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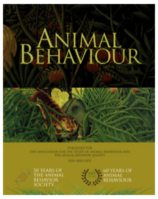

Review

Cooperating to compete: altruism, sexual selection and causes of male reproductive cooperation☆

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Competition among males for access to reproductive opportunities is a central tenet of behavioural biology that has critical implications for studies of mating systems, sexual selection and the evolution of numerous phenotypic traits. Given the expectation that males should compete vigorously for access to females, it may at first seem paradoxical that males in some species cooperate to reproduce, often resulting in the apparent sacrifice of direct fitness by some members of these cooperative partnerships. Because this form of cooperation lies at the interface between natural, sexual and kin selection, studies of the adaptive consequences of male reproductive cooperation may yield important insights into how complex and sometimes conflicting selective pressures shape individual behaviour. Here, we define and review examples of reproductive cooperation among male animals. We take an integrative approach to reviewing the potential causes of male–male cooperation, including potential adaptive hypotheses, ecological correlates, phylogenetic patterns and physiological mechanisms. The impact of male reproductive cooperation on sexual selection theory is also discussed. We conclude by outlining several important directions for future research, including efforts to improve understanding of the ecological and demographic contexts in which male reproductive cooperation occurs. Collectively, such analyses promise to improve our understanding of multiple fundamental concepts in evolutionary biology.

Classic sexual selection theory predicts that males should compete vigorously with one another for access to potential mates (Andersson, 1994; Bateman, 1948; Darwin, 1871; Dewsbury, 2005; Trivers, 1972). Such intrasexual competition is generally believed to be a powerful selective force that, in concert with female choice, has significantly shaped male phenotypes in most animal species (Andersson, 1994; Dale et al., 2007). In particular, reproductive competition among males is thought to have played a fundamental role in the evolution of traits such as morphological weaponry (Callander, Kahn, Maricic, Jennions, & Backwell, 2013), sexual dimorphism in body size (Andersson, 1994; Dale et al., 2007), and the highly conspicuous courtship displays observed in many species (Andersson, 1994; Petrie, Krupa, & Burke, 1999). A consistent expectation is that such traits are maintained because they increase the direct fitness of individual males.

Given the ubiquity of this expectation, biologists have long been intrigued by species in which males cooperate to secure access to mates. Such cooperation, which includes performing coordinated displays to attract females (peafowl, *Pavo cristatus*: Petrie et al., 1999; turkeys, *Meleagris gallopavo*: Krakauer, 2005; *Chiroxiphia* manakins: DuVal, 2007; Foster, 1981; McDonald & Potts, 1994), forming competitive coalitions to gain or defend access to females (dolphins, *Tursiops* sp.: Connor, Smolker, & Richards, 1992; lions, *Panthera leo*: Packer, Gilbert, Pusey, & Obrien, 1991) and even sharing parental care of the offspring of a single female (tamarins, *Saguinus* sp.: Díaz-Muñoz, 2011; Goldizen, 1987; humans, *Homo sapiens*: Crook & Crook, 1988; Smith, 1998), appears at first paradoxical because it is often associated with a loss of direct fitness for at least some participating males. Following the realization that indirect fitness benefits can explain apparently altruistic behaviour (Hamilton, 1963, 1964b), kin selection has frequently been invoked to explain such examples of reproductive altruism. Kin selection, however, cannot account for all occurrences of reproductive

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cooperation among males, most obviously in cases in which nonrelatives cooperate (Clutton-Brock, 2002). This raises intriguing questions about the ways in which natural selection, sexual selection and inclusive fitness interact to shape the reproductive behaviour of males. As more examples of reproductive cooperation have been examined, it has become clear that fitness consequences to males vary markedly among species (Canestrari, Marcos, & Baglione, 2005; Díaz-Muñoz, 2011; DuVal, 2007; Francisco, Gibbs, & Galetti, 2009; Kohda et al., 2009; Krakauer, 2005; Krakauer & DuVal, 2011; Wagner, Creel, Frank, & Kalinowski, 2007), suggesting a detailed, comparative exploration is needed to understand this phenomenon.

Because male reproductive cooperation stands at the intersection of sexual selection and inclusive fitness theory, it is integrally tied to some of the most active areas of research in evolutionary biology. However, male reproductive cooperation has received surprisingly little attention and has not, to our knowledge, been the subject of a general, synthetic review. More limited reviews were conducted on male cooperation in fish (Taborsky, 2009) and on cooperative displays in birds (Krakauer & DuVal, 2011). This review builds upon these papers by synthesizing the significance and exploring the taxonomic applicability of the concept of male reproductive cooperation. Specifically we aim to (1) define and summarize the multiple forms of male reproductive cooperation reported in the literature, (2) outline potential adaptive explanations for such cooperation, (3) explore the multifaceted 'causes' (ecological, demographic, phylogenetic, physiological) for male–male cooperation and (4) discuss the implications for sexual selection, in particular regarding patterns of variance in reproductive success and female mate choice. In addition to providing the first comprehensive review of male reproductive cooperation, this paper intends to enhance understanding of this phenomenon by outlining important directions for future research.

WHAT IS MALE REPRODUCTIVE COOPERATION?

We define male reproductive cooperation as occurring when two or more males, that would otherwise be (or are) reproductive competitors, engage in coordinated efforts to gain an advantage over other males in exclusive relation to reproduction. That is, males cooperate to attract, gain or maintain access to a female(s), or to assist her reproduction. Such coordination can include courtship displays, coalitionary aggression to defend or gain access to females or shared care of young. Our definition thus encapsulates the male reproductive cooperation outlined, but not explicitly defined, by Taborsky (2009) for fish. Individuals that cooperate to perform these activities accrue greater inclusive fitness than conspecifics that engage in these behaviours on their own. In this regard, our definition is consistent with the classic ecological concept of cooperation, which consists of interactions in which both participants benefit (Lidicker, 1979). The magnitude of these benefits, however, may not be equal. In particular, because benefits are assessed in terms of inclusive fitness, individual males may gain from cooperating even though they engage in reproductive altruism, meaning they appear to forgo direct fitness as a member of a cooperative male partnership.

We have deliberately set a broad definition for male reproductive cooperation. The key elements of our definition are that males are potential reproductive competitors and that they coordinate their cooperative behaviour. Future quantitative studies may wish to include or exclude the behaviours described herein depending on the question they address. Previous studies have reviewed and explained cooperation among males, but they were restricted to a single taxon (fish: Taborsky, 2009) or specific cooperative behaviour (competitive coalitions: Olson & Blumstein, 2009). In contrast, we emphasize the breadth of cooperative behaviours observed among males as well as the diversity of taxa involved to facilitate a more comprehensive exploration of this behaviour, given that it does not fit typical sexual roles emphasized in the literature.

Types of Male Reproductive Cooperation

To clarify our definition, we outline a few broad categories of male reproductive cooperation and consider both examples that fit our definition and those that do not. We note that our categories closely parallel the four types of cooperative reproduction proposed by Taborsky (2009) for fish.

Cooperative display coalitions

Cooperative display coalitions occur when two or more males congregate and coordinate their behaviours to attract and mate with females. Males within a display group are potentially forgoing solo display to attract females and may not have the chance to mate while they hold subordinate status. For example, manakins in the genus *Chiroxiphia* engage in elaborate multimale leapfrog dances to attract females (DuVal, 2007; McDonald, 1989a), and similar coordinated displays may be common in this family (Ryder, Blake, Parker, & Loiselle, 2011; Ryder, McDonald, Blake, Parker, & Loiselle, 2008). Other examples include wild turkeys (Krakauer, 2005) and peafowl (Petrie et al., 1999).

Competitive coalitions

Competitive coalitions occur when two or more males join forces to combat other males vying for access to a female. Perhaps the most familiar example of cooperative intrasexual competition for mates occurs in African lions, *Panthera leo*; males form coalitions to compete for access to females and the victor(s) of such contests mate with pride females. Males that form coalitions probably benefit by improving their chances of winning aggressive contests with competitors (relative to fighting alone), but they pay the certain cost of sharing breeding opportunities with females. This behaviour is also observed in feral horses, *Equus caballus* (Feh, 1999), dolphins (Connor et al., 1992) and baboons, *Papio cynocephalus anubis* (Bercovitch, 1988).

Our definition generally excludes male coalitions that are formed primarily to gain access to resources or to increase social rank. While these coalitions are sometimes shown to increase reproductive success, they typically do so secondarily, meaning they are the result of rank and not cooperative behaviour, and their reproductive benefits commingle with other survival benefits such as food and territory. Following this reasoning, male red howler monkeys, *Alouatta seniculus*, that form coalitions to gain access to and defend females (Pope, 1990) engage in male reproductive cooperation. In contrast, male macaques, *Macaca assamensis*, that form coalitions to ascend an intragroup dominance hierarchy do not meet our definition, even though they may increase their fitness as a consequence of their new rank (Schülke, Bhagavatula, Vigilant, & Ostner, 2010).

Cooperative polyandry

Cooperative polyandry is a breeding system in which two or more males mate with a single female and assist in rearing her young. For instance, male *Saguinus* tamarins, which are usually relatives, mate with a single female and carry dependent young (Díaz-Muñoz, 2011; Huck, Löttker, Böhle, & Heymann, 2005; Suarez, 2007). Other examples include Galapagos hawks, *Buteo galapagoensis* (Faaborg et al., 1995), some acorn woodpecker, *Melanerpes formicivorus*, groups (Haydock & Koenig, 2003), and certain human cultural groups from the Himalayas (Crook & Crook, 1988; Levine & Silk, 1997).

Cooperative parental care

Cooperative parental care occurs in species in which males engage in cooperative parental care, mate and gain paternity but do not form a polyandrous relationship with the female. These males are not helpers in the cooperative breeding sense (nonbreeding members, usually from previous brood: Cockburn, 1998; Skutch, 1935; Solomon & French, 1997), but instead are co-breeders (Dickinson, 2004) that may or may not have a social relationship with breeding females (i.e. a pair bond). For instance, subordinate males may assist a socially monogamous pair, as exemplified by immigrant male meerkats that compete for breeding opportunities and participate in brood care within a group (Griffin et al., 2003). Males may also provide care to offspring of multiple group females independent of social bonds. For example, male *Crotophaga* anis are socially monogamous, but multiple pairs share a nest (a crèche); all males sire young and provide care for nestlings (Riehl, 2012). Other examples include wild dogs, *Lycaon pictus* (Creel & Creel, 2002), pollinator fig wasps, *Kradibia tentacularis* (Suleman, Raja, & Compton, 2012), spider mites, *Schizotetranychus celarius* (Saito, 1986), and some populations of white-winged choughs, *Corcorax melanorhamphos* (Heinsohn, Dunn, Legge, & Double, 2000).

In contrast to co-breeders, nonbreeding male 'helpers' in cooperatively breeding societies do not fit our definition of male reproductive cooperation because they are not reproductive competitors. We realize designating individuals as reproductive competitors can be challenging, particularly in cooperative societies; this difficulty applies to many complex breeding groups (e.g. Hauber & Lacey, 2005). We emphasize the distinction between nonbreeding helpers and co-breeders, because these terms are often confused in the literature, and only the latter fall within our definition, provided there is coordinated cooperative behaviour.

Mutual tolerance and mate sharing

Mutual tolerance and mate sharing occur when two males share a territory and female, which they collectively, but often separately, defend. This behaviour is asocial and the only coordination evident is mutual tolerance by males. This pattern is observed in striped hyaenas, *Hyaena hyaena*, in which two males defend a territory containing a female; both males mate in the absence of a social relationship (Wagner, Frank, & Creel, 2008). Similar 'asocial polyandry' have been reported for kinkajous, *Potos flavus* (Kays & Gittleman, 2001), side-blotched lizards, *Uta stansburiana* (Sinervo & Clobert, 2003) and cheetahs, *Acinonyx jubatus* (Caro, 1994).

This type of male–male cooperation pushes the boundaries of our definition in that the behaviour is in essence asocial and coordination is minimal (i.e. males do not attack each other). Furthermore, behaviours in this category likely entangle survival benefits for males. However, we concur with Olson and Blumstein (2009), that cooperation between males is probably a continuum, with tolerance at one end of the spectrum and obligate joint participation at the other. Because intermediate forms of behaviour may be highly informative regarding the evolution of male–male cooperation, we have chosen to adopt a less restrictive perspective and to include mutual tolerance in our discussion.

We present the categories above as a heuristic tool to organize the broad array of behaviours encompassed by male reproductive cooperation. These categories may form interesting units of analysis in their own right. For example, the role of social and environmental factors in shaping competitive male coalitions has been evaluated by Olson and Blumstein (2009). Such analyses, to our knowledge, have not been conducted for cooperative polyandry, cooperative male parental care or cooperative male displays, leaving ample room for future study. Although some readers may view these categories as distinct phenomena, we believe that the overarching theme of male reproductive cooperation serves to unite these elements of male behaviour and may also be productively analysed.

WHO COOPERATES?

Occurrence of Male Reproductive Cooperation in Vertebrates

Male reproductive cooperation has not, to our knowledge, been systematically defined or categorized across taxa (but see Taborsky, 2009). Thus, to find peer-reviewed papers documenting examples of male reproductive cooperation, we conducted searches in ISI Web of Knowledge and Google Scholar to obtain the following exact phrase matches: 'male cooperation', 'cooperative polyandry', 'male alliance', 'male coalition', 'cooperative display', 'male mate sharing', 'male mutual tolerance'. If these searches yielded no results, we searched for any combination of the terms. Searches in Web of Science included the topic field, which examines article title, keywords and abstract. Google Scholar searches involved full text where available. In addition, for papers describing male reproductive cooperation, we examined associated references and cited articles to locate additional examples.

Table 1 details the examples identified by our searches and was used to generate figures in this manuscript. Although we attempted to be exhaustive, this list likely omits some species, because the descriptions of male behaviour may employ terminology not included in our search parameters. We expect that as researchers become more aware of the possibility of male cooperation, examples previously overlooked will be identified and we encourage interested researchers to build on the data set complied for this review.

THE WHY AND HOW OF COOPERATION

The 'cause' of any behaviour is complex and can be examined from a variety of perspectives depending upon the questions being examined. Following Tinbergen (1963), we view these different perspectives as nonexclusive, often complementary, explanations. Below, we explore proposed explanations for male reproductive cooperation using multiple levels of analysis (Sherman, 1988), both proximate and ultimate, and suggest areas for future research.

Fitness Benefits

Male reproductive cooperation may involve the apparent sacrifice of direct fitness by at least some members of cooperative partnerships. This apparent reproductive altruism parallels that found in many cooperatively breeding societies, leading to the logical application of inclusive fitness theory (Hamilton, 1964a), summarized by Brown (1987).

Indirect fitness benefits

Indirect fitness benefits may at least partially compensate males for apparent losses in current (or future) direct fitness benefits. A classic example of kin selection involves pairs of male wild turkeys that display together to attract females (Watts & Stokes, 1971). This would seem to impose a cost, as male wild turkeys can display and mate on their own. However, pairs are more successful at mating and siring chicks, and although only one member of the pair sires young, the second male is closely related and accrues greater fitness benefits than solo males (Krakauer, 2005).

Delayed (or future) fitness benefits

Delayed (or future) fitness benefits may lead to increased lifetime fitness despite current losses of reproductive opportunities. Such delayed benefits may be particularly relevant in cases in

Table 1
The diversity of animal species in which males engage in reproductive cooperation, as reported in the peer-reviewed literature

Species	Group	Order	Family	Type of male reproductive cooperation	Source
Chiroxiphia linearis	Birds	Passeriformes	Pipridae	Display	McDonald and Potts (1994)
Chiroxiphia lanceolata	Birds	Passeriformes	Pipridae	Display	DuVal (2007)
Chiroxiphia caudata	Birds	Passeriformes	Pipridae	Display	Foster (1981); Francisco et al. (2009)
Chiroxiphia pareola	Birds	Passeriformes	Pipridae	Display	Loiselle et al. (2006)
Pipra filicauda	Birds	Passeriformes	Pipridae	Display	Ryder et al. (2008, 2011)
Pipra fasciicauda	Birds	Passeriformes	Pipridae	Display	Robbins (1983)
Pipra serena	Birds	Passeriformes	Pipridae	Display	Prum (1985)
Meleagris gallopavo	Birds	Galliformes	Phasianidae	Display	Krakauer (2005); Watts and Stokes (1971)
Pavo cristatus	Birds	Galliformes	Phasianidae	Display	Petrie et al. (1999)
Moxostoma carinatum	Fish	Cypriniformes	Catostomidae	Display	Hackney, Tatum, and Spencer (1968)
Etheostoma blennioides	Fish	Perciformes	Percidae	Display	Fahy (1954)
Gallinula mortierii	Birds	Gruiformes	Rallidae	Cooperative polyandry	Goldizen, Buchan, Putland, Goldizen, and Krebs (2000); Goldizen, Putland, and Goldizen (1998); Maynard Smith and Ridpath (1972)
Prunella collaris	Birds	Passeriformes	Prunellidae	Cooperative polyandry	Davies et al. (1995); Hartley et al. (1995)
Sericornis frontalis	Birds	Passeriformes	Acanthizidae	Cooperative polyandry	Magrath and Whittingham (1997); Whittingham, Dunn, and Magrath (1997)
Melanerpes formicivorus	Birds	Piciformes	Picidae	Cooperative polyandry	Haydock and Koenig (2002)
Buteo galapagoensis	Birds	Falconiformes	Accipitridae	Cooperative polyandry	DeLay et al. (1996); Faaborg et al. (1995)
Eclectus parrots	Birds	Psittaciformes	Psittaculidae	Cooperative polyandry	Heinsohn, Ebert, Legge, and Peakall (2007)
Prunella modularis	Birds	Passeriformes	Prunellidae	Cooperative polyandry	Burke, Davies, Bruford, and Hatchwell (1989); Davies, Hatchwell, Robson, and Burke (1992)
Porphyrio porphyrio	Birds	Gruiformes	Rallidae	Cooperative polyandry	Craig and Jamieson (1990); Lambert, Millar, and Jack (1994)
Gallinula tenebrosa	Birds	Gruiformes	Rallidae	Cooperative polyandry	Garnett (1980)
Psophia leucoptera	Birds	Gruiformes	Psophiidae	Cooperative polyandry	Eason and Sherman (1995); Sherman (1995)
Corvus corone corone	Birds	Passeriformes	Corvidae	Cooperative polyandry	Baglione, Canestrari, Marcos, and Ekman (2003); Canestrari et al. (2005)
Corvus brachyrhynchos	Birds	Passeriformes	Corvidae	Cooperative polyandry	Townsend, Clark, McGowan, and Lovette (2009)
Gypaetus barbatus	Birds	Falconiformes	Accipitridae	Cooperative polyandry	Bertran, Margalida, and Arroyo (2009)
Cyanocorax morio	Birds	Passeriformes	Corvidae	Cooperative polyandry	Williams (2004)
Catharacta lonnbergi	Birds	Charadriiformes	Stercorariidae	Cooperative polyandry	Millar et al. (1994)
Melierax canorus	Birds	Falconiformes	Accipitridae	Cooperative polyandry	Malan (2005)
Calcarius pictus	Birds	Passeriformes	Calcariidae	Cooperative polyandry	Briskie (1992); Briskie, Montgomerie, and Põldmaa (1998)
Saguinus fuscicollis	Mammals	Primates	Callitrichinae	Cooperative polyandry	Goldizen, Mendelson, Van Vlaardingen, and Terborgh (1996); Terborgh and Goldizen (1985)
Saguinus mystax	Mammals	Primates	Callitrichinae	Cooperative polyandry	Huck, Löttker, and Heymann (2004); Huck, Löttker, Böhle, et al. (2005); Huck, Löttker, Heymann, et al. (2005)
Saguinus labiatus	Mammals	Primates	Callitrichinae	Cooperative polyandry	Suarez (2007)
Saguinus geoffroyi	Mammals	Primates	Callitrichinae	Cooperative polyandry	Díaz-Muñoz (2011)
Leontopithecus rosalia	Mammals	Primates	Callitrichinae	Cooperative polyandry	Baker, Dietz, and Kleiman (1993)
Symphalangus syndactylus	Mammals	Primates	Hylobatidae	Cooperative polyandry	Lappan (2007, 2008)
Homo sapiens	Mammals	Primates	Hominidae	Cooperative polyandry	Crook and Crook (1988); Levine and Silk (1997); Smith (1998)
Julidochromis transcriptus	Fish	Perciformes	Cichlidae	Cooperative polyandry	Kohda et al. (2009)
Chalinochromis brichardi	Fish	Perciformes	Cichlidae	Cooperative polyandry	Awata, Munehara, and Kohda (2005)
Neolamprologus pulcher	Fish	Perciformes	Cichlidae	Cooperative polyandry	Balshine-Earn, Neat, Reid, and Taborsky (1998); Dierkes, Heg, Taborsky, Skubic, and Achmann (2005); Dierkes, Taborsky, and Achmann (2008); Stiver, Dierkes, Taborsky, Lisle Gibbs, and Balshine (2005)
Julidochromis ornatus	Fish	Perciformes	Cichlidae	Cooperative polyandry	Awata et al. (2005); Awata, Heg, Munehara, and Kohda (2006)
Crotophaga major	Birds	Cuculiformes	Cuculidae	Cooperative parental care	Riehl (2011, 2012)
Corcorax melanorhamphos	Birds	Passeriformes	Corcoracidae	Cooperative parental care	Heinsohn et al. (2000)
Mungos mungo	Mammals	Carnivora	Herpestidae	Cooperative parental care	Keane et al. (1994)
Lycaon pictus	Mammals	Carnivora	Canidae	Cooperative parental care	Creel and Creel (2002)
Ochotona curzoniae	Mammals	Lagomorpha	Ochotonidae	Cooperative parental care	Dobson, Smith, and Gao (1998); Yin, Yang, Wei, and Zhang (2009)
Suricata suricatta	Mammals	Carnivora	Herpestidae	Cooperative parental care	Griffin et al. (2003)
Kradibia tentacularis	Insects	Hymenoptera	Agaonidae	Cooperative parental care	Suleman et al. (2012)
Pleistodontes imperialis	Insects	Hymenoptera	Agaonidae	Cooperative parental care	Zammit and Schwarz (2000)

Table 1 (*continued*)

Species	Group	Order	Family	Type of male reproductive cooperation	Source
Schizotetranychus celarius	Arachnids	Trombidiformes	Tetranychidae	Cooperative parental care	Saito (1986)
Nocomis micropogon	Fish	Cypriniformes	Cyprinidae	Cooperative parental care	Reighard (1943)
Notropis leptocephalus	Fish	Cypriniformes	Cyprinidae	Cooperative parental care	Wallin (1989)
Pelvicachromis pulcher	Fish	Perciformes	Cichlidae	Cooperative parental care	Martin and Taborsky (1997)
Hemilepidotus hemilepidotus	Fish	Scorpaeniformes	Cottidae	Cooperative parental care	DeMartini and Patten (1979)
Cebus capucinus	Mammals	Primates	Cebidae	Coalitions	Perry (1996)
Eulemur fulvus rufus	Mammals	Primates	Lemuridae	Coalitions	Ostner (2004)
Macaca sylvanus	Mammals	Primates	Cercopithecidae	Coalitions	Bissonnette, Bischofberger, and van Schaik (2010); Witt, Schmidt, and Schmitt (1981)
Alouatta seniculus	Mammals	Primates	Atelidae	Coalitions	Pope (1990)
Papio cynocephalus	Mammals	Primates	Cercopithecidae	Coalitions	Bercovitch (1988); Alberts, Watts, and Altmann (2003)
Hylobates lar	Mammals	Primates	Hylobatidae	Coalitions	Savini et al. (2009)
Pan troglodytes	Mammals	Primates	Hominidae	Coalitions	Watts (1998); Mitani, Merriwether, and Zhang (2000); Gilby et al. (2012)
Equus caballus	Mammals	Perissodactyla	Equidae	Coalitions	Feh (1999)
Tursiops sp.	Mammals	Cetacea	Delphinidae	Coalitions	Connor et al. (1992); Connor, Smolker, and Bejder (2006)
Panthera leo	Mammals	Carnivora	Felidae	Coalitions	Bygott, Bertram, and Hanby (1979); Packer et al. (1991)
Artibeus jamaicensis	Mammals	Chiroptera	Phyllostomidae	Coalitions	Ortega and Arita (2002); Ortega, Maldonado, Wilkinson, Arita, and Fleischer (2003)
Etheostoma olmstedi	Fish	Perciformes	Percidae	Coalitions	Stiver, Wolff, and Alonzo (2013)
Betta brownorum	Fish	Perciformes	Osphronemidae	Coalitions	Witte and Schmidt (1992)
Betta persephone	Fish	Perciformes	Osphronemidae	Coalitions	Witte and Schmidt (1992)
Parablennius sanguinolentus	Fish	Perciformes	Blenniidae	Coalitions	Oliveira et al. (2002); Santos (1985); Santos and Almada (1988)
Cyprinodon macularius	Fish	Cyprinodontiformes	Cyprinodontidae	Coalitions	Barlow (1961)
Amphiprion akallopisos	Fish	Perciformes	Pomacentridae	Coalitions	Fricke (1979)
Symphodus ocellatus	Fish	Perciformes	Labridae	Coalitions	Fiedler (2010); Lejeune (1985); Taborsky (1987)
Symphodus roissali	Fish	Perciformes	Labridae	Coalitions	Lejeune (1985)
Symphodus tinca	Fish	Perciformes	Labridae	Coalitions	Lejeune (1985)
Halichoeres maculipinna	Fish	Perciformes	Labridae	Coalitions	Thresher (1979)
Ourebia ourebi	Mammals	Artiodactyla	Bovidae	Mutual tolerance and mate sharing	Arcese (1999)
Herpestes sanguineus	Mammals	Carnivora	Herpestidae	Mutual tolerance and mate sharing	Waser, Keane, Creel, Elliott, and Minchella (1994)
Propithecus verreauxi	Mammals	Primates	Indriidae	Mutual tolerance and mate sharing	Kappeler, Mass, and Port (2009); Port, Johnstone, and Kappeler (2012)
Acinonyx jubatus	Mammals	Carnivora	Felidae	Mutual tolerance and mate sharing	Caro (1994)
Potos flavus	Mammals	Carnivora	Procyonidae	Mutual tolerance and mate sharing	Kays and Gittleman (2001)
Uta stansburiana	Lizards	Squamata	Phrynosomatidae	Mutual tolerance and mate sharing	Sinervo and Clobert (2003)
Catostomus commersonii	Fish	Cypriniformes	Catostomidae	Mutual tolerance and mate sharing	Reighard (1920)
Hypentelium nigricans	Fish	Cypriniformes	Catostomidae	Mutual tolerance and mate sharing	Raney and Lachner (1946)
Moxostoma aureolum	Fish	Cypriniformes	Catostomidae	Mutual tolerance and mate sharing	Reighard (1920)
Moxostoma duquesnei	Fish	Cypriniformes	Catostomidae	Mutual tolerance and mate sharing	Bowman (1970); Kwak and Skelly (1992)
Moxostoma macrolepidotum	Fish	Cypriniformes	Catostomidae	Mutual tolerance and mate sharing	Burr and Morris (1977); Jenkins (1970)
Moxostoma erythrurum	Fish	Cypriniformes	Catostomidae	Mutual tolerance and mate sharing	Jenkins (1970); Kwak and Skelly (1992)
Moxostoma valenciennesi	Fish	Cypriniformes	Catostomidae	Mutual tolerance and mate sharing	Jenkins (1970); Jenkins and Jenkins (1980)
Erimyzon oblongus	Fish	Cypriniformes	Catostomidae	Mutual tolerance and mate sharing	Page and Johnston (1990)

For each species, the taxonomic classification, type of male–male cooperation and source are listed. The data in this table are available in electronic form (FigShare repository http://dx.doi.org/10.6084/m9.figshare.843622).

which, as a result of reproductive cooperation, a male fails to sire young within a given breeding season but is not related to his presumably more successful cooperative companion. For example, lance-tailed manakins, *Chiroxiphia lanceolata*, form cooperative displays of unrelated males in which only one male typically mates. In the absence of immediate direct fitness opportunities and kin-selected benefits, subordinate males instead benefit from an increased future probability of becoming the breeder (DuVal, 2007; McDonald & Potts, 1994).

Current direct fitness benefits

Current direct fitness benefits are shared among some or all males in a group in many cooperative species, in contrast to previous examples that explain cooperation by males that are excluded from reproduction. For example, in cooperatively polyandrous Galapagos hawks, multiple males mate with a single breeding female and all of the males provision her young. Because male group-mates are not related (Faaborg et al., 1995), they cannot gain indirect fitness benefits from sharing care of young. Instead, males apparently have equal and random probability of siring young, resulting in shared paternity within and among breeding attempts (Faaborg et al., 1995).

As has been noted in the cooperative breeding literature, Brown's hypotheses (Brown, 1987) are not mutually exclusive and thus our understanding of the fitness benefits of cooperation may lie in determining their relative importance (Canestrari et al., 2005;

Dickinson, 2004). Indeed, it may be relatively common that males accrue multiple types of fitness, with the relative contributions varying in response to social and other conditions. For instance, Packer et al. (1991) reported that the relative contributions of indirect and direct fitness benefits in coalitions of male lions appear to vary in response to coalition size. Specifically, males in small coalitions tend to be unrelated and achieve roughly equal mating success, whereas males in large coalitions are generally close kin that partition direct fitness much less equitably, such that indirect fitness represents a more important component in larger groups. Increasingly, more studies have examined both indirect and direct fitness benefits and have revealed a diversity of fitness benefits to cooperating males. To this extent, reproductive skew models may help to quantify how fitness is partitioned and what factors promote or hinder cooperative groups (Kokko & Johnstone, 1999; Shen & Reeve, 2010).

Ecology, Demography and Social Structure

Ecological factors may have profound impacts on demography and social structure and, thus, on opportunities for male reproductive cooperation. Insights into the effects of ecology on such behaviour can be gleaned by studying cases of male–male cooperation that vary due to shifts in ecological conditions. For instance, lone male–female pairs of callitrichines cannot reproduce in the wild because of the high energetic demands of infant carrying (Goldizen, 1988), but they routinely do so in captivity, probably because of reduced energy needs. This observation highlights the apparent importance of male cooperation in meeting infant care demands in different ecological settings. Similarly, a theoretical model incorporating resource limitation (i.e. a limit on infant production) predicted cases of cooperative polyandry in the acorn woodpecker (Chao, 1997).

Territory quality also plays an important role in promoting male–male cooperation. For instance, while gibbons, *Hylobates lar*, are traditionally thought of as monogamous, the probability of polyandrous male partnerships increases in lower-quality territories (Savini, Boesch, & Reichard, 2009). Variation in resource availability has also been invoked to explain mutual male tolerance in asocial polyandry (Wagner et al., 2007) and cooperative male coalitions where resources dictate female distributions (Arcese, 1999).

Although limited mating opportunities are apparently key to most, if not all, male reproductive cooperation, these limits may be mediated by different factors. Cooperative male displays, for instance, seem to be associated with limits on social interactions (either via male–male competition, or via female mate choice) rather than limited physical resources such as food, breeding territories or nesting sites. Thus, the ecological basis of those limited mating opportunities is apparently linked to the type of male–male cooperation that results.

Phylogenetic History

While a phylogenetically controlled analysis of male reproductive cooperation is beyond the scope of this paper, some descriptive statistics on its taxonomic distribution are worth noting. We found 87 species that fit our definition in the peer-reviewed literature, representing 22 orders and 44 families of animals (Table 1). Most of the species identified are vertebrates, but we found two cases of male reproductive cooperation in insects and one in arachnids. Somewhat surprisingly, fish and birds each had 28 species with examples of male reproductive cooperation, while mammals had 27. Male reproductive cooperation appears to be fairly widely distributed among vertebrates, but at the ordinal level it is evident that some branches bear multiple species exhibiting the behaviour, while the majority of lineages are represented by only one or a few such species (Fig. 1). Thus, even in the absence of a formal phylogenetic analysis, it is evident that male reproductive cooperation has evolved multiple times within animals and, apparently, multiple times within three major lineages of vertebrates.

When the taxonomic distribution of each of the forms of male reproductive cooperation is considered, several interesting patterns emerge (Fig. 2). In fish, multiple examples of each type of male–male cooperation are evident. Coalitions are the most common form of reproductive cooperation among mammals, with no instances of cooperative displays. In contrast, cooperative polyandry is most common in birds, with no reports of either coalitions

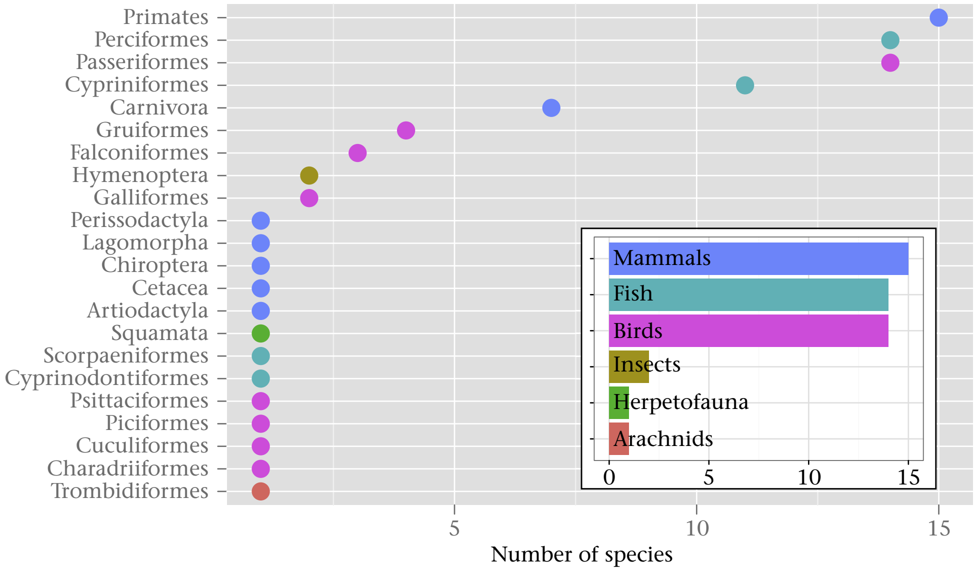

Figure 1. Male reproductive cooperation is widespread across animal orders, but many orders are represented by a single example. Coloured dots depict the number of species in each order that show an example of male–male cooperation. Colours correspond to the major animal groups labelled in the inset. The inset shows the number of species with male reproductive cooperation in each major group.

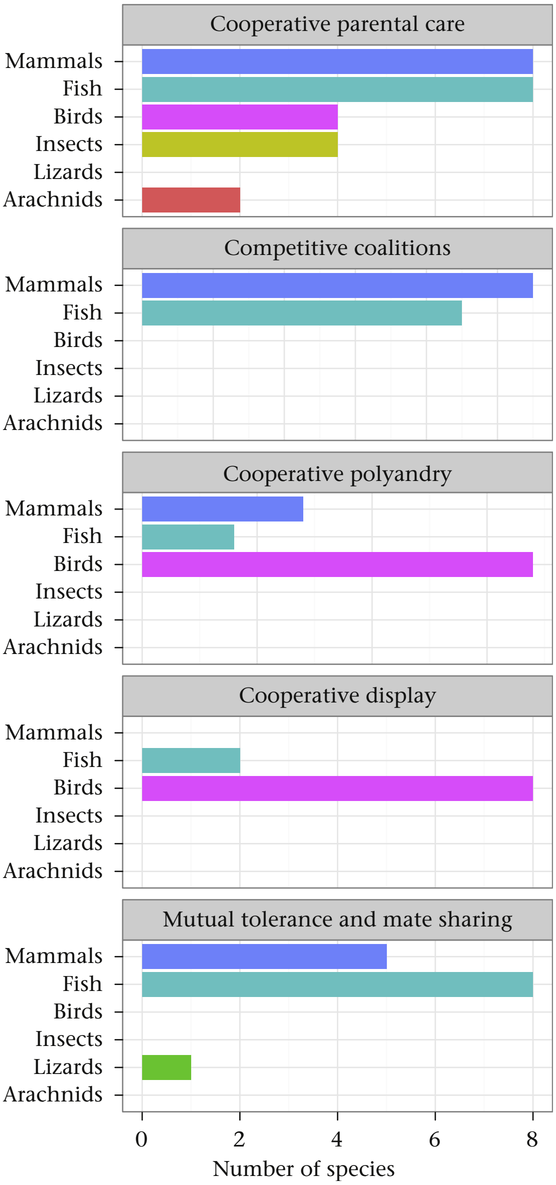

Figure 2. The different types of male reproductive cooperation are unevenly distributed among major animal groups.

or mutual tolerance. We find it intriguing that the relative frequency of the different forms of this cooperation varies across vertebrate lineages, suggesting that fundamental evolved (phylogenetic) differences in the biology of these organisms may have played a role in shaping opportunities for cooperative male behaviour.

We would like to emphasize that the taxonomic patterns are based on our initial survey of the literature and thus may not provide a definitive description of the phylogenetic distribution of this behaviour. Our purpose is to provide an overview of our current knowledge to promote identification of previously overlooked examples of male reproductive cooperation. Future research on male reproductive cooperation should benefit by considering both the ecological and evolutionary factors associated with this behaviour.

Physiological Mechanisms of Male Cooperation

Male reproductive cooperation raises the question of male relationships and the genetic, hormonal and neural underpinnings of cooperative behaviour. Mechanisms such as kin recognition, hormonal variations and cognitive abilities are likely to vary depending on the specific nature of male–male cooperation and the biological abilities of different species. However, none of these aspects of male cooperation has been well studied. We expect that the physiological mechanisms mediating male cooperation will vary substantially in species for which the average male partnership is shorter versus longer than a single breeding cycle.

In situations where male partnerships are long relative to a single breeding cycle, several mechanisms may be involved. When interactions among male relatives are common, kin recognition may facilitate male cooperation, encompassing mechanisms from individual recognition of kin due to a shared developmental environment to self-referential phenotype matching (Hauber & Sherman, 2001). Given that male relationships can involve extensive prosocial behaviour over extended periods (e.g. Garber, Encarnación, Moya, & Pruetz, 1993; Goldizen, 1989), hormonal mechanisms may facilitate this social bond. Hormones such as oxytocin and vasopressin have been studied primarily in the context of male–female monogamous pair bonds, but they also influence social aggregations (Goodson, Schrock, Klatt, Kabelik, & Kingsbury, 2009), increase trust in social situations (Kosfeld, Heinrichs, Zak, Fischbacher, & Fehr, 2005) and, importantly, in female–female relationships (Beery & Zucker, 2010). Whether these hormones also mediate male–male relationships remains an intriguing question. Furthermore, do males and females in cooperatively polyandrous situations develop hormonal profiles similar to pair-bonded monogamous species?

Males may also have other hormonal mechanisms to mediate behavioural changes in state, such as testosterone and glucocorticoids, in the presence of a male partner. An examination of the hormonal state of cooperatively polyandrous moustached tamarin, *Saguinus mystax*, males suggested little difference in testosterone and cortisol levels among males, despite differences in breeding success (Huck, Löttker, Heymann, & Heistermann, 2005). Hormonal profiles will likely vary according to the type of male cooperative behaviours: species with parental care might differ from species that form male coalitions for combat. Additionally, we speculate that behavioural feedbacks on hormone levels may differ from noncooperative species; for example, ‘winner’ and ‘loser’ effects (Hsu, Earley, & Wolf, 2005) may be less dramatic if male interactions occur in the context of both within- and among-group hierarchies. Experimental studies that manipulate male partner presence are likely to provide great insight into the physiological bases of male–male cooperation.

The physiological mechanisms regulating cooperative tendencies in temporary associations of males raise more questions. These mechanisms may be similar to those mediating long partnerships, but expressed in a context-dependent manner. Alternatively, transient male cooperation may involve complex cognitive functions that integrate cues from the social and ecological environment in near real-time. This seems probable in cases of cooperative aggression, and in particular in cases of intercession, in which a male must make decisions mid-conflict based on the identities of warring parties. These complex cognitive behaviours have been well documented in primates (de Waal & Tyack, 2003), but also occur in spotted hyaenas, *Crocuta crocuta* (Engh, Siebert, Greenberg, & Holekamp, 2005). These cognitive abilities are also likely to be manifested in reproductive contexts and represent productive targets for future research.

In summary, the mechanistic underpinnings of male reproductive cooperation seem to be particularly poorly understood. By conducting such analyses in a comparative framework it will eventually be possible to determine how these mechanisms vary with each type of cooperation. We believe that, as outlined here, the recognition of male reproductive cooperation as a single, overarching phenomenon will foster comparative investigation of the diverse mechanisms underlying specific examples of such cooperation.

MALE REPRODUCTIVE COOPERATION AND SEXUAL SELECTION

Sexual selection theory goes far beyond the basic construct taught in introductory biology courses, that of ardent males battling each other for the attention of coy females. Exceptions to this simplistic statement were pointed out by Darwin himself (e.g. sex-role reversed species: Darwin, 1871) and the variety of sexual roles explained by this theory has been expanded by decades of investigation into reproductive strategies (Emlen & Oring, 1977; West-Eberhard, 1979), including elaboration of female sexual traits, alternative mating tactics and strategies used by both sexes, and the importance of the social environment. Empirical and theoretical studies in areas such as sexual conflict and parental investment theory (Chapman, Arnqvist, Bangham, & Rowe, 2003; Kokko & Jennions, 2008), have revealed that the reproductive strategies of males and females are not as clearly distinct as textbook accounts would suggest. Therefore, much of the renewed interest in sexual selection has (rightly) focused on how the unexpected behaviours that some females exhibit fit into sexual selection theory. However, male cooperation in reproductive contexts has received relatively little attention, despite its potential to contribute to our understanding of sexual selection. Notably, because male reproductive cooperation brings together sexual selection and inclusive fitness theory (Rubenstein, 2012), it extends our thinking beyond the classic boundaries of male reproductive competition. Among the resulting questions, we pose two here. (1) How does the occurrence of male reproductive cooperation influence the action of sexual selection? (2) What is the full range of reproductive and social behaviours that can be thought of as sexually selected traits?

Variation in Reproductive Success, Male Competition and Trait Evolution

For sexual selection to alter phenotypic traits, these traits must be associated with differences in individual reproductive success. Reproductive cooperation among males has the potential to affect reproductive success of both males and females, thereby influencing the evolution of sexually selected traits. In general, variance in reproductive success is assumed to be greater for males, leading to the expectation that the intensity of sexual selection will also be greater for individuals of this sex. Depending upon the specific patterns of fitness involved, male reproductive cooperation may either increase or decrease variance in male reproductive success. In species in which direct fitness is restricted to the dominant individual in male partnerships, we expect greater variance in male reproductive success due to the presence of nonbreeding subordinates and to the failure of some males to form cooperative relationships. Sexual dimorphism in these species should be relatively pronounced. In contrast, in species in which reproduction is shared among partners, reproductive cooperation may serve to reduce variance in male reproductive success by increasing the number of individuals who achieve direct fitness; in these species, if all else is equal, sexual dimorphism may be comparatively modest. Although variance in reproductive success, intensity of sexual selection and sexual dimorphism are no doubt each shaped by multiple factors, reproductive cooperation among males generates testable predictions regarding the effects of variance in male reproductive success on phenotypic trait evolution.

The role of male cooperative behaviour in shaping sexually selected traits is unclear. For instance, in the case of sexual dimorphism, many cooperatively polyandrous species are monomorphic (e.g. Galapagos hawks), but species engaging in coalitionary aggression show marked dimorphism (e.g. lions). It seems likely that the specific adaptive function of cooperation contributes to the degree of dimorphism observed. Thus, because greater body size may enhance the ability of males to acquire or defend a pride of females, selection may favour greater dimorphism as compared to a species such as Geoffroy's tamarin, *Saguinus geoffroyi*, in which the primary benefit of male cooperation (cooperative care of young) seems unlikely to impose strong selection for sexual dimorphism. Kinship among cooperating individuals may also be an important factor, with kinship and indirect fitness benefits generally expected to reduce variance in male reproductive success, intensity of sexual selection, and thus sexual dimorphism. Among species lacking male parental care, however, there is no obvious relationship between the type of fitness benefit (e.g. direct, indirect) derived from male cooperation and the degree of sexual dimorphism. For example, three bird taxa with cooperative male display (wild turkeys, *Chiroxiphia* manakins, and ruffs, *Philomachus pugnax*), representing a range of reproductive sharing among males, have high levels of sexual dimorphism even compared to other members of their family without male cooperation. Thus, the influence of the type of male cooperation, reproductive sharing and male relatedness on sexually selected traits are prime targets for investigation.

Little empirical work has examined the role of male cooperative behaviour on sexual selection. A fascinating example is the evolution of male polymorphisms coincident with different status or roles. In bearded manakins (*Manacus* sp.), males of the yellow morph preferentially lek with (yellow) relatives, leading to increased reproductive success over white males and facilitating positive selection of the yellow morph in the population (Concannon, Stein, & Uy, 2012). Male cooperation can facilitate other selection patterns, such as in lazuli buntings, *Passerina amoena*, where mutual male tolerance of divergent male morphs causes disruptive selection on male traits (Greene et al., 2000). Empirical evidence also shows the potential for high levels of sexual dimorphism to evolve in the face of reproductive cooperation. Reproductive skew is pronounced population-wide in the long-tailed manakin, *Chiroxiphia linearis* (McDonald, 1989a, 1989b), notwithstanding male cooperation in displays to females. Thus, despite the relative rarity of male cooperation, we believe there is a tremendous opportunity to meld new theoretical research on the impact of this behaviour on classic models of sexual selection with empirical work to test models and reveal patterns that selection produces in nature.

Role of Female Choice

Classic sexual selection theory posits that female choice (intersexual selection) is a powerful force driving the evolution of male phenotypic traits. The selective pressures imposed by female mating preferences are traditionally assumed to lead to enhanced competition among males (intrasexual selection). Given this perspective on the relationship between inter- and intrasexual selection, how can female choice drive the evolution of reproductive cooperation among males?

The potential role of female choice in promoting cooperative male care of young is relatively straightforward. Females may be more successful, and thus prefer, multiple males to care for young. For example, in the cichlid *Julidochromis ornatus*, females that had two male helpers produced more offspring when controlling for group size (Awata, Kohda, Shibata, Hori, & Heg, 2010). Similarly, in closely related *Julidochromis ornatus*, experimental manipulations revealed that polyandrous females obtained more parental care by manipulating paternity allocation, leading to higher success than monogamous females (Kohda et al., 2009).

Not all examples of male reproductive cooperation relate to male care; in these species, what are the benefits to females that prefer male–male cooperation? It is possible that females prefer elaborate displays that require coordination by male partners, as may be the case in *Chiroxiphia* manakins (Trainer, McDonald, & Learn, 2002); in these species, multiple males can serve as an extended phenotype used by females to select males (Trainer & McDonald, 1995). Furthermore, coordinated teams of displaying males may allow more efficient mate assessment or harassment-free mating. With regard to the latter, cooperative coalitions of wild turkeys exclude other males from access to females and, because within-coalition dominance is determined prior to the breeding season (Krakauer, 2005), there is rarely squabbling among male partners over who gets to mate. Finally, females may also prefer groups of males because they are better than lone individuals at defending infants (e.g. redfronted lemurs, *Eulemur fulvus rufus*: Ostner, 2004; capuchin monkeys, *Cebus capucinus*: Fedigan, Rose, & Avila, 1996), or gaining access to resources in a given area (Savini et al., 2009). In summary, females may prefer cooperative males for multiple reasons, suggesting that intersexual selection is a key force favouring reproductive cooperation among males.

Novel Theoretical Approaches

We believe that studies of systems characterized by male reproductive cooperation offer tremendous opportunities to enhance our understanding of the full complexity of sexual selection and its effects on behavioural and other aspects of phenotypic variation. Although sexual selection theory has traditionally been dominated by the contributions of Bateman (1948) and Trivers (1972), there is growing awareness of alternative theoretical approaches. For example, the concept of dynamic mating markets (Noë & Hammerstein, 1994), newly applied to sexual selection (Patricelli, Krakauer, & McElreath, 2011), emphasizes multiple potential intersexual prospects and intrasexual competitors. Thus, the occurrence of cooperative partnerships as well as the opportunities and constraints that they impose become important factors for investigation. In addition to possessing attractive phenotypes, males must also have sufficient responsiveness and skill to achieve maximum fitness (Patricelli, Uy, Walsh, & Borgia, 2002). Recent debates about the utility of sexual selection theory highlight the need to expand the scope of sexual selection research beyond the single male–female dyad (Rubenstein, 2012). Accordingly, social network analysis has been used to explore how relations well beyond the dyadic level influence social relationships (Croft et al., 2006), including male–male cooperation (McDonald, 2007). We believe that systems characterized by male reproductive cooperation are ideal to fully realize the potential of a variety of selection models because (1) they include social behaviours not often considered in reproductive contexts, (2) male fitness is explicitly dependent on interactions with both same- and opposite-sex individuals and (3) female mate choice may be based on an extended multimale phenotype, challenging traditional conceptual and statistical approaches that assess differential reproductive success in relation to one or a few traits. Theoretical models incorporating these elements should generate significant new insights into how sexual selection shapes the morphology and behaviour of individuals.

A NOTE ABOUT COMPETITION

Animal social interactions are nuanced, and the occurrence of reproductive cooperation among males does not preclude competition among males, even among cooperating male partners. For instance, while cooperatively polyandrous male tamarins are famously prosocial (Goldizen, 1989) and have similar hormonal profiles (Huck, Löttker, Heymann, et al., 2005), available evidence points to intense sperm competition within male partnerships (Garber, Moya, Pruetz, & Ique, 1996; Harcourt, Purvis, & Liles, 1995). Similarly, although male lions cooperate to acquire or defend prides of females from other males, competition among coalition mates leads to rank-related differences in reproductive success (Packer et al., 1991).

Clearly, cooperation and competition among males are closely intertwined. While competition has historically received considerable attention from biologists, we hope to draw increased future attention to cooperation. Overstating the importance of competition can lead to neglecting important behaviours and subtly shape our views on evolutionary theory (Sussman, Garber, & Cheverud, 2005), influencing other fields of study (MacKinnon & Fuentes, 2005). We hope this review will encourage theoretical and empirical work on this underappreciated behaviour, thereby leading to a greater understanding of the balance between cooperation and conflict in evolution.

CONCLUSIONS

The ultimate goal of this paper was to highlight examples of male reproductive cooperation across animal taxa. We have identified an initial list of examples that we hope are used and extended by the research community. We believe that significant advances will emerge from future studies examining the causes, consequences and correlates of male reproductive cooperation. Investigations of the fitness consequences of this phenomenon will highlight the complex interplay between conflict and cooperation and should reveal the utility of inclusive fitness to explain more than just classic cases of cooperative breeding. Studies of the ecological factors associated with male reproductive cooperation will contribute to the long-standing debate regarding the role of ecology in generating social organization. Research into the physiological mechanisms underlying male reproductive cooperation represent, in our opinion, a largely unexplored wealth of information that will advance the study of the physiology and behaviour alike, merging proximate and ultimate approaches. Finally, we propose that male reproductive cooperation provides an important context for exploring new perspectives on sexual selection theory, which in turn may be greatly enhanced by considering cooperative interactions among individuals.

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References

Alberts, S. C., Watts, H. E., & Altmann, J. (2003). Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. *Animal Behaviour, 65*, 821–840.

Andersson, M. B. (1994). *Sexual selection*. Princeton, NJ, U.S.A.: Princeton University Press.

Arcese, P. (1999). Effect of auxiliary males on territory ownership in the oribi and the attributes of multimale groups. *Animal Behaviour, 57*, 61–71.

Awata, S., Heg, D., Munehara, H., & Kohda, M. (2006). Testis size depends on social status and the presence of male helpers in the cooperatively breeding cichlid *Julidochromis ornatus*. *Behavioral Ecology, 17*, 372–379.

Awata, S., Kohda, M., Shibata, J., Hori, M., & Heg, D. (2010). Group structure, nest size and reproductive success in the cooperatively breeding cichlid *Julidochromis ornatus*: a correlation study. *Ethology, 116*, 316–328.

Awata, S., Munehara, H., & Kohda, M. (2005). Social system and reproduction of helpers in a cooperatively breeding cichlid fish (*Julidochromis ornatus*) in Lake Tanganyika: field observations and parentage analyses. *Behavioral Ecology and Sociobiology, 58*, 506–516.

Baglione, V., Canestrari, D., Marcos, J., & Ekman, J. (2003). Kin selection in cooperative alliances of carrion crows. *Science, 300*, 1947–1949.

Baker, A. J., Dietz, J. M., & Kleiman, D. G. (1993). Behavioural evidence for monopolization of paternity in multi-male groups of golden lion tamarins. *Animal Behaviour, 46*, 1091–1103.

Balshine-Earn, S., Neat, F. C., Reid, H., & Taborsky, M. (1998). Paying to stay or paying to breed? Field evidence for direct benefits of helping behavior in a cooperatively breeding fish. *Behavioral Ecology, 9*, 432–438.

Barlow, G. W. (1961). Social behavior of the desert pupfish, *Cyprinodon macularius*, in the field and in the aquarium. *American Midland Naturalist, 65*, 339.

Bateman, A. J. (1948). Intra-sexual selection in *Drosophila*. *Heredity, 2*, 349–368.

Beery, A. K., & Zucker, I. (2010). Oxytocin and same-sex social behavior in female meadow voles. *Neuroscience, 169*, 665–673.

Bercovitch, F. B. (1988). Coalitions, cooperation and reproductive tactics among adult male baboons. *Animal Behaviour, 36*, 1198–1209.

Bertran, J., Margalida, A., & Arroyo, B. E. (2009). Agonistic behaviour and sexual conflict in atypical reproductive groups: the case of bearded vulture *Gypaetus barbatus* polyandrous trios. *Ethology, 115*, 429–438.

Bissonnette, A., Bischofberger, N., & van Schaik, C. P. (2010). Mating skew in Barbary macaque males: the role of female mating synchrony, female behavior, and male–male coalitions. *Behavioral Ecology and Sociobiology, 65*, 167–182.

Bowman, M. L. (1970). Life history of the black redhorse, *Moxostoma duquesnei* (Lesueur), in Missouri. *Transactions of the American Fisheries Society, 99*, 546–559.

Briskie, J. V. (1992). Copulation patterns and sperm competition in the polygynandrous Smith's longspur. *Auk, 109*, 563–575.

Briskie, J. V., Montgomerie, R., & Põldmaa, T. (1998). Paternity and paternal care in the polygynandrous Smith's longspur. *Behavioral Ecology and Sociobiology, 43*, 181–190.

Brown, J. L. (1987). *Helping and communal breeding in birds*. Princeton, NJ, U.S.A.: Princeton University Press.

Burke, T., Davies, N. B., Bruford, M. W., & Hatchwell, B. J. (1989). Parental care and mating behaviour of polyandrous dunnocks *Prunella modularis* related to paternity by DNA fingerprinting. *Nature, 338*, 249–251.

Burr, B. M., & Morris, M. A. (1977). Spawning behavior of the shorthead redhorse, *Moxostoma macrolepidotum*, in Big Rock Creek, Illinois. *Transactions of the American Fisheries Society, 106*, 80–82.

Bygott, J. D., Bertram, B. C., & Hanby, J. P. (1979). Male lions in large coalitions gain reproductive advantages. *Nature, 282*, 839–841.

Callander, S., Kahn, A. T., Maricic, T., Jennions, M. D., & Backwell, P. R. Y. (2013). Weapons or mating signals? Claw shape and mate choice in a fiddler crab. *Behavioral Ecology and Sociobiology, 67*, 1163–1167.

Canestrari, D., Marcos, J., & Baglione, V. (2005). Effect of parentage and relatedness on the individual contribution to cooperative chick care in carrion crows *Corvus corone corone*. *Behavioral Ecology and Sociobiology, 57*, 422–428.

Caro, T. M. (1994). *Cheetahs of the Serengeti Plains: Group living in an asocial species*. Chicago, IL, U.S.A.: University of Chicago Press.

Chao, L. (1997). Evolution of polyandry in a communal breeding system. *Behavioral Ecology, 8*, 668–674.

Chapman, T., Arnqvist, G., Bangham, J., & Rowe, L. (2003). Sexual conflict. *Trends in Ecology & Evolution, 18*, 41–47.

Clutton-Brock, T. (2002). Behavioral ecology – breeding together: kin selection and mutualism in cooperative vertebrates. *Science, 296*, 69–72.

Cockburn, A. (1998). Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology and Systematics, 29*, 141–177.

Concannon, M. R., Stein, A. C., & Uy, J. A. C. (2012). Kin selection may contribute to lek evolution and trait introgression across an avian hybrid zone. *Molecular Ecology, 21*, 1477–1486.

Connor, R. C., Smolker, R., & Bejder, L. (2006). Synchrony, social behaviour and alliance affiliation in Indian Ocean bottlenose dolphins, *Tursiops aduncus*. *Animal Behaviour, 72*, 1371–1378.

Connor, R. C., Smolker, R. A., & Richards, A. F. (1992). Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proceedings of the National Academy of Sciences of the United States of America, 89*, 987–990.

Craig, J. L., & Jamieson, I. G. (1990). Pukeko: different approaches and some different answers. In P. B. Stacey, & W. D. Koenig (Eds.), *Cooperative breeding in birds: Long term studies of ecology and behaviour* (pp. 385–412). Cambridge, MA, U.S.A.: Cambridge University Press.

Creel, S., & Creel, N. M. (2002). *The African wild dog: Behavior, ecology, and conservation*. Princeton, NJ, U.S.A.: Princeton University Press.

Croft, D. P., James, R., Thomas, P., Hathaway, C., Mawdsley, D., Laland, K. N., et al. (2006). Social structure and co-operative interactions in a wild population of guppies (*Poecilia reticulata*). *Behavioral Ecology and Sociobiology, 59*, 644–650.

Crook, J. H., & Crook, S. J. (1988). Tibetan polyandry: problems of adaptation and fitness. In L. Betzig, M. B. Mulder, & P. Turke (Eds.), *Human reproductive behaviour: A Darwinian perspective* (pp. 97–114). Cambridge, MA, U.S.A.: Cambridge University Press.

Dale, J., Dunn, P. O., Figuerola, J., Lislevand, T., Székely, T., & Whittingham, L. A. (2007). Sexual selection explains Rensch's rule of allometry for sexual size dimorphism. *Proceedings of the Royal Society B, 274*, 2971–2979.

Darwin, C. (1871). *The descent of man and selection in relation to sex*. London, U.K.: J. Murray.

Davies, N. B., Hartley, I. R., Hatchwell, B. J., Desrochers, A., Skeer, J., & Nebel, D. (1995). The polygynandrous mating system of the alpine accentor, *Prunella collaris*. I. Ecological causes and reproductive conflicts. *Animal Behaviour, 49*, 769–788.

Davies, N. B., Hatchwell, B. J., Robson, T., & Burke, T. (1992). Paternity and parental effort in dunnocks *Prunella modularis*: how good are male chick-feeding rules? *Animal Behaviour, 43*, 729–745.

DeLay, L. S., Faaborg, J., Naranjo, J., Paz, S. M., de Vries, T., & Parker, P. G. (1996). Paternal care in the cooperatively polyandrous Galapagos hawk. *Condor, 98*, 300–311.

DeMartini, E. E., & Patten, B. G. (1979). Egg guarding and reproductive biology of the red Irish lord, *Hemilepidotus hemilepidotus*. *Syesis, 12*, 41–55.

Dewsbury, D. A. (2005). The Darwin–Bateman paradigm in historical context. *Integrative and Comparative Biology, 45*, 831–837.

Díaz-Muñoz, S. L. (2011). Paternity and relatedness in a polyandrous nonhuman primate: testing adaptive hypotheses of male reproductive cooperation. *Animal Behaviour, 82*, 563–571.

Dickinson, J. (2004). A test of the importance of direct and indirect fitness benefits for helping decisions in western bluebirds. *Behavioral Ecology, 15*, 233–238.

Dierkes, P., Heg, D., Taborsky, M., Skubic, E., & Achmann, R. (2005). Genetic relatedness in groups is sex-specific and declines with age of helpers in a cooperatively breeding cichlid. *Ecology Letters, 8*, 968–975.

Dierkes, P., Taborsky, M., & Achmann, R. (2008). Multiple paternity in the cooperatively breeding fish *Neolamprologus pulcher*. *Behavioral Ecology and Sociobiology, 62*, 1581–1589.

Dobson, F. S., Smith, A. T., & Gao, W. X. (1998). Social and ecological influences on dispersal and philopatry in the plateau pika (*Ochotona curzoniae*). *Behavioral Ecology, 9*, 622–635.

DuVal, E. H. (2007). Adaptive advantages of cooperative courtship for subordinate male lance-tailed manakins. *American Naturalist, 169*, 423–432.

Eason, P. K., & Sherman, P. T. (1995). Dominance status, mating strategies and copulation success in cooperatively polyandrous white-winged trumpeters, *Psophia leucoptera* (Aves: Psophiidae). *Animal Behaviour, 49*, 725–736.

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

Engh, A. L., Siebert, E. R., Greenberg, D. A., & Holekamp, K. E. (2005). Patterns of alliance formation and postconflict aggression indicate spotted hyaenas recognize third-party relationships. *Animal Behaviour, 69*, 209–217.

Faaborg, J., Parker, P. G., DeLay, L., de Vries, T., Bednarz, J. C., Paz, S. M., et al. (1995). Confirmation of cooperative polyandry in the Galapagos hawk (*Buteo galapagoensis*). *Behavioral Ecology and Sociobiology, 36*, 83–90.

Fahy, W. E. (1954). The life history of the northern greenside darter, *Etheostoma b. blennioides* Rafinesque. *Journal of the Elisha Mitchell Scientific Society, 70*, 139–205.

Fedigan, L. M., Rose, L. M., & Avila, R. M. (1996). See how they grow: tracking capuchin monkey (*Cebus capucinus*) populations in regenerating Costa Rican dry forest. In M. Norconk, A. Rosenberger, & P. Garber (Eds.), *Adaptive radiations of neotropical primates* (pp. 289–307). New York, NY, U.S.A.: Plenum.

Feh, C. (1999). Alliances and reproductive success in Camargue stallions. *Animal Behaviour, 57*, 705–713.

Fiedler, K. (2010). Verhaltensstudien an lippfischen der gattung *Crenilabrus* (Labridae, Perciformes). *Zeitschrift für Tierpsychologie, 21*, 521–591.

Foster, M. S. (1981). Cooperative behavior and social organization of the swallow-tailed manakin (*Chiroxiphia caudata*). *Behavioral Ecology and Sociobiology, 9*, 167–177.

Francisco, M. R., Gibbs, H. L., & Galetti, P. M., Jr. (2009). Patterns of individual relatedness at blue manakin (*Chiroxiphia caudata*) leks. *Auk, 126*, 47–53.

Fricke, H. W. (1979). Mating system, resource defence and sex change in the anemonefish *Amphiprion akallopisos*. *Zeitschrift für Tierpsychologie, 50*, 313–326.

Garber, P. A., Encarnación, F., Moya, L., & Pruetz, J. D. (1993). Demographic and reproductive patterns in moustached tamarin monkeys (*Saguinus mystax*): implications for reconstructing platyrrhine mating systems. *American Journal of Primatology, 29*, 235–254.

Garber, P. A., Moya, L., Pruetz, J. D., & Ique, C. (1996). Social and seasonal influences on reproductive biology in male moustached tamarins (*Saguinus mystax*). *American Journal of Primatology, 38*, 29–46.

Garnett, S. T. (1980). The social organisation of the dusky moorhen, *Gallinula tenebrosa* Gould (Aves: Rallidae). *Wildlife Research, 7*, 103–112.

Gilby, I. C., Brent, L. J. N., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Goodall, J., et al. (2012). Fitness benefits of coalitionary aggression in male chimpanzees. *Behavioral Ecology and Sociobiology, 67*, 373–381.

Goldizen, A. W. (1987). Facultative polyandry and the role of infant-carrying in wild saddle-back tamarins (*Saguinus fuscicollis*). *Behavioral Ecology and Sociobiology, 20*, 99–109.

Goldizen, A. W. (1988). Tamarin and marmoset mating systems: unusual flexibility. *Trends in Ecology & Evolution, 3*, 36–40.

Goldizen, A. W. (1989). Social relationships in a cooperatively polyandrous group of tamarins (*Saguinus fuscicollis*). *Behavioral Ecology and Sociobiology, 24*, 79–89.

Goldizen, A. W., Buchan, J., Putland, D., Goldizen, A., & Krebs, E. (2000). Patterns of mate-sharing in a population of Tasmanian native hens *Gallinula mortierii*. *Ibis, 142*, 40–47.

Goldizen, A. W., Mendelson, J., Van Vlaardingen, M., & Terborgh, J. (1996). Saddle-back tamarin (*Saguinus fuscicollis*) reproductive strategies: evidence from a thirteen-year study of a marked population. *American Journal of Primatology, 38*, 57–83.

Goldizen, A. W., Putland, D., & Goldizen, A. (1998). Variable mating patterns in Tasmanian native hens (*Gallinula mortierii*): correlates of reproductive success. *Journal of Animal Ecology, 67*, 307–317.

Goodson, J. L., Schrock, S. E., Klatt, J. D., Kabelik, D., & Kingsbury, M. A. (2009). Mesotocin and nonapeptide receptors promote estrildid flocking behavior. *Science, 325*, 862–866.

Greene, E., Lyon, B. E., Muehter, V. R., Ratcliffe, L., Oliver, S. J., & Boag, P. T. (2000). Disruptive sexual selection for plumage coloration in a passerine bird. *Nature, 407*, 1000–1003.

Griffin, A. S., Pemberton, J. M., Brotherton, P., McIlrath, G., Gaynor, D., Kansky, R., et al. (2003). A genetic analysis of breeding success in the cooperative meerkat (*Suricata suricatta*). *Behavioral Ecology, 14*, 472–480.

Hackney, P. A., Tatum, W. M., & Spencer, L. S. (1968). Life history study of the river redhorse, *Moxostoma carinatum* (Cope), in the Cahaba River, Alabama, with notes on the management of the species as a sport fish. *Proceedings of the Southeast Association of Game and Fish Commissioners, 21*, 324–332.

Hamilton, W. D. (1963). The evolution of altruistic behavior. *American Naturalist, 97*, 354–356.

Hamilton, W. D. (1964a). The genetical evolution of social behaviour I. *Journal of Theoretical Biology, 7*, 1–16.

Hamilton, W. D. (1964b). The genetical evolution of social behaviour II. *Journal of Theoretical Biology, 7*, 17–52.

Harcourt, A. H., Purvis, A., & Liles, L. (1995). Sperm competition: mating system, not breeding season, affects testes size of primates. *Functional Ecology, 9*, 468–476.

Hartley, I. R., Davies, N. B., Hatchwell, B. J., Desrochers, A., Nebel, D., & Burke, T. (1995). The polygynandrous mating system of the alpine accentor, *Prunella collaris*. II. Multiple paternity and parental effort. *Animal Behaviour, 49*, 789–803.

Hauber, M. E., & Lacey, E. A. (2005). Bateman's principle in cooperatively breeding vertebrates: the effects of non-breeding alloparents on variability in female and male reproductive success. *Integrative and Comparative Biology, 45*, 903–914.

Hauber, M. E., & Sherman, P. W. (2001). Self-referent phenotype matching: theoretical considerations and empirical evidence. *Trends in Neurosciences, 24*, 609–616.

Haydock, J., & Koenig, W. D. (2002). Reproductive skew in the polygynandrous acorn woodpecker. *Proceedings of the National Academy of Sciences of the United States of America, 99*, 7178–7183.

Haydock, J., & Koenig, W. D. (2003). Patterns of reproductive skew in the polygynandrous acorn woodpecker. *American Naturalist, 162*, 277–289.

Heinsohn, R., Dunn, P., Legge, S., & Double, M. (2000). Coalitions of relatives and reproductive skew in cooperatively breeding white-winged choughs. *Proceedings of the Royal Society B, 267*, 243–249.

Heinsohn, R., Ebert, D., Legge, S., & Peakall, R. (2007). Genetic evidence for cooperative polyandry in reverse dichromatic *Eclectus* parrots. *Animal Behaviour, 74*, 1047–1054.

Hsu, Y., Earley, R. L., & Wolf, L. L. (2005). Modulation of aggressive behaviour by fighting experience: mechanisms and contest outcomes. *Biological Reviews, 81*, 33–74.

Huck, M., Löttker, P., & Heymann, E. (2004). Proximate mechanisms of reproductive monopolization in male moustached tamarins (*Saguinus mystax*). *American Journal of Primatology, 64*, 39–56.

Huck, M., Löttker, P., Böhle, U. R., & Heymann, E. W. (2005). Paternity and kinship patterns in polyandrous moustached tamarins (*Saguinus mystax*). *American Journal of Physical Anthropology, 127*, 449–464.

Huck, M., Löttker, P., Heymann, E., & Heistermann, M. (2005). Characterization and social correlates of fecal testosterone and cortisol excretion in wild male *Saguinus mystax*. *International Journal of Primatology, 26*, 159–179.

Jenkins, R. E. (1970). *Systematic studies of the catostomid fish tribe Moxostomatini* (Doctoral thesis, Cornell University, Ithaca, NY, USA).

Jenkins, R. E., & Jenkins, D. J. (1980). Reproductive behavior of the greater redhorse, *Moxostoma valenciennesi*, in the Thousand Islands region. *Canadian Field-Naturalist, 94*, 426–430.

Kappeler, P. M., Mass, V., & Port, M. (2009). Even adult sex ratios in lemurs: potential costs and benefits of subordinate males in Verreaux's sifaka (*Propithecus verreauxi*) in the Kirindy Forest CFPF, Madagascar. *American Journal of Physical Anthropology, 140*, 487–497.

Kays, R. W., & Gittleman, J. L. (2001). The social organization of the kinkajou *Potos flavus* (Procyonidae). *Journal of Zoology, 253*, 491–504.

Keane, B., Waser, P. M., Creel, S. R., Creel, N. M., Elliott, L. F., & Minchella, D. J. (1994). Subordinate reproduction in dwarf mongooses. *Animal Behaviour, 47*, 65–75.

Kohda, M., Heg, D., Makino, Y., Takeyama, T., Shibata, J.-Y., Watanabe, K., et al. (2009). Living on the wedge: female control of paternity in a cooperatively polyandrous cichlid. *Proceedings of the Royal Society B, 276*, 4207–4214.

Kokko, H., & Jennions, M. D. (2008). Parental investment, sexual selection and sex ratios. *Journal of Evolutionary Biology, 21*, 919–948.

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

Kosfeld, M., Heinrichs, M., Zak, P. J., Fischbacher, U., & Fehr, E. (2005). Oxytocin increases trust in humans. *Nature, 435*, 673–676.

Krakauer, A. (2005). Kin selection and cooperative courtship in wild turkeys. *Nature, 434*, 69–72.

Krakauer, A., & DuVal, E. H. (2011). Kin selection and cooperative courtship in birds. In C. A. Salmon, & T. K. Shackelford (Eds.), *The Oxford handbook of evolutionary family psychology* (pp. 230–247). New York, NY, U.S.A.: Oxford University Press.

Kwak, T. J., & Skelly, T. M. (1992). Spawning habitat, behavior, and morphology as isolating mechanisms of the golden redhorse, *Moxostoma erythrurum*, and the black redhorse, *M. duquesnei*, two syntopic fishes. *Environmental Biology of Fishes, 34*, 127–137.

Lambert, D. M., Millar, C. D., & Jack, K. (1994). Single- and multilocus DNA fingerprinting of communally breeding pukeko: do copulations or dominance ensure reproductive success? *Proceedings of the National Academy of Sciences of the United States of America, 91*, 9641–9645.

Lappan, S. (2007). Social relationships among males in multimale siamang groups. *International Journal of Primatology, 28*, 369–387.

Lappan, S. (2008). Male care of infants in a siamang (*Symphalangus syndactylus*) population including socially monogamous and polyandrous groups. *Behavioral Ecology and Sociobiology, 62*, 1307–1317.

Lejeune, P. (1985). Le comportement social des Labridés méditerranéens: Etude écoéthologique des comportements reproducteur et sociaux des Labridae méditerranéens des genres *Symphodus* (Rafinesque 1810) et *Coris* (Lacepede 1802). *Cahier d'Ethologie Appliquee, 5*, 1–208.

Levine, N. E., & Silk, J. B. (1997). Why polyandry fails: sources of instability in polyandrous marriages. *Current Anthropology, 38*, 375–398.

Lidicker, W. Z., Jr. (1979). A clarification of interactions in ecological systems. *Bioscience, 29*, 475–477.

Loiselle, B. A., Ryder, T. B., Duraes, R., Tori, W., Blake, J. G., & Parker, P. G. (2006). Kin selection does not explain male aggregation at leks of 4 manakin species. *Behavioral Ecology, 18*, 287–291.

MacKinnon, K. C., & Fuentes, A. (2005). Reassessing male aggression and dominance: the evidence from primatology. In S. McKinnon, & S. Silverman (Eds.), *Complexities: Beyond nature and nurture* (pp. 83–105). Chicago, IL, U.S.A.: University of Chicago Press.

Magrath, R. D., & Whittingham, L. A. (1997). Subordinate males are more likely to help if unrelated to the breeding female in cooperatively breeding white-browed scrubwrens. *Behavioral Ecology and Sociobiology, 41*, 185–192.

Malan, G. (2005). Reproductive partitioning among polyandrous alpha and beta pale chanting-goshawk males. *African Zoology, 40*, 213–222.

Martin, E., & Taborsky, M. (1997). Alternative male mating tactics in a cichlid, *Pelvicachromis pulcher*: a comparison of reproductive effort and success. *Behavioral Ecology and Sociobiology, 41*, 311–319.

Maynard Smith, J., & Ridpath, M. G. (1972). Wife sharing in the Tasmanian native hen, *Tribonyx mortierii*: a case of kin selection? *American Naturalist, 106*, 447–452.

McDonald, D. B. (1989a). Cooperation under sexual selection: age-graded changes in a lekking bird. *American Naturalist, 134*, 709–730.

McDonald, D. B. (1989b). Correlates of male mating success in a lekking bird with male–male cooperation. *Animal Behaviour, 37*, 1007–1022.

McDonald, D. B. (2007). Predicting fate from early connectivity in a social network. *Proceedings of the National Academy of Sciences of the United States of America, 104*, 10910–10914.

McDonald, D. B., & Potts, W. K. (1994). Cooperative display and relatedness among males in a lek-mating bird. *Science, 266*, 1030–1032.

Millar, C. D., Anthony, I., Lambert, D. M., Stapleton, P. M., Bergmann, C. C., Bellamy, A. R., et al. (1994). Patterns of reproductive success determined by DNA fingerprinting in a communally breeding oceanic bird. *Biological Journal of the Linnean Society, 52*, 31–48.

Mitani, J. C., Merriwether, D. A., & Zhang, C. (2000). Male affiliation, cooperation and kinship in wild chimpanzees. *Animal Behaviour, 59*, 885–893.

Noë, R., & Hammerstein, P. (1994). Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology, 35*, 1–11.

Oliveira, R. F., Carvalho, N., Miranda, J., Gonçalves, E. J., Grober, M., & Santos, R. S. (2002). The relationship between the presence of satellite males and nest-holders' mating success in the Azorean rock-pool blenny *Parablennius sanguinolentus parvicornis*. *Ethology, 108*, 223–235.

Olson, L. E., & Blumstein, D. T. (2009). A trait-based approach to understand the evolution of complex coalitions in male mammals. *Behavioral Ecology, 20*, 624–632.

Ortega, J., & Arita, H. T. (2002). Subordinate males in harem groups of Jamaican fruit-eating bats (*Artibeus jamaicensis*): satellites or sneaks? *Ethology, 108*, 1077–1091.

Ortega, J., Maldonado, J. E., Wilkinson, G. S., Arita, H. T., & Fleischer, R. C. (2003). Male dominance, paternity, and relatedness in the Jamaican fruit-eating bat (*Artibeus jamaicensis*). *Molecular Ecology, 12*, 2409–2415.

Ostner, J. (2004). Male life history and the unusual adult sex ratios of redfronted lemur, *Eulemur fulvus rufus*, groups. *Animal Behaviour, 67*, 249–259.

Packer, C., Gilbert, D., Pusey, A., & Obrien, S. (1991). A molecular genetic-analysis of kinship and cooperation in African lions. *Nature, 351*, 562–565.

Page, L. M., & Johnston, C. E. (1990). Spawning in the creek chubsucker, *Erimyzon oblongus*, with a review of spawning behavior in suckers (Catostomidae). *Environmental Biology of Fishes, 27*, 265–272.

Patricelli, G. L., Krakauer, A. H., & McElreath, R. (2011). Assets and tactics in a mating market: economic models of negotiation offer insights into animal courtship dynamics on the lek. *Current Zoology, 57*, 225–236.

Patricelli, G. L., Uy, J. A. C., Walsh, G., & Borgia, G. (2002). Sexual selection: male displays adjusted to female's response. *Nature, 415*, 279–280.

Perry, S. (1996). Intergroup encounters in wild white-faced capuchins (*Cebus capucinus*). *International Journal of Primatology, 17*, 309–330.

Petrie, M., Krupa, A., & Burke, T. (1999). Peacocks lek with relatives even in the absence of social and environmental cues. *Nature, 401*, 155–157.

Pope, T. R. (1990). The reproductive consequences of male cooperation in the red howler monkey: paternity exclusion in multi-male and single-male troops using genetic markers. *Behavioral Ecology and Sociobiology, 27*, 439–446.

Port, M., Johnstone, R. A., & Kappeler, P. M. (2012). The evolution of multimale groups in Verreaux's sifaka, or how to test an evolutionary demographic model. *Behavioral Ecology, 23*, 889–897.

Prum, R. O. (1985). Observations of the white-fronted manakin (*Pipra serena*) in Suriname. *Auk, 102*, 384–387.

Raney, E. C., & Lachner, E. A. (1946). Age, growth, and habits of the hog sucker, *Hypentelium nigricans* (LeSueur), in New York. *American Midland Naturalist, 36*, 76–86.

Reighard, J. (1920). The breeding behavior of the suckers and minnows. I. The suckers. *Biological Bulletin, 38*, 1–32.

Reighard, J. (1943). The breeding habits of the river chub, *Nocomis micropogon* (Cope). *Papers of the Michigan Academy of Science, Arts and Letters, 28*, 397–423.

Riehl, C. (2011). Living with strangers: direct benefits favour non-kin cooperation in a communally nesting bird. *Proceedings of the Royal Society B, 278*, 1728–1735.

Riehl, C. (2012). Mating system and reproductive skew in a communally breeding cuckoo: hard-working males do not sire more young. *Animal Behaviour, 84*, 707–714.

Robbins, M. B. (1983). The display repertoire of the band-tailed manakin (*Pipra fasciicauda*). *Wilson Bulletin, 95*, 321–504.

Rubenstein, D. R. (2012). Family feuds: social competition and sexual conflict in complex societies. *Philosophical Transactions of the Royal Society B: Biological Sciences, 367*, 2304–2313.

Ryder, T. B., Blake, J. G., Parker, P. G., & Loiselle, B. A. (2011). The composition, stability, and kinship of reproductive coalitions in a lekking bird. *Behavioral Ecology, 22*, 282–290.

Ryder, T. B., McDonald, D. B., Blake, J. G., Parker, P. G., & Loiselle, B. A. (2008). Social networks in the lek-mating wire-tailed manakin (*Pipra filicauda*). *Proceedings of the Royal Society B, 275*, 1367–1374.

Saito, Y. (1986). Prey kills predator: counter-attack success of a spider mite against its specific phytoseiid predator. *Experimental & Applied Acarology, 2*, 47–62.

Santos, R. S. (1985). Parentais e satelites: Tacticas alternativas de acasalamento nos machos de *Blennius sanguinolentus pallas* (Pisces: Blenniidae). *Arquipélago: Série ciências da natureza revista do Instituto Universitário dos Açores, 6*, 119–146.

Santos, R. S., & Almada, V. (1988). Intraspecific variation in reproductive tactics in males of the rocky intertidal fish *Blennius sanguinolentus* in Azores. In G. Chellazzi, & M. Vannini (Eds.), *Behavioral adaptations to intertidal life* (pp. 421–447). New York, NY, U.S.A.: Plenum.

Savini, T., Boesch, C., & Reichard, U. H. (2009). Varying ecological quality influences the probability of polyandry in white-handed gibbons (*Hylobates lar*) in Thailand. *Biotropica, 41*, 503–513.

Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social bonds enhance reproductive success in male macaques. *Current Biology, 20*, 2207–2210.

Shen, S. F., & Reeve, H. K. (2010). Reproductive skew theory unified: the general bordered tug-of-war model. *Journal of Theoretical Biology, 263*, 1–12.

Sherman, P. T. (1995). Social organization of cooperatively polyandrous white-winged trumpeters (*Psophia leucoptera*). *Auk, 112*, 296–309.

Sherman, P. W. (1988). The levels of analysis. *Animal Behaviour, 36*, 616–619.

Sinervo, B., & Clobert, J. (2003). Morphs, dispersal behavior, genetic similarity, and the evolution of cooperation. *Science, 300*, 1949–1951.

Skutch, A. F. (1935). Helpers at the nest. *Auk, 52*, 257–273.

Smith, E. A. (1998). Is Tibetan polyandry adaptive? *Human Nature, 9*, 225–261.

Solomon, N. G., & French, J. A. (1997). *Cooperative breeding in mammals*. Cambridge, U.K.: Cambridge University Press.

Stiver, K. A., Dierkes, P., Taborsky, M., Lisle Gibbs, H., & Balshine, S. (2005). Relatedness and helping in fish: examining the theoretical predictions. *Proceedings of the Royal Society B, 272*, 1593–1599.

Stiver, K. A., Wolff, S. H., & Alonzo, S. H. (2013). Sharing of potential nest sites by *Etheostoma olmstedi* males suggests mutual tolerance in an alloparental species. *PLoS One, 8*, e56041.

Suarez, S. S. (2007). *Paternity, relatedness, and socio-reproductive behavior in a population of wild red-bellied tamarins (*Saguinus labiatus*)* (Doctoral dissertation). Available from: ProQuest Dissertations and Theses database. (UMI No. 3247393).

Suleman, N., Raja, S., & Compton, S. G. (2012). Only pollinator fig wasps have males that collaborate to release their females from figs of an Asian fig tree. *Biology Letters, 8*, 344–346.

Sussman, R., Garber, P., & Cheverud, J. (2005). Importance of cooperation and affiliation in the evolution of primate sociality. *American Journal of Physical Anthropology, 128*, 84–97.

Taborsky, M. (1987). Cooperative behaviour in fish: coalitions, kin groups and reciprocity. In Y. Itō, J. L. Brown, & J. Kikkawa (Eds.), *Animal societies: Theories and facts* (pp. 29–237). Tokyo: Japan Scientific Societies Press.

Taborsky, M. (2009). Reproductive skew in cooperative fish groups: virtue and limitations of alternative modeling approaches. In R. Hager, & C. B. Jones (Eds.), *Reproductive skew in vertebrates: Proximate and ultimate causes* (pp. 265–304). Cambridge, U.K.: Cambridge University Press.

Terborgh, J., & Goldizen, A. W. (1985). On the mating system of the cooperatively breeding saddle-backed tamarin (*Saguinus fuscicollis*). *Behavioral Ecology and Sociobiology, 16*, 293–299.

Thresher, R. E. (1979). Social behavior and ecology of two sympatric wrasses (Labridae: Halichoeres spp.) off the coast of Florida. *Marine Biology, 53*, 161–172.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie, 20*, 410–433.

Townsend, A. K., Clark, A. B., McGowan, K. J., & Lovette, I. J. (2009). Reproductive partitioning and the assumptions of reproductive skew models in the cooperatively breeding American crow. *Animal Behaviour, 77*, 503–512.

Trainer, J. M., & McDonald, D. B. (1995). Singing performance, frequency matching and courtship success of long-tailed manakins (*Chiroxiphia linearis*). *Behavioral Ecology and Sociobiology, 37*, 249–254.

Trainer, J. M., McDonald, D. B., & Learn, W. A. (2002). The development of coordinated singing in cooperatively displaying long-tailed manakins. *Behavioral Ecology, 13*, 65–69.

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man, 1871–1971* (pp. 136–207). Chicago, IL, U.S.A.: Aldine.

de Waal, F. B. M., & Tyack, P. L. (2003). *Animal social complexity*. Cambridge, MA, U.S.A.: Harvard University Press.

Wagner, A. P., Creel, S., Frank, L. G., & Kalinowski, S. T. (2007). Patterns of relatedness and parentage in an asocial, polyandrous striped hyena population. *Molecular Ecology, 16*, 4356–4369.

Wagner, A. P., Frank, L. G., & Creel, S. (2008). Spatial grouping in behaviourally solitary striped hyaenas, *Hyaena hyaena*. *Animal Behaviour, 75*, 1131–1142.

Wallin, J. E. (1989). Bluehead chub (*Nocomis leptocephalus*) nests used by yellowfin shiners (*Notropis lutipinnis*). *Copeia, 1989*, 1077–1080.

Waser, P. M., Keane, B., Creel, S. R., Elliott, L. F., & Minchella, D. J. (1994). Possible male coalitions in a solitary mongoose. *Animal Behaviour, 47*, 289–294.

Watts, C. R., & Stokes, A. W. (1971). Social order of turkeys. *Scientific American, 224*, 112–118.

Watts, D. P. (1998). Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology, 44*, 43–55.

West-Eberhard, M. J. (1979). Sexual selection, social competition, and evolution. *Proceedings of the American Philosophical Society, 123*, 222–234.

Whittingham, L., Dunn, P., & Magrath, R. (1997). Relatedness, polyandry and extra-group paternity in the cooperatively-breeding white-browed scrubwren (*Sericornis frontalis*). *Behavioral Ecology and Sociobiology, 40*, 261–270.

Williams, D. (2004). Female control of reproductive skew in cooperatively breeding brown jays (*Cyanocorax morio*). *Behavioral Ecology and Sociobiology, 55*, 370–380.

Witt, R., Schmidt, C., & Schmitt, J. (1981). Social rank and darwinian fitness in a multimale group of Barbary macaques (*Macaca sylvana* Linnaeus, 1758). Dominance reversals and male reproductive success. *Folia Primatologica, 36*, 201–211.

Witte, K. E., & Schmidt, J. (1992). *Betta brownorum*, a new species of anabantoids (Teleostei: Belontiidae) from northwestern Borneo, with a key to the genus. *Ichthyological Exploration of Freshwaters, 2*, 305–330.

Yin, B., Yang, S., Wei, W., & Zhang, Y. (2009). Male reproductive success in plateau pikas (*Ochotona curzoniae*): a microsatellite analysis. *Mammalian Biology, 74*, 344–350.

Zammit, J., & Schwarz, M. P. (2000). Intersexual sibling interactions and male benevolence in a fig wasp. *Animal Behaviour, 60*, 695–701.