

SAE Biology Application: The Remainder Structure of Sex Unfolding — A Cross-Phylum Non-Adaptive Model of Same-Sex Sexual Behavior

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Abstract

This paper applies the Self-as-an-End (SAE) framework to biological sex determination, focusing on the subset of same-sex sexual behavior (SSB) most directly tied to sex differentiation mechanisms: exclusive same-sex partner preference (ESSP) — the stable behavioral pattern of choosing same-sex mates even when opposite-sex partners are available. The paper argues that biological sex is not a direct readout of DNA but the outcome of a physical unfolding process in which 5DD (Law of Replication) information unfolds through 7DD (Law of Differentiation) into 8DD (Law of Reproduction) structures. Physical processes necessarily carry remainder, and this remainder can manifest behaviorally as ESSP. By comparing four sex determination systems (mammalian XY, avian ZW, reptilian temperature-dependent, and fish social-signal systems) and a cross-phylum continuum of unfolding reversibility, the paper demonstrates that SSB is not a unitary phenomenon but a family of structurally distinct expressions of unfolding remainder under varying fixation conditions. The paper further distinguishes 8DD-level mating behavior from 9DD-level display behavior, identifies survival pressure as one important regulatory variable among several that modulate the behavioral expression rate of remainder, and advances four non-trivial predictions — each presented with supporting data and explicit falsification conditions.

Chapter 1. The Problem

Research on same-sex sexual behavior (SSB) in biology faces a fundamental categorical difficulty: SSB has been observed in over 1,500 species, yet these behaviors are grouped under a single descriptive category as though they shared a common cause. This unified labeling obscures a structural difference — sex determination mechanisms differ radically across taxa, and SSB in different species need not originate from the same biological level.

SSB as used in the existing literature is a very broad operational category, typically encompassing transient courtship, mounting, genital contact, copulation, and long-term pair bonding — heterogeneous behaviors that may serve entirely different functions. Cross-mammalian comparisons further show that SSB correlates systematically with sociality and other variables. This paper does not attempt a unified mechanism for all SSB. Instead, it focuses

on a specific subset: exclusive same-sex partner preference (ESSP) — the stable pattern of choosing same-sex mates when opposite-sex partners are available.

The SAE framework offers a way into this subset. In the SAE's DD sequence, sex formation involves three levels: 5DD (Law of Replication) provides DNA-level genetic information, 7DD (Law of Differentiation) differentiates homogeneous cells into heterogeneous tissues and organs, and 8DD (Law of Reproduction) organizes the differentiated outcome into sex-specific reproductive structures. Sex is not a direct readout of 5DD; it is the product of 5DD information unfolding through 7DD into 8DD.

This unfolding is a physical process. Physical processes have error rates. The core proposition of the chisel-construct cycle is that any construct necessarily produces remainder. Sex unfolding, as a construct, generates remainder that is not pathology, not defect, but a structural byproduct of the constructive process itself.

The central thesis of this paper is: the subset of SSB most directly linked to sex differentiation — namely ESSP — is best understood as the behavioral manifestation of unfolding remainder. Its specific form depends on three structural variables: the asymmetry between active and default unfolding pathways, the degree of reversibility in the unfolding process, and the modulation of behavioral expression rates by environmental factors including survival pressure. Different species occupy different positions on these three variables, and therefore their ESSP distribution patterns differ.

Asking "why does SSB exist" is like asking "why does sculpting produce debris" — the answer lies not in the uses of debris but in the structure of the sculpting act itself.

This is a quasi-subject-condition problem. The organisms analyzed in this paper lack 13DD (self) — they have chisel-construct cycles in operation, 8DD unfolding directions, and 9DD selection pressures, but no self to observe or resist their own constructive processes. In these quasi-subjects, ESSP is not an anomaly requiring special explanation but a structural property of the sex unfolding process. Extending this analysis to species with true subjectivity (13DD and above) would require additional DD-level variables and lies beyond the scope of this paper.

Chapter 2. Two-Dimensional Structure: Base Layer and Emergent Layer

2.1 Base Layer: The 5DD → 7DD → 8DD Unfolding Pathway

Sex formation is an ordered unfolding process. The fertilized egg occupies 6DD (Law of Self-Maintenance) in the DD sequence, carrying 5DD information (genetic combination) from both parents. After implantation, the embryo enters 7DD (Law of Differentiation) — from a homogeneous cell mass into three germ layers, then into organs. Sexual differentiation is a specific stage within the 7DD unfolding, whose outcome is organized into 8DD (Law of

Reproduction) structures: gonads, reproductive tracts, external genitalia, and the neural differentiation relevant to mate preference.

The critical feature of this process is that it is not accomplished in a single step. From 5DD information to 8DD structures, multiple sequential and parallel physical-chemical processes intervene, each with its own error distribution.

Consider mammals. At the 5DD level, the information is the sex chromosome combination (XX or XY). But between XY and "male body," at least the following steps occur: the SRY gene on the Y chromosome is activated; SRY protein drives undifferentiated gonads to develop as testes; testes secrete testosterone and AMH; testosterone is converted to DHT in target tissues; DHT drives masculinization of external genitalia. In parallel but with a different temporal window, testosterone crosses the blood-brain barrier and is converted by aromatase into estradiol, which drives sexual differentiation of specific brain regions — notably the sexually dimorphic nucleus (SDN-POA) and other neural structures associated with mate preference. Each step is an independent physical-chemical process.

Somatic sexual differentiation and mate-preference-related neural differentiation share a hormonal source but differ in temporal windows, receptor expression levels in target tissues, and spatial distribution of local enzyme activity. This constitutes two parallel but relatively independent unfolding processes. Desynchronization between them — the body completes masculinization while mate-preference neural circuitry differentiates to a different degree — is the core source of unfolding remainder.

It must be emphasized that contemporary neuroscience increasingly stresses that sexually differentiated behaviors are not produced by two wholly separate "male brain / female brain" modules, but are shaped by differential modulation of shared neural circuits, hormone levels, sex chromosome effects, and developmental timing. The "desynchronization" described here does not refer to a mismatch between two discrete brain types, but to the degree of sexual differentiation in mate-preference-related neural circuitry deviating along a continuous axis from the position typically matched to somatic sex.

2.2 Emergent Layer: Behavioral Manifestation of Unfolding Remainder

The base-layer remainder (desynchronization between somatic sexual differentiation and mate-preference neural differentiation) manifests at the emergent layer as a shift in behavioral preference. An individual whose body is fully masculinized but whose mate-preference neural circuitry is less differentiated in the male direction will show attraction patterns deviating from the "typical male" mode. This deviation is observed behaviorally as SSB.

The key insight at the emergent layer is: mate-choice direction follows the sexual differentiation direction of neural circuitry, not of the body. In "typical" individuals, the two are aligned, making this distinction invisible. Only when the two base-layer unfolding processes are desynchronized does their separation become behaviorally apparent.

This means that "same-sex sexual behavior" is an external observation made from the somatic level. From the perspective of mate-preference neural circuitry, a somatically male individual whose circuitry is differentiated toward the female direction pursuing males is, in its own neural mechanism, no different from a typical female pursuing males — both are mate choices driven by the same direction of neural differentiation. "Same-sex" is a somatic-level description, not a neural-mechanism-level description.

2.3 Three Structural Variables of the Base Layer

The distribution of unfolding remainder is not uniform. It is modulated by three structural variables:

Variable 1: Asymmetry between active and default pathways. In many species, sex unfolding is not symmetric — one direction is the "default pathway" (completed without additional signals) and the other is the "active pathway" (requiring additional hormonal or genetic signals to drive). The active pathway involves more steps; each additional step adds an error site. Therefore, the unfolding error rate of the active pathway is systematically higher than that of the default pathway.

Variable 2: Reversibility of the unfolding process. In some species (e.g., many fish), sex unfolding is reversible — individuals can transition from one sex to another during their lifetime. In others (e.g., mammals and birds), sex unfolding becomes highly fixed after the embryonic period. In reversible species, remainder can be corrected through re-unfolding; in highly fixed species, remainder becomes a long-term stable structure. Importantly, even in mammals, mate-preference-related behavioral neural circuits remain subject to dynamic modulation by circulating hormone levels in adulthood (activational effects). Thus, "highly fixed" refers to the hardware level (gonads, reproductive structures), while the software level (behavioral neural circuit activity states) retains a degree of environment-dependent fine-tuning.

Variable 3: Environmental modulation of expression rate. Unfolding remainder is a base-layer structural property, but whether it is expressed behaviorally depends on multiple environmental factors, among which 9DD selection pressure (survival pressure) is one structurally important variable. In species facing extremely harsh survival conditions, the cost of not pairing is individual death or offspring death, and survival pressure compresses the behavioral expression space of remainder — remainder persists at the neural differentiation level but is suppressed at the behavioral level. Other modulating factors include but are not limited to: population sex ratio, mate availability, social density, and reproductive cost.

Therefore, observed ESSP frequency does not equal the magnitude of unfolding remainder. $\text{ESSP frequency} = \text{remainder magnitude} \times \text{expression rate}$, where expression rate is jointly modulated by multiple environmental factors. This distinction is critical for correctly interpreting cross-species SSB data.

Chapter 3. Domain-Specific Distinctions

3.1 Four Sex Determination Systems

The biological world contains multiple sex determination mechanisms, each corresponding to a different 5DD → 8DD unfolding pathway.

Mammalian XX/XY system. The default pathway is feminization. XX individuals develop as female along the default pathway without additional active signals. XY individuals require the SRY gene to initiate the active masculinization program. Masculinization is therefore the active pathway in mammals, predicting a higher unfolding error rate in males than females. Existing data are directionally consistent: approximately 8-10% of domestic rams show exclusive same-sex partner preference (choosing rams over ewes even when ewes are available). This constitutes the cleanest ESSP sample in the present analytical framework — exclusive preference has been repeatedly verified under controlled conditions, and these rams' sexually dimorphic nucleus (oSDN) volume is significantly smaller than that of female-oriented rams, providing direct neuroanatomical evidence for the continuity of mate-preference neural differentiation. Systematic data on ewe ESSP are lacking; this data gap itself is informative — if female ESSP were equally common, it would be unlikely to have been entirely overlooked.

Avian ZZ/ZW system. Structurally reversed. Males (ZZ) carry homologous sex chromosomes; females (ZW) carry heterologous ones. The default pathway is masculinization; feminization requires active driving by genes on the W chromosome. Feminization is therefore the active pathway in birds, predicting a higher unfolding error rate in females than males. Currently, birds lack ESSP data equivalent to the ram studies (i.e., frequency of individuals who, under controlled conditions with opposite-sex partners available, exclusively choose same-sex mates). The 31% female-female pairing in a Laysan albatross population is important field data, but the colony sex ratio was significantly female-biased (59% female), so this figure primarily reflects an alternative pairing strategy under sex-ratio skew, not a clean measurement of unfolding error rate asymmetry. Systematic quantification of avian ESSP remains a major data gap.

Reptilian temperature-dependent sex determination (TSD). Some reptiles (crocodilians, sea turtles, some lizards) have sex determined by incubation temperature rather than sex chromosomes. In these systems, external temperature signals and internal genetic threshold mechanisms jointly act on sexual differentiation. When the two signals align, differentiation is clean; when they conflict (temperature driving one direction, genetic threshold driving the other), unfolding remainder increases. Data from the Australian jacky dragon (*Amphibolurus muricatus*) directly support this mechanism: in this species, whose sex determination is considered intermediate between classical TSD and cryptic genetic influence, ovotestis (containing both ovarian and testicular tissue) prevalence varies significantly across temperatures — 36% at 24°C (4/11), 45% at 34°C (5/11), 14% at 28°C (2/14). Researchers interpret this pattern as conflict between temperature signals and genetic thresholds (cryptic genetic influence under thermal override), not simply "the transitional temperature zone is most

uncertain." The higher ovotestis rates at the two extreme temperatures indicate that intermediate morphological states are most common when the conflict between external thermal signals and internal genetic thresholds is strongest.

Fish social-signal systems. Many fish have sex determined by social signals and reversible across the lifespan. Clownfish (protandrous: male-to-female) transition when the group's largest female dies, with the largest male converting to female. Cleaner wrasse (*Labroides dimidiatus*, protogynous) transition when the male is lost, with the largest female converting to male. Key data come from a field manipulation experiment on cleaner wrasse (56 widowed males, 48 monogamous pairs): when same-sex pairing occurred (male-male dyads), the smaller individual automatically assumed the "female position" and began sex change — the same-sex pairing itself triggered re-initiation of the unfolding process, and the dyad automatically converted toward a mixed-sex configuration.

3.2 The Reversibility Continuum

The four sex determination systems are distributed along a continuum of "unfolding reversibility":

Highest reversibility: fish social-signal systems. Sex can reverse across the lifespan. Unfolding remainder can self-correct through re-unfolding. Cleaner wrasse data confirm that same-sex dyads are developmentally unstable because the endocrine/gonadal system is poised to convert dyads toward mixed-sex configurations. Stable, long-term exclusive same-sex partner preference should be significantly rarer in such species because the system retains the capacity to re-unfold toward opposite-sex functional structures. Functional males in clownfish naturally carry ovotestes (both ovarian and testicular tissue), which is not pathology but normal structure maintaining the capacity for sex change.

Moderate reversibility: some amphibians. Some frog species develop according to genetic sex as tadpoles but can reverse sex under certain environmental conditions in adulthood. This reversal is less flexible than in fish but retains some corrective capacity.

Low reversibility: TSD reptiles. Sex is determined once by incubation temperature, but temperature fluctuations during incubation — and conflict with genetic thresholds — can produce incomplete sexual differentiation. The high ovotestis rates in jacky dragons under conflict conditions (36–45%) demonstrate that dual-channel signal conflict produces large numbers of intermediate-state individuals. Once hatching is complete, sex is typically irreversible.

Highly fixed: birds and mammals. Sex unfolding becomes highly fixed after the embryonic period; gonads and reproductive structures cannot naturally reverse in adults. Unfolding remainder becomes a long-term stable structural property at the hardware level. However, even in these species, mate-preference-related behavioral neural circuits remain subject to dynamic modulation by circulating hormones in adulthood (activational effects). "Highly fixed" thus refers to hardware (gonads, reproductive structures), while the software level (behavioral neural

circuit activity) retains a degree of environment-dependent fine-tuning. This means that even in mammals, behavioral expression of mate preference is not fully rigid but fluctuates within a range established by developmental organizational effects and modulated by adult activational effects.

The core prediction of this continuum: the lower the unfolding reversibility, the higher the probability that exclusive same-sex partner preference will appear as a stable behavioral pattern — because remainder cannot be corrected and persists as long-term behavioral deviation.

3.3 Behavioral Sexual Differentiation Grayscale and Role Assignment

Sex is not binary. Both somatic sexual differentiation and mate-preference neural circuit differentiation produce continuous values, not discrete endpoints.

In highly fixed species, when two somatically same-sex individuals with different neural circuit sexual differentiation grayscale values form a same-sex pair, their behavioral role assignment (active/receptive) reflects the relative difference between their two grayscale values, not an absolute property of either individual. Role resides not in the individual but in the grayscale difference within the relationship.

Systematic research on the broad-horned flour beetle (*Gnatocerus cornutus*) provides quantitative data: among 311 male-male dyads, 82% exhibited SSB, and 71% showed fixed roles (one male consistently active). The key finding: fixed-role dyads showed significantly lower aggression than role-switching dyads. This is precisely the prediction of the grayscale-difference model — large differences enable rapid role stabilization, small differences produce positional competition and elevated aggression. Another finding: body size differences did not significantly explain role assignment, implying that roles derive from an internal variable rather than externally visible physical attributes.

Cleaner wrasse data provide a complementary reference: in same-sex dyads, the smaller individual automatically assumed the "female position," with body size serving as a direct proxy for grayscale (in fish, body size directly maps to social sex).

An important qualification: the grayscale-difference model as the primary determinant of role assignment is most applicable in species with low social complexity where 9DD social competition is not prominent (e.g., beetles, fish). In species with high social complexity (e.g., primates), 9DD power-hierarchy dimensions may override 8DD grayscale differences — SSB roles may more strongly reflect current social dominance relationships than relative neural differentiation grayscale.

3.4 Display Behavior Is Not Same-Sex Sexual Behavior

A domain-specific distinction introduced in this paper: 9DD display behavior and 8DD mating behavior are not the same phenomenon and should not be included in the same statistics.

King penguin data from the Kerguelen Islands reveal the necessity of this distinction. Among 53 DNA-sexed displaying couples, 26.4% were male-male and 1.9% were female-female. But among 75 confirmed bonded pairs, male-male was only 1.3% and female-female 1.3%. Display-stage SSB and bonded-pair SSB differ by an order of magnitude.

Display behavior is 9DD-level social competition — individuals display their quality in the competitive arena, competing for social attention and position. The audience is the entire social field, not a specific mating target. Heterosexual individuals also engage in same-sex display competition; this has nothing to do with mate preference direction. The king penguin researchers themselves confirmed that display-stage male-male interactions are part of mate-search ecology rather than stable bonding. Males observed displaying with males subsequently paired with females significantly more slowly than males displaying with females — more likely reflecting positional disadvantage in display competition than mate-preference direction.

Therefore, large amounts of data recorded as "same-sex sexual behavior" in existing SSB research are actually 9DD display behavior rather than 8DD mating behavior. Once display behavior is stripped out, the true volume of 8DD-level mating SSB data shrinks dramatically, but the remaining data constitute a clean measurement of unfolding remainder. This methodological distinction is a prerequisite for correctly interpreting cross-species SSB frequency data.

3.5 Wild Populations and Captive Environments: Environmental Modulation of Expression Rates

Differences in ESSP frequency for the same species under different environmental conditions reveal the regulatory effect of environmental factors on remainder expression rates.

Penguins provide a striking contrast. Wild king penguin bonded-pair SSB was 1.3% (Kerguelen Islands, 1 male-male and 1 female-female among 75 pairs). In zoo environments, same-sex pairing proportions increase: among 93 Humboldt penguins at London Zoo (approximately balanced sex ratio), 3 of 34 nesting pairs were same-sex (approximately 9%). Twenty same-sex penguin pairs were reported across 16 major aquariums and zoos in Japan. Same-sex pairs have been documented at zoos in New York, Berlin, Odense, Sydney, London, and Valencia.

This frequency difference should not be reduced to a single factor. Multiple variables change simultaneously between wild and zoo environments: survival pressure (wild penguins face extremely harsh breeding conditions where failure to pair correctly can mean offspring death), mate availability (zoo populations are small with limited individual choice), social density (spatial constraints differ in zoos), and observational opportunity (behavior is more easily systematically observed in captivity). This paper proposes that 9DD-level survival pressure is one structurally important factor among these — it directly compresses the behavioral expression space of remainder. However, we acknowledge that existing data are insufficient to fully isolate survival pressure from other covariates.

One piece of evidence, however, suggests survival pressure's role cannot be dismissed: Bremerhaven Zoo in Germany attempted to break up three male-male penguin pairs by

introducing female penguins, but failed — zoo officials stated the bonds were "too strong." This is not opportunistic temporary behavior but a manifestation of genuine 8DD-level preference: same-sex partner choice persisted even when opposite-sex alternatives were available. This is structurally homologous to the 8-10% of rams with exclusive same-sex preference.

Therefore, correctly interpreting cross-species ESSP data requires distinguishing remainder magnitude (a base-layer property determined by genetic and developmental mechanisms) from behavioral expression rate (jointly modulated by survival pressure, sex ratio, mate availability, social density, reproductive cost, and other environmental factors). Wild-population SSB frequencies may systematically underestimate the true magnitude of unfolding remainder.

Chapter 4. Colonization and Cultivation

4.1 Forms of Colonization

Colonization in this domain takes three typical forms.

First: categorical colonization. Unified labels ("homosexuality," "SSB") flatten structurally distinct phenomena into a single category. Male ESSP in mammals, female-female cooperative breeding in sex-ratio-skewed bird populations, pan-sexual contact for social alliance in bonobos, dominance-establishing mounting in beetles — these are grouped under "SSB" but originate from entirely different DD levels. The first is a behavioral manifestation of 8DD unfolding remainder; the second is an alternative pairing strategy under demographic constraint; the third is 9DD-level social strategy; the fourth is a competitive substitute. Unified labeling compresses four different levels into one, obscuring actual mechanisms.

Second: the "natural/unnatural" framing. Evaluating biological behavior against "normal reproductive function," classifying everything not directly serving reproduction as "abnormal" or "a paradox requiring special explanation." This framework presupposes that 8DD reproductive function is the sole "legitimate" function of sexual behavior, then consigns all behavior not conforming to this presupposition to the category of "exceptions awaiting explanation." This is a typical form of institutional-layer colonization of the individual layer — compressing the multidimensional structure of behavior through a single functional definition.

Third: 9DD survival pressure colonizing 8DD remainder expression. This is the most primitive form of colonization, occurring at the level of individual behavior. In organisms without 13DD (self), 6DD (survival) and 8DD (reproduction) are the highest imperatives. When 9DD selection pressure dictates "fail to pair and die," the individual has no level of resource from which to say "no, I will follow my own unfolding direction." Remainder is suppressed not because it is absent but because there is no self to speak for it. The wild-versus-zoo penguin comparison suggests this form of colonization may be operative: the same species under different pressure conditions shows significantly different ESSP behavioral expression rates.

4.2 Forms of Cultivation

Cultivation means acknowledging that unfolding processes necessarily produce remainder, and that remainder is not pathology to be eliminated but a structural property of the chisel-construct cycle.

Specifically, cultivation requires three cognitive shifts.

First, from "why does SSB exist" to "what structure does SSB have." The former presupposes that SSB requires special explanation (why does it deviate from "normal"); the latter analyzes SSB as a behavioral manifestation of unfolding remainder, examining its internal structure.

Second, from unified category to structural differentiation. SSB in different species originates from different DD levels and should be analyzed separately. An effective analytical framework must distinguish at minimum: (a) ESSP driven by 8DD unfolding remainder (rams, zoo penguins), (b) 9DD-level display behavior (king penguin display-stage male-male interactions), (c) competitive substitutes (broad-horned flour beetle dominance mounting), (d) alternative pairing strategies under sex-ratio skew (albatross same-sex breeding), and (e) transitional pairing in reversible-unfolding species (cleaner wrasse auto-sex-change dyads).

Third, from "explaining anomaly" to "predicting distribution." The SAE framework does not ask "why are some individuals like this" but predicts the distribution pattern of unfolding remainder across species — which species have larger remainder, in which species remainder is expressed, and why.

Chapter 5. Theoretical Positioning

5.1 Dialogue with the "Ancestral Indiscriminate Mating" Hypothesis

A 2019 study in *Nature Ecology & Evolution* proposed the hypothesis of an "ancestral condition of indiscriminate sexual behaviors": early animals may not have differentiated between sexes when mating, and sex-selective mating evolved later alongside sexual dimorphism and recognition capabilities. Under this hypothesis, SSB is not a deviation requiring explanation but a residue of the ancestral state.

The SAE framework shares a structural resonance with this hypothesis: both refuse to treat SSB as anomalous. But SAE provides a more precise mechanism. The "ancestral indiscriminate" hypothesis is correct at the descriptive level but does not explain why SSB distribution patterns differ across species — if SSB were merely ancestral residue, it should attenuate uniformly across all species, yet the frequency and form of SSB vary enormously. The SAE unfolding-remainder model explains this variation: different species have different sex determination mechanisms, different pathway asymmetries, different reversibility levels, and different environmental modulation of expression rates, producing different remainder magnitudes and manifestation patterns.

5.2 Dialogue with the Adaptive-Explanation Approach

Extensive research has sought adaptive functions for SSB: social alliance, hierarchy establishment, kin altruism, same-sex co-parenting improving offspring survival, and so on. Each of these explanations has received data support in specific species.

The SAE framework does not deny these functional explanations but notes that they conflate two different questions. SSB as behavior can be co-opted at the 9DD social-competition level as a functional strategy, but this does not mean SSB originates at the 9DD level. Unfolding remainder is an 8DD-level structural property that exists prior to any functional co-optation. Some species' social systems co-opt this remainder as a social tool (approximately 60% of bonobo sexual activity occurs between females); other species' social systems do not co-opt it (8-10% of rams with exclusive same-sex preference serve no apparent social function).

The ESSP subset on which this paper focuses is precisely the set of behaviors least amenable to adaptive framing — individuals who, with opposite-sex partners available, exclusively choose same-sex mates. These individuals' behavior does not serve social alliance (because it is exclusive, not strategic), does not serve hierarchy establishment (because it persists regardless of social context), and does not serve alternative breeding (because it foregoes opposite-sex mating opportunity). It is the cleanest behavioral manifestation of unfolding remainder.

5.3 Dialogue with Developmental Biology

The organizational-activational hypothesis is the dominant framework in the sex differentiation field: embryonic-period hormones "organize" mate-preference-related neural structures (highly fixed), while adult-period hormones "activate" the already-organized neural circuits. This hypothesis is highly compatible with the SAE framework — "organization" corresponds to the 7DD → 8DD unfolding process; "activation" corresponds to the behavioral emergence of unfolding outcomes.

The SAE framework supplements this hypothesis in two ways. First, it explicitly positions the "organizational" stage as a chisel-construct process that necessarily produces remainder. The organizational-activational hypothesis describes the mechanism of unfolding; SAE adds the structural constraint that unfolding is necessarily imperfect. Ram data provide direct evidence: the oSDN volume of exclusively same-sex-preferring rams is significantly smaller than that of female-oriented rams, demonstrating the continuity of mate-preference neural differentiation and its association with unfolding remainder. Second, the SAE framework, by introducing the reversibility continuum, explicitly delimits the scope of the organizational-activational hypothesis: it describes the situation in highly fixed species (mammals, birds) and is not fully applicable to reversible-unfolding species (sex-changing fish), where "organization" is not a one-time highly fixed process but can be re-triggered by social signals.

Chapter 6. Non-Trivial Predictions

Prediction 1: Higher Unfolding Reversibility, Rarer Exclusive Same-Sex Partner Preference

[Prediction] In species with reversible sex unfolding, remainder can self-correct through re-unfolding. Therefore, in naturally sex-changing fish, stable and long-term ESSP should be significantly rarer. SSB in such species, if present, should be primarily transitional (temporary behavior before sex change completes) or social (9DD behavior unrelated to unfolding remainder).

[Supporting data] The cleaner wrasse field experiment directly supports this prediction. Same-sex pairing events occurred (at least 4 male-male dyads among 56 widowed males), but dyads were developmentally unstable — the smaller male began sex change, and dyads automatically converted toward mixed-sex configuration. Clownfish functional males naturally carry ovotestes, indicating that maintaining intermediate grayscale is a normal structural feature of such systems. Controlled mate-preference experiments directly measuring ESSP frequency in sex-changing fish are currently lacking.

[Falsification condition] If, in naturally sex-changing fish, a significant proportion of individuals maintain exclusive same-sex partner preference over extended periods (exceeding the normal sex-change timeline), despite available opposite-sex mates and open sex-change channels, this prediction fails.

Prediction 2: Active-Pathway Error Asymmetry Reverses Directionally Across Phyla

[Prediction] In mammals, masculinization is the active pathway; male ESSP is predicted to exceed female ESSP. In birds, feminization is the active pathway; female ESSP (at the bonding level, not the display level) is predicted to exceed male ESSP. In TSD reptiles, no active/default asymmetry exists; male and female ESSP are predicted to be closer to symmetric.

[Supporting data (partial)] Mammals: 8-10% exclusive same-sex preference in rams with systematic data; ewes lack equivalent systematic study. Giraffes show up to 94% male-male mounting vs. only 1% female-female. Birds: systematic ESSP quantification equivalent to the ram studies is currently lacking. The 31% female-female pairing in Laysan albatross primarily reflects alternative pairing strategy under sex-ratio skew and cannot serve directly as evidence for unfolding error rate asymmetry, though its direction is not inconsistent with the prediction. King penguin display-stage data (male-male 26.4% vs. female-female 1.9%) reflect 9DD display competition and are not applicable to testing this prediction. TSD reptile ESSP data are currently missing — the largest verification gap.

[Methodological warning] Cross-phylum ESSP comparisons must strip 9DD display behavior from statistics and control for population sex ratios. Any SSB frequency data including display behavior cannot cleanly test 8DD unfolding-remainder asymmetry.

[Falsification condition] If, after controlling for sex ratio and stripping display behavior, bonding-level data show that mammalian female ESSP systematically exceeds male ESSP, or avian male ESSP systematically exceeds female ESSP, the directionality claim of this prediction fails.

Prediction 3: In Low-Social-Complexity Species, SSB Pair Role Assignment Reflects Neural Differentiation Grayscale Difference

[Prediction] In species with low social complexity where 9DD social competition is not prominent, active/receptive role assignment in SSB dyads should be a property of the relationship, not the individual. Specific predictions: (a) the same individual can display different roles with different SSB partners; (b) fixed-role dyads show lower aggression than role-switching dyads (large grayscale difference → rapid role stabilization → reduced conflict); (c) in species with high social complexity (e.g., primates), 9DD power-hierarchy dimensions may override 8DD grayscale differences, with roles more strongly reflecting social dominance relationships.

[Supporting data] Flour beetle data directly support (b): fixed-role dyads showed significantly lower aggression than role-switching dyads. Body size failed to significantly explain role assignment, supporting derivation from an internal variable rather than externally visible attributes. Cleaner wrasse data support body size as a grayscale proxy. Adélie penguins show documented cases of reciprocal mounting, proving role switching is possible in avian SSB. High role dynamism and hierarchy dependence in primate SSB are directionally consistent with (c), but quantitative studies separating 8DD grayscale from 9DD hierarchy effects are lacking.

[Falsification condition] If, in low-social-complexity species, SSB role assignment is found to be entirely independent of dyad composition (the same individual always assumes the same role regardless of partner), and fixed/switching role status shows no association with within-dyad aggression, the grayscale-difference model fails.

Prediction 4: ESSP Frequency Differences for the Same Species Under Different Environmental Pressures Reflect Expression Rate Variation

[Prediction] Transferring the same species from high- to low-survival-pressure environments should increase ESSP behavioral expression rates, and vice versa. Unfolding remainder magnitude (determined by genetic and developmental mechanisms) is not affected by short-term environmental pressure changes. Therefore, $\text{ESSP frequency} = \text{remainder magnitude} \times \text{expression rate}$, where expression rate is jointly modulated by survival pressure, sex ratio, mate availability, social density, and other environmental factors.

[Supporting data] The wild-versus-zoo penguin comparison provides preliminary support. Wild king penguin bonded-pair SSB was approximately 1.3%; London Zoo Humboldt penguin same-sex pairing was approximately 9%. Zoo same-sex pairs showed ESSP characteristics (did not switch to opposite-sex partners when available). However, the existing comparison does not control for sex ratio, mate availability, or social density covariates, so the frequency difference cannot be wholly attributed to survival pressure alone.

[Ideal experimental design] Within the same species, control sex ratio and mate availability while systematically varying survival pressure or reproductive failure cost; measure ESSP frequency changes. If, under balanced sex ratio and ample mate availability, reducing reproductive failure cost still increases ESSP frequency, survival pressure's effect can be more cleanly isolated.

[Falsification condition] If, after controlling for sex ratio and mate availability, no significant ESSP frequency difference appears across different survival-pressure conditions, the claim that survival pressure is a key expression-rate modulator fails. If ESSP frequency differences are entirely explained by sex ratio and mate availability, the "remainder magnitude \times expression rate" separation model remains valid, but survival pressure is no longer a key variable within expression rate.

Chapter 7. Conclusion

7.1 Recovery

The core argument of this paper can be compressed into three propositions.

Proposition 1: Sex is the result of an unfolding process, not a direct readout of DNA. 5DD information unfolds through 7DD into 8DD, with each physical-chemical step carrying its own error distribution. Somatic sexual differentiation and mate-preference-related neural differentiation are two parallel but independent unfolding processes; their desynchronization is unfolding remainder.

Proposition 2: The magnitude and manifestation of unfolding remainder depend on species-level unfolding mechanics. Three structural variables — active/default pathway asymmetry, unfolding reversibility, and environmental modulation of expression rates — jointly determine the distribution and behavioral expression of remainder across species. In reversible-unfolding species, remainder self-corrects and stable ESSP is difficult to maintain. In highly fixed species, remainder becomes long-term structure. Active-pathway error rates exceed default-pathway rates, and which sex constitutes the active pathway reverses across phyla.

Proposition 3: Observed ESSP frequency does not equal unfolding remainder magnitude. ESSP frequency = remainder magnitude \times expression rate, where expression rate is jointly modulated by survival pressure, sex ratio, mate availability, and other environmental factors. Simultaneously, 9DD display behavior must be stripped from SSB statistics, or 8DD-level remainder measurement will be systematically distorted.

Asking "why does SSB exist" is like asking "why does sculpting produce debris" — the answer lies not in the uses of debris but in the structure of the sculpting act itself.

7.2 Contributions

This paper contributes to existing discussion at four levels.

First, it provides a unified analytical framework enabling cross-phylum comparison of ESSP under a single set of structural variables. Existing literature typically analyzes SSB within species; cross-phylum comparison has lacked a unified theoretical basis.

Second, it extracts the subset of SSB most directly linked to sex differentiation (ESSP) from the broad SSB category, shifting from "functional explanation" (what is it for) to "structural analysis" (what process does it come from). This does not preclude functional explanations but positions them as 9DD co-optation of 8DD remainder, distinct from the cause of remainder itself.

Third, it introduces the distinction between display behavior and mating behavior and an analytical framework for environmental modulation of expression rates, providing methodological tools for correct interpretation of SSB data.

Fourth, it advances four cross-phylum non-trivial predictions (unfolding reversibility, error-asymmetry reversal, grayscale-difference role assignment, environmental pressure modulating expression rate), each with explicit falsification conditions, rendering the model testable.

7.3 Open Questions

First, avian and TSD-reptile ESSP data for Prediction 2 are currently missing. Controlled-condition measurements (balanced sex ratio, opposite-sex available) of male and female ESSP frequency in birds and TSD reptiles are needed. In particular, whether TSD-reptile individuals incubated under thermal-genetic threshold conflict conditions show higher ESSP frequency is the key datum for testing the "dual-channel signal conflict amplifies remainder" hypothesis.

Second, the continuity of mate-preference-related neural differentiation currently has direct neuroanatomical support only from sheep oSDN data. Establishing continuous correlations between neuroanatomical measures and behavioral preference across more species is needed.

Third, this paper focuses on 8DD-level unfolding remainder. SSB in the biological world clearly does not all originate at this level. 9DD-level social competition (bonobo social-alliance SSB) and dominance competition (beetle dominance mounting) require separate modeling within the SAE framework. This paper consciously limits its analysis to the 8DD-level ESSP subset, leaving 9DD-level behavioral modeling to subsequent work.

Fourth, this paper's analytical framework (remainder magnitude \times expression rate) is sufficient for quasi-subjects lacking 13DD (self). In these species, 6DD (survival) and 8DD (reproduction) are the highest imperatives, and the individual has no level of resource to resist environmental suppression of remainder expression. Extending to species possessing self requires introducing additional DD-level variables — self can choose to bear costs in order to express 8DD unfolding direction even under continuing survival pressure — which lies beyond the scope of this paper.

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