CellPress
OPEN ACCESS

Trends in
Ecology & Evolution

Review

Socially transferred materials: why and how to study them

Sanja Maria Hakala,[1,*] Haruna Fujioka,[1,2] Katharina Gapp,[3] Ornela De Gasperin,[1,4] Eléonore Genzoni,[5] Rebecca M. Kilner,[6] Joris M. Koene,[7] Barbara König,[8,9] Timothy A. Linksvayer,[10] Marie-Pierre Meurville,[1] Matteo A. Negroni,[1] Hugo Palejowski,[5] Stuart Wigby,[11] and Adria C. LeBoeuf[1,*]

When biological material is transferred from one individual's body to another, as in ejaculate, eggs, and milk, secondary donor-produced molecules are often transferred along with the main cargo, and influence the physiology and fitness of the receiver. Both social and solitary animals exhibit such social transfers at certain life stages. The secondary, bioactive, and transfer-supporting components in socially transferred materials have evolved convergently to the point where they are used in applications across taxa and type of transfer. The composition of these materials is typically highly dynamic and context dependent, and their components drive the physiological and behavioral evolution of many taxa. Our establishment of the concept of socially transferred materials unifies this multidisciplinary topic and will benefit both theory and applications.

Highlights

Animal behavior, physiology, and fitness are influenced by materials transferred between conspecifics (e.g., milk or ejaculate), even in solitary taxa.

Such socially transferred materials are currently studied separately, without acknowledgment that they are instigators of evolutionary change and potent mechanisms for indirect genetic effects.

Recent methodological advances allow the linkage of socially transferred gene products to their physiological, behavioral, and fitness impacts, yet such integrative approaches are rarely used.

This conceptual framing and classification of socially transferred materials bridges proximate and ultimate scales and connects molecular biology to evolution.

The concept of socially transferred materials has the potential to bring about transformative innovation in fundamental research and also in applied fields, such as medicine and agriculture.

Molecules transferred between individuals are fundamental in evolution

All animals interact with other individuals of their own species at least some point in life; even solitary species are strongly impacted by their conspecifics (i.e., their fitness depends on both positive and negative social effects caused by their relatives, competitors, and mating partners). In addition to well-studied means of communication, such as visual, chemical, and auditory signals, animals have also evolved behaviors in which biological material is passed from one individual's body to another and directly affects the physiology of the receiver. The most notable examples are all highly fitness relevant: internal insemination, deposition of nutrition to offspring in eggs, and various other nutrition and symbiont transfer behaviors evolved in the context of parental care (Box 1) [1–6].

We define these **socially transferred materials** (see Glossary) as materials that are transferred between conspecifics and include components (i) metabolized by the donor, which (ii) induce a direct physiological response in the receiver, bypassing sensory organs, and (iii) benefitting the donor. Our definition is built on the definition of **allohormones** [7] and broadened to include the transfer of functional cells, and transfer to and from individuals that are not free-living, such as offspring developing inside the parent or anglerfish males living inside the females [8]. The only route to the evolution of nonfree-living individuals is via **social transfers**. A key distinction to separate socially transferred materials from pheromones is that components of socially transferred materials directly interact with the physiology of the receiver, while pheromones are detected by the sensory organs of the receiver. In this context, we do not consider mere collection of food for other individuals as a social transfer, unless the donor adds metabolized substances that target recipients. For example, some, but not all **nuptial gifts** are socially transferred materials [9].

Socially transferred materials typically involve both specialized behaviors and adapted morphological features, such as glands, which produce and secrete the transmitted components, or even full organs, such as penises, love darts, spermathecas, placentas, and nipples. Given that

[1]Department of Biology, Faculty of Science and Medicine, University of Fribourg, Fribourg, Switzerland
[2]Faculty of Environmental and Life Science, Okayama University, Okayama, Japan
[3]Department of Health Science Technology, ETH, Zurich, Zurich, Switzerland
[4]Instituto de Ecología, Xalapa, Veracruz, Mexico
[5]Department of Ecology and Evolution, University of Lausanne, Lausanne, Switzerland
[6]Department of Zoology, University of Cambridge, Cambridge, UK

the materials travel directly between individual bodies, they can have strong impacts on the physiology of the receivers. For example, when honeybee (*Apis mellifera*) larvae are fed royal jelly, a specific type of food secreted by the workers, they develop into queens instead of workers [10]; royal jelly also has longevity-enhancing components that are functional in taxa other than honeybees [11]. Similarly, although less dramatically, human milk affects the long-term health of offspring by protecting against infection, obesity, and diabetes [2,12]. Socially transferred materials have immediate impacts on behavior and physiology. For example, in the fruit fly *Drosophila melanogaster*, a seminal fluid protein 'sex peptide' reduces the willingness of females to mate, alters their dietary and resting preferences, and has major physiological effects, from enhanced egg production to immunological and metabolic changes [13]. Even though social transfers have been reported for hundreds of years across hundreds of taxa, only a few are well studied, and many of the molecular mechanisms in even the flagship transfers of milk and ejaculate are still poorly understood. We argue here that these materials are evolutionarily more important than currently appreciated.

With the help of emerging methodologies and theory, socially transferred materials fill an important gap in our understanding of evolution. The interacting phenotypes framework has proven useful for modeling and empirically studying the evolution and genetic architecture of traits involving interactions between conspecifics, which occur in all animals. This framework considers how the phenotype of an individual is directly affected by its own genotype (direct genetic effects) and indirectly affected by the genotypes of its interaction partners (indirect genetic effects) [14,15]. As such, it has been used to identify genes and alleles underlying variation in, and expression of, socially influenced traits [16,17]. However, apart from these few recent studies, this framework has mostly treated the mechanistic details by which genes influence traits as a black box. Socially transferred materials are likely to be central mechanisms of indirect genetic effects, and approaches that explicitly study these materials can help bridge the gap between mechanistic understanding and eco-evolutionary dynamics of interacting traits and genes.

Socially transferred materials typically comprise different components that are governed by different selection pressures, some social and others biophysical. Despite the diversity of impacts they exert on receivers, there are clear and currently unexplained commonalities in their components. Social transfers require a **vehicle**, a physical substance that enables the transmission of the primary cargo, such as ejaculate to transmit genetic material [6]; egg [18,19], milk [2,20,21], or mucus [22,23] to transmit nutritious components; or adapted forms of feces to transmit symbionts [24]. The primary cargo or **primary component** that is transferred, such as nutrition, genetic material, or symbionts, is the evolutionary driver for the transfer (Box 1). Over evolutionary time, this primary component is supplemented with **secondary components** (Table 1), which either have stabilizing and preserving functions for the whole vehicle or for some of the components, or function as allohormones to manipulate receivers. The functions of the various secondary components are not necessarily related to the functions of the primary components, and can be either beneficial or harmful for both the donor and the receiver. Currently, increasingly detailed data sets on the components of socially transferred materials are being produced, but there is no comprehensive, integrative effort toward studying their evolution and impact. Often, we have only a poor understanding of the various roles of secondary components or how they work in concert in these complex mixtures. Existing and emerging data sets must be connected with evolutionary theory to maximize the impact of research on socially transferred materials for multiple fields of biology.

In this review, we establish socially transferred materials as an integrative topic in biology. After defining them and discussing what is known on their evolution and composition (Box 1 and Table 1), we review theoretical frameworks and methodological directions to enable

[7]Amsterdam Institute for Life and Environment, Faculty of Science, Vrije Universiteit, Amsterdam, The Netherlands
[8]STIAS, Wallenberg Research Centre, Stellenbosch, South Africa
[9]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland
[10]Department of Biological Sciences, Texas Tech University, Lubbock, TX, USA
[11]Department of Evolution, Ecology, and Behaviour, University of Liverpool, Liverpool, UK

*Correspondence:
sanja.hakala@gmail.com (S.M. Hakala) and adria.leboeuf@gmail.com (A.C. LeBoeuf).

comprehensive future work (Figure 1). Understanding that social transfers are potent drivers of evolutionary change and creating a common framework for studying these materials will benefit each research domain from overarching theory to molecular pathways.

Convergent evolution of secondary components can reveal shared selection pressures

Socially transferred materials generally comprise a slew of different molecular components that can have similar molecular functions, even in completely different socially transferred materials and across taxa (Table 1). We hypothesize that, ultimately, this is because similar selection pressures (fitness costs, benefits, and fundamental physics and chemistry) shape the evolution of these transfers, regardless of their behavioral context. Here, we highlight similarities already observable in existing data sets, and call for a full comparative study of this topic.

Among the most consistent selection pressures for the composition of socially transferred materials are the risks of opening a direct physiological channel between bodies (e.g., [38]). For example, opening such a channel introduces significant potential for infection; sexually transmitted diseases are emblematic of this risk. Thus, social transfers commonly elicit an immune response in the receiver and, similarly reflecting this risk, many secondary components are defense related (e.g., antibodies, antioxidants, DNases, RNases, antimicrobial proteins and peptides, and even immune cells) [2]. These can function to protect transferred materials (e.g., [39]) or to enhance the defense system of the recipient [20,40]. When the social transfer is recurrent or sustained, the overall level of risk is especially high (e.g., placental viviparity can bring about problems such as gestational diabetes when physiological control mechanisms are compromised [41]), but it is typically balanced by high benefits and common interests between partners.

Orthologous genes are often co-opted across vastly different lineages for use in social transfers to ensure chemical stability and preservation, to transfer components, or to alter recipient physiology. Many molecular parallels can be found between proteins in the seminal fluid of *D. melanogaster* and the regurgitate transmitted mouth-to-mouth in *Camponotus floridanus* ant colonies, including esterase-6/juvenile hormone esterase, serpins, serine proteases, regucalcin, transferrin, lectins, and some uncharacterized but orthologous proteins [36,42]. Even across distant taxa, molecular commonalities can be observed: the nutritive fluid that ants feed to their colony members has molecular commonalities with mammalian milk, namely the abundant proliferation protein CREG1, lipoproteins or fatty acid-binding proteins, and antioxidant enzymes, such as xanthine dehydrogenase and superoxide dismutase [36,43].

An important class of secondary components in socially transferred materials are stabilizing molecules enabling the transfer of other molecules. Many of these may be convergently present in socially transferred materials across lineages, revealing that similar molecular pathways were co-opted repeatedly during the course of evolution. For example, protein families involved in RNA or lipid transport, or antioxidant activity, have been found across many socially transferred materials. In honey bee royal jelly, MRJP-3 has a key role in concentrating, stabilizing, and enhancing RNA bioavailability, facilitating social immunity and signaling among bees [44]. In an even more complex case, *Plataspidae* stinkbug females deliver essential symbionts to offspring via capsules laid simultaneously with the eggs, and a specific protein is responsible for stabilizing the symbiont in them [45]. Interestingly, tetraspanin is found in most socially transferred materials studied so far. This protein is a marker of exosomes (extracellular vesicles) [46], a major mode of cargo transmission between the cells of a multicellular organism. The presence of tetraspanin across social transfers indicates that exosomes have likely been co-opted from use in within-individual physiological processes to be used in across-individual physiological processes.

Glossary

Allohormones: substances that are transferred from one individual to another (free-living) member of the same species and that induce a direct physiological response, bypassing sensory organs.
Nuptial gift: materials transferred from one sex to the other during mating that can have positive, negative, or neutral effects on either sex. Some, but not all, nuptial gifts fit our definition of socially transferred materials (if metabolized components are added by the donor).
Primary component: main material that a social transfer has evolved to transmit from donor to receiver (e.g., genetic material, nutrition, or symbionts).
Secondary component: molecular and cellular components of socially transferred materials that are not the primary cargo, such as allohormones, stabilizing or transport molecules, even functional cells.
Social transfer (as used here): behavior through which socially transferred materials are passed between individuals and which evolved for this purpose (e.g., lactation and copulation).
Socially transferred material: materials transferred between conspecifics that include components (i) metabolized by the donor, which (ii) bring about a direct physiological response in the receiver, bypassing sensory organs, and (iii) that benefit the donor.
Trophallaxis: direct ingestion by one individual of material excreted, secreted or regurgitated by another.
Vehicle: combination of materials that evolved to allow socially transferred materials to be passed from one individual to another (e.g., egg, milk, ejaculate, mucus, specialized symbiont capsules, etc.).

Finally, although current studies mostly focus on the overall composition of socially transferred materials or the functions of specific components, it is likely that quantitative variability in composition is equally important and selected for. Many socially transferred materials appear to share similar response dynamics: their composition changes with the social and environmental context and individual condition (e.g., [47–49]). In addition to donor-induced plasticity in the socially transferred materials, it is likely that the responses of receivers are equally plastic, although, so far, the receiver side of these transfers has received little study. The constant evolutionary balance between cooperation and conflict between partners can push socially transferred materials to evolve to be increasingly complex, making them potent drivers of evolution (lactation is a major example of this; Figure 2).

Existing theoretical frameworks for understanding selection pressures acting on social transfers

Socially transferred materials are mostly studied at the proximate molecular level and, in many cases, studies do not explicitly link to evolutionary biology. We argue that this is hindering our ability to reach the full potential of this field.

Proximately, the secondary components in socially transferred materials can have complex and dynamically changing compositions, often with ample functional redundancy. Previous studies of communication signals have shown similar evolutionary paths toward seemingly unnecessary complexity, and their insights are valuable for studying socially transferred materials [78]. Multiple ideas have been put forward for why such complexity evolves: to balance the costs and benefits of single signals, or their mixture, or to increase robustness and counter transmission difficulties with noisy signals, or the physiological constraints of production. Additionally, there can be multiple messages delivered, by multiple donors to multiple receivers. It is also possible that some parts of a transferred material exist to eliminate cheaters (e.g., parasites or conspecific

Box 1. Classification of socially transferred materials based on primary components

Social transfers can be classified in many ways (Figure I), ranging from whether they disperse horizontally among individuals or vertically between parents and offspring, to whether they are synchronous or asynchronous in time, and whether they are more or less frequent or sustained**.** One of the most informative ways is to classify social transfers according to their primary components, with three main classes: the transfers of genetic material, nutrition, and symbionts.

Social transfers of genetic materia

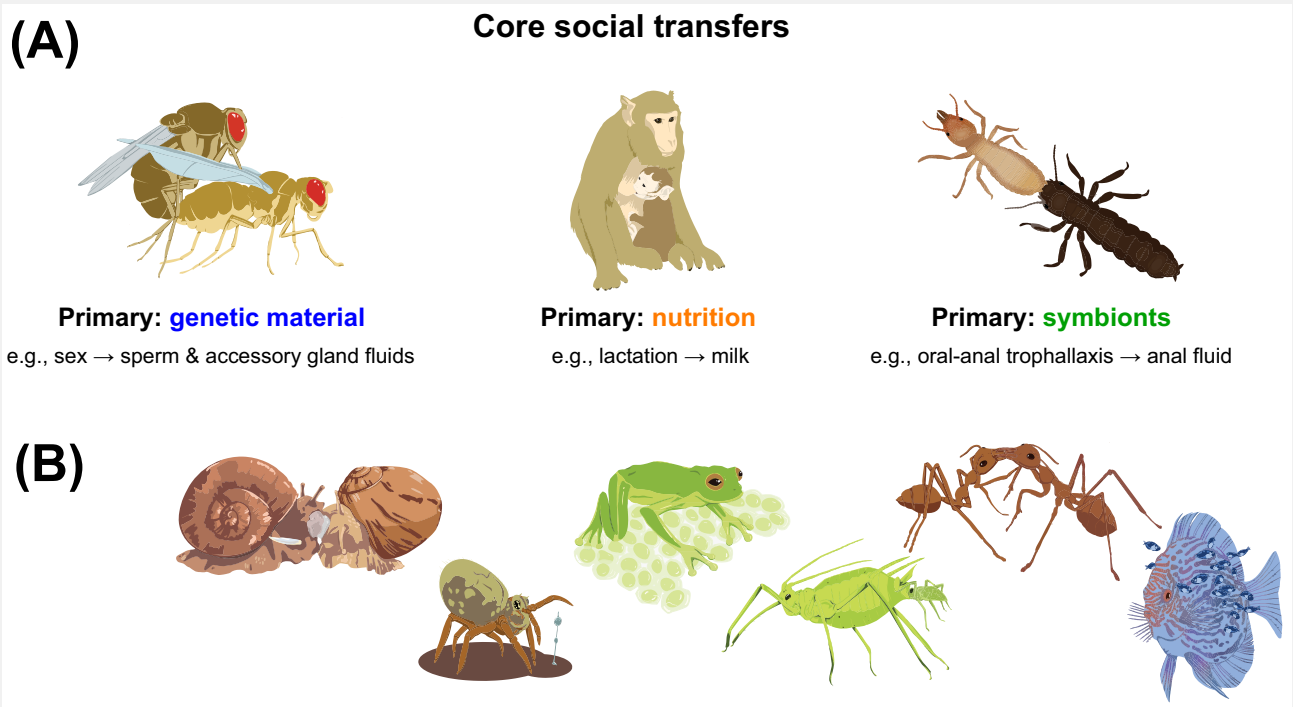
Transfers of genetic material include vertical transfers from parents to offspring, and horizontal transfers between mating partners. In vertical transfers of genetic material, ovules and sperm carry noncoding components that can exert epigenetic control over the gene expression of the offspring [25,26]. The secondary components in vertical social transfers often act out conflicts between parental genomes and conflicts between parents and offspring [27]. In horizontal transfers between mating partners, many secondary components in ejaculate and female reproductive fluids have major roles in sexually antagonistic arms races [28,29], which is similarly likely in materials such as mating plugs and nuptial gifts [9,30,31]. In some animals, mating involves the partners attaching to each other, even permanently (e.g., anglerfish [8]).

Social transfers of nutrition

Transfers of nutrition are usually related to parental care, which, in its most ancient form, is provisioning offspring with nutrition through the egg. Secondary components in eggs impact the hatching order, physiology, and success of offspring [18]. Care-associated materials can also be deposited outside eggs [25], or the parent or other relatives can lay trophic eggs for offspring to eat [32]. Many animals produce substances such as yolk and mucus [4,23], and some have even evolved specialized feeding organs, including mammary glands [21] or larval tubercles [33]. All forms of viviparity include social transfers, from invertebrates, such as tsetse flies and aphids [34], to the 142 independently evolved vertebrate cases [35]. In addition to offspring, material can also be transferred horizontally to mating partners, as nuptial gifts [9], or to other members of social groups, even generating a shared physiology, as in the case of many social insects [5,36].

Social transfers of symbionts

Transfers of symbionts are likely rarer than the aforementioned examples, but accumulating evidence suggests that symbionts are of such importance to animal physiology that specific behaviors for transferring them must have a larger evolutionary role than historically considered. Thus far, the secondary components in such transfers have received little to no study, apart from a few main examples, such as termite microbiome transfers [24]. It has been suggested that mammalian milk originally evolved to regulate bacterial communities [37]. Symbionts, and molecules supporting symbiotic relationships, are also common secondary components in all socially transferred materials (see Table 1 in the main text).



Primary cargo	Genetic material	Genetic material	Genetic material nutrition	Nutrition	Nutrition	Nutrition
Social transfer	**Love darts**	**Spermatophores**	**Eggs**	**Viviparity**	**Trophallaxis**	**Mucus**
Partner relatedness	Low	Low	High	High	High	High
Separation in time	Synchronous	Asynchronous	Asynchronous	Synchronous	Synchronous	Synchronous
Rate and duration	One-time, brief	One-time	One-time	One-time, sustained	Frequent, sustained	Frequent, sustained

Trends in Ecology & Evolution

Figure I. Examples of socially transferred materials in animals. (A) The three main classes of socially transferred material based on the primary components transmitted: genetic material (*Drosophila* ejaculate [42,48]), nutrition (mammalian milk [2,21]), and symbionts (termite anal fluids [24,38,54]). Although this review focuses on animals, the same principles and classifications can also be applied to other organisms. (B) Examples of social transfers and modes of classification based on relatedness of partners, whether the material is deposited at the same moment as it is consumed (synchronous) or is separated in time (asynchronous), and the rate and duration of the transfer. Examples shown from left to right: land snail love darts [28], springtail spermatophores [9], vertebrate eggs [19,49], aphid viviparity [34], ant **trophallaxis** [36], and *Discus* fish mucus [23].

competitors) and, thus, are the product of a completely different coevolutionary interaction beyond the donor and receiver. Redundancy may exist to allow maximal plasticity and robustness across different contexts, or as a legacy of past resistance in receivers. Overall, the history of research on animal signals highlights an important lesson: receiver fitness likely has a major role in shaping the components of socially transferred materials, just as it has in shaping communication signals.

Ultimately, costs and benefits for both donors and recipients drive the evolution of socially transferred materials. These can be measured as energetic costs, but more comprehensively in terms of direct and indirect fitness [79]. Thus, the inclusive fitness framework of kin selection theory is useful to understand the evolution of socially transferred materials across behavioral contexts,

Table 1. Molecular commonalities across socially transferred materials[a,b]

Molecule	Genetic material		Nutrition	
	Vertebrates	Invertebrates	Vertebrates	Invertebrates
Basic building blocks				
Sugars	Ejaculate [50]	Ejaculate [51]	Milk [20,52] (e.g., simple sugars, complex oligosaccharides) Regurgitate [3]	Eggs[c] Regurgitate [53]
Free amino acids	Ejaculate [50]	Ejaculate [50]	Milk [52]	Regurgitate [5,53] Excreta [54]
Lipids, fatty acids, triglycerides	Ejaculate [55–57] (e.g., cholesterol, glycosphingolipid, prostanoids)	Ejaculate [58]	Saliva [59] Milk [20,52] (e.g., fatty acids, gangliosides, cholesterol) Regurgitate [3] Eggs [19] (e.g., yolk lecithin, alkaloids)	Eggs[c] Regurgitate [5] (e.g., cholesterol, fatty acids, long-chain hydrocarbons)
Vitamins and minerals	Ejaculate [57,60] (e.g., vitamin D)		Milk [20,52] (e.g., magnesium, iron, calcium, vitamins A, D, E, and K) Regurgitate [3] Mucus [23] (e.g., calcium)	
Hormones				
Hormones	Ejaculate [57] (e.g., steroids, cortisol, renin, angiotensin)	Ejaculate [6] (e.g., Lucibufagin, JH)	Saliva [61] (e.g., ghrelin) Eggs [62] (e.g., steroid and thyroid hormones, cortisol) Mucus [23] (e.g., cortisol)	Regurgitate [5] (e.g., JH, vitellogenin)
RNA				
Small/noncoding RNA	Ejaculate [63–65]	Ejaculate [65]	Milk [20] Saliva [64]	Eggs[c] Regurgitate [5]
Nucleotides	Ejaculate [50]	Ejaculate [50]	Milk [52]	
Proteins				
Proteins	Ejaculate [57] (e.g., immunoregulatory factors, cytokines) FRF [66]	Ejaculate [58,67,68] Injection devices [39,69] FRF [70] (e.g., apolipophorins, transferrin, PPO, GluDH, HSPs, cathepsins, OBPs, est-6)	Milk [20] (e.g., casein, transferrin, α-, γ-, β-globulin, albumin, lysozyme, cathelicidins, XDH, CREG1, tetraspanin) Eggs [19] (e.g., ovalbumin, ovotransferrin, ovoinhibitor, avidin, cystatin, vitellogenin, lysozyme) Mucus [23,71] Regurgitate [3] Saliva [72]	Eggs [73] (e.g., vitellogenin) Regurgitate [36] (e.g., GluDH, apolipophorins, hexamerins, cathepsin, vitellogenin, CREG1, amylase, major royal jelly proteins, JH esterases, transferrins, serine proteases, serpins, OBPs, cathepsins, HSPs, XDH, SOD)
Antibodies and antimicrobials	Ejaculate [50] FRF [71]	Ejaculate [39,71]	Eggs [19] (e.g., IgY) Saliva [74] (e.g., IgG, IgM, IgA) Milk [20] Mucus [23] Regurgitate [3]	Regurgitate [5]
Cells				
Symbionts[d]	Ejaculate [71] FRF [71]	Ejaculate [75]	Mucus [22] Regurgitate [3]	Eggs [76] Regurgitate [77] Excreta [45]
Immunity cells	Ejaculate [50]	Ejaculate [50]	Milk [20] (e.g., neutrophils, lymphocytes, macrophages)	
Other cells	Ejaculate [50] (e.g., gland cells)	Ejaculate [50]	Milk [20] (e.g., stem cells)	

and helps in assessment of the inherent risks of opening a direct physiological channel between individuals. Given that kin selection is an intrinsic part of natural selection, this framework should be used for analyzing all intraspecific interactions, be they positive or negative, and with close relatives or not. The inclusive fitness framework best allows the formation of hypotheses for what kinds of socially transferred materials evolve under different levels of conflict. Secondary components can have both cooperative and competitive effects, and understanding their evolutionary role requires implementing an indirect fitness component in the analysis.

In theory, genes with social effects on fitness are expected to evolve more rapidly compared with genes that only influence an individual's own fitness [15,80]. All else being equal, these genes experience effectively relaxed selection, depending on the relatedness of interacting social partners. It has been shown empirically that evolution of socially transferred materials is indeed possible under relaxed selection [81]. By contrast, traits associated with the production and transfer of socially transferred materials can strongly affect the fitness of interacting partners, in some cases in opposing ways, potentially leading to evolutionary arms races and rapid phenotypic evolution.

The game theory approach may be fruitful when the payoffs of material transfer depend on not only the interacting partners themselves, but also their previous interactions and the strategies that conspecifics have taken, making selection somewhat frequency dependent: For example, the fecundity of a female can be stimulated by seminal fluid proteins from the male at the first mating. Then, later-mating males are selected to be sensitive to their position in the mating sequence [82,83] and to allocate resources accordingly (e.g., not investing in fecundity-stimulating proteins) [83]. The same principle likely applies in other contexts, such as investment in defensive components [84]. Furthermore, since socially transferred components can change the physiology of an individual, they can influence the subsequent social interactions of that individual, long after the donor has left the scene. For example, fecundity stimulation by one male can be seen as a service to its rivals, fundamentally changing the value of the resource that is being contested, altering the evolutionary pathways in line with fighting theory [85]. Contrastingly, in a simultaneous hermaphrodite, certain seminal fluid secondary components lower the future fecundity of the mating partner in the male role [86].

The aforementioned frameworks are ideal starting points for explaining the derived adaptations of socially transferred materials and also their potentially large role in driving evolution. With ecological and developmental feedback loops, these materials may provide positive feedback mechanisms and points of no return that create greater levels of cooperation, coordination, and social control (e.g., evolution of group living from parental care [87] or the evolution of lactation in mammals; Figure 2). In extreme cases, social transfers may evolve to integrate physiology across individuals, even leading to group-level metabolism, as in social insect colonies [36]. Looking further back in evolutionary time, we suggest that social transfers were an important step toward the evolution of multicellularity: indeed, from what else could the molecular mechanisms for

Notes to Table 1:
[a]The composition of socially transferred material has evolved convergently in different socially transferred materials and across taxa. We cite selected examples from vertebrates and invertebrates emphasizing known commonalities, and we encourage researchers to fill the gaps for their own study systems.
[b]Abbreviations: FRF, female reproductive fluids; GluDH, glucose dehydrogenase; HSP, heat shock protein; JH, juvenile hormone; SOC, superoxide dismutase; XDH, xanthine dehydrogenase.
[c]E. Genzoni, PhD thesis, University of Lausanne, 2022.
[d]Symbionts are special components because they are organisms of their own, not produced by the metabolism of the donor. Although some social transfers have clearly evolved to accomplish the basal transfer of symbionts [24], symbionts have likely entered other socially transferred materials as secondary components. Given that relatively little research has been done on them, they are not included as a main category here. However, symbionts are found in many socially transferred materials and, thus, are mentioned as secondary components.

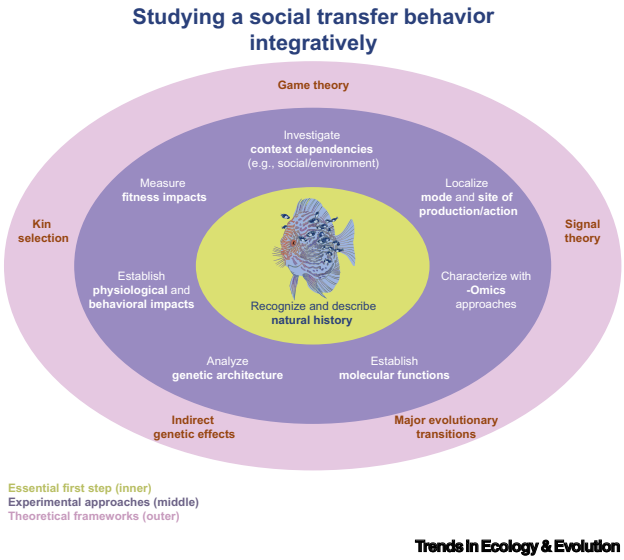


Figure 1. Complimentary research directions for the study of socially transferred materials. An integrative research program is needed to understand the evolution and functions of socially transferred materials. Using the complimentary research directions and theoretical frameworks shown here will aid in understanding the role of these materials as drivers of evolution and lead to a better proximate understanding of their functions in the molecular, physiological, and behavioral processes of organisms. Given that traditional natural-history studies regularly reported social transfers in various taxa, the study of socially transferred materials already has a strong foundation and rich literature to draw upon, even though many of the known transfers are yet to be inspected in detail. Additionally, new social transfers are still being discovered even in well studied systems, as illustrated by the recent discovery of a social role for ant pupal molting fluids [110]. The concentric rings illustrate the first essential step (inner circle), the experimental approaches (middle ring), and theoretical approaches (outer ring).

coordination among cells of a multicellular organisms have evolved than from social transfers among unicellular, cooperative organisms? If these same mechanisms are later co-opted from intraindividual control to interindividual control, the convergence across these materials becomes obvious. Thus, for understanding the evolution of socially transferred materials, it may be fruitful to consider multiple levels of biological organization [88].

Complementary research directions and novel methodologies

An integrative research program, pursued across taxa and for multiple social transfers, is needed to understand socially transferred materials and their role in evolution (Figure 1). First, before any of the complimentary directions mentioned below, recognizing a behavior that passes metabolized material between bodies relies on traditional natural-history approaches. In many taxa, these behaviors were described decades ago, but were never studied at the molecular level or in an evolutionary context.

Characterizing what is transmitted during the behavior is among the most common current research approaches, and a good starting point before more functional molecular studies. Comparative sequencing and transcriptomics, as well as metabolomic and proteomic studies, allow a view into the molecular content of transferred materials (e.g., [36,43]). Confirming which molecules originate in donors versus receivers requires extra care in study design. To determine how donor-derived components arrive in receivers and achieve their impacts, it is necessary to establish origin, processing, and degradation. Histological methods, such as *in situ* hybridization, are useful for characterizing tissue-specific expression and localization [67], as are tissue-specific gene expression measures (qPCR, single-cell RNA sequencing [68], and transcriptomics [89]) and mass spectrometry imaging techniques for tissue-specific protein or metabolite presence [90]. Transfer of proteins can be further tracked by incorporating stable isotopes in essential amino acids into donors and monitoring proteins found in receivers [91]. Other metabolic labeling methods can incorporate nucleic acid derivates (e.g., thiouridine) to label RNA or click chemistry

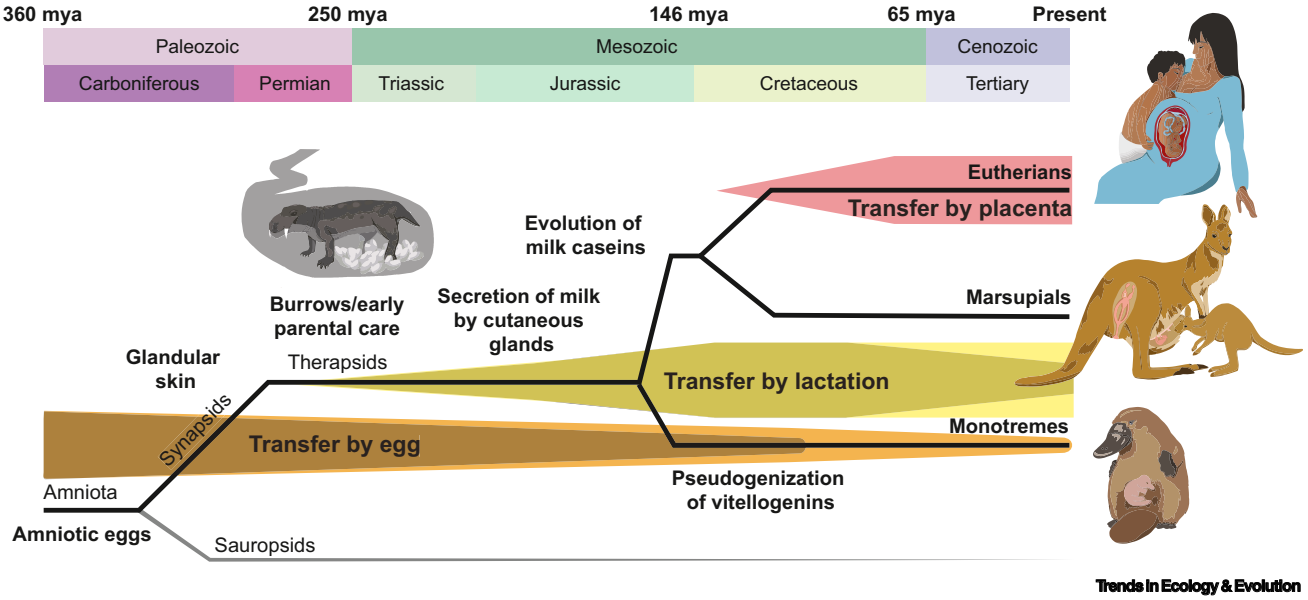


Figure 2. Evolution of nutrition-related socially transferred materials in mammals. Socially transferred materials are key innovations and drivers of evolution. During mammalian evolution, different types of vehicles, behaviors, and genes have replaced each other under the selection for better nutrition, care, and control over offspring. The amniotic egg was an evolutionary innovation that allowed for greater maternal nutrition provisioning. As critical pre-adaptations for the evolution of lactation, synapsids evolved glandular skin [21,37] and therapsids provided parental care [107]. Since then, highly adapted cutaneous glands evolved to secrete milk, possibly for nutrition or alternatively to regulate moisture, temperature, and/or bacterial communities around the eggs and offspring [37]. Either way, all extant mammals rely on milk for nutrition. This required the evolution of secretion pathways, glandular tissue, and genes such as those encoding the caseins, which are the major nutrient transfer components of milk [37]. This decreased the need for egg-derived nutrition; the three vitellogenins, major nutrient transfer components of egg in both vertebrates and invertebrates, became pseudogenes in most modern mammals [108]. Milk in marsupials is extremely complex and variable over development, more so than the milk of eutherian mammals [37]. In eutherians, when the placenta evolved to allow extended viviparity, it took over many of the functions of milk, even co-opting many of the same genes [109]. Here, the decreasing importance of first egg-derived components and later milk-derived components in some of the lineages is represented by variable highlight colors.

to label proteins, nucleic acids, or metabolites and to detect their modifications [92]. Many of the newest techniques are only available in model organisms, but recent innovations, especially with CRISPR, sequencing technology, click chemistry, and in the imaging and bioinformatic side of mass spectrometry, allow significant advances in non-model organisms too.

Current research regimens often do not inspect different environmental and physiological contexts to understand the dynamic nature of socially transferred materials and their effects, or inspect contexts that are too variable and end up diluting meaningful plasticity into noise around averages. Thus, for each social transfer, the effects of social and environmental contexts and individual conditions should be correlated with the topic of study, be it molecular composition of the material, responses of the receiver, or fitness. For example, developing assays that consistently show shifts in the composition of the transferred material with context will help identify the most interesting bioactive molecules for further investigation. Given that donor and receiver condition can have independent effects, tools such as cross-fostering or artificial insemination can help disentangle impacts. For example, a secondary component in ejaculate could enhance female fecundity, but its effect might vary with male and female age, either additively or synergistically.

To understand the importance of social transfers in the physiology of animals, establishing molecular functions is necessary. The impacts of single molecules on receivers are often context dependent [93] and hard to detect without controlled experimental paradigms. Single molecules may require the presence of other molecules and, thus, with the current single-molecule testing

approach, some effects may be missed. Assessing transfer routes of molecules can also reveal functionality in receivers, but in many cases, it is necessary to directly manipulate the molecules or the composition of the social transfer [68,94] or, if possible, the underlying genes or biosynthesis pathways in donors or receptors in receivers. Studying the target receptors or uptake of molecules in receivers is necessary to understand intraindividual molecular pathways, but it is challenging; although *D. melanogaster* seminal fluid proteins are well studied and many functions have been established in females, only a single receptor has been characterized [95]. Finally, pairing the current revolution in automated deep learning-based behavioral tracking in behavioral ecology [96] with tracking of transmitted molecules will allow researchers to interpret the effects of social transfers, on not only physiology but also behavior, in a quantitative and high-throughput manner.

Once socially transferred molecules have been identified, analyzing the underlying genetic architecture of these molecules, genomes, and behaviors becomes possible. Comparative genomics will allow the study of the evolutionary trajectories of socially transmitted molecules and could identify genomic changes associated with the evolution of social transfers. Recent studies revealed that some of these materials are not conserved but instead show rapid expansions of key gene families [17,29,81,94]. Special care must be taken in assigning gene orthologs in such studies, because, currently, annotation based on model organisms is the norm due to sparse characterization of gene function in other taxa. This easily leaves taxon-specific, fast-evolving, and novel genes unidentified, and creates a risk of misinterpreting their function. For example, *Megaponera analis* ants use the contents of their metapleural glands to disinfect the wounds of nestmates, and the most abundant protein in this socially transferred material has no orthology to any known protein, indicating a very young gene [97]. In addition to species-level comparisons, inspecting population-level genetic variation [68] would allow testing population genetic models of genes with indirect fitness effects [80].

Measuring fitness costs and benefits over socioecological contexts and evolutionary time will show how the dynamics of cooperation and conflict shape the evolutionary trajectories of socially transferred materials. This will help us understand the role of social transfers in the evolution of behavior and physiology, and such studies can be done even before the molecular composition of the material itself is known. In future work, when combined with detailed physiological and molecular data, understanding costs and benefits of these transfers may allow the manipulation of social transfers to develop practical applications (Box 2).

Concluding remarks

Socially transferred materials are an effective and taxonomically widespread means for one individual to impact another. The diverse molecular machineries of these materials show how evolution has brought about not only many fascinating solutions to direct and manipulate conspecifics, but also many commonalities across types of transfer and taxa. Several theoretical approaches can be used to study the evolution of these materials, and measuring and manipulating these materials offer new ways to test old evolutionary theories. Understanding the evolutionary role of socially transferred materials will also benefit other research fields, from molecular medicine to behavioral ecology.

Using the rich emerging data sets of the composition of socially transferred materials to study problems such as those detailed in the Outstanding questions (see Outstanding questions), will allow researchers to bridge the gap between ultimate and proximate scales of selection that has so long defined evolutionary biology. Inspecting socially transferred materials integratively and in the light of evolutionary theory will give us better insights into both their proximate functions and the ultimate role of social transfers as drivers of evolution.

Outstanding questions

How much convergent evolution is there across socially transferred materials? Enough data already exist to conduct initial meta-analyses for a limited number of transfers, and more data can be generated to fill the gaps for other taxa and transfers.

Is the convergence seen across socially transferred materials caused by a repurposing of molecular machinery evolved for multicellular coordination?

Where in gene regulatory networks are the genes for sending and receiving socially transferred materials, and what is their evolutionary age and rate of evolution? Are there genomic signatures of convergent evolution?

Is the evolutionary route always from simple material transfers of only primary components toward more complex transfers?

When social transfers occur in more cooperative or competitive contexts, does this affect how they evolve? Relatedness between partners and corresponding levels of cooperation and conflict should govern many aspects of social transfers, from rate of evolution to transfer frequency.

How do the costs and benefits of socially transferred materials change through evolutionary time? Are there events of runaway evolution from initially beneficial to highly costly?

How does the evolution of two-way transfers differ from unidirectional transfers? Do these have specific evolutionary constraints? Reproductive transfers in hermaphrodites would provide an excellent study system for these types of question.

Is the apparent plasticity of socially transferred materials and the responses of their receivers linked to robustness and dynamic context dependency? Is the full mixture of components ultimately more important than any single component?

What are the taxon-specific and universal principles of social transfers? Although this review focuses on animal research, similar material transfers occur in plants, fungi, and bacteria.

Box 2. Potential applications

Socially transferred materials can be used to screen for diagnostic biomarkers for diseases and conditions. This has already proven to be useful for monitoring fetus development with amniotic fluid biomarkers [98] or seminal fluid in connection to fertility [99]. Outside human medicine, similar applications are equally useful in agriculture and food science, as shown by the vast literature of bovine milk biomarkers (reviewed in [100]).

Secondary components of socially transferred materials can function outside the context and species in which they originally evolved. Egg yolk low-density lipoproteins or milk casein micelles protect sperm during preservation [101]. Royal jelly extends healthy aging and lifespan not only in honey bees, but also in other organisms [11]. Given that socially transferred components can be used across transfers and across taxa, secondary components may be used for future drug delivery given their functions in stabilization (e.g., RNA-binding proteins [44]) or packaging and delivery (e.g., extra-cellular vesicles [102]). In addition to drugs, the delivery of probiotic bacteria may benefit from the study of socially transferred materials, because many social transfers have evolved components to stabilize the transfer of symbionts across individuals. Recently, the severe acute respiratory syndrome-coronavirus 2 (SARS-CoV-2) pandemic has resulted in a renewed interest in the ability of maternal milk to transfer antibodies and other immune components [103].

The performance of socially transferred materials can be enhanced by altering their composition. Studies of such approaches have mostly focused on single functional molecules. For example, the agricultural industry benefits from understanding which molecules affect seminal fluid in *in vitro* fertilization [104] and sperm cryopreservation [105], which could be equally beneficial in conservation [106] or human medicine. In addition to improving the biological materials themselves, the composition of artificial substitutes, such as infant formula, can be altered. Understanding the context dependencies of natural milk could offer great improvements for more individually tailored formulas.

The aforementioned examples require mechanistic knowledge and proximate understanding of socially transferred materials. When this knowledge is placed in the evolutionary context, and especially when the underlying balance of benefits and costs is considered, different types of application can be found. Understanding how sexual or parent–offspring conflict shapes the composition of eggs, sperm, seminal fluid, or milk could help to push the conflict toward a desired outcome, for example in human fertility, animal breeding, or research. Understanding how a social insect colony uses socially transferred materials to produce colony-level physiological outcomes would allow targeted colony manipulation in pest ants and termites, and pollinating bees. Pest species could be controlled also using knowledge about how their mating partners manipulate their reproductive physiology. Applications for biocontrol may be possible even across species.

Acknowledgements

We thank Franziska Brenninger for the figure art, and all participants of the workshop 'Evolution and impact of socially exchanged materials' for discussions that shaped this work. A.C.L. was supported by the Swiss National Science Foundation (PR00P3_179776), S.H. by the Finnish Cultural Foundation, K.G. by the Swiss National Science Foundation (PR00P3_201543) and an SBFI-funded ERC starting grant, J.K. by the Dutch Research Council, R.K. by the Leverhulme Trust RPG-2018-232, and S.W. by a BBSRC grant (BB/V015249/1).

Declaration of interests

None declared by authors.

References

1. Chen, Z. *et al.* (2018) Prolonged milk provisioning in a jumping spider. *Science* 362, 1052–1055
2. de Weerth, C. *et al.* (2022) Human milk: from complex tailored nutrition to bioactive impact on child cognition and behavior. *Crit. Rev. Food Sci. Nutr.* Published online March 30, 2022. https://doi.org/10.1080/10408398.2022.2053058
3. Ding, J. *et al.* (2020) The composition and function of pigeon milk microbiota transmitted from parent pigeons to squabs. *Front. Microbiol.* 11, 1–10
4. Kern, C.C. *et al.* (2021) *C. elegans* feed yolk to their young in a form of primitive lactation. *Nat. Commun.* 12, 1–11
5. Meurville, M.-P. and LeBoeuf, A. (2021) Trophallaxis: the functions and evolution of social fluid exchange in ant colonies (Hymenoptera: Formicidae). *Myrmecological News* 10, 4136
6. Scolari, F. *et al.* (2021) Beyond sperm and male accessory gland proteins: exploring insect reproductive metabolomes. *Front. Physiol.* 12, 1–9
7. Koene, J.M. and Ter Maat, A. (2001) 'Allohormones': a class of bioactive substances favoured by sexual selection. *J. Comp. Physiol. - A Sensory, Neural, Behav. Physiol.* 187, 323–326
8. Swann, J.B. *et al.* (2020) The immunogenetics of sexual parasitism. *Science* 369, 1608–1615
9. Lewis, S. and South, A. (2012) The evolution of animal nuptial gifts. *Adv. Study Behav.* 44, 53–97
10. Maleszka, R. (2018) Beyond Royalactin and a master inducer explanation of phenotypic plasticity in honey bees. *Commun. Biol.* 8, 1–7
11. Kunugi, H. and Ali, A.M. (2019) Royal jelly and its components promote healthy aging and longevity: from animal models to humans. *Int. J. Mol. Sci.* 20, 1–26
12. Savino, F. *et al.* (2013) Advances on human milk hormones and protection against obesity. *Cell. Mol. Biol.* 59, 89–98
13. Hopkins, B.R. and Perry, J.C. (2022) The evolution of sex peptide: sexual conflict, cooperation, and coevolution. *Biol. Rev.* 97, 1426–1448
14. Baud, A. *et al.* (2022) Indirect genetic effects: a cross-disciplinary perspective on empirical studies. *J. Hered.* 113, 1–15
15. Bailey, N.W. *et al.* (2018) Indirect genetic effects in behavioral ecology: does behavior play a special role in evolution? *Behav. Ecol.* 29, 1–11

16. Brinker, T. *et al.* (2018) The genetic architecture of socially-affected traits: a GWAS for direct and indirect genetic effects on survival time in laying hens showing cannibalism. *Genet. Sel. Evol.* 50, 1–11
17. Warner, M.R. *et al.* (2019) Transcriptomic basis and evolution of the ant nurse-larval social interactome. *PLoS Genet.* 15, 1–20
18. Groothuis, T.G.G. *et al.* (2019) Revisiting mechanisms and functions of prenatal hormone-mediated maternal effects using avian species as a model. *Philos. Trans. R. Soc. B Biol. Sci.* 374, 1–9
19. Lesnierowski, G. and Stangierski, J. (2018) What's new in chicken egg research and technology for human health promotion? - A review. *Trends Food Sci. Technol.* 71, 46–51
20. Stannard, H.J. *et al.* (2020) Marsupial and monotreme milk - a review of its nutrient and immune properties. *PeerJ* 8, 1–31
21. Oftedal, O.T. (2012) The evolution of milk secretion and its ancient origins. *Animal* 6, 355–368
22. Sylvain, F.É. and Derome, N. (2017) Vertically and horizontally transmitted microbial symbionts shape the gut microbiota ontogenesis of a skin-mucus feeding discus fish progeny. *Sci. Rep.* 7, 1–14
23. Buckley, J. *et al.* (2010) Biparental mucus feeding: a unique example of parental care in an Amazonian cichlid. *J. Exp. Biol.* 213, 3787–3795
24. Nalepa, C.A. (2020) Origin of mutualism between termites and flagellated gut protists: transition from horizontal to vertical transmission. *Front. Ecol. Evol.* 8, 1–15
25. Finch, G. *et al.* (2020) Multi-level analysis of reproduction in an Antarctic midge identifies female and male accessory gland products that are altered by larval stress and impact progeny viability. *Sci. Rep.* 10, 1–27
26. Toker, I.A. *et al.* (2022) Transgenerational inheritance of sexual attractiveness via small RNAs enhances evolvability in *C. elegans*. *Dev. Cell* 57, 298–309
27. Haig, D. (2014) Coadaptation and conflict, misconception and muddle, in the evolution of genomic imprinting. *Heredity (Edinb).* 113, 96–103
28. Lodi, M. and Koene, J.M. (2017) Hidden female physiological resistance to male accessory gland substances in a simultaneous hermaphrodite. *J. Exp. Biol.* 220, 1026–1031
29. Wilburn, D.B. and Swanson, W.J. (2016) From molecules to mating: rapid evolution and biochemical studies of reproductive proteins. *J. Proteome* 135, 12–25
30. Browne, J.H. and Gwynne, D.T. (2022) Sexual selection on female copulatory devices in an insect with nuptial gifts. *bioRxiv* Published online March 27, 2022. https://doi.org/10.1101/2022.03.26.485942
31. Schneider, M.R. *et al.* (2016) The molecular basis and reproductive function(s) of copulatory plugs. *Mol. Reprod. Dev.* 83, 755–767
32. Peeters, C. (2017) Independent colony foundation in *Paraponera clavata* (Hymenoptera: Formicidae): First workers lay trophic eggs to feed queen's larvae. *Sociobiology* 64, 417–422
33. Villet, M.H. *et al.* (1990) Larval structures associated with larva-to-adult trophallaxis in *Platythyrea* (Hymenoptera: Formicidae). *Int. J. Insect Morphol. Embryol.* 19, 243–256
34. Ogawa, K. and Miura, T. (2014) Aphid polyphenisms: trans-generational developmental regulation through viviparity. *Front. Physiol.* 5, 1–11
35. Lemus, Y.S. and Garcia, C.M. (2022) Conflict and the evolution of viviparity in vertebrates. *Behav. Ecol. Sociobiol.* 76, 68
36. Hakala, S.M. *et al.* (2021) Biomarkers in a socially exchanged fluid reflect colony maturity, behavior, and distributed metabolism. *eLife* 10, 1–23
37. Lefèvre, C.M. *et al.* (2010) Evolution of lactation: ancient origin and extreme adaptations of the lactation system. *Annu. Rev. Genomics Hum. Genet.* 11, 219–238
38. Mirabito, D. and Rosengaus, R.B. (2016) A double-edged sword? The cost of proctodeal trophallaxis in termites. *Insect. Soc.* 63, 135–141
39. Otti, O. *et al.* (2013) In vitro antimicrobial sperm protection by an ejaculate-like substance. *Funct. Ecol.* 27, 219–226
40. Witkowska-Zimny, M. and Kaminska-El-Hassan, E. (2017) Cells of human breast milk. *Cell. Mol. Biol. Lett.* 22, 1–11
41. Buchanan, T.A. *et al.* (2007) What is gestational diabetes? *Diabetes Care* 30, 105–111
42. Wigby, S. *et al.* (2020) The *Drosophila* seminal proteome and its role in postcopulatory sexual selection: *Drosophila* seminal fluid proteins. *Philos. Trans. R. Soc. B Biol. Sci.* 375, 1–12
43. Zhang, L. *et al.* (2015) Bovine milk proteome in the first 9 days: protein interactions in maturation of the immune and digestive system of the newborn. *PLoS ONE* 10, 1–19
44. Maori, E. *et al.* (2019) A secreted RNA binding protein forms RNA-stabilizing granules in the honeybee royal jelly. *Mol. Cell* 74, 598–608
45. Koga, R. *et al.* (2021) Host's guardian protein counters degenerative symbiont evolution. *Proc. Natl. Acad. Sci. U. S. A.* 118, 1–9
46. Andreu, Z. and Yáñez-Mó, M. (2014) Tetraspanins in extracellular vesicle formation and function. *Front. Immunol.* 5, 1–12
47. Galante, L. *et al.* (2018) Sex-specific human milk composition: the role of infant sex in determining early life nutrition. *Nutrients* 10, 1–11
48. Hopkins, B.R. *et al.* (2019) Divergent allocation of sperm and the seminal proteome along a competition gradient in *Drosophila melanogaster*. *Proc. Natl. Acad. Sci. U. S. A.* 116, 17925–17933
49. Muriel, J. *et al.* (2019) Age-related patterns of yolk androgen deposition are consistent with adaptive brood reduction in spotless starlings. *Behav. Ecol. Sociobiol.* 73, 1–12
50. Perry, J.C. *et al.* (2013) The seminal symphony: how to compose an ejaculate. *Trends Ecol. Evol.* 28, 414–422
51. Cinelli, L.P. *et al.* (2009) Seminal fluid from sea urchin (*Lytechinus variegatus*) contains complex sulfated polysaccharides linked to protein. *Comp. Biochem. Physiol. Part B* 154, 108–112
52. Garwolińska, D. *et al.* (2018) Chemistry of human breast milk - c comprehensive review of the composition and role of milk metabolites in child development. *J. Agric. Food Chem.* 66, 11881–11896
53. Takashi, A. *et al.* (1991) Comparative study of the composition of hornet larval saliva, its effect on behaviour and role of trophallaxis. *Comp. Biochem. Physiol.* 99, 79–84
54. Fujita, A. *et al.* (2001) Distribution of lysozyme and protease, and amino acid concentration in the guts of a wood-feeding termite, *Reticulitermes speratus* (Kolbe): possible digestion of symbiont bacteria transferred by trophallaxis. *Physiol. Entomol.* 26, 116–123
55. Brouwers, J.F. *et al.* (2013) Distinct lipid compositions of two types of human prostasomes. *Proteomics* 13, 1660–1666
56. Walters, J.L.H. *et al.* (2020) Male infertility: shining a light on lipids and lipid-modulating enzymes in the male germline. *J. Clin. Med.* 9, 327
57. Vitku, J. *et al.* (2017) Occurrence and reproductive roles of hormones in seminal plasma. *Basic Clin. Androl.* 27, 1–12
58. Wainwright, S.M. *et al.* (2021) *Drosophila* Sex Peptide controls the assembly of lipid microcarriers in seminal fluid. *PNAS* 118, e2019622118
59. Sugiura, T. *et al.* (2002) Lysophosphatidic acid, a growth factor-like lipid, in the saliva. *J. Lipid Res.* 43, 2049–2055
60. Umbach, A.-K. *et al.* (2019) Concentrations of minerals in the canine prostatic fluid. *Reprod. Domest. Anim.* 54, 1064–1068
61. Aydin, S. *et al.* (2006) Biological rhythm of saliva ghrelin in humans. *Biol. Rhythm. Res.* 37, 169–177
62. von Engelhardt, N. *et al.* (2009) Steroids in chicken egg yolk: metabolism and uptake during early embryonic development. *Gen. Comp. Endocrinol.* 163, 175–183
63. Pratt, S.L. and Calcatera, S.M. (2017) Expression of microRNA in male reproductive tissues and their role in male fertility. *Reprod. Fertil. Dev.* 29, 24–31
64. Layne, T.R. *et al.* (2019) *microRNA detection in blood, urine, semen, and saliva stains after compromising*. 64 pp. 1831–1837
65. Hotzy, C. *et al.* (2021) *Evolutionary history of sexual selection affects microRNA profiles in Drosophila sperm*. 76 pp. 310–319
66. Itze-Mayrhofer, C. and Brem, G. (2020) Quantitative proteomic strategies to study reproduction in farm animal: female reproductive fluids. *J. Proteome* 225, 103884
67. Weber, M. *et al.* (2018) A targeted in situ hybridization screen identifies putative seminal fluid proteins in a simultaneously hermaphroditic flatworm. *BMC Evol. Biol.* 18, 1–13

68. Nakadera, Y. *et al.* (2020) Divergence of seminal fluid gene expression and function among natural snail populations. *J. Evol. Biol.* 33, 1440–1451
69. Immonen, E. *et al.* (2017) Mating changes sexually dimorphic gene expression in the seed beetle *Callosobruchus maculatus*. *Genome Biol. Evol.* 9, 677–699
70. McDonough-Goldstein, C.E. *et al.* (2021) Pronounced postmating response in the drosophila female reproductive tract fluid proteome. *Mol. Cell. Proteomics* 20, 100156
71. Rowe, M. *et al.* (2020) The reproductive microbiome: an emerging driver of sexual selection, sexual conflict, mating systems, and reproductive isolation. *Trends Ecol. Evol.* 35, 220–234
72. Iq, K.C. and Shu-Chien, A.C. (2011) Proteomics of buccal cavity mucus in female tilapia fish (*Oreochromis* spp.): a comparison between parental and non-parental fish. *PLoS ONE* 6, 2–8
73. McDonough-Goldstein, C.E. *et al.* (2021) *Drosophila* oocyte proteome composition covaries with female mating status. *Sci. Rep.* 11, 1–12
74. Mittal, S. *et al.* (2011) The diagnostic role of saliva - a review. *J Clin Exp Dent* 3, 314–320
75. Moran, N.A. and Dunbar, H.E. (2006) *Sexual acquisition of beneficial symbionts in aphids*. 103 pp. 12803–12806
76. Dedeine, F. *et al.* (2001) Removing symbiotic *Wolbachia* bacteria specifically inhibits oogenesis in a parasitic wasp. *Proc. Natl. Acad. Sci. U. S. A.* 98, 6247–6252
77. Wang, Y. and Rozen, D.E. (2017) Gut microbiota colonization and *Nicrophorus vespilloides* throughout development. *Appl. Environ. Microbiol.* 83, 1–13
78. Higham, J.P. and Hebets, E.A. (2013) An introduction to multimodal communication. *Behav. Ecol. Sociobiol.* 67, 1381–1388
79. Birch, J. (2017) *The Philosophy of Social Evolution*, Oxford University Press
80. Linksvayer, T.A. and Wade, M.J. (2009) Genes with social effects are expected to harbor more sequence variation within and between species. *Evolution* 63, 1685–1696
81. Patlar, B. *et al.* (2021) Nonadaptive molecular evolution of seminal fluid proteins in *Drosophila*. *Evolution* 75, 2102–2113
82. Alonzo, S.H. and Pizzari, T. (2010) Male fecundity stimulation: conflict and cooperation within and between the sexes: Model analyses and coevolutionary dynamics. *Am. Nat.* 175, 174–185
83. Sirot, L.K. *et al.* (2011) Protein-specific manipulation of ejaculate composition in response to female mating status in *Drosophila melanogaster*. *Proc. Natl. Acad. Sci. U. S. A.* 108, 9922–9926
84. Cotter, S.C. *et al.* (2010) Fitness costs associated with mounting a social immune response. *Ecol. Lett.* 13, 1114–1123
85. Hardy, I.C. and Briffa, M. (2013) *Animal Contests*, Cambridge University Press
86. Nakadera, Y. *et al.* (2014) Receipt of seminal fluid proteins causes reduction of male investment in a simultaneous hermaphrodite. *Curr. Biol.* 24, 859–862
87. Kazancio lu, E. *et al.* (2012) The evolution of social interactions changes predictions about interacting phenotypes. *Evolution (N. Y)* 66, 2056–2064
88. Szathmáry, E. (2015) Toward major evolutionary transitions theory 2.0. *Proc. Natl. Acad. Sci. U. S. A.* 112, 10104–10111
89. Matsushima, W. *et al.* (2019) Sequencing cell-type-specific transcriptomes with SLAM-ITseq. *Nat. Protoc.* 14, 2261–2278
90. Longuespée, R. *et al.* (2016) MALDI mass spectrometry imaging: a cutting-edge tool for fundamental and clinical histopathology. *Proteomics Clin. Appl.* 10, 701–719
91. Dittmar, G. and Selbach, M. (2015) SILAC for biomarker discovery. *Proteomics Clin. Appl.* 9, 301–306
92. van Delft, P. *et al.* (2017) The profile and dynamics of RNA modifications in animals. *ChemBioChem* 18, 979–984
93. Fricke, C. *et al.* (2013) Age-dependent female responses to a male ejaculate signal alter demographic opportunities for selection. *Proc. R. Soc. B Biol. Sci.* 280, 1–7
94. LeBoeuf, A.C. *et al.* (2018) Molecular evolution of juvenile hormone esterase-like proteins in a socially exchanged fluid. *Sci. Rep.* 8, 1–10
95. Yapici, N. *et al.* (2008) A receptor that mediates the post-mating switch in *Drosophila* reproductive behaviour. *Nature* 451, 33–37
96. Smith, J.E. and Pinter-Wollman, N. (2021) Observing the unwatchable: integrating automated sensing, naturalistic observations and animal social network analysis in the age of big data. *J. Anim. Ecol.* 90, 62–75
97. Frank, A.E.T. *et al.* (2022) Infection signaling and antimicrobial wound care in an ant society. *BioRxiv* Published online April 27, 2022. https://doi.org/10.1101/2022.04.26.489514
98. Huang, J. *et al.* (2017) Application of the amniotic fluid metabolome to the study of fetal malformations, using Down syndrome as a specific model. *Mol. Med. Rep.* 16, 7405–7415
99. Zarezadeh, R. *et al.* (2021) Omics in seminal plasma: an effective strategy for predicting sperm retrieval outcome in non-obstructive azoospermia. *Mol. Diagnosis Ther.* 25, 315–325
100. Zhu, D. *et al.* (2021) Milk biomarkers in relation to inherent and external factors based on metabolomics. *Trends Food Sci. Technol.* 109, 51–64
101. Bergeron, A. *et al.* (2007) Milk caseins decrease the binding of the major bovine seminal plasma proteins to sperm and prevent lipid loss from the sperm membrane during sperm storage. *Biol. Reprod.* 77, 120–126
102. Galley, J.D. and Besner, G.E. (2020) The therapeutic potential of breast milk-derived extracellular vesicles. *Nutrients* 12, 745
103. Jorgensen, S.C.J. *et al.* (2022) Role of maternal COVID-19 vaccination in providing immunological protection to the newborn. *Pharmacotherapy* 42, 58–70
104. París-Oller, E. *et al.* (2021) Reproductive fluids, used for the in vitro production of pig embryos, result in healthy offspring and avoid aberrant placental expression of PEG3 and LUM. *J. Anim. Sci. Biotechnol.* 12, 1–12
105. Dietrich, M.A. *et al.* (2017) Proteomic identification of seminal plasma proteins related to the freezability of carp semen. *J. Proteome* 162, 52–61
106. Anel-Lopez, L. *et al.* (2017) Improving sperm banking efficiency in endangered species through the use of a sperm selection method in brown bear (*Ursus arctos*) thawed sperm. *BMC Vet. Res.* 13, 1–8
107. Smith, R.M.H. *et al.* (2021) Neonate aggregation in the Permian dicynodont *Diictodon* (Therapsida, Anomodontia): evidence for a reproductive function for burrows? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 569, 110311
108. Brawand, D. *et al.* (2008) Loss of egg yolk genes in mammals and the origin of lactation and placentation. *PLoS Biol.* 6, 0507–0517
109. Guernsey, M.W. *et al.* (2017) Molecular conservation of marsupial and eutherian placentation and lactation. *eLife* 6, 1–19
110. Snir, O. *et al.* (2022) The pupal moulting fluid has evolved social functions in ants. *Nature* 612, 488–494