

Behavioral Ecology of Vertebrates

Unit 10. Sex Allocation

Module 4 Reproduction
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Learning, Discovering and Sharing Knowledge

In the previous unit, we talked about how the % monogamous relationships would be predicted to vary across species, populations and individuals within a population. In this unit, we look at how the % female tactics would vary both in terms of strategies (genotypes) and tactics (phenotypes) that switch with environmental conditions.

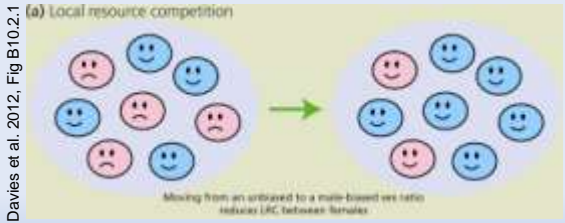
Learning Objectives (Davies et al. 2012:144)

Bias in male:female ratios- behavior or life-history?

- 1. Critique of folk psychology wording:** decisions, assumptions, manipulate, increase own fitness, mate quality
- 2. Sex allocation when relatives interact:** local resource competition/enhancement, local mate competition
- 3. Sex allocation in variable environments:** maternal condition, mate attractiveness, environmental sex determination, sex change

We need to practice critical thinking about some of the wording in this chapter. My major critique is that the theory of sex allocation is more relevant to a course on life history theory and evolution than to a course on behavioral ecology. Variation in the sex ratio is relevant to behavioral ecology, but it is a function of internal physiology, not really a behavioral response to a stimulus.

Davies et al. 2012, Fig B10.2.1



Moving from an unbiased to a male-biased sex ratio reduces LRC between females

Strong science requires precise use of words

1. CRITIQUE OF FOLK PSYCHOLOGY

The evolutionary theory associated with sex allocation is very complex. So the tendency in textbooks is to simplify the ideas with cartoons and by stating the ideas in terms of folk psychology. However, I believe the authors of this edition of the textbook do readers a dis-service by some of the wording they use. They use words like "fitness" in ways that are easily misinterpreted by readers who do not have a strong foundation in evolutionary theory.

1.1 Folk psychology (Davies et al. 2012:282,283)

1. "All sexually reproducing organisms must decide how to allocate resources to male and female reproduction"
2. "A huge variety of organisms...are manipulating the sex of their offspring in ways that increase their fitness"
3. "LRC among females reduces their value as offspring...investment in other daughters would be wasted"
4. "Throughout this book, we have assumed individuals act as if they are maximizing their fitness"

Let's practice our critical thinking skills! Which of these statements sounds like FP to you?

Lets take these one at a time and chat about why or why not.

1.2 Folk psychology (Davies et al. 2012:282,283)

#1 "All sexually reproducing organisms must decide how to allocate resources to male and female reproduction"

- If you could highlight one word or phrase that reduces the scientific credibility of this statement, which would it be?
- Why?
- How could you reword the statement to be more credible, from the logic of natural selection?

TIP: All, must decide

1.3 Folk psychology (Davies et al. 2012:282,283)

#2 "A huge variety of organisms...are manipulating the sex of their offspring in ways that increase their fitness"

- If you could highlight one word or phrase that reduces the scientific credibility of this statement, which would it be?
- Why?
- How could you reword the statement to be more credible, from the logic of natural selection?

TIP: Huge, manipulating, increase their fitness

1.4 Folk psychology (Davies et al. 2012:282,283)

#3 “LRC among females reduces their value as offspring...investment in other daughters would be wasted”

- If you could highlight one word or phrase that reduces the scientific credibility of this statement, which would it be?
- Why?
- How could you reword the statement to be more credible, from the logic of natural selection?

TIP: LRC: Local Resource Competition; value; wasted

1.5 Folk psychology (Davies et al. 2012:282,283)

#4 “Throughout this book, we have assumed individuals act as if they are maximizing their fitness”

- If you could highlight one word or phrase that reduces the scientific credibility of this statement, which would it be?
- Why?
- How could you reword the statement to be more credible, from the logic of natural selection?

TIP: Assumed; maximizing; their fitness


1.6 Poll- lets see if you understand

I want more practice identifying and rewording folk psychology statements

1. Highly disagree
2. Disagree
3. It depends
4. Agree
5. Highly agree

Let’s gauge your comfort level with FP. In response to this statement, which choice best expresses your view?

Davies et al. 2012, Fig 10.5



Deviations from 50:50 sex ratio

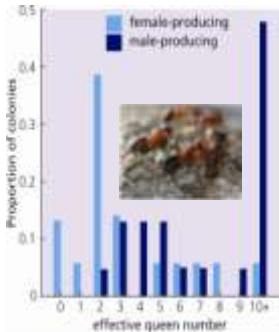
2. WHEN RELATIVES INTERACT

In the hymenoptera, we are used to species where an entire colony may be all female workers, like this parasitoid wasp, or honeybees. The prevailing hypothesis is that non-reproductive sisters help each other. We will learn more about the coefficient of relatedness in the next chapter. However, we find this deviation from a 50:50 sex ratio to be strange when it appears in vertebrates.

2.1 Local Resource Competition (LRC)

(Davies et al. 2012: 289, Fig. 10.3)

- Example: narrow-headed ant
 - Few queens = more female offspring
 - Many queens = more male offspring
- Why?
 - Variation in the extent of LRC across colonies (William & Keller (2000))
 - Lower resource availability limits dispersal of queens, therefore, benefit of producing new queens is reduced



(credit: K. Smith)

Life history of (*Formic exsecta*)? Resources? Colony size? Dispersal?]

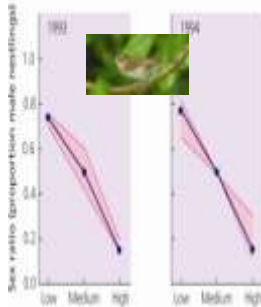
Can LRC “explain” sex ratio variation within species or populations? What do we mean by “explain”?

What is the hypothesis about the genotype? (fixed or conditional strategy?)

2.2 Local Resource Enhancement

(Davies et al. 2012: 293, Fig. 10.6)

- Example: Seychelles warbler
 - Female offspring stay and help in high quality territories
 - more females produced in high quality
 - Benefit only there when resources are plentiful (no competition)
- Observed –
 - high habitat quality = more female offspring;
 - low habitat quality = more male offspring



(credit: K. Smith)

Example: Seychelles warbler

Female offspring stay and help in high quality territories; more females produced in high quality
 Q: Is this cause/effect or correlation?

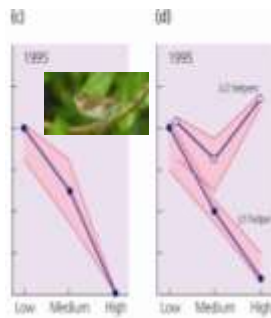
Benefit only there when resources are plentiful (no competition)

Komdeur et al. (1997) observed high habitat quality = more female offspring; low habitat quality = more male offspring (a)

2.2 Local Resource Enhancement

(Davies et al. 2012: 293, Fig. 10.6)

- Experiment (Komdeur et al. 1997)
- pairs moved from low to high quality territory
 - switched from 90% males to 85% females
- pairs moved from high to high
 - continued to have 80% female offspring
 - Further, >1 helper meant more sons (d)



(credit: K. Smith)

Komdeur et al. (1997) observed

Experiment – pairs moved from low to high quality switched from 90% males to 85% females & pairs moved from high to high continued to have 80% female offspring

Further, >1 helper meant more sons (d)

Davies et al. 2012 Fig. 10.12



“Pick” your own sex or that of your offspring?

3. VARIABLE ENVIRONMENTS

The second major set of hypotheses relates to strategies that have evolved in environments characterized by predictable fluctuations. This mantid shrimp switches between female tactics right after molting to male tactics in the hard shell phase.

3.1 Environmental Sex Determination

(Davies et al. 2012: 301, Fig. 10.10)

- Protogynous – female first (eg. Bluehead wrasse)
 - Old large males monopolize mating better
 - Remove male, largest female switches to male
- Protandry– male first (eg. clownfish)
 - Larger females produce more eggs
 - Remove female, largest male switches



(credit: K. Smith)

Sex change can be (a) female to male (ex. bluehead wrasse) or (b) male to female (ex. clownfish (*Amphiprion percula*))

Q: what is the hypothesis?

Natural selection favors individuals who mature as the sex whose fitness increases more slowly and then change to the other sex when older

If being old and big provides a greater benefit to one sex, then sex change is favored

Old large males monopolize mating so better to start as female and change to male later when older


Protandry– male first (ex. clownfish)

Reproductive success limited by the female’s ability to produce eggs, so the pair does better if the larger one is female

3.2 Trivers and Willard Hypothesis

(Davies et al. 2012: 297, Fig. 10.8)

- H: individuals should adjust the sex of their offspring based on environmental conditions
- Assumptions:
 - females in better condition have more resource and produce better offspring
 - higher quality offspring become higher quality adults
 - sons gain a greater fitness benefit from being higher quality adults
- Why would fitness of sons increase faster than daughters with improved maternal quality?



Credit: A. Marsh & J. Cantwell ; ed. By J. Packard

Trivers and Willard (1973) suggested that individuals should adjust the sex of their offspring based on environmental conditions.

-4 Assumptions:

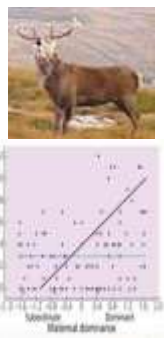
- Trivers and Willard **assumed** (C) would hold true when competition among males is intense, with the highest quality mates gaining a disproportionate share of matings. The consequence of these assumptions is shown in Fig 10.8, where fitness for sons increases faster than it does for daughters

- Low quality mothers will be selected to produce daughters, and high quality mothers produce sons

3.3 Maternal Condition

(Davies et al. 2012: 297, Fig 10.9)

- Example: Red Deer (Clutton Brock, et al., 1984)
 - Low body condition: 47% male calves
 - Good body condition: 61% male calves
- How would you test the 3 assumptions of Trivers?
- Genotype or phenotype?



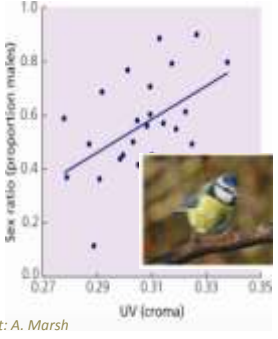
Credit: J. Cantwell

- Better habitat condition means females have greater resources to rear "higher quality" offspring.
- Offspring of "higher quality" grow into adults of "higher quality"
- Adult males of "high quality" have the greatest reproductive success
- Consequently, predicted under conditions of "high quality", females would have more male offspring, and more daughters under "poor" conditions

3.2 Mate Attractiveness

(Davies et al. 2012:298, Fig. 10.10)

- Blue tits- conditional
 - males: ultraviolet head patch varies
 - brighter UV patch produced more sons
- Treatment
 - UV block reversed effect (fewer sons)
- Variation in male or female genotype?



Credit: A. Marsh

Sheldon et al. (1999) showed that the same logic of Trivers and Willard (1973) can be applied to mate attractiveness in blue tits. Mate quality replaces maternal condition as factor on x axis from Fig 10.8. | Q: Does this imply that maternal condition is influenced by attractive male, or that male has good genes?

- Males have an ultraviolet patch on their head, which acts as a signal of quality. | What is meant by a signal of quality? Does this mean the males have better genes or provide more care?

Is not the hypothesis of better genes disproven by the UV block treatment? It is an effect on the females that changes the sex ratio, not the genotype of the males (otherwise blocked bright UV males would be predicted to produce more sons light unblocked bright UV males).

- Sons would benefit more from being higher quality. | What are we really saying here about the logic of natural selection? Are we saying there is a female sex linked genotype that both "chooses bright males" and "produces more males when more highly stimulated"? Do we know enough about the mechanisms? The heritability? Might this simply be neutral variation of the phenotype, not differential fitness?

Summary

(Davies et al. 2012:144)

Bias in male:female ratios- life-history not behavior

1. **Critique of folk psychology wording:** decisions, assumptions, manipulate, increase own fitness, mate quality
2. **Sex allocation when relatives interact:** local resource competition/enhancement, local mate competition
3. **Sex allocation in variable environments:** maternal condition, mate attractiveness, environmental sex determination, sex change

I encourage you to think of sex allocation as a life-history trait that influences the operational sex ratio NOT a behavioral decision. This is essentially understanding better what conditions influence the “female tactic” to increase or decrease in a population. We have learned that in some species there is a developmental trigger that influences the switch between female and male tactics in genotypes with a conditional genetic strategy. In other species, the trigger is conditional on the social or physical environment which may switch back and forth between good and poor conditions. In behavioral ecology models, it is the operational sex ratio that matters.