UNIT 9. PARENTAL CARE AND MATING SYSTEMS

SOURCES *(for powerpoint format: http://wfsc.tamu.edu/jpackard/behavior/wfsc622/powerpoints.zip)*

required: Chapter 9 in Krebs & Davies (1993:208-243)

remedial: "Rearing the Young" in Halliday 1994; "Arriving" in the Trials of Life video series

supplement: Chapter 11 in Blumstein, D.T. and Fernandez-Juricic, E. "A Primer of Conservation Behavior"

PARTS OF THIS LECTURE OUTLINE

1. Comparative approaches: fish, mammals and birds
2. Maternal Care (MC)- female strategies
3. Paternal Care (PC)- male strategies

TIP1: Last unit was about the coevolution of mating effort and parental effort. We established that those two traits are not necessarily sex-linked. In this unit, we go into more detail about the various hypotheses that have been tested for fish, mammals and birds. This diversity is wonderfully complex, and finding the "laws of nature" has defied many of the best minds. In this unit, we will look more at what are sex-linked patterns of parental care, specifically "Maternal Care" and "Paternal Care". The big picture overview is: where there is no paternal care, the distribution of females is influenced by food, predators and sociality. The pattern in the females may directly influence which male tactics have been most successful, or alternatively, males may indirectly compete for females by controlling the resources that attract females. Where males do provide paternal care, other factors have been identified, such as whether the care is "shareable" among several females (polygyny threshold hypothesis).

1. COMPARATIVE APPROACHES: FISH, MAMMALS AND BIRDS

1.1 **Comparative approaches: birds, mammals and fish**

1. Broad generalizations- relative frequency *(Krebs and Davies 1993:209 Table 9.1)* related to dispersal *(Krebs and Davies 1993:240 Table 9.5)*
   a. Fish:Paternal Care (PC)=>random or polygamous mating system (random dispersal)
   b. Mammals: Maternal Care (MC)=> polygynous mating system (males disperse)
   c. Birds: Paternal & Maternal Care (PC + MC)=> monogamous mating system (females disperse)

1.2 **Fish**

1. Paternal Care (PC)- Alternative Hypotheses *(Krebs and Davies 1993:211 Table 9.2)*
   a. H1: Paternity certainty associated with external fertilization (beware of cuckoldry!)
   b. H2: Order of gamete release (PC when female lays then leaves; H2 rejected)
   c. H3: Association (territoriality by male=> dual functions)
      i. external fertilization in a nest defended by male, e.g. stickleback male attracts multiple females to lay sequentially
      ii. male more closely associated with embryos=> care

1.3 **Mammals**

1. Maternal Care (MC): female group size, female range size, seasonality *Krebs and Davies 1993: 215 Fig. 9.1, Plate 9.1)*
   a. females solitary: small range defensible by male (dik-dik, marmosets, canids)
   b. females solitary: large range not defensible by male (impala, white-tailed deer)
   c. females social: large range not defensible by male (water buffalo, bison)
      i. predictable daily movement of female groups (Uganda kob, waterbuck, Grevy's zebra)
      ii. seasonal reproductive aggregation=> seasonal harem (red deer, elephant seal)
      iii. asynchronous estrous in female groups=>permanent harems (plains zebra, baboons)

TIP2: If you are experiencing a disconnect between the diagram in Figure 9.1 and the wording in this section of the outline, perhaps I can help clarify. You will see both sets of ideas in the literature. In the outline, the factors listed were female group size, female range size, and seasonality of breeding. In Figure 9.1, the factors are resource dispersion, predation and c:b of social living. Female group size is related to predation because there is safety in numbers in larger groups. Female range size is related to resource distribution, because where resources are scattered widely and sparsely, range size is bigger. Seasonality has an effect on both female sociality and male ability to defend female(s) in estrous. In seasons where resources are abundant and clumped, females may more readily tolerate other female competitors and group sizes increase. When females synchronize estrus and they remain in a group, the group may be easily defended by one male. However, if they synchronize estrous and break up in separate groups, one male is unlikely to defend all the females from his rivals (he has to run back and forth between groups and opportunistic sneakers may be active while he is gone).

1.4 **Birds**

1. Paternal & Maternal Care (PC + MC)
    a. monogamy- 90% of birds (insectivorous song-birds)
    b. polygyny: no cost to females
        i. e.g. yellow-headed black birds feed off-territory; indifferent to how many nests a male defends
    c. polygyny at a cost: PC is divided among females in polygynous territories
        i. red-winged blackbirds: females shared territories with more food *(Krebs and Davies 1993:230 Fig. 9.5)*
        ii. great reed warbler: females shared territories safer from predators *(Ezaki 1990 cited in Krebs and Davies 1993:232)*
        iii. pied flycatcher: second female's brood got less care *Krebs and Davies 1993:235 Fig.9.9)*

1.5. **Take-home message: comparative approaches to mating systems**

1. fish (no care or PC)
2. mammals (MC, M dispersal)
3. birds (PC, F dispersal)
4. e.g. sticklebacks; ungulates; blackbirds, great reed warblers

Part 1	**Study Questions for Chat & Quiz 9 "Parental Care and Mating Systems"**
1.1	Comparing fish, birds and mammals, how are mating systems related to sexual differences in dispersal? (TIP: relate to MC and PC)
1.2	What are 3 alternative hypotheses about why paternal care occurs in a surprising number of fish species? (TIP: Table 9.2)
1.3	In mammalian species that show primarily maternal care, what are the separate factors that influence female and male dispersion? (TIP: Figure 9.1)
1.4	Comparing birds, what are examples of species illustrating three divergent patterns of mating systems? (TIP: monogamy, polygyny with and without direct male care)
1.5	Comparing taxa as diverse as fish, birds and mammals, why has there been such a divergence in the co-evolution of maternal and paternal care?

2. MATERNAL CARE, NO PATERNAL CARE (MC)

2.1. **Field tests of hypothesis of Economic Defendability** ***(Emlen & Oring 1977 cited in Krebs and Davies 1993:217 Fig 9.2)***

1. H1: inelastic territory- # females defended by male depends on clumping
   a. varied OSR in grey-sided voles (females in cages: clumped or not clumped)
   b. no change in male territories; clumped=> polygyny, not clumped=> monogamy
2. H2: males defend sites chosen by females for spawning
   a. blue headed wrasse (females choose egg laying sites on coral reefs)
   b. replaced males=> no change; replaced females=> new sites

2.2. **Lekking- 4 alternative hypotheses HPHP** ***(Bradbury & Gibson 1983 cited in Krebs and Davies 1993:222)***

1. H1: "Hotspots"- males aggregate where females are *(Krebs and Davies 1993: 215 Fig. 9.1)*
   a. e.g. Uganda kob defended mating territories where females fed in marsh
   b. females are predictably found at this location
2. H2: Predation on males is reduced on leks *(Krebs and Davies 1993:223 Fig. 9.4)*
   a. e.g. Physalaemus frogs preyed on by bats in neotropics
   b. "safety in numbers"
3. H3: "Hotshots"- males aggregate to increase female attraction *(Krebs and Davies 1993:221 Fig. 9.3)*
   a. test 1: removed Hotshot=> females chose next popular male? (no: grouse)
   b. test 2: moved Hotshot's territory=> no change in popularity? (yes: fallow deer)
   c. it's the total activity at the site that is attractive to the females
4. H4: Prudent females pick vigorous male (safe territory +/or "good genes")
   a. yes: (sage grouse, black grouse)
   b. no: (multiple paternity in ruff shorebirds)
   c. the logic is that vigorous males keep away other annoying intruders

2.3. **Conditional strategy- Uganda kob, topi and fallow deer** ***(Clutton-Brock 1989 cited in Krebs and Davies 1993:221)***

1. C1: low population density=>resource-based territories or harems
   a. single females attracted to a resource=> resource was economically defendable
   b. females band together for predation defense=> harems
2. C2: high population density=> mating territories on lek *(Krebs and Davies 1993 Plate 9.1.c)*
   a. male competition was so intense that males switch to defending a small area
   b. cost of defending resource territory (or female group) was too high

2.4. **Take-home message re. no paternal care**

1. food distribution + predation=> female distribution=>economic defendability by males
2. e.g. voles, wrasse; lekking species; Uganda kob, fallow deer
3. this may also change seasonally, or during periods when female estrus is synchronized

Part 2	**Study Questions for Chat & Quiz 9 "Parental Care and Mating Systems"**
2.1	In relating resource distribution to mating systems without paternal care, how did Emlen and Oring apply the hypothesis of Economic Defendability to "defense of females as a resource"? (TIP: identify two alternative hypotheses)
2.2	What are 4 alternative hypotheses about the function of lekking? (TIP: HPHP)
2.3	Choose a species to explain a conditional mating strategy in males, where tactics change depending on population density? (TIP: choose an ungulate with no paternal care)
2.4	For vertebrates with no paternal care, what influences female distribution, and in turn, how does female defendability influence male distribution? (TIP: Fig. 9.1)

3. PATERNAL CARE PROVIDED (PC)

3.1 **H1: Monogamous mating system: sexual rivalry is high in both sexes, or no other options**

1. C1: obligate monogamy- death of one partner results in nest failure o e.g. seabirds, birds of prey, marmosets
2. C2: facultative monogamy- PC increases brood success, but not essential o e.g. cichlids, songbirds, wolves o threshold of desertion- male tradeoff (1 full brood = 2 half broods?)

3.2. **H2: Polygynous mating systems: polygyny threshold model** ***(Orians 1969 cited in Krebs and Davies 1993:232)***

1. Assumptions similar to Ideal Free Distribution Model *(Krebs and Davies 1993233-234: Fig. 9.7, 9.8)*
    a. male territories (resource patches) are high or low quality
    b. females are free to choose territories o under ideal conditions, females settle where benefits>costs
2. initially, all females choose monogamous males (good, then poor)
3. when all territories are full, new females share a male in good quality habitat
    a. benefits of good territory outweigh the costs of sharing a male

3.3. **H3: Polyandrous mating systems- derivation of polyandry from monogamy**

1. step 1: females that abandon nests are able to lay multiple clutches in a season and leave more offspring
    a. eg. phalarope shorebirds and spotted sandpipers -- species with long migrations; those females exhausted from migration and egg-laying that deserted nests to feed were more likely to recoup and lay again
    b. eg. jacana -- tropical species has high rate of nest failure from predation and flooding; those females that deserted to lay multiple nests "won the lottery" with floods and predators
2. step 2: males that accepted sole brood care, in environment of female abandonment, have more nestlings survive
    a. development of sequential polyandry involves steps 1 and 2
    b. eg. phalarope shorebirds
3. step 3: females that defended resource-based territories attracted more males and thus left more offspring
    a. development of resource-defence polyandry involves steps 1, 2, and 3
    b. eg. spotted sandpiper, jacana

3.4. **H4: Conditional mating system, e.g. dunnocks** ***(Davies 1992 cited in Krebs and Davies 1993:238 Fig 9.10)***

1. low food + few males=> monogamy (large F range, 1 M can only defend 1F)
2. high food + few males=>polygyny (small F range, 1 M can defend >1 F)
3. low food + many males=> polyandry (large F range; takes 2M to defend 1F)
4. high food + many males=> polygynandry (small F range; 2 M defend 2F)

3.5. Take-**home message: strategies of paternal care- to share or not to share?**

1. monogamy, polygyny, polyandry, conditional switching
2. distribution of females + importance of male care + risk of predation + OSR

Part 3	Study Questions for Chat & Quiz 9 "Parental Care and Mating Systems"
3.1	How would you test whether a monogamous mating system is obligate or facultative? (TIP: focus on the relative importance of paternal care)
3.2	Compare red-winged and yellow-headed blackbirds to explain the distinction between fixed and conditional reproductive strategies? (TIP: relate to obligate monogamy and the polygyny threshold model)
3.3	Describe the steps in the co-evolution of male and female strategies, where the ancestral mating system was monogamy and the derived system is polyandry? (TIP: refer to sequential and resource-defense polyandry)
3.4	Explain how resource distribution and the operational sex ratio influence the types of relationships observed in the conditional mating system of dunnocks? (TIP: refer to monogamous, polygynous, polyandrous and polygynandrous relationships)
3.5	For species with paternal care, what influences whether females choose monogamous, polygynous or polyandrous relationships? (TIP: take home message)

SUMMARY

1. **Comparative approaches: birds, mammals and fish**
    1. fish (no care or Paternal Care; random dispersal)
    2. mammals (Maternal Care , Male dispersal)
    3. birds (Paternal Care, Female dispersal)
    4. e.g. sticklebacks; ungulates; blackbirds, great reed warblers
2. **Maternal care with no paternal care**
    1. food distribution + predation=> female distribution=>economic defendability by males
    2. e.g. voles, wrasse; lekking species; Uganda kob, fallow deer
3. **Paternal care- to share or not to share?**
    1. Polygyny threshold (e.g. choice between monogamous & polygynous relationships in redwing blackbirds)
    2. conditional switching (e.g. dunnocks)
    3. distribution of females + importance of male care + risk of predation + OSR

Summary	Study Questions for Chat & Quiz 9 "Parental Care and Mating Systems"
4.1	What are the take home messages for this unit on mating systems
4.2	Given that there is a fundamental difference in the type of maternal and paternal care observed in vertebrates, what factors influenced co-evolution of male and female strategies? (TIP: focus on systems with and without paternal care)