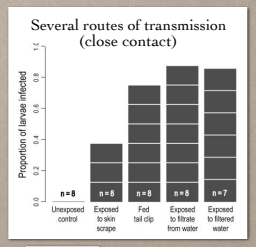
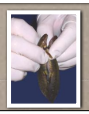
RANAVIRUSES ARE EASILY TRANSMITTED

- via water & fomites (given a high enough dose)
- direct contacts (even a single contact is sufficient)
- cannibalism, scavenging and necrophagy

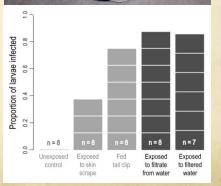
➡ Dose of inoculum seems to be the key





Routes of transmission: *via water*

- Essentially every dose-response study with ranavirus
  - BIV Cullen et al. 1995, Cullen & Owens 2002
  - ATV Brunner et al. 2005
  - FV3 Pearman et al. 2004, Hoverman et al. 2010, Warne et al. 2011
  - RUK Cunningham et al. 2007
  - LMBV Grant et al. 2003
- Small particles (filtered water) and chunky bits (filtrate) are both very infectious (Brunner et al. 2007)



Brunner et al. 2007

Routes of transmission: *via water*

Harp & Petranka (2006) added water (~2L) and pond substrate (~0.3kg) from ponds undergoing die-offs to kiddie pools with wood frog tadpoles

TABLE 1. Results of polymerase chain reaction assays for ranavirus detection in surviving wood frog tadpoles from Experiment 3.[a]

Experimental treatment			
Sediment	Water	No. of samples (% positive)	Pools (% positive)
Exposed	Unexposed	11 (45%)	83%
Exposed	Exposed	9 (44%)	67%
Unexposed	Unexposed	6 (0%)	0%
Unexposed	Exposed	6 (0%)	0%

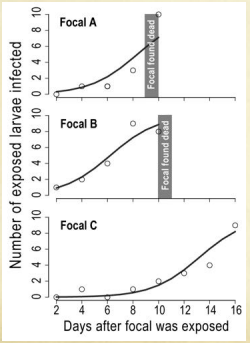
[a] Treatments reflect all combinations of exposed or unexposed sediment and water. Exposed samples were collected during an active ranavirus outbreak and unexposed samples from a pond without ranavirus. Data represent the number of samples analyzed, the percentage of samples that were positive (in parentheses), and the percentage of pools (n=6 per treatment) that were positive for ranavirus. Each sample reflects a pooled analysis of five tadpoles, and from one to three samples (5–15 tadpoles) were analyzed per pool.

Routes of transmission: *direct contact*

- ATV: one second, belly-to-belly contact caused infection in 18/21 *Ambystoma tigrinum* larvae (Brunner et al. 2007)
- BIV: 5/8 *Limnodynastes terraereginae* metamorphs co-housed with IP-injected frogs were infected (Cullen et al. 1995)*

*but not *L. caerulea* or *Cophixalus ornatus* adults (Cullen & Owen 2002)

Routes of transmission: *direct contact*



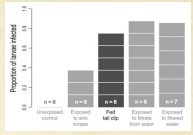
Brunner et al. 2007

- Infected *A. tigrinum* larvae become more infectious through time
- Carcasses are very infectious

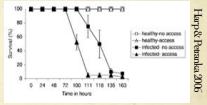
Routes of transmission: *consumption*

- Bits & pieces (nipping, biting)
  - Fed tail clips form ATV-exposed larvae (Brunner et al. 2005)
  - Orally inoculated 3 anuran spp with FV3 (Hoverman et al. 2010)
- Cannibalism

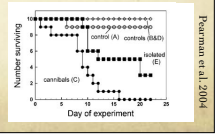
- Necrophagy/scavenging
  - Tadpoles with access to FV3-infected carcasses get sick and die faster (Harp & Petranka 2006, Pearman et al. 2004)



Brunner et al. 2007



Harp & Petranka 2006



Pearman et al. 2004

Routes of transmission: *vertical*

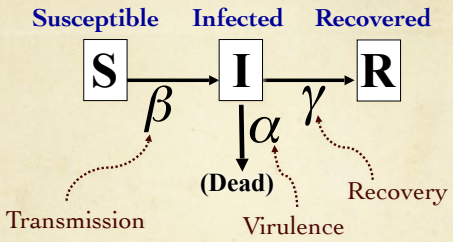
- 60% of wood frog tadpoles raised from eggs in lab "weakly positive" for FV3-like virus (Greer et al. 2005)
- FV3-contaminated wood frog eggs: 4/5 field-collected & 1/3 laid in captivity (Duffus et al. 2008)
  - Only 1/59 tadpoles tested from these four clutches was positive by PCR

Contamination or true vertical transmission?

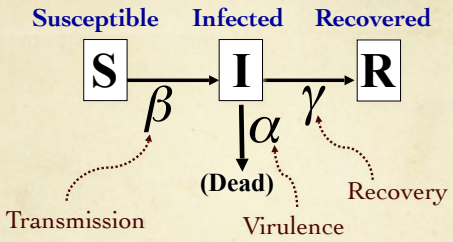
Vertical transmission is rare

unimportant for epidemic dynamics

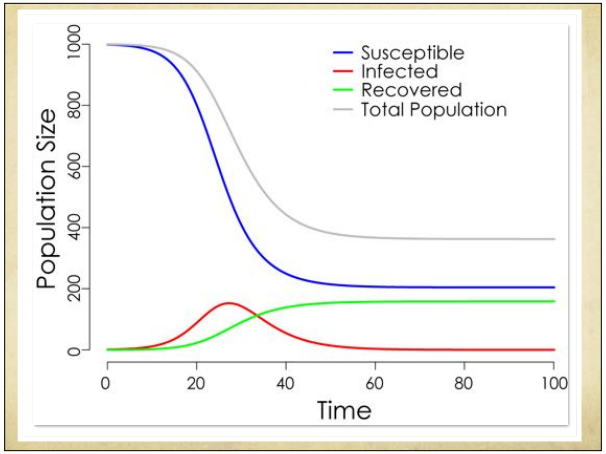
potentially important for year-to-year persistence



- Central to understanding dynamics of disease
- Used to predict the spread and impact of disease, and the efficacy of control strategies

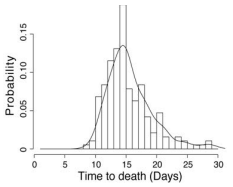


- Relate mechanisms and patterns
- Scale individual-level processes to the populations and landscapes



Ranavirus virulence & recovery

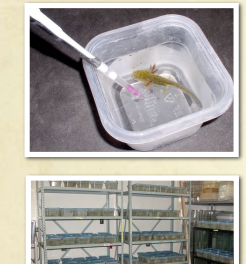
Generally lethal within about 2-3 weeks



- Survivors often chronically infected
- No immunity

Brunner et al. 2004, 2007

Ranavirus virulence & recovery



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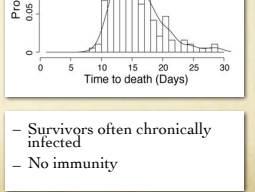

- Survivors often chronically infected
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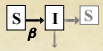
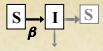
Brunner et al. 2004, 2007

Unpacking the transmission term



$$contacts \times (I/N) \times P(\text{inf} \mid contact) \times S$$

Unpacking the transmission term



$$contacts \times (I/N) \times P(\text{inf} \mid contact) \times S$$

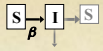
Contact rate increases with density

$$cN \times (I/N) \times P(\text{inf} \mid contact) \times S$$
$$c \times P(\text{inf} \mid contact) \times I \times S$$
$$\beta \times I \times S$$

Contact rate is constant (density-independent)

$$c \times (I/N) \times P(\text{inf} \mid contact) \times S$$
$$c \times P(\text{inf} \mid contact) \times (I/N) \times S$$
$$\beta \times (I/N) \times S$$

Unpacking the transmission term



$$contacts \times (I/N) \times P(\text{inf} \mid contact) \times S$$

Contact rate increases with density

$$\beta IS$$

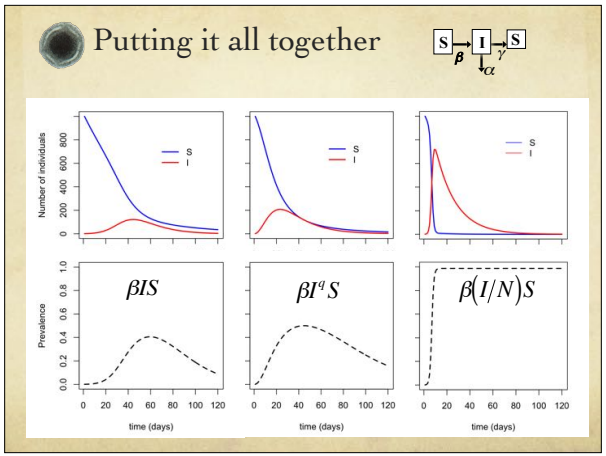
- Disease fades out before host goes extinct
- Culling is an effective control measure

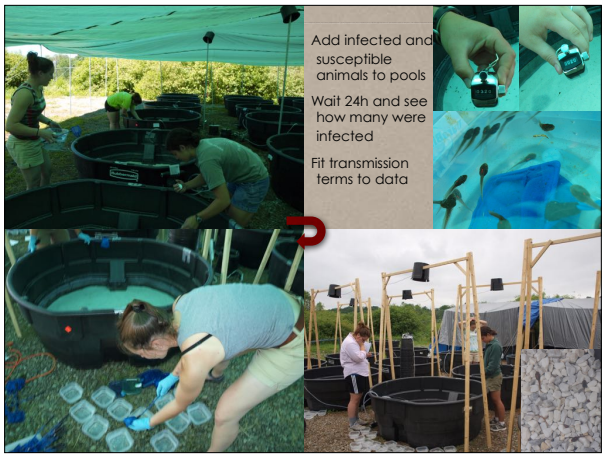
Contact rate is constant (density-independent)

$$\beta(I/N)S$$

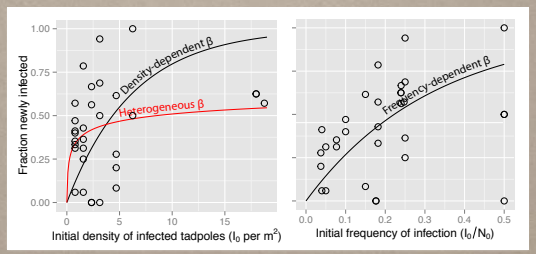
- Transmission continues as host goes extinct
- Culling will not control disease

Putting it all together





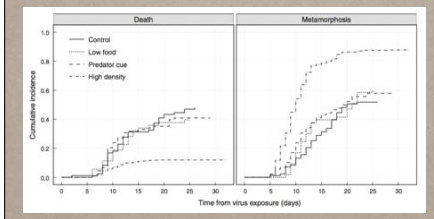
TRANSMISSION IS RAPID

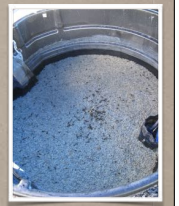


$$\frac{dI}{dt} = \beta IS \qquad \frac{dI}{dt} = \beta\left(\frac{I}{N}\right)S$$

$$\frac{dI}{dt} = k\ln\left(1+\frac{\bar{\beta}I}{k}\right)S$$

EPIDEMICS ARE RAPID

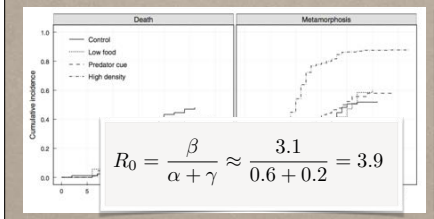




Virtually every individual was infected
But many metamorphosed (rather than died)

Reeve, B. C., E. J. Crespi, C. M. Whipps, and J. L. Brunner. 2013. Natural stressors and ranavirus susceptibility in larval wood frogs (*Rana sylvatica*). EcoHealth 10:190-200.

EPIDEMICS ARE RAPID



$$R_0 = \frac{\beta}{\alpha + \gamma} \approx \frac{3.1}{0.6 + 0.2} = 3.9$$

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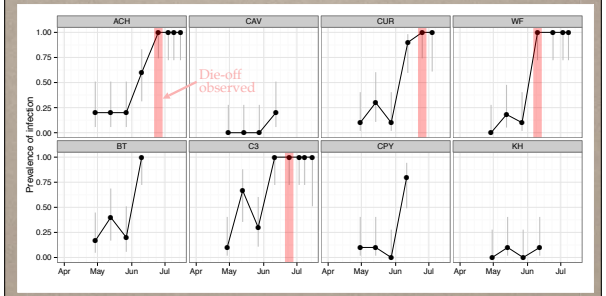
RANAVIRUS EPIDEMIOLOGY & STRESS AT YALE MEYERS FOREST

RANAVIRUS & STRESSORS



RV infection uncoupled from mortality

RV prevalence increases prior to mortality event

Transmission summary

Routes of transmission

1) Most transmission occurs by "close contact"
2) Build up of virus in the environment, particularly substrate, may increase transmission
3) Cannibalism & Necrophagy/ Scavenging are probably very important

Form of transmission

1) Frequency-dependent (over most host densities)
2) Dose-dependent transmission from the environment is like density-dependent transmission
3) Transmission via scavenging is an added term (keep track of carcasses) and should lead to accelerating epidemics