

ZOOL 567 – Lit Review 3: Annotated Bibliographies (final)

The bibliographies were organized into three categories according to the three main mating behaviors observed in snails: 1) choosy for larger mates, 2) choosy for mates of relatively similar size (i.e., size-assortative mating), 3) random mating/mate choice irrespective of size. Then, the articles were arranged in chronological order (earliest to latest) in each subcategory. There are 10 articles in total.

1) Mating behavior – choosy for larger mates

Cardoso, R. S., Costa, D. S., & Loureiro, V. F. (2007). Mating behaviour of the marine snail *Littoraria flava* (Mollusca: Caenogastropoda) on a boulder shore of south-east Brazil. *Journal of the Marine Biological Association of the United Kingdom*, 87(4), 947-952. <https://doi.org/10.1017/S0025315407053210>

Summary: This study observes how the *Littoraria* genus marine snail selects mates based on size. It was understood sexual selection of size exists in *Littorina* as the males choose to mate with larger females since there is a positive correlation between size and fecundity. However, there has been evidence from prior research indicating that mating behaviors in *Littoraria* snails may be affected by other factors other than size. Cardoso et al. (2007) were interested in observing the effect of size on mating and copulation, as well as if individuals perceive others' size by their shell size. They observed *Littoraria flava* in particular since it was not well studied. Cardoso et al. observed the mating of *L. flava* in an artificial rocky shore in Flexeira Beach, Brazil. They observed every mating pair and potential mate (females near mating pairs that did not mate but could potentially mate) and recorded sizes and copulation times. They also measured the shell lengths of all snails on the study site (both mating and non-mating). The snails were later sub-categorized into sexes (male and female) and then into sizes (small and large) to create four treatment groups in total. A t-test was conducted to compare the sizes between the mating and non-mating snails. An ANOVA test was conducted to analyze variances in copulation times between mating pairs. It was discovered that *L. flava* mating can consist of partners of equal sizes, but males strongly preferred mating with larger females. This is significant because it implies that *L. flava* can mate on a size-assortative basis; however, males prefer selecting larger females. Additionally, larger females had longer copulation times than smaller females, suggesting that larger females are more reproductively successful. However, the data suggested that being a larger male does not equate to higher mating success.

Contribution: This research advances knowledge as it focuses on the mating behaviors of a snail species that was previously not well-studied. This study helps confirm that size is an important trait in sexual selection for females, but less so for males. It agrees with Ng & Williams (2014) that snails can adopt size-assortative mating but prefer larger mates. This study also raises future questions about potential factors that could also strongly influence mating behavior such as intraspecific competition for mates and resource availability. I chose this article because it provides evidence that males strongly prefer larger female mates.

Dillen, L., Jordaens, K., van Dongen, S., & Backeljau, T. (2010). Effects of body size on courtship role, mating frequency and sperm transfer in the land snail *Succinea putris*. *Animal Behaviour*, 79(5), 1125-1133. <https://doi.org/10.1016/j.anbehav.2010.02.010>

Summary: This article investigates how body size is involved in mating behaviors of *Succinea putris* (hermaphroditic land snail species). There are two courtship roles that hermaphroditic snails can adopt during mating: the active role (actively initiates mating by mounting onto passive individual's shell) and the passive role (individual waits to be approached by active individual). From prior knowledge, individuals will choose mates that increase their reproductive success, and this may be linked to body size (i.e., larger partners can transfer more sperm). Dillen et al. (2010) were interested to see if the body sizes of two potential partners may predict likelihood of mating. The objectives of this study were to determine if the body sizes of two partners affects motivations to mate, courtship role determination (who will be the active and passive partners), and the number of sperm that is transferred during copulation. 900 sexually mature *S. putris* snails that were at least 9 mm in shell height were collected during their mating season. The snails were then subdivided as either "small" or "large". They paired different combinations of sizes and tagged a focal individual (to examine courtship role determination) and allowed them to mate. The researchers created 262 pairs; however, only considered the 99 pairs that copulated. The data indicated that smaller snails adopted the active role. However, the researchers speculated that hermaphrodites generally prefer playing the active role since fitness is a function of the number of matings they initiate. Therefore, they were inconclusive that size is involved in courtship role determination. A large partner and small partner were most likely to mate, suggesting that smaller individuals prefer mating with relatively larger snails. Lastly, the study confirmed that larger size correlates with higher sperm transfer. This signifies that smaller individuals select larger mates to increase their reproductive success.

Contribution: This research advances knowledge as it confirms *S. putris* (hermaphrodites) have size preferences for their mates which was previously not well researched. This article helps confirm that size is an important trait in snail/hermaphroditic mating. Additionally, it supports previous knowledge that larger mates are preferred for increasing reproductive success. This study raises future questions regarding how hermaphroditic snails allocate energy and resources during reproduction and how courtship roles are determined. I selected this article as it discusses how body size influences mating behavior, as well as proposed reasons why larger sizes are preferred in snail mating.

Saltin, S. H., Schade, H., & Johannesson, K. (2013). Preference of males for large females causes a partial mating barrier between a large and a small ecotype of *Littorina fabalis* (W. Turton, 1825). *Journal of Molluscan Studies*, 79(2), 128-132.
<https://doi.org/10.1093/mollus/eyt003>

Summary: This article examines how male *Littorina fabalis* (marine snails) select their mates based on size. It was known that males of the *Littorina* genus actively find mates while females are passive and rarely reject males. It was understood that optimal female mates for many taxa are large since larger females are generally more fecund. Additionally, *L. fabalis* males invest a lot of energy into finding their female mate (ex. producing mucous to move and follow the female's mucous trail) and increase their risks (ex. predation); therefore, they are choosy. It was known that males of a similar species (*Littorina saxatilis*) adopt size-assortative mating; however, the mating strategy in *L. fabalis* was still undetermined. Saltin et al. (2013) were interested to see if *L. fabalis* mate on a size-assortative basis and determine if the mate preferences of *L. fabalis* based on size created mating barriers that impede gene flow due to the lack of hybridity of sizes in mating. The researchers collected individuals from two ecotypes (variants) of *L. fabalis* ("small and sheltered" (SS) and "large and moderately exposed" (LM)). The researchers paired individuals of the different ecotypes to test if males were choosy for larger females. They also paired individuals of the same ecotype to test if they adopt size-assortative mating. These pairs were then allowed to mate. The mating behaviors of males were observed (i.e., whether males decided to follow a female's mucous trail and initiate copulation). It was discovered that LM males strongly preferred females of their own ecotype; however, they could mate with SS females. SS males preferred to mate with LM females or the largest SS females. Both cases signify that males strongly preferred larger female mates, providing evidence that there is a partial mating barrier between larger males and smaller females.

Contribution: This article advances knowledge by providing evidence that size is a trait in sexual selection in snails. Additionally, it supports other findings that the active mate is choosy for larger passive mates. This article also raises further questions. When comparing the results of *L. fabalis* versus *L. saxatilis*, the mating barriers based on size differences are stronger in *L. saxatilis*. Further studies could examine why magnitudes of mating barriers are different among species. I chose this article because it studied exactly what I was interested in. Additionally, it supports many of the other articles that I selected.

2) Mating behavior – Choosy for mates that are of similar size to themselves (size-assortative mating)

Yu, T. L. & Wang, L. M. (2013). Mate choice and mechanical constraint on size-assortative pairing success in a simultaneous hermaphroditic pond snail *Radix lagotis* (Gastropoda: Pulmonata) on the Tibetan Plateau. *Ethology*, 119(9), 738-744.
<https://doi.org/10.1111/eth.12114>

Summary: This study examines how body size influences mating patterns and mating success in *Radix lagotis* (hermaphroditic pond snail species). From prior studies, evidence for size-assortative mating patterns in hermaphrodites has been ambiguous and inconclusive. However, it was assumed that mating patterns in hermaphroditic gastropods are size-dependent since body size positively correlates with fecundity. Yu & Wang (2013) were interested in providing evidence to support size-assortative mating in hermaphrodites by observing *R. lagotis*. They conducted experiments to test whether individuals choose mates discriminately based on size and whether differences in size between two partners affects copulation efficiency. The researchers conducted a field study by randomly collecting 221 mating pairs and 150 unpaired individuals from their natural habitat. Each individual's body mass was indicated by their shell volume and then they were either categorized as "large" or "small". The researchers also conducted experiments under laboratory conditions. For the first experiment, they tagged a focal individual and allowed them to pick a mate from two options of different sizes. This was repeated with 44 replicates. For the second experiment, they paired different combinations of sizes and observed whether copulation was attempted and successful and recorded successful copulation duration. This was repeated with 34 replicates. The results from the field study show that mating pairs were of similar size. This suggested size-assortative mating in *R. lagotis*. In the laboratory experiments, most of the successful and longer copulations constituted of mating pairs featuring two large individuals. These results also support that *R. lagotis* prefer mating on a size-assortative basis. However, most of the tagged individuals chose the larger individual to mate with. The researchers observed that smaller individuals had shorter copulatory organs, restricting their abilities to inseminate others. This was suggested to be a mechanical constraint in smaller individuals, resulting in less successful copulations.

Contribution: This article advances knowledge by finding evidence to support size-assortative mating in hermaphroditic gastropods. Previous research on the adoption of size-assortative mating in hermaphrodites was ambiguous. This study supports the assumption that mating patterns in hermaphroditic gastropods are size-dependent. The researchers also encourage future extensive studies on the mechanisms of mate choice in hermaphrodites. I chose this article since it is relevant to my topic about mate choice based on size in snails. Additionally, this article complements several of my other articles about size-assortative mating.

Ng, T. P. T., & Williams, G. A. (2014). Size-dependent male mate preference and its association with size-assortative mating in a mangrove snail, *Littoraria arduiniana*. *Ethology*, 120(10), 995-1002. <https://doi.org/10.1111/eth.12271>

Summary: This article investigated how a particular species of mangrove snail (*Littoraria arduiniana*) mate. Previously, it was assumed that all males generally prefer large female mates; however, there was slight evidence suggesting that males of different sizes have different preferences in mate size. Ng & Williams (2014) were interested to see how males selected their mates by size and how males “battle” each other when there is only one female. It was hypothesized that size-assortative mating (males choosing females of the same size as them) was a result of size-dependent mate preference by the male (i.e., large and small males had different preferences in female mate size based to their own size). To explore these questions and hypotheses, Ng & Williams separated males and females based on size (large and small). They mated different combinations of sizes of males and females. They observed each step of snail mating: 1) male follows female’s mucous trail, 2) shell mounting (male climbs onto female shell to “claim” it), and 3) copulation (sperm transfer process), and examined if the male would follow the female’s mucous trail, frequency of shell mounting, and duration of copulation for each of the 18 replicates per mating combination. They also observed male physical aggression in “mating battles” (males fighting for a large female). The data indicated that large males strongly preferred to mate with large females, but small males were less choosy on the size of their mate. This suggests that size-assortative mating does generally exist in *L. arduiniana* due to male size-dependent mate selection; however, small males can also mate with larger females. Additionally, during mate battles, it was discovered that large males were always able to defeat the small males for the large female during any mating stage, suggesting large size to be an advantage for males.

Contribution: This article helps confirm that an important trait in snail sexual selection is size. The research advances knowledge as it confirms that *L. arduiniana* snails mate in a size-assortative basis which was previously undetermined in prior studies. This study also raises further questions or studies using different snail species and observing other factors that may be important in sexual selection (ex. age). I chose this article because it provides important background knowledge on how snails choose their mates based on size and intra-specific competition between males for a large female mate, suggesting that female size is important in mating.

Kimura, K., Hirano, T., & Chiba, S. (2015). Assortative mating with respect to size in the simultaneously hermaphroditic land snail *Bradybaena pellucida*. *Acta Ethologica*, 18(3), 265-268. <https://doi.org/10.1007/s10211-014-0211-7>.

Summary: This study examines how body size plays an important factor in sexual selection in *Bradybaena pellucida* (simultaneous hermaphroditic land snails). It was known that body size is an important trait in sexual selection across many species since larger body size correlates with increased gamete production, and therefore, increased reproductive success. In hermaphroditic animals with reciprocal intromission (i.e., each partner plays both male and female roles in each mating event), it is expected that they choose mates who are similar in size to themselves (i.e., size-assortative mating). However, from previous studies, the mating patterns of hermaphrodites have been inconclusive since many of these studies have yielded different results. Kimura et al. (2015) examined the relationship between body size and fecundity in *B. pellucida*, as well as if *B. pellucida* mate on a size-assortative basis as expected in hermaphrodites. The researchers collected *B. pellucida* of various sizes and allowed them to sexually mature in the laboratory. The researchers then measured each snail's shell volume as an indicator of body size. When testing the correlation between body size and fecundity, the researchers randomly created 25 pairs of snails and let them mate. They then counted the number of hatched eggs for each mating pair. When testing the correlation between body size and mate selection, the researchers randomly separated 600 *B. pelludica* snails of various sizes into 30 groups of 20. Each group was then allowed to mate. The researchers only recorded the sizes of the first pair of snails to initiate mating. It was determined that there is a positive correlation between the number of eggs produced and body size. Additionally, there was slight evidence that the smallest and largest individuals can mate with each other; however, *B. pellucida* on average preferred mates who are of similar size, suggesting size-assortative mating.

Contribution: This article advances knowledge by helping to confirm that *B. pellucida* mate on a size-assortative basis. Based on prior studies regarding size in hermaphroditic sexual selection, this was inconclusive due to the variation of results. This article also encourages future studies such as examining potential mechanical constraints that prevent snails of significantly different sizes from mating, even though there is slight evidence that conveys that this mating is possible. I chose this article because it answers the question that I was interested in; however, it contradicts some other articles that claim individuals prefer larger mates.

3) Mating behavior – Mate selection is random or does not depend on size

Baur, B. (1992). Random mating by size in the simultaneously hermaphroditic land snail *Arianta arbustorum*: Experiments and an explanation. *Animal Behaviour*, 43(3), 511-518.
[https://doi.org/10.1016/S0003-3472\(05\)80109-5](https://doi.org/10.1016/S0003-3472(05)80109-5)

Summary: This article investigates how hermaphroditic land snails mate based on size. From previous studies, there was evidence that marine snails adopt size-assortative mating (individuals select mates who are similar in size to them); however, past research was inconclusive on how land snails mate since several studies have yielded ambiguous results. Baur (1992) investigated if *Arianta arbustorum* (a hermaphroditic land snail species) were selective of size when choosing mates as well as determine if being larger is advantageous in mating success. Baur first observed *A. arbustorum* mating in their natural habitat (subalpine forest) and recorded the shell volumes of both mating and non-mating snails. Afterwards, in laboratory conditions, the snails were subdivided into three groups: small, medium, and large. Each snail shell was labelled with a unique number. A snail from each size group was placed into an arena. Baur recorded time it took to initiate courtship (when a mating pair first orally contacted each other), courtship duration (how long they contacted each other for), and which sized individuals engaged in the courtship. This was repeated for 40 trials. In both the field and laboratory experiments, it was suggested that *A. arbustorum* do not discriminate mates based on size, but they appear to mate with whoever they see first. Baur proposed that this may be because *A. arbustorum* try to limit risks of predation, desiccations, and energy costs during mate searching. This is significant because it suggests that random mating (choosing mates with no regard to their genetic makeup) dominates in land snails because unlike marine snails, they may face more constraints and try to initiate mating as soon as possible to increase their reproductive success. Additionally, it was presumed that being larger does not appear to provide increases in mating success, further supporting random mating in *A. arbustorum*.

Contribution: This article advances knowledge regarding how land snails choose mates as it was previously inconclusive. It confirms that land snails do not mate on a size-assortative basis unlike marine snails. This study also helps guide future research such as determining what constraints impact land snail mating behavior. I chose this article since it is about how snails select mates; however, it opposes many of my other articles. Most of the articles that I have state that size is an important trait when it comes to selecting mates, and large mates are preferred since they may provide higher reproductive success.

Chaine, A. & Angeloni, L. (2005). Size-dependent mating and gender choice in a simultaneous hermaphrodite, *Bulla gouldiana*. *Behavioral Ecology and Sociobiology*, 59(1), 58-68.
<https://doi.org/10.1007/s00265-005-0009-8>

Summary: This article observes if size is involved in *Bulla gouldiana* (a hermaphroditic snail species) mating behaviors. Although it was known that sexual selection of traits applies to hermaphrodites, there were not many studies focusing on what these traits were. However, it was speculated that hermaphrodites are more limited in sexual selection for traits involved in mate acquisition compared to non-hermaphrodites. Prior to this study, little research was done on the mating behaviors of hermaphrodites; however, it was believed that hermaphrodites adopt size-dependent mating strategies. Chaine & Angeloni (2005) were interested to determine if body size (relative or absolute) can affect mate choice and duration of mating in *B. gouldiana*. Chaine & Angeloni studied a *B. gouldiana* population in the field and recorded the mass and sexual role (sperm donor or sperm recipient) of each mating individual. The researchers also conducted mating experiments in the lab. Sexually mature *B. gouldiana* of a range of body sizes were randomly collected from a single population. Each individual was isolated for one week in a 25C seawater tank to stimulate reproductive receptivity. Afterwards, 127 mating experiments were conducted (2 hours each), mating several combinations of sizes. The researchers recorded every behavior and their duration. Sex role was determined by which individual mounted the other and extruded its penis (male role/sperm donor) and which individual received the intromission (female role/sperm recipient). There was only slight evidence that being larger may increase the probabilities of being mated and longer copulation times. However, it was ultimately determined that *B. gouldiana* do not adopt size-dependent mating strategies. Therefore, the results indicate that size is not a significant factor in mate choice and success. The researchers believed that there was size-dependent mating patterns in hermaphrodites; however, *B. gouldiana* did not strongly support this.

Contribution: This study attempts to synthesize knowledge on if size is a trait in sexual selection in hermaphroditic snails. Although there is limited information on size-dependent mating strategies in hermaphrodites, this study contradicts previous findings and assumptions since it was observed that *B. gouldiana* do not adopt size-dependent mating strategies. This study stimulates future research to find other mating strategies in hermaphrodites. I chose this article because it examines if size is a trait that is selected for in snail mating; however, it conflicts with some of my other articles as it suggests that size is not a significant factor.

Koene, J. M., Montagne-Wajer, K., Ter Maat, A. (2007). Aspects of body size and mate choice in the simultaneously hermaphroditic pond snail *Lymnaea stagnalis*. *Animal Biology*, 57(2), 247-259. <https://doi.org/10.1163/157075607780377983>

Summary: This study examines if there is a relationship between body size and likelihood of being selected for mating in the simultaneously hermaphroditic pond snail *Lymnaea stagnalis*. Researchers knew that body size was a signal of resource allocation to reproduction in simultaneous hermaphrodites. In hermaphroditic animals, reproductive success of the female function was correlated with body size since larger individuals can produce more eggs and hold more sperm. There was ample evidence that some hermaphroditic species select larger partners for higher reproductive success; however, there were also species that have not been reported to select mates based on size. Koene et al. (2007) were interested to see if body size correlates with egg production, if size differences between two individuals impact their ability to copulate, and if body size affects mate choice in *L. stagnalis*. Mature *L. stagnalis* were cultured in the laboratory and their sizes were measured using their shell height. The researchers collected 62 snails and divided them into four different size groups. These snails were then isolated, and their egg production was measured by counting the number of eggs in each egg mass they produced. To test if size differences impact copulation potential, the researchers created three mating treatments: two large, one small and one large, and two small and see if they mated. To test if size impacts mate choice, the researchers tagged a focal individual and placed them in a tank with a large, small, and similar-sized snail and let them choose their mate. It was determined that there was a positive correlation between body size and egg production. However, *L. stagnalis* did not appear to prefer larger mates nor mates of the same size. This suggested that mating in *L. stagnalis* is either random or that there is another trait involved in sexual selection.

Contribution: The authors synthesize knowledge by suggesting that size does not apply to sexual selection in *L. stagnalis*. This study has both supported and contradicted previous findings since it was known that not all hermaphrodites choose mates based on size; however, there are also many that do. This study also encourages future research of sexual selection in *L. stagnalis*. I selected this study because it was relevant to my topic of how body size could be a factor in mate choice of snails. However, this study does contradict with some of the other articles that I have selected.

Nakadera, Y. & Koene, J. M. (2013). Reproductive strategies in hermaphroditic gastropods: Conceptual and empirical approaches. *Canadian Journal of Zoology*, 91(6), 367-381. <https://doi.org/10.1139/cjz-2012-0272>.

Summary: This article attempts to describe the reproductive strategies of hermaphroditic gastropods (sea slugs and snails). Reproductive strategies include behavioral, morphological, and physiological traits that optimize reproductive success. In the past, hermaphroditic mating and their sexual reproduction strategies have been overlooked. It was understood that hermaphrodites possess both male and female reproductive strategies/traits, making them difficult to study. There are gaps in knowledge of what these reproductive strategies are. Nakadera & Koene (2014) conducted a literature review by examining several primary articles that discuss traits involved in hermaphroditic sexual reproduction and evaluating whether these traits are reproductive strategies, as well as determine some complications of hermaphroditic sexual reproduction. These traits were subdivided between sex-biased traits (traits that the male or female has that influences reproductive success; ex. male accessory glands, seminal fluid) and shared cost traits (traits that both males and females have that influence reproductive success; ex. size). Some of the reproductive strategies the authors suggested include the presence of love darts (organ that stabs mate to initiate mating and increases reproductive success of the male), promiscuity (may enhance female reproductive success), and virginity of mate (may increase chances of mating). It was suggested that body size was not a reproductive strategy. The researchers were ultimately inconclusive on which reproductive strategies were the most beneficial because diversity of these strategies exist among hermaphroditic gastropods. Additionally, there was limited information; therefore, the authors encourage future empirical research such as molecular genotyping methods to test the significance of these traits on reproductive success. They suggest that studying shared cost traits are complex because these traits may affect both sex functions in hermaphrodites (i.e., it is complex to understand which sex is optimizing reproductive success), but sex-biased traits should be more straightforward to study.

Contribution: This article attempts to advance knowledge on the field of hermaphroditic gastropod sexual reproduction since it has previously been overlooked. It focuses on the unique and complex physiological, behavioral, and morphological reproductive traits of hermaphroditic gastropods. This article agrees with previous studies that hermaphroditic mating is complex and requires proper empirical approaches to understand more as major gaps of knowledge remain. This was selected for my literature review because it touches on my topic (mate selection based on size); however, it contradicts the primary articles that I selected since it suggests that mate quality is independent of body size.