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Opinion

Social regulation of reproduction: control or signal?

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Traditionally, dominant breeders have been considered to be able to control the reproduction of other individuals in multimember groups that have high variance in reproductive success/reproductive skew (e.g., forced sterility/coercion of conspecifics in eusocial animals; sex-change suppression in sequential hermaphrodites). These actions are typically presented as active impositions by reproductively dominant individuals. However, how can individuals regulate the reproductive physiology of others? Alternatively, all contestants make reproductive decisions, and less successful individuals self-downregulate reproduction in the presence of dominant breeders. Shifting perspective from a top-down manipulation to a broader view, which includes all contenders, and using a multitaxon approach, we propose a unifying framework for the resolution of reproductive skew conflicts based on signalling rather than control, along a continuum of levels of strategic regulation of reproduction.

Reproductive skew: an overview

'If each male secures two or more females, many males cannot pair' [1]

Inequality in mating success 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 disparity is extremely high, **reproductive skew**; see Glossary) is exacerbated in **cooperative animal societies** – in many highly social/**eusocial animals** (mammals, insects, crustaceans) only very few individuals in the group/colony reproduce [2] and the others (e.g., workers in eusocial animals, helpers in cooperative breeding birds and mammals) typically defend the nest and help to raise the young of the dominant breeder [3,4]). Less disproportionate skews are found in other breeding systems, along a continuum (Figure 1). Finally, noncooperative breeders (i.e., with no **alloparental care**) rely on permanent or temporary mating aggregations where, for example, a few males monopolize most mating events (harem polygyny).

The concept of reproductive skew typically implies some type of reproductive hierarchy, or rank order, in which a few individuals are the main, if not the only, breeders; they apparently prevent the reproduction of other individuals by imposing functional sterility, delaying their reproductive attempts, or – in sequential hermaphrodites – dictating the timing of sex change. In this view, reproductively less successful individuals pursue their own reproductive interests only (or mostly) when breeders die, leave, or are experimentally removed. If this is the case, how does a single individual, or a pair, control the reproductive physiology of many others? If

Highlights
Reproductive skew and variance in reproductive success describe uneven distributions of reproduction where disparity is extreme or smaller in extent, respectively, but remains relevant.

Theoretical reproductive skew models often assume allocation of reproduction under dominant control. We propose to revert this view and consider a bilateral decision rather than a top-down manipulation.

Strategic self-regulation of reproduction represents an evolutionary stable and parsimonious resolution of the conflict, where each individual makes reproductive decisions based on current social/ecological conditions. Less successful breeders can still gain indirect and/or future benefits.

We describe a unifying framework for understanding the uneven sharing of reproduction in animals from invertebrates to vertebrates, and from separate-sex animals to sequential and simultaneous hermaphrodites.

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the control works as an imposed 'contraceptive pill' [6], how can breeders avoid being affected themselves, and how can they avoid counteradaptations (arms races) by nonbreeders?

We provide a concise historical account of the evolutionary mechanisms behind reproductive skew, and revise the current interpretation of how reproductive skew is achieved. We suggest moving from a dominant-focused narrative to a broader one which includes the benefits reproductively subordinate individuals gain when they respond to **honest signalling** by dominant breeders and regulate their reproduction strategically. In other words, instead of an imposed control, where only breeders make decisions, we look for evidence of interactive use of signals (weapons, ornaments, **badges of status**) and/or other phenotypic traits, including posture and behaviour, which act as cues of, for example, fighting ability, motivational state, or health condition among the contestants. We finally address rare cases where true **manipulation** is likely to occur. Throughout our analysis we refer to control as an evolutionary mechanism of imposition, coercion, or manipulation (*sensu* [8]) where the breeder increases its fitness by means of any proximate mechanism which triggers changes in the reproductive output of another – the breeder receives reproductive advantages, the latter pays costs.

Using a multisystem and multitaxon approach, which considers different factors in the socioecological context (group size, sex ratio, territorial defence, relatedness, inbreeding avoidance, resource limitations), we propose a unified framework for a more parsimonious resolution of the reproductive conflict based on honest signalling and individual decision making rather than on top-down control. Contestants exchange signals which convey information about their respective qualities (e.g., fecundity, size, fighting ability) and allow informed reproductive decisions. Successful individuals (dominant breeders) gain direct immediate fitness benefits; subordinates can leave and breed elsewhere or remain for indirect and/or future benefits and/or use **alternative mating/reproductive tactics** [9,10]. When the relative quality assessment does not end with a consensus evaluation, the conflict escalates. If subordinates challenge the decision later on, then aggression, eviction, infanticide, and **policing** are used as retaliation against transgressive subordinates (acting as **social sanctions**).

Social control of reproduction

Sexual reproduction implies some level of interaction between individuals: even broadcast spawners rely on coordination between partners when they release their gametes in the environment. More complex interactions are found in increasingly complex social contexts where some individuals monopolise matings and increase their reproductive success, typically at the expense of same-sex rivals. Such monopolization is often based on some form of reproductive dominance, where, for example, alpha males sire most of the offspring and subordinate males attain limited reproductive success, mainly via **alternative mating tactics** [9,10] and/or female control (synchronous oestrous cycles [11] or post-mating cryptic choice [12]).

Typically, reproductive monopoly in resource/harem defence polygyny involves overt aggression (e.g., male elephant seals, *Mirounga angustirostris* [13]) and results in control of reproduction. However, in the scientific literature the term 'social control of reproduction' has gained a more specific meaning which goes beyond aggressive exclusion of sexual rivals from an area or mate. We find reference to social control in instances such as caste determination and/or reproductive conflict in social hymenopterans [14], mammals [15], crustaceans [16], cooperative

breeders [17], and sequential hermaphrodites [18]. The term 'social control' here typically implies a process that is actively initiated by dominant breeders which triggers temporary or permanent phenotypic (behavioural, morphological, and physiological, including hormonal) changes in group members, regulates their reproductive output, and ultimately determines the reproductive skew. However, what is dominance (Box 1)? Dominance/subordinance interactions imply that opponents meet, exchange signals, assess relative quality, and make decisions about their relative ranks. Why should we use this paradigm for resource competition and a different one, based on manipulation, for reproductive competition (*sensu* [19])?

Resolving the reproductive conflict

Reproductive skew implies that one or a few individuals gain a larger than average share of reproduction: this sets a reproductive conflict which would typically result in an actual contest (e.g., [13]). Initially, reproductive skew was strictly associated with the concept of complete control of reproduction by dominants, but this was later relaxed to partial control [2] (Box 1).

According to the 'social control' view, some individuals actively suppress the reproduction of others by means of aggression or chemical control, and/or by displaying phenotypic traits (e.g., visual, acoustical, behavioural, or morphological, including body size) that diminish the fertility of receivers. This hypothesis implies that breeders manipulate (*sensu* [8]) the reproductive physiology of others to their own fitness advantage. There have been strong debates about the magnitude of reproductive control and the proximate mechanisms of active suppression/inhibition of the reproductive potential of non-breeders. If acknowledgment of breeding dominance mitigates the conflict with limited costs with respect to overt aggression, then non-breeders become active players who self-limit their reproductive output in view of current/future, direct/indirect advantages, thereby making the best of a bad situation (see Table I in Box 1). Self-downregulation represents a (undeliberate) response that subordinates have evolved to the perception of their relatively poor competitive ability. The central question is therefore – do breeders directly control group reproduction, or do all contestants self-regulate reproduction in response to reciprocal cue/signal assessment? In other words, do breeders determine the reproductive output of the entire group, or do both breeders and non-breeders express strategic decision-making processes based on the assessment of their reciprocal qualities?

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

In the 1990s honest-signalling models started to emerge in different fields of behavioural sciences, and the evolutionary mechanisms underlying reproductive control were questioned in social insects. At that time, queens (reproductively dominant females) were considered to be capable of inhibiting worker reproduction via queen pheromones (i.e., chemicals) that directly manipulate worker reproductive physiology such that workers would behave in ways that increased queen fitness at their own expense [25]. In a now renowned paper, Keller and Nonacs [37] questioned this paradigm and asked whether queen pheromones, rather than manipulative agents, are honest signals of fertility. They proposed that workers, which do not mate but have functional ovaries, responded to queen signals by foregoing reproduction and gaining inclusive fitness benefits. They noted the lack of evidence that queen pheromones actively suppress worker reproduction and that valid alternative explanations are available; for instance, owing to **kin selection**, workers have genetic interests in preventing the reproduction of nestmate workers (worker **policing** [27,37]). Moreover, it was difficult to explain how queen pheromones were evolutionarily stable [37]: pheromonal queen control would have resulted

queens and/or other workers as the result of honest queen signalling, especially when the genetic interests of the queen and the workers are aligned.
Reproductive skew: unequal partitioning of reproduction within a group. In highly skewed societies, only one or few individuals reproduce and the others delay or forego reproduction.
Social monitoring: tracking the signals and behaviours of other members of the group/population and adjusting one's own phenotypic traits (e.g., behaviour, body size) accordingly.
Social parasitism: a form of parasitism where the parasites exploit the host workforce and/or parental care (with fitness costs for the host). This includes (i) facultative (intraspecific) social parasitism where, typically, a female of a free-living species adopts a parasitic lifestyle by usurping a conspecific female nest (e.g., the paper wasp *Polistes biglumis*; Box 2) and (ii) obligate (interspecific) social parasitism where, typically, parasites do not establish their colonies independently and the invasion of host colonies is the only available reproductive option. Some obligate social parasites do not produce a worker caste and rely on host workers to rear their offspring (e.g., *Polistes atrimandibularis*, a social parasite of *P. biglumis*).
Social sanction: any form of retaliation against dishonest signallers or subordinates who do not yield to other group members. Typically, social sanctions imply aggression, policing, infanticide, and/or group eviction.
Strategic growth: adaptive, plastic adjustment in body size as a function of social context.

General trend in relatedness

Variance in reproductive success

General trend in group size

Solitary breeders **Noncooperative breeders** **Cooperative breeders** **Eusocial breeders**
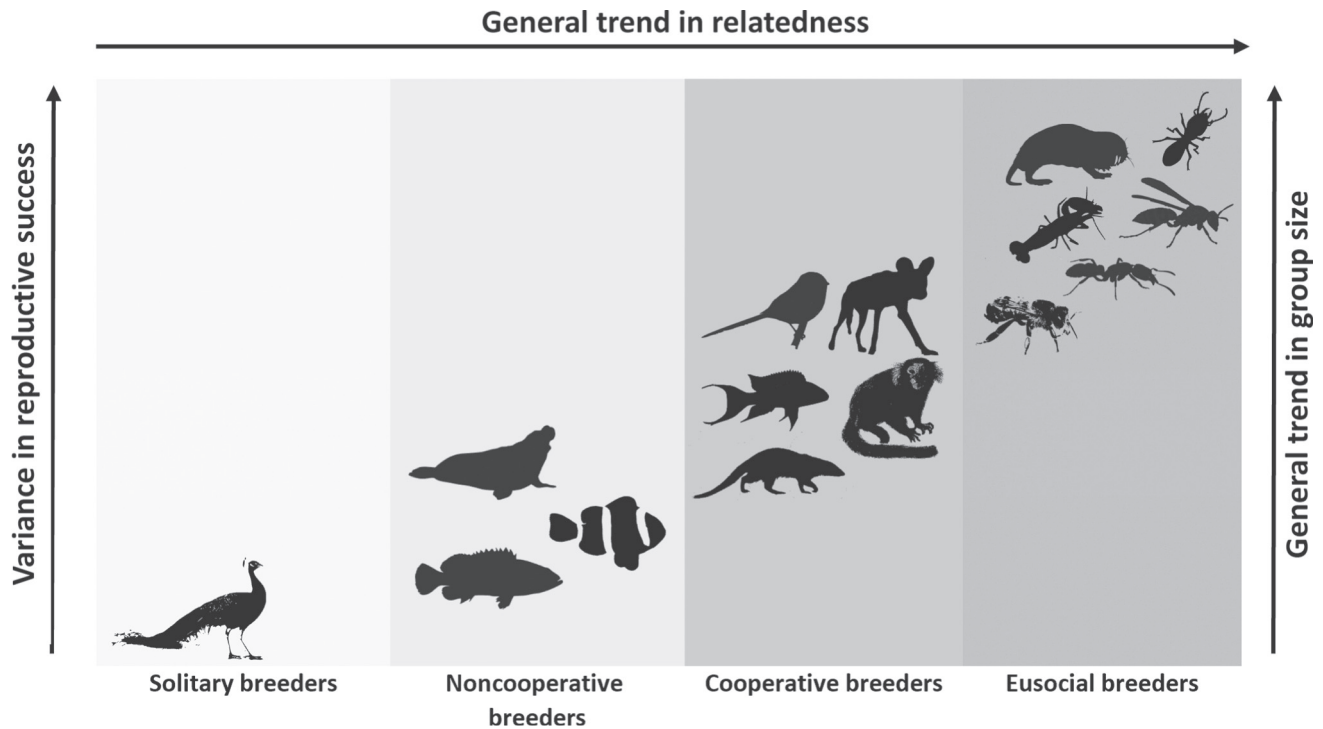
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Figure 1. Increasing levels of variance in reproductive success, up to reproductive skew (only one or a few individuals reproduce; top right corner), are common across taxa and breeding systems. Inequality in reproduction can be driven by high levels of relatedness (kin selection), especially in large groups/colonies (but see *Polistes* social wasps [5]). Mammals (here exemplified by naked mole-rats) are included as 'eusocial breeders', even if the criteria for eusociality are not fully satisfied for this group [6,7]. Silhouettes of representative examples (solitary breeders: *Pavo cristatus* peacocks; noncooperative breeders: *Epinephelus merra* honeycomb groupers, *Amphiprion clarkii* clownfish, *Mirounga angustirostris* elephant seals; cooperative breeders: *Neolamprologus pulcher* daffodil cichlids, *Callithrix jacchus* marmosets, *Aegithalos caudatus* long-tailed tits, *Lycaon pictus* African wild dogs, *Mungos mungo* banded mongooses; eusocial breeders: *Apis mellifera* honey-bees, *Polistes* wasps, ponerine ants, Termopsidae termites, *Synalpheus regalis* snapping shrimp, *Heterocephalus glaber* naked mole-rats).

in an arms race where selection would have favoured workers that resisted manipulation and, on the other side, queens that produced new control-effective doses and compounds [38] – whereas we now know that queen pheromones are highly conserved in Hymenoptera [39] (Table 1). Similarly, it was unclear how queen pheromones would have affected worker fertility without affecting that of the queen [37]. The change in perspectives on 'social control' of reproduction, that started in 1993 in social insects [37], has been limited to this taxon for a long time.

Change in perspective: from social insects to sequential hermaphrodites

The first theoretical evolutionary models of sex allocation in sequential hermaphrodites focused on individual advantage and addressed the relationship between body size and sex-specific fertility. The size-advantage hypothesis predicted that individuals change sex when they grow to a size where fertility in the second sex is higher than that in the first [72]. With increasing focus on the social context, dominant breeders of the second sex (which gain the highest reproductive output [73]) were expected to control groupmate timing of sex change to their own advantage (mirroring queen control of worker reproduction in social insects).

In female-first sex-changing fishes (protogynous, typically haremic [73]), this idea stemmed from simple experiments where removing the dominant male from the group 'allowed' the largest female to change sex and become male [74]. Because subordinates changed sex only after the removal of the dominant, it was inferred that dominants coercively kept subordinates in the reproductively less rewarding sex by physical intimidation and/or chemical manipulation [18] (Table 1). However, such proximate mechanisms are unpractical, particularly in large groups. Moreover, the largest female is not necessarily the one that changes sex [65], suggesting individual decision making.

A similar rationale was applied to some male-first sex-changing fishes (protandrous, typically monogamous [73]). Clownfishes live in symbiosis with anemones, a scarce resource: each anemone hosts a reproductive pair (a large female and her male partner) and smaller non-breeders. The removal of the female seemed to 'allow' the breeding male to become a female and the largest non-breeder to develop as the breeding male, suggesting top-down manipulation. However, remaining at the anemone and queuing for breeding positions is an adaptive choice associated with

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Box 1. Dominance and reproductive skew models

The term 'dominance' is broadly used to convey rank and identify winners (dominants) or losers (subordinates), where dominants gain priority access to limited resources [20]. We use the term 'dominant' here in the sense of 'dominant breeders' – individuals who achieve higher reproductive success than others. In many social contexts dominants express specific phenotypic trait values (in size, physical condition, fecundity, morphology, behaviour, or personality) and/or motivational states (e.g., winning/losing previous encounters) that contribute to the power asymmetry between contestants [21] as they display their fighting abilities and willingness to escalate the conflict (e.g., the fighting sequence in the cichlid *Nannacara anomala* [22] or the 'parallel walk' in red deer, *Cervus elaphus* [23]). Therefore, dominance/subordinance interactions imply active use of signals, reciprocal assessment, and decision making by each contestant.

Once ranks are established, individuals may further develop signals that advertise their rank (including badges of status [24]). In queenless ponerine ants, for instance, workers develop rank-specific odour profiles after establishing their ranks via fighting [25]; in the cichlid *Astatotilapia burtoni,* new reproductively dominant males develop bright colours and territorial behaviour minutes after gaining dominant status [26]. Once in place, high ranks and associated advantages may be enforced by retaliatory measures against transgressing subordinates (i.e., social sanctions such as displays, aggression, policing, infanticide, and group eviction [20,27]).

Reproductive skew models assume a game-theoretic decision in which, under dominant control, subordinates either acquiesce or leave the group [2]. Initial models were dominant-centred and based on group-living benefits, reproductive options outside the group (ecological constraints), and breeder/non-breeder relatedness (Table I).
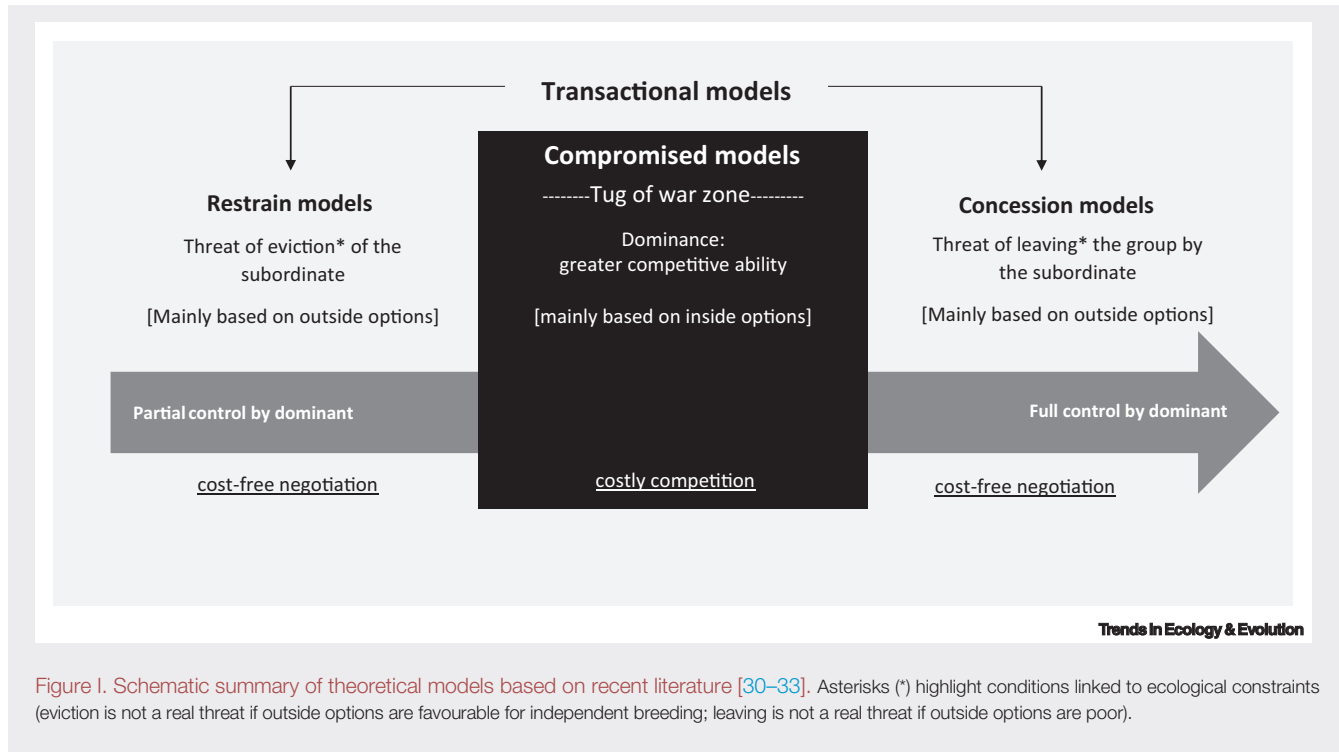
Dominant breeders retain subordinates by granting them reproductive concessions (transactional concession models), or subordinates give up part of their reproductive share (transactional restrain models) under the threat of eviction by dominant breeders [28]. The tug-of-war models instead imply that a compromise is reached based on the current competitive abilities of subordinates (Figure I). Combinations of transactional and compromise models (synthetic models [29,30]) which include ecological constraints and 'inside options' (costly competition) have been formulated, but overall the narrative is typically still focused on dominant breeder control [31–33].

It has been claimed that the application of theoretical reproductive-skew models to real data does not fully comply with the assumptions and/or predictions of the models and is of 'limited use for analysing individual strategies' [34], making the formulation of unifying skew models unlikely [35,36]. We propose here to replace dominant-centred reproductive skew models with a framework in which all individuals respond to cues/signals from their opponents and, given current outside options and within-group relatedness, make reproductive decisions.

Table I. Benefits of breeding in the social group (for reproductively dominant individuals) and staying in the social group and self-downregulating reproduction (for reproductively subordinate individuals) in contexts with some level of reproductive skew[a]

Contestant	Type of benefit	Benefit
Reproductively dominant	Direct	More partners/helpers increase dominant reproductive success
Reproductively subordinate	Indirect/current	Inclusive fitness (R) Inbreeding avoidance (R)
	Best of a bad situation/future	Queuing for breeding positions (EC) Mitigated aggression Eviction avoidance

[a]The table includes details on the variables included in early theoretical models: the option of breeding outside the group (ecological constraint, EC) and the relatedness between breeders and non-breeders (R), which implies kin selection (e.g., in eusocial insects) and/or inbreeding avoidance (e.g., in 'eusocial' mammals and cooperative-breeding birds).

Figure I. Schematic summary of theoretical models based on recent literature [30–33]. Asterisks (*) highlight conditions linked to ecological constraints (eviction is not a real threat if outside options are favourable for independent breeding; leaving is not a real threat if outside options are poor).

unfavourable outside options (see Table I in Box 1 and Table 1) [75], to the point that non-breeders stop growing and avoid challenging the breeding pair [76] (i.e., **strategic growth** [43]).

We propose that, in sequential hermaphrodites, selection has favoured individuals that make their reproductive decision (here, timing of sex change) after monitoring the social context and assessing relative sex-specific fertility (Table 1). The cues/signals used to assess relative breeding 'ranks' include phenotypic traits (body size, colouration, behaviour, etc.) and population sex ratio – so much that the timing of sex change is affected by overfishing which depletes fish populations of the largest individuals, typically belonging to the second sex [77]). Population density and sex ratio can also trigger alternative reproductive tactics; for example, males that opportunistically delay sex change when they receive high fitness returns in the first sex (e.g., in male-first *Crepidula* slipper snails [78]) and individuals that develop directly as the second sex [79].

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

According to sex allocation theory [80], simultaneous hermaphrodites are expected to adjust their allocation to the two sexual functions depending on mating opportunities [80,81]. Such an individual-benefit perspective has been largely applied (reviewed in [69,70]), and the relevant social cues/signals have been identified in some species (e.g., [82,83]). Instead, it was easier to explain the decision to change sex in sequential hermaphrodites (following dominant removal) as the result of the manipulation of some individuals by others. However, why should we apply different theoretical approaches to similar sexual systems in which individuals express their two sexes either simultaneously or sequentially – self-adjustment of sex allocation in simultaneous

Table 1. Comparison of the two contrasting hypotheses of signalling versus control using representative examples across multiple taxa[a,b]

	Signal hypothesis		Control hypothesis	
	Subordinates respond to dominants' signals by downregulating their reproductive output in their own best interest		Subordinates are manipulated to decrease their reproductive output against their own reproductive interests	
	Prediction	Evidence (or lack of)	Prediction	Evidence (or lack of)
Eusocial insects	Aligned genetic interests of queen and workers (kin selection) should select for workers that respond to queen pheromones as honest fertility signal; transgressing workers are socially sanctioned	Workers perform policing behaviours as the result of queen fertility signals (e.g., cuticular hydrocarbons) [27,37]	Contrasting fitness interests of queen and workers should select for chemical queen control of worker reproduction (irrespective of colony kin structure)	Chemical queen control is uncommon [39], except in parasitic relationships (see Box 2 in the main text for **social parasitism**; e.g., in *Polistes* wasps [40,41])
	Signals used in reproductive conflict should be honest and 'uncheatable' indices of fertility	Queen pheromones correlate with fertility in many species, supporting their 'honesty' as fertility signals [27]	If queen pheromones are manipulative agents that suppress worker reproduction, they should be uncorrelated with queen fertility	The mandibular 'queen substance' in honeybee is uncorrelated with fertility, but its function is unclear [42]
	Queen pheromones should be highly conserved across taxa because, being honest signals, they do not trigger any arms race	Queen pheromones have cross-activity across unrelated hymenopteran species, supporting highly conserved signalling [39]	Control pheromones should be constantly renewed during evolution to maintain effectiveness (as a consequence of the arms race where workers are selected for resisting manipulation and queens for overcoming worker resistance)	
'Eusocial' mammals	High within-group relatedness should result in individuals avoiding mating with relatives as a response to inbreeding avoidance (individual decision making)	Individuals avoid mating with related individuals [7]	If dominants suppress subordinate reproduction, a 'physiological block to reproduction' [15] should occur (e.g., via oestrogens produced by dominant females that affect non-breeders)	Ingestion of faecal oestrogens do not result in diminished fertility [6]
	If subordinate breeders gain direct benefits from group living and/or queuing for breeding positions, they should downregulate traits that trigger social sanctions	Because dominants are usually the largest individuals, subordinates strategically regulate their own body growth [43]		
Eusocial crustaceans	High within-group relatedness (e.g., via direct larval development and/or natal philopatry [44]) should result in individuals avoiding mating with relatives as a response to inbreeding avoidance (individual decision making)	There is support for colony-mate recognition (via kin recognition or familiarity [45]), a prerequisite for inbreeding avoidance	If breeders have control of worker reproduction, chemical mechanisms should be identified that inhibit worker gonadal maturation	No evidence of chemical mechanisms (also, some colonies have multiple queens, which questions the control abilities of breeders [46])
Cooperatively breeding birds	High within-group relatedness should result in individuals avoiding mating with relatives (inbreeding avoidance) as individual decision making	There is support for inbreeding avoidance [47,48]		
	Subordinate breeders should gain direct benefits from group living, especially if there are ecological constraints to dispersal and limited opportunity to meet mature, opposite-sex non-relatives;	Non-kin helpers gain future [49] and/or direct benefits [50] (group foraging, reduced predation risk [51]); social sanctions (e.g., infanticide) is used by both dominant and subordinate females, similarly		

Table 1. (continued)

	Signal hypothesis		Control hypothesis	
	Subordinates respond to dominants' signals by downregulating their reproductive output in their own best interest		Subordinates are manipulated to decrease their reproductive output against their own reproductive interests	
	Prediction	Evidence (or lack of)	Prediction	Evidence (or lack of)
	they should queue for breeding position	to policing in social insects [52]		
Cooperatively breeding carnivores	In females, age and body size should act as honest cues of reproductive dominance (only old and large females reproduce owing to the high energy costs of reproduction). Subordinates in good condition could reproduce (and elicit social sanctioning)	Subordinates sometimes reproduce [17]; dominant and other subordinate females retaliate by imposing social sanctions (e.g., infanticide) [53,54]	If the suppression of subordinate reproduction occurs via stress-related hormonal mechanisms, levels of adrenal glucocorticoids and/or gonadal steroids should be rank-dependent	Endocrine hormone levels do not always correlate with rank [54]
	If subordinate breeders gain direct benefits from group living and queue for breeding positions, they should monitor the social environment for replacing vacant positions	Evidence that social monitoring is widespread is emerging (e.g., in dwarf mongooses [55,56])	If subordinate breeders refrain from reproduction under threat of eviction and/or infanticide, they should be able to associate the long-term consequences of mating (becoming pregnant/giving birth) with aggressive retaliations occurring weeks/months after mating	
Social primates	Rank should be advertised by signals and/or badges of status	Flanged males in orang-utans and 'fatted' males in mandrills signal their dominant rank [57]	If subordinate breeders refrain from reproduction under threat of eviction and/or infanticide, they should be able to associate the long-term consequences of mating (becoming pregnant/giving birth) with aggressive retaliations occurring weeks/months after mating	
	Subordinate females should be socially sanctioned if they do not self-downregulate reproduction in response to cues/signals by the breeding pair	Infanticide [58] is a means of sanctioning transgressive subordinates	Subordinate reproduction should be inhibited via chemical mechanisms initiated by breeders	Suppression of ovulation in subordinate females (triggered by scent marking by dominants) and diminished sperm cell production in subordinate males [59] are used as evidence of suppression of subordinate (alternatively, they could result from self-downregulation after assessment of signals conveyed by scent marking)
Cooperatively breeding fishes	Low, but extant, within-group relatedness should favour group living and helping behaviour (kin selection) where non-breeders queue for breeding positions. Subordinate fish should downregulate traits that trigger social sanctions; all individuals should signal their quality and fighting ability	Partial support for kin selection theory [60]; subordinates strategically downregulate body growth and avoid aggression by (large) dominants [61]; chemical signals (urine) are used in territorial contests [62]	Dominants should chemically suppress subordinate reproduction	Smaller gonads in subordinates are used as evidence of reproductive suppression [63] but might be the consequence of self-downregulation in response to social cues

Table 1. (continued)

| | Signal hypothesis | | Control hypothesis | |
| | Subordinates respond to dominants' signals by downregulating their reproductive output in their own best interest | | Subordinates are manipulated to decrease their reproductive output against their own reproductive interests | |
	Prediction	Evidence (or lack of)	Prediction	Evidence (or lack of)
Sequential hermaphrodites: female-first sex-changing fishes	**Territorial harems**			
	Females (first-sex individuals) should self-delay/forego sex change in response to large-male signals; they should queue for the male breeding position	There is evidence of considerable display of visual cues [64]; signals or sanctions may be less effective at the group periphery, and this might explain why some females change sex even if the male is present [18]; the largest female does not necessarily change sex [65]	Sex change should be based on direct suppression by large dominant males	Dominant male removal triggers subordinate sex-change; some females at the group periphery (where control is weaker) change sex even if the male is present [18]
	Temporal spawning aggregations			
	Sex-change decisions should be based on the assessment of social factors such as population sex ratio and relative body size; sex change could be delayed if current reproductive output is high	The process of 'sex ratio induction' triggers sex change when mortality or recruitment changes the sex ratio of the group [66]. Once interpreted as social control, it may be regarded as signalling (via social monitoring)		
Sequential hermaphrodites: male-first sex-changing fishes	**Monogamy (under strong ecological constraints: e.g., limited territories/anemones)**			
	Subordinate breeders should gain direct benefits from group living; they should stay in the group and queue for replacing breeding positions. The need to stay in the group should select for the ability to opportunistically adjust a plethora of traits and signals which advertise reproductive condition (e.g., body size; other cues and signals)	Non-breeders downregulate their body growth and avoid aggression/eviction [43,67] Breeder/non-breeder clownfish use body size, behavioural displays, and UV-based visual signals in dominance/subordinance interactions [68]	Sex change should be based on direct suppression by the dominant breeding pair. If subordinate breeders give up reproduction under the threat of eviction, they should be able to associate sexual maturation with aggressive retaliation and the potential outcome of being evicted	
	Monogamy or random mating (no apparent strong ecological constraints)			
	Sex-change decisions should be based on the assessment of social factors such as population sex ratio and relative body size	The process of 'sex ratio induction' triggers sex change when mortality or recruitment changes the group sex ratio [66]. Once regarded as social control, it may be interpreted as signalling (via social monitoring)	Individuals should change sex as a response to social control	The process of 'sex ratio induction' triggers sex change when mortality or recruitment change group sex ratio [66]. Once regarded as social control, it may be interpreted as signalling
Simultaneous hermaphrodites	Individuals should change their sex allocation in response to social environment: in other words, they invest relatively more in one or the other sexual function depending on current mating opportunities	Individuals adjust their sex allocation to current mating opportunities [69,70]	Individual sex-allocation decisions should be affected by partners	Sperm donors manipulate the uptake and/or use of sperm by their partners, thus increasing their paternity share (e.g., antagonistic coevolution in snails, earthworms, and flat-worms [71]; see Box 2 in the main text)

[a]Following the work of Oi et al. [27] in social insects; see also Table 2 in [2].
[b]Predictions and instances of empirical evidence, when available, are reported. Empty boxes indicate absence of predictions or evidence.

hermaphrodites, but lack of it in sequential hermaphrodites? What proximate mechanisms would allow individuals of one sex to prevent sex change in others? Even if manipulation can indeed occur (simultaneous hermaphrodites not only provide an excellent playground to test decisions on partitioning of resources to male and female functions [84] but also provide examples of actual manipulation of reproduction [80]; Box 2), it often fails to explain sex-change decisions.

Concluding remarks

Animals constantly check their environment to obtain relevant social information and make decisions [91]. This includes constant **social monitoring** and consequent behavioural and physiological adjustments to current social context (e.g., [92,93]), even outside the species boundary [94]. Why would they not use the information obtained to also adjust their reproduction? Indeed, theoretical models and empirical studies show that individuals adjust their offspring number and sex ratio and/or sex allocation to current conditions [95]. However, somewhere along the way it became easier to consider non-breeder reproductive responses as manipulations imposed by breeders rather than individual decisions, even though evidence for the underlying proximate mechanisms was lacking (see Outstanding questions). Nonetheless, the use of signals rather than control is a more parsimonious and evolution-compatible perspective to explain the social regulation of reproduction. Active manipulation by dominant breeders (i) is not evolutionarily stable (a 'mutant' non-breeder who reproduces because it does not perceive/respond to manipulative agents would spread its genes to the next generation), (ii) would fuel arms races (breeders should increase the magnitude of the manipulative agents and/or change their nature – e.g., novel chemical compounds, behaviours, visual displays – to retain its effectiveness), and (iii) is less parsimonious because it requires that subordinates learn complex associations of the long-term potential consequences of mating (e.g., eviction or infanticide; see Table 1 for predictions for the control hypothesis as applied to social carnivores, primates, and sequential hermaphrodites). Finally, (iv) it fails to explain alternative reproductive tactics.

Box 2. The continuum of strategic regulation of reproduction

Reproductive conflicts can be graded along a continuum, and a multisystem and multitaxon approach is useful to broaden our understanding of their evolutionary mechanisms and resolutions (Figure I). In the perspective of variance in lifetime reproductive success, that extends to extreme reproductive skews in animal societies, the establishment and maintenance of dominant breeding positions [20] is the most relevant evolutionary mechanism to establish the actual share of reproduction – that is often considered to be the sole prerogative of winners. A change in perspective, with a focus on all contestants – who assess their reciprocal, honest signals and make strategic decisions based on current social context (including kinship and ecological constraints), provides a more parsimonious evolutionary mechanism of conflict resolution (Figure I).

Costly aggressive encounters are employed to establish reproductive hierarchies [13,20], often combined with signals/ritualized displays and assessment from both sides. Signalling mitigates costs because contestants assess their relative qualities and less successful individuals avoid fights by leaving and breeding elsewhere. If instead they remain, they can avoid challenging the dominant directly (strategic regulation of reproduction for indirect/delayed benefits) and/or adopt alternative routes to reproduction (including satellite behaviours, sneaky matings, coalitions, and alliances [36]). In our view, these tactics are neither concessions by dominants (as depicted in concession models) nor failures to refrain from reproduction (as depicted in restrain models). They are measurable outcomes of the strategic options of subordinates which can trigger retaliation through social sanctions.

At one end of the continuum, there are cases where one individual clearly increases its fitness at the expense of others. In simultaneous hermaphrodites, sperm donors manipulate the uptake and/or use of donated sperm by their partners, usually not without resistance, as reported in snails [85], earthworms [86], and flatworms [71]. These are real cases of intraspecific manipulation of reproduction that add to interspecific examples: obligate social insect parasites [40] invade the colony of another species, take over the reproductively dominant position using chemical deception, and manipulate the host reproductive output [40,87,88]. Interestingly, intraspecific (facultative) social parasites switch from signalling to manipulating depending on the context: free-living species of *Polistes* social wasps use cuticular compounds as honest signals of fertility in their own colonies, but use them as manipulative compounds if they behave as facultative social parasites in the nest of a conspecific female [41,89]. More extreme cases are parasites which castrate their hosts, such as the parasitic barnacle *Sacculina carcini* [90]).

Outstanding questions

What are the key experiments to discriminate between the signalling versus control hypotheses? The classical experiment of removing the reproductively dominant individual (s) from the group and measuring changes in the reproductive status of subordinates alters the social context and fails to discriminate between whether subordinates respond to the end of manipulation by the dominant individual or to the new social context. In fact, the challenging experiments necessary to distinguish between honest signalling and dominant control remain to be conducted. Could facultative social parasites (e.g., *Polistes* wasps or other social insects) or hermaphrodites be convenient model systems?

Why is within-species reproductive manipulation still observed, albeit in rare cases (see main text)? Can the 'strategic regulation of reproduction' view help to investigate the evolution of low-skew societies?

What are the proximate mechanisms underlying strategic regulation of reproduction? Are the mechanisms used consistently across taxa, mating systems, or ecological conditions? How are stress-related effects associated with the regulation of reproduction (i.e., is socially induced stress a form of control of reproduction)? Are stress-related effects associated with the regulation of reproduction consistent across taxa? If not, why?

Why is reproductive competition regulated via overt aggression in some taxa and via signalling/ displaying in others? Why is the relative importance of signals/display versus overt aggression different among taxa? Is this associated with the amount of social interaction (e.g., species that live in groups have evolved diverse types of signalling and displays, whereas those that interact and compete for relatively short time-periods have not)?

Can we trace the mechanisms underlying social sanctioning? How are transgressing signallers identified? What matched/mismatched cues/ signals allow such identification? What are the mechanisms that initiate

Figure I. Reproductive conflict across taxa and mating systems, from signalling to arms race (true manipulation). The resolution of competitive contests is mediated by honest signalling and aggression in different combinations (grey triangles). The exchange of honest signals between opponents has two different outcomes: (i) in the breeder-to-be, the assessment of its higher relative quality triggers the onset of a physiological status favourable to reproduction (or sex change in sex-changers); by contrast, (ii) in the non-breeder-to-be, the assessment of its lower relative quality triggers physiological changes which make reproduction (or sex change) unlikely. Social sanctions are used when the established reproductive ranks are not acknowledged/respected. Therefore, signal exchanges among contestants result in strategic self-regulation of reproduction (e.g., in female-first sex-changing fish, *Anthias squamipinnis*, as well as in termites), whereas mainly physical aggression occurs where signals have not evolved as a way to reduce direct contests – possibly because animals interact for limited time-periods, for example, in haremic-like groups (e.g., elephant seals, *Mirounga angustirostris*). Arms races (involving adaptations and counter-adaptations) occur, for example, in the simultaneously hermaphroditic snail *Cornu aspersum* and in the flatworm *Macrostomum lignano*, or in coevolving interspecific interactions (e.g., in the obligate social parasite *Polistes atrimandibularis*, here photographed with its host *Polistes biglumis*). Photo credits are given in the acknowledgments.

sanctioning (i.e., that underlie the association between perceiving mismatched cues/signals and attacking the dishonest signallers)? How fast should dishonest signallers be sanctioned? How fast should they conform to honest signalling? To what extent are social sanctions effective in bringing transgressing signallers back into line? Is there resistance to social sanctions? Are social sanctions involved in arms races? What are the conditions that allow honest signals to be used as agents of manipulation in different contexts?

Indeed, reproductively subordinate individuals and less successful breeders often choose to stay and forego/postpone reproduction [96] when leaving the group (or colony, nest, anemone, etc.), and breeding elsewhere is risky whereas staying increases their fitness either indirectly (via kin selection) or directly (by increasing survival chances, queuing for replacing breeding positions, or adopting alternative mating tactics). Similarly to the switch in perspective that occurred in social insects – from queen control to queen signals [37] – and following the recent revisitation of the social control of body size (**strategic growth** [43]), we propose here to consider 'social control of reproduction' as an adaptive response to the social context by all contestants and redefine it as 'strategic regulation of reproduction'. Our work broadens the applicability of the argument initiated for social insects to a large number of taxa where the effects of social environment on reproduction are apparent – from invertebrates to vertebrates, from separate-sex animals to sequential and simultaneous hermaphrodites. The use of the traditional dominant-focused view might obscure reproductive adaptations by limiting investigations into responses to cues and signals and into proximate mechanisms for self-downregulation of reproduction. The new perspective we propose results instead in a more parsimonious, evolutionarily stable, and comprehensive framework for understanding reproductive conflicts in animals.

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Declaration of interests

The authors declare no conflicts of interest.

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