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An alternative hypothesis for the evolution of same-sex sexual behaviour in animals

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Same-sex sexual behaviour (SSB) has been recorded in over 1,500 animal species with a widespread distribution across most major clades. Evolutionary biologists have long sought to uncover the adaptive origins of 'homosexual behaviour' in an attempt to resolve this apparent Darwinian paradox: how has SSB repeatedly evolved and persisted despite its presumed fitness costs? This question implicitly assumes that 'heterosexual' or exclusive different-sex sexual behaviour (DSB) is the baseline condition for animals, from which SSB has evolved. We question the idea that SSB necessarily presents an evolutionary conundrum, and suggest that the literature includes unchecked assumptions regarding the costs, benefits and origins of SSB. Instead, we offer an alternative null hypothesis for the evolutionary origin of SSB that, through a subtle shift in perspective, moves away from the expectation that the origin and maintenance of SSB is a problem in need of a solution. We argue that the frequently implicit assumption of DSB as ancestral has not been rigorously examined, and instead hypothesize an ancestral condition of indiscriminate sexual behaviours directed towards all sexes. By shifting the lens through which we study animal sexual behaviour, we can more fruitfully examine the evolutionary history of diverse sexual strategies.

Since Charles Darwin[1,2] first recognized natural and sexual selection as engines of evolutionary change, considerations of sex and fitness in evolutionary biology have largely focused on sexual behaviours between individuals inferred to have fertilization-compatible gametes, commonly termed 'heterosexuality'. To avoid any conflation with terms for human sexual identities (Box 1) and to more accurately describe the observations of specific interactions among individuals, we refer to these behaviours as different-sex sexual behaviours (DSBs; Box 1). Because individual fitness is broadly understood to be a function of survival and reproduction, these DSBs, which can potentially lead to the production of offspring, have clear consequences for fitness. However, animals also exhibit an array of sexual behaviours that cannot be classified as DSBs and do not seem capable of directly resulting in reproductive success. These include sexual behaviours directed at individuals of the same sex[3], different species[4], dead bodies[5], inanimate objects[6] and self-stimulatory behaviours[7]. Same-sex sexual behaviours (SSBs; Box 1) are among the most widely observed and discussed of the non-DSB sexual behaviours. SSB is widespread across animals, with recorded observations in over 1,500 animal species including all major vertebrate clades as well as diverse invertebrate groups[8–11] (Fig. 1 and Table 1). These observations have been recorded from captive individuals, under laboratory conditions, and in wild populations of animals found in myriad ecological conditions. However, most of what we know about the incidence of SSB is the result of opportunistic and haphazard observations[3,12].

With growing recognition of the prevalence of SSB, evolutionary biologists have devoted greater attention to addressing what is often considered an evolutionary conundrum or 'Darwinian paradox': how has SSB evolved and persisted if it cannot result in reproduction and therefore must reduce the fitness of individuals, and may result in population extinction if all individuals in a population engaged solely in SSB[13] (for example, refs. [14–16])? Efforts to resolve this apparent paradox have taken the form of taxon-specific searches for adaptive and non-adaptive explanations of SSB (reviewed in refs. [8,11]). Briefly, adaptive hypotheses (for example, kin selection, overdominance, intrasexual conflict, sexual antagonism) hold that SSB evolves due to indirect fitness benefits and assume that alleles or epigenetic marks coding directly or indirectly for SSB must be beneficial for them to arise and be maintained over evolutionary time[14,17–20]. In contrast, non-adaptive or maladaptive hypotheses (for example, mistaken identity, prison effect, infection) consider SSB a 'fundamentally erroneous tactic'[16] and posit that they derive from either pleiotropic effects or constraints of other aspects of animals' biology[21] (reviewed in refs. [8,11,12]).

Many of these explanatory hypotheses are based on a few key assumptions, which are often implicit rather than explicitly stated. First, SSB research appears to take for granted that the costs of SSB are high — and thus adaptive hypotheses assume that benefits of SSB must be even greater to account for its persistence, whereas non-adaptive hypotheses assume that SSB will be strongly selected against when possible. Second, these hypotheses seem to assume that SSB has independent origins in many animal lineages by framing SSB as a trait that arose in each study system from an ancestral population with exclusive DSB (Box 1) and which subsequently became more common through adaptive or non-adaptive processes.

We question these assumptions and propose an alternative explanation for the prevalence of SSB: that the ancestral condition for sexual behaviour in animals included both DSB and SSB, and that various evolutionary processes, adaptive or otherwise, have shaped the persistence and expression of SSB in different lineages, but need not explain its origins. Indeed, when we observe a particular trait so prevalent within a clade, a reasonable hypothesis to explain such an evolutionary pattern is that the trait likely arose near the clade's origins[22]. Yet, to our knowledge, this hypothesis has not been applied to thinking about the evolution of SSB. While the most parsimonious

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Box 1 | Terminology and disclaimers

We recognize the complexity involved in discussing sexual behaviour across animals while maintaining an inclusive view of sex, sexuality and gender in humans. In considering the ideas presented here, we have grappled with how to not exclude important human contexts while also not conflating human sexuality with sexual behaviours seen in other animal taxa[86]. To avoid anthropomorphization, we have drawn a distinction between human attributes of gender and sexuality (both of which are categories based on self-identification of personal identity, attraction, and sexual or romantic preference) and the scientific terminology of sex and sexual behaviours, which can be used to describe specific characteristics and traits observed in non-human animals (see Box 2). Thus, we deliberately do not use terms such as 'heterosexual' or 'homosexual' in the manuscript, except in quotations, to prevent any conflation between human sexuality and non-human animal sexual behaviours[8,99]. Instead, we refer to same-sex sexual behaviour (SSB) and different-sex sexual behaviour (DSB), which more accurately describe the observation of sexual interactions.

Specifically, we use the terms SSB and DSB to refer to discrete sexual interactions among individuals, acknowledging that it may be difficult to categorize behaviours among more than two individuals. When aggregating sexual behaviours across an individual's lifetime or across multiple individuals in a population, the degree of SSB or DSB exhibited by individuals or populations becomes a continuous, rather than a categorical, trait (Fig. 2a). It is important to note that SSB and DSB are not mutually exclusive behaviours, and that knowing the prevalence of DSB in an individual or population may not predict anything about the prevalence of SSB, and vice versa; animals demonstrating SSB may sometimes demonstrate more DSB, not less as is often assumed[11,100]. We use the terms exclusive DSB (individual level: all sexual behaviours of an individual are DSB; population level: all individuals in a population only engage in DSB) and exclusive SSB (individual level: all sexual behaviours of an individual are SSB; population level: all individuals in a population only engage in SSB) to describe the theoretical extremes of this continuous variation in sexual behaviour.

Human cultural constructions of sexual behaviours have impacted hypotheses surrounding SSB evolution, particularly in social vertebrates and other primates[8,43]. Much discussion of adaptive and non-adaptive explanations for the evolution of SSB has been explored using humans as a study system rather than other species[8], and certain concepts have clearly been inspired or motivated by human socio–political contexts. For example, the 'prison effect'[8], which posits that individuals engage in SSB when the opportunity to mate with different sexes is removed, is named after the popular perception that single-sex contexts, like prisons, encourage 'situational homosexuality' among inmates[101]. We note that measuring human sexual behaviours accurately and ethically is notoriously difficult[102,103], making control measures difficult to obtain, and the coercive aspects of a prison context exacerbate these problems[101]. This historic focus on human sexual behaviours has often led evolutionary biologists to understand the origins of a widespread animal behaviour through the social context of a single terminal node[86].

Because of the inevitable role biases can play in shaping researcher perspectives in all fields, we consider it important to acknowledge that although the authors represent multiple genders, sexualities and scientific subdisciplines, all are cisgender biologists who live and have been educated in a predominantly Euro–American cultural context and scientific tradition. Our goal is that the ideas we present here lead to a productive, careful discussion of the diversity, functions and evolution of animal sexual behaviour and that this discussion is inclusive of people of diverse sexes, genders and sexualities.

solution may not always be correct, the hypothesis that SSB derives from a single evolutionary origin is certainly a neglected consideration in the study of SSB.

Further, we discuss how this new hypothesis of ancestral sexual behaviour that includes DSB and SSB might reshape how scientists think about and study SSB in extant taxa. In doing so, we aim to redefine the null hypothesis in studies of SSB—put simply, we are proposing a shift from asking 'Why engage in SSB?' to 'Why not?'. Such shifts in our collective null models have been advocated for in various aspects of sexual behaviour (for example, arbitrary trait choice in mate selection[23] and the existence of female mate choice itself (reviewed in refs. [24,25]); territoriality[26,27]; female multiple mating[28–31]) and have prompted changes in empirical research conducted in those domains (for example, refs. [32–36]). We contend that such a shift in what we consider the baseline for sexual behaviours will spark new hypotheses and avenues of research into SSB that, regardless of whether our predictions prove correct, will help us better understand the diversity in sexual behaviours across animals.

A new model for the evolution of sexual behaviour

We propose that indiscriminate sexual behaviour, or sexual behaviour without sex-based mate identification resulting in the expression of both SSB and DSB, is the most likely ancestral condition of sexually reproducing animals. We reason that the perfectly targeted DSB assumed in current models are more likely a derived trait that arose after the evolution of sexual behaviours in an ancestral anisogamous, multicellular, immobile species[37] (Box 2). Moreover, as exclusive DSB requires mechanisms of mate recognition (beyond molecular mechanisms of fertilization compatibility), it logically can only occur subsequent to the evolution of perceivable sexual polymorphism (for example, body size and shape, colours, chemical and auditory signals, and so on). Evidence in support of these critiques comes from echinoderms, an early branching lineage that most likely bears close resemblance to the ancestral organisms in which sexual behaviours evolved, and which often express both SSB and DSB[38–40].

Further, we suggest that selection would only act against SSB in ecological or social contexts where its costs become prohibitive. Absent such costs in particular lineages, SSB may be retained, because reproductive fitness is likely often maximized at intermediate mixtures of sexual behaviours that balance the costs of specifically targeting fertilization-compatible mates with the benefits of an increased number of mating opportunities[13,41,42]. Thus, the expression of both DSB and SSB, to varying degrees across individuals' lifetimes and across individuals in a population, may be the norm for most animal species, representing the legacy of an ancestral condition of indiscriminate sexual behaviour that remains either neutral or, in some contexts, advantageous (Fig. 2b).

Costs and benefits of SSB. Our hypothesis emerges from considering the relative costs and benefits of sexual behaviour. In the case of SSB, the implicit assumption of most research is that the costs are high, spurring a search for equally large benefits to explain the persistence of the costly behaviour. The adaptive hypotheses for the

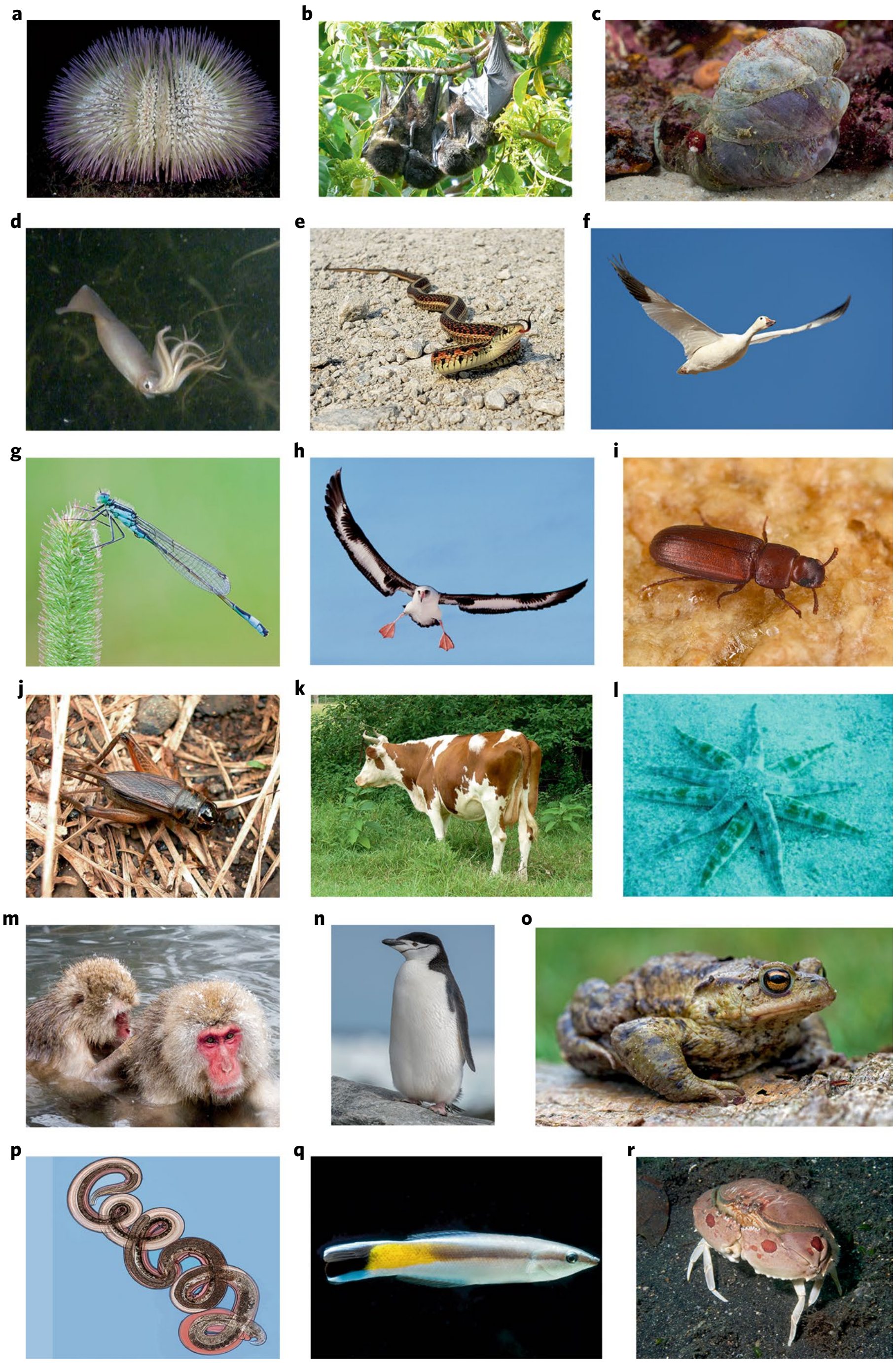

Fig. 1 | Examples of species with documented SSB demonstrate the widespread distribution of SSB in animals. a, Variegated sea urchin (*Lytechinus variegatus*). **b**, Bonin flying fox (*Pteropus pselaphon*). **c**, Common slipper shell (*Crepidula fornicata*). **d**, Humboldt squid (*Dosidicus gigas*). **e**, Garter snake (*Thamnophis sirtalis*). **f**, Snow goose (*Anser caerulescens*). **g**, Damselfly (*Ischnura elegans*). **h**, Laysan albatross (*Phoebastria immutabilis*). **i**, Red flour beetle (*Tribolium castaneum*). **j**, Field cricket (*Teleogryllus oceanicus*). **k**, Domestic cow (*Bos taurus*). **l**, Sea star (*Archaster angulatus*). **m**, Japanese macaque (*Macaca fuscata*). **n**, Chinstrap penguin (*Pygoscelis antarcticus*). **o**, Common toad (*Bufo bufo*). **p**, Rat gastrointestinal roundworm (*Nippostrongylus brasiliensis*). **q**, Bluestreak cleaner wrasse (*Labroides dimidiatus*). **r**, Box crab (*Calappa sp.*). Species in which SSB has been documented span a wide variety of taxa. While socially complex vertebrates such as mammals (**b**,**k**,**m**) and birds (**f**,**h**,**n**) are often the first species that come to mind when discussing SSB, within vertebrates these behaviours have also been documented in squamates (**e**), amphibians (**o**) and fish (**q**), as well as in invertebrates such as echinoderms (**a**,**l**), arthropods including insects (**g**,**i**,**j**) and crustaceans (**r**), nematodes (**p**) and molluscs (**c**,**d**). Note that this is a non-exhaustive list of taxa with documented SSB. See Table 1 for a list of behavioural descriptions and citations for taxa depicted here. Credit: **a**, Leo Francini/Alamy Stock Photo; **b**, reproduced from ref. [87], © 2016 Norimasa Sugita under a Creative Commons licence CC BY 4.0; **c**, blickwinkel/Alamy Stock Photo; **d**, NOAA (https://oceanexplorer.noaa.gov/explorations/06davidson/logs/summary/media/squid_600.html); **e**, © Aaron Goodwin; **f**, robertharding/Alamy Stock Photo; **g**, Alex Fieldhouse/Alamy Stock Photo; **h**, Frans Lanting Studio/Alamy Stock Photo; **i**, Photo by Peggy Greb, USDA Agricultural Research Service; **j**, Gerald McCormack; **k**, pxhere under a Creative Commons licence CCO 1.0; **l**, reproduced from ref. [40], Springer; **m**, Brian Jeffery Beggerly under a Creative Commons licence CC BY 2.0; **n**, National Geographic Image Collection/Alamy Stock Photo; **o**, Arterra Picture Library/Alamy Stock Photo; **p**, reproduced from ref. [98], © 2013 Nieuwenhuizen et al. under a Creative Commons licence CC BY 4.0; **q**, blickwinkel/Alamy Stock Photo; **r**, Hal Beral/VWPics/Alamy Stock Photo

Table 1 | Descriptions of SSBs expressed by diverse species across the animal phylogeny (depicted in Fig. 1), along with the associated citations documenting these behaviours

Figure	Common name	Species	Behavioural description	Reference
1a	Variegated sea urchin	*Lytechinus variegatus*	These sea urchins are broadcast spawners that often aggregate together before releasing gametes. Aggregations reflect the sex distribution across the population: there is no evidence that sea urchins can distinguish the sex of prospective partners.	39
1b	Bonin flying fox	*Pteropus pselaphon*	In the wild, male flying foxes engage in same-sex genital licking of erect penises within all-male social clusters. The behaviour is unrelated to allogrooming (which the species does not engage in).	87
1c	Common slipper shell	*Crepidula fornicata*	Slipper shells are sequential hermaphrodites that are first sexually mature as males and later transition to female. Smaller, more mobile males join aggregations of larger animals to permanently associate and mate with. When given a choice, a substantial minority of males choose to associate with other males.	88
1d	Humboldt squid	*Dosidicus gigas*	Males have been observed with visible spermatangia on their mantles, indicative of mating by another male. The spermatangia are found in the same location and at similar numbers as are usually deposited on females.	44
1e	Garter snake	*Thamnophis sirtalis*	Mating in this species often occurs in large balls of males attempting to copulate with a single focal snake, sometimes a receptive female but also sometimes a male snake releasing similar pheromones to a receptive female.	89
1f	Snow goose	*Anser caerulescens*	Both male–male mounting and female–female pairs raising the young of both individuals together have been recorded in snow geese.	75
1g	Damselfly	*Ischnura elegans*	In this species, andromorphic females that mimic the colour pattern of male damselflies can be common in some conditions. Males often court and form copulatory pairings with other males, particularly when there are many andromorphic females present.	21
1h	Laysan albatross	*Phoebastria immutabilis*	Nearly one third of Laysan albatross pairs raising chicks on one Oahu population were female–female; both females involved in such pairs reproduce within the pair year to year.	90
1i	Red flour beetle	*Tribolium castaneum*	Male red flour beetles often pair with and attempt to copulate with other males, including release of spermatophores and other behaviours common to male–female matings.	91
1j	Field cricket	*Teleogryllus oceanicus*	Male crickets frequently court one another, including courtship song, courtship posturing and mounting one another.	62
1k	Domestic cattle	*Bos taurus*	Cattle in mixed-sex herds will sometimes congregate into all-female subgroups when some or all females are in estrus. In these groups, females engage in the same courtship behaviours common to mating bulls, including genital licking, chin rubbing and mounting.	92
1l	Sea star	*Archaster angulatus*	While sea stars are broadcast spawners, in this species they do pair together with males mounting females before releasing gametes. Pairs remain in position for up to 24 h. Male-on-male pairings are not uncommon in wild conditions.	40
1m	Japanese macaque	*Macaca fuscata*	Female snow macaques routinely pair off and form temporary but exclusive relationships with other females, during which they engage in same-sex mounting complete with pelvic thrusting. Females will compete with males for access to other females and will sometimes preferentially associate with other females rather than available males.	93
1n	Chinstrap penguin	*Pygoscelis antarcticus*	Famously, two captive-bred chinstrap penguins at the Central Park Zoo formed a pair-bond and attempted to incubate an egg; when provided with a fertile egg from another nest they successfully co-reared a chick together. Same-sex pairings are also quite common in related Gentoo and Adélie penguins.	75,94
1o	Common toad	*Bufo bufo*	Male toads do not discriminate between sex, receptivity or species when seeking partners for amplexus; when grasped, males mounted by other males use a specific release call to trigger release by the mounting male.	61
1p	Rat gastrointestinal roundworm	*Nippostrongylus brasiliensis*	Chemotactic attraction between males and females is common in a variety of nematode species, but same-sex chemotaxis is not. In this species, males predominantly approach females, whereas females exhibit equal chemotactic approaches to other females and to males.	95
1q	Bluestreak cleaner wrasse	*Labroides dimidiatus*	These wrasse are sequential hermaphrodites that begin sexual maturity as females and, in the absence of a resident male, the largest female transitions to become a male. However, these females begin spawning with other females and assuming 'male' courtship roles and behaviour well before the reproductive transition is complete, beginning ~1 h after male removal.	96
1r	Box crab	*Calappa sp.*	Male crabs have been observed copulating with one another for extended periods of time in excess of 18 d continuously.	97

Note that this is not an exhaustive list of species exhibiting SSB.

Box 2 | Definition of sexual behaviours in relation to sexual reproduction

The astonishing diversity in reproductive modes and systems within and among animals renders the task of defining sexual behaviours dismayingly difficult. Moreover, because humans are likely better at recognizing behaviours that may be sexual in species that have sex in similar ways to us, we note that there is likely observer bias in the scientific recognition, description and understanding of sexual behaviours across animals[12] (Box 1). Thus, we have tried to develop working definitions for sexual behaviour in animals—and the related concepts of sex and sexual reproduction—that appreciate natural variation and represent how most biological traits vary continuously.

We use a broad definition of animal sexual behaviours to include any behaviour that may contribute to reproductive success, such as behaviours that are employed in mating, courtship or pair bonding, no matter the context in which they are observed[3,12]. Reproductive success requires the production of offspring through sexual reproduction: the combination of genetic material to form progeny typically involving the fusion of gametes of different sizes (anisogamy). Thus, especially for gonochoristic systems where individuals produce only one type of gamete, sex is used to classify individuals based on the type of gamete they produce (typically females: larger cytoplasm-bearing gametes (eggs); or males: smaller, primarily DNA-bearing gametes (sperm)). Notably, these definitions cannot adequately describe individuals that do not produce gametes, and operational definitions of sex in many taxa often rely on secondary, more visible traits. Recognizing these limitations, for the purposes of this Perspective, we have relied on the gametic definitions of sex to broadly ground our understanding of sexual behaviours directed towards 'same sex' versus 'different sex' individuals.

By the above definitions, sexual behaviours necessarily evolved subsequent to the evolution of sexual reproduction. However, there is a surprising dearth of theoretical work investigating the ancestral origin of sexual behaviours. One notable exception is Parker's[37] model, which postulates that mobility, behavioural complexity, copulation and internal fertilization (which can be interpreted as including sexual behaviours) evolved in an anisogamous, multicellular, immobile species. In this Perspective, we situate the most recent common ancestor of extant animals with sexual behaviours at a similar evolutionary origin. However, this does not preclude the possibility of multiple origins of sexual behaviour, or that organisms other than multicellular anisogamous animals may have sexual behaviours. Notably, we deviate from the logic of Parker's[37,51,52] models that specifically hypothesize that this transition necessarily results in strong selection for 'female targeting' sexual behaviours in males. We further suggest that these models reflect a predominant implicit assumption that sexual behaviours evolved exclusively directed towards individuals of a different sex—an assumption questioned by our hypothesis.

evolution of SSB may indeed prove valuable in explaining the prevalence of the behaviour in particular clades, especially in species with complex social systems such as primates[43] where potential benefits of SSB are easier to identify. However, particularly when we consider the possibility of ancestral indiscriminate sexual behaviours, SSB need not confer large benefits to persist. Instead, we suggest the costs of SSB may be minimal in many cases (sensu refs. [44,45]), particularly in species with high mating frequencies relative to their reproductive output. Thus, the ubiquity and persistence of SSB can be largely explained by ancestral origins coupled with weak selection acting against a trait whose costs to fitness are far lower than other hindrances to higher reproductive success (for example, infertility or mate competition).

Insight into the potentially low costs of SSB can be gleaned from the rich literature investigating heterospecific sexual behaviour, or sexual behaviour directed towards other species. While there are certainly demonstrated examples of high costs associated with heterospecific sexual behaviour[46,47] (also termed reproductive interference), recent research has also revealed that in some taxa, heterospecific sexual behaviour can persist because its costs are lower than the costs of reducing mating efforts or of additional mechanisms for conspecific mate recognition[48,49]. For example, a recent study found that when closely related squash bug species were placed together in exclosures, heterospecific mating was common, but individuals that engaged in the behaviour also had high mating rates with conspecifics and had similar hatching success to individuals that were not allowed to mate with heterospecifics[50]. Similarly, SSB could have relatively low costs in species that invest little in individual mating attempts.

Costs and benefits of DSB. Both adaptive and non-adaptive hypotheses explaining the evolution of SSB are implicitly derived from the premise that the ancestral state is a population with exclusive DSB into which alleles coding for SSB have invaded, and that engaging in relatively less DSB is tightly associated with reduced fitness. This premise is also found in the few models that describe the evolution of sexual behaviours, which hypothesize that DSB, specifically 'female targeting' by males, would rapidly evolve in ancestral broadcast spawners due to selection pressures from high post-copulatory sperm competition[37,51,52] (Box 2). These models assume that because DSB is essential for sexual reproduction, selection will strongly favour high levels of DSB. By extension, they also assume that males with better 'female targeting', that is, higher levels of DSB, will have increased reproductive success.

However, this is often not the case—factors such as mate competition, mating order, mate age, gamete quality, sperm concentration and post-copulatory choice by females play important roles in determining whether or not DSB results in the production of offspring[32,53–55]. Furthermore, in many animal species, DSB is not limited to unique occasions of fertilization and may also have many non-reproductive functions[3,56,57], indicating that 'excess' sexual behaviours need not significantly reduce fitness[3,41]. In contrast, increasingly discriminating mate selection and sex-specific behaviours can come at the cost of missed mating opportunities as well as the cost of behavioural and morphological secondary sex characteristics (by which different-sex individuals that are potentially fertilization-compatible mates can be identified)[13,16,58,59]. For example, male burying beetles engage in more SSB when the perceived costs of missed mating opportunities with females were higher[60], suggesting that exclusive DSB could be disadvantageous when mating opportunities are rare.

In sum, we argue that while increasing degrees of DSB could maximize the likelihood of fertilization and, by extension, fitness in certain, perhaps widespread, conditions, it does not follow that more DSB is the only viable strategy necessary for high fitness. Exclusive DSB, rather than representing the baseline strategy for sexually reproducing animals, may represent a derived trait that evolved only after the development of secondary sex characteristics that facilitate mate identification and access, and is only adaptive in specific contexts.

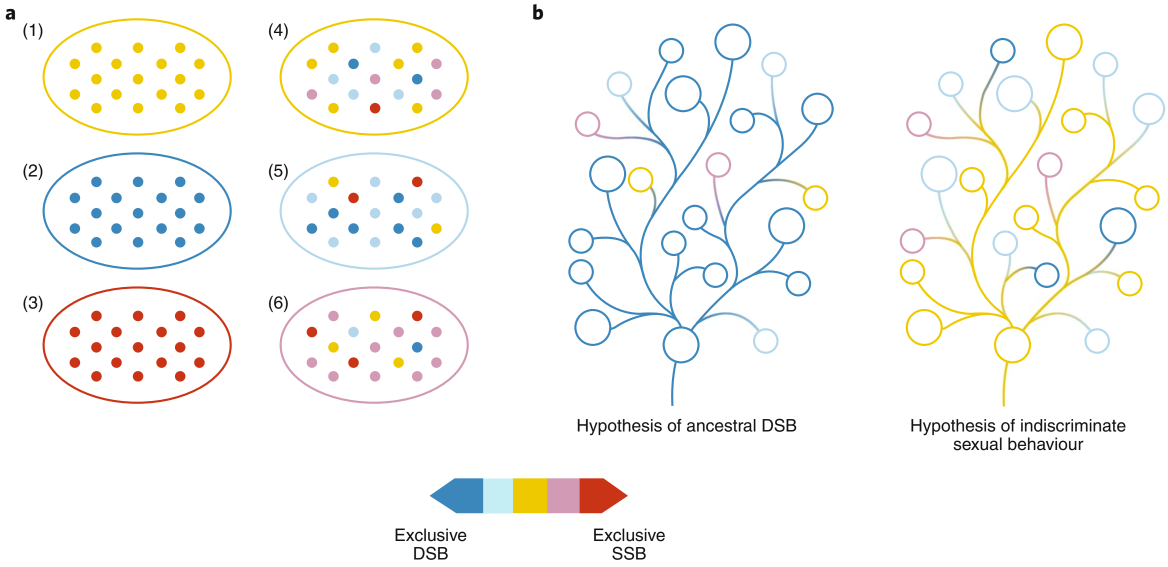

Fig. 2 | Conceptual representation of the variation in SSB and DSB that is possible at the individual and population, and species levels. a, Across their lifetimes, individuals may vary in the frequencies at which they express SSB or DSB, and populations can hypothetically be either monomorphic or polymorphic for SSB and DSB. Monomorphic populations could be comprised (1) entirely of individuals expressing both SSB and DSB across their lifetimes, or of (2) individuals who all express exclusive DSB, or of (3) individuals who all express exclusive SSB. We note, however, that a population comprised entirely of exclusive SSB individuals would likely go extinct. Populations may also be highly polymorphic, with some comprised of (4) individuals expressing greater frequencies of either SSB or DSB, some predominantly comprised of (5) individuals that largely engage in DSB but some individuals that express higher frequency of SSB, and the reverse (6) where most individuals exhibit higher frequencies of SSB but some are more often engaged in DSB. The polymorphic populations conceptualized here represent a small subset of the spectrum of possibilities that may exist within populations in nature. **b**, Macroevolutionary hypotheses of the evolution of SSB and DSB can be depicted through phylogenetic representations with the current, dominant hypothesis of ancestral exclusive DSB (left) and our proposed hypothesis of ancestral indiscriminate sexual behaviours (right). For both hypotheses, the ancestral animal reproduces sexually and is anisogamous (Box 2). Under the hypothesis of ancestral DSB, the most recent common ancestor to animals with sexual behaviour expressed exclusive DSB. This reproductive mode is then maintained with the exception of a few terminal nodes that have evolved greater levels of SSB. In contrast, our proposed hypothesis suggests the most recent common ancestor to animals with sexual behaviour expressed indiscriminate sexual behaviours with a mixture of SSB and DSB. This new hypothesis influences the perception of mixtures of sexual behaviours in extant species, suggesting that both those with more DSB or SSB might have been subject to selective pressures. Further, this hypothesis suggests that, on closer inspection, we will likely find most species to express a mixture of both DSB and SSB.

Shifting the baseline. Until now, evolutionary biologists have asked why SSB has evolved and how it can persist despite the obvious costs. We counter by questioning whether the obvious costs to SSB are really so obvious after all. We ask whether and when investing in costly mate recognition systems and potentially limiting mating opportunities through hyper-selectivity would evolve if generalist strategies of sexual behaviour allow for sufficiently high probabilities of fertilization and have sufficiently low costs[11,16,61–63]. Herein lies the crux of our argument: any individual adaptive or non-adaptive hypothesis put forward to explain the 'purpose' of SSB in animals may well explain its persistence, including the secondary non-reproductive functions for which SSB has been co-opted. However, the origins of SSB may lie not in recent evolutionary events producing those functions but in the earliest forms of sexual behaviours.

This seemingly subtle distinction rests on the crucial notion that the initial conditions of a population undergoing evolutionary change can have significant, even directional, impacts on its evolutionary trajectory[64–66]. Expected costs, benefits and likelihoods of particular evolutionary trajectories differ depending on whether we assume there has been selection for a given trait that is initially uncommon, or for or against a trait that is initially common. Thus, by shifting assumptions about the origins of these sexual behaviours, our hypothesis greatly alters the selective regimes that could give rise to the diversity of sexual behaviours we observe in animals today.

Our argument aligns with prior critiques of fields of research that are narrowly focused on adaptive evolution. A focus on adaptation can lead to the interpretation that extant traits are the most recent manifestation of evolutionary change under strong natural selection, rather than emergent properties borne of weak or absent selection, fluctuating selective pressures and biological constraints[67–69]. Under a hypothesis with SSB as predominantly neutral, it is therefore conceivable that depending on the lineage and ecological context, selection for DSB and against SSB may be strong, selection against SSB may be negligible, and in some cases selection for a higher degree or specific type of SSB may be strong. Indeed, it has previously been suggested that SSB initially arose as a neutral variant in non-human primates, and various emergent sociosexual benefits later reinforced selection for the trait[43]. We extend this hypothesis to propose that variation in mate targeting is ancestral to all sexually reproducing, gonochoristic animals. Thus, we predict the astonishing diversity of sexual behaviours present in animals to be the result of varying degrees of adaptive and non-adaptive processes (including drift) acting on existing continuous variation in the extent of DSB or SSB expressed across individuals, populations and species.

Implications for studying SSB

Considering the null hypothesis of indiscriminate sexual behaviour as the ancestral condition points to new directions for studying the evolution and ecology of SSB.

Phylogenetic comparisons. Our hypothesis naturally lends itself to exploration through phylogenetic comparative methods, tracing the

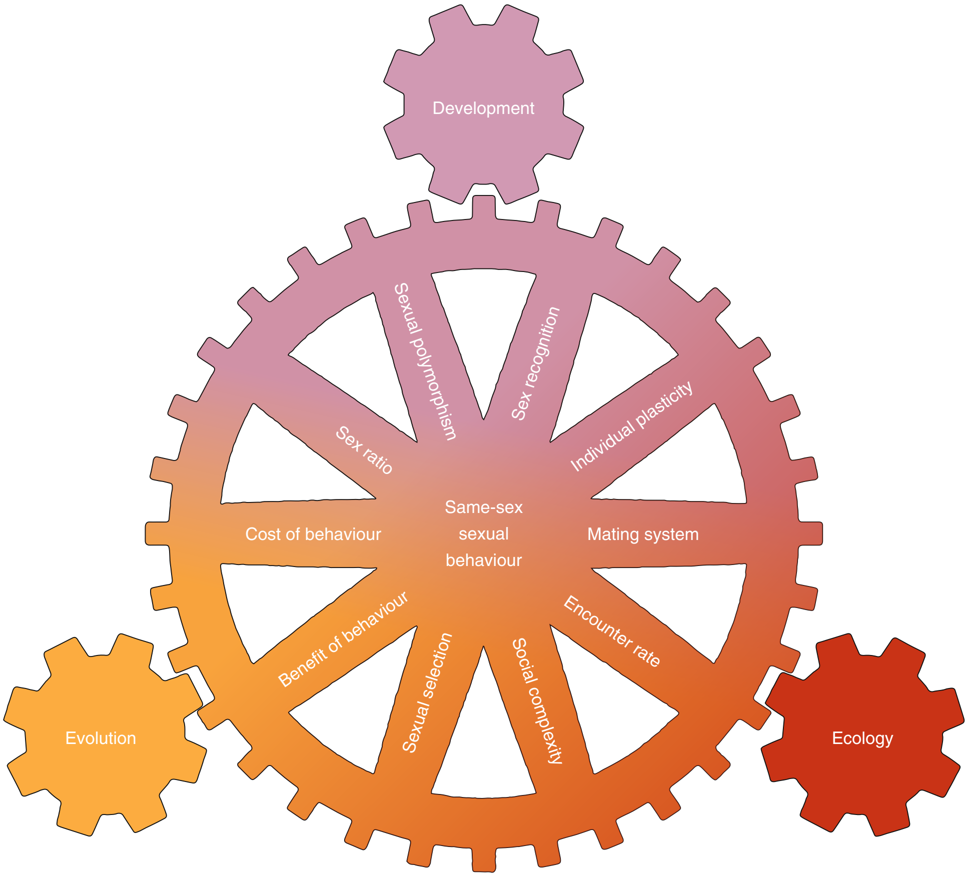

Fig. 3 | Ecological, evolutionary and developmental factors may influence the expression of SSB. Our hypothesis of an ancestral state of indiscriminate sexual behaviours comprising a mix of SSB and DSB generates a deeper consideration of the factors that influence the levels of SSB in a population or species. We suggest that just as mating systems, among other traits, are influenced by a combination of evolutionary, ecological and developmental factors, so is the prevalence of SSB. In addition to the costs and benefits that have been the primary axis of analysis for SSB thus far, research into the expression of SSB should also include consideration of how costs and benefits vary with factors such as levels of sexual selection, sexual polymorphism and sex recognition as well as encounter rate and social complexity, in addition to individual plasticity. Considering the complex determinants of levels of SSB and DSB will lead to more accurate and complete understanding of these behaviours predicated on ecology and behaviour, rather than untested assumptions about which behaviours are normal or paradoxical. We note that, while some research has considered the relationships between SSB and several factors including sex ratios, sex recognition and encounter rates, many other ecological, evolutionary and developmental factors that may influence or be influenced by SSB have rarely been systematically explored.

presence and prevalence of SSB across animal clades to assess the probability of ancestral origins. Indeed, detailed studies of SSB with this approach would allow for testing evolutionary hypotheses for the origin and maintenance of SSB beyond those that seek to resolve the evolutionary conundrum of SSB solely within the context of a particular taxon. Currently, however, such an analysis is impossible, due to a lack of reliable data. While SSB is documented in hundreds of species across animals, our understanding of the prevalence of SSB both within and among animal species is incomplete largely due to three main biases that seem to be present in current discussions of SSB.

First, many records of SSB come from incidental observations, and far more may have gone unreported because researchers either did not recognize behaviours or considered them shameful, unimportant or simply irrelevant to the studies they were conducting[12,20] (Box 1). Furthermore, SSB is often categorized as aggression, displays of dominance or social bonding and thus set apart from other sexual behaviours[12]. We contend that DSB can also be part of social dynamics, and the a priori designation of DSB as sexual and SSB as non-sexual hinders the retrieval of such data for any meta-analysis of sexual behaviour. Second, when researchers perceive species as sexually monomorphic, sex may be assigned solely based on observed mating behaviours by researchers who assume these behaviours are appropriate indicators of gametic sex. Thus, scientists may observe a sexual behaviour and incorrectly infer that it is DSB while in reality, both individuals may be of the same sex. Third, experimental mating studies are often designed to only present focal individuals with possible mates of a different sex. As a result, these studies preclude the possibility of observing SSB.

Thus, limited data as well as sampling bias impede a quantitative phylogenetic analysis across animals at this time. We predict that as behavioural ecologists and evolutionary biologists conduct rigorous and systematic research that does not assume SSB to be anomalous, SSB is likely to be found even more frequently than the incidental observations in a wide diversity of species would indicate. A concerted effort to understand the natural history of SSB across populations, species and lineages would provide an invaluable baseline for understanding the evolutionary dynamics of sexual behaviour.

Ecology and natural history of SSB. As long as explorations of animal sexual behaviour are predicated on the consideration of SSB as an evolutionary conundrum, the widespread prevalence of SSB across varied taxa in social and ecological conditions will remain confusing and unresolved. Reframing this question within our hypothesis will encourage new avenues of research into how various aspects of a species' ecology, evolution and development can impact and interact with the expression of sexual behaviours (for example, ref. [70]) (Fig. 3). In addition, our hypothesis prompts researchers to explore the abiotic and biotic conditions associated with the costs and benefits of different expressions of SSB among individuals, populations and species. Such research will require measuring what types of sexual behaviours individuals engage in, and how often those behaviours are found in either an SSB or DSB context. Further, it prompts investigations of how variation within or among individuals in age, size, hormone levels, sexually polymorphic traits, gametic sex and social position can impact the expression of sexual behaviours. For example, differences in the expression of SSB in males and females have already been the subject of some research in both human[71] and non-human[45,72,73] animal systems. The costs and benefits of SSB and DSB may differ among sexes due to sex-based variation in mating effort, reproductive investment and social systems. Accordingly, greater understanding of the contexts in which the sexes differ in their sexual behaviours should elucidate the factors that relax or strengthen selection for both SSB and DSB. In addition, research has shown that the ecological and population dynamics that impact sex ratios, encounter rates and levels of pre-copulatory sexual selection can influence mating system evolution[29,74]. Similarly, an area of research investigating how these factors can also impact the expression of SSB (for example, refs. [16,42,60,62,75]) is ripe for further development.

How research can untangle whether SSB is costly, beneficial or neutral remains a challenging question. The answer to this question likely varies across and within species; thus, appreciating intraspecific variation in SSB along with interspecific variation will help advance our understanding of the ecological conditions and evolutionary drivers shaping SSB in animals. Such research will also help elucidate the role of SSB as a component in the complex sexual networks that influence how sexual selection operates within and among species[76,77].

Concluding remarks

If any other trait had been observed in such a diverse array of taxa as SSB, it likely would be widely accepted that the trait was an ancestral condition present in some of the earliest animal clades. The notion that SSB has arisen convergently in so many different lineages only makes intuitive sense from a heteronormative world view in which 'heterosexual' behaviour is framed as the 'natural order' for sexually reproducing species, and 'homosexuality' is viewed as a recent aberration whose existence must be explained and justified[12]. Thus, the heteronormative and patriarchal Euro–American cultural norms persistent across evolutionary biology have influenced the discussion of sexual behaviours[9,30,78–84], keeping this discussion focused predominantly on DSB, a single type of sexual behaviour deemed culturally acceptable[85,86] (Box 1).

Questioning these biases creates room for potentially more parsimonious hypotheses regarding the evolution of sexual behaviour. As research into the representation of sexual behaviour across species continues, we suggest that species expressing both SSB and DSB will turn out to be as or more common than species with exclusive DSB, which may be a rarity in nature. Questions surrounding selection for and against varying degrees of DSB and SSB offer exciting opportunities for evolutionary biology. Because of the paucity of research in this area, any expansion of our hypothesis at this point would be speculative. But we are excited to see how relaxing the traditional constraints imposed on evolutionary theory of sexual behaviours will allow for a broader and more thorough understanding of the multivalent roles that these behaviours play in the ecology and evolution of animals. The notion that SSB is a recently evolved and distinct phenomenon from 'heterosexual' sex, rather than one component of the messy and tangled spectrum of behaviours, traits and strategies we clumsily refer to as 'sex' and 'sexual behaviour', is symptomatic of the kinds of binary essentialism that hinder not only social liberation and equity, but also scientific discovery.

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Competing interests

The authors declare no competing interests.

Additional information

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