## An integrodifference model for invasion of blowflies

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## Outline

(1) The System and the Model
(2) Dynamics
(3) Parameterization and conclusions

## Chrysomya albiceps invasion

- In the 1970's, Chrysomya albiceps, along with other blowfly species, was introduced in South America.
- In the subsequent years, it proceeded to invade most of South America, and had a strong impact on native species.



## Life cycle

- Life cycle: adults $\rightarrow$ eggs $\rightarrow$ larvae.
- Adults have short life span (usually less than 2 weeks).
- Females oviposit around 1 week after emergence, and at most two times.
- Larvae feed upon carrion and grow until emerging into an adult.


## Prout Model

- Population is limited by larval competition for carrion.
- Not only survival, but also fecundity of the adult, are strongly affected by density at larval stage.
- Cannibalism in the larval stage also plays a role.
- Prout introduced this two-stage discrete-time model for larvae (v) and adults density (u) (Prout 1985):

$$
\begin{aligned}
u_{t} & =S^{*} v_{t} e^{-s v_{t}} \\
v_{t+\Delta t} & =\frac{1}{2} F^{*} u_{t} e^{-f v_{t}}
\end{aligned}
$$

- $S^{*}$ and $F^{*}$ are maximum survival and fecundity in abundant meat, while $f$ and $s$ are density-dependent parameters.
- $\Delta t$ is the generational time, comprising egg to emergence plus the time until female oviposition (egg-to-egg time).


## Ricker equation

- We can rewrite the system as a single equation for larvae only, yielding:

$$
v_{t+\Delta t}=\frac{1}{2} S^{*} F^{*} v_{t} e^{-(s+f) v_{t}}
$$

- This is the well-known Ricker equation (Ricker 1954).
- Parameters are as before. It's important to notice that all of them can be directly measured in laboratory.


## Spread in discrete time evolution

- In order to introduce spatial dynamics, we employ a redistribution kernel $K(\delta)$ (Kot 1992).
- It can be thought of as the probability of an individual at $x$ to be at $x+\delta$ after the dispersal stage. So the equation for a population which only spreads is

$$
u_{t+\Delta t}(x)=\int_{-\infty}^{+\infty} u_{t}(x+\delta) K(\delta) d \delta
$$

- To conserve the total population, $K$ has to be normalized, i.e., $\int_{-\infty}^{\infty} K=1$.


## Spread in discrete time evolution <br> Brownian movement

- We assume a simple Brownian motion for the movement of flies.
- This leads to a Gaussian redistribution kernel:

$$
K(\delta)=\frac{1}{\sigma \sqrt{\pi}} e^{-\delta^{2} / \sigma^{2}}
$$

- Here $\sigma$ is the key parameter that measures the distance of spread in one generation.
- Adults can be thought of as agents of spread only, and the spread distance is, in fact, how far they lay eggs.


## The model

- Plugging the Ricker equation discussed earlier into the dispersal equation, we arrive at

$$
v_{t+1}(x)=\frac{F^{*} S^{*}}{2 \sigma \sqrt{\pi}} \int_{-\infty}^{+\infty} v_{t}(x+\delta) e^{-(s+f) v_{t}(x+\delta)} e^{-\delta^{2} / \sigma^{2}} d \delta
$$

- Next, we will discuss the dynamical behavior implied by this model.


## Complex spatio-temporal dynamics





Figure: Population density evolution, with $F^{*} S^{*}=57, s+f=0.5$ and $\sigma=0.1$, starting from a small, localized initial condition.

- The (non-spatial) Ricker equation, is known to present a bifurcation route (period-doubling) to chaos.
- With space dynamics included, we see a complex behavior of solutions, which oscillate irregularly in both space and time.
- Although mathematically exciting, this is not observable in field measurements due to the coarse-grained nature of the data.


## Invasion front: constant velocity

- We are interested in the study of a process of invasion.
- The solution defines a front of invasion, separating a region without blowflies, and another with them.
- After a few generations, the front attains a constant velocity.
- We analyse the dependence of the velocity on the parameters.


Figure: Successive population densities showing the front of invasion.

## Dependence on $F^{*} S^{*}$



- The velocity $c$ increases with the linear coefficient of the growth function.
- It can be shown that $c \propto \sqrt{F^{*} S^{*}}$.
Figure: Propagation speed as a function of the parameter's product $F^{*} S^{*}$. Here $\sigma=0.1$ and $s+f=0.5$.


## Dependence on $\sigma$ and $f+s$

- Since the only spatial scale is defined by $\sigma$, it's to be expected that the velocity is proportional to it. That's indeed the case.
- By taking $f$ and $s$ constant, we are assuming a homogeneous medium.
- This assumption can only be valid at large scales - of hundreds of kilometers.
- But these parameters have no impact on the velocity of invasion.


## Physiological data

- The fertility and survival data were taken from the literature (Godoy et. al. 2001).
- Larval development time is dependent on temperature. We considered average temperatures in the region ranging from 17 to $25^{\circ} \mathrm{C}$. The time until oviposition ranges from 5 to 10 days, giving a total egg-to-egg time between 15 and 35 days (Al-Misned et. al. 2002).
- The ranges of parameters are summarized below.

$$
\begin{array}{cc}
F^{*} & 150-300 \\
\hline S^{*} & 0.4-0.6 \\
\hline \Delta t & 15-35 \text { days }
\end{array}
$$

## Capture-recapture experiment

- Capture-recapture experiment was performed in 1982 in a national park in South Africa (Braack 1986).
- 16,000 radioactively marked flies were released from a central point, and recaptured 5 to 7 days later in traps distributed through the park.
- $0.82 \%$ were recaptured.


Figure: Map of the northern Kruger National Park to show Central Release Point of radioactive flies and positions of traps for subsequent recapture of blowflies.
Reproduced from (Braack 1986).

## Capture-recapture experiment



Figure: Least squares fit of one-generation dispersal data.

- We reworked published data, to compensate for measure effort.
- For each range of distance, we calculate number of recaptures / (Area $\times$ number of traps).
- Then we fit a Gaussian to the (mirrored) histogram. We obtain a value for $\sigma$ between $7-14 k m$.


## A prediction for velocity

We have completely parameterized the model, and are able to calculate a "prediction" for the invasion velocity.

With the ranges of parameters taken into account, this yields a velocity of $1.2 \mathrm{~km} /$ day $\pm 0.9$.

## Observed data in South America invasion

- Historical observations (Baumgartnet and Greenberg 1984) allow us to determine roughly the date of arrival of Chrysomya albiceps at several locations. This provides an approximate observed velocity for the invasion front.

The velocity observed was of $1.5-1.8 \mathrm{~km} /$ day .

So, we have a reasonable agreement with the expected velocity from the model.

## Summary

- We build a model for blowfly invasion.
- This model is parameterized with laboratory and field data.
- We compare the invasion velocity so predicted with observational data, and obtain good agreement.

It's feasible to get realistic predictions using data from lab experiments, as long as one takes into account the variability that may exist in the population.

# Thanks for your attention! 

## References I

If Prout，T．，McChesney，F．，The American Naturalist，126，521－558，（1985）
Ricker，W．E．，Journal of the Fisheries Research Board，11：559－623 （1954）
國 Kot，M．，J．Math．Biol．30：413－436（1992）
䍰 Godoy，W．A．C．Von Zuben，F．J．，Von Zuben，C．J．，dos Reis，S．F．Mem． Inst．Oswaldo Cruz，96（5），627－634（2001）
國 Fahad A．M．AI－Misned，Mikky A．Amoudi and Salah．S．M．Abou－Fannah， J．King Saud Univ．，15，9－58（2002）
R Braack，L．E．O，Retief，P．F．，Onderstepoort J．Vet．Res．，53，13－18（1986）
國 Baumgartner，D．L．，Greenberg，B．，Journal of Medical Entomology，21，1， 105－113（1984）

