Modeling effects of harvest on firefly population persistence

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ABSTRACT

North American fireflies in the genus *Photinus* are commercially harvested to extract the enzyme luciferase, despite the availability of a synthetic recombinant enzyme. Our goal was to examine the potential effects of harvesting on *Photinus* population persistence. Using estimated demographic parameters for *Photinus*, we developed a stochastic simulation population model to understand combined effects of demography, harvest rate, delayed larval development, and environmental stochasticity on population persistence of fireflies. With no harvest and low environmental stochasticity, modeled populations tended to reach carrying capacity. We found that average population size of adult fireflies decreased with increasing harvest rate and increasing environmental stochasticity. At the highest modeled growth rate ($\lambda = 2.8$) the population failed to persist only when environmental stochasticity was high and harvest rate was $\geq 60\%$. Once harvest was introduced, only populations with high growth rates consistently persisted. Long-term, sustainable *Photinus* harvest rates based on survey data suggest that harvest rates >10% are acceptable only if $\lambda > 1.6$. Our modeling results suggest that *Photinus* populations might tolerate low harvest levels, although in the absence of more precise data on vital rates and the amount of environmental stochasticity, the exact level is unknown. To further examine sustainability, harvest rates should be monitored and standardized surveys conducted to document firefly population changes.

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1. Introduction

One of the most common causes of current species extinctions is overharvest, or overkill (Brook et al., 2008; Yiming and Wilcove, 2005). The effect of harvest on population viability is central to hunting and other sustained yield programs and has been well studied for species of commercial concern, mostly vertebrates and trees (e.g., Ellner and Fieberg, 2003; Gustafson, 1996; Taylor et al., 2005). Many efforts have been made to determine sustainable harvesting practices for species commonly collected or exploited by human commerce, such as wild fish (Conover and Munch, 2002), parrots (Beissinger and Bucher, 1992), and sharks (Gallucci et al., 2006). Sustainable harvest practices for invertebrates have received less attention (Dunn, 2005). Most invertebrate harvesting studies have focused on commercial species that humans use as food or bait, such as abalone, oysters, crabs, tunicates, sponges, and annelids (New, 1995; Reynolds et al., 2001). There are many insect groups harvested for taxonomic collections, such as birdwing butterflies, Papilionidae (Marshall, 1982; Owen, 1971) and beetles, Coleoptera (New, 1995). However, effects of such harvest on population persistence have seldom been quantified, and current insect harvest practices are considered by some to be unsustainable (e.g., butterflies, Kurdna, 1986; Petanidou et al., 1991; USFWS, 1997).

Fireflies (Coleoptera: Lampyridae) are charismatic insects that attract considerable public attention. Firefly harvesting has been virtually ignored, despite recent concerns about their conservation status (Takeda et al., 2006). The bioluminescent displays of certain synchronously flashing fireflies appeal to ecotourists (e.g., *Photinus carolinus* in Great Smoky Mountains National Park, USA (Faust, 2010), *Pteroptyx tener* in Kuala Selangor, Malaysia (Wong and Yeap, 2012)). There have been widespread reports of declining firefly populations (Khoo et al., 2009; Wong and Yeap, 2012; L.F. Faust, unpubl. data), although the lack of systematic monitoring means that most evidence is anecdotal. Although purported firefly declines might be partially attributed to habitat destruction, pesticides, and light pollution, overharvest may also have a substantial impact. In the USA, fireflies are harvested commercially to extract luciferase (Howes, 1993; Sigma-Aldrich, 2010), an enzyme that catalyzes light production when adenosine triphosphate (ATP) is present. Until 1985, luciferase could be obtained

only by harvesting live fireflies (mainly *Photinus* spp. in the USA), but once the *Photinus pyralis* luciferase gene was cloned (de Wet et al., 1985) synthetic luciferase could be produced in large quantities.

Although it is no longer necessary to harvest fireflies to extract luciferase, commercial firefly harvesting continues. For example, during the summer of 2008 collectors in one Tennessee county reportedly harvested 1584 g of fireflies (The Oak Ridger, 2008). At approximately 40 mg wet weight per *Photinus* individual (S. Lewis, unpubl. data), this represents approximately 40,000 male fireflies. Harvesting has the potential to impact *Photinus* firefly populations in the USA, but no studies have evaluated what harvest levels these insect populations can sustain. Here we use a pattern-oriented modeling approach (e.g., Grimm et al., 1996; Wichmann et al., 2003) to examine the potential effects of harvest on firefly population size and persistence. Because stochasticity affects population persistence, we first developed a deterministic model to allow us to investigate the effects of variation in demography and harvest rate on population growth and equilibrium population size. We then included demographic stochasticity but kept the environment constant, followed by adding environmental stochasticity to determine the combined influence of both sources of stochasticity on population persistence. We next examined how different larval development strategies might affect population persistence. Finally, we performed a sensitivity analysis to evaluate which of our estimated parameters has the greatest impact of population persistence.

2. Methods

2.1. The model

We developed a stage-structured model of an insect population that has a single reproductive period per year, after which adults die. The model includes harvest of adults of both sexes, although in some species of *Photinus* only the males are harvested. Eggs usually develop into adults within a single year, but the model allows for prolonged larval development, as seen in some species, where some larvae take more than one year to reach adulthood (e.g., Hovestadt et al., 2007). Because we used the model to analyze the consequences of extending the larval stage beyond a single year, only a fraction of larvae become adults after one year. We used the model to investigate how population persistence is affected if larvae postpone development with a fixed probability, e.g. as a diversified bet-hedging strategy (Philippi and Seger, 1989), and if the delayed larval development is a result of phenotypic plasticity caused by environmental signals (Danforth, 1999; Danks, 1992). Finally, the model incorporates the probability that adult females become mated, to allow us to investigate one type of Allee effect when population density becomes low.

As the purpose of the model is to investigate the risk of population extinction due to harvesting, we included demographic stochasticity by considering population size as a discrete stochastic variable affected by probabilistic demographic events. We added increasing levels of environmental stochasticity to the model, thereby enabling us to explore whether prolonged larval development is a beneficial strategy in an unpredictable environment.

In our model, we considered three developmental stages in the life cycle of fireflies: eggs (E), larvae (L) and adults (A). Adults consist of females (A_f) and males (A_m), and larvae consist of those that have spent approximately i years in the larval stage (L_i), so that $L = \sum_{i=1}^{\Psi} L_i$, where Ψ is the maximum number of years an individual can spend in the larval stage.

2.2. Deterministic model

The number of eggs produced by A_f adult females in year t is denoted $E(t)$, and the expected number of young larvae that will develop from these eggs is

$$L_0(t) = p_e E(t) \tag{1}$$

where p_e is the probability that an egg develops into a larva.

The probability that a larva survives the first year is denoted p_{l0}. We determined that a proportion of surviving larvae do not pupate and therefore start on their second larval year (denoted b). Larvae that do not emerge after the second year die. Thus, the number of larvae that are approximately one-year old in the following year becomes

$$L_1(t+1) = p_{l0} L_0(t) \tag{2}$$

while the number of two-year old larvae in year $t+1$ is the number of one-year old larvae that remain larvae and survive for an extra year, i.e.

$$L_2(t+1) = p_{l1} b_1 L_1(t) \tag{3}$$

or, in general, for individuals spending $i+1$ year in the larval stage as

$$L_{i+1}(t+1) = p_{li} b_i L_i(t) \tag{4}$$

We assumed that the probability of a larva surviving from one year to the next declines with larval density due to intraspecific interactions such as competition for resources and cannibalism (Evans, 1991; Inouye, 1999; Lee and Seybold, 2010; Miller, 1964; Peckarsky, 1991). A general model for the decrease in survival rate of larvae during their ith year is

$$p_{li} = p_{mi} \exp\left(-\sum_{j=0}^{\Psi} c_{ij} L_j\right) \tag{5}$$

where p_{mi} is the survival rate of age i larvae in the absence of intraspecific competition. c_{ij} expresses the influence of competition on survival rate exerted by larvae of age j on larvae of age i.

Larval competition may prolong development time (Danks, 1992; Gerber, 1984), so the proportion of larvae taking an extra year to develop will increase with population size. We modeled the proportion of larvae postponing pupation as

$$b_i = 1 - (1 - b_{mi}) \exp\left(-\delta_i \sum_{j=0}^{\Psi} c_{ij} L_j\right) \tag{6}$$

where b_{mi} is the proportion of larvae of age i that do not pupate in the absence of intraspecific competition and δ_i is a constant expressing the effect of competition on development of larvae. Note that by varying b_{mi} and δ_i, Eq. (6) can model delayed larval development as a fixed proportion of all larvae (when $b_{mi} > 0$ and $\delta_i = 0$), as a variable proportion dependent on larval density (when $b_{mi} = 0$ and $\delta_i > 0$), as a mixture of the two strategies (when $b_{mi} > 0$ and $\delta_i > 0$), or as the absence of developmental delay (when $b_{mi} = 0$ and $\delta_i = 0$).

In year $t+1$, expected recruitment of adults comes from larvae that have spent one or more years in that stage. The probability that a larva survives pupation and reaches reproductive maturity is denoted p_a, so the expected number of adults in year $t+1$ is

$$A(t+1) = \sum_{i=1}^{\Psi} (1 - b_i) p_a L_i(t+1) \tag{7}$$

of which $A_f(t+1) = fA(t+1)$ are females and $A_m(t+1) = (1-f)A(t+1)$ are males ($0 \le f \le 1$).