Sexual selection, breeding systems and sexual conflict

András Kosztolányi

Department of Ecology
University of Veterinary Medicine Budapest

Eötvös Loránd University, 13th November 2018
Outline

• Anisogamy and sexual selection

• Breeding systems
  • mating systems
  • parental care systems

• Conflict over parental care
  • case studies in the Kentish plover
Short CV

- **1990-1996:** Biology MSc, Eötvös University
- **1996-1999:** PhD student, University of Debrecen
- **2002-2004:** University of Debrecen
- **2004-2007:** University of Bath
- **2007-2012:** Department of Etology, Eötvös University
  Magyary Zoltán post-doc and OTKA grants
- **2012-2014:** University of Debrecen
  MTA-DE „Lendület” Behavioural Ecology Research Group
- **2014-** Szent István University
  (2016- University of Veterinary Medicine Budapest)
Short CV

- **1990-1996**: Biology MSc, Eötvös University
- **1996-1999**: PhD student, University of Debrecen
- **2002-2004**: University of Debrecen
- **2004-2007**: University of Bath
- **2007-2012**: Department of Etology, Eötvös University  
  Magyary Zoltán post-doc and OTKA grants
- **2012-2014**: University of Debrecen  
  MTA-DE „Lendület” Behavioural Ecology Research Group
- **2014-**: Szent István University  
  (2016- University of Veterinary Medicine Budapest)
Main interest

• Evolution of breeding systems and parental care
• Cooperation and conflict over care between parents

• Model systems:
  • Shorebirds, Kentish plover (1996 –)
  • Biparental Geotrupidae beetle (2012 –)
Anisogamy and sexual selection
Anisogamy → sexual conflict

- Bateman (1948)
  - **males**: more mates → higher reproductive success → *to mate with as many female as it can*
  - **females**: more mates → reproductive success does not increase → *to find the best quality male*

- *Males and females have a antagonistic view about mating rates*
Anisogamy → sexual conflict

- **Antagonistic view of males and females about mating rates**

<table>
<thead>
<tr>
<th>Species</th>
<th>Maximum number of offspring produced during lifetime</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elephant seal</td>
<td>Male: 100</td>
</tr>
<tr>
<td></td>
<td>Female: 8</td>
</tr>
<tr>
<td>Red deer</td>
<td>Male: 24</td>
</tr>
<tr>
<td></td>
<td>Female: 14</td>
</tr>
<tr>
<td>Man</td>
<td>Male: 888</td>
</tr>
<tr>
<td></td>
<td>Female: 69</td>
</tr>
<tr>
<td>Kittiwake gull</td>
<td>Male: 26</td>
</tr>
<tr>
<td></td>
<td>Female: 28</td>
</tr>
</tbody>
</table>

The data for man came from the Guinness Book of Records: the male was Moulay Ismail the Bloodthirsty, Emperor of Morocco, the woman had her children in 27 pregnancies. The data for elephant seals are from Le Boeuf and Reiter (1988), for red deer from Clutton-Brock et al. (1982). In the monogamous kittiwake, where male and female invest similarly in each offspring, the difference in maximum reproductive output is negligible (Clutton-Brock, 1983).
Anisogamy → sexual selection

- The main reasons for sexual selection
  - anisogamy
  - 1:1 sex ratio is ESS (Fisher 1930)

- **Sexual selection**: traits advantageous *in competition for mates*
  - intrasexual selection (competition *within* a sex for mates)
  - intersexual selection (competition *within* a sex for the preference of the other sex)

- Sexually selected traits (large weapons or elaborate ornaments) may decrease survival → *net benefit should be positive*
Intrasexual selection

- **Before copulation**
  - competition (larger, stronger, more aggressive wins)
  - mate guarding
- **After copulation**
  - sperm removal
  - sperm competition
  - mate guarding, copulatory plugs
  - induced abortion, infanticide
Intersexual selection

- **Before copulation**
  - mate choice (traits, ornaments that the females “like”)

- **After copulation**
  - cryptic female choice

Feral fowl (Pizzari & Birkhead 2000)

Field cricket (Tregenza & Wedell 2002)
Why do females choose?

- **Direct (non-genetic) benefits**
  - access to resources, e.g. food
  - nuptial gifts

- **Genetic benefits**
  - Female “gains” only sperm
  - Theories:
    - sexy son/runaway selection/fisher’s hypothesis
      - positive feedback between trait and preference
      - female’s son will be also preferred
      - empirical evidence is scarce
    - Good gene/handicap hypothesis
      - only good quality males can afford condition dependent ornaments
Breeding systems

- Breeding system (Reynolds, 1996)
  - **Mating system**: number of mates for females and males
  - **Parental care system**: number and sex of caring parents
Relationship between parental care and mating systems

- Emlen and Oring (1977)

  Parental care system → OSR → Mating system

- Maynard Smith (1977)

  OSR → Mating opportunities → Parental care system
Relationship between parental care and mating systems

- Emlen and Oring (1977)
- Maynard Smith (1977)
Bidirectional relationships between parental care and mating systems

- Székely et al. (2000):

![Diagram showing bidirectional relationships between parental care and mating systems](image)
Mating systems

- Monogamy
- Polygamy
  - polygyny
  - polyandry
  - polygynandry
Polygyny

- Most common breeding system (cf. anisogamy)
- One male monopolizes the eggs of several females (and also the females)
- The method of monopolization depends on
  - distribution of females
  - length of fertile period of females
Harem or female-defense polygyny

- A group of females can be defended
- Females form groups e.g. because of predation or feeding
Resource-defense polygyny

- Distribution of resources is patchy
- Resource patches can be defended
- A polygyny-threshold model (Orians, 1969): an already mated male on the better territory is a better choice if the difference in territory quality > PT
Scramble competition polygyny

- Neither females nor resource can be defended

- E.g. short reproductive season, females are widely dispersed or in large groups

- Scramble competition for mating

Horseshoe crab
Lek polygyny

- lek: in Swedish “play”
- Females gain only sperm from the male
- Mating success is very skewed
- In a few species (~35 birds, ~7 males, few frogs and insects)
Lek: Why do males aggregate?

- Not mutually exclusive hypotheses
  - **Hotspot**: places where females occur frequently
  - **Dilution effect**: reduced predation
  - **Hotshot**: males are around the preferred male
  - **Stimulus pooling**: more males increase female attraction
Lek: Why do males aggregate?

- Not mutually exclusive hypotheses
  - **Hotspot**: places where females occur frequently
  - **Dilution effect**: reduced predation
  - **Hotshot**: males are around the preferred male
  - **Stimulus pooling**: more males increase female attraction

**Lek paradox**

- Selective female choice → directional selection → why do not variance diminish?

- **Condition dependent costly signals**
  - Condition is influenced by many genes → not a single gene is under selection be female choice → variance maintained
Monogamy

• For males polygyny would be optimal

• Why do monogamy evolve?
  • **Mate guarding hypothesis**: to ensure mating and paternity (e.g. harlequin shrimp)
  • **Mate assistance hypothesis**: male parental care is essential for offspring survival (e.g. seahorse)
  • **Female-enforced monogamy**: female does not allow the male to attract more females (e.g. *Nicrophorus defodiens* burying beetle)
Monogamy: birds vs. mammals

- **Mammals**: ~4% of species are monogamous
- **Birds**: ~96% of species are monogamous (socially! → see later)
Monogamy: birds vs. mammals

- **Mammals**: ~4% of species are monogamous

- **Birds**: ~96% of species are monogamous (socially! → see later)

- **Mammals**:
  - large initial investment into the offspring be the female
  - the offspring is attached to the female
  - male cannot be an effective parent → *polygyny*

- **Birds**:
  - after laying the eggs male can be an effective parent → *biparental care and monogamy*
Social vs. genetic mating system

• In some socially monogamous bird species even 50% of the offspring can be extra-pair (EPY = extra-pair young).

• For males EPC (extra-pair copulation) is beneficial: they parasitize the parental care of other males.

• For males EPC can be costly: their mate can engage in EPC if she is not guarded constantly during the fertile period.

• For females EPC can be beneficial: genetic (good genes) or direct benefits (ensure fertilization, EPC male can help with parental care or allow feeding on his territory).

• For females EPC can be costly: Her mate may reduce parental care if cuckoldry is expected.
Polyandry

- In relatively few species
- A female monopolize the sperm and parental care of several males
- Often with sex role reversal
- Territory defence or male defence polyandry
Dunnock: polygynandry

- Frederick Orpen Morris (1856): humble life of the dunnock
Dunnock: polygynandry

- Conflict:
  - For males polygyny is optimal
  - For females polyandry is optimal
- When none of them wins: polygynandry
Parental care and parental investment

- **Parental care** (Clutton-Brock 1991)
  - any parental behaviour that increases the survival of offspring
  - may not entail costs for the parent(s)

- **Parental investment** (Trivers 1972):
  - any parental behaviour that increases the survival of offspring
  - decreases the investments of the parent into other offspring
  - may not be proportional to the resources devoted to offspring (e.g. energy spent on nest defence vs. predation during nest defence)
Why is conflict over care?

- Care is **beneficial** because it increases the survival of the young
- **BUT** care is **costly** for the parent:
  - *cost of reproduction*: reduced survival or future breeding success
  - the caring parent may be *predated* whilst caring
  - *lost opportunities* for mating
Why is conflict over care?

- Care is **beneficial** because it increases the survival of the young
- **BUT** care is **costly** for the parent:
  - *cost of reproduction*: reduced survival or future breeding success
  - the caring parent may be *predated* whilst caring
  - *lost opportunities* for mating

**Therefore, both parents would prefer the other to do the hard work of parental care** (Lessells 1999, Houston et al. 2005)
Why is conflict over care?

- Care is **beneficial** because it increases the survival of the young
- **BUT** care is **costly** for the parent:
  - *cost of reproduction*: reduced survival or future breeding success
  - the caring parent may be *predated* whilst caring
  - *lost opportunities* for mating

Therefore, both parents would prefer the other to do the hard work of parental care (Lessells 1999, Houston et al. 2005)

- Conflict over care in penduline tits
  - no biparental care
  - ~40% of nests is deserted by both parents
  - up to 7 mates during a breeding season
Why is conflict over care?

- Care is **beneficial** because it increases the survival of the young
- **BUT** care is **costly** for the parent:
  - *cost of reproduction*: reduced survival or future breeding success
  - the caring parent may be *predated* whilst caring
  - *lost opportunities* for mating

Therefore, both parents would prefer the other to do the hard work of parental care
(Lessells 1999, Houston et al. 2005)

- Conflict over care in penduline tits
  - no biparental care
  - ~40% of nests is deserted by both parents
  - up to 7 mates during a breeding season

Family life is not ideal
**Parental care in shorebirds**

- Majority of bird species: biparental care
- Shorebirds
  - sandpipers, plovers and allies, approx. 200 species
  - variable parental care

**Cooperation**
- Avocets
  - © J. van der Kam
- Oystercatchers
  - © T. Székely

**Conflict**
- Phalaropes
  - © J.D. Reynolds
- Ruff
  - © RSPB

Both parents provide care

One parent provides care
Parental care in shorebirds

Variation within and between populations of the same species

Székely et al. 2006 BioScience; Székely et al. 2007 J Ornithol
Parental care in shorebirds

Variation within and between populations of the same species

Shorebirds: good model system to understand how biparental care evolves

Székely et al. 2006 BioScience; Székely et al. 2007 J Ornithol
Why study Kentish plover?

Kentish plover (*Charadrius alexandrinus*)

- **Natural history**
  - common 40–44 g insectivorous shorebird that breed in many countries
  - nest on the ground on shores and saltmarshes
  - adult males and females have distinct plumages

- **Diverse breeding system**
  - biparental incubation of eggs BUT after hatching one parent (*usually the female*) may desert the brood
  - deserted parent cares alone until the chicks die or fledge
  - deserting parent may remate

---

Male

Female

Precocial chick

© R. Sauli

© K. Hyun-tae
Why study Kentish plover?

Kentish plover (*Charadrius alexandrinus*)

- **Natural history**
  - common 40–44 g insectivorous shorebird that breed in many countries
  - nest on the ground on shores and saltmarshes
  - adult males and females have distinct plumages

- **Diverse breeding system**
  - biparental incubation of eggs BUT after hatching one parent (*usually the female*) may desert the brood
  - deserted parent cares alone until the chicks die or fledge
  - deserting parent may remate

Monogamy, polygyny and polyandry along with biparental, male-only and female-only care all occur within a single population.
Why study Kentish plover?
Why study Kentish plover?
Why study Kentish plover?

© Kis J.
Why study Kentish plover?
Parental cooperation in Kentish plover

One of the handful of species in which several factors influencing cooperation between parents have been identified

Cooperation ....................................................... Conflict

Life history
large family......................................................................... small family
late breading........................................................................ early breading
Székely & Cuthill 2000 Proc Roy Soc B

Ambient environment
harsh environment.......................................................... mild environment
AlRashidi et al. 2011 Anim Behav
rich food............................................................................ poor food
Kosztolányi et al. 2006 J Anim Ecol
high predation...................................................................... low predation
Amat et al. 1999 Ibis

Social environment
even sex ratio........................................................................ biased sex ratio
Székely et al. 1999 Behav Ecol; Kosztolányi et al. 2011 J Evol Biol
Parental cooperation in Kentish plover

One of the handful of species in which several factors influencing cooperation between parents have been identified.

Cooperation

Life history
- large family vs. small family
- late breading vs. early breading
  - Székely & Cuthill 2000 Proc Roy Soc B

Conflict

Ambient environment
- harsh environment vs. mild environment
  - AlRashidi et al. 2011 Anim Behav
- rich food vs. poor food
  - Kosztolányi et al. 2006 J Anim Ecol
- high predation vs. low predation
  - Amat et al. 1999 Ibis

Social environment
- even sex ratio vs. biased sex ratio
  - Székely et al. 1999 Behav Ecol; Kosztolányi et al. 2011 J Evol Biol
Effect of ambient environment on cooperation: temperature

- Recording for 24 hours
- incubation behaviour
- temperature at ground level

Fieldwork:
United Arab Emirates
Effect of ambient environment on cooperation: temperature
Effect of ambient environment on cooperation: temperature
Effect of ambient environment on cooperation: temperature

- 6-8 h
- 12-14 h
- 18-20 h
Effect of ambient environment on cooperation: temperature

- High ambient temperature → **more cooperation**

Mixed-effects model; time factor × female incubation interaction $F_{11,274} = 4.4$, $p < 0.001$

AlRashidi et al. Frontiers in Zoology 7:1
Effect of ambient environment on cooperation: cover

- Experimentally changing nests cover
- Behavioural data:
  - baseline (24 hours)
  - manipulated (24 hours)
- Fieldwork:
  Farasan Islands

Original  After manipulation

Cover added  Cover removed

AlRashidi et al. 2011 Anim Behav 82: 235–243
Effect of ambient environment on cooperation: cover

- Experimentally changing nests cover
- Behavioural data:
  - baseline (24 hours)
  - manipulated (24 hours)
- Fieldwork:
  Farasan Islands

Original

After manipulation

AlRashidi et al. 2011 Anim Behav 82: 235–243
Effect of ambient environment on cooperation: cover

- Change compared to baseline (mean ± SE, n = 20 nests)
Effect of ambient environment on cooperation:

- Change compared to baseline (mean ± SE, \( n = 20 \) nests)
Effect of ambient environment on cooperation: cover

- Change compared to baseline (mean ± SE, n = 20 nests)

More sunlight → higher temperature → more cooperation

Mixed-effects models, total incubation, treatment: $F_{1,18} = 7.66, p = 0.013$; number of changeovers: treatment × time period interaction: $F_{11,198} = 4.54, p < 0.001$
Biparental incubation: cooperation or conflict?

- **Objective:** to test how males and females respond to changed levels of parental effort of their mate
- **Manipulation:** *cooling* the nest at low ambient temperatures → *increasing the cost* of incubation

- **Fieldwork:** United Arab Emirates
- **Protocol:** matched design for each nest
  - day 1: baseline
  - day 2: targeting one parent (male 22h-04h or female 05h-09h)
  - day 3: targeting the other parent (male or female, random order)

*Kosztolányi et al. 2009 Behav Ecol 20: 446–452*
Biparental incubation: cooperation or conflict?

- Data collection and manipulation:
  1. Camera and digital video recorder (*incubation behaviour*)
  2. Balance under the nest and a data logger (*body mass*)
  3. Temperature sensors and data logger (*ambient and nest temperature*)
  4. Remote controlled Peltier device (*cooling the nest*)
- Data were recorded every 20s

Kosztolányi et al. 2009 Behav Ecol 20: 446–452
Biparental incubation: cooperation or conflict?

- Data collection and manipulation:
  1. Camera and digital video recorder (incubation behaviour)
  2. Balance under the nest and a data logger (body mass)
  3. Temperature sensors and data logger (ambient and nest temperature)
  4. Remote controlled Peltier device (cooling the nest)
- Data were recorded every 20s

Kosztolányi et al. 2009 Behav Ecol 20: 446–452
Biparental incubation: cooperation or conflict?

- Data collection and manipulation:
  1. Camera and digital video recorder (*incubation behaviour*)
  2. Balance under the nest and a data logger (*body mass*)
  3. Temperature sensors and data logger (*ambient and nest temperature*)
  4. Remote controlled Peltier device (*cooling the nest*)

- Data were recorded every 20s

Kosztolányi et al. 2009 Behav Ecol 20: 446–452
Biparental incubation: cooperation or conflict?

- Data collection and manipulation:
  1. Camera and digital video recorder (*incubation behaviour*)
  2. Balance under the nest and a data logger (*body mass*)
  3. Temperature sensors and data logger (*ambient and nest temperature*)
  4. Remote controlled Peltier device (*cooling the nest*)
- Data were recorded every 20s

Kosztolányi et al. 2009 Behav Ecol 20: 446–452
Biparental incubation: cooperation or conflict?

- Data collection and manipulation:
  1. Camera and digital video recorder (*incubation behaviour*)
  2. Balance under the nest and a data logger (*body mass*)
  3. Temperature sensors and data logger (*ambient and nest temperature*)
  4. Remote controlled Peltier device (*cooling the nest*)
- Data were recorded every 20s

Kosztolányi et al. 2009 Behav Ecol 20: 446–452
Biparental incubation: cooperation or conflict?

- Data collection and manipulation:
  1. Camera and digital video recorder (*incubation behaviour*)
  2. Balance under the nest and a data logger (*body mass*)
  3. Temperature sensors and data logger (*ambient and nest temperature*)
  4. Remote controlled Peltier device (*cooling the nest*)
- Data were recorded every 20s

Kosztolányi et al. 2009 Behav Ecol 20: 446–452
Biparental incubation: cooperation or conflict?

Kosztolányi et al. 2009 Behav Ecol 20: 446–452
Biparental incubation: cooperation or conflict?
Biparental incubation: cooperation or conflict?

Kosztolányi et al. 2009 Behav Ecol 20: 446–452
Biparental incubation: cooperation or conflict?

Kosztolányi et al. 2009 Behav Ecol 20: 446–452
Biparental incubation: cooperation or conflict?

Kosztolányi et al. 2009 Behav Ecol 20: 446–452
Biparental incubation: cooperation or conflict?

Red arrows and shaded areas: mean and 95% CI
Biparental incubation: cooperation or conflict?

Red arrows and shaded areas: mean and 95% CI

<table>
<thead>
<tr>
<th>Compensation: 35°-135°</th>
</tr>
</thead>
<tbody>
<tr>
<td>Absolute deviation of vectors from 45° (mean and 95% CI)</td>
</tr>
<tr>
<td>Male manipulation</td>
</tr>
<tr>
<td>Female manipulation</td>
</tr>
</tbody>
</table>
Biparental incubation: cooperation or conflict?

Red arrows and shaded areas: mean and 95% CI

### Absolute deviation of vectors from 45° (mean and 95% CI)

<table>
<thead>
<tr>
<th></th>
<th>Male manipulation</th>
<th>Female manipulation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male manipulation</td>
<td>68.3° (57.0°-79.6°)</td>
<td>70.2° (56.8°-83.7°)</td>
</tr>
</tbody>
</table>

Compensation: 35°-135°

**Trade-off:**
- response to mate behaviour → usually **compensation**
- biparenatal incubation **BUT** conflict

Kosztolányi et al. 2009 Behav Ecol 20: 446–452
Summary and conclusions

- Two forms of sexual selection: intra and inter
- Females’s benefit of choosiness: direct and indirect (genetic)
- Breeding systems
  - Mating systems: polygyny, monogamy, polyandry, polygynandry
  - Social mating system ≠ genetic mating system
  - Parental care systems: biparental, female-only, male-only, none
- Parental care:
  - family life is not ideal ← conflict between the parents
- Parental cooperation in Kentish plover
  - High temperature may promote cooperation
  - The cooperation between the parents is full of conflicts
Collaborators and funding

Tamás Székely  
Univ Bath

Innes C Cuthill  
Univ Bristol

Clemens Küpper  
Max Planck

Monif AlRashidi  
Univ Hail

- OTKA
- Biotechnology and Biological Sciences Research Council, UK
- The Royal Society, UK
- Environment Agency, Abu Dhabi
- Magyary Zoltán Felsőoktatási Közalapítvány

Thank you for your attention!