Mating System Evolution

Inbreeding and Outbreeding

Lecture 8: Spring 2013
Mating system = who you mate with

• Outcrossing rate = $t$

• Ranges from 0 to 1.0 where 0 is total obligate selfing and 1.0 is obligate outcrossing.
Mating system & breeding system of plants & animals

Animals:
   Mobility
   Most dioecious, but some hermaphroditic (still require mate), fission, and parthenogenetic

Plants:
   Lack mobility
   Many hermaphroditic
   selfing ----> outcrossing ----> dioecy

Breeding system = *Attributes of the flowers within an individual that may influence gamete transfer among conspecifics*
Evolution of Mating Systems

Breeding System Variation in Plants

Selfing ←----------------→ Outcrossing
**Terminology**

**Inbreeding depression** = relative performance of progeny resulting from matings between relatives versus between two unrelated individuals.

**Fitness** = the quantity and quality of progeny produced by an individual.

**Selfing or self mating** = a decline in heterozygosity by 50% each generation selfing occurs. The most extreme form of inbreeding.

**Outcrossing** or outcrossed mating = mating between unrelated individuals.
Issues in Conservation and Restoration Biology

➢ Anthropogenic:
  • Land development
  • Over exploitation
  • Species Translocations
  • Pollution

➢ Ecological:
  • Environmental fluctuations
  • Environmental catastrophes
  • Fragmentation
  • Meta-population dynamics
  • Allele and edge effects
  • Small effective number (Ne) (Lande 1997)
Issues in Conservation and Restoration Biology

Genetic:

- Maladaptive hybrids
- Selective breeding and harvesting
- Small population size
- Decreased genetic variation
- Inbreeding depression
- Fixation of new mutations

(Lande 1997)
Mating System Variation: Animals and Plants

Proportion of Species

Selfing ←------- Mixed-mating------→ Outcrossing

(Redrawn from Jarne & Auld 2006)
Evolution of Mating Systems

Ecological Advantages to Selfing:
Reproductive Assurance Hypothesis (Darwin 1876)

Genetic Advantage of Selfing:
50% Genetic Transmission Advantage (Fisher 1941)

Genetic Disadvantage of Selfing
Inbreeding Depression (Darwin 1876)
Ecological Advantages to Selfing:

- Pollination/reproductive assurance (Darwin 1876)
- If pollinators become rare
- Survival at low population densities
- Promotion of local adaptation
- Lower costs of reproduction
- Colonizing ability: long distance colonization (Baker 1955)
Evolution of selfing:

• Selfing poplns thought to be evolved from outcrossing poplns

• Selfing has evolved repeatedly in plant kingdom

• Darwin’s early observation in 1876
  “Nature abhors self-fertilization”

• A lot of theory but not a lot of empirical data on many of the hypotheses for the evolution of selfing
Reproductive Assurance

(1) Reproductive assurance (RA)

– 1st proposed by Darwin 1876

– Initially viewed as a rare event, favored by natural selection under special environmental conditions
(2) Lack of pollinators

– Darlington 1939 – autogamy arises under environmental conditions occur that prevent effective pollination by normal vectors

– Hagerup 1951 – suggested that extra moisture in Northern oceanic climates limit good weather days for flying by insects

– Barrett 1980s – tristyly found in continental Brazil but a selfing morph found on Jamaica at edge of range of *Eicchornia paniculata*
RA Hypotheses

(3) Long distance colonization (Baker’s rule 1955)

– Single propagule following long distance dispersal will succeed only if individual is autogamous thus allowing a new population to establish

– Autogamy is a characteristic of a successful colonizing species (Baker and Stebbins 1965; Stebbins 1970)
RA Hypotheses

(4) Competition for limited # of pollinator vectors among plant species

- Grant and Grant 1965
- May be more intense for SI species (Levin 1972)
- May expect a divergence in flowering phenology between two competing species for pollinator visits
(5) Local adaptation

- Selection for autogamy arises when environmental conditions allow only a narrow range of genotypes to survive or reproduce (i.e., following a bottleneck) Mather 1953;1973

- The gain in immediate fitness via an increase in local adaptation might overcompensate for the decrease in long-term fitness through a loss of genetic flexibility (Jain 1976)
Reproductive Assurance or enhancement of gamete transmission? (Lloyd 1979)

• Prior selfing - ~ to complete selfing

• Competing selfing –
  – self and outcross pollen compete for the same ovules
  – Pollen equally effective

• Delayed selfing – increase opportunity for outcrossing first, then selfing allowed if all ovules not fertilized
RA Hypotheses

(6) Restrict gene flow

- Autogamy arises as a mechanism to restrict gene flow between closely related sympatric species


- Genetic neighborhood small (Fenster 1991 a, b; Evolution)
(6) Restrict gene flow (cont.)
   – Levin 1975
     • Argued that selection for autogamy occurs whenever two taxa produce sterile hybrids and share pollinators in a mixed population
     • Reproductive isolating mechanisms – prezygotic and post zygotic
     • Cleistogamous flowers reduce gene flow since often produced underground (violets, touch me nots)
RA Hypothesis

(7) Selection might be favored on the basis of rapid fixation of favorable recessive alleles (Haldane 1932)

(8) Enhance survival at low population densities

(9) Lower cost of reproduction – shunt resources for larger flowers to other traits that might improve survival.

How many of these hypotheses can apply to animal systems?
Selfing *Mimulus micranthus*

Mixed-mating *Mimulus guttatus*

However, a recent review has noted that many plant species with specialize pollination systems also exhibit RA, since there is often more variation in pollinator service.
Reproductive assurance of specialized flowers: delayed selfing
RA Hypotheses

(10) Automatic selection hypothesis

– Fisher 1941

– Gene for autogamy spreads throughout an outcrossing population w/o significant inbreeding depression (>50%) and no pollen discounting.
Gene Contribution to the Next Generation

- Automatic selection hypothesis (Fisher 1941)
- 50% transmission advantage of selfing
- Genetic Advantage to selfing

<table>
<thead>
<tr>
<th></th>
<th>Outcross</th>
<th>Self</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maternal seed</td>
<td>0.5</td>
<td>1.0</td>
</tr>
<tr>
<td>Sired seed</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>Total</td>
<td>1.0</td>
<td>1.5</td>
</tr>
</tbody>
</table>
Why aren’t all populations selfing or inbreeding?
Gene Contribution to the Next Generation

- Cost of Outcrossing: Only contributing $\frac{1}{2}$ of your genes in both your pollen and ovules compared to another individual who can also self and have 1.5 advantage.

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<th>Outcross</th>
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</tr>
<tr>
<td>Total</td>
<td>1.0</td>
<td>1.5</td>
</tr>
</tbody>
</table>
Thus:

• If only outcross, one contributes 50% of genes in both their pollen and ovules compared to another individual who can both self and outcross, having a 1.5 advantage.

• If Inbreeding depression > 50% then outcrossing maintained

• If Inbreeding depression < 50% then selfing may evolve
Issues with respect to expression of inbreeding depression

- Population level
- Individual level
- Species level
- Role of environment on detection of inbreeding depression?
- Abiotic and biotic factors?
What factors determine whether a population can purge its genetic load?

• Genetic basis of inbreeding depression?

  Partial Dominance (Dominance) vs. Overdominance
  
  \[\begin{align*}
  &AA &Aa &aa \\
  &vs. &AA &Aa &aa
  \end{align*}\]

• Mating system?

  Outcrossing Species vs. Selfing Species

\[\textit{M. guttatus} \quad \textit{M. micranthus}\]
Evolution of Mating Systems

The relationship between mating system and the genetics of inbreeding depression

<table>
<thead>
<tr>
<th>Genetic Basis</th>
<th>Purging of Genetic Load</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominance</td>
<td>Selfer $&gt;&gt;$ Outcresser</td>
</tr>
<tr>
<td>Overdominance</td>
<td>Selfer $=$ Outcresser</td>
</tr>
</tbody>
</table>

Can one purge the genetic load from a population?
Glasshouse Inbreeding Depression Studies: Tests of Purging

1) Comparison of inbreeding depression in selfing *M. micranthus* and mixed-mating *M. guttatus*.

2) Consequences of 5 generations of serial inbreeding in *M. guttatus* across the entire lifespan.

3) Quantifying the level of dominance responsible for the expression of inbreeding depression in *M. guttatus* and *M. micranthus*.
1st Approach:

Carr and Dudash (AJB 1996)
Carr and Dudash (AJB 1996)
Relative Performance in Flower Production

2nd Approach:

Dudash et al. Evolution 1997
Genetic basis of inbreeding depression: Can genetic load be purged?

3rd Approach:

M. guttatus  M. micranthus

North Carolina 3 Breeding Design

AA  P1  Aa  F1  F2  B2

P2  aa  Aa  AA

B1

(Dudash & Carr Nature 1998)
What factors determine whether a population can purge its genetic load?

• Genetic basis of inbreeding depression?
  Partial Dominance (Dominance) :  AA  Aa  aa

• Mating system?
  Selfing Species has Lower Inbreeding Depression than Outcrossing Species

(M. guttatus  M. micranthus)

Factors that influence ability to purge

- Genetic basis of inbreeding depression (dominance vs. overdominance)
- Natural selection reduces frequency of deleterious alleles
- Effects of prior inbreeding in reducing effects of new inbreeding
- Impact of new mutations
- Role of environment in expression of inbreeding depression
Mating System Variation: Animals and Plants

Why mixed mating?

Proportion of Species

Selfing ←------- Mixed-mating------→ Outcrossing

(Lande & Schemske 1985, Redrawn from Jarne & Auld 2006)
How can mixed-mating strategies be maintained in nature?

- Balance of immediate & long-term fitness (Mather 1943)
- Ecological conditions (Stebbins 1950)
- Loss of local adaptation in a novel habitat (Ronce et al. 2009)
Plants
Selfing and subsequent inbreeding depression in Animals

~ 1/3 of all animals capable of some form of selfing ~ hermaphrodites

Inbreeding avoidance mechanisms?

Prezygotic -

Postzygotic -
Animals with Hermaphroditic phyla (Jarne & Auld 2006)

- Molluscs
- Trematodes
- Cnidarians

Hydras, anemones, jelly fish, corals
THE INBREEDING COEFFICIENT \((F)\)

The inbreeding coefficient of an individual refers to how closely related its parents are. When parents are unrelated, offspring \(F = 0\), for completely inbred individuals \(F = 1\).

Levels of inbreeding in offspring for different kinds of relationships among parents are:

<table>
<thead>
<tr>
<th>Parents</th>
<th>Offspring (F)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unrelated</td>
<td>0</td>
</tr>
<tr>
<td>Brother-sister, mother-son, or father-daughter</td>
<td>0.25</td>
</tr>
<tr>
<td>Half brother-half-sister (half sibs)</td>
<td>0.125</td>
</tr>
<tr>
<td>First-cousins</td>
<td>0.0625</td>
</tr>
<tr>
<td>Second-cousins</td>
<td>0.0156</td>
</tr>
<tr>
<td>Self-fertilization (or selfing) ~ Plants</td>
<td>0.5</td>
</tr>
</tbody>
</table>
Inbreeding depression for different components of fitness in wild species of animals with a 25% increase in inbreeding coefficient. Inbreeding depression is % reduction of inbred compared to outbred individuals.

<table>
<thead>
<tr>
<th>Species</th>
<th>Character</th>
<th>Inbreeding depression %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deer mice</td>
<td>Litter size</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>Survival to weaning</td>
<td>8</td>
</tr>
<tr>
<td>House mice (wild)</td>
<td>Litter size</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>Body wt at 53 days</td>
<td>-10</td>
</tr>
<tr>
<td></td>
<td>Nesting behaviour</td>
<td>10</td>
</tr>
<tr>
<td>Japanese quail</td>
<td>Reproduction and survival</td>
<td>64</td>
</tr>
<tr>
<td></td>
<td>Fertility</td>
<td>21</td>
</tr>
<tr>
<td></td>
<td>Survival 0-5 wks</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>Body weight</td>
<td>4</td>
</tr>
<tr>
<td>Chukar partridges</td>
<td>Reproduction and survival</td>
<td>58</td>
</tr>
<tr>
<td></td>
<td>Egg production</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>Body weight</td>
<td>1</td>
</tr>
<tr>
<td>Rainbow trout</td>
<td>Hatchability</td>
<td>-10, 9, 14</td>
</tr>
<tr>
<td></td>
<td>Fry survival</td>
<td>8, 11</td>
</tr>
<tr>
<td></td>
<td>Wt at 150 days</td>
<td>12</td>
</tr>
<tr>
<td>Zebra fish</td>
<td>Hatchability</td>
<td>89</td>
</tr>
<tr>
<td></td>
<td>Survival to 30 days</td>
<td>43</td>
</tr>
<tr>
<td></td>
<td>Length at 30 days</td>
<td>43</td>
</tr>
<tr>
<td></td>
<td>Length at 30 days</td>
<td>11</td>
</tr>
<tr>
<td>Channel catfish</td>
<td>Hatchability</td>
<td>-11</td>
</tr>
<tr>
<td></td>
<td>Body weight at 4 wks</td>
<td>43</td>
</tr>
<tr>
<td></td>
<td>Body weight at 12 wks</td>
<td>7</td>
</tr>
</tbody>
</table>
*Sabatia angularis* (Gentianaceae)

Herkogamy and Dichogamy

Male fn

Female fn
Inbreeding depression measured in three environments in *Sabatia angularis* (Gentianaceae)

The environment matters!

Dudash (Evolution 1990)
Outbreeding depression

**Definition:**
offspring from crosses between individuals from different populations have lower fitness than progeny from crosses between individuals from the same population

Opposite of inbreeding depression

Optimal outcrossing distance – Price & Waser 1979
Outbreeding depression

3 Mechanisms proposed to generate outbreeding depression:

1) Chromosomal differences
   Post zygotic vs. prezygotic isolating mechanisms

2) Adaptive differentiation among populations

3) Population bottlenecks and genetic drift
Investigations of inbreeding vs. outbreeding depression

Inbreeding depression: 4,204 publications

Outbreeding depression: 731 publications

Why are we interested in the expression of outbreeding depression?
Genetic Rescue – outcrossing to reduce effects from inbreeding

- Increases genetic diversity

- Observed subsequent fitness increases of small isolated inbred populations

- Fear of outbreeding depression is preventing genetic management of fragmented populations (Frankham et al. 2011)
Genetic rescue from crosses between different poplns:

**Mammals**
- African elephant, lion and wild dog
- Black rhinoceros
- Bighorn sheep
- Columbia Basin pygmy rabbit
- Florida panther
- Golden lion tamarin
- Mexican wolf

**Birds**
- Greater prairie chicken in Illinois
- Red-cockaded woodpecker

**Reptile**
- Swedish adder

**Plants**
- Button wrinklewort
- Lakeside daisy population in Illinois
- Marsh grass of Parnassus
- Mauna Kea silversword (Hawaii)
- Brown’s banksia
- Round leafed honeysuckle
Why is genetic rescue so important?

- What factors are contributing to the need for genetic rescue?

- Are all local populations (~demes) of a species similar?

- Examples from our readings?
Highlights

• Variability in both plant and animal mating systems
• Evolution of selfing from outcrossing
• Reproductive assurance common in nature
• Transmission bias associated with self matings
• Inbreeding depression - major force preventing evolution of selfing
• Purging of genetic load
• Inbreeding in nature and factors that influence expression of inbreeding depression
• Many species can benefit from crossing between populations with little fear of long term effects of outbreeding depression