Social regulation of reproduction: control or signal?

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Traditionally, dominant breeders have been considered able to control other individuals' reproduction in multi-member groups with high variance in reproductive success/reproductive skew (e.g., *forced sterility* on subordinate conspecifics in eusocial animals; *suppression* of sex change in sequential hermaphrodites). These actions are typically presented as active *impositions* by reproductively dominant individuals. However, how can individuals regulate the physiological reproductive state of others? Alternatively, less reproductively successful individuals could self-restrain from reproduction in presence of dominant breeders. Shifting perspective from a top-down manipulation to a broader view (which includes all contestants) and using a multi-taxa approach, we propose a resolution of reproductive-skew conflicts based on signalling rather than control, along a continuum of levels of strategic regulation of reproduction.

Highlights

"Reproductive skew" and "variance in lifetime reproductive success" often describe an uneven distribution of reproductive success, the first focusing on systems where the reproduction disparity is extremely high, the latter referring to any system, including those where the degree of skew is smaller in extent, but still relevant.

Theoretical models of reproductive skew in general tend to present the allocation of reproduction based on dominant control (adopting the dominants' perspective). Here we propose to revert this view and consider a bilateral decision rather than a top-down control.

For social systems and groups to be maintained, the conflict on the unequal sharing of reproductive success needs to be resolved. A strategic self-induced regulation of reproduction represents a low cost and parsimonious resolution of the conflict, based on indirect and/or future benefits to individuals that accept social subordination. This is particularly true under kin selection, ecological constraints (e.g., limited nesting sites or territories) and/or when group members queue for reproductively dominant breeding positions.

Reproductive skew

"*if each male secures two or more females, many males cannot pair*" [1]

Inequality in **mating success** (see Glossary) is one of the consequences of intrasexual competition and is at the basis of the theory of sexual selection. It typically results in high variance in lifetime **reproductive success** between same-sex individuals within the population. Unequal distribution of reproduction (or, when reproduction disparity is extremely high, "**reproductive skew**") is exacerbated in **cooperative society** (Figure 1): in many **eusocial animals** (insects, mammals, crustaceans) only very few individuals in the colony reproduce [2]. Less disproportionate skews are found in other cooperative breeding systems, along a continuum [3,4]. In all of these systems, some individuals not only do not reproduce (or have reduced/delayed reproduction) but may also cooperate with the dominant breeders to defend the nest and raise their young (e.g., workers in eusocial animals, helpers in cooperative breeding birds and mammals [5,6]). Non-cooperative breeders (i.e., with no **alloparental care**) rely on permanent or temporary mating aggregations where, for example, alpha males monopolize most mating events (harem polygyny) [7].

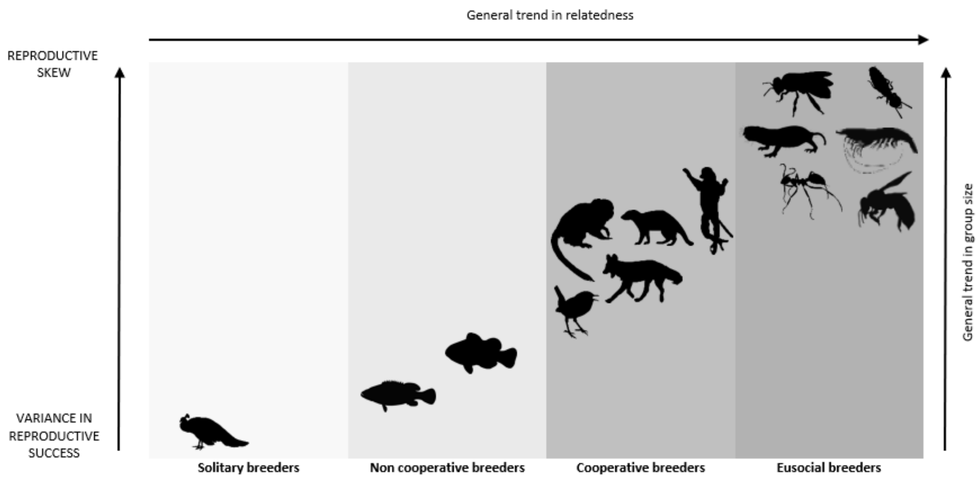

Figure 1. Increasing levels of variance in reproductive success, up to reproductive skew, are common across taxa and mating strategies, often (but not always) driven by high levels of relatedness (kin selection) and frequently higher in large groups/colonies (but see *Polistes* social wasps [8]). Representative silhouettes of selected examples are from phylopic.org (see full credit in the acknowledgements).

All the definitions of reproductive skew imply some kind of reproductive hierarchy, or rank order, where few reproductively dominant individuals are the main, if not the only, breeders: they apparently regulate reproductive competition by preventing other individuals from reproducing via total or partial functional sterility in rivals, delaying their reproductive attempts or - in **sequential hermaphrodites** - affecting their sex change (temporal sex allocation [9]). In this view, reproductively less successful individuals are able to pursue their reproductive interests only when the dominant breeders die, leave or are experimentally removed. If this is the case, how does a single individual of one sex control the status of many others?

Providing a concise historical account on the proposed mechanisms behind reproductive skew, we revise the way we usually interpret how reproductive skew is reached and suggest to move from a dominant-focused narrative to a broader one, considering also the benefits reproductively subordinate individuals obtain when they restrain their own reproduction in the presence of dominant breeders. In other words, instead of an imposed control, where only the breeders make decisions, we look for evidence of a more interactive use of signals between the contestants. Throughout our analysis, we refer to control as a form of imposition and **manipulation** (following the definition commonly accepted in parasitology [10]), where breeders increase their own fitness at the expenses of other group or population members. Using simultaneous hermaphrodites and parasites as examples, we finally address cases where real manipulation is likely to occur.

With a multi-systems and multi-taxa approach, which considers different factors in the socio-ecological contexts (group size, sex ratio, resource limitations, territorial defence, degree of relatedness), we propose a more parsimonious resolution of the reproductive conflict based on honest signalling and individual decision-making, rather than control, which might apply to social contexts with reproductive skew and result in the unequal share of mating opportunities we see in animal societies. Aggression, physical intimidation and punishment (eviction, infanticide, and **policing)** can still be used as reinforcing mechanisms or the sole form of control (e.g., aggression-based breeding dominance) in groups where dominant breeders can forcefully maintain their status (e.g., sea lions; red deer; some primitively eusocial wasps lacking morphological castes). Otherwise, the signaller and the recipient exchange signals which convey information of their reciprocal quality (e.g., fecundity, size, fighting ability) and allow both of them to take a decision in view of direct immediate benefits for the dominant breeders or indirect and/or future benefits for the others, which comply with the bad situation, making the best of it. Alternatively, the latter can compete or desert.

Social control of reproduction

Sexual reproduction implies some level of interaction between individuals: even broadcast spawners, when releasing their gametes in the environment, rely on a certain degree of coordination between partners [11]. More complex interactions are found with increasingly complex social context, where some individuals mate with multiple partners, typically at the expenses of same sex rivals, increasing their **reproductive success**. Since the seminal paper of Emlen and Oring [7], ecological factors (which allow to control the direct access to mates and/or essential resources) have been connected with the evolution of **polygamy**. Such monopolization is often based on some form of hierarchical reproductive dominance, where, for example, alpha males sire the majority of the offspring, even when other males are present. Typically, reproductive monopoly in resource/harem defence polygyny is obtained and maintained with overt physical competition and aggressive encounters (e.g., among male elephant seals [12]) and represents a form of control of reproduction.

However, in the scientific literature the term "social control of reproduction" has gained a more specific meaning, which goes beyond the aggressive exclusion of sexual rivals from an area or a mate. Thus, for example, we find reference to social control in multiple instances such as caste determination and reproduction and queen/worker conflict in eusocial hymenopterans [13,14], mammals and crustaceans [15,16]; reproduction in cooperative breeders [17]; temporal sex allocation in sequential hermaphrodites, where subordinates delay or forego sex change [18,19]. In these cases, the term "social control" often implies a mechanism actively initiated by the dominant breeder(s), which usually triggers temporarily or permanent phenotypic changes in group members (behavioural, morphological and physiological, including hormonal changes), regulates their reproductive output and ultimately determines the reproductive skew. But what is dominance (Box 1)? And does dominance in general, and breeding dominance in this case, exacerbate conflicts, or does it resolve them [20]?

BOX 1 – Dominance and reproductive skew models

The term dominance is broadly used to convey ranks (from the initial observations of peck-order [21]) and to define winner (dominant) or loser (subordinate) status. Dominants gain priority access to limited resources (including mates). Here we use the term dominant in the sense of "dominant breeders": individuals who have higher reproductive output than others when competing for access to mates and exhibit some form of power asymmetry (surpassing others in traits relevant to mate competition [22]). In many social contexts, hierarchies are first established: dominants have specific phenotypic traits (size, physical condition, fecundity, behavioural or personality traits) or states (winner or loser status from previous encounters) that contribute to the relative power asymmetry between contestants. Opponents displays their fighting abilities and willingness to escalate the conflict in a sequential assessment (e.g., the fighting sequence in the cichlid *Nannacara anomala* [23] or the “parallel walk” in red deer, *Cervus elaphus* [24]) up to the most dangerous fights. After the relative rank has been established, signals may be produced to advertise it: in queenless ponerine ants, for example, workers compete for reproduction via overt aggression; once a dominance hierarchy has been established, pheromones signal the reciprocal rank [25]. Similarly, in the cichlid *Astatotilapia burtoni* [26] only reproductively dominant males exhibit territorial behaviour and bright colors: these traits are showcased within minutes of gaining dominant status [26]. Finally, once established and advertised, such a rank might need to be maintained/enforced (via aggressive behaviours, policing, infanticide and eviction [27]).

Reproductive skew models [28–30] assume a game-theoretic decision, where subordinates decide to stay (if they increase or gain fitness returns comparable to being solitary [31]) or leave the group (not always a feasible option). Initial models were based on the benefit of breeding in a group (to the main advantage of dominant breeders), the possibility of reproducing outside the group (ecological constraint) and the relatedness between breeders and non-breeders (Table I).

Table I. Benefits of breeding in social contexts with some level of reproductive skew, with details on the other two variables used in early theoretical models: the option of breeding outside the group (ecological constraint, EC) and the relatedness between breeders and non-breeders (R) which imply kin selection (e.g., eusocial insects) as well inbreeding avoidance (eusocial mammals).

CONTESTANTS	**TYPE OF BENEFIT**	
Reproductively DOMINANT	DIRECT	More partners/helpers
Reproductively SUBORDINATE	INDIRECT/CURRENT	Inclusive fitness [R] Inbreeding avoidance [R]
	BEST OF A BAD SITUATION/FUTURE	Queuing [EC] Habitat saturation [EC] Reduced aggression Eviction avoidance

Dominant breeders could retain subordinate ones allowing for some reproductive concessions (transactional concession models) or subordinates give up part of their reproductive share (transactional restrain models, under threat of eviction by dominant breeders [32]). The tug-of-war models instead imply that a compromise should be reached, based on the limited but current competitive abilities of subordinates (Figure I). Combinations of transactional and compromise models (synthetic models [28,29]), and the addition of "outside options" (ecological constraints) and "inside options" (costly competition) have been proposed, but overall the narrative is still focused on the dominant-breeder control of group/population members [33–35].

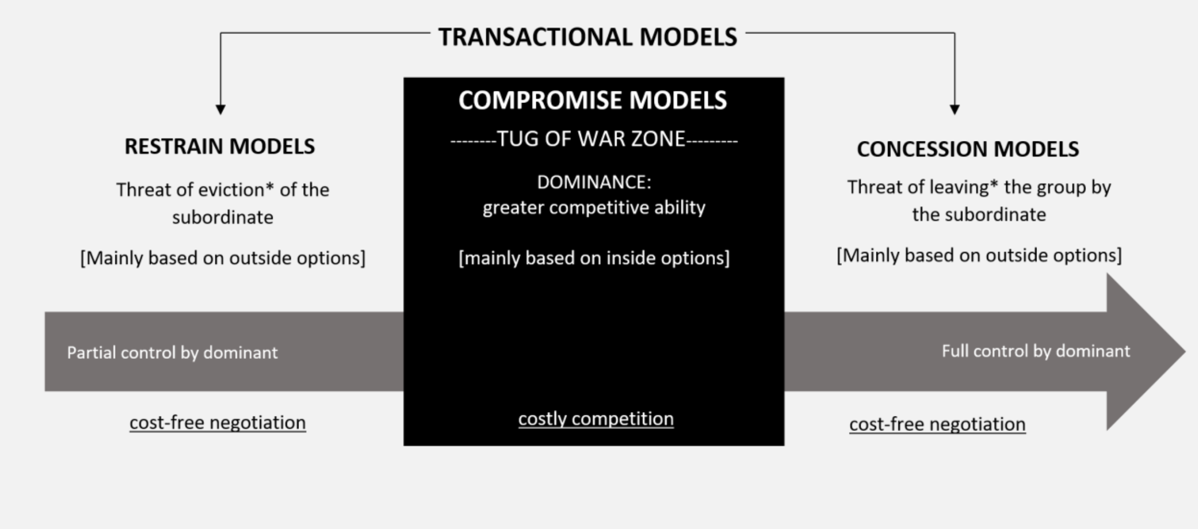

Figure I. Schematic summary of theoretical models, based on recent literature [29,33–35].

A change of perspective: does the resolution of the conflict need to be costly?

Reproductive skew implies that one/few individual(s) gains a larger than average share of reproduction: this sets a reproductive conflict, which would typically result in an actual contest (e.g., [12]). However, in social contexts, less costly resolutions (in terms of injury and energetic costs) than actual fights might be beneficial to all contestants. Initially, reproductive skew has been strictly associated with the concept of a complete control of reproduction by the dominant [31], later relaxed into a partial control [32] (Box 1).

According to the dominant breeder view, some individuals actively suppress the reproduction of other group members (as shown in articles titles [18,19,36,37]), by releasing chemical signals/pheromones, and/or exhibiting visual signals or aggressive behaviours, and/or displaying morphological traits (including body size) that diminish receivers' fertility. This hypothesis is therefore strictly associated with the expectation that reproductively dominant individuals **manipulate** (*sensu* [10]) the reproductive physiology of others and gain fitness advantages at the their expenses. There has been a strong debate about the level of control and the underlying mechanisms of suppression behind it, especially whether they consist in active suppression/inhibition of the reproductive potential of individuals by dominant breeders. If the recognition of breeding dominance can resolve the conflict with limited costs with respect to reiterated aggression, then "subordinate" individuals become active players, who restrain their own reproductive output. Self-restrained reproduction might be triggered by a variety of reasons, from current/future and/or direct/indirect advantages, making the best of a bad situation (Table I) but represents a response to a signal/assessment of rank, rather than a manipulation.

So, the main question is: do dominant breeders directly control the reproduction of group members or are the latter responding to signals? In other words, are dominant breeders making all decisions about the reproductive output in the group/population or are both dominant breeders and non-breeders making decisions about their own reproduction based on the assessment of their reciprocal qualities?

Historical change in perspective: the role of queen pheromones in social insects

In 1991, honest signalling models started to emerge in different fields of behavioural sciences [38] and the mechanisms underlying the control of reproduction was questioned in social insects. At the time, queens (dominant reproductive females) were considered capable of inhibiting the reproduction of workers by means of chemical compounds: queen pheromones were typically interpreted as a means of direct coercive manipulation of workers, so that workers would behave in ways that increased the queen's fitness at their own expenses [25,39,40]. With a now renown paper, Keller and Nonacs [41] questioned this perspective, asking whether queen pheromones, rather than being manipulative agents that queens use to impose worker sterility, were honest signals of fertility. If this was the case, workers, which do not mate but have functional ovaries [42], would respond to such signals by self-restraining from reproduction, still at the benefit of their own inclusive fitness. They noted the lack of evidence that queen pheromones actively suppress worker reproduction, while valid alternative explanations often existed; for instance, due to **kin selection**, workers may have selfish genetic interests in preventing nestmate workers from reproducing (worker policing [41,43,44]). Moreover, it would be difficult to explain how such pheromones are evolutionarily maintained [41]: pheromonal queen control is expected to result in an arms race where workers are under strong selection to resist manipulation and, in turn, queens would be selected to increase the amount of pheromone or produce new control-effective compounds [45] – whereas we now know such signals are highly conserved in Hymenoptera [40] (Table 1).

Table 1. Predictions of the two contrasting hypotheses of signalling (SH) *vs*. control (CH) using selected examples across multiple taxa (following the work of Oi et al. [44] in social insects). Proposed proximate mechanisms are listed and instances of empirical evidence are reported. For sequentially hermaphroditic fishes please refer to Table 2.

	Predictions		**Mechanisms**	**Empirical support**
Taxon/Social system	**Signal Hypothesis (SH): subordinates respond to dominant's signals by self-restraining their reproductive output as this is their best option**	**Control Hypothesis (CH): subordinates are manipulated to decrease their fertility output against their own reproductive interests**	**Proposed mechanism used by dominant and response by subordinate**	**The hypothesis with the best empirical support is reported (SH or CH)**
Social insects	Genetic interests: queens and workers are related (kin selection) so subordinates gain indirect genetic benefits	The control does not depend on the kin structure of the colony	SH: queens release pheromones which function as fertility signals; self-restrained ovary development in the workers (not imposed: some workers reproduce) CH: queens release "control" pheromones that chemically sterilize all workers from laying eggs	SH: evidence of worker **policing** [41,43,44] maximizing indirect genetic benefit (workers care for eggs laid by their mother and destroy those laid by sisters) CH: not common, but see box 2 for **facultative intraspecific parasitism**, e.g., in *Polistes* wasps [46]
	Signals are honest and "uncheatable indices of fertility" [44]; they correlate with ovarian activity	The level of control depends on the size of the colony, rather than queen fertility (though colony size and fertility often correlate)	SH: queen pheromones reflect queen's fertility; workers/subordinates give up reproduction based on benefit gained CH: production of queen "control" pheromones depends on colony size (larger colonies might require larger production)	SH: strong evidence in many species of pheromones as honest signal (see [44]) CH: some cuticular compounds in honeybees correlate with colony size more than with fertility [47]

	Signals reflect fecundity so they are conserved across different social insect taxa	Control mechanisms need to be constantly changed to maintain effectiveness as workers may evolve counter-adaptations (mechanisms not conserved)	SH: queen pheromones highly conserved across different taxa CH: arms race expected. Workers selected to resist manipulation; queens selected to produce new/more effective control pheromones	SH: cross-activity of pheromones supports highly conserved signalling [40]
Eusocial mammals: naked mole-rats (*Heterocephalus glaber*) and Damaraland mole-rats (*Fukomys damarensis*)	Genetic interests: queens and workers are related to some extent (kin selection); reduced inbreeding depression as members of the colony are related to some extent	"Physiological block to reproduction" by queens on non-breeding females [15] Queens increase fecundity and reduce workload [48]	SH: direct interactions with the breeding queen; no evidence of pheromonal control of reproduction by queens notwithstanding vast empirical approach [49] CH: possible transfer of oestrogens from dominant female to non-breeders via coprophagy may alter oestrogen levels in the latter [50]	SH: mating with related individuals is avoided [49] CH: no evidence that ingestion of faecal oestrogens results in diminished fertility, although coprophagy reported (see [49])
	Future benefits: queueing for breeder position			SH: Subordinates restrain their own growth to avoid aggression by dominants [51]
Eusocial crustaceans: caridean snapping shrimp, genus *Synalpheus*	Ecological constraints: benefit in living in host sponges (shelter and food provision); shared resource defence	One or multiple queens in the colony; non-breeders increase the dominants' reproductive success by helping in cooperative defence of the colony [52]	CH: chemical mechanisms postulated [53] but no evidence	SH: Presence of the queen "suppresses" gonadal development in workers; no aggression [53]
	Genetic interests: queens and workers are related in some species (kin selection); reduced inbreeding depression		SH: direct development favours natal philopatry and within group relatedness [52]	
Cooperative breeding birds	Genetic interests: Kin selection in some	Non-breeding subordinates increase the dominant		SH: Ability to discriminate kins [54]

(e.g., chestnut-crowned babbler, *Pomatostomus ruficeps*)	species/inbreeding avoidance	reproductive success by helping at the nest		
	Future benefit: queueing for breeder position		CH: aggressive behaviour	SH: In some species helpers at the nest are not close relatives, but instead help for future benefits [55] or direct advantage of foraging in groups and diminish predation risk [56] However, no signalling by helpers of their contribution (as a rent payment) was detected [57] CH: dominant females prevent subordinate ones from access to nests and thus to laying ([58] but see [59]); no aggression towards non-related helpers [57]
Cooperative breeding carnivores: dwarf mongooses (*Helogale parvula*), African wild dogs (*Lycaon pictus*) and wolves (*Canis lupus*)	High energetic costs of reproduction for females: age and body mass can be interpreted as honest signal of reproductive dominance	Behavioural suppression of reproduction in males; endocrine and behavioural in females [60]	SH: subordinates recognize reproductive dominance signals and self-restrain reproduction: enforcement by infanticide can be used by both dominant and subordinate females, similarly to policing in social insects (e.g., in meerkats [61]) CH: endocrine suppression of subordinates' reproduction by dominant: adrenal glucocorticoids and gonadal steroids are expected to be correlated with rank [62]	SH: not always endocrine levels correlate with ranks; subordinates sometimes reproduce; infanticide [62]
	Benefits from group living (e.g., protection from predators); queueing for breeder position (breeders are under predation threat as well as non-breeders; Radford, pers. comm.)			SH: No mechanisms identified. Evidence for widespread **social monitoring** (e.g., in dwarf mongooses [63,64])

Social primates, e.g., marmosets (*Callithrix jacchus*); Verreaux's sifakas (*Propithecus verreauxi*); white-faced capuchins (*Cebus capucinus*), and more	Benefits from group living; queuing for breeding positions	Non reproductive subordinates increase the number of offspring (sired by the dominant) helping with parental care [65,66]	SH: Self-restrained reproduction following chemo-signals by the breeding pair (anal scent marking) where subordinate females may stay and queue for breeding opportunities, or leave the group; attempts to breed by subordinate females are reported; reinforcement by infanticide and eviction from the group [66] CH: Hypothesized suppression of ovulation in subordinate females (via scent marking) and diminished sperm cell production in subordinate males [66]	SH: Possible inbreeding avoidance; evidence of infanticide as a deterrent of reproduction in subordinates marmosets [67] CH: no evidence
Semi-solitary orang-utans (*Pongo pygmaeus)* and mandrills (*Mandrillus sphinx*) (subordinate and dominant males have different secondary sexual traits [68])	Genetic interests: dominant and subordinate males are related (kin selection: indirect genetic benefits)	The control does not depend on the kinship, dominant males monopolize access to females	SH: flanged males in orang-utans and "fatted" males in mandrills signal their dominant rank; subordinate males self-restrain from developing full secondary sexual traits in a sort of alternative reproductive strategy; only some reproduce	SH: no evidence CH: no evidence

Change in perspective: from social insects to sequential hermaphrodites

As queens in social insects were considered able to inhibit reproduction in other females, in sequential hermaphrodites dominant breeders of the second sex (i.e., the sex with the highest reproductive output [69]) were considered capable of suppressing conspecifics' sex change at their advantage. This idea stemmed from simple experiments in female-first sex-changing fishes (protogynous, characterized often by a haremic system [69]) where removing the dominant male from the group "allowed" a large female to change sex and become a male [70]. As subordinates changed their reproductive strategy only after the removal of the dominant, it was assumed that the dominant coercively kept them in the reproductively less-rewarding sex, either by physical intimidation or by chemical manipulation (Table 1,2). Nonetheless, in the case of fish, "active domination" [18] is not always feasible in large groups and other proximate mechanisms have not been reported, to our knowledge. Moreover, not always the largest female is the one changing sex [71].

A similar "aggressive dominance" has been reported mainly in one instance of male-first sex-changers (protandrous, characterized often by a monogamous system [69]): the clownfishes (subfamily Amphiprioninae; Table 2). These fishes live in symbiosis with anemones, a scarce resource [72]. Each anemone hosts a reproductive pair (a large dominant female and her male partner) and many smaller nonbreeders. Here, the removal of the female seemed to "allow" the breeding male to change sex to female and the largest non-breeder to develop as the breeding male [73]. Yet, staying at the anemone as a non-breeder is an adaptive choice (rather than an imposition), as young clownfish evicted from the anemone would almost certainly die, to the point that they restrain their own growth to avoid challenging the breeding pair ([74]; see strategic growth below). In the situation of habitat saturation (Table I, 2), reducing eviction from the group while queuing for future reproduction represents the best choice (Table 2). In other protandrous species, sex change is often regulated by body size and/or population sex ratio (Table 2). Individuals of male-first sex-changers can also delay sex change if they are obtaining high reproductive success as males (e.g., the slipper snail *Crepidula* [75]).

Thus, we propose that also in sequential hermaphrodites, decisions about reproduction (in this case, sex change) are individual decisions based on the social contexts (Table 2). The relevant social cues used to assess their own breeding position vary; for instance, female-first sex-changers with haremic nuptial system base their decision on relative morphological and behavioural cues, whereas if they reproduce in spawning aggregations use their own relative size and population sex ratio, which nonetheless indicates they monitor the social contest.

Similarly, male-first sex-changers also base their sex change decisions either on individual cues (e.g., relative body size in clownfish with territorial anemones [76]), or on the sex ratio of the population (solitary breeders and species with random mating). This social monitoring is affected by anthropogenic interference: overfishing depletes the population of the largest individuals, which exhibit the second sex [71]. The density and sex ratio of the population can also trigger alternative reproductive strategies, such as the presence of non sex-changers (primary males and females): individuals that develop directly the second sex and keep it throughout life [72].

Table 2. Predictions of the two contrasting hypotheses of signalling (SH) *vs.* control (CH) using selected examples across sequentially hermaphroditic fishes. In each sexual system (protogyny: female first sex-change; protandry: male-first sex change), different strategies of social regulation/control of reproduction based on mating system and ecological/social conditions are highlighted.

SEXUAL SYSTEM	MATING SYSTEM	ECOLOGICAL/SOCIAL CONDITIONS	SIGNAL OR CONTROL?
PROTOGYNY ♀ → ♂	TERRITORIAL HAREMS	Individuals of the first sex (female) choose to delay or skip sex change in the presence of a larger male	SH: regulation of sex change based on aggressive display, sexual dimorphism (colour - dichromatism - and behaviour) efficient even through glass (as found in *Anthias anthias* [70]); in *Labroides dimidiatus* sex change even in the presence of males in females at the periphery of the male territory, where male-female interactions are scarce [18] not always the larger female change sex [71]
			CH: control of sex change based on aggression (when dominant is removed the subordinate change sex)
	TEMPORAL SPAWNING AGGREGATIONS	Sex change based on population sex ratio and relative size (better to be a large male to compete with other males in the spawning grounds). Possibility of delaying sex change with current reproductive outcome	SH: *Sex ratio induction* [77]
PROTANDRY ♂ → ♀	MONOGAMY with ecological constraints	Individuals change sex when breeding positions are vacant (e.g., in clownfish, after queueing at the anemone, as dispersing involves predation risk [72])	SH: The dominant female grows bigger and signal her reproductive dominance (size-based hierarchy); the reproductive males is the second largest fish; non-breeders restrain their own growth and gonadal development thus avoiding aggression/eviction [51,78]
			CH: aggressive dominance by dominant couple
	MONOGAMY or RANDOM MATING with no ecological constraints	Sex change based on population sex ratio and relative size	SH: *Sex ratio induction* [77]

Lessons from simultaneous hermaphrodites: from self-adjustment of sex allocation to manipulation of reproduction

Ten years before Keller and Nonacs' paper [41], Charnov [9] proposed that sex allocation was an adaptive response to social conditions: each individual was expected to adjust its resource investment in reproductive traits as a function of current mating opportunities [9]. This perspective was also successfully applied to hermaphrodites, who were expected to change their allocation to the female or the male sexual function depending on mating opportunities [9]. However, while for *simultaneous* hermaphrodites the individual benefit perspective has been largely applied in subsequent studies (as reviewed in [79,80]) and the origin of the relevant social signals identified in some species (e.g., [81,82]), it was often easier to explain the decision to change sex in *sequential* hermaphrodites as the result of the manipulation of one sex over the other. But why two similar systems, in which individuals act as both sexes either simultaneously or sequentially, should be explained with two different theoretical approaches: self-adjustment of sex allocation in the former, but lack of it in the latter? And how can individuals of one sex prevent the change of sex of others? Even if manipulation can indeed occur (simultaneous hermaphrodites not only can be used as a great playground to test decisions on partitioning of male and female functions [83], but also provide examples of actual manipulation of reproduction (Box 2) [84]), in most cases manipulation does not explain sex-change decisions.

BOX 2 - The social regulation of reproduction continuum

As shown for eusociality [4], reproductive modes and strategies [69,85], also reproductive conflicts can be seen along a gradient, a continuum (often taxon-specific), where a multi-systems and multi-taxa approach can broaden up our understanding of reproductive conflicts and allow for a better interpretation of their resolution (Figure II). In the perspective of variance in lifetime reproductive success, up to extreme reproductive skews in animal societies, the establishment and maintenance of a dominant breeding position [27] is considered the most relevant mechanism to establish the actual share of mating opportunities, often considered the sole prerogative of winners. A change of perspective, with a focus on both contenders [86], who all assess honest signals and make their decisions based on current social context (including kinship and ecological constraints), represents a more parsimonious mechanism of conflict resolution, enforced when necessary (figure II). At one end of the continuum, there are cases of true manipulation (increased fitness of one individual at the expenses of others). Interesting examples (with corresponding arms races) are found in simultaneous hermaphrodites (intraspecific manipulation) and parasites (interspecific manipulation).

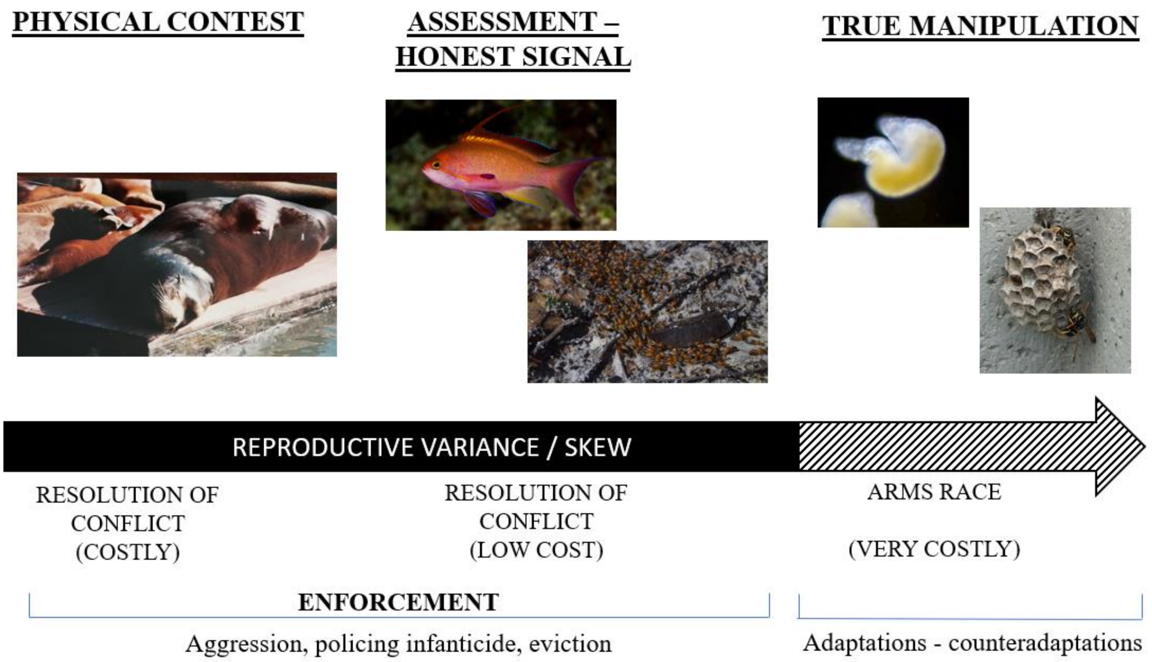

Figure II: Resolution of reproductive conflict, across taxa and mating system. Physical contest can be used in many haremic-like societies where dominant males aggressively monopolize access to mates (e.g., California sea lions, *Zalophus californianus*). Less costly resolution (often used in larger groups, with high reproductive skew) can be obtained by reciprocal assessment of dominance breeding status by both reproductively dominant and subordinate individuals, as proposed for sequential hermaphrodites (female-first sex changing *Anthias squamipinis* fish, courtesy of Nuno Vasco Rodruigues) and eusocial animals (such as termites). Reproductive monopoly can be enforced by aggression, policing, infanticide and eviction. An active arms race (involving adaptations and counter-adaptations) occurs in intraspecific reproductive conflicts (e.g., in simultaneous hermaphrodites: *Macrostomum lignano* courtesy of Lukas Schärer) or interspecific ones (e.g., in social parasites, photo of *Polistes biglumis* and its social parasite *Polistes atrimandibularis*).

In simultaneous hermaphrodites, sperm donors can manipulate partners' sperm uptake and/or use, usually not without resistance: for example, antagonistic coevolution has been described in the flatworm *Macrostomum lignano* [87] (whose seminal fluid contains compounds which affect the partner propensity to remove received sperm) and ways to manipulate partners' use of own sperm has been reported in snails [88,89] and earthworms [90]. These are real cases of intraspecific manipulation of reproduction, adding to interspecific examples: in **obligate social insect parasites** [91,92] a female can invade the colony of another species, take over the reproductively dominant position using chemical mimicry, camouflage and/or chemical insignificance and manipulate the host reproductive output [91,93]. Interestingly, facultative social parasites can switch from signalling to manipulating: *Polistes* social wasps use cuticular compounds as honest signals of fertility in their own colony, or as manipulative compounds when they act as social parasites [94,95].

More extreme cases are parasites which castrate their hosts, e.g., parasitic barnacle *Sacculina carcini,* whose castrating mechanism is well known (destruction of the androgenic gland in male crabs [96]). We could thus think about manipulative social control of reproduction as a form of intraspecific castration or imposed contraceptive pill [49]. But the main question remains: how can this control be performed?

Concluding remarks

Animals constantly check their environment, get relevant information about it and make decisions. This includes a constant **social monitoring** and consequent behavioural adjustment to the current social context (e.g., [97,98]). Why shouldn't they use this info to adjust also their reproduction? Indeed, theoretical models and empirical studies show us that individuals adjust the number and sex ratio of their offspring and/or their own sex allocation to current condition [9,99,100]. However, somewhere along the way it became easier to consider reproductive decisions (limitation or delay of reproduction by some group members) as manipulations imposed by dominant breeders on the other group/population members rather than responses by any individual to current condition, even though evidence for the underlying proximate mechanisms was lacking (see outstanding questions). Indeed "subordinates" and less successful breeders often choose to stay and restrain their own reproduction [86] if leaving the group (or colony, nest, anemone, etc.) is risky whereas staying increases their fitness either indirectly (via kin selection) or directly by increasing their survival chances and allowing some even small probability to inherit the breeding position (e.g., by queueing and replacing the breeding positions). Similarly to the switch of perspective occurred in social insects - from control to signal for queen pheromones [41] - and following the recent revisitation of social control of size (**strategic growth** [51]) we should consider "social control of reproduction" as an adaptive and active response to breeding dominants rather than a passively received, imposed manipulation from them, and possibly redefine it as "strategic regulation of reproduction". The use of the traditional ("dominant") view might conceal reproductive adaptations, including responses to signals and mechanisms for self-restraining of reproduction. The new perspective we propose results instead in a more effective and less costly resolution of reproductive conflicts in animal societies.

Outstanding questions

What are the key experiments to test signalling ("subordinates" assessing the presence of a dominant breeder and restraining their own reproduction) *vs.* control (dominant breeders actively manipulating the reproduction of other group/population members)? The classical experiment of removing the reproductively dominant individual(s) changes the social context and fails to disentangle whether the subordinates' change in reproductive status is associated to the end of the dominant manipulation or to subordinate(s) perceiving the changed social context and updating the appropriate reproductive decision. In fact, the challenging experiments or observations required to unravel between dominant breeder(s) manipulation and honest signalling of breeding dominance have yet to be conducted. Could facultative social parasites (e.g., *Polistes* wasps [95]) or hermaphrodites be convenient model systems?

How do organisms assess their social environment (conspecific breeding/fighting ability, population sex ratio or densities…)? Are mechanisms consistent across taxa and mating systems?

What are the proximate mechanisms underlying strategic regulation of reproduction?

What mechanisms/behaviours are used to establish dominance? What characteristics identify winners? How consistent are they across taxa and mating systems?

Can the view of the "strategic regulation of reproduction" help to investigate the evolution of low-skew societies?

Glossary

Alloparental care: care of young provided by individuals who are not the parents.

Cooperative animal society: social group, where reproduction is restricted to dominant pairs and the rest of the group help in foraging, defence and mainly caring for offspring other than their own; often characterized by the presence of a specific territory/nest.

Eusocial animals: definition coined initially for social insects with reproductive division of labour, overlapping generations and cooperative care of young [15]; for eusocial mammals see [48,49].

Obligate social parasites: social insects that rely on the worker caste of another species to rear their brood, as they lack workers and produce only reproductive individuals. They invade the host nest, kill or subdue the resident queen and take over her breeding role [101].

Kin selection: indirect inclusive fitness obtained by the fitness of close relatives.

Mating success: effectiveness in securing one or more mates.

Manipulation: alteration of behaviour and/or physiology of other individuals for individual benefit (at the expenses of others). It has been initially addressed in parasites [10,102], where it is clear how the benefit to the parasite is detrimental to the host.

Facultative intraspecific parasitism: social insects of free-living species that invade the nest of a conspecific female and take over her breeding role [103] (see Box 2).

Policing: behaviour in social hymenopterans. In worker policing, workers remove and destroy eggs laid by other workers; also, queens can destroy eggs laid by workers.

Polygamy: one member of one sex mating with multiple members of the opposite sex. **Polygyny** (one male mating with multiple females) is more common than **polyandry** (one female mating with multiple males), as males are often less limited than females in the number of gametes they can produce/offspring they nurture (but this is not always the case for social insects, where males do not generally defend harems [104,105]); for females, increased reproductive success may depend more on getting help in rearing offspring rather than on multiple mating, as in **eusocial animals** (see [106] and current discussion on Bateman's principles [107]).

Reproductive skew: unequal partitioning of reproduction within a social group. In highly skewed societies, only one or few individuals reproduce, while the others delay or forgo reproduction completely.

Reproductive success: successful production of offspring. Can be calculated for breeding attempts, seasons, years or lifetime.

Sequential hermaphroditism: sex change. Each individual is able to produce gametes of the two sexes but not at the same time: they develop as one sex and later change to the opposite sex.

Simultaneous hermaphroditism: Each individual is able to produce gametes of the two sexes at the same time; with the exception of self-compatible species, they need a partner to reproduce.

Social monitoring: tracking signals and behaviours of other members of the group/population and adjusting behaviour and/or relationships appropriately.

Strategic growth: Adaptive plastic adjustment in body size as a function of social context [51].

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Silhouettes in figure 1 courtesy of: Cathy (peacock http://www.phylopic.org/image/631543cd-0e41-43b6-a325-335a06b2045e/), Christoph Schomburg (shrimp http://www.phylopic.org/image/aed2513d-2386-4218-b913-384838c0107b/), Steven Traver (naked mole-rat http://www.phylopic.org/image/7a7d8226-aa19-4f6f-8afa-f039cc860d7e/) Richard J. Harris (wasp http://www.phylopic.org/image/10daab45-21e7-4d2a-97e0-9809e0a3eb5b/), Mattia Menchetti (bee http://www.phylopic.org/image/b199a5f5-20c4-4cc9-9c54-1b51578c2487/), Lily Hughes (clownfish http://www.phylopic.org/image/ca160bcf-f2b8-4d2d-80bd-426f1f51be72/), Melissa Broussard (termite http://www.phylopic.org/image/188d20e7-a6da-4d7c-99e1-52935c2b0c6d/), Margot Michaud (mongoose http://www.phylopic.org/image/147096a8-7d0e-41ba-9301-f30dd06fbce5/), T. Michael Keesey (ant http://www.phylopic.org/image/c2ce58fd-bc12-4557-9617-c5c5e31f3820/; primate https://beta.phylopic.org/images/8856a7d8-eae6-4fdb-a4ad-9618ec066376; wild dog https://beta.phylopic.org/images/0bdb6532-0fa9-4ae7-992c-5b04a58d04d2); Anthony Caravaggi (bird https://beta.phylopic.org/images/e38c264a-8989-4e69-a6c1-7778b919980d); Christopher Kenaley (fish https://beta.phylopic.org/images/86c40d81-2613-4bb4-ad57-fb460be56ae5); Kai Caspar (primate https://beta.phylopic.org/images/cbfc863c-9ca3-441e-

9e38-95876fe19203). Photos in figure II are from the authors, unless otherwise specified: we are grateful to Nuno Vasco Rodrigues and Lukas Schärer for sharing their photos with us.

References

1 Darwin, C. (1871) *The descent of man: and selection in relation to sex*, John Murray, London, England

2 Keller, L. and Reeve, H.K. (1994) Partitioning of reproduction in animal societies. *Trends in Ecology & Evolution* 9, 98–102

3 Keller, L. and Perrin, N. (1995) Quantifying the level of eusociality. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 260, 311–315

4 Sherman, P.W. *et al.* (1995) The eusociality continuum. *Behavioral Ecology* 6, 102–108

5 Boomsma, J.J. (2013) Beyond promiscuity: mate-choice commitments in social breeding. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368, 20120050

6 Downing, P.A. *et al.* (2016) How to make a sterile helper. *BioEssays* 39, e201600136

7 Emlen, S.T. and Oring, L.W. (1977) Ecology, sexual selection, and the evolution of mating systems. *Science* 197, 215–223

8 Jandt, J. *et al.* (2014) Polistes paper wasps: a model genus for the study of social dominance hierarchies. *Insectes Sociaux* 61, 11–27

9 Charnov, E.L. (1982) *The Theory of Sex Allocation*, Princeton University Press.

10 Hughes, D.P. and Libersat, F. (2019) Parasite manipulation of host behavior. *Current Biology* 29, R45–R47

11 Wangensteen, O.S. *et al.* (2016) Reproductive strategies in marine invertebrates and the structuring of marine animal forests. In: Rossi S., Bramanti L., Gori A., Orejas Saco del Valle C. (eds) *Marine Animal Forests*. Springer, Cham

12 Lindenfors, P. *et al.* (2002) Phylogenetic analyses of sexual selection and sexual size dimorphism in pinnipeds. *Behavioral Ecology and Sociobiology* 52, 188–193

13 Brian, M. (1980) Social control over sex and caste in bees, wasps and ants. *Biological Reviews* 55, 379–415

14 Wheeler, D.E. (1986) Developmental and physiological determinants of caste in social Hymenoptera: evolutionary implications. *The American Naturalist* 128, 13–34

15 Faulkes, C.G. and Bennett, N.C. (2001) Family values: group dynamics and social control of reproduction in African mole-rats. *Trends in Ecology & Evolution* 16, 184–

190

16 Chak, S.T. *et al.* (2015) Social behaviour and recognition in decapod shrimps, with emphasis on the Caridea. In *Social Recognition in Invertebrates* pp. 57–84, Springer

17 Cant, M.A. (2014) Cooperative breeding. *The Princeton guide to evolution*

18 Robertson, D. (1972) Social control of sex reversal in a coral-reef fish. *Science* 177, 1007–1009

19 Warner, R.R. *et al.* (1996) Social control of sex change in the shelf limpet, *Crepidula norrisiarum:* size-specific responses to local group composition. *Journal of Experimental Marine Biology and Ecology* 204, 155–167

20 Preuschoft, S. and van Schaik, C.P. (2000) Dominance and communication. Conflict management in various social settings. In: *Natual conflict resolution*, Aureli, F. and De Waal, F.B.M (eds) pp. 77–105

21 Drews, C. (1993) The concept and definition of dominance in animal behaviour. *Behaviour* 125, 283–313

22 Davidian, E. *et al.* (2022) The eco-evolutionary landscape of power relationships between males and females. *Trends in Ecology & Evolution* 37, 706–718

23 Enquist, M. *et al.* (1990) A test of the sequential assessment game: fighting in the cichlid fish *Nannacara anomala*. *Animal Behaviour* 40, 1–14

24 Van Staaden, M.J. *et al.* (2011) Signaling aggression. In *Advances in genetics* 75pp. 23–49, Elsevier

25 Conte, Y.L. and Hefetz, A. (2008) Primer pheromones in social hymenoptera. *Annual Review of Entomology* 53, 523–542

26 Burmeister, S.S. *et al.* (2005) Rapid behavioral and genomic responses to social opportunity. *PLoS Biol.* 3, e363

27 Tibbetts, E.A. *et al.* (2022) The establishment and maintenance of dominance hierarchies. *Philosophical Transactions of the Royal Society B* 377, 20200450

28 Johnstone, R.A. (2000) Models of reproductive skew: a review and synthesis. *Ethology* 106, 5–26

29 Buston, P.M. *et al.* (2007) Reproductive skew and the evolution of group dissolution tactics: a synthesis of concession and restraint models. *Animal Behaviour* 74, 1643–1654

30 Nonacs, P. and Hager, R. (2011) The past, present and future of reproductive skew theory and experiments. *Biological reviews of the Cambridge Philosophical Society* 86, 271–98

31 Vehrencamp, S.L. (1983) Optimal degree of skew in cooperative societies. *American Zoologist* 23, 327–335

32 Johnstone, R.A. and Cant, M.A. (1999) Reproductive skew and the threat of eviction: a new perspective. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 266, 275–279

33 Buston, P.M. and Zink, A.G. (2009) Reproductive skew and the evolution of conflict resolution: a synthesis of transactional and tug-of-war models. *Behavioral Ecology* 20, 672–684

34 Johnstone, R.A. and Cant, M.A. (2009) Models of reproductive skew: outside options and the resolution of reproductive conflict. *Reproductive skew in vertebrates: proximate and ultimate causes*

35 Reeve, H.K. and Shen, S.-F. (2006) A missing model in reproductive skew theory: the bordered tug-of-war. *Proceedings of the National Academy of Sciences* 103, 8430–4

36 Faulkes, C. *et al.* (1990) Social suppression of ovarian cyclicity in captive and wild colonies of naked mole-rats, *Heterocephalus glaber. Reproduction* 88, 559–568

37 Fitzpatrick, J.L. *et al.* (2006) Male reproductive suppression in the cooperatively breeding fish *Neolamprologus pulcher. Behavioral Ecology* 17, 25–33

38 Godfray, H.C.J. (1991) Signalling of need by offspring to their parents. *Nature* 352, 328–330

39 Fletcher, D.J. and Ross, K.G. (1985) Regulation of reproduction in eusocial Hymenoptera. *Annual Review of Entomology* 30, 319–343

40 Van Oystaeyen, A. *et al.* (2014) Conserved class of queen pheromones stops social insect workers from reproducing. *Science* 343, 287–290

41 Keller, L. and Nonacs, P. (1993) The role of queen pheromones in social insects: queen control or queen signal? *Animal Behaviour* 45, 787–794

42 Oster, G.F. and Wilson, E.O. (1978) Caste and ecology in the social insects. *Monographs in Population Biology* 12, 1–352

43 Wenseleers, T. and Ratnieks, F.L. (2006) Enforced altruism in insect societies. *Nature* 444, 50–50

44 Oi, C.A. *et al.* (2015) The origin and evolution of social insect queen pheromones: novel hypotheses and outstanding problems. *BioEssays* 37, 808–821

45 Heinze, J. and d' Ettorre, P. (2009) Honest and dishonest communication in social Hymenoptera. *Journal of Experimental Biology* 212, 1775–1779

46 Cervo, R. *et al.* (2015) Visual recognition in social wasps. In *Social recognition in invertebrates* pp. 125–145, Springer

47 Strauss, K. *et al.* (2008) The role of the queen mandibular gland pheromone in honeybees (*Apis mellifera*): honest signal or suppressive agent? *Behavioral Ecology and Sociobiology* 62, 1523–1531

48 Houslay, T.M. *et al.* (2020) Benefits of cooperation in captive Damaraland mole-rats. *Behavioral Ecology* 31, 711–718

49 Buffenstein, R. *et al.* (2022) The naked truth: a comprehensive clarification and classification of current "myths" in naked mole-rat biology. *Biological Reviews* 97, 115–140

50 Watarai, A. *et al.* (2018) Responses to pup vocalizations in subordinate naked mole-rats are induced by estradiol ingested through coprophagy of queen's feces. *Proceedings of the National Academy of Sciences* 115, 9264–9269

51 Buston, P. and Clutton-Brock, T. (2022) Strategic growth in social vertebrates. *Trends in Ecology & Evolution* 37, 694–705

52 Hultgren, K. *et al.* (2017) Sociality in shrimps. In *Comparative social evolution* pp. 224–250, Cambridge University Press Cambridge

53 Chak, S.T.C. *et al.* (2015) Reproductive skew drives patterns of sexual dimorphism in sponge-dwelling snapping shrimps. *Proceedings of the Royal Society B: Biological Sciences* 282, 20150342

54 Leedale, A.E. *et al.* (2020) Cost, risk, and avoidance of inbreeding in a cooperatively breeding bird. *Proceedings of the National Academy of Sciences* 117, 15724–15730

55 Kokko, H. and Johnstone, R.A. (1999) Social queuing in animal societies: a dynamic model of reproductive skew. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 266, 571–578

56 Sorato, E. *et al.* (2012) Effects of predation risk on foraging behaviour and group size: adaptations in a social cooperative species. *Animal Behaviour* 84, 823–834

57 Nomano, F.Y. *et al.* (2015) Unrelated helpers neither signal contributions nor suffer retribution in chestnut-crowed babblers. *Behavioral Ecology* 26, 986–995

58 Raihani, N.J. and Clutton-Brock, T.H. (2010) Higher reproductive skew among birds than mammals in cooperatively breeding species. *Biology Letters* 6, 630–632

59 Magrath, R.D. and Heinsohn, R.G. (2000) Reproductive skew in birds: models, problems and prospects. *Journal of Avian Biology* 31, 247–258

60 Creel, S. *et al.* (1992) Behavioural and endocrine mechanisms of reproductive suppression in Serenge dwarf mongooses. *Animal Behaviour* 43, 231–245

61 Young, A.J. and Clutton-Brock, T. (2006) Infanticide by subordinates influences reproductive sharing in cooperatively breeding meerkats. *Biology Letters* 2, 385–7

62 Creel, S. (2022) A retrospective view of early research on dominance, stress and reproduction in cooperatively breeding carnivores. *Hormones and Behavior* 140, 105119

63 Kern, J.M. and Radford, A.N. (2018) Experimental evidence for delayed contingent cooperation among wild dwarf mongooses. *Proceedings of the National Academy of Sciences* 115, 6255–6260

64 Morris-Drake, A. *et al.* (2021) Experimental evidence for delayed post-conflict management behaviour in wild dwarf mongooses. *Elife* 10, e69196

65 Port, M. and Kappeler, P.M. (2010) The utility of reproductive skew models in the study of male primates, a critical evaluation. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews* 19, 46–56

66 Schiel, N. and Souto, A. (2017) The common marmoset: an overview of its natural history, ecology and behavior. *Developmental Neurobiology* 77, 244–262

67 Saltzman, W. *et al.* (2009) Reproductive skew in female common marmosets: what can proximate mechanisms tell us about ultimate causes? *Proc. Biol. Sci.* 276, 389–99

68 Utami, S.S. *et al.* (2002) Male bimaturism and reproductive success in Sumatran orang-utans. *Behavioral Ecology* 13, 643–652

69 Benvenuto, C. *et al.* (2017) Ecological and evolutionary consequences of alternative sex-change pathways in fish. *Scientific Reports* 7, 9084

70 Fishelson, L. (1970) Protogynous sex reversal in the fish Anthias squamipinnis (Teleostei, Anthiidae) regulated by the presence or absence of a male fish. *Nature* 227, 90–91

71 Munday, P.L. *et al.* (2006) Diversity and flexibility of sex-change strategies in animals. *Trends in Ecology & Evolution* 21, 89–95

72 Branconi, R. *et al.* (2020) Ecological and social constraints combine to promote evolution of non-breeding strategies in clownfish. *Communications biology* 3, 1–7

73 Fricke, H. and Fricke, S. (1977) Monogamy and sex change by aggressive dominance in coral reef fish. *Nature* 266, 830–832

74 Rueger, T. *et al.* (2018) Reproductive control via the threat of eviction in the clown anemonefish. *Proceedings of the Royal Society of London B: Biological Sciences* 285, 20181295

75 Brante, A. *et al.* (2016) The relationship between sex change and reproductive success in a protandric marine gastropod. *Scientific Reports* 6, 29439

76 Wong, M.Y.L. *et al.* (2007) The threat of punishment enforces peaceful cooperation and stabilizes queues in a coral-reef fish. *Proceedings of the Royal Society of London B: Biological Sciences* 274, 1093–9

77 Ross, R.M. (1990) The evolution of sex-change mechanisms in fishes. *Environmental Biology of Fishes* 29, 81–93

78 Rueger, T. *et al.* (2021) The next frontier in understanding the evolution of coral reef fish societies. *Frontiers in Marine Science* 8, 665780

79 Koene, J.M. (2017) Sex determination and gender expression: reproductive investment in snails. *Molecular Reproduction and Development* 84, 132–143

80 Schärer, L. and Ramm, S. (2016) Hermaphrodites. *The Encyclopedia of Evolutionary Biology* 2,

81 Picchi, L. and Lorenzi, M.C. (2019) Gender-related behaviors: evidence for a trade-off between sexual functions in a hermaphrodite. *Behavioral Ecology* 30, 770–784

82 Schleicherová, D. *et al.* (2006) How outcrossing hermaphrodites sense the presence of conspecifics and suppress female allocation. *Behavioral Ecology* 17, 1–5

83 Leonard, J.L. (2006) Sexual selection: lessons from hermaphrodite mating systems. *Integrative and Comparative Biology* 46, 349–367

84 Schärer, L. *et al.* (2015) Sexual conflict in hermaphrodites. *Cold Spring Harbor Perspectives in Biology* 7, a017673

85 Ah-King, M. and Nylin, S. (2010) Sex in an evolutionary perspective: just another reaction norm. *Evolutionary Biology* 37, 234–246

86 Shimoji, H. and Dobata, S. (2022) The build-up of dominance hierarchies in eusocial insects. *Philosophical Transactions of the Royal Society B* 377, 20200437

87 Patlar, B. *et al.* (2020) Seminal fluid-mediated manipulation of post-mating behavior in a simultaneous hermaphrodite. *Current Biology* 30, 143–149

88 Lodi, M. *et al.* (2017) High level of sperm competition may increase transfer of accessory gland products carried by the love dart of land snails. *Ecology and Evolution* 7, 11148–11156

89 Lodi, M. and Koene, J.M. (2017) Hidden female physiological resistance to male accessory gland substances in a simultaneous hermaphrodite. *Journal of Experimental Biology* 220, 1026–1031

90 Koene, J.M. *et al.* (2005) Piercing the partner's skin influences sperm uptake in the earthworm *Lumbricus terrestris. Behavioral Ecology and Sociobiology* 59, 243–249

91 Lhomme, P. and Hines, H.M. (2018) Reproductive dominance strategies in insect social parasites. *Journal of Chemical Ecology* 44, 838–850

92 Cini, A. *et al.* (2019) Inquiline social parasites as tools to unlock the secrets of insect sociality. *Philosophical Transactions of the Royal Society B* 374, 20180193

93 Bagnères, A.-G. *et al.* (1996) Chemical usurpation of a nest by paper wasp parasites. *Science* 272, 889–892

94 Lorenzi, M.C. *et al.* (2011) Facultative social parasites mark host nests with branched hydrocarbons. *Animal Behaviour* 82, 1143–1149

95 Lorenzi, M.C. *et al.* (2007) The chemical strategies used by Polistes nimphus social wasp usurpers (Hymenoptera Vespidae). *Biological Journal of the Linnean Society* 91, 505–512

96 Chassard-Bouchaud, C. and Hubert, M. (1976) On the fine structure of the regressing ecdysial glands of *Carcinus maenas* L. (Crustacea Decapoda) parasitized by *Sacculina carcini* Thompson. *Cell and Tissue Research* 167, 351–361

97 Taborsky, B. and Oliveira, R.F. (2012) Social competence: an evolutionary approach. *Trends in Ecology & Evolution* 27, 679–688

98 Reber, S.A. *et al.* (2013) Social monitoring via close calls in meerkats. *Proceedings of the Royal Society B: Biological Sciences* 280, 20131013

99 Booksmythe, I. *et al.* (2018) *Daphnia* females adjust sex allocation in response to current sex ratio and density. *Ecology Letters* 21, 629–637

100 Booksmythe, I. *et al.* (2017) Facultative adjustment of the offspring sex ratio and male attractiveness: a systematic review and meta-analysis. *Biological Reviews* 92, 108–134

101 Hölldobler, B. and Wilson, E.O. (1990) *The ants*, Belknap Press.

102 De Jong-Brink, M. and Koene, J.M. (2005) Parasitic manipulation: going beyond behaviour. *Behavioural Processes* 68, 229–233

103 Cervo, R. (2006) *Polistes* wasps and their social parasites: an overview. *Annales Zoologici Fennici*, 43, 531–549

104 Griffin, M.J. *et al.* (2019) Insect harem polygyny: when is a harem not a harem? *Behavioral Ecology and Sociobiology* 73, 40

105 Boomsma, J.J. (2007) Kin selection versus sexual selection: why the ends do not meet. *Current Biology* 17, R673–83

106 Ross, L. *et al.* (2013) Ecology, not the genetics of sex determination, determines who helps in eusocial populations. *Current Biology* 23, 2383–2387

107 Tang-Martínez, Z. (2016) Rethinking Bateman's principles: challenging persistent myths of sexually reluctant females and promiscuous males. *The Journal of Sex Research* 53, 532–559