Behavioral Ecology of Vertebrates

Unit 9. Mating Systems

Module 4 Reproduction

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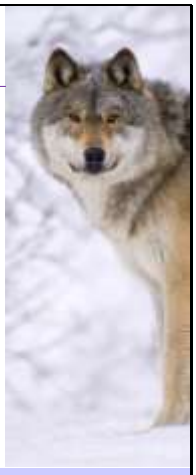


Learning, Discovering and Sharing Knowledge

Previously, we have examined how the physical and social environments have shaped behavioral strategies. We established that the sex that give the most parental care is the one that is a valued resource for which the other sex competes. We have examined how this sexual competition has been shaped by "force" or by "charm". Now we put these ideas together to explore the amazing diversity of mating systems.

Learning Objectives (Davies et al. 2012, Table 9.3)

Hierarchical approach (broad themes):

1. **Life history constraints:** paternal care (mammals/ birds), offspring (altricial/precocial), diet, litter-size, life-span
2. **Ecological factors:** resources (food, safety, companions) influence female clumping; female behavior influences male options to monopolize mates ("hotspot", "hotshot", switcher)
3. **Social "conflicts" within a species**: switching between monogamous, polygynous, and polyandrous relationships depends on resources and operational sex ratio

This is the direction that the thinking is going in Behavioral Ecology. Different approaches for asking questions at different levels in the biological hierarchy. These themes are implicit throughout Chapter 9, but they are not pulled together explicitly until the last pages. Today, I will try to make this thinking more explicit and explain the reasoning. Notice that on a continuum of "highly heritable" to "learned", the traits associated with life-history constraints are more genetic, and the traits examined under the theoretical framework of social conflicts and more learned.

Comparisons between taxonomic orders

1. LIFE HISTORY CONSTRAINTS

Before behavioral ecologists had the technology for following marked individuals and measuring paternity, they relied on comparisons of widely different taxonomic groups to understand genetic variation. This is what we refer to life history constraints, and it applies to comparisons across taxonomic orders or families as different as mammals and amphibians.

9.1 Mating Systems *(Davies et al. 2012: 224, Table. 9.1)*

Mating System	Who? (per season)	Parental care	Mate Access Strategies
Monogamy	♂+♀ (may pair for life)	Often both	Partners defend each other
Polygyny	♂+♀♀	Female (most or all)	Males: Female defense, resource defense, leks, or scramble competition
Polyandry	♀+♂♂	Male (most or all)	Female defense
Promiscuity	♀+♂♂ ♂+♀♀		Varied
Polygamy	Non-monogamous ♂ and or ♀		Varied

(credit: N. Spear)

This is the way the terms are defined in every textbook. It is useful as a broad overview. However, I hope to convince you today that it is no longer useful to refer to a "monogamous system" as if a species has a gene for monogamy. Rather, we should be looking at the % monogamous relationships in each population, and how populations vary within each species.

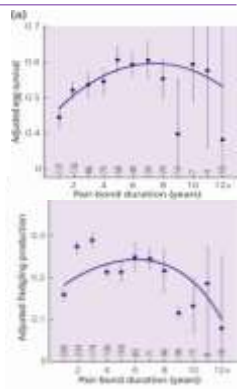
1.1 Monogamy (Davies et al. 2012:264)

- Oystercatchers (shorebird)
  - Where have you seen them?
- Mostly monogamous relationships
  - How would you test this?
- Both maternal & paternal care (obligate)
  - How would you test this?

Test of monogamous relationships (TIP: need evidence of both social and genetic fidelity). Test of obligate care (TIP: remove one and see if the brood survives)

1.2 Monogamy (Davies et al. 2012:264)

- Increased success (eggs, fledglings) with duration of the pair bond
  - What age is the peak?
  - Why the decline after peak?
  - What is "adjusted"?
- More experience improves behavioral coordination
  - Why is there 8% "divorce"?
  - Are "divorcees" polygynous?

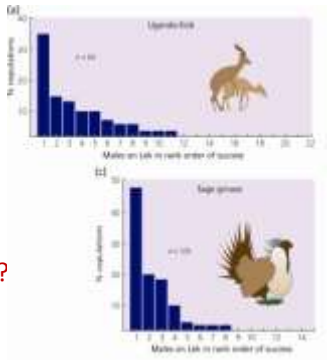


Credit: A. Marsh (edited by J. Packard)

Newly formed pairs are not as successful as those that have been together longer; senescence after peak (5-7 yr). "adjusted" measures control statistically for other effects including age of males and females, individual identity, and territory quantity. There is an initial cost of breeding with a new partner. Those that deserted mates gained increased survival and reproductive success on better territory. Initiators of divorce gained while victims lost.

1.3 Polygynous (Davies et al. 2012, Fig. 9.4)

- No paternal care
  - Why in mammals?
  - Why in birds?
  - Which sex competes?
- High variance in male reproductive success
  - Why does this matter?
  - Season or lifetime?



Credit: A. Marsh (edited by J. Packard)

Newly formed pairs are not as successful as those that have been together longer; senescence after peak (5-7 yr). "adjusted" measures control statistically for other effects including age of males and females, individual identity, and territory quantity. There is an initial cost of breeding with a new partner. Those that deserted mates gained increased survival and reproductive success on better territory. Initiators of divorce gained while victims lost.

1.3 Polyandry (Davies et al. 2012: 278, Fig. 9.13)

- African jacana
  - Other species?
- No maternal care
  - Why sex role reversal?
- High variance in female reproductive success
  - Why does this matter?
  - Season or lifetime?
- Variation in paternity
  - What is a "monandrous" relationship?

Other species? Florida snail kite, phalarope, spotted sandpipers. Sex role reversal: (a) small clutch size of 4, (b) incubation constraints, (c.) variable resources (flood/drought cycles), (d) female defends large territory in which several males nest, incubate the eggs and care for young. Why matter? Females compete for both mates and extra-pair copulations. Highly variable over lifetime, due to unpredictable floods. Monandrous relationships: 100% paternity assurance. Polyandrous: 41% of male's brood sired by co-male.

2.3 Polygynandry (Davies et al. 2012: 277)

- African lions- no paternal care *(Packer et al. 1991)*
- Polyandrous, polygynous and monogamous relationships depending on resources/competitors
- Polyandry Threshold Model *(Gowaty, 1981):*
  - males prefer unpaired female in good territory
  - males accept paired female when the other option would be an unpaired female in poor territory
- Are lions a good fit to Polyandry Threshold Model?
  - Advantages for females?
  - Advantages for males?
- Does male "lifetime fitness" increase with polyandrous relationships?

Photo credit: Beverley Joubert

Credit: J. Travis (edited by J. Packard)

Davies et al. (2012) use polyandrous relationships in lions as an example of the "Polyandry threshold model". We need to practice critical thinking! | Good fit? Males don't have a choice between paired and unpaired females, they form coalitions based on relationships with brothers and peers| Advantages for females: defense against intruders; Advantages for males: coalition defends food resources, territory & females when threatened. | "Lifetime fitness" does not make sense. Lifetime reproductive success is dependent on a variety of factors, there is not a genotype for "accept a partner in a coalition" or "do not accept a partner". The heritable strategy is conditional, switching between tactics depending on the physical (food to feed large groups) and social environment (availability of coalition partners). Fitness is a characteristic of a genotype, not an individual.

1.4 Poll- lets see if you understand

Premise for debate: *"There is not monogamy, polygyny, polyandry in an entire species…only variation in % monogamous, polygamous or polyandrous relationships."* Do you agree?

a) Yes
b) No
c) It depends

Davies et al. 2012, Fig 9.8

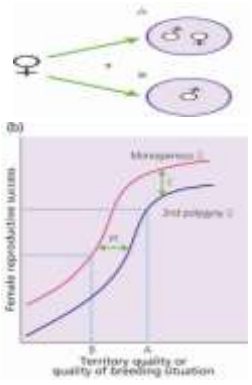
Comparisons across genera (related species)

2. ECOLOGICAL FACTORS

Classic comparison between red-winged blackbirds and yellow-headed blackbirds. Yellow-heads eat seeds outside the marsh, nest over land and females settle randomly in the marsh. Red-wings' territories vary in quality, one male can monopolize a site: good habitat in center of marsh where predators cannot walk on water. More insect food in the center of the marsh. Females have a choice between accepting a paired male in the center of the marsh, or an unpaired male with a poor territory at the edge of the marsh.

2.1 Polygyny Threshold Model (Davies et al. 2012, Fig. 9.9)

- Polygyny Threshold Model *(Orians, 1969)*
- Males who control and defend the best resources gain the most mates
- Females choose polygyny if costs are outweighed by access to good resources

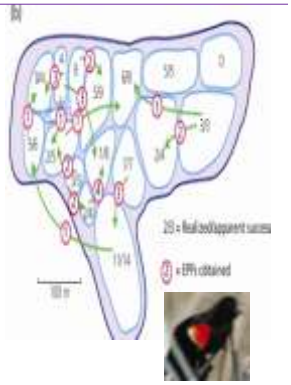


Credit: T. Harrington (edited by J. Packard)

Lets clarify what is the "polygyny threshold model", in contrast to the muddled "polyandry threshold model" that Davies et al (mistakenly) tried to apply to the lions.

2.1 Cost of polygynous relations *(Davies et al. 2012: 268, Fig. 9.8)*

- No cost to females *(e.g. yellow headed blackbirds)*
  - where males contribute very little parental care, females do not "suffer" from polygyny
  - What do we mean by "suffer"?
- Cost to females *(e.g. red-winged blackbirds)*
  - Females share either resources the male controls (e.g., nest sites, food) or paternal care
- Cost to males- paternity
  - Did males copulate exclusively with females in their territories?
  - Is EPF adaptive?

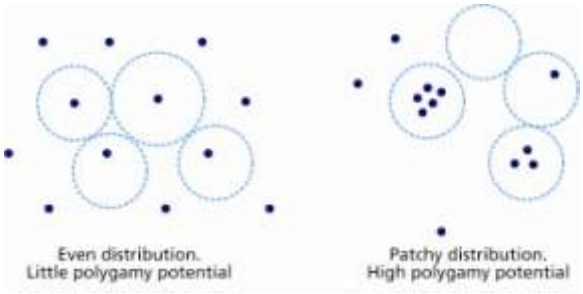


Credit: K. Smith (edited by J. Packard)

Red-winged blackbirds (*Agelaius phoeniceus*) are an example of polygyny costing females reproductive success in terms of paternal care (but not if you measure nest survival due to predation)

- Reduced male assistance leads to reduced reproductive success
- Females choose to settle in territories of monogamous males *except* when territory quality was higher
- Female choice for higher quality habitat over monogamy is adaptive because cost of losing a nest to predators is greater than the cost of sharing paternal care

2.2 Clumped resources (Davies et al. 2012, Fig. 9.2)



Which species? Yellow- head or red-wing?

Remember in Module 2 when we talked about the Ideal Free Distribution? We predicted that individuals would go to where there were more resources. Yellow head BB would be an example of an even distribution of resources with little polygamy potential. Red wing BB illustrates a system with patchy distribution and high polygamy potential because the resources are clumped. This is the basis for the Ecological Model (next slide).

9.3 Ecological model *(Davies et al. 2012: 224, Fig. 9.1)*

Mating Systems with no Male Parental Care

Tendencies: ♀ reproductive success limited by resources (other than males)
♂ reproductive success limited by access to ♀

Dispersion: ♀ dispersion depends on resource dispersion (in space & time)
♂ dispersion depends on ♀ dispersion

Credit: N. Spear (edited by J. Packard)

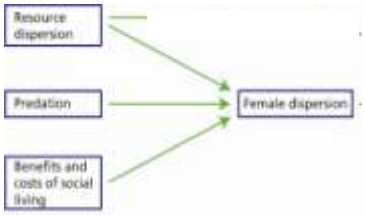
This is the "mantra" we discussed as the take home message from Fossil Rim field trip. Examples (a) monogamous dik diks live in forests where they find highly nutritious leaves and fruits in relatively small territories, females disperse and each male defends one female, (b) polygynous Uganda kob defend a small territory on a lek where female movements are predictable (like blackbuck at FR), (c) multi-male herds of water buffalo form where large aggregations of females cannot be monopolized by the males, so they wander with the females (like addax at FR).

9.5 Ecological model- females *(Davies et al. 2012: 224)*

Why is ♀ reproductive success limited by resources (other than males)?

Why does ♀ dispersion depends on resource dispersion (in space & time)?

How does predation & social living fit in with this?



Credit: N. Spear (edited by J. Packard)

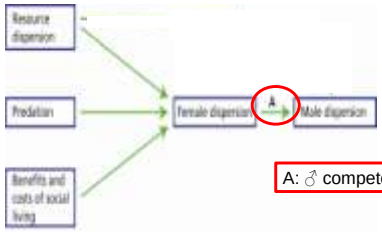
In the simple view, distribution of resources influences female clumping. However, in Module 3 when we look at factors influencing group living, we also learned that predation and communal care of young may influence female groups

9.6 Ecological model- males *(Davies et al. 2012: 224, Fig. 9.1)*

Why is ♂ reproductive success limited by access to ♀?

What do we mean by ♂ dispersion depends on ♀ dispersion?

What would be an example? What is missing from this diagram?



Credit: N. Spear (edited by J. Packard)

Whatever influences the females, if they are clumped, then one male can monopolize them. Remember that we learned this in Module 3. I am thinking of the sable at Fossil Rim, where one male follows the female group around wherever they go and will use force to exclude any rivals from this harem. However, there is also indirect competition among males.

9.6 Ecological model- males *(Davies et al. 2012: 224, Fig. 9.1)*

What is your favorite example of "harem" defense?

Do males defend females if they are not clumped?

What is your favorite example of "resource" defense?

Do males "anticipate" or learn?

B: ♂ competes indirectly for ♀: ♂ "anticipates" how resources influence ♀ dispersion and ♂ competes for resource-rich sites

Credit: N. Spear (edited by J. Packard)

We also need to add in the indirect competition by males. I am thinking of the blackbuck at Fossil Rim. They learned female movements and set up territories where the females pass through. If a male copulates with a female on his territory, then he "indirectly" removes her as a "resource' available to other males in the population. It might seem he has anticipated where to find females in the future, but actually he has learned from past experience.

2.5 Poll- lets see if you understand

Premise for debate: *"in species with no paternal care, the % monogamous and polygamous relationships in a population depends on:*

- *how resource distribution affects clumping in females*
- *options for males to monopolize females"*

a) I agree
b) I disagree
c) It depends

Lets dialogue more about this using the elearning discussion tool

Davies et al. 2012 Fig. 9.12

Comparing relationships within a species

3. SOCIAL "CONFLICT"

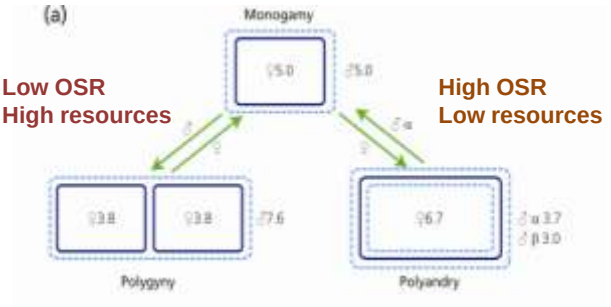
Dunnocks are a small sparrow-like bird that builds nests in the hedges in the British Isles. Davies and his studies did a series of studies that revealed individuals switch between different types of relationships. He turned this study into investigation of what he calls social conflict. In my personal opinion, I guess it depends on the "eye of the beholder" whether this is conflict or opportunity. (Maybe like newspapers, stories about conflict sells more books than stories about opportunity.)

3.1 Dunnocks (switch) (Davies et al. 2012:276)

- Female territories expand with scarce resources
- If high OSR, one male cannot exclude another
- Polygynandrous relationships

In the dunnocks, when food is scarce, females forage over really big territories. So big that a beta male might copulate with one female while the alpha male is looking for the female in another territory. Davies described conditions of polygynandry in dunnocks as a "Stalemate". Several males overlapping the territories of several females does not fit optimal predictions: from female perspective, paternal care is shared; from male perspective, paternity is shared; beta male more likely to provide care if has attained more copulations; beta male is more likely younger

3.2 Dunnocks (switch) (Davies et al. 2012:276)



Davies described this study of the dunnocks better in the previous edition. Where there is lots of food, females have small territories and at a low OSR (Few males to females), one male can monopolize several females. When resources decline and female territories expand, one male may not be able to exclude another male, particularly if there are a lot of males around. Females are more likely than males to die over a harsh winter.

2.3 Variable Mating Systems (Davies et al. 2012: 276)

- Polygynous relations (one male & several females)
  - Least successful for females due to sharing male with other females – less assistance with parental care.
- Monogamous relations (one male & one female)
  - Good success for female due to not sharing time/assistance.
- Polyandrous relations (one female & several males)
  - Greater success for female due to additional help with parental care.
- Polygynandrous (two males share two females)
  - Stalemate!
  - What do we mean by a stalemate?

Photo Credit: Damon Bay (Dunnock Diary)

J.Travis

Credit: T. Harrington (edited by J. Packard)

Clearly, dunnocks are an example of a variable mating system, which results in changing percentages of these four different types of relationships. Since there are costs and benefits associated with each of these tactics, no one tactic prevails, rather the emergent mating system reflects the % of monogamous and % polygamous relationships under the conditions at the time the study was done.

2.2 Social "conflict" (Davies et al. 2012: 271)

- Red-Winged Blackbirds are example of conflicting costs and benefits for each sex
- Polygynous females
  - Benefits: by choosing polygyny on good territory rather than monogamy on poor territory due to lower nest predation
  - Costs: by sharing paternal care, young are fed less frequently due to reduced male assistance (Pribil, 2000)
- Polygynous males
  - Benefits of multiple clutches in territory
  - Costs of reduced "paternity assurance"

Photo Credit: John & Barbara Gerlach

J.Travis

Credit: T. Harrington (edited by J. Packard)

From a proximate perspective, what we predict would be "best" for females is different that the prediction based on what is "best" for females. This does not imply that the individual count up their own "units of reproductive fitness" when making decisions! How could they?! But it leads to interesting testable hypotheses that are consistent with our understanding of how conditional strategies play out under changing conditions.

3.4 Poll- lets see if you understand

Premise for debate: *"For species that switch between types of relationships depending on fluctuations in resources & OSR, it is best to limit analysis using "social conflict" models to comparisons of individuals within one species"*

a) I agree
b) I disagree
c) It depends

Lets dialogue more about this using the elearning discussion tool

Summary (Davies et al. 2012, Table 9.3)

Hierarchical approach (e.g. order, genus, species):

1. **Life history constraints**: paternal care (mammals/ birds), offspring (altricial/precocial), diet, litter-size, life-span
2. **Ecological factors:** resources (food, safety, companions) influence female clumping; female behavior influences male options to monopolize mates ("hotspot", "hotshot", switcher)
3. **Social "conflicts" within a species**: switching between monogamous, polygynous, and polyandrous relationships depends on resources and operational sex ratio

Our take-home messages about mating systems!