Problem choice: Chemical Espionage
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Additional Problem C
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A Mathematical Model of Chemical Espionage: Executive Summary

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Model Structure

Our model captures the interactions between *Pieris brassicae* (henceforth referred to as "butterflies"), and the parasitoid species *Trichogramma brassicae* and *Costeria glomerata* (henceforth referred to as "wasps"), based on the presence of an anti-aphrodisiac chemical signal, benzyl cyanide (BC)[5]. A diagram of the model can be found in Figure 1 of the Appendix, where the populations are: $E(t)$, the butterfly eggs, $F_v(t)$, the virgin female butterflies, $F_m(t)$, the mated female butterflies, $M(t)$, the male butterflies, and $W(t)$, the wasps, where t is time in days, justified in *Model Parameters, Initial Conditions and Further Assumptions*. Differential equations that represent changes in each population can be found as Equations 1-5 in the Appendix. In order to generate a comprehensive, yet general model of such interactions, experimental observations of interactions between both wasp species and the butterfly species will be used to inform a general female wasp population, W, in the model. W is female because only female wasps lay eggs, so the relevant *direct* interaction between the species is between (mated) females of both species only, though reproduction within the populations contributes indirectly. For simplicity, it is assumed that the rate of reproduction of the wasps is constant so that inclusion of a male wasp population in the model is not necessary. Therefore, the total population of wasps would be $2W$ if males were accounted for in the model, assuming there is a 50/50 distribution of male and female wasps. This model is accurate during mating seasons; that is, it does not currently consider variable environmental conditions, though it can be relatively easily augmented to do so. Our model attempts to find a "best balance" of the system, which we define as a case where the BC's level of effectiveness in these interactions allows both species to persist (neither become extinct). The BC effectiveness is accounted for in the model as the effectiveness of both the mating interaction between M and F_v and the effectiveness of the parasitic interaction between F_m and W, discussed further in the *Model Parameters, Initial Conditions and Further Assumptions* section The long-term behavior of the populations, disregarding seasonal limitations, depends on the effectiveness of these interactions based on anti-aphrodisiac presence. While the butterflies can certainly survive without the wasps, the wasps would fare poorly without the parasitism of the butterflies, so the long-term behavior should also consider these relationships.

A key assumption of our model is that generations of both species are *discrete*, meaning that mating between F_v and M occurs around the same time. This is a reasonable assumption, as in many locations that the butterflies inhabit, such as the UK, only two generations of butterflies occur due to seasonal limitations[2]. Most insects "overwinter", or hibernate as eggs[3], so it is fair to assume that once temperature conditions allow, the overwintered eggs will hatch around the same time, producing the first generation of adults that year around the same time. This discrete quality of insect generations also allows for clearer visualization of population behavior. One study of this butterfly population witnessed 75,000 butterflies in one location in 1.5 days, which they estimated to be a "small proportion" of the total local population[4], so we set our original total population of adult butterflies to be 750,000, assuming it to be 50% male and 50% female. We decided that with this population sample, a fair carrying capacity for the entire adult butterfly population would be 1,000,000. Because the butterflies feed and breed on plants of the genus *Brassicae*[6], which includes cabbage and cauliflower, access to these plants would impose such a limit on the population. For readability, our simulation included approximate population values divided by 10,000. Therefore, the carrying capacity parameter values are 50 for F_m and 50 for M, assuming the rapid occurrence of mating between males and females drives F_v to 0 fast enough to not require a carrying capacity.

Because wasps occupy a higher trophic level, or predator level than the butterflies due to their parasitic nature, their population would naturally be lower, so we estimated a carrying capacity for the entire wasp population to be 700,000. This would indicate a carrying capacity of 350,000 for W (35 once divided), since this is only female wasps. This limit to the wasp population primarily relies on the wasps' access to butterfly eggs for food early in life. These carrying capacities are included in the corresponding equations (3, 4 and 5) as logistic terms.

The butterfly occupies four distinct stages in its life cycle: egg, larva, pupa, and adult. For the sake of simplicity in our model, we chose to include only egg and adult populations, as these stages are the most relevant to the issues of reproduction and wasp parasitism. However, it should be noted that there exists a time delay between the transition between the egg and butterfly stages; in reality the butterfly occupies the egg population for 3-18 days and the adult population for 3-12 days, leaving a delay of 22-69 days when the butterfly occupies the larva and pupa stages, during which other parasites, such as various bacteria, can lower the survival rate of butterflies to the adult stage[8]. This is accounted for by including a high death rate for E, $d_E = 0.6$, that does not contribute to the wasp population. Because of these durations of life stages, we chose our time unit, t to be days. It should also be noted that it is appropriate to assume these intermediate life stages to be in E, as adult butterflies are the only life stage capable of mating. Following this, we assume F_m to be a *terminal state*, or that once females mate, they cannot return to F_v. This is appropriate, as female butterflies are typically monogamous[7], so F_m would not participate in additional mating. Considering multiple sources, we estimated a fair butterfly lifespan to be 30-60 days.

The discrete generations, life cycle, and estimated total butterfly population size gives rise to our choice of initial conditions. Continuing to divide realistic populations by 10,000 and choosing t_0 to be right after the overwintered eggs "hatch" (including time delay for unincluded life stages), $E(0) = 0$, $F_v(0) = 36.38$ (99% of females), $F_m(0) = 1.125$ (1% of females), $M(0) = 37.5$ (50% of the total original butterfly population), and $W(0) = 20$ (estimated lower than 75% of carrying capacity due to lack of host species). Remaining parameters include: $b = 20$, or the number of eggs laid by each mated female[1], which is multiplied by d_Fm in equation 1 in order to avoid double-counting female butterflies that remain in F_m after mating, $d_{Fm} > d_M, dW > d_{Fv}$, the natural death rates of the corresponding populations, $\lambda = 0.01$, the proportion of eggs that become adults (based on 0.74% survival rate in literature[9]), $\alpha = 0.2$, the proportion of mating interaction between F_v and M, $\omega = 0.07$, the proportion of parasitic interaction between F_m and W (value chosen based on 7.1% successful parasitism[10]), and finally $\sigma = 0.0071$, the estimated increase in ω and α based on the presence of BC, based on error bounds on ω[10].

Results

The resulting behavior of this model with these parameters and conditions can be seen in Figure 2 of the Appendix. Some behavior aligns with our intended behavior: Fv rapidly decreases as Fm increases, E increases as (Fm increases, E slowly drops off as eggs become adults, (Fm and (M slowly drop off as this generation dies out, and W increases with increased access to (E. However, this all occurs in a third of the intended time frame (1 generation being a minimum of 30 days). Further, it was hoped that all populations would cycle in different amplitudes and periods in response to egg hatching, parasitism and life span, but instead, these populations became steady, only reflecting activity of a single generation. So while we were able to generate realistic population dynamics for a single generation, this result does not yet provide a quantification of the "best balance" of this system such that all populations can persist in expected cyclic manners, assuming the realistic seasonal limits cause these discrete generations and do not contain enough generations to even out to steady population points.

In the long run, or the case of longer mating seasons where generations do not remain discrete, population behavior depends on the mating and parasitic interactions and most importantly, σ, the parameter reflecting BC's effect on these interactions, the following scenarios would be expected: 1) both the total butterfly population and W could be driven to extinction, 2) both could persist, or 3) the butterflies could persist and wasps could be driven to extinction, but W cannot persist without the persistence of the butterflies due to their parasitic relationship. In order to gain a better sense of accurate population dynamics, different parameters could be tested, and further model structure considerations could be made until the model reflects realistic, documented population behavior.

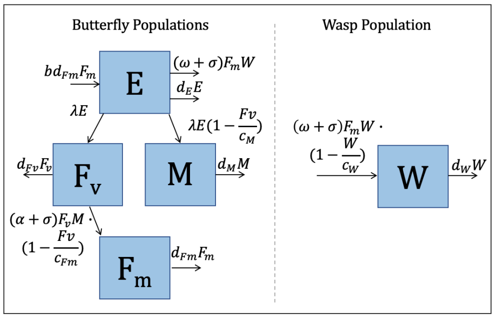

Figure 1: Model diagram

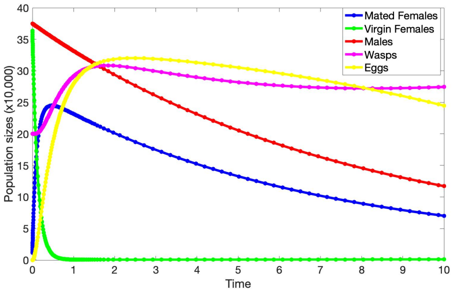

Figure 2: Model behavior with discussed parameter and initial condition values

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