

Reproductive Social Behavior: Cooperative Games to Replace Sexual Selection

Joan Roughgarden,^{1*} Meeko Oishi,² Erol Akçay¹

Theories about sexual selection can be traced back to Darwin in 1871. He proposed that males fertilize as many females as possible with inexpensive sperm, whereas females, with a limited supply of large eggs, select the genetically highest quality males to endow their offspring with superior capabilities. Since its proposal, problems with this narrative have continued to accumulate, and it is our view that sexual selection theory needs to be replaced. We suggest an approach that relies on the exchange of direct ecological benefits among cooperating animals without reference to genetic benefits. This approach can be expressed mathematically in a branch of game theory that pertains to bargaining and side payments.

A recent review of diversity in animal reproductive social behavior (1) raises questions about Darwin's 1871 theory of sexual selection (2). Unlike the theories of evolution through common descent and of evolutionary change by natural selection, Darwin's theory of sexual selection has continually drawn criticism from evolutionists, notably Huxley in 1938 (3). Darwin wrote "Males of almost all animals have stronger passions than females" and "the female... with the rarest of exceptions is less eager than the male... she is coy." Darwin explained these templates as resulting from females choosing mates who are "vigorous and well-armed... just as man can improve the breed of his game-cocks by the selection of those birds which are victorious in the cock-pit." He continues, "Many female progenitors of the peacock must... have... by the continued preference of the most beautiful males, rendered the peacock the most splendid of living birds."

Since 1871, sexual selection theory has often been restated (4), yet contemporary definitions share Darwin's central narrative: "We now understand... Males, who can produce many offspring with only minimal investment, spread their genes most effectively by mating promiscuously... Female reproductive output is far more constrained by the metabolic costs of producing eggs or offspring, and thus a female's interests are served more by mate quality than by mate quantity" (5). This narrative is taught in biology textbooks (6), is axiomatic to evolutionary psychology (7), and is broadcast in popular media (8).

¹Department of Biological Sciences, Stanford University, Stanford, CA 94305–5020, USA. ²Sandia National Laboratory, Post Office Box 5800, Albuquerque, NM 87185–1137, USA.

*To whom correspondence should be addressed. E-mail: joan.roughgarden@stanford.edu

The reproductive social behavior of most species has not been studied, but a great many of those that have been do not conform to Darwinian sexual-selection templates. We suggest that sexual selection is always mistaken, even where gender roles superficially match the Darwinian templates.

There are fundamental problems that universally undercut all applications of sexual selection theory to any species, including the contradiction between sexual selection's rationale and the reason for sexual versus asexual reproduction, the difficulty of sustaining a stable hierarchy of genetic quality within a gene pool in the face of continued directional selection for high-ranked genotypes, and the use of different fitness definitions for males and females. These and other fatal problems are detailed in the references accompanying table S1.

We think that the notion of females choosing the genetically best males is mistaken. Studies repeatedly show that females exert choice to increase number, not genetic quality, of offspring and not to express an arbitrary feminine aesthetic. Instead, we suggest that animals cooperate to rear the largest number of offspring possible, because offspring are investments held in common. We therefore propose replacing sexual selection theory with an approach to explaining reproductive social behavior that has its basis in cooperative game theory. We introduce a notion of allocating time into various relationships to maximize cooperative, or "team," fitness. In this theory, we can observe that diverse social organizations emerge from how individuals accrue direct benefits from the relationships they develop with one another within diverse ecological contexts.

Cooperative Games in Reproductive Social Behavior

Here, we explain reproductive social behavior in developmental time, not evolutionary time.

A social system develops from the interaction of individuals just as body parts develop from the interaction of tissues. In our model, each animal acts continually as an individual or as a team member, and the value of an action is scored by how it contributes to that animal's average fitness accumulation rate (9). An individual's actions involve obtaining and exchanging direct benefits to increase the number of offspring successfully reared (10–14). We further envision a future two-tier theory that will embed this phenotypic treatment within an overarching evolutionary-genetic model.

Maynard Smith introduced game theory to biology in the 1980s, including the evolutionary stable strategy (ESS), a population-genetic counterpart to the Nash competitive equilibrium (NCE) of game theory (15). A competitive game ends when an NCE is attained, i.e., the state where each player cannot better its position, given the positions of the other players. In competitive games, the players do not communicate.

In cooperative games, players make threats, promises, and side payments to each other; play together as teams; and form and dissolve coalitions. Cooperative games usually end up at different solutions to an NCE. Nash also investigated cooperative games and introduced the concept of a Nash bargaining solution (NBS) as an outcome of these games (16).

Logic of bargaining and side payments. To illustrate, consider a "payoff matrix" that indicates the direct benefit each player receives in every scenario (17):

		Player 2	
		A	B
Player 1	A	(2, 6)	(10, 5)
	B	(4, 8)	(0, 0)

In the upper left, for example, (2, 6) represents a benefit of 2 to player 1 and 6 to player 2 whenever player 1 does action A at the same time as player 2 also does action A. The symbols A and B may have different meanings for each player, because they may be different types of individual: one female and the other male, or one with territory and the other without. Individual competitive play in this example winds up at the lower left, an NCE, because player 2 always moves into the left column ($6 > 5$ and $8 > 0$), and, once in the left column, player 1 always moves down ($4 > 2$). This outcome does not result in cooperative play.

Once this NCE has been attained, player 1 observes it could attain a benefit of 10 if player 2 could be induced to play B when it plays A. Player 1 may therefore "threaten" player 2 by promising to play A, which will reduce player 2's benefit from 8 to 6. For this threat to be

credible, player 1 must demonstrate a willingness to suffer a loss itself from 4 to 2. In response to a credible threat, player 2 can negotiate to play B sometimes when player 1 is playing A, in return for player 1 not carrying out the threat too often. Conversely, player 2 can also counter-threaten player 1. These threats establish a “threat point,” i.e., the greatest benefit each can receive is when the other is playing to hurt its opponent the most. Nash suggested that the rational outcome of negotiation is the set of “coordinated” plays by both players acting together as a team that maximizes the “product” of the average benefits each player receives relative to its threat points. We call this product of individual fitnesses the team fitness function. Its maximum is the NBS.

Continuing from the NBS, player 1 may promise a side payment to player 2 to induce it to play B when player 1 plays A. If player 1 offers 4 to player 2, then the upper right entry of the payoff matrix becomes (6, 9). In this new game, the upper right is more profitable than the lower left to both players. The lower left remains an NCE, however, and the upper right becomes an NCE too. If the players find themselves in the lower left, they may agree to play jointly as a team, with player 1 playing A and player 2 playing B, which will then move them to the upper right. Assuming player 1 continues to honor the promised side payment, the upper right is stable even if the players sometimes dissolve into individual play, because the upper right is both an NCE and an NBS.

How might we use this logic to explain social behavior as a cooperative process? The economic and game-theoretic literature presents many models of bargaining tactics to attain an NBS (18–23). Here, we offer an approach tailored to how reproductive social behavior may develop.

State variables for social dynamics. We suppose each player has a time budget and can allocate a fraction of time into playing each strategy. We assume the animals continually adjust their time allocations into various social relationships to increase their average fitness accumulation rates. Suppose the animals are playing as individuals. If an animal is spending, say, 50% of its time doing A, which is more profitable than doing B, then in the next hour we assume it will increase the time spent doing A and reduce the time spent doing B. Meanwhile, the other animal is also adjusting its time allocations into its A and B actions. A social system then emerges from the simultaneous mutual adjusting of each player’s time allocations into the actions most profitable to themselves. When the players play independently, the two state variables are $p_1(t)$ and $p_2(t)$, which are the fractions of seconds during hour t that player 1 and player 2 each play their strategy A.

Alternatively, the animals may play jointly as a team. If the team is spending, say, 50% of

its time jointly playing AA, which is more profitable than playing AB, BA, or BB, the team will increase its fraction of time playing AA and reduce the time playing the other combinations. A mixed team strategy is quite possible too, in which the team plays a pair of combinations, say AB and BA, at some best ratio of time. Team play requires four state variables: $x_{AA}(t)$, $x_{AB}(t)$, $x_{BA}(t)$, and $x_{BB}(t)$ are the fraction of seconds during hour t that player 1 and player 2 jointly play each possible pair of strategies. When the animals form a team after playing as individuals or when the team dissolves into individual play after playing as a team, the dynamics for their time allocations switch from the equations that describe individual play to those that describe team play and vice versa, a problem in the optimal control of hybrid dynamical systems (24–27).

The direct benefits each receives from their interactions with the others are summarized in the payoff matrix whose entries are $w_{ij,k}$, which is the fitness accumulation rate obtained by player k when player 1 plays strategy i and player 2 plays strategy j .

Individual play dynamics. If the individuals independently adjust their time allocations to increase their own average fitness accumulation rates, then the time allocation dynamics consist of two coupled equations. Each individual adjusts its time allocation to climb the gradient of its own average fitness accumulation rate (28).

$$\frac{dp_i}{dt} = \frac{1}{w_i(p_1, p_2)} \left(\frac{\partial w_i(p_1, p_2)}{\partial p_i} \right) p_i (1 - p_i)$$

where $i \in \{1, 2\}$ and the individual average fitness accumulation rates are $w_i(p_1, p_2) = p_1 p_2 w_{AA,i} + p_1 (1 - p_2) w_{AB,i} + (1 - p_1) p_2 w_{BA,i} + (1 - p_1) (1 - p_2) w_{BB,i}$.

Team play dynamics. In team play, the team adjusts its time allocation into the four possible combination plays by climbing the gradient of the team fitness accumulation rate (29).

$$\frac{dx_{ij}}{dt} = \frac{1}{w_1(x_{AA}, x_{AB}, x_{BA}, x_{BB}) w_2(x_{AA}, x_{AB}, x_{BA}, x_{BB})} \times \left\{ \frac{\partial^* [w_1(x_{AA}, x_{AB}, x_{BA}, x_{BB}) w_2(x_{AA}, x_{AB}, x_{BA}, x_{BB})]}{\partial^* x_{ij}} \right\} \times x_{ij} (1 - x_{ij})$$

where $ij \in \{AA, AB, BA, BB\}$ and ∂^* is a directional partial derivative indicating that, as some variable is changed, the remaining variables alter in unison as a block in the opposite direction, preserving the sum of the $x_{ij}(t)$ equal to one. To form the team fitness accumulation rate, let v_i be the threat point to player i , i.e., player i ’s best fitness accumulation rate when the other player is playing to minimize it. The individual average fitness accumulation rates in light of the threat point are $w_i(x_{AA}, x_{AB}, x_{BA}, x_{BB}) = x_{AA}(w_{AA,i} - v_i) +$

$x_{AB}(w_{AB,i} - v_i) + x_{BA}(w_{BA,i} - v_i) + x_{BB}(w_{BB,i} - v_i)$ where $i \in \{1, 2\}$. The team fitness accumulation rate is then the product of these individual fitness accumulation rates.

Hence, in the scenario where individual play leads to the competitive solution (NCE) consisting of player 1 playing B and player 2 playing A, a payoff of 4 is yielded to player 1 and 8 to player 2 (Fig. 1). In contrast, team play leads to the bargaining solution (NBS), which consists of playing the combination AB about a quarter of the time and BA about three-quarters of the time, yielding a payoff of about 6 to player 1 and 7 to player 2.

Biological approaches to cooperation have relied on altruism theory and usually wrestle with how to prevent cheaters and free riders (30). The bargaining approach to cooperation does not suffer from difficulties with cheating. Should an animal decide not to cooperate, then the other party reverts to the threat point, which is worse for the noncooperator than the bargaining solution. Instead, the difficult issue for the cooperative game approach is whether the animals can carry out team play and can discern the team fitness function whose gradient they should climb. Many animal behaviors involving physical intimacy, such as grooming, traveling, and sleeping in close proximity, making reciprocal interlocking vocalizations, and same-sex and between-sex sexuality could all promote coordinated action. Further, we hypothesize that a sense of friendship resides in animal bonding, a joy or synergy in the spirit of cooperation that allows animals to sense and experience the product, not merely the sum, of their individual well-beings.

Economic approaches to cooperation have focused on repeated games. These encompass what are known as folk theorems, in which many kinds of equilibria are possible in infinitely repeated games, including mutually beneficial ones labeled “cooperative” (30–32). The classic example is the tit-for-tat strategy in the repeated prisoner’s dilemma game (33). In repeated games, one party can punish another. When players discern that certain moves lead to punishments, the individuals can wind up moving to a mutually beneficial equilibrium, creating the illusion of cooperation. Our dynamics constitute a repeated game too, because we assume the animals are playing continuously as they adjust their time allocations to actions A and B, if they are playing as individuals, or to AA, AB, BA, and BB, if they are playing as a team. The main difference between previous approaches and ours is how the game is played: Through reciprocal calls and physical intimacy, players perceive team fitness and act accordingly rather than play solely as individuals. Communication during courtship permits bargaining and promises of side payments. The distinction between our proposition and previous work is apparent in the use of the word “cooperative,”

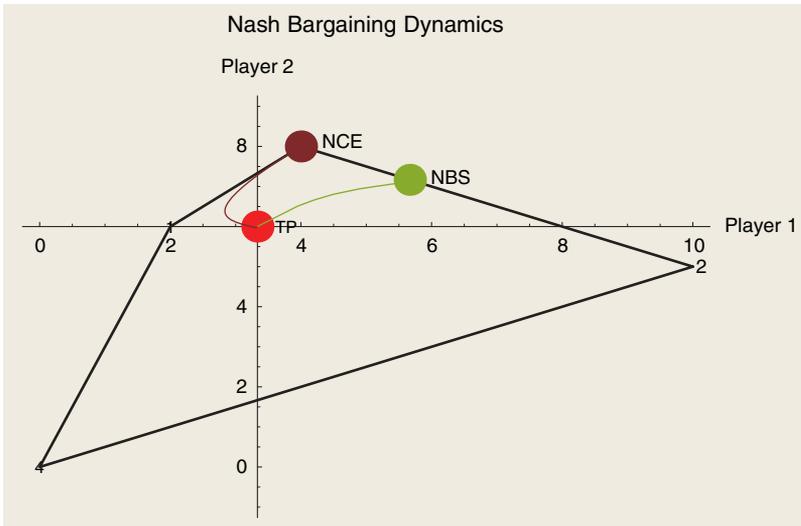


Fig. 1. Comparison of social system resulting from individual play versus team play. The corners of the polygon represent the fitness payoffs at the pure strategies (each player individually chooses to play one strategy 100% of the time). The origin is placed at the threat point (TP) of (2/3, 6) to player 1 and player 2, respectively. The trajectory of payoffs each player receives as the social system develops is depicted in brown for individual play and green for team play. Starting at the threat point, individual play culminates at the competitive-equilibrium social system (NCE) where player 1 always plays B and player 2 always plays A, yielding payoffs of 4 and 8, respectively. Starting from the same point, team play culminates at the bargaining-solution social system (NBS) where player 1 and player 2 jointly play AB 5/18 of the time and jointly play BA 13/18 of the time, yielding payoffs to player 1 and player 2 of 5.7 and 7.2, respectively.

which means only a mutually beneficial outcome in previous work but describes a process of perceiving and playing the game in our work.

Peacock wrasse game. Peacock wrasses (*Symphodus tinca*) live in shallow rocky habitat off the Corsican coast (34, 35). Females choose whether to lay eggs in a male’s nest or to broadcast their eggs over the sea floor. Males defending eggs against predators lose weight and suffer higher mortality. They abandon nests that haven’t accumulated many eggs. Abandoned eggs quickly attract predators. The following game may account for when a cooperative male-female association forms versus when male and female pursue their reproductive objectives independently:

		Male	
		Search	Stay
Female	Broadcast	(1, 1)	(0, 0)
	Deposit	(0, 0)	(2, 2)

The female can lay eggs in a territory and the male can remain there to guard them, forming a cooperative couple with both receiving the maximum fitness of 2. Alternatively, they may both remain single, with the female broadcasting her eggs on the sea floor and the male independently searching for them. If so, each receives a fitness of 1, reflecting the loss of some exposed eggs and

the failure of the male to find some of them. Or, the female could lay eggs in a territory that the male decides to abandon, resulting in a fitness of 0 for both. Conversely, the male could set up a territory that the female declines to lay eggs in, again resulting in a fitness of 0 for both because the female’s eggs spread over the ocean floor are not fertilized. Given this scheme of payoffs, what social system develops?

Under individual play, broadcast-search and deposit-stay are both locally stable Nash competitive equilibria. If we assume the noncooperative solution of broadcast-search is primitive, yielding a fitness of 1 to each, how can the peacock wrasse develop the cooperative solution of deposit-stay that will yield a fitness of 2 for each? Perhaps they bargain.

The female could deposit eggs in a territory-like space regardless of whether the male is there. She might lose them all, but she has driven the male’s fitness to 0. Conversely, the male might defend a territory without eggs. His fitness will be 0, but so will the female’s. Indeed, the threat point is (2/3, 2/3); the best the female can do if the male is trying to minimize her fitness and vice versa for the male. Because 2/3 is less than 1 that each is presently receiving, both need to alter their relationship. With courtship and intimate physical contact, they can synchronize activities and play as a team instead of as individuals. The dynamics of team play quickly converge to the cooperative solu-

tion of deposit-stay because this is the state with the highest team fitness. In this way, cooperative reproductive social behavior emerges from enlightened Darwinian self-interest.

Team play is not the only dynamic capable of reaching the deposit-stay equilibrium. This outcome is also the risk-dominant and payoff-dominant equilibrium (36, 37).

Oystercatcher game. In the Eurasian oystercatcher (*Haematopus ostralegus*), a sexually monomorphic wading bird common on mudflats, some reproductive groups consist of threesomes with one male and two females, whereas most consist of one male and one female (38–40). The threesomes occur in two forms, aggressive and cooperative.

In an aggressive threesome, each female defends her own nest, and the male defends a territory encompassing both females. The females lay eggs about two weeks apart. The females attack each other frequently throughout the day. The male contributes most of his parental care to the first-laid eggs, leaving the second nest often unguarded.

In a cooperative threesome, the two females share one nest; both lay eggs in it together, about one day apart; and all three birds defend it together. The females mate with each other frequently during the day, only slightly less often than they do with the male. The females also sit together and preen their feathers together.

How might cooperation instead of aggression develop in oystercatcher threesomes? Consider a three-player game with two females and one male. The benefit each player receives corresponds to the number of their own young successfully fledged. Each female has the option of befriending or attacking the other female. The male has the choice of providing care for offspring of female 1 or female 2. We list the payoffs and strategies in the order (female 1, female 2, male).

To develop the payoff matrix, first suppose male guards female 1’s nest and ignores female 2’s nest, unless both females share the same nest. When both females befriend each other, the brood consists of two offspring from each, corresponding to benefits of (2, 2, 4). Next, when female 1 attacks female 2, suppose the benefits are (3, 0, 3), indicating that female 1 benefits from male’s undivided attention and raises a brood of three eggs consisting only of her offspring, whereas female 2 loses everything because male is leaving her nest unguarded; meanwhile male sees his total payoff drop to three. Alternatively, if female 2 attacks female 1, then female 1 retains some of her eggs because of male’s protection, while female 2 can raise two eggs, resulting in payoffs of (1, 2, 3). The asymmetry, (3, 0, 3) and (1, 2, 3), highlights male’s care of only female 1’s offspring. Lastly, when the females attack each other, both suffer, resulting in payoffs of (1, 1, 2). This situation, where male

helps female 1, is summarized in the first matrix below, and a similar argument for when male helps female 2 leads to the second matrix below:

Male: help 1	Female 2	
	Befriend	Attack
Befriend	(2, 2, 4)	(1, 2, 3)
Female 1	Attack	(3, 0, 3) (1, 1, 2)

Male: help 2	Female 2	
	Befriend	Attack
Befriend	(2, 2, 4)	(0, 3, 3)
Female 1	Attack	(2, 1, 3) (1, 1, 2)

Four Nash competitive equilibria correspond to both females attacking each other, (attack, attack, help 1) and (attack, attack, help 2), and to the female without the male's support attacking the female who does have his support, (befriend, attack, help 1) and (attack, befriend, help 2).

The threat point for each player is found by assuming the other two players are playing jointly against them. For example, female 2's threat point is found from the following two-player game, in which a coalition's payoff is the sum of the payoffs to its members:

	Coalition of female 1 and male			
	Befriend, help 1	Befriend, help 2	Attack, help 1	Attack, help 2
Female 2	Befriend (2, 2, 4)	(2, 2, 4)	(3, 0, 3)	(2, 1, 3)
	Attack (1, 2, 3)	(0, 3, 3)	(1, 1, 2)	(1, 1, 2)

The female 1–male coalition can play four strategies, and female 2, two strategies. If this coalition plays to minimize female 2, it will move to the third column, (attack, help 1), and then the best female 2 can do is move to the bottom row, (attack), yielding her a payoff of 1. This is threat point against female 2, the best she can do in the worst case. This logic yields the following threat points for all individual players:

Coalition structure	Threat point
{Female 1, male} versus {female 2}	1
{Female 2, male} versus {female 1}	1
{Female 1, female 2} versus {male}	2

In a fully cooperative game, the three players choose their strategies jointly. The NBS max-

imizes the product of the three players' benefits. The NBS is to play (befriend, befriend, help 1) 50% of the time and (befriend, befriend, help 2) the remaining time. This solution is attained through team-play dynamics and represents the two females caring for their offspring jointly and the male splitting his efforts equally between the offspring of female 1 and female 2, as automatically occurs when both females share the same nest.

Conclusion

Cooperative game theory is the mathematical basis for social selection, an alternative to sexual selection theory (I). The key elements to social selection are: (i) Reproductive social behavior and sexual reproduction are cooperative. Sexual conflict derives from negotiation breakdown. In sexual selection, sexual conflict is primitive and cooperation derived, whereas in social selection sexual cooperation is primitive and conflict derived. Hence, sexual selection and social selection are mutually exclusive theories. (ii) Within reproductive social groups, organisms bargain and trade direct ecological benefits to maximize number of young reared. (iii) Reproductive groups are coalitions of one or both sexes that may include prezygotic "helpers," such as the white-collared male ruff and feminine male bluegill sunfish who assist in courtship, together with postzygotic helpers who assist in raising offspring. Families are reproductive groups whose participants share kinship. (iv) Secondary sex characters are social-inclusionary (SI) traits that permit participating in the species' social system, and exclusion is reproductively lethal. Two types of SI traits include (i) co-operation facilitators like mutual grooming and preening, interlocking vocalizations, between-sex and same-sex sexuality, and other intimacies promoting coordinated team play and the perception of team fitness and (ii) expensive, functionally useless badges like the peacock's tail that are admission tickets to monopolistic resource-controlling coalitions. Any imperfection in an admission ticket is the target of prejudice. In social selection theory, cooperation and team play coexist with prejudice and exclusion.

References and Notes

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5. J. Coyne, "Charm schools," *Times Literary Supplement*, 30 July 2004.
6. "Male birds are often beautiful; and the female of the species is a drab, camouflaged creature..."

[because] female birds just want to mate with males decked out in finery... Why have colorful appearances evolved so rarely [in animals other than birds]?... [because] flight may allow bird species to indulge the taste for gaudiness that many females apparently have (41)."

7. "Because women in our evolutionary past risked enormous investment as a consequence of having sex, evolution favored women who were highly selective about their mates... A man in human evolutionary history could walk away from a casual coupling having lost only a few hours of time (42)."
8. "Males fighting for females is the elastic in the jockstrap of evolution, therefore women are hardwired to 'size up' and appreciate male competition (43)."
9. An individual's rate of fitness accumulation is the integrand in the demographic formula for an animal's lifetime reproductive success, $R_0 = \int_0^{\infty} m(x)l(x) dx$. $m(x)$ is fecundity per time at age x , and $l(x)$ is the probability of living to age x or more; their product is a fitness accumulation rate. In developmental time, animals choose actions to increase their instantaneous $m(x)l(x)$. Lifetime fitness, R_0 , needed in evolutionary models, is the fitness accumulated during the expected lifespan.
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28. These equations resemble coevolution between two species, each with one haploid locus containing two alleles. Here, the notion of a "seconds pool" replaces that of a gene pool, profitable seconds beget more profitable seconds with haploid inheritance, and the time-allocation variables change as each individual climbs their own adaptive surface, by analogy to the adaptive topography metaphor of population genetics.
29. These equations resemble evolution within a single species at one haploid locus containing four alleles, where here the "seconds pool" replaces the gene pool.
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Supporting Online Material

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Table S1

References and Notes

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