed and presents the challenge of inferring egg limitation rates from what in many cases is indirect evidence (Heimpel and Rosenheim 1998; West and Rivero 2000). The most direct evidence of egg limitation comes from dissections of female insects. Dissections of live females at the end of the day's oviposition activity is a sensible approach for exploring egg limitation in synovigenic species, which continue to mature eggs as adults and for whom egg limitation is therefore temporary. However, interpreting egg load data for synovigenic species can be difficult. Females may lack mature eggs because they are young and have not matured eggs, because they have matured and laid all their eggs, or because they have matured and then resorbed all their eggs (Papaj 2000). These different routes to egglessness have very different implications for population dynamics and oviposition behavior, but the route followed by a female is difficult if not impossible to ascertain from simple dissection. For proovigenic insects, which do not mature eggs as adults, dissections of live females do not produce good measures of egg limitation, because egg-laying activity is truncated by the sampling event itself.

Empirical studies that have argued for the preeminence of time limitation have emphasized the difficulty of finding hosts, particularly for parasitoids, or the importance of inclement weather, which may limit the time available for foraging and oviposition by parasitoids and especially by herbivores (Miller 1979; Courtney and Duggan 1983; Leather et al. 1985; Watt 1992; Freeman and Ittyeipe 1993; Tammaru et al. 1996; Weisser et al. 1997; Doak et al. 2006; Hanski and Saccheri 2006; Gotthard et al. 2007; Saastamoinen 2007).

Study System and Analytical Approach

Our aim was to measure as directly as possible time limitation, egg limitation, and realized lifetime reproduction in a natural insect population. Of course, no single case study can resolve the controversy of the relative importance of time limitation versus egg limitation; our goal, therefore, was to take one step forward by capitalizing on the special opportunities provided by the simplified reproductive biology of the adult female gall midge *Rhopalomyia californica* (Rosenheim et al. 2007). We borrowed a key technique developed by Thomas et al. (1980), who collected adult female spruce budworm cadavers in the field and dissected them to quantify unlaid eggs. We extended this technique in three ways. First, to avoid the interpretational challenges associated with the complex ovarian dynamics of synovigenic species such as the spruce budworm, we chose to work with *R. californica*, which matures all of its eggs before emerging as an adult and does not resorb eggs (Rosenheim et al. 2007). For this species, egg loads decrease only through oviposition. *Rhopalomyia californica* induces galls only on the shrub *Baccharis pilularis*, where small clutches of eggs are laid on shoot tips (mean clutch size = 1.92 ± 0.09 [SE], $N = 584$, for two samples taken in 2006, where a clutch was defined as eggs that are within one egg width of each other). Because we can estimate initial egg loads from the size of the female, dissections of females provide an estimate of cumulative oviposition success up to the time the female is collected. By sampling females that had died naturally in the field and quantifying the residual egg load, we obtained a direct measure of permanent egg limitation. Second, we needed to correct our measures of egg limitation for the potentially biasing effects of predation. We could sample only those females that were not killed by predators and who died from other causes (e.g., exhaustion of their nutrient reserves; *R. californica* do not feed as

$$\begin{aligned}\text{Cost of oviposition} &= \text{lost opportunities for fitness returns from eggs to be laid in the future}\\ &= \begin{pmatrix}\text{Cost mediated by}\\ \text{the use of an egg}\end{pmatrix} + \begin{pmatrix}\text{Cost mediated by the use}\\ \text{of time to deposit the egg}\end{pmatrix}\\ &= \begin{pmatrix}\text{Number of eggs that}\\ \text{cannot be laid in}\\ \text{the future, because}\\ \text{an egg was laid on}\\ \text{the present host,}\\ \text{assuming egg}\\ \text{limitation}\end{pmatrix} \bullet \begin{pmatrix}\text{Fitness returns}\\ \text{per egg laid}\end{pmatrix} \bullet \begin{pmatrix}\text{Probability of}\\ \text{egg limitation}\end{pmatrix} + \begin{pmatrix}\text{Number of eggs that}\\ \text{cannot be laid in}\\ \text{the future, because}\\ \text{of the time that was}\\ \text{used was to lay an}\\ \text{egg on the present}\\ \text{host, assuming time}\\ \text{limitation}\end{pmatrix} \bullet \begin{pmatrix}\text{Fitness returns}\\ \text{per egg laid}\end{pmatrix} \bullet \begin{pmatrix}\text{Probability of}\\ \text{time limitation}\end{pmatrix}\\ &= (1)\bullet(\Delta W)\bullet(P_{egg-lim}) + (T_{ovip})\bullet(r_{ovip})\bullet(\Delta W)\bullet(P_{time-lim})\end{aligned}$$

Figure 1: A simple model for decomposing the total cost of oviposition into the components contributed by time costs and egg costs; ΔW is the expected fitness return per egg laid, $P_{\text{egg-lim}}$ is the probability of egg limitation, T_{ovip} is the time required to deposit an egg, r_{ovip} is the rate of oviposition, and $P_{\text{time-lim}}$ is the probability of time limitation.

adults). If females who avoided predation had, on average, greater longevities than females killed by predators, then they might also have had greater opportunities to lay all their eggs, and thus our sample of females on pan traps would overestimate egg limitation rates. Therefore, we quantified the predation rate for females, allowing us to apply the needed corrections. Third, the temporally compressed adult life stage of *R. californica* (most females emerge at dawn, lay their eggs, and die before the midafternoon) allowed us to easily test the hypothesis that inclement weather is a primary cause of females failing to lay their full lifetime complement of eggs.

We used our field-based estimates of time limitation and egg limitation in *R. californica* to parameterize a simple model (Rosenheim 1999*b*) to decompose the total cost of oviposition for *R. californica* into the components contributed by time costs and egg costs (see fig. 1). From figure 1, the relative contribution of egg costs, C_{egg}, to the total cost of oviposition is then

$$C_{\text{egg}} = \frac{P_{\text{egg-lim}}}{P_{\text{egg-lim}} + (T_{\text{ovip}})(r_{\text{ovip}})(P_{\text{time-lim}})}. \tag{1}$$

The relative contributions of egg costs and time costs to the total cost of oviposition are important, because these costs are predicted to shape many aspects of insect reproductive behavior.

What does the natural history of gall midges tell us about the likely importance of time limitation versus egg limitation? The typically ephemeral adult life stage of gall midges, combined with their moderately high fecundities, have led some researchers to argue that the reproductive biology of gall midges is dominated by time limitation (Hinz 1998; Harris et al. 2003). Indeed, life table studies for two gall midge species concluded that failure to lay the full egg complement was the dominant source of reproductive shortfall or mortality in the midge life cycle (*Taxomyia taxi* and *Asphondylia boerhaaviae* were estimated to lay only 7.3% and 5.6% of their lifetime complement of eggs, respectively; Redfern and Cameron 1978; Freeman and Geoghagen 1989). Although it may be globally easier for female herbivores to find hosts than it is for female parasitoids, thereby increasing the likelihood of observing egg limitation, female herbivores still need to distinguish between suitable and unsuitable oviposition sites, and extensive foraging may be required to find high-quality host plants or plant organs (Bernays and Chapman 1994). Researchers have argued that gall midges are valuable models for the study of insect-plant interactions, because they share with longer-lived insect herbivores the same suite of selective oviposition behaviors (Harris and Rose 1989). For example, gall midges discriminate against lower-quality hosts both before and after alighting and avoid ovipositing on host plants that already bear eggs or larvae of other midges (Harris and Rose 1989; Harris et al. 2003, 2006). All these observations might lead some to conclude that time limitation should be the preeminent influence on the reproductive ecology of these insects.

Material and Methods

Lifetime Reproduction in the Field

Our study site was located just north of the University of California Stebbins Cold Canyon Preserve (38.5122°N, 122.0968°W). *Baccharis pilularis* was the dominant shrub. To sample midges that had completed their lifetime reproduction, we placed dry pan traps beneath *B. pilularis* to capture midges as they died and fell from the plant canopy. Pan traps were white plastic cafeteria trays (35 cm × 45 cm, NSF, Huntington Beach, CA) that we fitted with two layers of mesh in which the dead midges lodged securely. Live midges were never observed entangled in the mesh. In 2003 only, pans were deployed early each morning and collected late in the afternoon after the day's cohort of midges had died. In 2004–2006, pans were left in the field 24 h per day and emptied in daily checks. In some cases, heavy rain delayed checks until a subsequent day. Traps were deployed March 5–May 16, 2003; February 19–March 10, 2004; March 7–April 6, 2005; and February 23–April 4, 2006.

Dead midges were held on ice and transported to a laboratory freezer (-20°C), where they were held until dissection (not more than 5 days). Only egg counts from midges whose abdomens still presented soft internal tissues were retained for analyses. We also excluded cases in which midge abdomens contained any eggs that had deteriorated or been digested, liberating the bright red yolk into the abdominal cavity. Across all years of the study, 310 of 367 dead females collected in our pan traps (84.5%) satisfied our criteria and allowed residual egg load estimates. Midges were then slide mounted, and the length of each hind tibia was measured with an ocular micrometer as an index of body size. In cases where hind tibias were unavailable (midges are delicate insects, and dead specimens often lacked some legs), other body parts were measured (midtibia lengths, fore tibia lengths, mesonotum length), and hind tibia lengths were estimated from linear regressions.

We reared a sample of midges each year to establish regression equations that allowed us to estimate a female's initial egg load from her size (table A1 in the online edition of the *American Naturalist*). In 2003 (March 26–April 7) and 2004 (March 16–17), we collected galls from the periphery of our main study site and held them in the laboratory for not more than 1 week to collect emerging females, which were dissected and measured. In 2005 (March 15–30) and 2006 (March 23–April 14), we enclosed 50–85 galls across our study site in polyester mesh sleeves and checked them daily in the early morning hours to collect newly emerged females for dissection and measurement.

We used the regression equations for hind tibia length, midtibia length, fore tibia length, and mesonotum length, in that order of preference based on which measurements were available, to estimate initial egg load for female midges that were collected dead in the field. Some dissectible dead midges did not yield any of these measurements; in these cases (2003, $n = 2$; 2004, $n = 12$; 2005, $n = 1$; 2006, $n = 1$), we assigned the mean starting egg load estimated for that year's sample of dead midges, but these midges were excluded from analyses of midge size effects.

Predation Rates

We conducted focal observations of freely foraging midges in the field to estimate the rate of contact with predatory arthropods and spiderwebs and the actual predation rate. Observers searched *B. pilularis* bushes to locate midges and then followed midges for as long as possible, using a handheld computer to record midge behavior (resting, walking, flying, probing/ovipositing) and any contacts with predators. To reduce any possible disruption of predators, we observed midges from a distance of 0.5–1.0 m, avoided contacts with the host plant, and minimized our movement. Although our presence would have prevented birds from foraging near the focal midge, we only very rarely observed birds foraging on *B. pilularis* anywhere on our site, and we therefore suspect that invertebrates were the dominant predators. A total of 231 midges were observed for a total of 82.1 h between March 12 and May 12, 2003; February 9 and April 23, 2004; March 7 and April 11, 2005; and February 21 and April 19, 2006.

Observations were conducted during all daylight hours when midges could be found in the field. Adult female midges move through two distinct phases of activity (Rosenheim et al. 2007). Immediately following eclosion from the pupa, there is a period during which midges mate but are otherwise almost entirely immobile; because all known midge predators rely on prey movement to detect or capture prey, we expected predation risk to be low during this rest period. There follows a period of active search for oviposition sites and laying eggs, which we expected to be riskier. Thus, we calculated separate estimates of predation rate for the rest and oviposition phases of activity.

During these observations, we occasionally observed predators that had captured midges (the focal midge or others) but had not yet fully consumed them. These captured midges were collected, held on ice, and returned to the lab for dissection and measurement to determine their egg loads at the time of capture.

Standard errors for predator contact and predation rates were calculated from 1,000 bootstrapped samples. For a description of how our estimates of egg limitation and mean proportion of eggs laid were corrected for predation, see appendix B in the online edition of the *American Naturalist.*

Midges Collected Live

To provide an independent assessment of egg limitation in midge populations, we collected samples of live midges in the field at different times during the morning and early

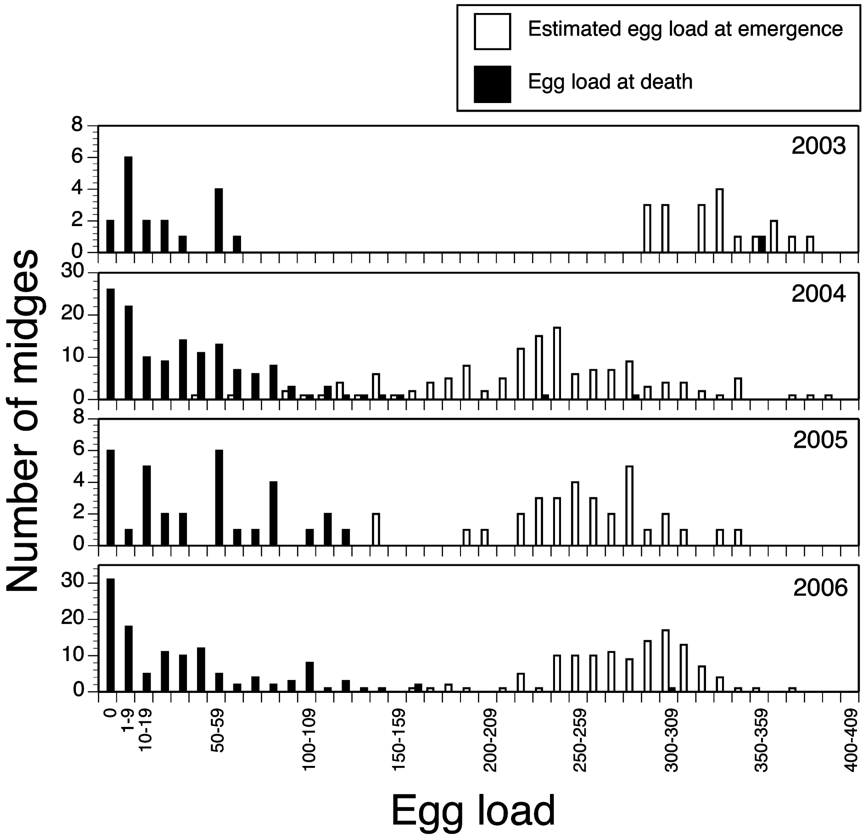

Figure 2: Observed egg load distributions for female midges at the time of their death (*solid bars*) and projected initial egg loads of the same sample of females, based on regressions of egg load versus body size for reared midges (*open bars*), 2003–2006. Note that the 0–9 egg load class has been divided into two subclasses to display the eggless females separately. Mean ± SE egg loads: 2003, 332.7 ± 6.2 at emergence versus 39.1 ± 18.3 at death ($n = 139$); 2004, 234.9 ± 5.4 at emergence versus 39.6 ± 3.8 at death ($n = 19$); 2005, 258.6 ± 8.2 at emergence versus 45.7 ± 7.0 at death ($n = 32$); 2006, 282.1 ± 3.4 at emergence versus 38.6 ± 4.4 at death ($n = 120$).

afternoon on March 12 and 19, 2004, and March 8 and 10, 2005. Midges were captured while they were either resting (early morning sample, March 8, 2005) or ovipositing (all other samples). Midges were placed on ice and returned to the laboratory for dissection and measurement. Mean female size did not change significantly across the daily samples (data not shown).

Weather Effects on Midge Reproduction

To assess the hypothesis that the ability of midges to lay their lifetime complement of eggs was impeded by bad weather, we obtained weather data from a National Oceanic and Atmospheric Administration climatological station (Markley Cove 38.4939°N, 122.1249°W) located 3.5 km southwest of our field site. Six variables were used to describe daily weather conditions, with values reflecting the 24-h period beginning at 0830 hours (near the peak of female emergence); means ± SD for these variables were as follows: temperature at 0830 hours, 9.4° ± 4.9°C (range: 2.8°–20.0°C); cloud cover at 0830 hours (clear, partly cloudy, cloudy, fog, rain); maximum daily temperature, 21.1° ± 6.2°C (range: 9.4°–28.9°C); wind speed (total distance moved over 24 h), 32.1 ± 16.0 km (range: 3.2–96.6 km); rainfall (over a 24-h period) 1.98 ± 5.11 mm (range: 0.0–27.9 mm); and evapotranspiration (water evaporating over a 24-h period), 2.18 ± 1.33 mm (range: 0.0–4.83 mm).

Egg load data for females collected at death were not distributed normally. We therefore used simple bivariate nonparametric correlations to explore the effects of the individual weather variables. Following Conover (1999), we assessed the importance of all the weather variables considered simultaneously while controlling for effects of year and midge size by rank transforming all the continuous variables and performing a multiple regression with year and cloud cover as categorical variables. Means are presented ±1 SE unless otherwise noted.

Results

Lifetime Reproduction in the Field

In each of the four years of the study, female midges laid a large proportion (>80%) of their estimated total lifetime complement of eggs (fig. 2; table 1). Approximately one in five midges completely exhausted their egg supply before dying (egg limitation; table 1), whereas the remaining females, consistently the majority of the population, died with eggs remaining in their ovaries (time limitation). Thus, for most sampled midges, realized lifetime reproduction approached or actually reached the maximum value obtainable, as defined by the absolute constraint of their full egg complement. Nevertheless, egg limitation was a minority condition within the population.

Predation on Female Midges

We observed midges ($N = 26$) for a total of 25.1 h during the posteclosion rest period; only one contact with a predator and no instances of actual predation were recorded. These data yield an estimated predator contact rate of $0.040 \pm 0.041\ \mathrm{h}^{-1}$ and a predation rate of zero. The one predator that contacted a resting phase midge was a cantharid beetle, which is known to eat aphids but which we never observed to eat midges. We observed midges ($N = 205$) for a total of 57.0 h during the oviposition period and recorded 12 contacts with predators and three instances of actual predation. These data yield a predator contact rate of $0.213 \pm 0.066\ \mathrm{h}^{-1}$ and a predation rate of $0.052 \pm 0.030\ \mathrm{h}^{-1}$. Of the 12 contacts with predators, 10 were with predators known to be potentially lethal (spiders or their webs), and two were with predators not known to be lethal (ants). Thus, it is during the period of active oviposition that midges appear to incur a substantial risk of predation.

Twenty-eight midges were collected out of the grasp of predators. Of these, 20 had intact abdomens, with no signs that eggs had been subject to extraoral digestion. These females bore an average of 64.3 ± 18.9 eggs (range: 0–318; see "Egg Loads for Midges Captured by Predators" in app. B for the distribution of egg loads), and based on midge size, we estimate that they had laid 0.780 ± 0.052 (range: 0.172–1.0) of their lifetime complement of eggs before being captured.

We corrected our estimates of egg limitation and the mean proportion of the lifetime complement of eggs successfully laid for the effects of predation (table 1). The correction produced a modest decrease in our estimate of egg limitation (approximately one in six females completely exhausted their eggs), whereas we still estimate that females consistently laid >80% of their lifetime egg complement. Our conclusion that female lifetime reproduction can be constrained by egg limitation does not, therefore, appear to be an artifact generated by the biasing role of predation.

Egg Loads of Live Midges

Some readers may question the reliability of data obtained by dissecting dead insects. Our interpretation of the egg load data obtained from dead midges suggests that if we collect live midges in the field over the course of a day, we should observe declining egg loads and the eventual appearance of females whose egg inventories have been entirely exhausted. Indeed, live females collected over the course of 4 days revealed these patterns (fig. 3). Egg loads declined rapidly over the course of the day (Spearman's rank correlation: March 12, 2004, $\rho = -0.87$, $N = 40$, $P < .0001$; March 19, 2004, $\rho = -0.55$, $N = 12$, $P = .063$; March 8, 2005, $\rho = -0.83$, $N = 42$, $P < .0001$; March 10, 2005, $\rho = -0.58$, $N = 16$, $P = .019$), and eggless females appeared in the early afternoon (logistic regression model for all dates combined; time of day effect, $\chi^2 = 18.0$, $\mathrm{df} = 1$, $P < .0001$; effect of date NS). Thus, dissections of live females confirmed the inference that midges are laying most, and in some cases all, of their lifetime complement of eggs.

Weather Effects on Midge Reproduction

We evaluated the hypothesis that inclement weather is a primary factor preventing oviposition. Bivariate regressions of six weather variables on the number of eggs remaining unlaid at the time of midge death ($N = 310$ observations) revealed weak but statistically significant roles for two variables; more eggs remained unlaid on days with higher maximum temperatures (Spearman's $\rho = 0.130$, $P = .022$), and fewer eggs remained unlaid on days with greater rainfall (Spearman's $\rho = -0.119$, $P = .036$). All other variables were nonsignificant (cloud cover at 0830 hours, Kruskal-Wallis test $\chi^2 = 4.2$, $P = .38$; temperature at 0830 hours, Spearman's $\rho = 0.028$, $P = .62$; wind speed, Spearman's $\rho = -0.042$, $P = .47$; evapotranspiration, Spearman's $\rho = 0.094$, $P = .10$). A multivariate model that included year and midge size as covariates along with the six weather variables explained only a very small amount of the variation in the number of unlaid eggs ($R^2 = 0.06$). Only two variables made statistically significant contributions to the model; daily high temperatures were again positively correlated with the number of unlaid eggs ($F = 6.0$, $\mathrm{df} = 1, 280$, $P = .015$), whereas rainfall was again negatively correlated with the number of unlaid eggs ($F = 4.1$, $\mathrm{df} = 1, 280$, $P = .043$). Thus, the minor role revealed for weather suggests that midges perform slightly better under cooler, wetter conditions.

Table 1: Observed rates of egg limitation and projected proportion of total lifetime egg complement laid in the gall midge *Rhopalomyia californica*

Year (*n*)	Observed proportion of females egg limited	Proportion of females egg limited, corrected for predation	Estimated proportion of eggs laid	Estimated proportion of eggs laid, corrected for predation
2003 (19)	.105 ± .070	.086 ± .059	.889 ± .048	.870 ± .042
2004 (139)	.187 ± .033	.150 ± .034	.812 ± .019	.806 ± .019
2005 (32)	.188 ± .069	.153 ± .062	.819 ± .028	.811 ± .025
2006 (120)	.258 ± .040	.212 ± .042	.867 ± .014	.850 ± .019
Total (310)	.210 ± .023	.171 ± .029	.838 ± .012	.829 ± .016

Note: Shown are means ± 1 SE (bootstrapped estimate).

Size Effects on Midge Reproduction

Neither the absolute number of eggs remaining unlaid at the time of death nor the estimated proportion of the total lifetime complement of eggs successfully laid was significantly correlated with midge size (hind tibia length) (Spearman's rank correlation, $N = 294$, $\rho = 0.075$, $P = .20$ and $\rho = 0.029$, $P = .62$, respectively). Midge size also had no effect on the risk of completely exhausting the egg supply (logistic regression, likelihood ratio, $\chi^2 = 0.003$, $N = 294$, $P = .96$). Although there was a marginally nonsignificant positive correlation between midge size and the probability of being captured by predators (logistic regression for the combined sample of midges collected from pan traps and from predators, with year as a blocking factor, $\chi^2 = 3.7$, $N = 320$, $P = .053$), because midges captured by predators had usually already deposited most of their eggs (see above), this would have a negligible effect on expected midge fitness. Taken together, these results mean that because larger midges started life with more eggs, midge size was the primary determinant of the estimated total number of eggs laid by the females sampled by our pan traps (ANCOVA: effect of midge size, $F = 137.9$, df = 1, 289, $P < .0001$; effect of year, $F = 34.5$, df = 3, 289, $P < .0001$).

The Cost of Oviposition in Rhopalomyia californica

We used our field-based estimate of egg limitation in *R. californica* to parameterize equation (1), which decomposes the total cost of oviposition for *R. californica* into the components contributed by time costs and egg costs. Our estimates were (i) $P_{\text{egg-lim}} = 0.17$, (ii) $T_{\text{ovip}} = 10$ s (J. A. Rosenheim, unpublished data), and (iii) $P_{\text{time-lim}} = 1–0.17 = 0.83$. The last parameter, r_{ovip}, was coarsely estimated as the mean observed number of eggs laid across all years of the study (232) divided by the total period of active oviposition (taken as 4 h; see Rosenheim et al. 2007), equaling 58 eggs h^{-1}. With these parameter estimates, the model suggests that the egg contributes 57% of the total cost of oviposition, with time costs contributing the remaining 43% of the total costs. Thus, despite the fact that egg limitation is a minority condition in the population (17% of females are egg limited), time and egg costs are similar in magnitude, and oviposition behavior of this midge is expected to be responsive to both of these cost components.

Discussion

We have reported the first direct field measures of egg limitation, time limitation, and lifetime reproduction for an insect that must forage actively to locate a series of oviposition sites. We find that females lay on average a large proportion of their lifetime complement of eggs (mean estimate 82.9%) and incur a moderate risk of completely exhausting their lifetime egg supply (mean estimate 17%). Thus, the number of eggs matured, itself strongly correlated with body size, is the primary determinant of realized lifetime reproduction. As predicted by theory (Rosenheim 1996, 1999*a*; Sevenster et al. 1998; Ellers et al. 2000; Rosenheim et al. 2000; van Baalen 2000) and as generally supported by the empirical record (Heimpel and Rosenheim 1998; West and Rivero 2000), complete egg limitation is a minority condition in the population but is not trivially rare. Time costs and egg costs make similar contributions to the overall cost of oviposition, and thus, neither should be ignored when analyzing reproductive behavior.

We have found that *Rhopalomyia californica* lays a larger proportion of its eggs than does any of the 18 species reviewed by Courtney (1984), yet it incurs only a modest risk of egg limitation. Thus, *R. californica* appears to have largely solved the challenge of balancing its investment in reproduction versus the soma in a stochastic environment. How has it done this? We suggest that the midge's ecology has suppressed the sources of stochasticity in reproductive opportunity, including variation in host availability and variation in the time available to lay eggs, as follows.

Variation in host availability has been reduced by the midge's use of a perennial host and its habit of ovipositing extensively on the host on which the female herself de-

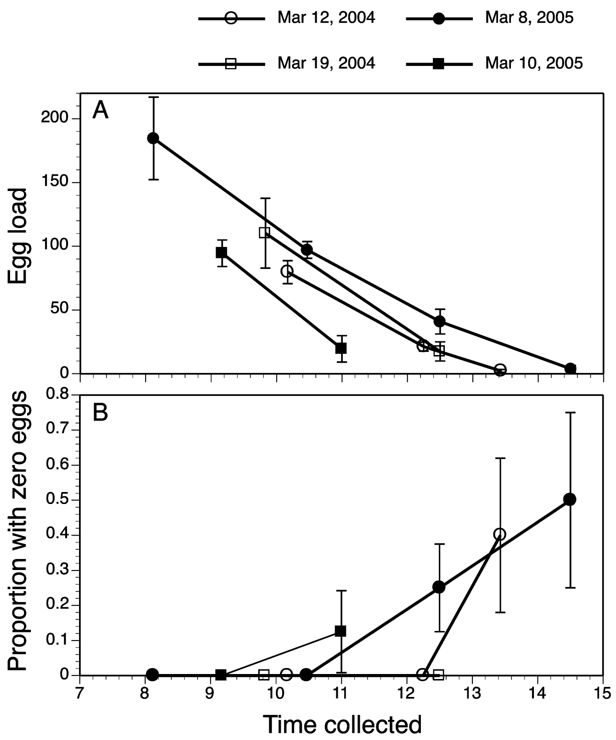

Figure 3: Egg loads of female midges collected live in the field at different times of the day. Shown are the mean ± SE egg load for live females (*A*) and the mean ± binomial SE proportion of females who had completely exhausted their egg supply (*B*). Sample sizes for successive collections: March 12, 2004: 17, 18, 5; March 19, 2004: 10, 2; March 8, 2005: 12, 14, 12, 4; March 10, 2005: 8, 8.

veloped or perhaps on adjacent plants (Briggs and Latto 2000; Rosenheim et al. 2007). Midges do not emerge from their galls on days with stormy weather (Rosenheim et al. 2007). Their very short adult lives give them an unusual ability to employ the shortest of forecasts to identify periods of permissive weather that will cover their entire adult lives.

The impact of predation was minimized in two ways. First, by compressing the adult life stage into just a few hours, midges usually senesce and die before they can be preyed on. Second, the midges that were killed had usually already laid most of their eggs. Midges resting shortly after emergence remain immobile and thus incur a low risk of predation. Furthermore, females initiating oviposition expressed the highest rates of oviposition (Rosenheim et al. 2007), thereby reducing the risk that predation would occur before most eggs were laid. Young, heavily egg-laden females also appear to fly less (Rosenheim et al. 2007), thereby reducing their exposure to some predators. Whereas it has been suggested that heavily egg-laden midges have impaired flight capacities (Gagné 1994) and might therefore be expected to have diminished abilities to escape from predators (Roitberg et al. 2003), our data suggest that it is primarily females with depleted egg loads that are being preyed on. Because midges do not feed as adults, they are insensitive to variation in food availability, unlike those herbivores and parasitoids that feed as adults and for whom food availability can be a major source of variation in adult fecundity and longevity.

Finally, by laying eggs in small clutches, *R. californica* reduces the total number of suitable oviposition sites that must be located in comparison with species that lay eggs singly (Courtney 1984; Mangel and Heimpel 1998). In addition, *R. californica* at our study site often laid multiple clutches on a single tip of *Baccharis pilularis*, further reducing the total time needed for reproduction (J. A. Rosenheim, unpublished data). Plasticity in the number of eggs laid per clutch and the number of clutches laid per *B. pilularis* tip, unexplored in this system, could be a further means of matching the rate of oviposition with the egg load and time remaining in the adult stage (Mangel and Heimpel 1998).

Proovigenic Species as Model Systems in Insect Ecology

Any time a species is chosen as a study organism because of special advantages that it offers, it raises the question of whether the "specialness" also prevents us from generalizing the results. Do the simplified ovarian dynamics and ephemeral adult stage of *R. californica* mean that lessons learned from this midge are not relevant more broadly?

Here we offer two observations supporting the use of *R. californica* and, by extension, other strictly proovigenic insects as models for studies of insect reproduction. First, female *R. californica* and other insect herbivores and parasitoids share the same fundamental challenges: they must search for oviposition sites and oviposit while avoiding predators, and they must do this under potentially variable weather conditions. As argued by Harris and colleagues (Harris and Rose 1989; Harris et al. 2003, 2006), midges are useful models of plant-insect interactions expressly because they exhibit the same suite of selective oviposition behaviors as do longer-lived herbivores. Second, the empirical record suggests that proovigenic and synovigenic insects are quantitatively similar in their balanced expression of time limitation versus egg limitation (Redfern and Cameron 1978; Courtney 1984; Freeman and Geoghagen 1989; Driessen and Hemerik 1992; Heimpel and Rosenheim 1998; Rosenheim 1999*b*; West and Rivero 2000; de Vries and Harlan 2005; Jepsen et al. 2007). Synovigenic, but not proovigenic, species may be able to adjust egg maturation and resorption rates in response to fluctuating reproductive opportunity (Papaj 2000), but all egg maturation rates have an upper limit, which can be overwhelmed by opportunities to oviposit in host-rich habitats (Heimpel et al. 1998; Casas et al. 2000). We conclude that the simplified ovarian dynamics of strictly proovigenic species make them valuable models for addressing problems that may be nearly intractable when working with synovigenic species.

Direct estimates of egg limitation are needed for other species, including both proovigenic and synovigenic species. For this study and for others that use traps to collect samples of insect cadavers to quantify unlaid eggs, a key issue is whether the traps produce a biased sample of the female population. One source of bias that we have addressed here is predation. Another possible bias is generated by placing pan traps under the host plant. Some female herbivores or parasitoids may fail to locate host plants during some or all of their foraging period; in this case, placing pan traps below host plants will overestimate reproductive success and egg limitation. We suggest that this source of bias was minimal in our study of *R. californica*. Direct observations of foraging midges and colonization experiments demonstrate that females typically initiate oviposition on their natal host plant (Rosenheim et al. 2007) and move only very short distances over their lifetimes to reproduce on the natal host plant or adjacent host plants (estimated mean lifetime dispersal = 1.7 m; Briggs and Latto 2000). Furthermore, their host plant, *B. pilularis*, was a dominant member of the plant community at our study site and is dominant at many sites where the midge occurs; any potentially rare longer-distance dispersal events would likely have led to encounters with other hosts. When studying mobile herbivores that oviposit on more scattered host plants, it may be useful to sample under both host and nonhost plants to quantify any possible bias associated with sampling location.

Conclusions

The results of this study and the full empirical record are most compatible with a view of insects balancing the risks of time limitation versus egg limitation. Even when egg limitation is a minority condition within the population, as it is for *R. californica*, egg costs make substantial contributions to the overall cost of oviposition. Thus, neither egg limitation nor time limitation can be safely ignored.

A key remaining challenge is to distinguish between two views of constraints on insect reproduction. One view is that all insect herbivores and parasitoids have the same long-term mean expectation of time limitation versus egg limitation and therefore that all the variability we see in the empirical record reflects the underlying spatial and temporal stochasticity of the environment. A second view is that at least some of the variation in the empirical record instead reflects real interspecific differences in the importance of time costs versus egg costs. Theory suggests three important candidates for traits that may modulate the relative importance of time costs versus egg costs across species. First, the mean number of eggs laid per oviposition site is likely to be important (Weis et al. 1983; Courtney 1984; Mangel and Heimpel 1998; Rosenheim 1999*a*). At one end of the spectrum are species that lay eggs singly and that therefore must identify a large number of suitable oviposition sites to lay their full complement of eggs. At the other end of the spectrum are females, often flightless and sessile, that lay all of their eggs in one clutch and for which the task of laying their full complement of eggs is thus greatly simplified (Mason et al. 1977; Sopow and Quiring 1998; Rhainds and Ho 2002). Between these extremes are synovigenic species that may lay all, or nearly all, of their available eggs in a single daily clutch (Tatar 1991; Ekbom and Ferdinand 2003) and that therefore experience daily recurrences of egg limitation; there also are species whose clutch size decisions may change in response to the perceived risk of time and egg limitation (Rosenheim and Rosen 1991; Mangel and Heimpel 1998; Casas et al. 2000). Second, the cost of the mature oocyte itself may shape the evolution of egg limitation (Rosenheim 1996; Ellers et al. 2000). Substantial interspecific variation in egg size exists in insect herbivores and parasitoids. Some species produce heavily yolked eggs, whereas some parasitoids have shifted much of the burden of provisioning the embryo onto the host insect by producing eggs that absorb amino acids and other key nutrients directly from the host's hemolymph (Ferkovich and Dillard 1986). Third, the magnitude of stochastic temporal and spatial variation in reproductive opportunities may be important (Sevenster et al. 1998; Ellers et al. 2000; van Baalen 2000). Theoretical and empirical studies in each of these areas will allow us to build a sound understanding of the cost of insect oviposition and how that cost may constrain reproductive success.

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