Mating Games and Signalling

• Reading: pp 571-592, ch 23
• Signal design for mate attraction and courtship
• Searching vs signaling for mates
• Courtship control and persistence
• Mechanisms of mate choice
Mate attraction signal rules

• Signals designed to attract potential mates from a distance
  – large signal range
  – high locatability
  – high duty cycle
  – species specific
  – stereotyped (low modulation level)
  – arbitrary form-content linkage
Expect species specificity of mate attraction signal when females emit the signal since they have more to lose from a hybrid mating
Species differences in cricket calls

Species differences are encoded in temporal patterns.
Species differences in firefly flashing signals

(A) *Photuris*
- consanguines
- greeni
- macdermotti
- versicolor Florida
- ignitus
- ordens
- ranytoxus
- punctualatus
- magnellus
- pennsylvanica
- lucicrescens
- "little red"

Time (sec)
Species differences in fiddler crab and fence lizard displays

Species differences in facial patterns

Figure 18.3 Facial color patterns in African guenons. African guenons in the genus *Cercopithecus* often live in mixed species troops and use conspicuous, colorful skin spots and hair tufts as the primary species recognition mechanism. The colors used include white, black, brown, yellow, blue, and red. (After Kingdon 1988.)
Species differences in bird song

Species differences are encoded in frequency range, INI, note structure.
Sexual imprinting and sympatric speciation

**indigobirds reared by black-bellied firefinches**

- indigobird mimics black-bellied firefinch song
- indigobird imprinted on black-bellied firefinch

**mate choice**

- parasitism of novel or alternate host

**host choice**

- black-bellied firefinch
- African firefinch

**OR**

- indigobird mimics African firefinch song
- indigobird imprinted on African firefinch

Convergence in mate attraction signals

- Habitat effects
  - Bird song
    - whistles in forest, trills in open habitats
  - Lizard head bobbing
    - bob shape on ground, interbob interval for arboreal species

- Signaling sex and modality
  - Males tend to use auditory or visual signals
  - Females more likely to use chemical signals
## Courtship signal design rules

### Table 18.3 Design rules and modality-specific mechanisms for courtship signals

<table>
<thead>
<tr>
<th>Design feature</th>
<th>Rule</th>
<th>Visual mechanisms</th>
<th>Auditory mechanisms</th>
<th>Olfactory mechanisms</th>
<th>Tactile mechanisms</th>
</tr>
</thead>
<tbody>
<tr>
<td>Range</td>
<td>Short</td>
<td>Low color contrast, Subtle movement display</td>
<td>Soft unstructured sounds</td>
<td>Contact chemical, Volatile, rapid fadeout chemical</td>
<td>By definition</td>
</tr>
<tr>
<td>Locatability</td>
<td>Receiver and Nest site</td>
<td>Directed display, Pointing</td>
<td>Beam sound, Countercalling</td>
<td>Directed flow, Add visual component</td>
<td>Herding</td>
</tr>
<tr>
<td>Duty cycle</td>
<td>High for short period</td>
<td>Flashing color, High display repetition rate</td>
<td>High repetition rate</td>
<td>Contact chemical</td>
<td>Hold, High touch rate</td>
</tr>
<tr>
<td>ID level</td>
<td>Species and Sex</td>
<td>Sexual dimorphism</td>
<td>Sex-specific sound pattern</td>
<td>Sex-specific chemicals</td>
<td>Sex specific pattern</td>
</tr>
<tr>
<td>Modulation level</td>
<td>Graded</td>
<td>Display rate</td>
<td>Repetition rate</td>
<td>Poor</td>
<td>Vary pressure</td>
</tr>
<tr>
<td>Form-content linkage</td>
<td>Linked: Intentions, Parent skill, Courtship feed, Calm</td>
<td>Nesting behavior, Submissive</td>
<td>High frequency, Repertoire</td>
<td>Receptivity, Hormone manip</td>
<td>Mount, Nuptial gift, Lick genitals, Stroke</td>
</tr>
</tbody>
</table>
Form-content linkage in courtship

Male leg wave

Blackbird points to nest

Kudu chin push

Guinea pig rumba dance
Courtship can facilitate copulation synchronization
Static vs dynamic calling displays in tree frogs

Static components:
Convey information about species differences.
Females prefer mode.

Dynamic components:
Convey information about individual differences.
Females prefer extremes.
Sexual selection and signalling

- Mate attraction and courtship signalling is influenced by
  - The operational sex ratio
  - The male mating strategy
  - The relative importance of intrasexual (male-male competition) vs intersexual (female mate choice) selection
Consequences of anisogamy

- Females produce few costly, large, immobile, and well-provisioned eggs
- Males produce many small mobile sperm, and can fertilize many females
- Males compete for access to receptive females
- Sedentary males compete by sperm competition (e.g. sea urchin)
- Mobile males can either search for females, defend resources, or wait for females to encounter them (most vertebrates)
Male mating strategies

- If sedentary, compete by sperm competition
  - equip gametes for competition
  - produce many gametes
- If mobile, strategy depends on resource distribution
  - Search for and defend females
    - long-term association (monogamy or permanent harem)
    - dominance hierarchy determines access to females
    - short-term associations during receptive period
    - coercion
  - Defend resources needed by females
    - breeding or feeding sites
  - Advertise to attract females
    - display on leks
Mobility game

• Continuous asymmetric scramble with equal sex ratio
• Operational sex ratio skewed towards sex with shortest gamete + recovery time
• Each sex seeks strategy that minimizes its cycle time given partner behavior
• 2 ESS’s: male search and female signal or female search and male signal
• Male searching more common due to female costs
Mate searching patterns

Males tend to search if female location is predictable

Females tend to search when there is resource defense since males are tied to resources

Nonsearching sex emits attraction signals

Exaggerated signals are given by males due to sexual selection

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Table 23.2 Patterns of searching sex, long-distance advertising sex, and mating system in a variety of mobile animals

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Searching sex</th>
<th>Signaling sex and modality</th>
<th>Mating system</th>
</tr>
</thead>
<tbody>
<tr>
<td>Insects</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crickets, katydids, grasshoppers, cicadas</td>
<td>F</td>
<td>M/Aud</td>
<td>Burrow defense, nuptial gift or self-advertisement</td>
</tr>
<tr>
<td>Bark beetle, carrion beetle, boll weevil</td>
<td>F</td>
<td>M/Olf</td>
<td>Oviposition site defense or self-advertisement</td>
</tr>
<tr>
<td>Hawaiian Drosophila, fireflies, hill-topping and swarming species, dragonflies</td>
<td>F</td>
<td>M/Vis</td>
<td>Self-advertisement or oviposition site defense</td>
</tr>
<tr>
<td>Some bees, other nectivores, parasitoids, dung beetles</td>
<td>F</td>
<td>none</td>
<td>Defense of food sites, males grab females</td>
</tr>
<tr>
<td>Most moths</td>
<td>M</td>
<td>F/Olf</td>
<td>Female defense</td>
</tr>
<tr>
<td>Many Hymenoptera, Diptera, some butterflies, scarab beetle</td>
<td>M</td>
<td>none</td>
<td>Males wait at female emergence site</td>
</tr>
<tr>
<td>Many butterflies, solitary bees</td>
<td>M</td>
<td>F/Vis</td>
<td>Female defense, male patrolling</td>
</tr>
<tr>
<td>Fish</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reptiles and Amphibians</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Urodeles</td>
<td>M</td>
<td>F/Vis</td>
<td>Female defense</td>
</tr>
<tr>
<td>Anurans</td>
<td>F</td>
<td>M/Aud</td>
<td>Oviposition site defense or self-advertisement</td>
</tr>
<tr>
<td>Lizards</td>
<td>M</td>
<td>F/Vis</td>
<td>Resource defense</td>
</tr>
<tr>
<td>Geckos</td>
<td>F</td>
<td>M/Aud</td>
<td>Resource defense</td>
</tr>
<tr>
<td>Snakes</td>
<td>M</td>
<td>F/Olf</td>
<td>Female defense</td>
</tr>
<tr>
<td>Birds</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Most songbirds, many nonpasserines</td>
<td>F</td>
<td>M/Aud + Vis</td>
<td>Resource defense or self-advertisement</td>
</tr>
<tr>
<td>Ducks, geese</td>
<td>M</td>
<td>M/Vis</td>
<td>Female defense</td>
</tr>
<tr>
<td>Some corvids, quail</td>
<td>M</td>
<td>F/Aud</td>
<td>Female defense</td>
</tr>
<tr>
<td>Mammals</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Most primates</td>
<td>M</td>
<td>F/Olf + Vis</td>
<td>Female defense</td>
</tr>
<tr>
<td>Chimpanzee, gorilla</td>
<td>F</td>
<td>M/Aud</td>
<td>Resource defense</td>
</tr>
<tr>
<td>Most rodents</td>
<td>M</td>
<td>F/Olf</td>
<td>Female defense</td>
</tr>
<tr>
<td>Pika, house mouse, white-lined bat</td>
<td>F</td>
<td>M/Aud + Olf</td>
<td>Resource defense</td>
</tr>
<tr>
<td>Horses</td>
<td>M</td>
<td>F/Olf</td>
<td>Female defense</td>
</tr>
<tr>
<td>Most ungulates</td>
<td>F</td>
<td>M/Vis + Olf</td>
<td>Resource defense</td>
</tr>
</tbody>
</table>

Note: Aud = auditory; Olf = olfactory; Vis = visual.
Courtship duration patterns

- Females control courtship in male resource defense and self-advertisement systems
  - courtship prolonged, involves many male displays
  - e.g. most birds, lekking and paternal care species
- Females also control courtship in predatory species
  - Male signals often submissive
  - e.g. spiders, preying mantis, lions
- Males control courtship in female defense systems
  - courtship is often short or absent, or may be aggressive and violent in male dominance systems
  - some insect males mate with females before eclosion
  - some bats mate while females hibernate
  - some sea slugs use “love darts”- hypodermic penises
Mechanisms of mate choice

• Direct benefits (choice influences mate fecundity or survival)

• Indirect benefits (genes passed to offspring)
  – Fisher’s process - predicts arbitrary traits
  – Good genes - predicts traits indicate genetic quality
    • Condition dependent indicator traits
    • Revealing indicator traits
Direct benefits of assortative mating in Australian frogs

Figure 23.11 Benefits of female preference for call frequency. In the Australian frog *Litoria naevosa*...
Fisher’s runaway process

• If
  – a female exhibits preference for a male trait, and
  – there is no cost to females to express this preference

• Then
  – both sons and daughters of this female will carry genes for both the preference and the trait
  – This creates a genetic correlation between preference and trait

• This correlation between preference and trait
  – leads to a “runaway” increase in the male trait until
  – further increase in the male trait is opposed by natural selection

• Predicts extravagant, arbitrary traits
Arbitrary traits in birds-of-paradise?
Population variation in bowers

- Am. inornatus (Fak fak)
- Am. inornatus (Arfak)
- Archboldia
- Am. macgregoriae
- Prionodura
- Am. sublaris
- Scenopoeetes
- Sericus
- Ptilonorhynchus (satin bowerbird)
- C. maculata
- C. lauterbachii
- C. cerviniventris
- C. nuchalis
- Ai. melanotis
- Ai. crassirostris
- Menura (superb lyrebird)

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Good genes models for female choice

- Females do not get direct benefits from males
- Females choose males with best overall genetic quality in order to maximize offspring viability
- Predicts mating signals that depend on male condition and thereby indicate male quality
  - Assumes that male quality is heritable
Condition dependent trait

Only males in good condition can make a large investment in a trait which then has less affect on their survival.
Barn swallow tail length indicates parasite resistance

Females prefer long tails

Long tails are costly

Parasites influence tail length

Resistance correlates with paternal tail length

But, males do provide parental care and tails may improve flight

Effect of spot removal on mate success

Do peacock trains indicate male quality?

PETRIE M 1991 PEAHENS PREFER PEACOCKS WITH ELABORATE TRAINS ANIMAL BEHAVIOUR 41: 323-331.


Effect of spots on offspring survival

Ornaments and good genes. Peacocks with more eyespots on their tails produced offspring that survived better when released from captivity into an English woodland park. Source: Petrie [924].
Female preference for repertoire size in *Acrocephalus* warblers

(A) Response to playbacks  (B) Offspring recruitment

Repertoire size may reveal condition during early development when males learn songs
Good genes and female choice

• But, meta-analysis revealed that only 1.5% of the variation in viability is explained by preferred male traits (Moller & Alatalo 1999)

• Sexual selection can accelerate loss of deleterious mutations, according to theory (Whitlock 2009) and data (Hollis and Houle 2009)

• More studies are needed that link mate choice to known genetic variation in viability

Post-copulation calls

• Unique vocalizations given by males and/or females
• Function is unclear, several hypotheses exist:
  – Orgasm synchrony (humans and gibbons)
  – Subordinate females may use them to increase rank by soliciting future support from male (baboons)
  – Recruit additional mates and elicit male-male competition in elephant seals
  – Honest advertisement of male quality in rhesus monkeys since calling males are often attacked
  – Advertise mate guarding (male rat ultrasound)
Sex-role reversal