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22 May – 2 June 2008, Leipzig & Bad Schandau (Germany)

Talk 5:
Quantifying the consequences of reproductive asynchrony in natural populations

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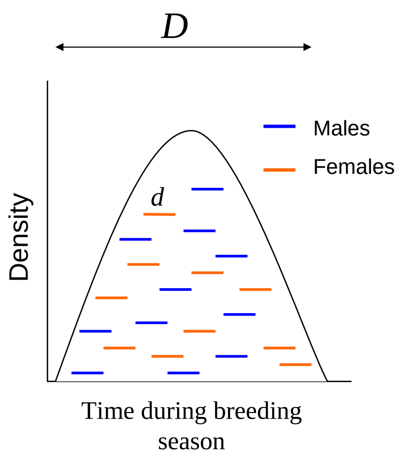
Reproductive Asynchrony

Common in diverse taxa in seasonal environments

Long population-level breeding period (*D*)

Short(er) individual-level breeding period (*d*)



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Contrasting selection pressures

Advantage:

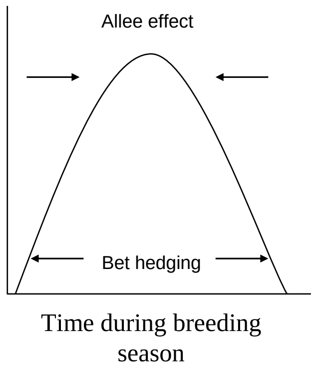
Asyn. can be a bet-hedging strategy in unpredictable environments

- -Growing seasons of variable length
- -Inter-year differences in optimal times for reproduction

Disadvantage: (Calabrese & Fagan 2004)

Reduced temporal overlap of potential mates can lead to female reproductive failure

- -Pop. growth rate decreases at low densities
- -Pop. can crash if Allee threshold crossed



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Magnitude of negative effects unknown in nature

C&F approach not easy to connect to data

- -Restrictive assumptions about reproductive biol.
- -Model not designed to be fit to data

Goals:

Develop a modeling framework that remedies above limitations

Use it to quantify % of females that fail to mate (q^*) in natural *Parnassius* butterfly populations

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Characteristics of an appropriate approach

Males and females modeled separately
- -Likely to have diff. reproductive timing strategies and be characterized by diff. parameters

Avg. individual lifespan shorter than pop.-level reproductive period
- -Definition of asynchrony

Females not guaranteed to mate before dying
- -Goal is to quantify proportion that fail to mate

Can be readily fit to data (preferably using maximum likelihood)

Flexible mating biology assumptions
- -Accommodate a range of species
- -Use model selection to learn about mating biol.

Build on the Zonneveld model

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Female and male densities

$$\frac{dF}{dt} = F_0 g(t, \theta_f) - \alpha_f F \qquad \frac{dM}{dt} = M_0 g(t, \theta_m) - \alpha_m M$$

Emergence function

$$g(t, \theta) = \frac{\lambda}{\Gamma(\mu)} (\lambda t)^{\mu - 1} Exp(-\lambda t)$$

Zonneveld 1991; 1992; 1996a, b; Zonneveld & Metz 1991

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Build on the Zonneveld model

Unmated female density

$$\frac{dU}{dt} = F_0 g(t, \theta_f) - c(\bullet)MU - \alpha_f U$$

Cumulative mated female density

$$\frac{dR}{dt} = c(\bullet)MU$$

Proportion of unmated females

$$q(t) = 1 - \frac{R(t)}{F_0}$$

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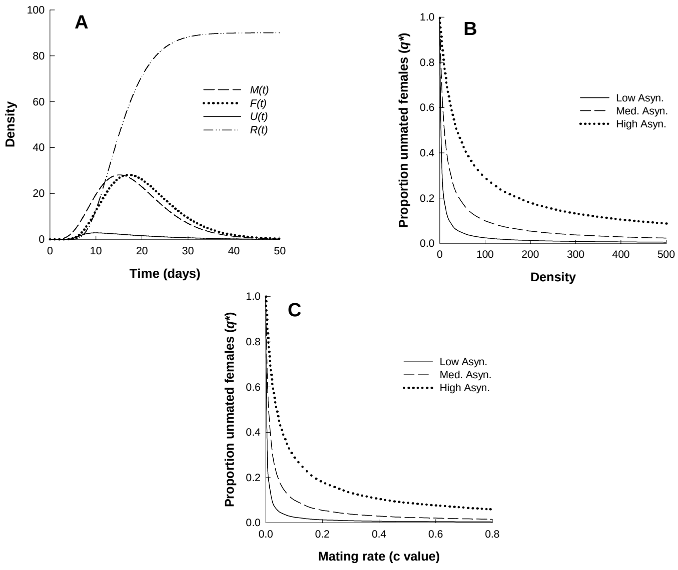
Model behavior



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Species-specific mating biology

Framework must allow for species-specific mating factors

These factors may affect (lower) q^* by inc. mating efficiency when mates are rare

Define time-dependant variables on which mating efficiency may hinge

Incorporate these vars. into mating factor sub-models and fit each to data

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Mating factor sub-models

Model No.	Model Name	Functional Form	No. Fitted Parameters
1	Constant	$c = w$	1
2	Male Age	$c(t,w) = w\bar{a}_m(t)$	1
3	Power Male Age	$c(t,w,y) = w(\bar{a}_m(t))^y$	2
4	Inv. Male Age	$c(t,w) = \frac{w}{1+\bar{a}_m(t)}$	1
5	Inv. Power Male Age	$c(t,w,y) = \frac{w}{(1+\bar{a}_m(t))^y}$	2
6	Male Size	$c(t,w) = wb(t)$	1
7	Power Male Size	$c(t,w,y) = w(b(t))^y$	2
8	Inv. Male Density	$c(t,w) = \frac{w}{(1+M(t))}$	1
9	Inv. Power Male Density	$c(t,w,y) = \frac{w}{(1+M(t))^y}$	2
10	Female Lifetime Reprod. Opportunities	$c(t,w,y) = \frac{w}{1+y\,h(t)}$	2

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Benefits of mating factor sub-model approach

1) *q** can be calculated for each sub-model

- Allows examination of the effects of alternative mating biol. assumptions

2) Likelihood/AIC-based model selection can be employed to identify most likely given data

-What part of the range of *q** values receives most support from data?

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Study species and data

Both Species:

-Discrete, non-overlapping generations
-Univoltine
-Monandrous females
-Males place sphragis (mating plug) over female abdomen

Parnassius clodius

-Studied in Grand Teton national park in Wyoming,USA (1998 – 2000)
-2000 data: 14 counts of males, mated and unmated females in one large meadow across the flight period

Parnassius smintheus

-Studied in Alberta, Canada (1995 – 2002)
-1996 data: 14 counts across flight period from several nearby small meadows

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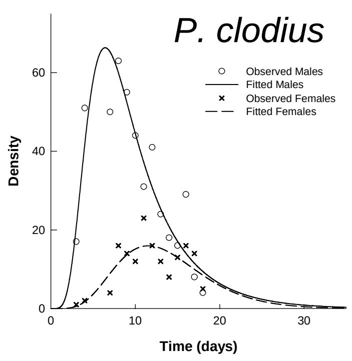
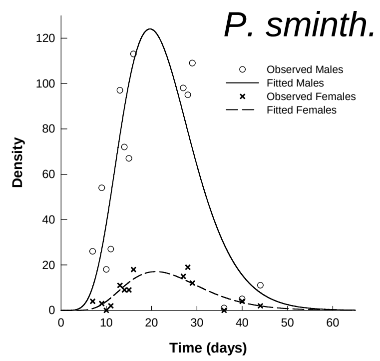
Results: Basic population parameters





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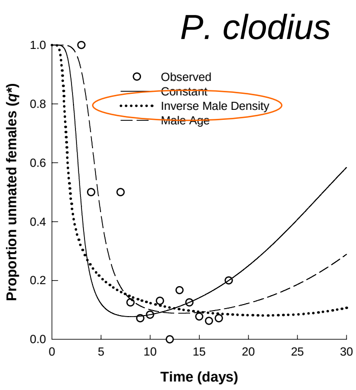
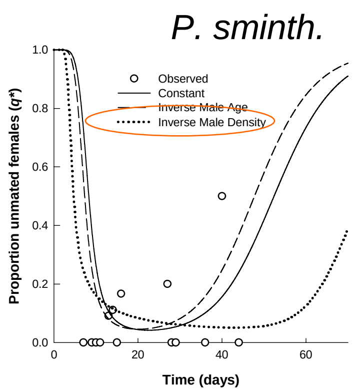
Results: Mating factor sub-models





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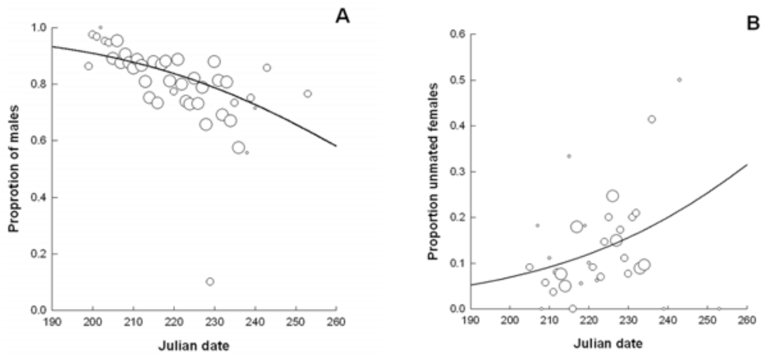
Results: Suppl. analyses for *P. sminth.*



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Results: % of females mateless (*q**)

	Asyn. (d/D)	Min.	Max.	Best-Fit	Model-Averaged
P. clodius	0.06	11.3%	18.6%	13.1%	13.8%
P. sminth.	0.08	6.5%	11.1%	8.1%	8.8%

Female mating success

Species	% Fems. Unmated	Asyn. (*d/D*)	Notes	Source
Speckled wood (*Parage aegeria*)	4% (n = 53)	0.2-0.33	Species was "quite abundant" in study area, suggesting high dens.	Wickman & Wiklund 1983
Light brown apple moth (*Epiphyas postvittana*)	13% (n=289)	N/A	Lab exp. manipulating length of fem. exposure to males	Danthanarayana & Gu 1991
Bagworm (*Matisa plana*)	6 – 18%	N/A	Fems. emerge 6d before males, fem lifespan 7d	Rhainds et al. 1999
Glanville frittilary (Melitaea cinxia)	18% (n = 147)	0.1	Low dens. Patches had higher % unmated	Kuussaari et al. 1998

Based on a summary by Kokko & Mappes 2005

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Conclusions

Data on female reproductive success should be recorded when possible!

Incorporation of alternative mating factors modulates, but doesn't eliminate neg. effects of asyn.

Male dens. sub-model supported for both spp. despite qualitative difference in datasets

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Conclusions

A large % of females in each pop. expected to die mateless

Pop. growth rates must exceed 7% (low) to 23%(high)

q^* expected to increase with decreasing density
$\Rightarrow$ Allee effect

Asynchrony may be a more important issue in sparse populations than has been recognized.

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