

COMPARATIVE COGNITION & BEHAVIOR REVIEWS

Where Is the Lust? Reproductive Affects at the Emergence of Experience

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Discussions of the adaptive origins of sentience focus on survival-related affects such as pain, hunger, and thirst. Yet reproduction is primary to fitness, and reproductive behavior often demands the same persistence and goal-directed flexibility that valenced experience is hypothesized to support. We ask whether a reproductive affect, the felt pull toward mating (here: lust), is as fundamental as pain in the evolution of sentience, providing a positive counterweight to competing homeostatic needs. We outline the rationale, comparative clues, and empirical approaches, and we argue that we may need to attend not only to those that hurt but to those that want.

Keywords: animal awareness, sentience, consciousness, pain, lust, motivation, trade-off

Survival, Reproduction, and the Origins of Felt Experience

Discussions of the adaptive origins of awareness are dominated by survival-oriented examples: the sting of pain, the pang of hunger, the grip of thirst. These are commonly considered homeostatic affects—consciously felt, valenced bodily signals that motivate behavior to correct internal imbalances (Damasio & Damasio, 2022; Panksepp, 2005). Such feelings are argued to connect internal physiological states to flexible behavioral responses in unpredictable environments, making them prime candidates for the first forms of felt experience. In evolutionary narratives it is often argued that sentience, taken as the capacity for valenced experience, arose to help organisms stay alive by avoiding dangers and maintaining homeostasis (Damasio & Damasio, 2022; Ginsburg & Jablonka, 2019; Veit, 2023). Here, the proposed link runs through behavioral flexibility. Valenced experience is thought to support more than fast, reflexive, local stimulus–response routines, instead enabling integrative, context-sensitive

control over extended and internally competing behavioral programs. In this sense, valenced experience allows for greater “complexity,” navigating richer, noisier decision contexts through integrative, flexible behavioral control.

Reproductively relevant affects and behaviors, by contrast, are often diminished in these accounts. Influential frameworks of animal affect place sexual desires (hereafter lust, for shorthand) in a later emerging and more cognitively and affectively laden category, implying it evolved only after “basic” homeostatic drives such as hunger or pain had established a baseline of felt experience. Panksepp’s (2005) seminal model of primary emotions, for example, classifies “LUST” as a prototypical emotional system, presumed to have evolved after the more fundamental survival-related homeostatic affects. Tinbergen’s (1951) ethological hierarchy similarly cast reproductive behaviors as “luxury” actions, expressed only when survival needs are met. While Rolls’s (2014) distinction between survival- and reproduction-linked emotions treat mating motivation as a later, higher-order system. A similar move appears in Loewenstein’s (1996) discussion of “visceral

factors,” where hunger, thirst, sexual desire, and pain are identified as powerful motivators, but again in a way that reinforces the survival-first framing. The prevailing throughline is that felt experience first evolved to keep organisms alive, and only later was extended to support reproductive pursuits such as mate seeking and courtship.

From an evolutionary perspective, however, treating reproduction as secondary lacks sense. Survival is not an end in itself; it matters only as a means to reproduction. This is explicit in core evolutionary theory. Darwin distinguished sexual selection from natural selection but treated both as fundamental routes by which selection shapes adaptation via survival and reproduction, a framing that has since been richly developed across evolutionary biology (Andersson, 1994; Darwin, 1871). Omitting reproductive affects from accounts of basal sentience may thus underestimate how much of early experience was shaped by the demands of reproduction as well as self-preservation. If pain is often cast as the paradigmatic negative feeling that allows organisms to minimize harms, reproduction plausibly demands a counterpart: a positive pull strong enough to motivate persistence and support the flexible behavioral pursuit of opportunities even when self-preservation is at stake. We follow the common view that such a pull is positively valenced—an experience widely described across philosophy, psychology, and the arts as elating, engaging, and often intrinsically enjoyable (Dickinson, 2005; Oberg, 2018; Panksepp, 2005; Richards, 2015). We are perhaps the very first creatures capable of feeling needed not only to register threats with aversion but also to weigh them against vital opportunities via attraction, so that felt experience could serve as a mechanism for evaluating trade-offs and flexibly shifting behavior between survival and reproduction.

Lust as Pain’s Counterweight

If pain is the quintessential negative-valenced homeostatic affect, lust can be seen as its positive-valenced reflection. Pain, on common accounts, is typically associated with physical damage, and it motivates animals to

withdraw from harm, learn from the encounter, and/or recuperate from injury (Craig, 2003a; Damasio & Damasio, 2022; Klein, 2015). Other homeostatic affects such as hunger and thirst can likewise be propulsive, sustaining approach and persistence even in the face of competing survival demands. What sets lust apart is that it functions as a dedicated motivational engine for reproduction: It signals a chance to mate and urges approach, flexible engagement, sustained effort, and evaluation until mating is achieved. Crucially, reproduction requires its own felt urgency, because opportunities to reproduce must often be weighed against hunger, thirst, pain, or danger. Without dedicated reproductive affects, reproduction would risk being consistently outcompeted by survival imperatives. Like pain, lust is intense and can motivationally dominate, capable of reorganizing behavior from moments to days (Cooke et al., 2006; Pfaus et al., 2001; Warner, 1927), and both can override other priorities when they surge (Eccleston & Crombez, 1999; Pfaus et al., 2001; Woolf & Walters, 1991).

Pain usually outranks other motivations: An animal in acute pain will often abandon foraging or exploration to tend to its injury. Yet the priority of pain has limits. Starving animals may persist in foraging despite painful wounds if starvation is the greater threat (Craig, 2003b). Sexual motivation shows the same kind of context-dependent dominance, with animals in the grip of a mating drive frequently ignoring hunger, thirst, fatigue, or danger. Male and female rats will cross electrified grids to interact with receptive partners (Meyerson et al., 1973; Warner, 1927); salmon will fight upstream with the goal of mating, and go without feeding until death (Cooke et al., 2006); and male mantids and spiders will mate even while being cannibalized by their partners (Andrade, 1996; Barry et al., 2008). Sexual arousal can also blunt other drives directly and reorganize motivational priorities by producing analgesia, suppressing competing needs, and even reversing the valence of normally aversive cues (Pfaus et al., 2001). These cases show that reproductive affect can rival, and often dominate, the motivational power of pain, thereby supporting a view of its role as a foundational counterweight rather than a late addition to the affective repertoire.

Lust, under such a view, is not a late-arriving luxury but an equally primal drive. If pain evolved early to push organisms away from harm, then complementary states evolved to pull them toward vital mating opportunities. Hunger and thirst can likewise be propulsive, directing behavior toward sustenance, but lust is distinctive in supplying the reproductive pull needed to trade off against survival costs. Rather than a sequential hierarchy, then,

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pain and lust may have been mutually defining poles of affective life—repulsive and propulsive together—establishing the contrasts that made felt experience adaptive at the origins.

Might Sex Demand Feeling?

In functional terms, a reproductive affect is as deeply grounded as any survival affect. The evolutionary stakes of reproduction are absolute: Survival only serves reproduction in the end. Selection favors mechanisms that drive organisms to seize mating opportunities even when doing so is costly or risky. A felt mating urge could provide a powerful motivational engine to ensure reproduction is not easily deemphasized, especially when obstacles must be overcome or other needs temporarily set aside.

The stronger reasons to expect reproductive affects, however, lie in the demands of sexual reproduction itself. Courtship and mating interactions are rarely reflexive; they are often prolonged, complex, conditional sequences of behavior. An animal must often decide which mate to pursue, how long to persist in their behavior or pursuit, when to change tactics or try elsewhere, how to attend to predators and contend with rivals, and when to give up (Andersson, 1994; Jennions & Petrie, 1997). These decisions require integrating factors both environmental and internal, including signals from mates and competitors, seasonal cues, reserves of energy and hormones, and prior experiences (Candolin, 2003; Rosenthal, 2017). This flexible, persistent, and evaluative negotiation of priorities is exactly the kind of challenge for which felt experience is thought to have adaptively evolved (Damasio & Damasio, 2022; Ginsburg & Jablonka, 2019; Veit, 2023). A lust-driven animal can remain on task through this complexity, sustaining effort and adjusting behavior despite setbacks. In short, a felt drive to reproduce could keep an organism engaged in pursuing mates in a way that a rigid set of reflexive responses cannot, especially under challenging and dynamic conditions.

In many species, sexual interactions involve an asymmetry between the sexes, with one sex actively courting and the other evaluating mates (Andersson, 1994). Reproductive affect is likely to support each strategy, albeit through different functions: facilitating persistence and flexibility on the courting side, and providing an evaluative currency on the choosing side. Importantly, both pursuit and choice may require a positively valenced drive that can compete with pain and other homeostatic survival affects at the same functional level so that reproductive priorities can win trade-offs against survival-oriented demands.

On the courting side, lust may mediate between conflicting needs. Many animals will forego food, safety, even life itself for a chance to reproduce, showing the mating drive can override hunger, pain, or fear (Barry et al., 2008; Pfaus et al., 2001; Warner, 1927). On the choosing side, reproductive contexts frequently involve intensive evaluation. Selecting a mate is one of the most consequential choices an organism faces. Well-supported theory in sexual selection emphasises the role of mate choice in securing genetic benefits and in interpreting honest signals of partner quality and condition (Andersson, 1994; Kirkpatrick, 1996; Zahavi, 1975). Affect here may serve as a common currency for weighing such options and trade-offs: assessing partner quality and compatibility, interpreting courtship signals in the context of rivals and predators, and deciding where to invest mating effort. It is plausible that sentient affective states evolved in part as tools for navigating these nuanced decisions, thereby allowing animals to flexibly balance priorities when choosing mates just as they do when avoiding dangers.

In nearby discussions, some authors have argued that mate choice is partly an aesthetic phenomenon, in the sense that receiver-side hedonic evaluation can itself be an evolutionary force (Prum, 2012). We flag this mainly as a parallel debate about valuation, but it is not our target. Our claim concerns basal, homeostatic-style positive affect that can sit at the same functional level as pain or hunger in mediating trade-offs, rather than the later-emerging, higher-order aesthetic emotions of preference and “beauty” emphasised (Prum, 2012), and convincingly criticized (Patricelli et al., 2019), in the sexual selection literature.

Together, these dual pressures—the need for a drive strong enough to override competing demands, and the need for an evaluative capacity to navigate complex choices—make lust as plausible a foundation for sentience as homeostatic affects. If negative affect evolved to secure survival, positive affect may have coevolved to secure reproduction. This symmetry suggests that the roots of experience were not singular but braided from the beginning.

Comparative Clues

Do animals at the frontiers of debate about animal sentience exhibit signs of a reproductive drive so powerful it sometimes overwhelms other needs and supports flexible, goal-directed behavior? We cannot directly access what an animal feels and experiences, but behavior and physiology provide compelling clues.

In arthropods, mating effort can eclipse even the most basic survival imperatives. In *Lispe* flies, for instance,

males perform elaborate multistage dances in which they flexibly track the quality of sunlight and local viewing environments to amplify the brilliance of their visual signals to females, despite the ubiquitous risk of predation (White et al., 2020; White & Latty, 2020). More dramatically, some species court at the cost of their lives. Male praying mantises and orb-weaving spiders will continue to mate even while being cannibalized by their partners, as stated earlier (Andrade, 1996; Barry et al., 2008). Such cases highlight a drive so strong that males risk, or proactively forfeit, their survival for a single reproductive opportunity.

Among cephalopods, the power of reproductive motivation is expressed through remarkable flexibility. Male cuttlefish strategically disguise themselves as females to slip past rivals, switching tactics depending on the social setting (Brown et al., 2012). Octopuses likewise sustain courtship in the face of escalating threats, including fights with rivals and the risk of being attacked or cannibalized by females (Hanlon & Forsythe, 2008). These behaviors point to a reproductive drive capable of overriding self-preservation and sustaining inventive strategies in unpredictable contexts.

In fish, salmon epitomize reproductive single-mindedness. During their spawning migration, Pacific salmon cease feeding altogether, diverting all energetic reserves to the journey upstream—a journey that ends in exhaustion and death (Cooke et al., 2006; Hendry & Berg, 1999). Even those that survive the breeding season often take unusual risks while spawning, reflecting a temporary override of fear and self-preservation.

We cannot be certain whether these animals experience lust or desire in the way humans do, but the parallels across taxa are striking. Sexual motivation has the capacity to suppress hunger, dampen responses to pain, and promote risky behavior, and in many species it clearly eclipses competing needs. We are rightly cautious in attributing subjective states, but comparative evidence suggests that reproductive affects may be both widespread and ancient, rather than a late-emerging trait restricted to large-brained species.

Rethinking the Search for Feeling

If reproductive affects are a basal feature that co-evolved alongside pain and other survival-related drives, then our approach to studying animal awareness should broaden accordingly. Empirical work has understandably foregrounded negative states such as pain, fear, and stress, both for ethical reasons and because defensive responses to threats are conspicuous, are experimentally tractable,

and have long served as the paradigmatic test cases for animal sentience. Yet frameworks that consign lust or positive desire to a “higher” status risk overlooking a fundamental strand in affective evolution. In its rudimentary form, lust need not be a rich emotion; it may be better seen as a primary motivational state akin to hunger, deeply grounded in biology and plausibly present at the origins of mind.

In terms of method, the evidential strategies developed for pain and homeostatic affects can be productively translated to the reproductive domain. Popular capacity-based frameworks that integrate behavioral and neurophysiological evidence (e.g., Crump et al., 2022), for example, could be readily adapted. The relevant capacities are already visible: persistence with courtship attempts despite repeated failure or risk; trade-offs where mating opportunities are weighed against food, safety, or rest; and the expression of flexible, rich behaviors—deception, innovation, targeted display—that far exceed what stereotyped, reflexive responses alone would allow, as stated earlier (Andersson, 1994; Pfau et al., 2001). Cross-species analogies further strengthen the case. Among vertebrates, lust is variously invoked to explain persistence in the face of costs or the invention of novel tactics to secure partners, and the same explanatory lens can plausibly be extended to taxa such as cephalopods or insects, where examples of deceptive mimicry, extreme risk-taking, and prolonged courtship abound (Andrade, 1996; Barry et al., 2008; Hanlon & Forsythe, 2008; White & Latty, 2020).

Applying the same standards to lust and to pain would give a more balanced picture of animal awareness. Trade-offs to avoid harm are readily treated as evidence of feeling, yet extreme persistence in mating is often overlooked or downplayed. The caveat applies on both sides: Defensive and courtship behaviors alike may sometimes be automatic rather than felt. What matters is whether flexible, sustained action in the kinds of noisy, competing contexts described earlier is parsimoniously explained by the presence of a felt experience. If reproduction is recognized as a foundational basis for affect in the way that survival is for pain, the evolutionary timeline of sentience may need to be revised, with survival and reproduction sharing the stage from the outset.

Where Are the Horny Bugs?

The search for animal sentience has long followed the trail of suffering: We look for animals that respond to injury in ways that suggest they feel pain. That approach has been fruitful, but incomplete. Reproduction is just as

fundamental to evolutionary persistence as survival, and in many species the breeding game demands as much behavioral flexibility, complex decision making, and sacrifice of other needs as any survival challenge.

So, where are the horny bugs? They are likely right alongside the hurting ones, wherever life's challenges make it worthwhile to feel something at all. Insects driven to extraordinary lengths by the urge to reproduce may be telling us something important about why awareness arose in the first place. In mapping sentience across the animal kingdom, we must focus not only on species that suffer but also on those that strive and persist. Answers to questions of consciousness may lie as much in the grip of desire as in the shadow of pain.

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