

CAN THE ANCESTRAL INDISCRIMINATE SEXUAL BEHAVIOUR HYPOTHESIS EXPLAIN THE EXISTENCE OF SAME-SEX SEXUAL BEHAVIOUR IN THE ANIMAL KINGDOM?

ABSTRACT

Same-sex sexual behaviour (SSB) is widespread across animal taxa despite its presumed fitness costs. The literature has attempted to justify this by endeavouring to uncover its adaptive and maladaptive origins, in an attempt to resolve its repeated evolution. However, this includes the unchecked assumption that the earliest species exhibited exclusive different-sex sexual behaviour (DSB), from which SSB evolved. This notion is challenged by the ancestral indiscriminate sexual behaviour (ISB) hypothesis, which states that sexual behaviour first evolved as a trait that was non-targeted towards particular sexes, resulting in expression of both SSB and DSB, from which condition SSB has persisted. By shifting the evolutionary baseline of sexual behaviour, we can depart from a ‘justification-based’ perspective of SSB that has perhaps been influenced by a propensity of heteronormativity in the literature, and instead reconcile the widespread nature of such behaviour with its ancestral condition.

1. Introduction

Same-sex sexual behaviour (SSB) is the performance of actions between conspecifics of the same sex that are used in opposite-sex courtship or mating interactions. This is different from same-sex sexual preference (SSP), which is when individuals are more likely to undergo SSB even if different-sex partners are available (Bailey & Zuk, 2009; Poiani, 2010). Traditionally, biologists have considered the evolution of SSP and SSB a conundrum in that it cannot result in reproduction, and thus is often presumed to reduce fitness (Bagemihl, 1999). Investing in any sexual behaviour can be costly as it increases an individual's vulnerability to disease, predation and physical damage (Lehtonen et al., 2012). In addition to these costs, SSB might reduce lifetime reproductive success, for example if sperm production is limited (Sales et al., 2018) or if the amount of time individuals express different-sex sexual behaviour (DSB) is reduced. This is documented in humans, where individuals expressing SSP conceive on average 80% fewer offspring (Gavrilets & Rice, 2006).

Despite this, SSB is widespread across the animal kingdom and is maintained in some populations at frequencies higher than the theoretical mutation rate (Gavrilets & Rice, 2006). There have been 1500 recorded observations in different species (Bailey & Zuk, 2009; Roughgarden, 2004; Terry, 2000), which is likely to be lower than the actual frequency due to incorrect classification of sexes in sexually monomorphic species and a lack of studies that are not derived from haphazard observations (Bagemihl, 1999; Sommer & Vasey, 2006). SSB has therefore been posed as a 'Darwinian Paradox': why would individuals invest resources into SSB if it does not directly result in reproduction? The literature has aimed to answer this through adaptive (e.g. Gavrilets & Rice, 2006; Mizumoto et al., 2016) and nonadaptive (e.g. Sales et al., 2018; Van Gossum et al., 2005) taxon-specific justifications for its existence. This has led to a general conjecture that independent origins of SSB have arisen from an ancestral condition of DSB. Additionally, theory often assumes that the costs of SSB are always high, such that if it evolved adaptively then there must be large benefits, and if it persists maladaptively then it will be strongly selected against (Monk et al., 2019).

However, the widespread notion of SSB repeatedly evolving despite high fitness costs includes unchecked assumptions on the benefits of exclusive DSB and costs of SSB. Moreover, it implicitly assumes that exclusive DSB is the baseline condition for animals, from which SSB has evolved (Monk et al., 2019). This essay will challenge the assumption that SSB has repeatedly evolved from an ancestral condition of exclusive DSB, and will instead reconcile the persistence of SSB with an ancestral state of indiscriminate sexual behaviour (ISB). This will be done by discussing the theory of the ancestral ISB hypothesis, before considering how

it might explain the persistence of SSB due to high costs of evolving towards exclusive DSB and the low costs of retaining SSB.

2. Ancestral Indiscriminate Sexual Behaviour: Theory

Indiscriminate sexual behaviour (ISB) is the performance of actions attributed to courtship or mating interactions without sex-based mate identification, resulting in expression of both SSB and DSB. It has recently been proposed that ISB is the baseline condition of animals that exhibit sexual behaviour (Monk et al., 2019). This suggests that SSB, as opposed to newly arising from a condition of exclusive DSB, might have persisted from a behavioural repertoire that included SSB itself: this framework is hereafter referred to as the ancestral ISB hypothesis.

Sexual behaviour is extraordinarily diverse and difficult to define due to the range of animal mating systems and reproductive modes. It can broadly be described as behaviour employed during mating or courtship that may contribute to reproductive success, irrespective of the context in which it is observed (Sommer & Vasey, 2006). Reproductive success in sexually reproducing animals is dependent on the production of offspring through sexual reproduction, defined as the fusion of two gametes in the process of fertilisation (Hine & Martin, 2019). From an evolutionary perspective, evolution of sexual reproduction generated gamete competition. Furthermore, disruptive selection acted on variation in gamete size resulting in gamete asymmetry (Parker et al., 1972). In gonochoristic systems, given individuals produce one of two distinct gamete sizes, and sex is used to classify members depending on which size they produce. Typically, a male produces microgametes (sperm) while a female produces macrogametes (eggs) (Parker, 2011).

Directed sexual behaviour must have evolved subsequent to sexual reproduction, because such behaviour cannot be directed towards a particular sex if those sexes are not yet defined prior to evolution of gamete dimorphism (Monk et al., 2019). Research into the origin of sexual behaviour is profoundly lacking, but one exception and generally accepted hypothesis from Parker (2014) states that it evolved in anisogamous, multicellular broadcast spawners with limited mobility: hereafter referred to as the ancestral species. However, Parker suggests that this evolutionary transition resulted in strong selection for female-targeting in males (Parker et al., 1972), assuming that ancestral sexual behaviour arose as exclusive DSB (Monk et al., 2019), a notion that is challenged by the ancestral ISB hypothesis.

The ancestral ISB hypothesis reasons that perfectly-targeted DSB is a derived trait that evolved subsequent to non-targeted sexual behaviour. Moreover, it argues that exclusive DSB requires sex-specific mate recognition beyond the molecular mechanisms that control

fertilisation compatibility. Such recognition could only arise after the evolution of detectable sexual polymorphism, which was not likely to exist in the ancestral species (Monk et al., 2019). These critiques are supported by evidence that both SSB and DSB are expressed in echinoderms (Keesing et al., 2011; McCarthy & Young, 2002), an early-branching phylum with traits that resemble Parker's (2014) aforementioned description of the ancestral species. Young and colleagues (1992) demonstrate that the echinoid *Stylocidaris lineata* expresses SSB in their breeding aggregations. The proportion of DSB versus SSB occurs at frequencies predicted by chance on the basis of sex ratio, where a population with a 1 : 1 sex ratio produced male-female pairs ~50% of the time. The authors suggest that the sexual aggregations are not a result of any form of sex recognition. Similar behaviour may have been expressed in the ancestral species, and therefore only in derived species did exclusive DSB using mate recognition evolve. Such evolution might have proceeded in a coevolutionary type scenario: some individuals' fitness is increased by detecting cues which inform that the emitter is a different sex, thus leading to greater reproductive success following such pairs' sexual behaviours. This would cause selection to favour such sex-specific cues, ultimately resulting in coevolution of sexual polymorphism and sex-specific mate recognition.

The ancestral ISB hypothesis further suggests that selection would only act against SSB in the ancestral species' diverging populations when the costs become overly prohibitive in specific socio-ecological conditions. Outside such conditions, SSB might be retained at intermediate levels. This is because if the costs of SSB are not high, fitness might be maximised by expressing sexual behaviour towards all conspecifics, increasing the number of mating opportunities, and not suffering potential costs of targeting exclusively different-sex individuals (Han & Brooks, 2015; Savolainen & Hodgson, 2016). Therefore, the expression of SSB in extant species may have not been selected against from an ancestral condition of ISB, and thus has been retained as either neutral or advantageous (Monk et al., 2019).

This baseline shift in the ancestral state of sexual behaviour means that rather than studying the 'purpose' of SSB as an explanation for its evolution in specific lineages, its existence can instead be studied as a relic from a set of ancestral behaviours (Monk et al., 2019). The importance of this difference between the ancestral ISB hypothesis and other hypotheses that attempt to explain SSB's evolution lies in the notion that the initial conditions of a diverging population undergoing change has significant effects on its evolutionary trajectory (Futuyma, 2010; Levin, 2012). The likelihood of a particular trajectory differs depending on whether selection is acting on a trait that is initially common, or uncommon. By

shifting the baseline in the origins of sexual behaviour, the selective regimes that might have given rise to the current widespread nature of SSB in the animal kingdom are relaxed.

The ancestral ISB hypothesis can only explain the existence of SSB if evidence supports that: (a) exclusive DSB did not evolve in the ancestral species and its diverging lineages; and (b) SSB persisted in early lineages without incurring high costs. Such evidence in support of the hypothesis will be assessed through the remainder of this essay.

3. Persistence of SSB from Ancestral ISB: Evidence & Speculation

(a) Why would exclusive DSB not evolve in the ancestral species?

Exclusive DSB would be disadvantageous compared to ISB under conditions that might have been present in the ancestral species, and therefore might not have evolved (Monk et al., 2019). One of the few models that hypothesise the origin of sexual behaviour states that ‘female-targeting’ by males rapidly evolved in ancestral broadcast spawners, assuming it would be selected due to increased fertilisation success in conditions of sperm competition or limitation (Parker, 1984; Parker, 2014). However, males expressing proportionally more DSB are not necessarily favoured by selection in both these conditions. As demonstrated by Levitan (2004), selection acting on sexual traits in broadcast spawners is highly density-dependent, with only specific conditions of low-density and resultant sperm limitation strongly selecting for female-targeting. Furthermore, conditions in the ancestral species likely meant that selection acted on other factors that increase fertilisation success alongside a strategy of ISB. In these conditions, it is likely that sperm and eggs would regularly meet in spawning events, without the need for female-targeting, due to water flow and close proximity of males and females in aggregations (Shuster & Wade, 2003). Therefore, these conditions would lead to strong selection on gamete traits, such as egg adaptations to decrease polyspermy and high sperm count and quality to ensure zygotic success following fertilisation (Levitan, 2002; Levitan, 2004). Furthermore, these traits might be greater determinants of reproductive success in the ancestral species compared to the relative proportion of DSB expressed, and so there is little validity in assuming that the ancestral conditions would necessitate evolution towards exclusive DSB. This is supported by extant populations of broadcast spawners, where McCarthy & Young (2002) demonstrate that pre-spawning aggregations of urchins reflect the sex distribution across the population, with no evidence of female-targeting behaviour.

In early lineages, in addition to the conditions selecting for factors that increase fertilisation success alongside ISB, evolving increasingly exclusive and discriminating DSB could be costly due to missed mating opportunities (Monk et al., 2019; Sales et al., 2018). This

is conceivable in the ancestral species, where individuals displaying greater discriminatory mate selection might have lower fertilisation success than those which distribute their gametes more widely to all conspecifics during a spawning event. Therefore, despite expression of SSB being erroneous, it would occur as part of the ISB strategy because its costs are less consequential than potentially missed mating opportunities (Sales et al., 2018; Savolainen & Hodgson, 2016). Furthermore, exclusive DSB would be particularly unfavourable if spawning events, and by extension mating opportunities, were rare, because in this case the cost of missed matings would be higher. This has been demonstrated by male burying beetles, which express more SSB when the apparent costs of missed mating opportunities are greater (Engel et al., 2015). Additionally, evolving towards exclusive DSB would be particularly disadvantageous if the conditions required costly secondary sexual characteristics for sex identification (Hasegawa & Arai, 2018; Martins et al., 2018).

In short, while exclusive DSB might increase reproductive success compared to alternative strategies in some cases, it is not the only viable fitness-increasing strategy, and therefore higher relative proportions of DSB will not always be favourably selected. This could be the case in the ancestral species, where due to the spawning conditions and certain costs of evolving towards exclusive DSB, a generalist strategy of ISB might have been favoured. Therefore, rather than indicating a baseline strategy of animals, exclusive DSB might be a trait that arose after ISB, evolving subsequent to secondary sexual characteristics and only in particular contexts in derived populations (Monk et al., 2019).

(b) Could SSB persist due to low costs?

If SSB need not incur high costs in diverging lineages of the ancestral species, then this would support the theory that it has persisted from a baseline condition of ISB rather than having multiple independent origins. Its widespread nature would then largely be explained by its origins from ISB coupled with weak, or absent, selection acting against it (Monk et al., 2019). Evidence of the costs of SSB being minimal can be gleaned from species with high mating rates relative to their reproductive output. For example, Hoving et al. (2019) demonstrate that a semelparous life-cycle, brief mating events and group-living in the Humboldt squid leads to expression of male SSB at frequencies similar to DSB. Such results in this species would be in line with the hypothesis that low costs for individual mating events, and the gain in reproductive output by mating with as many individuals as possible, might be consistent with expressing ISB. Furthermore, such studies that suggest the low costs of SSB (e.g. Hoving et al., 2019; MacFarlane et al., 2010) support that ISB, and by extension some SSB, could have

been retained in the ancestral species' diverging lineages. Moreover, selection acting against ISB might have been relatively weak in these lineages compared to other obstructions of reproductive success with much higher fitness costs, such as mate competition or infertility (Monk et al., 2019).

As well as considering the potential low cost of retaining SSB by making comparisons with extant populations, insight may be gleaned by assessing the ubiquity of other sexual behaviour that does not directly lead to reproductive success (Monk et al., 2019). Heterospecific sexual behaviour is an interspecific interaction during mate acquisition caused by incorrect species recognition (Gröning & Hochkirch, 2008). Such behaviour is comparable to SSB because it appears maladaptive in that it does not directly result in offspring production. Some literature suggests that heterospecific behaviour exists because its costs are lower than the costs inflicted if mating efforts are reduced or for evolving additional mechanisms of conspecific mate recognition (Drury et al., 2019; Takakura et al., 2015). For example, a study that enclosed related species of squash bugs together demonstrated that heterospecific sexual behaviour was common, but individuals still had high mating rates with conspecifics and similar hatching success as those that were inhibited from expressing heterospecific sexual behaviour (Greenway et al., 2019; Monk et al., 2019). It might be that SSB is comparable to this and could persist with relatively low costs, particularly in species with high mating rates that do not invest much into single matings. If SSB did persist in early lineages due to low costs, then the ISB hypothesis is not mutually exclusive to other adaptive hypotheses of SSB's evolution. Instead, it suggests that in conditions where SSB confers benefits, selection acted to increase its expression from pre-existing SSB, instead of requiring new mutations to arise, thus relaxing the constraints for its evolution.

In total, evidence that the costs of SSB might be much lower than often assumed in the literature can be gleaned from extant populations that express such behaviour and demonstrate other seemingly maladaptive sexual behaviour. From this, it can be extrapolated that from a condition of ISB, SSB might have low enough costs to persist in diverging lineages, in frequencies that differ within species, populations and an individual's lifespan.

4. Concluding Remarks

The ancestral ISB hypothesis reconciles the widespread existence of SSB with behaviour expressed in ancestral species, stating that SSB has persisted from a condition of ISB as opposed to repeatedly evolving as a novel trait in separate lineages. The hypothesis suggests that in the ancestral species, and its earliest lineages, ISB might have maximised fitness by

balancing costs of evolving towards exclusive DSB with benefits of more mating opportunities. It further suggests that SSB has persisted from this condition in some lineages without incurring high costs.

Other traits that are as comparably diverse across animal taxa are widely accepted to be present in some ancestral condition (Monk et al., 2019), yet SSB has almost exclusively been studied as a costly trait which has convergently arisen in distinct lineages. While this ‘justification-based’ research has some rationale due to the seemingly direct reproductive costs, no other trait with comparable fitness implications has been studied with similarly unchecked assumptions, receiving attention with regard to how it has repeatedly evolved and why selection has not eliminated it (Savolainen & Hodgson, 2016). In part, this may be due to a heteronormative stance and Euro-American cultural norms affecting how the topic has been discussed and studied, particularly in the 20th Century when much of the literature was developed (Monk et al., 2019). But by shifting the baseline in sexual behaviour evolution, the ancestral ISB hypothesis suggests that selection has acted on pre-existing SSB in early animal lineages. Thus, traditional constraints imposed on the theory of how SSB exists in populations can be relaxed, and SSB’s persistence is reconciled with the ancestral condition of sexual behaviour in the animal kingdom.

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