| Sexual Selection |
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## Sexual Selection

Intra-sexual selection: selection on traits $\qquad$ or behaviours that increase the ability of one sex to compete directly with one $\qquad$ another for fertilizations (e.g., fighting, sperm competition)

Inter-sexual selection: selection on traits or behaviours that increase the attractiveness of one sex to the other.

## Definition of the Sexes

Female: the sex producing large, immobile, food-rich gametes called eggs.

Male: the sex producing small, mobile, food-absent gametes called sperm ("little more than self-propelled DNA").

## Definition of the Sexes <br> Anisogamy: the production by the sexes of different sized gametes. <br> Isogamy: the production by the sexes of equivalent sized gametes.



## Bateman's Principle

"Sperm is cheap"
Male reproductive success is limited by access to females, whilst female reproductive success is limited by access to resources.

Can lead to a conflict between the sexes, with females being the choosy sex.

| Rates of Reproduction |  |  |  |
| :--- | :---: | :---: | :---: |
|  | Maximum number of offspring <br> produced during lifetime |  |  |
| Species | Male | Female |  |
| Elephant seal | 100 | 8 | $12 \times$ |
| Red deer | 24 | 14 | $2 \times$ |
| Human | 888 | 69 | $13 \times$ |
| Kittiwake gull | 26 | 28 | $1 \times$ |

## Reproductive Effort

Reproductive effort: the total investment made by an individual into reproduction. Includes parental effort, gametic effort and mating effort. (All other effort can be considered somatic effort.)

Parental effort: the sum of an individual's parental $\qquad$ investment in its offspring over its lifetime.

Gametic effort: the total investment made by an individual into the production of gametes.

Mating effort: the total investment made by an individual into acquiring or securing a mate.

## Reproductive Effort



Trivers (1972) stated that parental effort should include all investment into offspring. Thus, Trivers would include gametic effort as parental effort.
Promiscuous or
Polygamous
Opportunity for
Mexual selection

## Opportunity for Sexual Selection

(Trivers 1972)
Opportunity for sexual selection = relative parental effort made by males versus females ( $\mathrm{PE}_{8} / \mathrm{PE}_{\phi}$ )

When $\mathrm{PE}_{\widehat{\delta}} / \mathrm{PE}_{\phi} \ll 1$, there is a high opportunity for sexual selection to act on males.

When $\mathrm{PE}_{\hat{6}} / \mathrm{PE}_{t}=1$, there is little opportunity for sexual selection to act on either sex.

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## Male Reed Warbler Song



1. Male reed warblers stand at the tops of brush and sing for females.
2. Females prefer males with complex songs both as social and extra-pair mates.


## Why are Females Choosy?

## a) Direct Benefits

1.Shelter for female or offspring
2. Defence from predators
3. Parental care of offspring $\qquad$
4.Food (for female)
5.Fertility assurance (sperm to fertilize all eggs)
6.Absence of parasites or disease $\qquad$
7.Reduced mate search time

| Direct Benefits: Bullfrogs |  |
| :---: | :---: |
|  | 1. Males defend breeding territories in ponds or small lakes. <br> 2. Some territories are better than others. <br> 3. High quality territories have warmer water an less dense vegetation. |
|  | 4. Warm water facilitates egg development and less dense vegetation reduces predation by leeches because eggs can form into a tight ball. |

## Direct Benefits: Bullfrogs

5. Males compete with one another for the best territories. Generally the biggest and strongest males are successful at obtaining and holding the best territories
6. Intra-sexual selection for body size, strength, and fighting ability.
7. Females prefer to mate with males on high quality territories (inter-sexual selection).

## Direct Benefits: Katydids



1. Males produce a large protein-rich spermatophore (may weight close to $30 \%$ of male's weight), which he gives to a female during copulation.
2. A female eats the spermatophore and uses the energy to make eggs. $\qquad$
3. Females prefer large males because these males produce larger spermatophores.
4. Large males reject small females as possible mates because they can not produce enough eggs $\rightarrow$ mutual mate choice.

## b) Indirect Benefits

1. Good genes.
2. These might increase offspring growth rate, disease resistance, survivorship, competitiveness, etc.
3. They might also increase the attractiveness of sons (or daughters).



## Indirect Benefits: Gray Tree Frogs

|  | Father |  |  |
| :--- | :---: | :---: | :---: |
| Growth rate | $\mathbf{L o n g}$ call | Short call |  |
| Time of meta. | early | $=$ |  |
| Weight at meta. | $\mathbf{+}$ | late |  |
| Larval survival | $\mathbf{+}$ | $=$ |  |


|  | Selection for Good Genes |
| :--- | :--- | :--- |

## Fisherian Runaway Selection

1. Suppose that there is variation in a male trait such as tail length.
2. Suppose that there is also variation in female preference for tail length - some females like small tails, others like long tails.
3. Assume that there is a genetic basis for the male trait and the female preference.
4. Over time the genes for female preference will become 'linked' to the genes for the male trait: preference for long tail - long tail preference for short tail - short tail

## Fisherian Runaway Selection



## Fisherian Runaway Selection

Stalk-eyed Flies

1. Carry their eyes on the ends of long thin appendages.
2. In both sexes bigger flies have longer eyestalks, but males have longer stalks for their size than females. $\qquad$
$\qquad$
3. In the evening, the flies congregate beneath overhanging steam bank, they cling in small groups to dangling roots.
4. Males and females often mate on the roots.


## Stalk-eyed Flies <br> (Wilkinson \& Reillo 1994)

1. Males and females separated immediately $\qquad$ after emergence from their pupae.
2. Set-up three artificial breeding lines:
i) Control: 10 males and 25 females picked at random;
ii) Long treatment: 10 males with the longest
$\qquad$ eyestalks and 25 females picked at random;
iii) Short treatment: 10 males with the shortest eyestalks and 25 females picked at random.

## Stalk-eyed Flies <br> (Wilkinson \& Reillo 1994)

$\qquad$
3. Three populations (control and two treatments) were bred for 13 generations, at which time there was significant differences in average eyestalk length (short < control < long).
4. Paired-choice tests then performed to determine female preference for male eyestalk length in each population.

## Stalk-eyed Flies

(Wilkinson \& Reillo 1994)
5. Two males, one from the short line and the other from the long line, were placed in a cage with five $\qquad$ females (from one of the two treatments).
6. Males had same body size, but differed in eyestalk length.
7. The cage was divided down the middle with a clear plastic barrier containing a hole just big enough to allow females to pass through, but not males.
8. Preference of females was then observed (i.e., number of females on either side of cage).


## Stalk-eyed Flies

9. Wilkinson \& Reillo selected on male eyestalk length, and found a correlated response in female preference for eyestalk length.
10. Experiment shows:
i) female stalk-eyed flies are choosy;
ii) both male eyestalk length and female preference are heritable;
iii) selection on one trait can produce an evolutionary response in another trait.

Genetic correlation between trait and preference, consistent with Fisherian runaway selection

## Zahavi's Handicap Principle

1. Proposed that the peacock's tail was a day-to-day handicap to the male.
2. Females prefer long tails or some other elaborate trait precisely because they are handicaps and therefore act as an "honest" signal of male quality.
3. A male with a long tail must be of superior quality because he is still alive and well.
4. Thus, predation, disease or energetic constraints keep the signal honest.
5. The handicap model assumes that the superior quality of the male must be heritable (i.e., have a genetic component = good genes).

## Zahavi's Handicap Principle

Benefit = number of matings
Cost $=$ survivorship


## Zahavi's Handicap Principle

1. In the handicap model the good genes are genes for utilitarian aspects of survival and reproduction.
2. The Fisherian model assumes that the genes are purely for attracting females.
3. The handicap model requires that the degree of exaggeration of the trait (e.g., size of a peacock's tail) is contingent on the males genetic quality.
4. High quality males produce larger displays. This is sometimes referred to as condition-dependent handicaps.

Question: Why do females prefer males with longer tails and why don't all males simply generate long tails?
> Møller experimentally elongated the tails of some
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$\qquad$ males and compared these to males that had their tails cut and reattached, but had similar lengths to the experimental males. Males were similar in body size.
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## Barn Swallows <br> (Møller 1988, 1989, 1990)

1. Found that males with experimentally elongated tails were handicapped in their foraging:
a) they caught smaller, less profitable prey items;
b) they grew poorer quality feathers and shorter tails in subsequent molts.
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$\qquad$
Tail size is an honest indicator of male quality (e.g., foraging efficiency).

## Barn Swallows

Does male tail size indicate genetic quality - a $\qquad$ benefit that could be passed onto a female's offspring (indirect benefits)? $\qquad$

1. Swallows are parasitized by a blood-sucking mite, which infects parents and offspring.
2. Mite's lifecycle is very short (days) and therefore during nestling phase of swallows many mites can build up on offspring.
3. Mites reduce offspring growth rate.
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## Barn Swallows

(Møller 1988, 1989, 1990)

1. To test if mite infection (i.e., resistance to infection) was heritable, Møller exchanged half the nestlings $\qquad$ between pairs of nests soon after hatching.


Number of mites on male parent
Male tail length

