Density-Dependent Selection Model for the Evolution of Sociality of
Ceratina (Neoceratina) australensis

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Abstract

Ceratina (Neoceratina) australensis, the Australian small carpenter bee, is socially polymorphic with both solitary and social nests present in the same population. Solitary nests contain a single adult female and her developing brood and social nests contain two adult females and their brood. Solitary nests tend to produce more offspring per female than social nests, but only when a species of parasitic wasp is absent. When the wasp is abundant, solitary nests suffer high levels of parasitism and loss of brood. Thus, solitary nests do worse in the presence of wasps and better in their absence. The parasitic wasp does better when solitary nests are common, and worse when they are rare. The interactions with this nest parasite are hypothesized to allow maintenance of both nest types in bee populations: when solitary nests are dense, the wasp increases in numbers, which leads to an advantage for social nests, and vice versa. To address this hypothesis, several mathematical models were developed to capture the biology of this system. The models were analyzed to determine whether a stable equilibrium with both social and solitary nests was possible. Such an equilibrium was found, but only for a very small region of the parameter space. This restriction might explain why the occurrence of socially polymorphic species, where the advantage of sociality is driven by predators/parasites, is rare.

Introduction

Several species are observed to be solitary- once an offspring is mature enough to live without the care of its parents, it ventures off alone. However, in some species, offspring don't venture off alone but instead form groups, either staying with the parental group, which may include other related individuals or forming groups with unrelated individuals. Across different types of social groups, there exists a range of cooperation for foraging, caring for offspring, and defense. Living in groups has both benefits and costs. For example, shoaling behavior in fish is seen as a trade-off between a reduction in predation and increased competition for food (Hoare 2000). Evolutionary biologists have long studied why stable social groups only appear to exist in certain species. Much research has been done on the highly social species found in insects, such as ants, bees, wasps and termites (Wilson 1971). However, not all species in these groups are social, implying that the fitness consequences of group living must vary – sometimes it is favored and sometimes it isn't. While progress can be made to understand the evolution of sociality by comparing social and nonsocial species using a comparative approach, a species that shows both group and solitary living allows the fitness effects of each to be directly measured. In this thesis, I consider a bee species that shows variation in group living.

Ceratina (Neoceratina) australensis, the Australian small carpenter bee (Figure 1) is an oddity in the *Ceratina* genus because it has been observed to be socially polymorphic, with both social and solitary nests observed within a single population (Rehan 2010). The female bees build nests within dead giant fennel (*Ferula communis*) stems that resemble a hollow tube with four to five subunits (Figure 2). Both social and solitary bee nests have a single entrance. Social nests arise when the female bee that founded the nest ("the foundress') acquires a nestmate. This nestmate is often a daughter bee that remains in her natal nest, giving the nest two 'queens.' The foundress and the nestmate create a division of labor within the nest. The foundress actively reproduces and forages while the nestmate remains to guard the entrance to the nest. The nestmate is, however, able to reproduce and will take ownership of the nest if the foundress dies.

Social nesting insects have defense mechanisms that involve cooperation. In the caste system, the soldier caste may have enhanced physical traits to attack predators

(Gruter 2012). Without a soldier caste, organisms may display aggressive behavior or release alarm pheromones. One defense mechanism involves guarding the entrance to the nest. Theoretically, if the entrance is blocked then a predator can't enter the nest as easily, or at all. Solitary nests, however, are likely to be much more susceptible to predation because one queen can't stay at the entrance defending the nest and also forage so that she can nurture her offspring efficiently.

One hypothesis for the evolution of sociality in *C. australensis* is as a defense against predation by a species of chalcid wasp from the genus *Eurytoma* (Figure 3). This parasitoid wasp reproduces by laying eggs in bee larvae. Wasps then hatch and feed on the bee larvae, resulting in their death. A nest is most likely to become parasitized when the nest entrance is unguarded. For nests with one queen, this occurs whenever it leaves to gather food. Therefore, having two queen bees in a nest is expected to provide an advantage against predation and increase the survival of larvae (Rehan 2010, 2014).

To test whether wasp predation can favor the evolution of sociality in bees, we modeled a three variable system, explicitly following social bees, solitary (asocial) bees, and wasps. We created a system of three difference equations, one for each species and then varied the parameters of the model to examine how mortality, reproduction and parasitism rates altered the outcomes. We used analytical approaches, numerical approaches, and simulations to gain insight into the behavior of the model. The model included all of the parameters that are likely to affect the evolution of sociality in this system (Table 1.2). A constraint we placed on the parameters of the model, based on the biology of the interaction, was that survival of larvae in social nests was better than in solitary nests with parasitism but was worse without parasitism. In addition to determining when sociality was favored, we were especially interested in determining whether there are conditions under which both solitary and social bees, and their wasp parasitoids can be maintained in the population.

Methodology

Table 1.1: Variables	
Variable	Definition
S[t]	The number of social nests at time t
A[t]	The number of solitary nests at time t
W[t]	The number of wasps at time t

Table 1.2: Parameters		
Parameter	Definition	Range
k	Maximum parasitism rate	[0,1]
Z	Number of wasps to achieve 50% parasitism	$(0,\infty)$
m	Bee mortality rate	[0,1)
mW	Wasp mortality rate	[0,1)
bW	Wasp birth rate	
bau	# of bees that emerge from a solitary unparasitized nest	
bap	# of bees that emerge from a solitary parasitized nest	
bsu	# of bees that emerge from a social unparasitized nest	
bsp	# of bees that emerge from a social parasitized nest	
Assumptions: 2bau > bsu ≥ bau > bsp > bap ≥ 0		

Model Building

The life cycle (Figures 4 and 5) consists of surviving adult bees building nests and laying eggs, which then hatch into larvae if they are not parasitized. Larvae become adults in the nest and then these adults leave the nests in order to build new ones that will start the next generation. Bee mortality occurs after bees leave the nest and before they begin building a new nest. Eggs parasitized by wasps die. We censured the life cycle when offspring emerged from the nests. All nests in a population were synchronous. Each generation thus follows the same cycle: a portion of the adult bees die and then the survivors build nests (either social or solitary/antisocial). Some of the nests are parasitized, which depends on the density of wasps in the area. Parasitized nests produce fewer offspring than unparasitized nests. In addition, solitary nests lose more offspring when they are parasitized than do social nests. These assumptions imply that larval production is such that unparasitized, solitary nests (bau) > unparasitized, social nests (bsu) > parasitized, social nests (bsp) > parasitized, solitary nests (bap). Bee birth rate was assumed to be density dependent, implying it is resource limited perhaps due to pollen or nectar availability. Mathematically, we simply divided bee birth rate parameters by the total bee population (using one individual per solitary nest and two per social nest) plus a constant value of 1. As the bee population increases, birth rate declines. We used the variable A to track asocial/solitary bees and the variable S to track social bees.

Wasp reproduction is dependent on how many bee nests are in the area, how protected (social versus solitary) the nests are, how many bee larvae are in the nests, and how many eggs one female wasp can lay per bee larvae.

An appropriate method to model this system is using a nonlinear discrete time model where the parameter t would represent the number of generations.

The software program Mathematica (Wolfram Mathematica 11 Student Edition, version 11.3.0.0) was used to run all our simulations and help with equilibrium identification and stability analyses. For numerical analyses, we wrote functions that calculated the equilibria and their stability for various parameter inputs. For the simulations, we followed the frequencies of the three variables for various parameter values. For numerical analyses, we used randomly chosen parameter combinations to determine how frequently particular equilibria existed and their stability.

Model Analysis

Since field experiments have shown the existence of social nests, solitary nests, and wasps coexisting within an area, we sought to see if our nonlinear discrete time model showed such an equilibrium. In theory, these are all the possible equilibria of our system, where a non-zero entry indicates a positive value at equilibrium:

Equilibrium point as (A[t], S[t], W[t])
$(0, 0, 0)$
$(\hat{A}, 0, 0)$
$(0, \hat{S}, 0)$
$(0, 0, \hat{W})$
$(\hat{A}, \hat{S}, 0)$
$(\hat{A}, 0, \hat{W})$
$(0, \hat{S}, \hat{W})$
$(\hat{A}, \hat{S}, \hat{W})$

To determine if these equilibria existed in our system, we used Mathematica to solve for the equilibria. An equilibrium is defined as the values of the variables ($\hat{A}$, $\hat{S}$ and $\hat{W}$) at which their frequencies do not change from one generation to the next, ie A[t+1] = A[t] = $\hat{A}$, S[t+1] = S[t] = $\hat{S}$, and W[t+1] =W[t] = $\hat{W}$. These were the six equilibria that were found to be possible, given the biological constraints on the parameters:

Equilibrium point as (A[t], S[t], W[t])
1.$(0, 0, 0)$
2.$(\frac{bau(1-m)-m}{m}, 0, 0)$
3.$(0, \frac{bsu(1-m)-2m}{2m}, 0)$
4.$(\hat{A}, 0, \hat{W})$[1]
5.$(0, \hat{S}, \hat{W})$[2]
6.$(\hat{A}, \hat{S}, \hat{W})$[3]

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[1] See Appendix for values of $\hat{A}$ and $\hat{W}$
[2] See Appendix for values of $\hat{S}$ and $\hat{W}$
[3] See Appendix for values of $\hat{A}$, $\hat{S}$, and $\hat{W}$

Note that for equilibria 4, 5 and 6, the values of Â, Ŝ and Ŵ are too complicated to include in the table.

Two of the possible equilibria did not exist in our system. The equilibrium (0, 0, Ŵ) does not exist because wasps need bee larvae in order to reproduce, so they cannot persist in their absence. The equilibrium (Â, Ŝ, 0) does not exist because in the absence of wasps, all bee nests are unparasitized and so social bees lose out to solitary bees. Since bau > bsu, the solitary population will always outperform the social population in the absence of wasps.

To test the existence and stability of these equilibria, we found the characteristic polynomial of the Jacobian of our three equations. The characteristic polynomial is used to determine the eigenvalues of the linearized system at the equilibrium. If any of the eigenvalues is greater than one, the equilibrium is unstable and a population is not expected to remain there. For complex eigenvalues ($\lambda = \alpha + \beta i$), the equivalent condition for instability is that $\sqrt{\alpha^2 + \beta^2} > 1$. If all of the eigenvalues are less than one, the equilibrium is stable and a population is expected to remain at that equilibrium indefinitely. The non-evaluated Jacobian, J (A, S, W), is shown in the appendix. Below are examples of the Jacobian evaluated at certain equilibrium points (from above).

$J(0, 0, 0) =$

$$
\begin{pmatrix}
-(1 + \text{bau})\ (-1 + m) & 0 & 0 \\
0 & -\frac{1}{2}\ (2 + \text{bsu})\ (-1 + m) & 0 \\
0 & 0 & 0
\end{pmatrix}
$$

$J(\hat{A}, 0, 0) =$

$$
\begin{pmatrix}
\frac{\text{bau}\ (-1+m)^2 + m^2}{\text{bau} - \text{bau}\ m} & m\left(-1 + \frac{m}{\text{bau} - \text{bau}\ m}\right) & \frac{(\text{bap} - \text{bau})\ k\ (\text{bau}\ (-1+m) + m)\ (-1+mW)}{\text{bau}\ Z} \\
0 & 1 + \left(-1 + \frac{\text{bsu}}{2\ \text{bau}}\right) m & 0 \\
0 & 0 & -\frac{(\text{bap} - \text{bau})\ bW\ k\ (\text{bau}\ (-1+m) + m)\ (-1+mW)}{\text{bau}\ Z}
\end{pmatrix}
$$

$J(0, \hat{S}, 0) =$

$$
\begin{pmatrix}
1 + \left(-1 + \frac{2\ \text{bAU}}{\text{bsu}}\right) m & 0 & 0 \\
m\left(-1 + \frac{2\ m}{\text{bsu} - \text{bsu}\ m}\right) & \frac{\text{bsu}\ (-1+m)^2 + 2\ m^2}{\text{bsu} - \text{bsu}\ m} & \frac{(\text{bsp} - \text{bsu})\ k\ (\text{bsu}\ (-1+m) + 2\ m)\ (-1+mW)}{2\ \text{bsu}\ Z} \\
0 & 0 & -\frac{(\text{bsp} - \text{bsu})\ bW\ k\ (\text{bsu}\ (-1+m) + 2\ m)\ (-1+mW)}{2\ \text{bsu}\ Z}
\end{pmatrix}
$$

Results

To analyze the stability of the equilibria, we first determined the characteristic polynomial by taking the determinant of [J (A, S, W)-λI], where J(A, S, W) is the Jacobian, I is a 3 by 3 identity matrix, and λ is the variable lambda. The values of lambda that make the characteristic polynomial at each equilibrium zero are the eigenvalues for perturbations around the equilibrium. Each equilibrium had three corresponding lambda values (corresponding to perturbations in social bees, asocial bees and wasps).

The Zero State

The (0, 0, 0) equilibrium exists when there are no bees or wasps in a certain area. By evaluating the Jacobian at (0,0,0), we discovered its eigenvalues that help determine when rare bees or wasps could establish a new colony.

There were three eigenvalues found for this equilibrium. The first eigenvalue is λ_1 = bau (1-m)+(1-m). If the birth survival rate of solitary bees is greater than the mortality rate (bau (1-m) > m), λ_1 is greater than 1. The second eigenvalue is λ_2 = (1/2)bsu(1-m)+2(1-m) and λ_2 is greater than one when bsu(1-m)-2m>0. The third eigenvalue is λ_3 = 0. This means that a rare wasp cannot invade a new area but solitary and social bees can if their birth rates are high enough to overcome non-parasitoid induced mortality.

Solitary Bees Only

The (Â, 0, 0) equilibrium exists when bau (1-m) > m or when the birth rate is higher than the death rate. We evaluated the Jacobian at this equilibrium and found three eigenvalues. The first eigenvalue is $\lambda_1 = 1 - m + (\frac{bsu}{2bau})m$. Since bsu < 2bau, the third term is less than m and so the sum of λ_1 is less than 1. This eigenvalue is the one that is associated with the introduction of social bees and indicates that in the absence of wasps, social bees cannot invade a population of solitary bees. The second eigenvalue was $\lambda_2 = \frac{bau(1-m)^2+m^2}{bau(1-m)}$, which is less than one. This was found by manipulating the fraction:

bau(1-m)^2 + m^2 – bau(1-m) < 0 → -m bau(1-m)+m^2 < 0, which is true because bau(1-m) > m for (Â, 0, 0) to exist and therefore the first term is more negative than m^2. Since λ_2 is less than one, (Â, 0, 0) is stable to perturbations of A (solitary bees). Basically, when

solitary bees are at this equilibrium their birth and death rates are equal. Above the equilibrium, birthrates decline and below, they increase due to density dependence. The third eigenvalue is $\lambda_3 = \frac{(bau-bap)bWk(bau(1-m)-m)(1-mW)}{bauZ}$, which can be either greater than or less than one. This eigenvalue is more likely to be greater than one under the following conditions: small Z, small mW, large (bau-bap), large bW, and large k. That is, when wasps are good at finding nests and produce a lot of offspring, they will invade. If all three eigenvalues are less than one, then the $(\hat{A}, 0, 0)$ equilibrium is globally stable.

Social Bees Only

The $(0, \hat{S}, 0)$ equilibrium exists when bsu(1-m) > 2m, that is the birth rate must be higher than the death rate. We evaluated the Jacobian at this equilibrium and found three eigenvalues. The first eigenvalue is $\lambda_1 = 1 - m + (\frac{2bau}{bsu})m$, which is greater than one because since bsu < 2bau, the third term is greater than m and so the total sum is greater than one. This means that a population of only social bees is unstable to the invasion of solitary bees, which makes sense based on the biology of the system (social nesting is advantageous only in the presence of wasps). The second eigenvalue was $\lambda_2 = \frac{bsu(1-m)^2+2m^2}{bsu(1-m)}$, which is less than one. This was found by manipulating the fraction: $bsu(1-m)^2 + 2m^2 - bsu(1-m) < 0 \rightarrow$ -m bsu(1-m) + $2m^2 < 0$, which is true because bsu(1-m) > 2m for $(0, \hat{S}, 0)$ to exist and therefore the first term is more negative than $2m^2$. Since λ_2 is less than one, $(0, \hat{S}, 0)$ is stable to perturbations of S (social bees). As for the solitary equilibrium, this result is due to the density dependence of the birth rate. The third eigenvalue was $\lambda_3 = \frac{(bsu-bsp)bWk(bsu(1-m)-2m)(1-mW)}{2bsuZ}$, which can be either greater than or less than one. This eigenvalue is more likely to be greater than one under the following conditions: small Z, small mW, large (bau-bap), large bW, and large k, as before. Since λ_1 is always greater one, the $(0, \hat{S}, 0)$ equilibrium is globally unstable.

Two Variable and Three Variable State

The $(\hat{A}, 0, \hat{W})$, $(0, \hat{S}, \hat{W})$, and $(\hat{A}, \hat{S}, \hat{W})$ equilibria were too complex for us to easily evaluate the Jacobian and find the eigenvalues. However, simulations showed that these equilibria do exist under certain parameter conditions and that they can be stable.

Simulations

To examine the likelihood of obtaining different outcomes, we created a Mathematica function that randomly chose all the parameter values and then determined all equilibria and their stability. We performed ten thousand simulations with randomly drawn parameter combinations and found the following:

Equilibria Present	Number	Stable Equilibria*
{(0,0,0)}	1500	(0, 0, 0)
{(0,0,0), (Â,0,0)}	1455	(Â, 0, 0)
{(0,0,0), (Â,0,0), (Â,0,Ŵ)}	20	(Â, 0, Ŵ)
{(0,0,0), (0,Ŝ,0), (Â,0,0)}	6131	(Â, 0, 0)
{(0,0,0), (Â,0,0), (0,Ŝ,0), (Â,0,Ŵ)}	769	(Â, 0, Ŵ)
{(0,0,0), (Â,0,0), (0,Ŝ,0), (Â,0,Ŵ), (Â,Ŝ,Ŵ)}	15	(Â, Ŝ, Ŵ)
{(0,0,0), (Â,0,0), (0,Ŝ,0), (Â,0,Ŵ), (0,Ŝ,Ŵ)}	101	(Â, 0, Ŵ)
{(0,0,0), (Â,0,0), (0,Ŝ,0), (Â,0,Ŵ), (0,Ŝ,Ŵ), (Â,Ŝ,Ŵ)}	9	(Â, Ŝ, Ŵ)

* all other equilibria are unstable

These data indicate that 15% of randomly drawn parameter combinations have birth and death rates that prevent bees from replacing themselves in the absence of wasps. Another ~15% of parameter combinations have values that prevent wasps from replacing themselves, even when all bees are solitary. Together, these 30% of simulations are of little biological interest since they represent cases where each species cannot actually exist under any conditions. In the remaining simulations, loss of the wasp is the most common occurrence, occurring 87% of the time (6131 of 7045 simulations). While this tells us something about the difficulty of maintain a specialist parasitoid wasp, in nature both species co-exist and so it is the remaining 914 simulations that are our main interest. Within this group, the most common outcome is coexistence of the solitary bee with the wasp, occurring in ~97% of outcomes (890 of 914 simulations). In only ~3% of situations in which both the bee and wasp coexist at equilibrium is the social bee expected to be present. In all 24 cases in which an equilibrium with the social bee is stable, the solitary bee is also present.

Discussion

Our research has determined that there are conditions under which bees and wasps can coexist. When that happens, it is most likely that all of the bees that prevail will be solitary. Rarely, there can be both solitary and social bees with their wasp parasitoids maintained in the population. This suggests that one of the reasons for rarely observing mixed strategies within a single population is that it is rare that the parameters will be just right to give such an equilibrium. Overall, we find that the conditions for the maintenance of both bee types includes relatively high parasitism ($k > 0.5$) and wasp birthrate (bW) but relatively low bee ($m < 0.5$) and wasp ($mW < 0.5$) mortality.

Why do solitary bees tend to be stably maintained in populations, while social bees lose out? To answer the question, it is worth considering what happens with the wasp. When social bees are doing well, wasp parasitism declines and so wasp density declines. Declines in wasp densities leads to a decline in wasp parasitism. Thus an equilibrium with wasps and social bees is likely to be readily invaded by solitary bees because of the low parasitism. This conjecture is supported by the fact that we never saw an equilibrium with just social bees and wasps that was stable to the invasion of solitary bees.

The next steps in this modeling effort are twofold. First will be to use experimental estimates of the parameters from the *Ceratina (Neoceratina) australensis* and *Eurystoma sp.* interaction to see if they predict a stable equilibrium containing both bee types. Second is to use the insight gained regarding stability from the simulations to help with the analytical proofs for the existence and stability of all equilibria.

Appendix

Equations Represented in a Module

```
Beesandwaspsgraphed[a0_, s0_, w0_, k_, Z_, m_, mW_, bau0_, bap0_, bsu0_, bsp0_, bW_, gens_] := Module[{A, S, W},

  A[0] = a0; (*antisocial nests at time 0*)
  S[0] = s0; (*social nests at time 0*)
  W[0] = w0; (*wasps at time 0*)

  (*recursions for bees*)
  A[t_] := A[t] = (1 - m) (A[t - 1]) + (bau0 / (1 + A[t - 1] + S[t - 1])) A[t - 1] (1 - m) (1 - k (1 - mW) W[-1 + t] / (Z + (1 - mW) W[-1 + t])) +
    (bap0 / (1 + A[t - 1] + S[t - 1])) A[t - 1] (1 - m) (k (1 - mW) W[-1 + t] / (Z + (1 - mW) W[-1 + t]));

  S[t_] := S[t] = (1 - m) (S[t - 1]) + (bsu0 / (1 + A[t - 1] + S[t - 1])) (S[t - 1] / 2) (1 - m) (1 - k (1 - mW) W[-1 + t] / (Z + (1 - mW) W[-1 + t])) +
    (bsp0 / (1 + A[t - 1] + S[t - 1])) (S[t - 1] / 2) (1 - m) (k (1 - mW) W[-1 + t] / (Z + (1 - mW) W[-1 + t]));

  (*recursion for wasps*)
  W[t_] :=
   W[t] = (k * (1 - mW) W[t - 1] / (Z + (1 - mW) W[t - 1]))
     ((1 - m) (A[t - 1]) bW ((bau0 - bap0) / (1 + A[t - 1] + S[t - 1])) + (1 - m) (S[t - 1] / 2) bW ((bsu0 - bsp0) / (1 + A[t - 1] + S[t - 1])));

  MatrixForm[{" = last social "ToString[S[gens]], " = last antisocial "ToString[A[gens]], " = last wasp "ToString[W[gens]],
    " = maximum parasitism rate"ToString[k], " = number of wasps to give 50% parasiticm"ToString[Z], " = mortality rate of bees"ToString[m],
    " = mortality rate of wasps"ToString[mW], " = birth rate of unparasitized, solitary bees"ToString[bau0],
    " = birth rate of parasitized, solitary bees"ToString[bap0], " = birth rate of unparasitized, social bees"ToString[bsu0],
    " = birth rate of parasitized, social bees"ToString[bsp0], " = birth rate of wasps"ToString[bW], "Antisocial = blue line",
    "Social = red line", "Wasps = green line",
    ListPlot[{Table[{i, A[i]}, {i, 0, gens}], Table[{i, S[i]}, {i, 0, gens}], Table[{i, W[i]}, {i, 0, gens}]},
     AxesLabel → {"Generations", "Population Size"}, PlotStyle → {Blue, Red, Green}, Joined → True, ImageSize → 375]}
  ]
]
```

Jacobian

J(A, S, W)=

$$
\left\{\left\{-\frac{(-1+m)\left((-1+mW)\left(A^2+2A(1+S)-(-1+bAU(-1+kw)-bAPkw-S)(1+S)\right)W-\left(A^2+2A(1+S)+(1+S)(1+bAU+S)\right)Z\right)}{(1+A+S)^2((-1+mW)W-Z)},\right.\right.
$$

$$
-\frac{A(-1+m)(-bAPkw(-1+mW)W+bAU((-1+kw)(-1+mW)W+Z))}{(1+A+S)^2((-1+mW)W-Z)},\ \frac{A(bAP-bAU)kw(-1+m)(-1+mW)Z}{(1+A+S)(W-mWW+Z)^2}\right\},\left\{-\frac{(-1+m)S(-bSPkw(-1+mW)W+bSU((-1+kw)(-1+mW)W+Z))}{2(1+A+S)^2((-1+mW)W-Z)},\right.
$$

$$
-\frac{1}{2(1+A+S)^2((-1+mW)W-Z)}(-1+m)\left((-1+mW)\left(2+2A^2+bSU+bSPkw-bSUkw+4S+2S^2+A(4+bSU+bSPkw-bSUkw+4S)\right)W-\left(2A^2+bSU+2(1+S)^2+A(4+bSU+4S)\right)Z\right),
$$

$$
\left.\frac{(bSP-bSU)kw(-1+m)(-1+mW)SZ}{2(1+A+S)(W-mWW+Z)^2}\right\},\left\{\frac{bWkw(-1+m)(-1+mW)((-bSP+bSU)S+2bAP(1+S)-2bAU(1+S))W}{2(1+A+S)^2((-1+mW)W-Z)},\right.
$$

$$
\left.\left.\frac{(bSP+A(-2bAP+2bAU+bSP-bSU)-bSU)bWkw(-1+m)(-1+mW)W}{2(1+A+S)^2((-1+mW)W-Z)},\ -\frac{bWkw(-1+m)(-1+mW)(2A(bAP-bAU)+(bSP-bSU)S)Z}{2(1+A+S)(W-mWW+Z)^2}\right\}\right\}
$$

Equilibria

$(\hat{A}, 0, \hat{W})$:

$\hat{A} =$

$$-\frac{1}{2\,(bap - bau)\,bW\,k\,m\,(-1 + mW)^2}$$
$$\big(-bap\,bau\,bW\,k + bau^2\,bW\,k - bap^2\,bW\,k^2 + 2\,bap\,bau\,bW\,k^2 - bau^2\,bW\,k^2 + bap\,bW\,k\,m - bau\,bW\,k\,m + bap\,bau\,bW\,k\,m - bau^2\,bW\,k\,m +$$
$$bap^2\,bW\,k^2\,m - 2\,bap\,bau\,bW\,k^2\,m + bau^2\,bW\,k^2\,m + 2\,bap\,bau\,bW\,k\,mW - 2\,bau^2\,bW\,k\,mW + 2\,bap^2\,bW\,k^2\,mW - 4\,bap\,bau\,bW\,k^2\,mW +$$
$$2\,bau^2\,bW\,k^2\,mW - 2\,bap\,bW\,k\,m\,mW + 2\,bau\,bW\,k\,m\,mW - 2\,bap\,bau\,bW\,k\,m\,mW + 2\,bau^2\,bW\,k\,m\,mW - 2\,bap^2\,bW\,k^2\,m\,mW +$$
$$4\,bap\,bau\,bW\,k^2\,m\,mW - 2\,bau^2\,bW\,k^2\,m\,mW - bap\,bau\,bW\,k\,mW^2 + bau^2\,bW\,k\,mW^2 - bap^2\,bW\,k^2\,mW^2 + 2\,bap\,bau\,bW\,k^2\,mW^2 -$$
$$bau^2\,bW\,k^2\,mW^2 + bap\,bW\,k\,m\,mW^2 - bau\,bW\,k\,m\,mW^2 + bap\,bau\,bW\,k\,m\,mW^2 - bau^2\,bW\,k\,m\,mW^2 + bap^2\,bW\,k^2\,m\,mW^2 - 2\,bap\,bau\,bW\,k^2\,m\,mW^2 +$$
$$bau^2\,bW\,k^2\,m\,mW^2 - bap\,k\,Z + bau\,k\,Z + bap\,k\,mW\,Z - bau\,k\,mW\,Z +$$
$$\sqrt{\big((-1 + mW)^2}$$
$$\big(4\,(bau\,(-1 + k) - bap\,k)\,Z\,(bap\,bW\,k\,(bau\,(-1 + m) + m)\,(-1 + mW) + bau\,(-bW\,k\,m\,(-1 + mW) + bau\,bW\,k\,(-1 + m + mW - m\,mW) + Z)) +$$
$$\big(bap^2\,bW\,k^2\,(-1 + m)\,(-1 + mW) + bap\,k\,(-bau\,bW\,(-1 + 2\,k)\,(-1 + m)\,(-1 + mW) + bW\,m\,(-1 + mW) + Z) +$$
$$bau\,(bW\,k\,m + bau\,bW\,(-1 + k)\,k\,(-1 + m)\,(-1 + mW) - bW\,k\,m\,mW + 2\,Z - k\,Z))^2\big)\big)\big)$$

$\hat{W} =$

$$-\frac{1}{2\,(bau\,(-1 + k) - bap\,k)\,(-1 + mW)^2}$$
$$\big(-bap\,bau\,bW\,k + bau^2\,bW\,k - bap^2\,bW\,k^2 + 2\,bap\,bau\,bW\,k^2 - bau^2\,bW\,k^2 + bap\,bW\,k\,m - bau\,bW\,k\,m + bap\,bau\,bW\,k\,m - bau^2\,bW\,k\,m +$$
$$bap^2\,bW\,k^2\,m - 2\,bap\,bau\,bW\,k^2\,m + bau^2\,bW\,k^2\,m + 2\,bap\,bau\,bW\,k\,mW - 2\,bau^2\,bW\,k\,mW + 2\,bap^2\,bW\,k^2\,mW - 4\,bap\,bau\,bW\,k^2\,mW +$$
$$2\,bau^2\,bW\,k^2\,mW - 2\,bap\,bW\,k\,m\,mW + 2\,bau\,bW\,k\,m\,mW - 2\,bap\,bau\,bW\,k\,m\,mW + 2\,bau^2\,bW\,k\,m\,mW - 2\,bap^2\,bW\,k^2\,m\,mW +$$
$$4\,bap\,bau\,bW\,k^2\,m\,mW - 2\,bau^2\,bW\,k^2\,m\,mW - bap\,bau\,bW\,k\,mW^2 + bau^2\,bW\,k\,mW^2 - bap^2\,bW\,k^2\,mW^2 + 2\,bap\,bau\,bW\,k^2\,mW^2 -$$
$$bau^2\,bW\,k^2\,mW^2 + bap\,bW\,k\,m\,mW^2 - bau\,bW\,k\,m\,mW^2 + bap\,bau\,bW\,k\,m\,mW^2 - bau^2\,bW\,k\,m\,mW^2 + bap^2\,bW\,k^2\,m\,mW^2 - 2\,bap\,bau\,bW\,k^2\,m\,mW^2 +$$
$$bau^2\,bW\,k^2\,m\,mW^2 - 2\,bau\,Z - bap\,k\,Z + bau\,k\,Z + 2\,bau\,mW\,Z + bap\,k\,mW\,Z - bau\,k\,mW\,Z +$$
$$\sqrt{\big((-1 + mW)^2}$$
$$\big(4\,(bau\,(-1 + k) - bap\,k)\,Z\,(bap\,bW\,k\,(bau\,(-1 + m) + m)\,(-1 + mW) + bau\,(-bW\,k\,m\,(-1 + mW) + bau\,bW\,k\,(-1 + m + mW - m\,mW) + Z)) +$$
$$\big(bap^2\,bW\,k^2\,(-1 + m)\,(-1 + mW) + bap\,k\,(-bau\,bW\,(-1 + 2\,k)\,(-1 + m)\,(-1 + mW) + bW\,m\,(-1 + mW) + Z) +$$
$$bau\,(bW\,k\,m + bau\,bW\,(-1 + k)\,k\,(-1 + m)\,(-1 + mW) - bW\,k\,m\,mW + 2\,Z - k\,Z))^2\big)\big)\big)$$

$(0, \hat{S}, \hat{W})$;

$\hat{S} =$

$$-\frac{1}{4\,(bsp - bsu)\,bW\,k\,m\,(-1 + mW)^2}$$
$$\big(-bsp\,bsu\,bW\,k + bsu^2\,bW\,k - bsp^2\,bW\,k^2 + 2\,bsp\,bsu\,bW\,k^2 - bsu^2\,bW\,k^2 + 2\,bsp\,bW\,k\,m - 2\,bsu\,bW\,k\,m + bsp\,bsu\,bW\,k\,m - bsu^2\,bW\,k\,m +$$
$$bsp^2\,bW\,k^2\,m - 2\,bsp\,bsu\,bW\,k^2\,m + bsu^2\,bW\,k^2\,m + 2\,bsp\,bsu\,bW\,k\,mW - 2\,bsu^2\,bW\,k\,mW + 2\,bsp^2\,bW\,k^2\,mW - 4\,bsp\,bsu\,bW\,k^2\,mW +$$
$$2\,bsu^2\,bW\,k^2\,mW - 4\,bsp\,bW\,k\,m\,mW + 4\,bsu\,bW\,k\,m\,mW - 2\,bsp\,bsu\,bW\,k\,m\,mW + 2\,bsu^2\,bW\,k\,m\,mW - 2\,bsp^2\,bW\,k^2\,m\,mW +$$
$$4\,bsp\,bsu\,bW\,k^2\,m\,mW - 2\,bsu^2\,bW\,k^2\,m\,mW - bsp\,bsu\,bW\,k\,mW^2 + bsu^2\,bW\,k\,mW^2 - bsp^2\,bW\,k^2\,mW^2 + 2\,bsp\,bsu\,bW\,k^2\,mW^2 -$$
$$bsu^2\,bW\,k^2\,mW^2 + 2\,bsp\,bW\,k\,m\,mW^2 - 2\,bsu\,bW\,k\,m\,mW^2 + bsp\,bsu\,bW\,k\,m\,mW^2 - bsu^2\,bW\,k\,m\,mW^2 + bsp^2\,bW\,k^2\,m\,mW^2 -$$
$$2\,bsp\,bsu\,bW\,k^2\,m\,mW^2 + bsu^2\,bW\,k^2\,m\,mW^2 - 2\,bsp\,k\,Z + 2\,bsu\,k\,Z + 2\,bsp\,k\,mW\,Z - 2\,bsu\,k\,mW\,Z +$$
$$\sqrt{\big((-1 + mW)^2}$$
$$\big(-8\,(bsu\,(-1 + k) - bsp\,k)\,(-bsp\,bW\,k\,(bsu\,(-1 + m) + 2\,m)\,(-1 + mW) + bsu\,(bsu\,bW\,k\,(-1 + m)\,(-1 + mW) + 2\,bW\,k\,m\,(-1 + mW) - 2\,Z))\,Z +$$
$$\big(bsp^2\,bW\,k^2\,(-1 + m)\,(-1 + mW) + bsu\,(2\,bW\,k\,m + bsu\,bW\,(-1 + k)\,k\,(-1 + m)\,(-1 + mW) - 2\,bW\,k\,m\,mW + 4\,Z - 2\,k\,Z) +$$
$$bsp\,k\,(-bsu\,bW\,(-1 + 2\,k)\,(-1 + m)\,(-1 + mW) + 2\,(bW\,m\,(-1 + mW) + Z)))^2\big)\big)\big)$$

$$\hat{W} =$$

$$-\frac{1}{4\,(bsu\,(-1+k)-bsp\,k)\,(-1+mW)^2}$$

$$\Big(-bsp\,bsu\,bW\,k+bsu^2\,bW\,k-bsp^2\,bW\,k^2+2\,bsp\,bsu\,bW\,k^2-bsu^2\,bW\,k^2+2\,bsp\,bW\,k\,m-2\,bsu\,bW\,k\,m+bsp\,bsu\,bW\,k\,m-bsu^2\,bW\,k\,m+$$

$$bsp^2\,bW\,k^2\,m-2\,bsp\,bsu\,bW\,k^2\,m+bsu^2\,bW\,k^2\,m+2\,bsp\,bsu\,bW\,k\,mW-2\,bsu^2\,bW\,k\,mW+2\,bsp^2\,bW\,k^2\,mW-4\,bsp\,bsu\,bW\,k^2\,mW+$$

$$2\,bsu^2\,bW\,k^2\,mW-4\,bsp\,bW\,k\,m\,mW+4\,bsu\,bW\,k\,m\,mW-2\,bsp\,bsu\,bW\,k\,m\,mW+2\,bsu^2\,bW\,k\,m\,mW-2\,bsp^2\,bW\,k^2\,m\,mW+$$

$$4\,bsp\,bsu\,bW\,k^2\,m\,mW-2\,bsu^2\,bW\,k^2\,m\,mW-bsp\,bsu\,bW\,k\,mW^2+bsu^2\,bW\,k\,mW^2-bsp^2\,bW\,k^2\,mW^2+2\,bsp\,bsu\,bW\,k^2\,mW^2-$$

$$bsu^2\,bW\,k^2\,mW^2+2\,bsp\,bW\,k\,m\,mW^2-2\,bsu\,bW\,k\,m\,mW^2+bsp\,bsu\,bW\,k\,m\,mW^2-bsu^2\,bW\,k\,m\,mW^2+bsp^2\,bW\,k^2\,m\,mW^2-$$

$$2\,bsp\,bsu\,bW\,k^2\,m\,mW^2+bsu^2\,bW\,k^2\,m\,mW^2-4\,bsu\,Z-2\,bsp\,k\,Z+2\,bsu\,k\,Z+4\,bsu\,mW\,Z+2\,bsp\,k\,mW\,Z-2\,bsu\,k\,mW\,Z+$$

$$\sqrt{\Big((-1+mW)^2}$$

$$\big(-8\,(bsu\,(-1+k)-bsp\,k)\,(-bsp\,bW\,k\,(bsu\,(-1+m)+2\,m)\,(-1+mW)+bsu\,(bsu\,bW\,k\,(-1+m)\,(-1+mW)+2\,bW\,k\,m\,(-1+mW)-2\,Z))\,Z+$$

$$\big(bsp^2\,bW\,k^2\,(-1+m)\,(-1+mW)+bsu\,(2\,bW\,k\,m+bsu\,bW\,(-1+k)\,k\,(-1+m)\,(-1+mW)-2\,bW\,k\,m\,mW+4\,Z-2\,k\,Z)+$$

$$bsp\,k\,(-bsu\,bW\,(-1+2\,k)\,(-1+m)\,(-1+mW)+2\,(bW\,m\,(-1+mW)+Z))\big)^2\big)\Big)\Big)$$

$$(\hat{A},\,\hat{S},\,\hat{W}):$$

$$\hat{A} =$$

$$-\Big(\Big(\big((bsp-bsu)^2\,bW\,(bsu+bsp\,k-bsu\,k)\,m\,(-1+mW)+$$

$$2\,bau^2\,\big(bsp^2\,bW\,(-1+k)\,(-1+m)\,(-1+mW)-bsp\,bsu\,bW\,(-1+k)\,(-1+m)\,(-1+mW)+2\,bsu\,bW\,m\,(-1+k+mW-k\,mW)+$$

$$2\,bsp\,(bW\,(-1+k)\,m\,(-1+mW)+Z)\big)+$$

$$bau\,(bsp-bsu)\,\big(-bsp\,bsu\,bW\,(-1+k)\,(-1+m)\,(-1+mW)+bsp^2\,bW\,k\,(-1+m)\,(-1+mW)+4\,bsu\,bW\,m\,(-1+k+mW-k\,mW)+$$

$$2\,bsp\,(bW\,(-1+2\,k)\,m\,(-1+mW)+Z)\big)-$$

$$bap\,(bsp-bsu)\,\big(-bsu^2\,bW\,(-1+k)\,(-1+m)\,(-1+mW)+bsp\,bsu\,bW\,k\,(-1+m)\,(-1+mW)+4\,bsp\,bW\,k\,m\,(-1+mW)+$$

$$2\,bsu\,(bW\,m\,(-1-2\,k\,(-1+mW)+mW)+Z)\big)-$$

$$2\,bap\,bau\,\big(-bsu^2\,bW\,(-1+k)\,(-1+m)\,(-1+mW)+bsp^2\,bW\,k\,(-1+m)\,(-1+mW)+bsp\,bsu\,bW\,(-1+m+mW-m\,mW)+$$

$$2\,bsp\,(bW\,(-1+2\,k)\,m\,(-1+mW)+Z)+2\,bsu\,(bW\,m\,(-1-2\,k\,(-1+mW)+mW)+Z)\big)+$$

$$2\,bap^2\,\big(bsp\,bW\,k\,(bsu\,(-1+m)+2\,m)\,(-1+mW)+bsu\,(-2\,bW\,k\,m\,(-1+mW)+bsu\,bW\,k\,(-1+m+mW-m\,mW)+2\,Z)\big)\Big)\Big/$$

$$\Big((2\,bap-2\,bau-bsp+bsu)^2\,bW\,(bsu+2\,bau\,(-1+k)+(-2\,bap+bsp)\,k-bsu\,k)\,m\,(-1+mW)\Big)\Big)$$

$$\hat{S} =$$

$$\Big(2$$

$$\Big(2\,bap^3\,bW\,k\,(bsu\,(-1+m)+2\,m)\,(-1+mW)+$$

$$bap^2\,\big(bsu^2\,bW\,(-1+k)\,(-1+m)\,(-1+mW)-4\,bsp\,bW\,k\,m\,(-1+mW)-$$

$$2\,bau\,bW\,(bsp\,k\,(-1+m)+bsu\,(-1+2\,k)\,(-1+m)+2\,(-1+3\,k)\,m)\,(-1+mW)+bsp\,bsu\,bW\,k\,(-1+m+mW-m\,mW)+$$

$$2\,bsu\,(bW\,(-1+2\,k)\,m\,(-1+mW)+Z)\big)+$$

$$bau\,\big(-2\,bau^2\,bW\,(-1+k)\,(bsp\,(-1+m)+2\,m)\,(-1+mW)-(bsp-bsu)\,(bsp\,bW\,k\,m\,(-1+mW)+bsu\,bW\,m\,(-1+k+mW-k\,mW)-bsp\,Z)+$$

$$bau\,\big(bsp\,bsu\,bW\,(-1+k)\,(-1+m)\,(-1+mW)+4\,bsu\,bW\,(-1+k)\,m\,(-1+mW)+bsp^2\,bW\,k\,(-1+m+mW-m\,mW)+$$

$$2\,bsp\,(bW\,m\,(-1-2\,k\,(-1+mW)+mW)+Z)\big)\big)+$$

$$bap\,\big(2\,bau^2\,bW\,(bsu\,(-1+k)\,(-1+m)+bsp\,(-1+2\,k)\,(-1+m)+2\,(-2+3\,k)\,m)\,(-1+mW)+$$

$$(bsp-bsu)\,(bsp\,bW\,k\,m\,(-1+mW)-bsu\,(bW\,(-1+k)\,m\,(-1+mW)+Z))+$$

$$bau\,\big(bsp^2\,bW\,k\,(-1+m)\,(-1+mW)+bsp\,(bsu\,bW\,(-1+m)\,(-1+mW)+2\,bW\,(-1+4\,k)\,m\,(-1+mW)-2\,Z)+$$

$$bsu\,(-bsu\,bW\,(-1+k)\,(-1+m)\,(-1+mW)-2\,(bW\,(-3+4\,k)\,m\,(-1+mW)+Z))\big)\big)\Big)\Big)\Big/$$

$$\Big((2\,bap-2\,bau-bsp+bsu)^2\,bW\,(bsu+2\,bau\,(-1+k)+(-2\,bap+bsp)\,k-bsu\,k)\,m\,(-1+mW)\Big)$$

$$\hat{W} =$$

$$\frac{(-2\,bau+bsu)\,Z}{(bsu+2\,bau\,(-1+k)+(-2\,bap+bsp)\,k-bsu\,k)\,(-1+mW)}$$

Figures

Figure 1: A close-up photo of *Ceratina (Neoceratina) australensis,* the Australian small carpenter bee. Credit: Marc Newman

Figure 2: The nest of an Australian small carpenter bee in a giant fennel stem.

Credit: Sandra Rehan, The Rehan Lab @ UNH

Figure 3: A species of chalcid wasps from the genus *Eurytoma.* Credit: waspweb.org

Mortality
m

Nesting Adults
$(1-m)A[t]$

Adult Bees
$A[t]$

Eggs Produced
$b_A \dfrac{A[t](1-m)}{(1+A[t]+S[t])}$

Nest are not Parasitized
$\left(1 - \dfrac{kW[t](1-m)}{Z+(1-m)W[t]}\right)$

Nest are Parasitized
$\left(\dfrac{kW[t](1-m)}{Z+(1-m)W[t]}\right)$

Unparasitized Larvae
$b_{au}\dfrac{A[t](1-m)}{(1+A[t]+S[t])}\left(1 - \dfrac{kW[t](1-m)}{Z+(1-m)W[t]}\right) +$
$b_{ap}\dfrac{A[t](1-m)}{(1+A[t]+S[t])}\left(\dfrac{kW[t](1-m)}{Z+(1-m)W[t]}\right)$

Parasitized Larvae

Wasps are Born
$(b_{au} - b_{ap})\dfrac{A[t](1-m)}{(1+A[t]+S[t])}\left(\dfrac{kW[t](1-m)}{Z+(1-m)W[t]}\right)bW$

Figure 4: The above flowchart represents the life cycle of a solitary bee population. Adult bees that survive mortality become nesting adult bees. These adults produced eggs that have a chance of being parasitized. When nests are parasitized, not all bee larvae survive. Those that do survive, give rise to bees and those who don't survive, give rise to wasps. Bee larvae from nests that are not parasitized give rise to all bees.

Mortality
m

Nesting Adults
$(1-m)S[t]$

Adult Bees
$S[t]$

Eggs Produced
$b_s \dfrac{S[t](1-m)}{2(1+A[t]+S[t])}$

Nest are not Parasitized
$\left(1 - \dfrac{kW[t](1-m)}{Z+(1-m)W[t]}\right)$

Nest are Parasitized
$\left(\dfrac{kW[t](1-m)}{Z+(1-m)W[t]}\right)$

Unparasitized Larvae
$b_{su}\dfrac{S[t](1-m)}{2(1+A[t]+S[t])}\left(1-\dfrac{kW[t](1-m)}{Z+(1-m)W[t]}\right) +$
$b_{sp}\dfrac{S[t](1-m)}{2(1+A[t]+S[t])}\left(\dfrac{kW[t](1-m)}{Z+(1-m)W[t]}\right)$

Parasitized Larvae

Wasps are Born
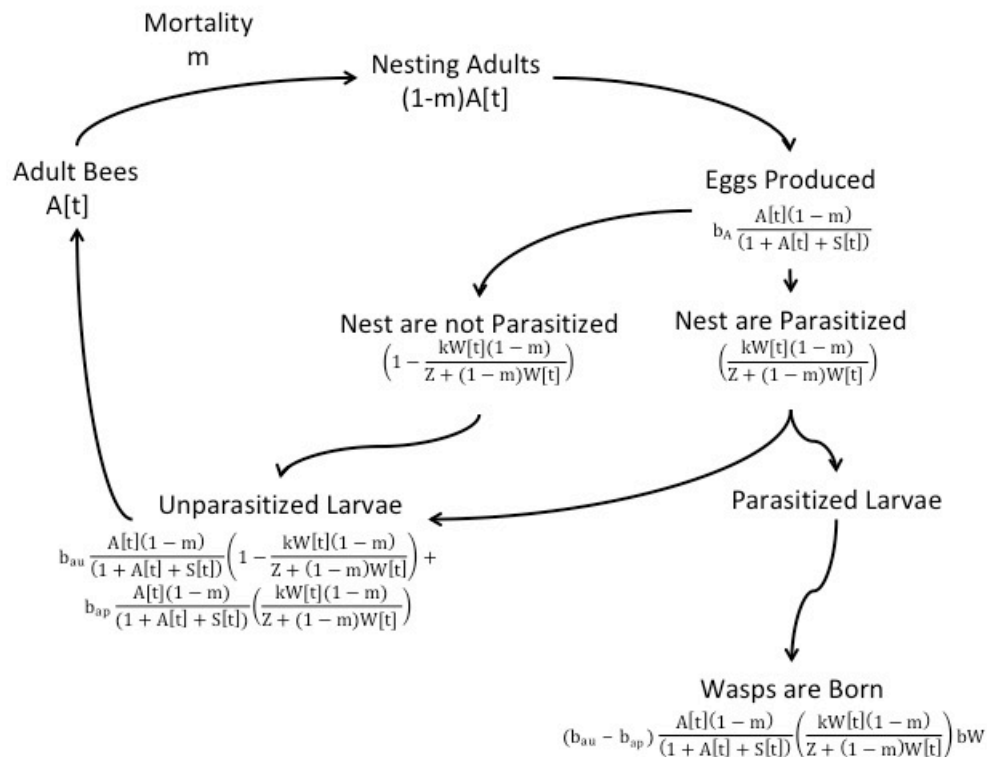$(b_{su}-b_{sp})\dfrac{S[t](1-m)}{2(1+A[t]+S[t])}\left(\dfrac{kW[t](1-m)}{Z+(1-m)W[t]}\right)bW$
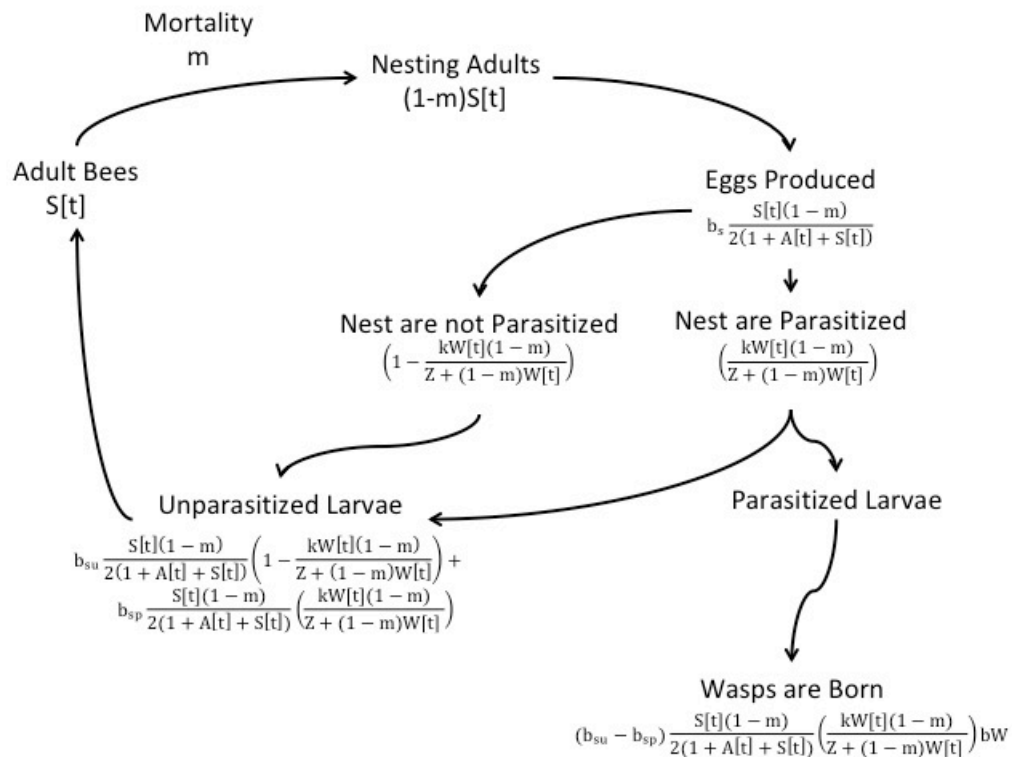
Figure 5: The above flowchart represents the life cycle of a social bee population. Adult bees that survive mortality become nesting adult bees. These adults produced eggs that have a chance of being parasitized. When nests are parasitized, not all bee larvae survive. Those that do survive, give rise to bees and those who don't survive, give rise to wasps. Bee larvae from nests that are not parasitized give rise to all bees.

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