Sexual Selection & Mate Choice in the Three-Spined Stickleback

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Brief Background about the Three Spined Stickleback

- Kingdom - Animalia
- Phylum - Chordata
- Class - Actinopterygii
- Order - Gasterosteiformes
- Family - Gasterosteidae
- Genus - Gasterosteus
- Species - aculaetus

- Common in Northern temperate climates (Europe, Japan, Alaska, etc.)
- Less than 10 cm long
- Unusual feature - they have no scales
- Bony armour plates
- Three heavy spines spaced on back
- Related to pipefish and sea horses

- Found in fresh water lakes and streams
- Extremely morphologically diverse
- Males have red throats and shiny blue-green eyes
  - Parasitized males show decreased throat colouration
- Males are territorial - build and protect nests and provide parental care for fry for approx 10 days

- Red throats can elicit aggression in other males and used for courting ripe females
- Degree of colouration gives indication of male quality/condition factor
- Response to red colouration is not universal with all the species
- Males develop blue-green irises upon maturation

Benefit of Study

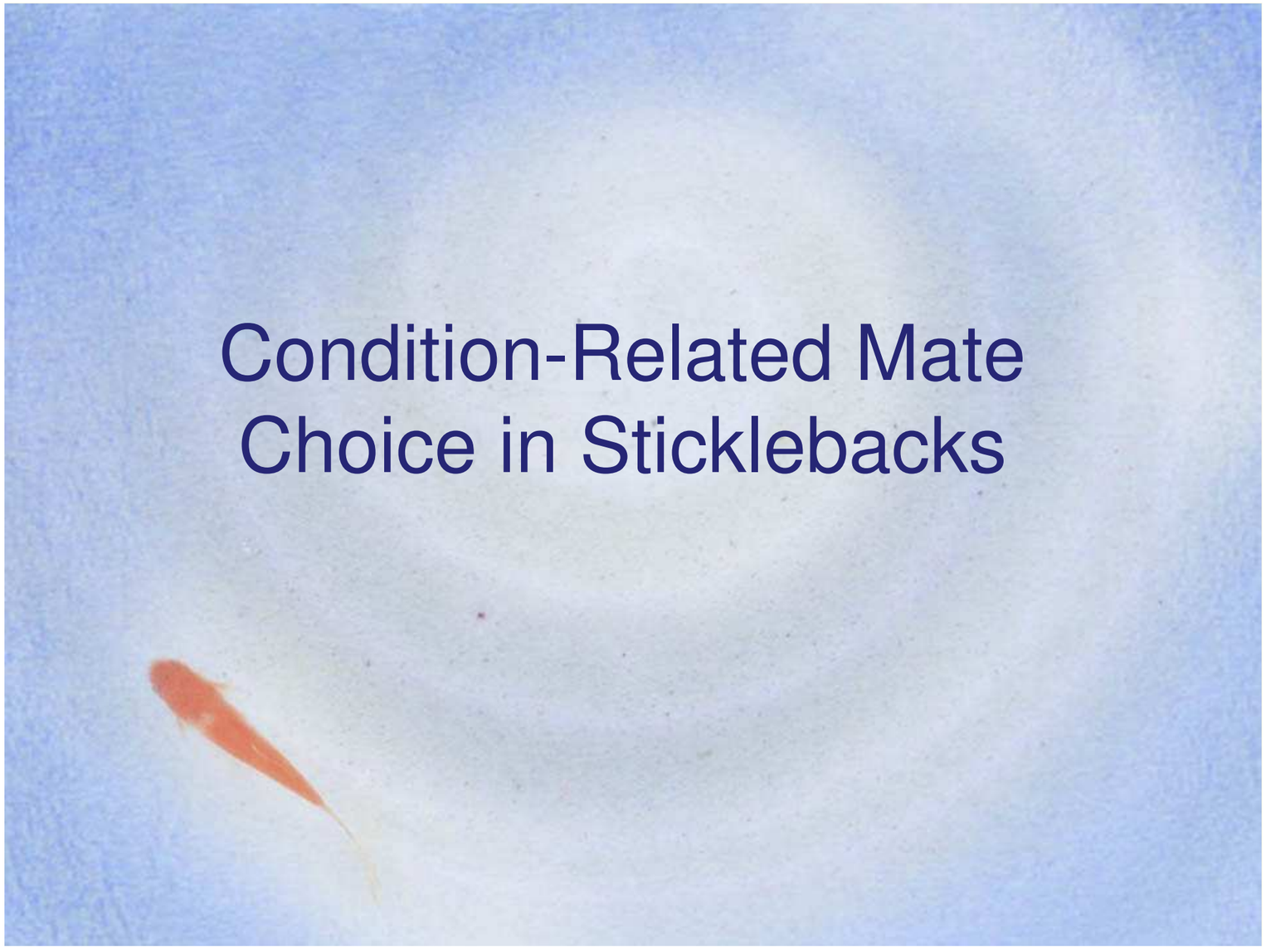
- Entire genome sequenced of a female fish from a lake in Alaska

- Major research organism for evolutionary biologists understanding genetic changes involved in adapting to new environments, as well as, intensive sexual selection.

Prof. Dr. Theo C. M. Bakker

- Explores evolutionary processes in ecosystems
- Main interest in selective forces that drive the evolution of life history, behavioural and morphological traits in animal populations
- He is also interested in underlying population genetic processes

- His current research is in evolutionary ecology of natural and sexual selection in three-spined sticklebacks (*Gasterosteus aculeatus*, Gasterosteidae) and *Pelvicachromis taeniatus* (Cichlidae)…


Condition-Related Mate
Choice in Sticklebacks

Hypotheses / Issues

- Sexual selection through female mate choice
- Heritability estimates of mate choice
- Covariance of condition dependence (CD)

Basic Definitions

- Heritability
- Condition Dependence (CD)
- Condition Factor
- Pleiotrophic Effects

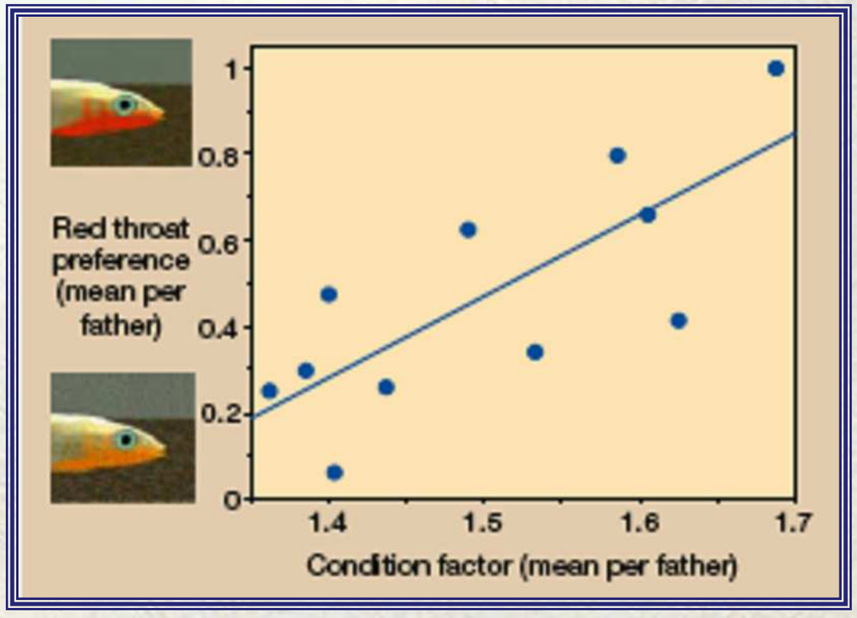
In This Study…

- Bred and wild-caught stickleback parents used in standardized lab conditions

- Removed offspring from fathers' nests 1 hour after fertilization and transferred to winter conditions until reached adult body size.

- After becoming reproductive (ripe), lab-bred females were given 2-minute choices between 2 computer simulated courting males.

Heritability & Mate Choice Findings



- Figure 1 Relation between mean male winter condition (body mass) per group in non-reproductive winter conditions and mean red breeding colouration preference of ripe females

Heritability Findings

- The offspring from different fathers significantly differed in condition ($P < 0.001$) and in female preference for red breeding colouration ($P < 0.02$).

- There was no significant female preference for bright red breeding colouration over bright orange breeding colouration ($P > 0.71$).

Female Mate Choice Findings

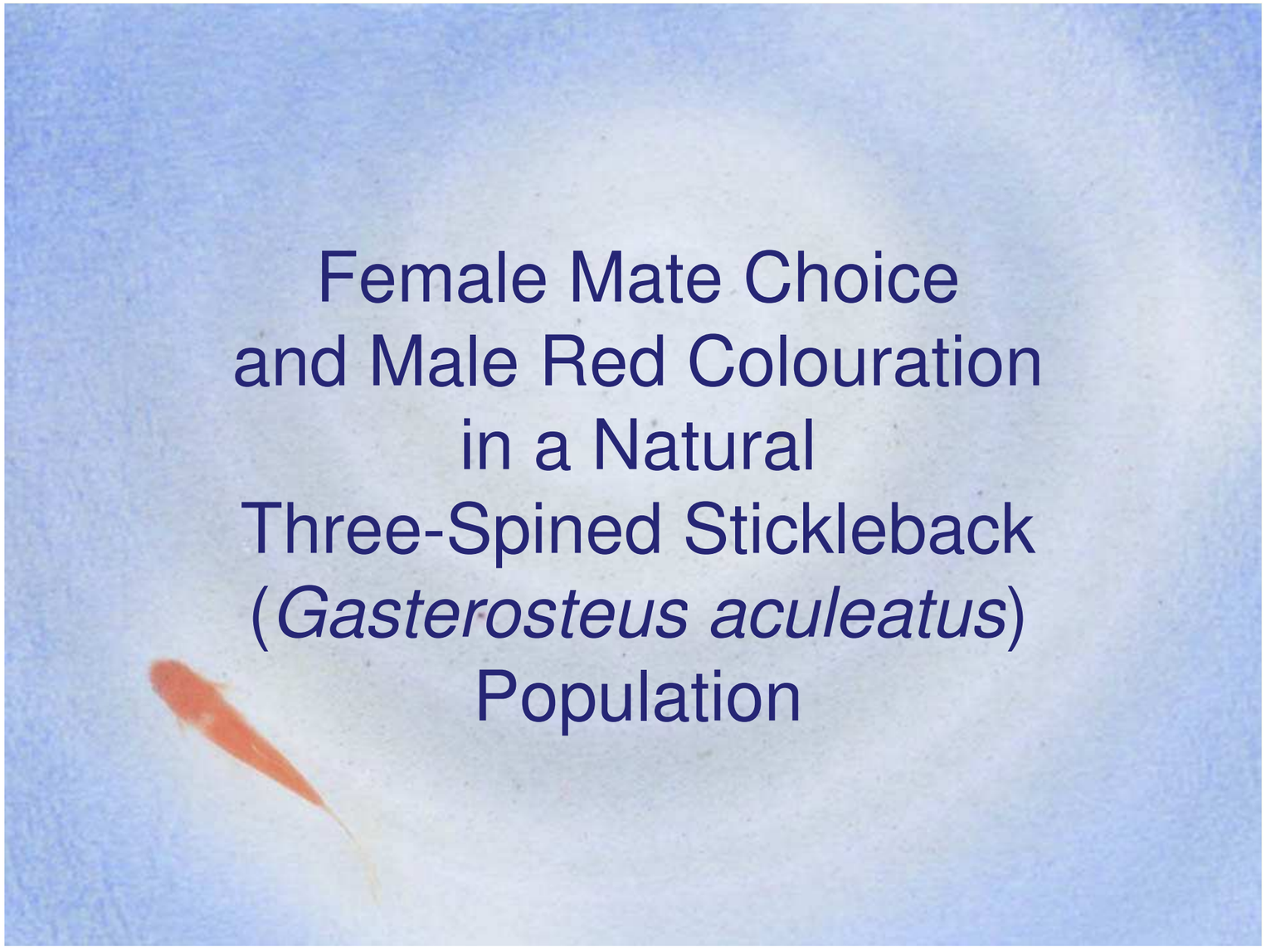
- Females from groups with a high average condition factor before reproduction preferred redder coloured males.

- Females from groups with a low average condition factor before reproduction preferred orange coloured males.

Conclusions

- Dependent covariance of mate preference with condition and breeding colouration.

- High genetic variance in condition and coloration may be occurring in population, caused by pleiotrophic effects?


Female Mate Choice
and Male Red Colouration
in a Natural
Three-Spined Stickleback
(*Gasterosteus aculeatus*)
Population

Hypotheses / Issues

- Influence of males' physical condition on the expression of red breeding colouration

- Males breeding behaviour

- Female choice relationship to the intensity of the males red breeding colouration

Basic Definitions

- Sexual Dichromatism
- Heterospecific Predation

In This Study…

- Freshwater sticklebacks observed in a natural habitat (with summer conditions in the lab):

1. Male courtship was instigated for nest development and egg receiving; where red intensity, number of eggs and condition are analyzed.

http://www.arkive.org/species/ARK/fish/Gasterosteus_aculeatus_aculeatus/Gasterosteus_ac_ac_09b.html?movietype=wmMed

http://www.arkive.org/species/ARK/fish/Gasterosteus_aculeatus_aculeatus/Gasterosteus_ac_ac_09a.html?movietype=wmMed

* only 20% of nests counted due to water conditions.

2. Female mate choice of 2 courting males dependent on red breeding colouration.

Intensity of Colouration Findings

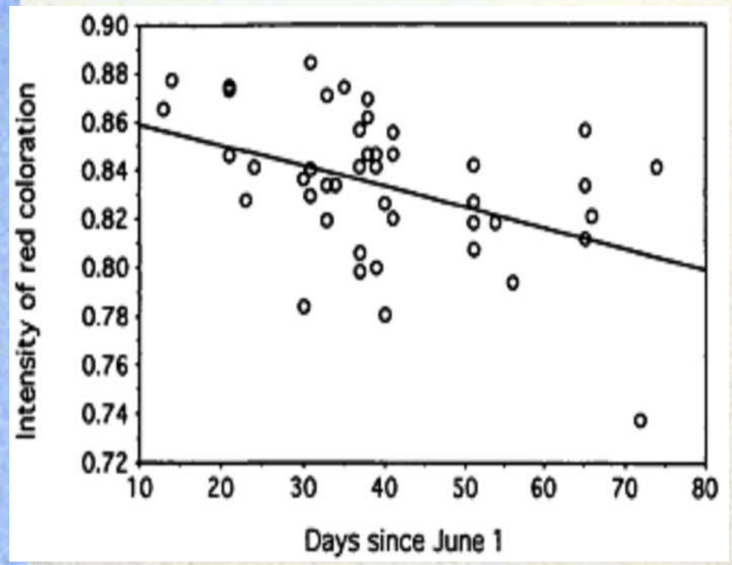


Figure 1 Correlation between intensity of red breeding colouration of reproductively active males during the breeding season

- Intensity of red colouration significantly negatively correlated with breeding season ($P < 0.005$).
- Majority of males complete only 1 breeding cycle (1/51 males recaptured).

Intensity of Colouration Findings

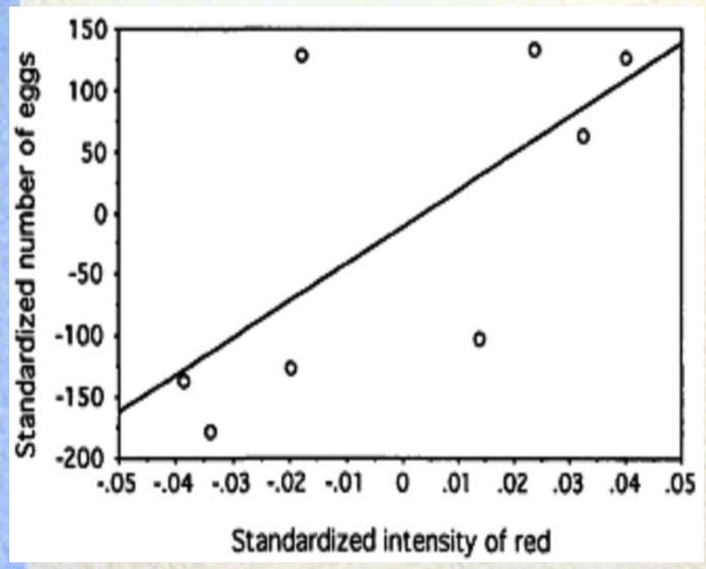
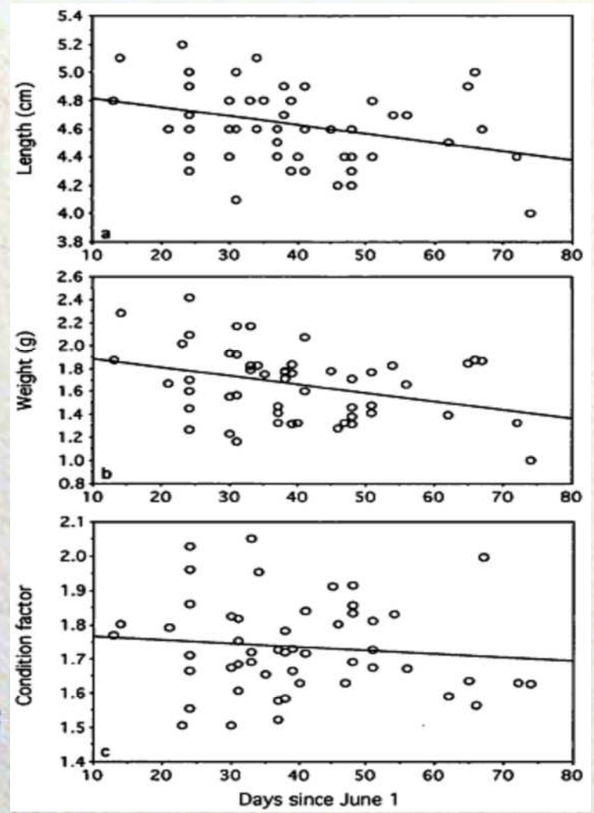


Figure 2 Correlation between the maximum of intensity of red breeding colouration and the number of eggs in nest

- Number of eggs significantly positively correlated to the intensity of red breeding colouration ($P < 0.05$).
- Increases in red breeding colouration, increases the eggs received in male developed nests.

Male Condition Factor Findings



- Length ($P < 0.017$) and weight ($P < 0.013$) significantly negatively correlated with breeding season.
- Condition factor did not show a significant correlation ($P > 0.44$).
- WHY?

Figure 3 Changes in (a) length in cm, (b) weight in g, and (c) overall condition factor

Preference of Female Findings

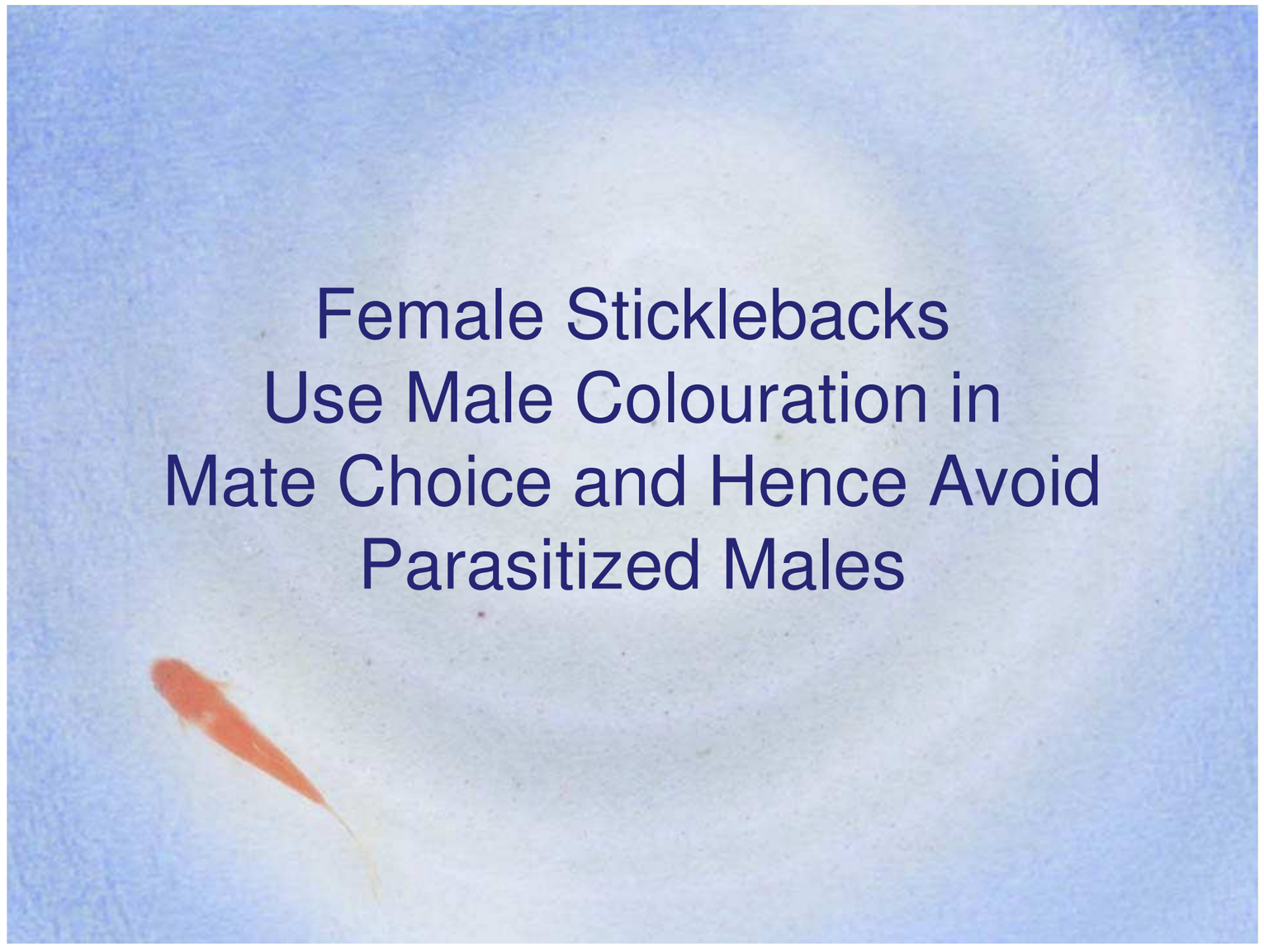
- Ripe females of this population significantly prefer redder males ($P < 0.01$).
- The sexual dichromatism acts as a decision-making tool made by the female to choose a mate.

Conclusions

- Increase in red breeding colouration in courting males, the more attractive the population to ripe females.

- Changes in red breeding colouration intensity, male condition and eggs received, may be attributed to:
  - Biotic / abiotic factors
  - Development and location of nests
  - Water currents
  - Predation
  - Aggression / defensive / paternal care behaviour

Female Sticklebacks Use Male Colouration in Mate Choice and Hence Avoid Parasitized Males



Hypotheses / Issues

- Sexual selection of male ornaments reveal male's condition (ie. parasitization)

- Females recognize formerly parasitized males by lower intensity breeding colouration

- Additive genetic variation for parasite resistant genes

- Intersexual selection on males is more important than intrasexual selection

Basic Definitions

- Additive Genetic Variation
- Intersexual Selection
- Intrasexual Selection

In This Study…

- Separation of male and female stickleback (in the lab) and female choice govern the following procedures:

1. White and green light conditions partitioned between females and courting males with varying breeding colouration intensity.

2. Bright males contained in 2 tanks (control, and parasite infected using “white spot” ciliate) while viewed by females to choose.

White Light & Green Light

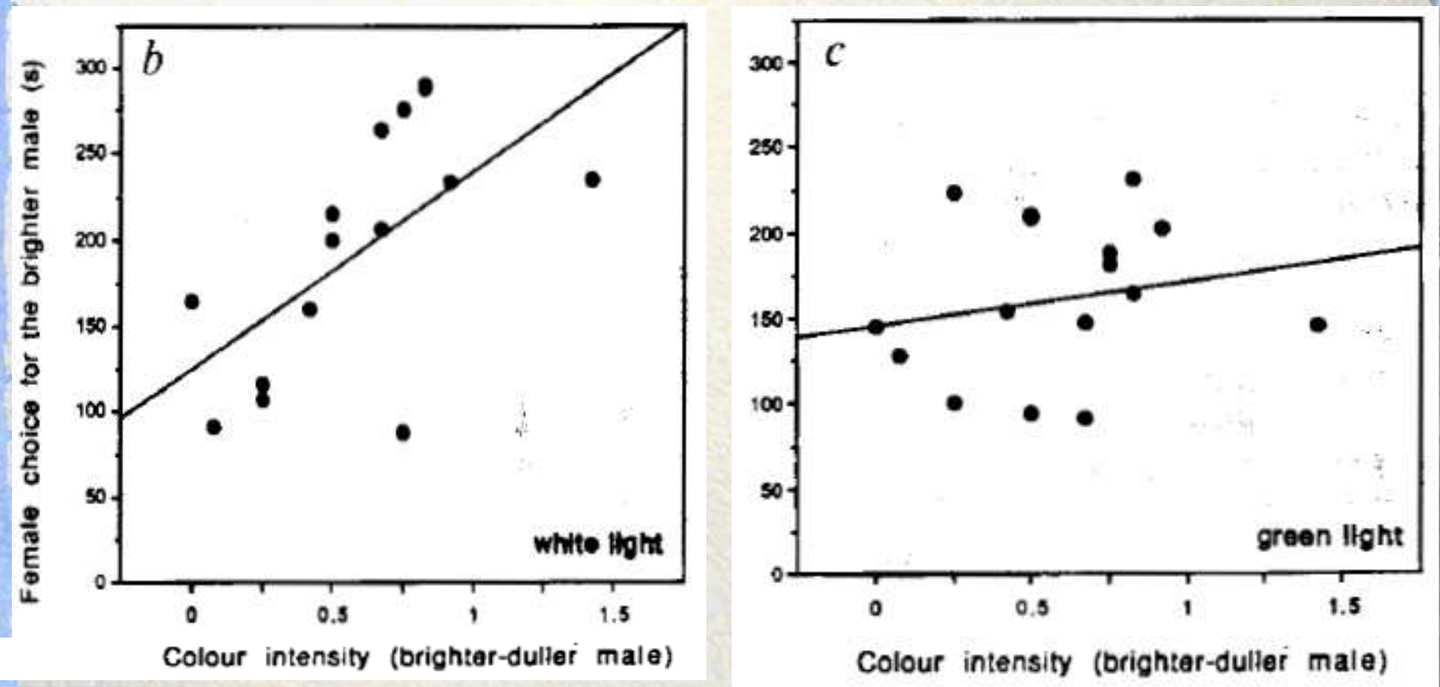


Figure 2 Contrast of colour intensity and female mate choice with (b) white light ($P < 0.01$) and (c) green light ($P = 0.75$).

White/Green & Female Choice

- Green light conditions prevented the cue of red breeding colouration by females.

- White light conditions allowed the cue of red breeding colouration by females.

Parasitization & Female Choice

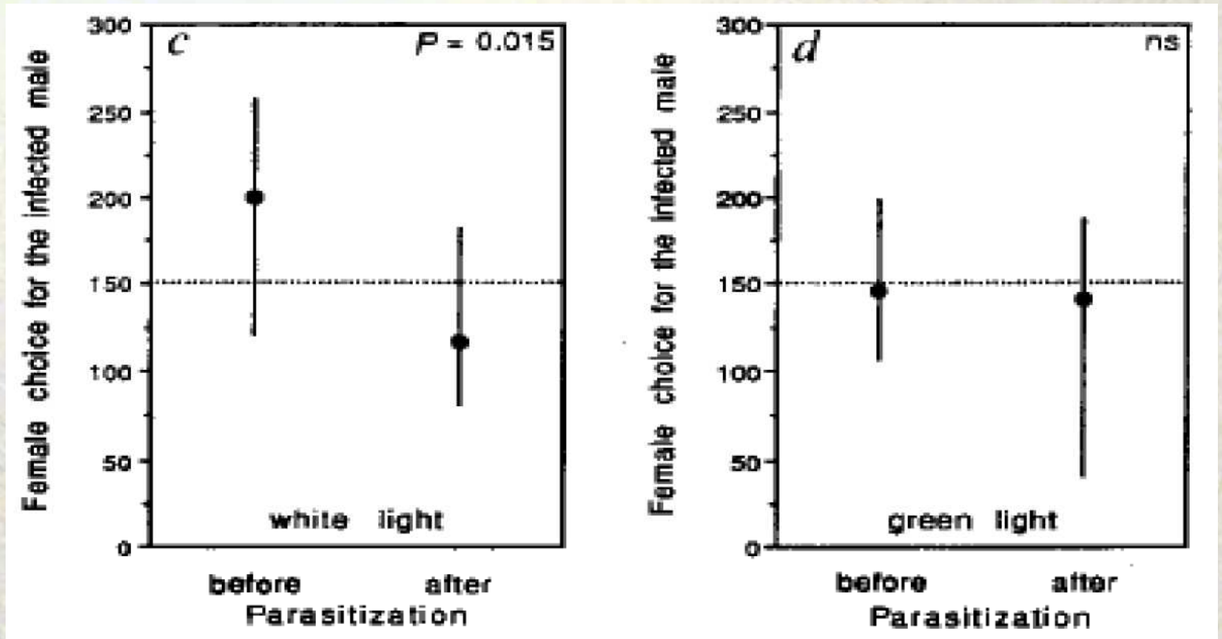


Figure 3 Female choice for the infected before parasitization of the brighter male (with ciliate) and after recovery from parasite under (c) white light from 3 different females, and (d) green light from 4 different females

Parasitization & Female Choice

- Females can recognize formerly infected (parasitized) males in white light conditions.

- Green light conditions construe the visual recognition of breeding colouration.

- Implication of female detection prior to parasitization of males.

Conclusions

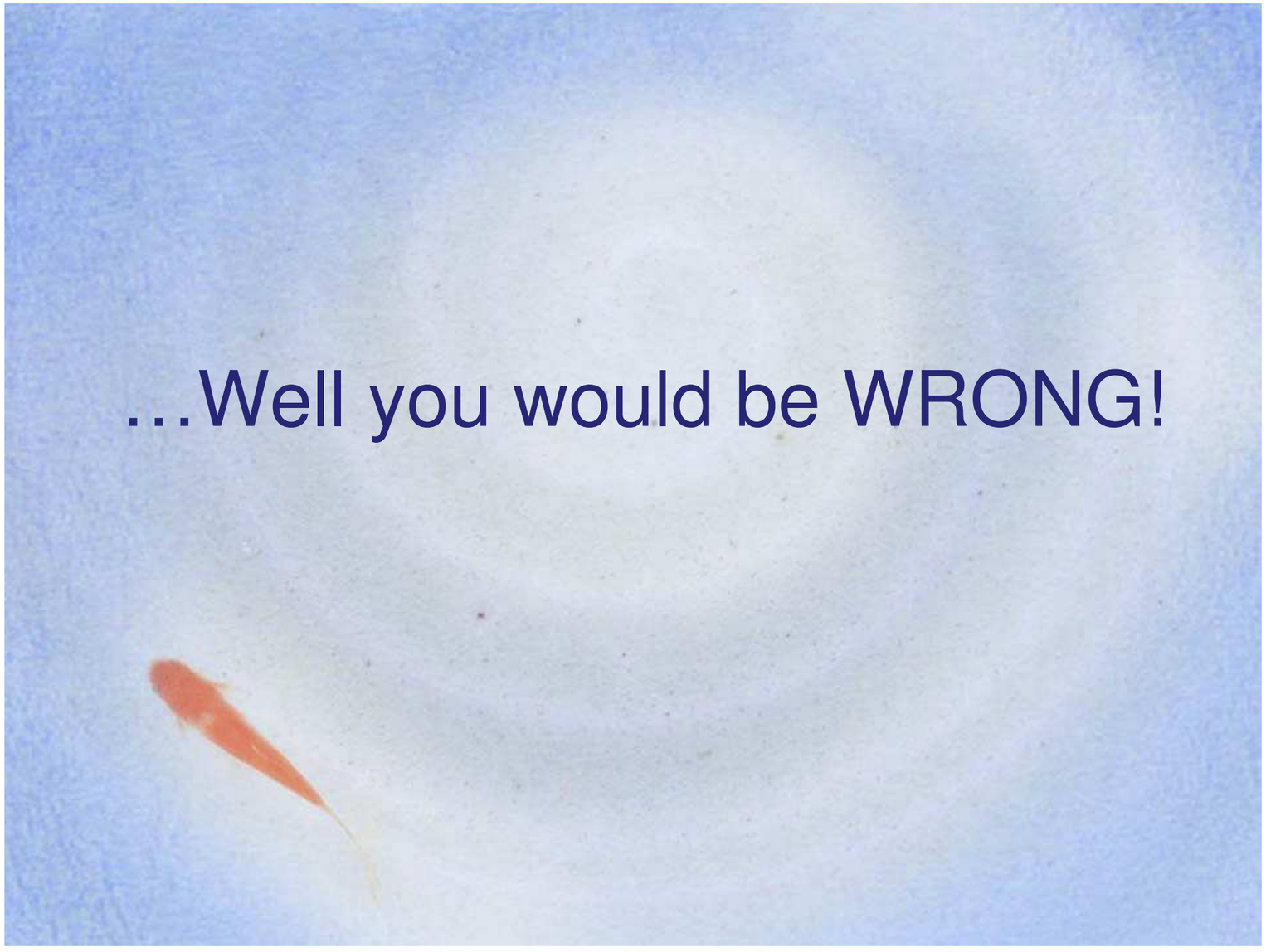
- Females prefer to mate with males handicapped by secondary sexual ornaments (red breeding colouration).

- No use of male courtship intensity in decision-making.

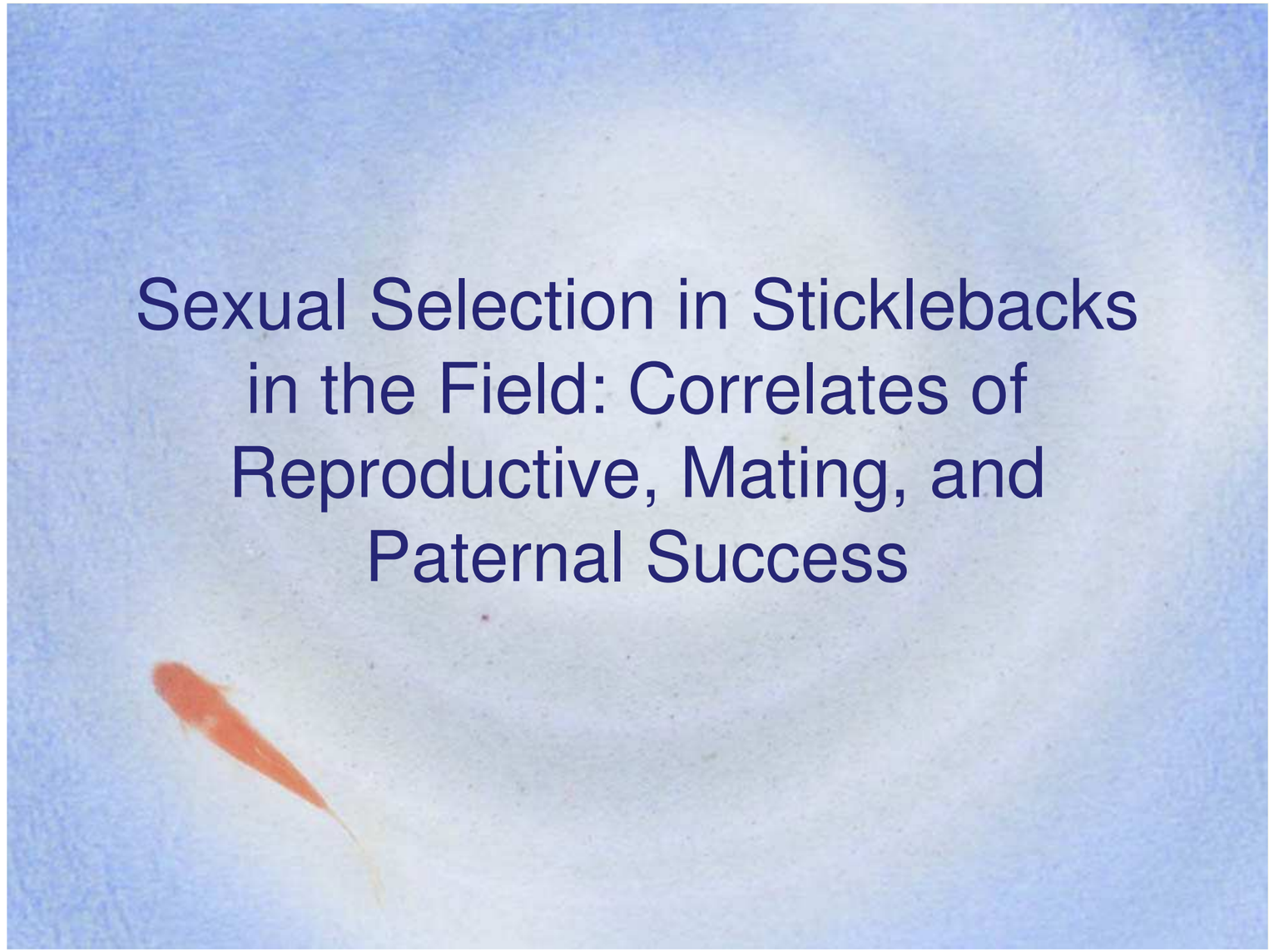
- Any agent influencing condition affects intensity of breeding colouration and females mate choice.

- Intersexual selection is most important since females primarily choose mates dependent on visual appearance.


At this point, is everything
clear to everyone?


…Well you would be WRONG!

Sexual Selection in Sticklebacks in the Field: Correlates of Reproductive, Mating, and Paternal Success



Sexual selection in sticklebacks in the field

- Female mate choice powerful selective force on male secondary sexual traits
- Female choosiness can evolve for 3 reasons
- Rewarded with direct fitness benefits (paternal care)
- Offspring of choosy females will inherit either genes for attractiveness or
- Inherit genes for viability

4 hypotheses to explain the evolution of complex displays

- Multiple message hypothesis
- Redundant signal hypothesis
- Unreliable signal hypothesis
- Multiple context hypothesis
- Reproductive Success
- Mating Success
- Paternal Success

- Experiment was conducted in an unmanipulated natural setting to understand how sexual selection actually operates

In This Study…

- 2 stickleback populations differing in ecology
- Test which males traits and nest-site traits are correlated with reproductive success
- For one population paternal success and mating success were measured separately in order to determine whether paternal success and mating success are correlated and whether females prefer good fathers

Wohlensee population

- Breeding season 1993 2m square littoral zone
- Shallow water (10 - 25cm) preferred breeding site
- Parasite present, orange yellow worm, *Pomphorhynchus laevis*
- Reduces stickleback fitness

- 15 males studied in early group (April)
- Second similar sized group studied in May
- Checked males daily for changes in group composition, nest positions, and willingness of males to show courtship to a dummy of a ripe female.

- Measured colour intensity of males with a densitometer

- Length and mass were measured to calculate their condition

- Males were killed to determine the severity of parasite infection

Roche population

- Breeding season 1995 small channel
- Depth varied between 50 - 80 cm
- Sparse vegetation
- High current
- Low parasite loads, none prevailing in this population

- 69 males sampled
- Data on paternal success for 45 of the males (15 June, 19 May, 11 July)
- Determined colour intensity of throat and eyes
- Length and mass calculated for condition

- Nests were present at 3 depths (65 cm, 45 cm, 20 cm)
- Current measured at each depth (stronger at depth)
- Measured temperature and concentration of dissolved oxygen
- Recorded whether nest was hidden
- Eggs present in nest were counted to determine parental success

Figure 1

- June sample in Roche population
- Number of eggs collected by males
- Peaks at stages 15-16 (approx 3 days)
- Males collect eggs for about 3 days then provide care
- Decreases due to egg mortality

- Paternal success determined by the number of eggs that survive to hatching

- Males : clean, oxygenates, defends eggs ensuring survival

Wohlensee population early group

- One male trait that correlated with reproductive success was male SIZE
- Bigger males produced more progeny

- Table 1

Wohlensee, reproductive success	
Early group n = 13	$r^2 = 0.36$
Body Size	0.60

- Figure 2

Wohlensee population late group

- Positive correlation between egg number and intensity of red throat colouration
- Negative relation between egg number and presence of parasite

- Table 1

Wohlensee, reproductive success	
Late Group n= 10	r = 0.79
Red intensity of throat	0.49
Presence of parasite	-0.56

- Figure 3

Roche population May sample

- Reproductive success correlated with depth, distance upstream, number of snails (predators), number of intruders, number of female approaches
- Mating success - only nests with higher temperature had higher success

- Table 1

Roche, May		
Mating success	n = 10	r = 0.72
Number of snails	0.70	
Date of start of nest	- 0.61	

June sample

Table 1

Roche, June		
Reproductive success	n = 36	r = 0.21
Body size	0.31	
Presence of plant	0.31	
Mating success	n = 23	r = 0.51
Body size	0.62	
Presence of plant	0.47	
Condition	0.36	
Standard [oxygen]	0.32	

June sample

- Larger males and males with hidden nests had higher reproductive success
- Mating success was also higher
- Males with successful nests had intense blue eyes and nests in stronger currents
- Unknown whether it is nest concealment or depth that is the relative factor

July sample

Table 1

Roche, July		
Reproductive success	n = 11	r = 0.74
Body size	0.49	
Proportion of females in headup	- 0.85	
Mating sucess	n = 10	r = 0.64
Body size	0.83	
Red intensity of throat	- 0.91	
Mating success, largest male excluded	n = 9	r = 0.63
Body size	0.28	
Red intensity	- 0.21	

July sample

- Reproductive success was positively correlated with number of spawnings per hour
- Larger males produced more offspring
- Mating success - larger males with less intense red throats had higher mating success
- Paternal success associated with green eye intensity

Pooled Roche samples

- Only trait that was significantly positively correlated was males size
- Red intensity had a non-significant negative correlation
- Table 1

Roche, pooled		
Reproductive success	n = 66	r = 0.13
Body size	0.28	
Red intensity	-0.21	
Mating success	n = 44	r = 0.20
Body size	0.41	
Red intensity	-0.20	

- Therefore, overall the male trait that was most significant was body size

- Better paternal care preferred by females

- Large body size more advantageous in male-male competition

http://www.arkive.org/species/ARK/fish/Gasterosteus_aculeatus_aculeatus/Gasterosteus_ac_ac_12.html?movietype=wmMed

Interesting findings

- Roche samples - no association between throat colour and reproductive/mating success

Possible Explanations

- In lab, variations in male traits were minimized. In field, females prefer males with other traits not just red colouration
- Redder males have more aggression, which may reduce mating possibilities
- Costs of choice in the field (eg predation) may reduce females choosing redder males
- A female-biased operational sex ratio may reduce female choosiness
- Mating advantage of redder males might not result in acquiring more eggs, but in acquiring eggs of better quality, mutual mate choice
- Present tests may have had insufficient power to detect the advantage of red intensity

Explanation for redness in Wohlensee late population

- Positive correlation with red colouration
- Males had very low reproductive success
- The availability of ripe females was limited
- Females may have preferred redder males for genetic benefits more that paternal care

- Territory traits also important in reproductive success
- Females more likely to choose nests that are concealed
- Nests were also in the deepest levels of the stream with higher water velocity (better water exchange)
- Out of reach of predators (grey heron)

- Redder males did NOT have higher mating success, therefore were not better fathers

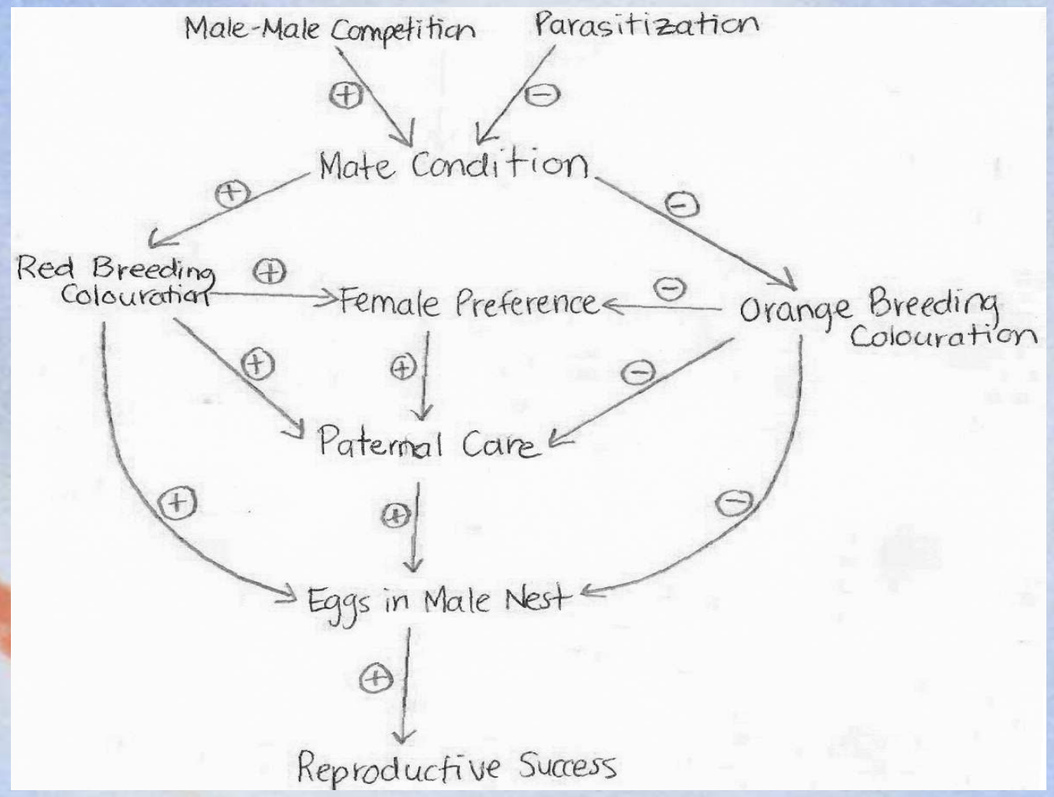
- Further research is needed to determine the correlation between red colouration and paternal quality

- In conclusion, findings agree with the multiple message hypothesis of sexual ornamentation

- The multiple sexual traits revealed different aspects of male quality: females find larger males attractive for better paternal quality, but red males are preferred for better genetic qualities

Discussion of Behavioural and Developmental Pathway

Laboratory Conditions Pathway



Natural Habitat Conditions Pathway