

ZOOL 567- Annotated Bibliography

Courtship roles

Masonjones, H. D., & Lewis, S. M. (2000). Differences in potential reproductive rates of male and female seahorses related to courtship roles. *Animal Behaviour*, 59(1), 11-20.

<https://doi.org/10.1006/anbe.1999.1269>

Summary: This article investigated the relationship between courtship roles and potential reproductive rates when comparing male and female seahorses, *Hippocampus zosterae*. Prior research minimally proves whether males who invest dominantly in parental care devote more care per offspring than females. Masonjones and Lewis (2000) sought to measure potential reproductive rates in male and female dwarf seahorses to determine if a higher potential reproductive rate will be the sex that competes more intensely for the opposite sex. To investigate this hypothesis, two measures were calculated: 1) the maximum number of offspring produced per breeding cycle when an unlimited number of mates were available and 2) the time each sex was not available for mating; through pairing sexually isolated males and females with reciprocal sexual partners and measuring the time it took for each sex to prepare to mate. This was followed by executing experiments that measured gestation time. Results showed that females took 2 days longer to mate than males and were unable to reproduce (time out) for 1.2x longer than males. This led to males being able to produce 17% more offspring in one breeding season than females. Additional experiments were completed using calculations to determine length of gestation (which was used as a measure to aid in getting an estimate of total reproductive cycle duration), potential reproductive rate, along with reproductive 'time out.' These results indicate that the research's hypothesis was supported as males competed more intensely for access to the opposite sex having the higher potential reproductive rate. This study provides further confirmation of traditional courtship roles that the sex having higher potential reproductive rates equates to having less access to the opposite sex. Future areas of research could include comparing how relative parental investments and potential reproductive rates can indicate courtship roles and competition for the opposite sex.

Word Count- 300

Contribution: This article was chosen to be part of my literature review because within the article it highlights courtship roles within seahorses and puts emphasis on how male seahorses provide the parental care which is the focus of my topic. This article advances knowledge in the field by posing good future direction in possible studies looking at different species in their courtship roles. The model of traditional courtship roles was supported by these research findings in seahorses. Measuring potential reproductive rates using equations provided a quantitative analysis of courtship roles supporting previous work on the topic.

Word Count- 95

Sex roles

Vincent, A., Ahnesjö, I., Berglund, A., & Rosenqvist, G. (1992). Pipefishes and seahorses: Are they all sex role reversed? *Trends in Ecology & Evolution*, 7(7), 237-241.

[https://doi.org/10.1016/0169-5347\(92\)90052-D](https://doi.org/10.1016/0169-5347(92)90052-D).

Summary: This article reviews research that highlights male pregnancy in both seahorses and pipefishes which has led to the speculation that females that are the ones to compete more intensely for access to mates. This is said due to the inference that males limit female reproduction. The studies of Syngathid fish regarding the reproductive ecology have only been explored within 10 years of this article. Therefore, further research completed has proven that it can be either sex that is the predominant competitor for mates in various species, expanding literature. A link has been detected in the family that comprises pipefishes and seahorses between mating patterns and sex roles. However, such research done does not exclusively associate sex role reversal with male parental care. Sex role reversal defined by females competing more intensely than males for access to mates in comparison to the usual pattern tests our theoretical understanding of the evolution of sex differences. Seahorses and pipefishes have displayed one of the classic examples of sex role reversal through highly specialized male pregnancy that decreases the male reproductive rate, therefore resulting in more intense female competition for males along with greater sexual selection pressures on females. Evidence with *Hippocampus fuscus* (Sri Lankan seahorse) display these seahorses are not sex role reversed despite limited space for brooding and lengthy care periods. The predominant competitors for access to mates are males exemplified: 1) in courtship, where males exhibit greater amounts of behavior patterns and 2) distinguished aggressive behaviors in courtship (tail wrestling and snapping with the snout) were seen in males. It has been found that monogamous species are considered to have “conventional” sex roles, whereas sex role reversed species are polygamous. Future research to understand ecological and social factors that may be linked to promoting different mating patterns within the Syngnathidae family.

Word count- 300

Contribution: This review summarizes that despite male pregnancy and parental care seen in both seahorses and pipefishes does not signify that females are the sex that compete more intensely for access to mates. Several studies have shown that the predominant competitors for mates are males which prove a traditional sex role. This article has linked an association where species with “conventional” sex roles are monogamous, whereas sex role reversed species are polygamous. Finding out whether this a causal relationship is unidentified but could be useful information. As a review, this article consists of applicable information on the mating behaviors of seahorses.

Word count- 100

Vincent, A. C. J. (1994). Seahorses exhibit conventional sex roles in mating competition, despite male pregnancy. *Behaviour*, 128(1/2), 135-151.
<https://doi.org/10.1163/156853994X00082>.

Summary: This article highlights that pregnancy is undergone by males in seahorses and mentions the assumption that seahorses were considered sex-role reversed since male reproduction is limited by the pregnancy, thus signifying a female-biased operational sex ratio (OSR). The research done by Vincent (1994) studied this assumption, as it is mentioned that no prior literature has investigated this speculation. Vincent (1994) used the species *Hippocampus fuscus* to examine the prediction of whether females compete more intensely than males for access to mates. The investigation of interactive behaviours and states was recorded using a video camera. Courtship behaviours (ex. colour heightening, approaching, departing) and behaviours characterized with competition (ex. Snapping, struggling, and wrestling, intruding) were observed on a hand-held computer. The findings of the study were observationally and comparatively obtained. Major findings of the experiment were contradictory to assumptions, despite pregnancy occurring in male seahorses. Through observations, it was concluded that *H. fuscus* demonstrated conventional sex roles. This was inferred from the following inspections: 1) levels of male intrasexual competition were significantly higher than during female intrasexual competition (in terms of behaviours common to both sexes), and 2) aggressive behaviours were only exhibited by males. Although competition was seen in females, occurrences were to a much lesser extent than exhibited by males. Intrasexual competition and mate choice were noted to likely involve establishing which individual successfully mated, although the results of the experiment do not confirm the significance of these two processes. Contrary to predictions made and despite male pregnancy, the significance of the findings shows that *H. fuscus* revealed conventional sex roles. Future studies should aim to investigate how intrasexual competition and mate choice may influence successful mating seen in seahorses. An examination of the influence of male pregnancy on the OSR, despite conventional sex roles should also be assessed.

Word count- 299

Contribution: This article advances knowledge in the field by studying the unique conventional sex roles displayed in seahorses, despite male pregnancy. Vincent (1994) challenged the assumption posed that seahorses exhibit sex-role reversal, proving it to be wrong using comparative and observational experimental approaches. Conventional sex roles seen in *H. fuscus* demonstrated by greater intrasexual competition in males and substantial aggressive behaviours in males compared to females. This article will be useful in my literature review as it highlights the type of sex role seen in seahorses that can be linked to mate selection, and ultimately mating behaviours.

Word count- 96

Mate selection

Naud, M-J., Curtis, J. M. R., Woodall, L. C., & Gaspar, M. B. (2009). Mate choice, operational sex ratio, and social promiscuity in a wild population of the long-snouted seahorse *Hippocampus guttulatus*. *Behavioral Ecology*, 20(1), 160-164. <https://doi-org.ezproxy.lib.ucalgary.ca/10.1093/beheco/arn128>

Summary: This article examined social interactions and mate choice in *Hippocampus guttulatus* male and female seahorses with relation to operational sex ratio (OSR). OSR, defined as the ratio of sexually active males to females in a population is believed to be one of the several factors influencing which behaviour is displayed by which sex in a population. Existing literature on OSR and mate choice in seahorses is scarce compared to a selection of more readily studied pipefishes. Therefore, this article presents an extension of evidence of social promiscuity, size-assortative mating, and an OSR on seahorses. Naud et al. (2009) aimed to do the following: 1) characterize social interactions, 2) calculate OSR in wild *Hippocampus guttulatus*, and 3) evaluate effects of familiarity and body size on mate choice in free-living males and females. SCUBA divers observed and recorded individuals engaging in social interaction, greeting, courtship, mating, or aggression, along with the reproductive status of adult seahorses. Greetings were distinguished by body brightening along with at least 2 of 4 common ritualistic behaviours. Courtship, meaning readiness to mate was characterized by greeting behaviours, pointing (female lifting head toward surface) and pumping (male contracting pouch) or rising (pair swimming vertically). Mating, exhibited by rising and transfer of eggs, while aggression was noted when individuals engaged in tail wrestling, chasing or rapid snout strikes (snapping). The degree of social promiscuity along with size-assortative mating, also investigated. The results of the study propose choosiness in male *H. guttulatus* especially toward larger females and tendencies to be more competitive, suggesting sexual selection acting more strongly on females in such a system. Future studies should include more studies on mate choice with a large study population to further investigate influences driving seahorse mating systems. Such studies as this provide valuable information on connections between OSR and sex roles.

Word count- 300

Contribution: This article highlights social interactions and mate choice in *Hippocampus guttulatus* populations relating to OSR that provide evidence of the choosier and more competitive sex in mate selection. Several social behaviours were noted that enabled researchers to propose sexual selection acting more strongly on females in this system. With few existing literature on mate choice in seahorses, this article has contributed worthy knowledge on mate choice and OSR. Through observations made on social interactions, this article was included in my literature review providing evidence on the choosiness and competitive nature when it comes to mate selection in seahorses.

Word count- 98

Mattle, B. & Wilson, A. B. (2009). Body size preferences in the pot-bellied seahorse *Hippocampus abdominalis*: Choosy males and indiscriminate females. *Behavioral Ecology and Sociobiology*, 63(10), 1403-1410. <https://doi.org/10.1007/s00265-009-0804-8>.

Summary: This article investigated the significance of body size in reproductive decision-making seen in *H. abdominalis* raising interest in both sexes potential mating partners of different sizes. Strong preference for larger females suggested sexual selection may act strongly on female body size in *H. abdominalis* consistent with prior knowledge on the importance of female body size for reproductive output of this species. Previous studies exhibited flexibility of sex roles in *H. abdominalis* gave inspiration to complete an experimental study to explore the role of body size in both female and male mate selection. Testing of the hypothesis that females show no body size preference, while males do to confirm whether female body size is the key determinant of offspring number and size in *H. abdominalis*. Seahorses were anesthetized to place in tanks and tag with a visible fluorescent tag, a photo was taken along with a measurement of weight. Seahorses were placed in different experimental tanks and each individual was offered a choice between two seahorses of the opposite sex belonging to different size classes. The mate-choice experiments were conducted during a time where seahorses are mostly actively reproductive (first hours of daylight). Recordings on digital video cameras located in the test tanks were connected to a computer generating films. Results demonstrated seahorse courtship behavior that involved increasingly intense interactions between mating partners. The study showed that mating behaviors in *H. abdominalis* vary significantly between males and females, providing evidence for the hypothesis presented. The significance of the study highlights the differences in courtship behavior between males and females proving highly discriminate males and indiscriminate females. Future studies should aim to study larger and more balanced populations to decrease possibility of statistical errors as well as attempt to investigate chemical cues concerning mate-choice decision of seahorses.

Word count- 295

Contribution: This article was selected to be part of my literature as it provides knowledge on the behaviours associated with mate-choice decision seen in seahorses. Body size preference has been noted to be an important factor in male mate selection suggesting they are discriminate whereas vague courtship behaviors were detected in females therefore proposing them as being indiscriminate. Previous studies suggest the importance of female body size for reproductive output of this species to maximize the reproductive success of males, this study has reaffirmed these findings through differences in courtship behaviours between males and females.

Word count- 94

Bahr, A., Sommer, S., Mattle, B., & Wilson, A. B. (2012). Mutual mate choice in the potbellied seahorse (*Hippocampus abdominalis*). *Behavioral Ecology*, 23(4), 869-878.
<https://doi.org/10.1093/beheco/ars045>.

Summary: This article highlighted that mate choice decisions may be influenced by a multitude of behavioral, morphological, olfactory, and vocal signals that vary between environmental conditions along with between the sexes. Prior research has studied such traits in isolation, so this study serves to investigate the impact of 2 key traits (olfactory cues and body size) on mate choice decision in *Hippocampus abdominalis* in a hierarchical experimental design (1. Olfactory cues only, 2. Olfactory cues and body size, and 3. Free interaction) to examine influences under increasing levels of multimodal stimulation. Methods included the collection of fin clips of anesthetized animals used for genetic analysis and photos of the animals to determine measurements. An experiment was conducted providing individuals of both sexes olfactory cues from differing Major Histocompatibility Class II beta-chains [MHIIb] which is linked to possible advantages to the choosy individual of factors such as immunity and inbreeding. 3 different olfactory stimuli varying in their MHIIb dissimilarity to the focal individual were used to test the preference of subjects. Secondly, the importance of olfactory and visual cues in individual preference was observed by offering male and female seahorses a choice between a large and small partner, then looking at MHIIb diversity. Lastly, the free interaction and mating of individuals was investigated to see whether mate choice was influenced by MHIIb and/or body size preferences. Results of these various experiments showed: 1) female preference for MHIIb-dissimilar stimuli than for MHIIb-similar cues and 2) male preference for larger females. Together, these results indicate that male and female seahorses have preferences for morphological and olfactory traits in mate choice decisions, concluding the existence of mutual mate choice in this species. As this study did, future work should examine multivariate interactions between traits to expand the limited existing body of research.

Word count- 297

Contribution: This article advances knowledge in the field as it serves as evidence of studying the integration of multiple mating cues and both male and female perspectives to investigate mate choice and sexual selection more deeply. This article provides support that there exists mutual mate choice in the *H. abdominalis* species, where males prefer and mate with larger females, whereas females prefer and mate with MHIIb-dissimilar males. This was included in my literature review as it outlines that not only males prefer certain traits in mate selection, but females do as well, as other research articles have only shown male preference.

Word count- 100

Bahr, A., & Wilson, A. B. (2011). Impact of sex-role reversal on the diversity of major histocompatibility complex: Insights from the seahorse (*Hippocampus abdominalis*). *BMC Evolutionary Biology*, 11(1), 121. <https://doi.org/10.1186/1471-2148-11-121>.

Summary: This article examines the major histocompatibility complex (MHC/MH) which is known to play a role in both immune function and olfactory-mediated mate choice. Further investigation presents an ideal system in the effects of these two selective forces on genetic diversity. Seahorses display highly developed male parental care, female-female competition, and mate choice that serves as an ideal study subject to present MH-odor mate choice cues which are expected to influence the intensity of sexual selection. Mating patterns in which individuals with different phenotypes mate with one another are suspected to promote MHC diversity and increase the number of heterozygote individuals in natural populations, therefore assuming sexual selection can contribute to MHC allelic diversity. Prior knowledge focuses on species that exhibit conventional sex roles, with choosy females and competitive males. This study aims to characterize MH-variation in sex-role reversed populations of *Hippocampus abdominalis* that exhibit a highly developed form of male parental care. Location of a highly variable copy of the MHIIb locus in this species like those of conventional sex roles species was done through the genome sequencing and transcriptome screening of brood pouches tissues in male seahorses. The samples of MHIIb are found in male brood pouch tissues and may suggest functional activity in the molecules during male pregnancy. Complete MHIIb sequences were obtained from the male subjects and analyzed. This study yielded the first data on the pattern of MH diversity in *H. abdominalis* which was concluded to be similar in structure to that in other vertebrates, containing high genetic diversity. Determining whether MH-odor cues are used in mate choice decisions in this species of seahorse are ongoing, and future aims to explore these findings would help highlight the roles of both natural and sexual selection in exhibiting high levels of MHIIb diversity found in the seahorse.

Word count- 299

Contribution: This article advances knowledge taking into consideration the MHC analysis of species exhibiting sex-role reversed mate choice, whereas prior findings focused mostly on species that display conventional sex roles. This article supports previous findings (above reference) in literature that MHC plays a role in immune function and olfactory-mediated mate choice suggesting males and females may differ in their ability to detect odor cues. This article was included in my literature review because one of the authors from a previous source I have used also wrote this, and I believe this is an expansion of the work the author started.

Word count- 99

Monogamy in seahorses

Wilson, A. B., & Martin-Smith, K. M. (2007). Genetic monogamy despite social promiscuity in the pot-bellied seahorse (*Hippocampus abdominalis*). *Molecular Ecology*, 16(11), 2345-2352. <https://doi.org/10.1111/j.1365-294X.2007.03243.x>.

Summary: This article talks about sexual selection theory having a positive correlation between relative parental investment and mate choice. Although it is seen in syngnathid fishes (seahorses and pipefishes) that males brood offspring due to evolved specialized brooding structures, all seahorses are known to exhibit conventional sex roles with more male-male competition for access to mates along with strict genetic monogamy. Prior studies have addressed explanations on the lack of multiple mating in seahorse species, but specific hypotheses have not been explicitly addressed. This study aims to explore genetic monogamy despite social promiscuity in *Hippocampus abdominalis* populations and it hypothesizes plasticity in sex roles of the species, subject to local population density and sex ratio. The use of novel microsatellite markers was used to determine genetic mating patterns in low- and high-density field populations, as well as the examination of genetic mating patterns in captive populations at extremely high densities. *Hippocampus abdominalis* subjects were used to record courtship behavior in fieldwork carried out between 2000-2005. Genomic DNA was extracted, amplified, and sequenced from male brood pouches and embryos. In all observations of observed courtship behaviour, reproduction was seen with a single female and single male, suggesting monogamy. Genetic assessment of extracted DNA indicated that all males had mated monogamously. From the results, it was concluded that there is plasticity in sex roles and that the strength of intrasexual competition and mate choice may be influenced by factors such as sex ratio and population density. Future studies should explore whether unmated females involved in promiscuous courtship behavior are more likely to contribute to subsequent broods. Future work in the lab could be done to determine whether the lack of multiple mating in male seahorses is because of behavioural restrictions, or due to the complex reproductive systems of males.

Word count- 296

Contribution: This article advances knowledge in the field of mating behavior in seahorses by studying it from a genetic scope. DNA extraction, amplification and sequencing of male brood pouches and embryos proved the genetic monogamy in seahorse mating behavior. The genetic analysis supported previous findings that have concluded that all seahorse species mate monogamously. This article was included in my literature review to expand on mating behaviors seen in seahorses, despite promiscuous courtship behavior observed, seahorses exhibit a unique characteristic of being known to monogamy. Also, the future work proposed could lead to useful knowledge to add in the literature.

Word count- 99

Vincent, A. C. J., & Sadler, L. M. (1995). Faithful pair bonds in wild seahorses, *Hippocampus whitei*. *Animal Behaviour*, 50(6), 1557-1569. [https://doi.org/10.1016/0003-3472\(95\)80011-5](https://doi.org/10.1016/0003-3472(95)80011-5).

Summary: This article investigated animal mating patterns said to be influenced by both ecological and social factors and was the first during its time to study whether male and female *Hippocampus whitei* forming pairs mated repeatedly and exclusively. Faithful pair bonds have been apparent in seahorses through clear visual evidence of having mated (female transfers eggs, male becoming pregnant) inferring sexually faithful pair bonding. Mated pairs do not disjoin unless a partner disappears or dies. The observational field study completed explored mating patterns in a wild population of *H. whitei*. The duration of the study was from November 1991- mid-April 1992, with the breeding season for *H. whitei* starting mid-late October (thus, the studying failed to observe matings at the beginning of the season). Individual seahorses were tagged with discs that hung around their necks. Observations of movement and social interactions were noted each day, and location, reproductive state, and activities of seahorses were noted as observed. Results indicated that the seahorses exhibited both social and sexual monogamy through the inspection of: 1) partners performing daily greeting rituals, 2) mating only with one another, and 3) abstained opportunities to interact with other individuals. Seahorses were seen to never abandon their partners that were injured or unable to reproduce, only if their mate disappeared or died, thus confirming faithfulness. Greetings were concluded to be significant reinforcers of pair bondings and a confirmation of presence of their partner. Suggestions were made behind males possibly insisting on monogamy due to reasons decreasing their reproductive success such as increased risk of receiving only a partial clutch of eggs or costs of female polygamy being high regarding an increased risk of disease or parasites. The future work suggested by this article is to determine whether it is a possibility that male seahorses can impose monogamy.

Word count- 299

Contribution: This article advanced knowledge in the field as it was the first of its kind to study whether *Hippocampus whitei* forming pairs mated repeatedly and exclusively. Faithful pair bonds including social and sexual monogamy have been confirmed within the Syngnathidae family, and this study adds to existing literature. This article questioned and proposed reasoning behind monogamy, suggesting future work to determine if it is the male that may impose monogamy. Information highlighted in this article will be useful in displaying examples of another species of seahorse along with knowledge on the role that greetings play within seahorse mating behavior.

Word count- 99