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Sex, Love, or War? A Representation of 20 Years of Research on the Social Interactions of Animals

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To navigate through a social world, animals may form temporary or long-term associations with others, recognize kin and discriminate between familiar and unfamiliar conspecifics, protect themselves and their resources, fight and compete for the best mates, and produce offspring that require various forms of care. The purpose of the current paper was to summarize the publication trends of research investigating animal social interactions over the last 20 years. We selected 8 journals for their diverse representation of animal taxa and examined the number of published articles representing research on affiliative, agonistic, and sexual social interactions. Out of 18,993 published articles, social interactions were studied in 5.5% to 30.8% of the published articles per journal between 1993-2013 (N = 4,273). Agonistic social interactions (43%) were the most frequently published topic with affiliative social interactions representing less than a third (30%) of the articles and sexual social interactions accounting for the remaining articles (27%). Mammalian social interactions were investigated the most (38.5%) with invertebrate (22%) and avian (21%) social interactions following closely behind. Observational research and experimental research designs were used to explore different social interactions. Social interactions were studied most often in laboratory settings (45%), then semi-natural field settings (32.5%), and less often in natural habitats (19%). Interestingly, the rates of the different types of social interactions, certain taxa, type of research study, and research setting remained relatively consistent across the 20 year period. Some fluctuations occurred in the frequency of specific topics and taxa within various years; however, research on mate choice, parental care, environmental influences, and group composition was consistently conducted across the years. While many aspects of social interactions in a broad range of taxa have been studied, there are many areas that are still sparse and in need of additional research.

To navigate through a social existence, animals may form temporary or long-term associations with others, recognize kin and discriminate between familiar and unfamiliar conspecifics, protect themselves and their resources, fight and compete for the best mates, and produce offspring that require various forms of care. Our knowledge about social interactions of animals is myriad as the availability of species, ease of experimentation, funding access, and the research interests of the scientists have shaped this vast body. A variety of texts summarize the basics of animal behavior using specific, and often, unique examples to highlight key points (Bolhuis & Giraldeau, 2005; Bolhuis & Hogan, 1999). With the exception of this special issue, only a handful of journal articles have attempted to describe the current state of the literature examining animal social interactions (Banks, Piggott, Stow, & Taylor, 2007; Choleris & Kavaliers, 1999; Dukas, 2008; Galef & Laland, 2005; Krause, Lusseau, & James, 2009; Nakamura, 2009; Pepperberg, 2011; Rosa Salva, Regolin, Mascalzoni, & Vallortigara, 2012; Yuying, Earley, & Wolf, 2006). While these reviews are limited to specific aspects of social interaction due to the inherent difficulty in organizing such a diverse array of literature, they are critical to our understanding of the status of research on social interactions in animals.

Beginning with a topic that is related to cognition (see Beran, Parrish, Perdue, & Washburn, 2014 in this issue), Rosa Salva and colleagues (2012) describe the importance of lateralization in visual recognition and processing of various stimuli that facilitate social interactions within species. For example, Karenina, Giljov, Glazov and Malashichev (2013) recently observed that beluga calves (*Delphinapterus leucas*) in their natural habitat prefer to swim on the left side of their mothers presumably to process their mother's proximity

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and behavior. This finding was supported by another study in which dolphins (*Tursiops aduncas*) preferred to initiate tactile contact with a swim partner positioned to their left (Sakai, Hishii, Takeda, & Kohshima, 2006), with both studies suggesting that cetaceans may monitor the actions of a preferred or familiar conspecific with their right hemispheres (Karenina et al., 2013; Sakai et al., 2006). Banks, Piggot, Stow, and Taylor (2007) described the difficulty social species may face living in environments in which habitats are fragmented, as disjointed habitats lead to fewer opportunities to engage in social interactions. Another study reviewed the various mediators and outcomes of fighting contests between animals (Yuving, Earley, & Wolf, 2006). The results of this review indicated that the neuroendocrine mechanisms underlying these contests were important but difficult to synthesize into a cohesive understanding, leading the authors to conclude that additional research was needed (Yuving et al., 2006). Using primates as an example, Nakamura (2009) emphasized the importance of focusing on the social interaction itself in order to fully understand the functions and consequences of those social interactions. While the component behaviors are critical to recognizing a social interaction, they are not sufficient to understanding the larger picture (Nakamura, 2009). Network theory and modeling allows researchers to begin to look at the social interaction within small or large settings. These techniques allow researchers to understand the influences of social interactions on group compositions and long-term associations (Krause, Lusseau, & James, 2009). Other studies reviewing the role of social learning in the behavioral fitness of a species reiterate the importance of studying social interactions. Whether an insect or a mammal, social interactions provide individuals opportunities to learn new behaviors or to manipulate old behaviors in novel ways (see Blaser & Belizzi, 2014 this issue, Choleris & Kavaliers, 1999; Dukas, 2008; Galef & Lelund, 2005). Finally, social interactions are also critical to the development of cognitive abilities as highlighted by Pepperberg (2011) in her review on the importance of social interactions in avian cognition.

Unlike many other species-typical behaviors, social interactions require two conditions: the presence of two or more animals and an exchange of behaviors in which one animal initiates a behavior and the other animal produces a response to the initiator. Affiliative social interactions involve behaviors that function to create and/or strengthen bonds, repair existing bonds, or achieve beneficial reciprocity between two or more animals. A variety of behaviors are displayed during affiliative interactions (i.e., grooming, playing, greeting, touching, and altruistic behaviors; Connor, 2002). For example, primate grooming preserves cohesion, and as group size increases, grooming time increases (Lehmann, Korstjens, & Dunbar, 2007). Young and adult dolphins play cooperatively both in human care and in their natural habitat, suggesting that play may facilitate bond development and maintenance (Kuczaj & Highfill, 2005). Black-and-White Colobus monkeys (*Colobus guereza*) greet each other through embracing or non-sexual mounting following agonistic behavior or during a non-agonistic reunion with another individual (Kutsukake, Suetsugu, & Hasegawa, 2006). Giraffe (*Giraffa camelopardalis*), in human care, establish relationships and indicate preferences by approaching and examining each other socially, or necking, rubbing heads, or bumping one another (Bashaw, Bercovitch, Bloomsmith, & Maple, 2007). Finally, female mule deer (*Odocoileus hemionus*) respond with strong defensiveness to distress calls of fawns despite the doe's reproductive status, her relation to the fawn, or the presence of her own fawns (Lingle, Rendall, Wilson, Deyoung, & Pellis, 2007).

Agonistic social interactions involve behaviors that are aggressive, threatening, or submissive (Swedell, 2012). Examples of aggressive behaviors include hitting, kicking, biting, scratching, or other direct contact that aims to wound or challenge. Threatening behavior can involve non-contact displays such as growling, tooth display, pounding/thumping, head-tossing, lunging, or inflated display of body parts. Submissive behavior can be demonstrated through vocalization, avoidance, flinching, pacifying posture, and tucking or flattening of certain body parts (Connor, 2002). A majority of agonistic behavior in California male sea lions (*Zalophus californianus*) involves calling or chasing displays rather than costly direct body conflict (Jacobs, Hernandez-Camacho, Young, & Gerber, 2008). Bred captive sows (*Sus scrofa domesticus*) use bites, head knocks, and body knocks to establish social hierarchy (Seguin, Friendship, Kirkwood, Zanella, & Widowski, 2006). For meerkats (*Suricata suricatta*), avoidance rather than submission is a more successful strategy in preventing repeat aggressive encounters with conspecifics (Kutsukake & Clutton-Brock, 2008). In

an extreme example of agonistic social interactions, many animals, from insects to mammals, display filial cannibalism or infanticide (Fox, 1975). This agonistic act may be intentional or unintentional and appears to be an adaptive mechanism to increasing the fitness of a group or a species.

Sexual (i.e., socio-sexual) social interactions consist of many types of behaviors between individuals that may involve genital-to-genital contact (e.g., intromission attempts, copulations, or reciprocal genital stimulation), selection of partners based on various displays (e.g., armaments, coloration, gifts), mate guarding, sexual conflict (e.g., sperm competition, cannibalism), and many other aspects (Elgar, 2005; Moller, 2005). Comb-footed spiders (*Anelosimus studiosus*) display non-conceptive sexual play in which male and female spiders practice courting one another (Pruitt, Burghardt, & Riechert, 2012). Depending on the type of fly (*Drosophila* spp.), male flies will dance, "sing," or present females with silk-covered food nuptials to elicit copulation (Ryan, 2005). Males from many taxa often guard their mates from rival males to ensure reproductive success (Elgar, 2005). Additionally, some animals will consume their mates following copulation (e.g., female spiders, Sasaki & Iwahashi, 1995).

The purpose of the current study was to examine publication trends during the last 20 years of research in which social interactions were investigated. Using a sample of journals known to publish behavioral research on a broad range of taxa, we examined each research study involving social interactions. Each study was coded for type of social interaction, taxon investigated, type of research method, setting in which the research study was conducted, specific topic of interest, and year of publication. Several questions guided our review:

1. How often were social interactions studied as compared to other types of behaviors between 1993 and 2013?
2. Did the number of articles published on social interactions change during that time frame?
3. What types of social interactions were studied and did they change over time?
4. Did interest in specific social interaction topics fluctuate over time?
5. Was there a priority in topics examined and published during the last five years?
6. What types of animals were studied and did interest in various animals change over time?
7. Finally, what research methods and settings were used to study the social interactions?

Method

Sample

Sixty-nine journals that publish research about social interactions on a broad range of non-human animals were reviewed for this study (Table 1). This list presented in Table 1 is not exhaustive as there are many taxon-specific and topic-specific journals that may publish research on social interactions. For the purpose of this study, we narrowed our final selection of journals to review using the following criteria: 1. a broad range of taxa were published within the journal, 2. the articles reflected diverse behavioral interactions, 3. articles represented original research studies that used different methodologies, and 4. the journal had a minimum of a 20-year publication history. Eight journals were identified as our final selection: *Animal Behaviour, Applied Animal Behavior Science, Behavioral Ecology & Sociobiology, Behaviour, Behavioral Processes, International Journal of Comparative Psychology, Journal of Comparative Psychology, and Ethology*. After excluding all reviews of books, commentaries, theoretical papers, and letters to the editor, we reviewed 18,993 articles. Of these articles, 4,273 articles reflected research studies involving a social interaction of some type. This final sample represented 22.5% of the available articles published across the eight selected journals.

Variables

The articles were coded for a number of measures including the type of social interaction (i.e., *agonistic, affiliative*, and *sexual*), the specific topic for each social interaction (i.e., a subtopic – Table 2), the particular taxon under study, the type of research design, and the type of research setting. We defined agonistic social interactions as interaction behaviors between two or more animals that were aggressive, threatening, or submissive in nature; affiliative social interactions as interaction behaviors that served to create and/or strengthen bonds, repair existing bonds, or achieve beneficial reciprocity between two or more animals; and sexual social interactions as interaction behaviors between two or more animals that related specifically to sex, including genital-to-genital contact, mate selection, and mate guarding. Thirty-two subtopics were developed to capture aspects of the focus of each study, which are

summarized in Table 2. Subject taxa were categorized as *mammal*, *reptile*, *amphibian*, *bird*, *fish*, or *invertebrate*. Research design for each study was classified as either *experimental* or *observational*. Experimental designs involved some type of manipulation within the study whereas observational designs involved studies in which naturally existing differences were studied. Research settings were identified as *lab*, *semi-natural field*, *natural habitat*, *zoo*, and *not included* (see Table 3 for operational definitions).

Table 1
Journals publishing research on animal social interactions

Acoustical Physics	Comparative Biochemistry & Physiology Part B	Mammal Review
American Journal of Veterinary Research	Conservation Biology	Marine Biology
American Journal of Primatology	Ecological Applications	Marine Environmental Research
Anatomia, Histologia, Embryologia: Journal of Veterinary Medicine Series C	Ecology	Marine Fisheries Review
Animal Behaviour	**Ethology**	Marine Mammal Science
Animal Cognition	Fisheries Science	Molecular Ecology
Animal Learning & Behavior	Fishery Bulletin	Molecular Ecology Notes
Annual Reviews	Folia Primatologica	Journal of the Acoustical Society of America
Anthrozoos	ICES Journal of Marine Science	Natural History
Applied Animal Behaviour Science	**International Journal of Comparative Psychology**	Nature
Aquatic Mammals	International Journal of Primatology	New Zealand Journal of Marine & Freshwater Research
Aquatic Toxicology	Journal of Animal Ecology	Pacific Science
Arctic	Journal of Applied Ecology	Polar Biology
Behavioral & Brain Sciences	Journal of Comparative Physiology B: Biochemical, Systemic, & Environmental Physiology	Primates
Behavioral Ecology and Sociobiology	**Journal of Comparative Psychology**	Proceedings: Biological Sciences
Behaviour	Journal of Experimental Biology	Science
Behavioural Brain Research	Journal of Experimental Marine Biology & Ecology	Science of the Total Environment
Behavioural Processes	Journal of Experimental Psychology	Sensory Systems
Bioacoustics	Journal of Heredity	Veterinary Immunology & Immunopathology
Biological Conservation	Journal of Mammology	Veterinary Microbiology
Bioscience	Journal of Parasitology	Veterinary Record
Brain, Behavior & Evolution	Journal of Primatology	Wildlife Conservation
Canadian Journal of Zoology	Journal of Wildlife Diseases	Zoo Biology

Note. **Bolded** journals were used for the current article.

Procedure

Two coders identified potential articles and coded the selected articles. Two local universities were used to access online journal databases to search for peer-reviewed articles pertaining to "social interactions of animals." After selecting the specific journals that met our criteria, we examined all of the articles published within each journal from the years 1993 to 2013. We scanned the titles and abstracts to identify the topic of each article and to determine whether the study involved investigation of agonistic, affiliative, or sexual social interactions. Topics related to agonistic social interactions contained key words such as "fighting," "competition," "contest," "submission," "dominance," "displacement," "aggression," "infanticide," "siblicide," "territorial," "predatory," "injuries," and "cannibalism." Examples of key words within affiliative interaction topics included "cooperation," "mutualism," "grooming," "altruism," "adoption," "parental care," "sharing," "social bonds," and "play." Topics specific to sexual social interaction behavior often featured key words like, "copulation," "breeding," "courtship display," "mating," and "mate choice."

When further clarification was necessary, we read the articles in full text to ensure that the contents met the criteria for agonistic, affiliative, and sexual interactions among animals. If an article pertained to one of these three interaction categories but the study did not involve pure social interaction (such as utilizing playbacks or animal models), then the article was excluded from selection. Articles specific to our interests were documented within Microsoft Excel 2007 spreadsheet. Each documentation included the journal name, article title, authors of the study, type of social interaction studied, associated subtopic, subject taxon category, sample size, year that the article was published, setting of the research, and the type of study. The total number of articles published each month was also documented to ascertain the overall publishing trends for each journal per year.

Table 2
Operational definitions of subtopics

Categories	Operational Definitions
Aggression	Social interactions involving aggression, conflicts, infanticide, etc.
Behavioral	Social interactions pertaining to general behaviors involving defense, and other responses
Cognition	Social interactions involving recognition or decision making or memory
Competition	Social interactions that involved competition or contests for territory and resources
Cooperation	Social interactions associated with individuals working or cooperating together
Courtship	Social interactions associated with sexual courting and display
Development	Social interactions involving changes over time, focusing on young and adolescent influences
Dominance	Social interactions involving the importance of status
Emotion	Social interactions involving the study of emotions
Environment	Social interactions affected by any external stimulus or context (i.e. resource distribution, group influences, territories)
Foraging	Social interactions involving foraging or finding food
Genetics	Social interactions associated with kinship or the influence of genetics
Group Composition	Any study investigating effects, such as audience effects, upon social interactions within a group of individuals that varies in size and characteristics
Hormones	Social interactions influenced by any pheromone/hormone or other chemical injection
Laterality	Social interactions that are influenced by lateralization
Learning	Social interactions associated with any conditioning, previous experience, priming, long-term memory, or familiarity with previously-encountered individuals
Mate Choice	Social interactions related to anything about sex, mate choices, sex ratios, ornaments, and sexual conflicts
Networks	Social interactions involving any kind of affiliation research looking at relationships, cohesion, and cooperation.
Neurobiology	Social interactions influenced by any neurotransmitters, brain areas and processes, etc.
Nursing	Social interactions involving nursing, suckling, or weaning
Offspring	Social interactions involving hatchlings or young
Olfaction	Social interactions involving the effect of smells or odor detection/scents
Parental Care	Social interactions involving behaviors that adult animals direct toward offspring
Personality	Social interactions affected by behavioral syndromes and individual stable characteristics
Physiological	Social interactions involving the effect of any body, anatomical stimulus, or change (i.e., coloration change or appendages lost/gained)
Play	Social interactions involving play
Reconciliation	Social interactions following conflict that serve to repair bonds
Separation	Social interactions influenced by the isolation or separation of individuals from groups or parents
Sex Differences	Social interaction studies looking at differences between the sexes
Social Cues	Social interactions pertaining to physiological-sensory signals or behavioral signals that are used to indicate a subject's status
Stress	Social interactions affected by stress
Vocalization	Social interactions involving sounds & vocals

All data were analyzed using IBM SPSS® 19.0. Chi square goodness of fit tests, chi square tests of independence, binomial tests, and Spearman correlations were used to explore the various trends in publications on non-human animal research investigating social interactions. All data are represented as frequencies or percentages unless otherwise noted.

Table 3
Operational definitions of types of settings

Categories	Operational Definitions
Lab	A setting where a study is conducted within an artificial, controlled environment whereby experimental conditions are easily manipulated.
Field	A setting whereby research is conducted within a natural or semi-natural habitat that allows some control by the experimenter, and subjects are able to behave as they normally would without significant human interference (e.g., nature preserves, pastures, farms). Subjects may be wild or captive.
Natural Habitat	A totally natural setting where animals live freely in their wild habitat without human control. (e.g., forests, lakes, oceans, mountain ranges, prairies, etc.)
Zoo	A setting that consists of an enclosure or constructed habitat that mimics a natural environment for a species but allows more subject control compared to field and natural settings.
Not Included	This category applies if a study does not specify a research setting.

Results

Overall Trends

Many journals publish articles about social interactions in non-human animals (Table 1). We identified 4,273 articles in which social interactions were studied from the almost 19,000 articles processed from the eight journals examined. On average, about 23% ± 16% of the published research studies involved social interactions. Individual journals ranged between 6% and 56% in their publication of articles regarding social interactions (Table 4), and also varied in the total number of research studies they published each year, with *Animal Behaviour* publishing significantly more articles in general ($\chi^2(7, N = 4{,}273) = 3{,}891.62$, $p < 0.001$). Overall, agonistic social interactions (n = 1,819, 42.7%) were studied significantly more than affiliative interactions (n = 1,275, 29.9%) and sexual interactions (n = 1,147, 26.9%) ($\chi^2(2, N = 4{,}241) = 180.12$, $p < 0.001$). The articles were then sub-divided into more specific topics for a finer analysis. Thirty-two topics were identified with mate choice, parental care, environmental factors, and group composition occurring the most often across the articles ($\chi^2(31, N = 4{,}261) = 5{,}805.59$, $p < 0.001$, Table 3 for topics). Six taxa were represented across the journals with mammals (n = 1,632) representing the most frequently studied taxon and reptiles (n = 122) and amphibians (n = 86) representing the least studied taxa ($\chi^2(5, N = 4{,}239) = 2{,}393.63$, $p < 0.001$; Figure 1). Interestingly, the research studies were divided fairly equally between observational (n = 992, 48.4%) and experimental (n = 903, 44.0%) research paradigms although the results of a binomial test indicated that observational research occurred significantly more often than experimental research (p = 0.043). Finally, studies were conducted significantly more than expected by chance in both laboratory (n = 856, 45.0%) and semi-natural field settings (n = 617, 32.5%); natural habitats (n = 358, 19.0%) were used less often than expected by chance.

Table 4
Article frequencies per category for each journal

	AB	AAS	BEH	BES	BP	ETH	IJCP	JCP
Total Articles	5901	2929	1560	3040	2279	697	388	2199
Social Interactions	1807	422	452	646	292	390	23	241
% of Articles	30.6	14.4	29.0	21.3	12.8	56.0	5.9	11.0
Agonistic Interactions	849	237	176	223	139	126	6	63
Affiliative Interactions	454	118	125	181	107	135	13	142
Sexual Interactions	504	46	149	241	44	124	4	36

Note. AB = *Animal Behaviour*; AAS = *Applied Animal Science*; BEH = *Behaviour*; BES = *Behavioral Ecology & Sociobiology*, BP = *Behavioral Processes;* ETH = *Ethology*; IJCP = *International Journal of Comparative Psychology;* JCP = *Journal of Comparative Psychology*

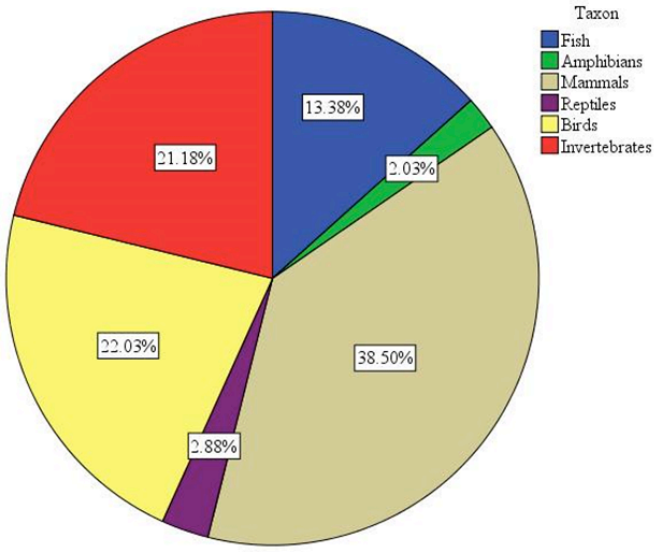

Figure 1. Percentage breakdown of taxa represented across all articles involving social interactions.

Trends Across the Years

Each journal showed some fluctuations in the number of articles they published on social interactions across the 20-year period in five year increments (Figure 2). Spearman correlations were conducted for each journal to determine if any trends existed in the frequency of publications on social interactions across the years. The results indicated that two journals published more articles on social interactions recently: *Behavioral Ecology and Sociobiology* (r_s = 0.71, p < 0.001) and *International Journal of Comparative Psychology* (r_s = 0.65, p < 0.001). To further investigate the yearly trends, we conducted a series of chi square tests of independence for each of the major variables – type of social interactions, taxon, specific subtopic, type of study, and study setting.

Type of Social Interactions. The represented percentage of each type of social interaction remained relatively consistent over the years, the results of the chi square test of independence indicated that there was a relationship between the two variables (χ^2(40, N = 4,241) = 87.68, p < 0.001, V = 0.102; Figure 3). Although the overall analysis indicated that agonistic interactions occurred more frequently than affiliative interactions across all articles, this trend was replicated only for the initial years of the study (i.e., 1993, 1995, 1997) in which agonistic interactions were studied more than expected by chance. In 1999 and 2003, sexual interactions were examined at significantly higher rates than expected by chance. Finally, in 2000, 2002, and 2013, affiliative interactions were examined at significantly higher rates than expected by chance.

Specific Subtopics. The publication frequency across years on specific topics was extremely diversified (Table 5). A statistically significant relationship was found between year and the specific topics (χ^2(620, N = 4,261) = 802.50, p < 0.001, V = 0.097); however, given the inconsistent results and the very small effect size, interpretation of these results is difficult. A detailed examination of the results did not support any clear trends across the different articles.

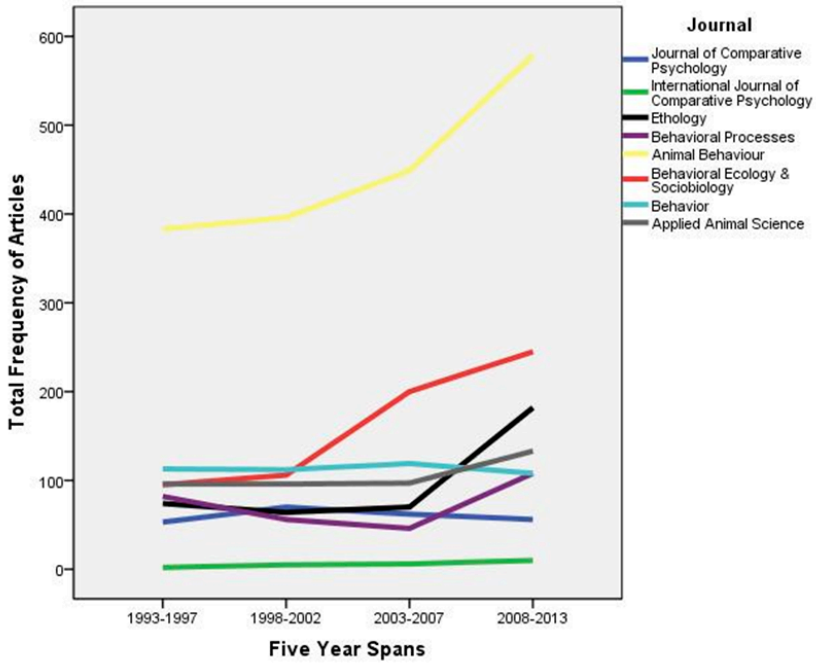

Figure 2. Number of articles on social interactions per journal from 1993-2013.

Aside from mate choice, parental care, group composition, and environmental influences, few other topics were consistently studied across the years. Interestingly, slightly different results appeared when subtopics were examined across the journals. Mate choice continued to the lead the way as one of the most popular topics across journals, but several other subtopics emerged as important publication trends, including the influence of foraging demands, the presence of offspring, learning effects, associations between individuals, and play interactions.

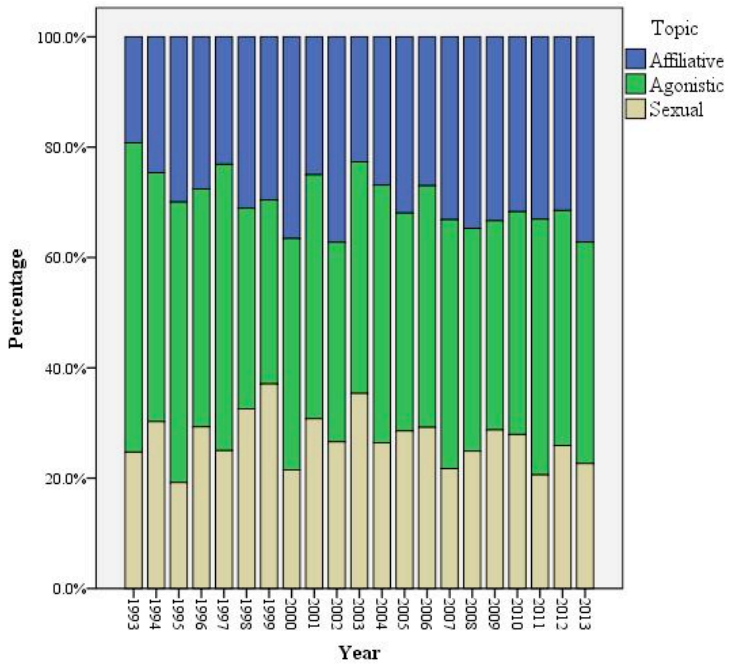

Figure 3. Percentage of articles on types of social interactions from 1993-2013

Table 5
Frequencies for specific sub-topics per journal

	AB	AAS	BEH	BES	BP	ETH	IJCP	JCP	TOTAL
Aggression	36	0	**41**	14	0	14	0	7	112
Behavioral	67	**33**	7	25	**22**	**34**	3	7	198
Cognition	19	0	1	2	0	6	0	**10**	38
Competition	**19**	1	3	0	0	0	0	0	23
Cooperation	**55**	0	2	11	2	6	0	3	79
Courtship	90	14	27	43	14	**62**	0	10	260
Development	11	7	4	6	**8**	3	1	4	44
Dominance	86	30	30	24	**33**	26	1	11	241
Emotion	0	0	0	0	2	0	0	**1**	3
Environmental Factors	143	**69**	32	32	10	13	4	8	311
Foraging	42	8	5	16	**15**	**19**	0	4	109
Genetics	33	**12**	7	13	2	1	0	3	71
Group Composition	94	77	25	50	15	26	0	11	298
Hormones	44	11	5	14	**12**	10	0	7	103
Laterality	3	0	0	1	0	0	0	0	4
Learning	37	4	2	14	12	4	**4**	**13**	90
Mate Choice	**401**	19	**103**	**158**	31	54	0	29	795
Networks-Associations	42	5	**25**	14	0	12	1	**19**	118
Neurobiology	1	0	0	1	**4**	0	0	1	7
Nursing	4	**10**	0	3	4	4	**2**	4	31
Offspring	**55**	0	3	**22**	0	3	0	3	86
Olfaction	27	3	3	7	6	3	0	3	52
Parental Care	140	46	49	59	31	30	2	25	382
Personality	13	**20**	3	4	0	2	0	2	44
Physiology	111	23	21	32	19	17	1	7	231
Play	14	**10**	6	1	4	4	**2**	**12**	53
Reconciliation	18	1	8	0	6	6	1	3	43
Separation	1	2	0	0	**4**	3	0	2	12
Sex Differences	28	8	3	**25**	9	1	1	4	79
Social Cues	**70**	1	9	12	12	9	0	3	116
Stress	2	**4**	0	1	0	0	0	0	7
Vocalization	101	3	28	31	15	18	0	25	221

Note. AB = *Animal Behaviour*; AAS = *Applied Animal Science*; BEH = *Behaviour*; BES = *Behavioral Ecology & Sociobiology*, BP = *Behavioral Processes;* ETH = *Ethology*; IJCP = *International Journal of Comparative Psychology;* JCP = *Journal of Comparative Psychology*. **Bolded** numbers represent the categories that occurred at frequencies significantly above chance. **Bolded** topics represent topics that occurred significantly above chance.

Taxa. The results of the chi square test of independence indicated that the use of certain taxa was related to the year of publication ($\chi^2(100, N = 4{,}239) = 157.77$, $p < 0.001$, $V = 0.086$). Like the previous analysis, a detailed examination of the results did not produce any specific trends in publication across the years. In 2002 and 2004, reptiles were studied significantly more frequently than expected by chance, as were amphibians in 1993, fish in 2005, and invertebrates in 2009. Despite these slight changes in publication frequency, the use of taxa also remained relatively consistent across the years with mammals the most often studied taxon followed by birds and invertebrates (Figure 4).

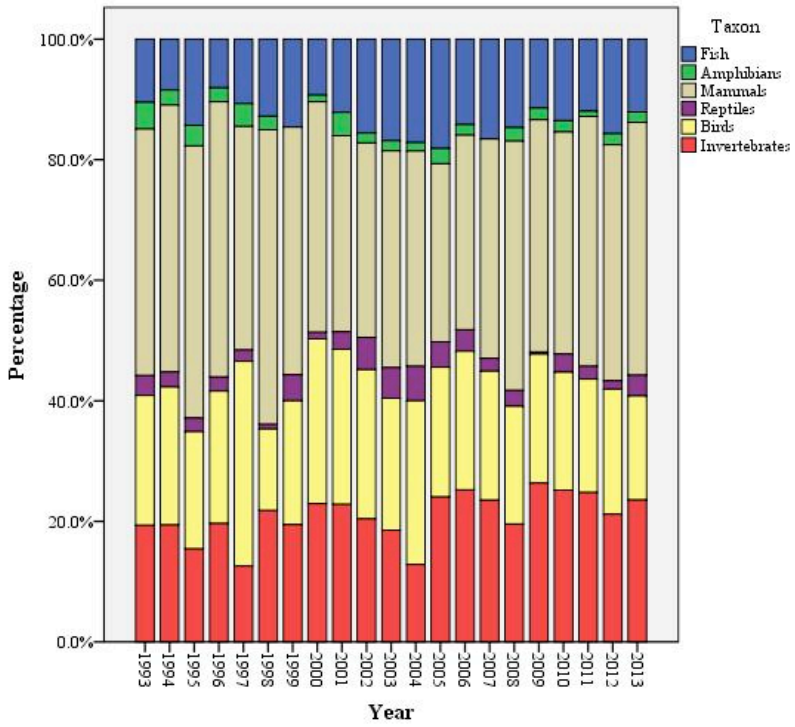

Figure 4. Percentage of articles by taxa from 1993-2013.

Research Methods. The results of a chi square test of independence indicated the presence of a statistically significant relationship between year and the type of study method used ($\chi^2(20, N = 1{,}895) = 46.74$, $p = 0.001$, $V = 0.157$). As before, no clear trend emerged in the use of research methods across the years. The frequencies of observational and experimental methods were distributed as expected by chance across each year with only a few years in which the type of research used fluctuated some. In 1993 and 2009, experimental methodologies occurred more often than expected by chance and in 2008 and 2013, observational methodologies occurred more often than expected by chance.

Research Setting. The results of a chi square test of independence indicated a significant relationship between the year and the study setting used to conduct the study ($\chi^2(60, N = 1{,}895) = 122.69$, $p < 0.001$, $V = 0.147$). In 1993 and 2002, laboratory settings were used more than expected by chance. In 2007, field settings and controlled and uncontrolled settings were used more than expected by chance. Natural habitat was represented significantly more often than chance in 2008 and 2012 and a mix of research settings was again observed more often than expected by chance in 2011 and 2013.

Interactions Across Variables

We conducted several additional analyses to explore the relationship between various variables to better understand publication trends in research involving social interactions. In particular, we were interested in determining if the type of social interaction studied was related to taxa, specific topics, type of research method used, or the setting in which the research was conducted.

Social interaction and taxa. The results of a chi square test of independence indicated that the type of social interaction studied was related to the taxa studied ($\chi^2(60, N = 1{,}895) = 122.69$, $p < 0.001$, $V = 0.147$). Mammals and birds were used significantly more than expected by chance when affiliative social interactions were studied while fish and reptiles were used significantly more than expected by chance to study agonistic social interactions (Figure 5). Interestingly, invertebrates, fish, and amphibians were used significantly more than expected by chance to study sexual social interactions.

Social interaction and type of research study. The results of a chi square test of independence indicated that a relationship existed between the type of research study conducted and the type of social interaction studied ($\chi^2(2, N = 1{,}866) = 36.69$, $p < 0.001$, $V = 0.140$). Observational research was used significantly more often than expected by chance to study affiliative social interactions ($n = 390$, 61.5%) and significantly less often than expected by chance to study agonistic social interactions ($n = 361$, 45.9%). In contrast, experimental research was used to study agonistic social interactions significantly more often than expected by chance ($n = 426$, 54.1%) and to study affilitative social interactions significantly less often than expected by chance ($n = 244$, 38.5%). Sexual social interactions were studied with both types of research methods at fairly equal rates (observational, $n = 217$, 48.8% and experimental, $n = 228$, 51.2%).

Social interaction and research setting. A significant relationship between the type of social interaction and the setting used to conduct the study was found ($\chi^2(6, N = 1{,}864) = 153.31$, $p < 0.001$, $V = 0.203$; Figure 6). The results indicated that sexual social interactions were studied significantly more than expected by chance in laboratory settings than either in a controlled field setting or a natural habitat. Agonistic social interactions were studied significantly more than expected by chance in a controlled field setting than in a laboratory or a natural habitat setting. Finally, affiliative social interactions were studied significantly more than expected by chance in a natural habitat or in a combination of research settings.

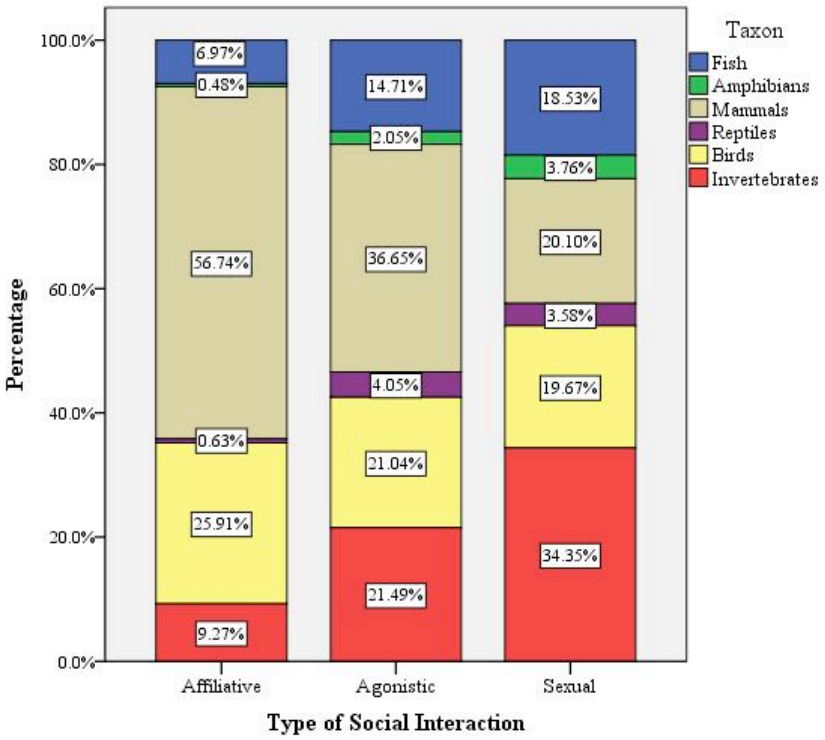

Figure 5. Percentage of articles by taxa per type of social interaction.

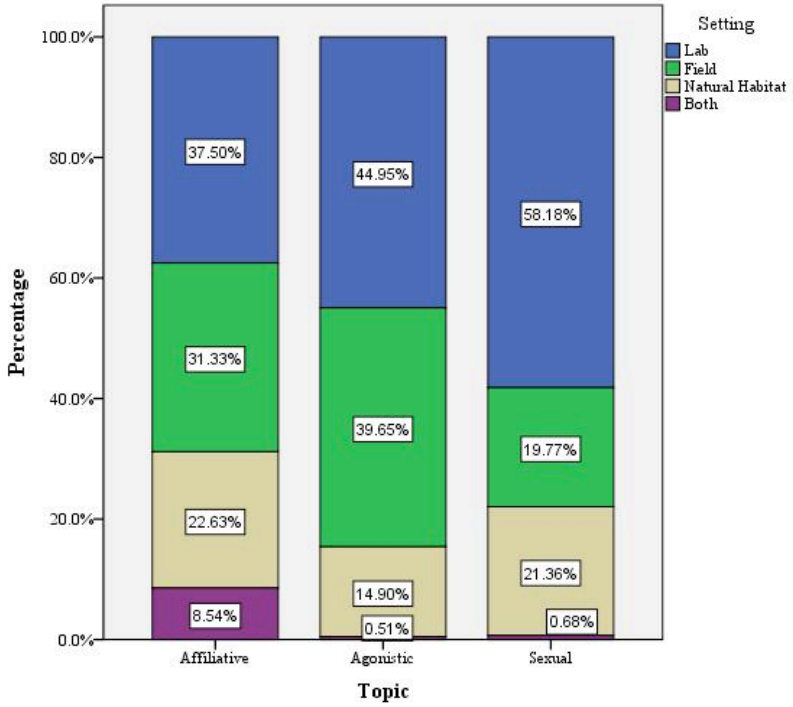

Figure 6. Percentage of articles by setting per type of social interaction.

Trends Between 2008-2013

A final set of chi square tests of independence was conducted to determine if any clear trends existed for research investigating different types of social interactions. Of the different variables of interest (e.g., taxa, type of study) only the type of study conducted may have changed in the last five years ($\chi^2(5, N = 543) = 26.54, p < 0.001, V = 0.221$); no other relationship between the year and each variable was discovered. The results of the significant analysis indicated that slightly more observational studies were conducted across each of the last five years than experimental studies with the exception of 2009 when experimental studies ($n = 65$, 67%) were conducted significantly more than expected by chance.

Given that each variable was not influenced by the year, the data were collapsed across the five-year period to determine if any overall trends could be detected. A series of chi square goodness of fit tests was conducted for each major variable: type of interaction studied, specific topic identified, taxa, and type of research setting. Agonistic interactions continued to be the most frequently studied social interaction ($n = 582$, 41.2%) followed by affiliative interaction ($n = 472$, 33.4%) and sexual interactions ($n = 358$, 25.4%) ($\chi^2(2, N = 1,412) = 53.31, p < 0.001$). Specific topics remained the same as observed in the 20-year data with studies on mate choice ($n = 238$, 16.8%), parental care ($n = 109$, 7.7%), group compositions ($n = 104$, 7.3%), environment ($n = 95$, 6.7%), and vocalizations ($n = 82$, 5.8%) representing the most frequently occurring topic of interest ($\chi 2$ (30, $N = 1,417$) = 1,402.63, $p < 0.001$). The taxa studied also followed the 20-year trend with mammals ($n = 564$, 39.7%), invertebrates ($n = 333$, 23.5%), and birds ($n = 279$, 19.7%) representing the taxa most frequently studied ($\chi^2(5, N = 1,419) = 879.92, p < 0.001$). Finally, the most recent data for type of research setting were also similar to the 20-year trends such that research conducted in laboratories ($n = 216$, 38.9%) and field settings ($n = 169$, 30.3%) occurred significantly more often than expected by chance with research conducted in multiple types of settings ($n = 28$, 5.0%) occurring with significantly less frequency than expected by chance ($\chi^2(3, N = 555) = 138.08, p < 0.001$).

Brief Comparison of Results to Articles Published in *Science* and *Nature*

To ascertain the scientific impact of research on social interactions in non-human animals, we conducted a brief review using *Google Scholar* to determine the most frequently cited articles on the three types of social interactions as published by *Science* and *Nature* during our 20 year period. The results for *Science* produced 23 articles for affiliative social interactions, 12 articles for agonistic social interactions, and 16 articles for sexual social interactions. Of these articles, six had been cited 100 or more times in subsequent publications and included studies on affiliative social interactions investigating lions and birds, studies of agonistic social interactions involving primates and genetically-altered mice, and studies of sexual social interactions examining protozoans and spiders. The results for *Nature* produced 32 articles for affiliative social interactions, 5 articles for agonistic social interactions, and 6 articles for sexual social interactions. Of these articles, all but two had been cited more than 100 times in subsequent publications and included studies investigating mainly mammals (primates and rodents) but included all major animal groups (affiliative interactions), mainly mammals (agonistic interactions), and birds and mammals (sexual interactions).

Sub-topics of interest for *Science* included cooperation (McDonald & Potts, 1994, 174 citations), conflict resolution (de Waal, 2000, 268 citations), courtship and mating practices (Andrade, 1996, 222 citations; Packer, Pusey, & Eberly, 2001, 99 citations; West, Herre, & Sheldon, 2000, 102 citations). *Nature,* included a wider range of sub-topics with many involving genetic, hormonal, or neurophysiological functions of various social behaviors. The two most frequently cited articles involving affiliative social interactions included a study on brown capuchin monkeys (*Cebus apella*) responding to inequitable food conditions (Brosnan & De Waal, 2003, 773 citations) and a study with mice whose social behavior is affected by the loss of the oxytocin gene (Ferguson, Young, Hearn, Matzuk, Insel, & Winslow, 2000, 524 citations). The two most frequently cited articles for agonistic interactions included the cognitive ability of Pinyon jays (*Gymnorhinus*

cyanocephalus) to deduce social dominance (Paz-y-Mino, Bond, Kamil, & Balda, 2004, 147 citations) and an increase in hormones while fish watch fights (Oliveira, Lopes, Carneiro, & Canário, 2001, 142 citations). Finally, the two most frequently cited article involving sexual social interactions included the unexpected finding that female birds increased their offspring's fitness through extra-pair matings (Foerster, Delhey, Johnsen, Lifjeld, & Kempenaers, 2003, 320 citations) and evidence for a neural circuit in female mice that activates during male sexual behavior (Kimchi, Xu, & Dulac, 2007, 174 citations).

Discussion

Our goal for the current study was to understand the trends in research investigating non-human animal social interactions published over the last 20 years. Previous reviews had concentrated on specific types or aspects of social interactions such as the mediators of contest outcomes in agonistic encounters (Yuving et al., 2006), the role of lateralization in recognizing others during social interactions (Rosa Salva et al., 2012), and the importance of social interactions in the development of cognition in birds (Pepperberg, 2011). To date, the extant literature on social interactions of non-human animals has not been organized in a way that facilitated our understanding of the research findings. To understand these trends in order to develop future priorities, we had to organize the current literature. First, we needed to determine what portion of the available research concerned research about social interactions. Second, we needed to identify which topics had been explored fully and which topics had been studied less frequently. Third, we needed to summarize how the research was being conducted in terms of subjects, research design, and research setting as this information may provide knowledge for future endeavors. Finally, we needed to explore whether or not changes in publication trends had occurred over the last 20 years.

Overall Trends

One commonality across all the reviews prepared for this special issue was the overwhelming volume and breadth of available literature to review. Trying to decide what journals to examine much less what aspect of social interactions to summarize was extremely difficult. With more than 50 journals from which to choose, we limited our selection to eight journals that best represented a diverse set of taxa and topics involving social interactions. From these eight journals, we had almost 19,000 articles from which to gather our final sample of about 4,300 articles.

Articles about non-human social interactions represented a little over a fifth of the total articles published by these eight journals. Each journal, however, published articles investigating social interactions at differing rates (Table 4). The *International Journal of Comparative Psychology* and *Journal of Comparative Psychology* published the fewest number of articles on social interactions (6% and 10%, respectively) while *Ethology* published the largest number of articles (56%). Each journal varied across the 20 year period in the number of articles they published on social interactions with two journals (*Behavioral Ecology & Sociobiology* & *Ethology*) showing an increase in articles investigating social interactions by the end of the 20-year period (Figure 2).

Overall, articles investigating agonistic social interactions were the most frequently published topic. Many of these articles involved the effects of different group compositions (Leca, Gunst, Thierry, & Petit, 2003), environmental factors such as resource distribution or housing (Moinard, Mendi, Nicol, & Green, 2003), the role of dominance (Verbeek, Boon & Drent, 1996), the outcome of contests (Sneddon, Huntingford, & Taylor, 1997), or general aggressive behavioral interactions (Pereira & Kappeler, 1997). Affiliative interactions were the next most frequent type of social interaction. These articles tended to involve parental care and nursing (Hakkarainen & Korpimäki, 1994), play (Bekoff, 1995), networks or associations (Van Hoof & Van Schaik, 1994), and cooperative interactions (Huang & Robinson, 1996). Finally, sexual interactions were studied the least often across the journals. These articles investigated mate choice

(Seehausen & van Alphen, 1998), courtship (Alberts, Altmann, & Wilson, 1996), sex differences (Kvarnemo, Forsgren, & Magnhagen, 1995), the influence of hormones (Hunt, Hahn, & Wingfield, 1997), and the importance of sensory systems in selecting mates (Kortet & Hedrick, 2005). Mammals were the most frequently studied animal followed by birds and invertebrates. Research methodology was almost equally divided between observational and experimental research with most of it divided between laboratory and field settings; about 20% of the research was conducted in a natural habitat. The above references represent the most frequently cited article on each topic included in our dataset.

Specific Trends

Types of social interaction. The results of this study suggested that very few trends existed in the research topic of social interactions. Across the 20-year period, research on agonistic social interactions occurred more often than expected during the early part of this period. In contrast, research on affiliative social interactions did not become more popular until about halfway through the review period. Still, even with the changes in relative importance, the research on agonistic behavior continued to be prolific and outnumbered the other two topics for every year but 2002, when research on affiliative interactions outnumbered the research on agonistic interactions and sexual interactions. While we did not examine the reasons behind the popularity of agonistic interactions for researchers, it seems plausible that understanding the factors involved in agonistic encounters may elucidate possible solutions in decreasing the number of these encounters with animals in controlled environments or a better understanding of various evolutionary pressures that shaped current populations. It is important to know the determinants and outcomes of agonistic interactions when considering the health and welfare of different animals. For example, Banks and colleagues (2007) indicated that the more dispersed and fragmented habitats became for certain species, the greater the pressure on the species to survive. Thus, finding a mate becomes harder, which may in turn lead to an increase in competition within sexes as they attempt to entice mates.

Additional analyses also indicated preferences of using various taxa to investigate certain social interactions. Research examining agonistic interactions tended to overuse fish and reptiles (Figure 6). In contrast, research investigating affiliative interactions tended to over-represent mammals and birds. Interestingly, research regarding sexual interactions was more likely to use fish, amphibians, and invertebrates, presumably because more components of these taxa may be manipulated allowing for investigations in the causal contributions of sexual selection, sexual conflict, and other mate choice determinants. This conclusion is supported by follow-up analyses indicating that research on sexual interactions tended to be performed in the laboratory with experimental paradigms. Furthermore, research on affiliative interactions was more likely to be performed in the natural habitat or field setting and tended to be observational in nature.

When we examined specific subtopics over time, the results were scattered and myriad. Mate choice, group composition, parental care, and environmental influences were consistently the most studied subtopics over the years. After these topics, certain topics appeared and then disappeared in their importance; for example, cooperation and competition, dominance, emotion, personality, neurobiology, vocalizations, and stress all emerged as important aspects to study at different points across the 20-year period. Furthermore, different subtopics were emphasized by different journals as indicated in Table 5.

Other research considerations over time. A brief examination of the results suggested that the taxa studied varied over the years but with little consistency. Research with mammals included everything from free-ranging aquatic mammals to small and large terrestrial mammals. At times, fish, birds, reptiles, and invertebrates contributed significantly to the type of taxa studied, but in general most research studies on social interactions involved mammals. When the research setting was considered, studies conducted in laboratory settings occurred more frequently in the first 10 years of the study while the importance of field settings and natural habitats was emphasized more frequently over the latter half of the period. More recently, conducting

research in two types of settings has increased, although this is still not performed consistently, likely because of the difficulty of accessing wild and captive subjects of the same species. Perhaps most intriguing is the fact that both observational and experimental studies were performed almost equally across the majority of the years. This trend is important as it highlights the importance of conducting research using both uncontrolled and controlled designs, which increases the overall generalizability of the findings as they have been validated and replicated in different contexts.

Areas of Priority During the Last Five Years

Using the last five years of publications, we explored the same questions addressed by our analyses of the full dataset. The results produced very similar outcomes, with agonistic social interactions consistently producing more research articles than the other two types of social interactions. The same four subtopics continued to be pursued by researchers, as was the use of mammals, invertebrates, and birds in research on social interactions. Both laboratory and field settings continued to be important and observational and experimental research were performed equally. It is clear from these data that certain topics (i.e., mate choice, group composition, parental care, and environmental factors) within social interactions will continue to be pursued. Understanding the factors that influence agonistic interactions between animals or the importance of various affiliative behaviors in the development and maintenance of bonds are all critical to the survival of social species. Likewise, understanding the factors that influence the choice of a mate in a variety of animals is valuable.

Future Directions

The results of this study indicated that the study of social interactions holds a significant place in the study of animal behavior despite the limited number of journals examined. Given that such a broad range of taxa engage in social interactions, this topic will clearly remain popular and critical to our understanding of animals and the importance of their social and physical environments. Social interactions are often embedded within and difficult to disentangle from many of the topics pursued in this special issue including animal welfare and conservation issues, immunological functioning, learning, and cognition. While the number of papers on social interactions fluctuated some over the years for each journal, they seemed to be produced at relatively stable rates. Interestingly, the three major types of social interactions identified were relatively stable and fairly equally represented across the years. However, if a call for action was provided, we would suggest that additional research on the courtship and mate choice behaviors and interactions exhibited by larger mammals would be of interest. Although we have quite a bit of knowledge about invertebrates, fish, birds, and some small mammals, we know much less about these aspects of larger mammals (e.g., elephants, marine mammals, rhinoceroses, hippopotamuses, big cats, wolves), and in particular, how socio-sexual knowledge and interactions develop over their lifespans. If we are going to be able to support species in their natural environments or in human care, we need to understand all the aspects we can about these social interactions. Similarly, understanding the influence of group compositions and the importance of associations between individuals is also critical.

We would also recommend that researchers continue to diversify their settings or collaborate more often with other researchers doing research in the settings that are different from their own. While manipulation and control are important in determining the causes of various interactions, these studies should also be replicated in natural environments so that the validity of the conclusions may be evaluated. Finally, we also believe that as our understanding of the various systems (e.g., neural, physiological, and behavioral) becomes more advanced, the interaction between the neuro-physiological mechanisms and the behavior exhibited during social interactions will become increasingly important. This trend has already begun as indicated by the results of our brief examination of the publications on social interactions in *Science* and *Nature*. Working with animal models from the fish, bird, and invertebrate taxa will continue to be critical to

our understanding of social interactions as these taxa represent experimental research that can be conducted relatively quickly because of their shorter life spans and the availability of greater experimental controls. We also encourage similar types of review studies be performed for specific taxa or genera. There is clearly a need for studies investigating the current state of specific types of social interactions as we attempt to make sense and organize the vast corpus of research on social interactions (see MacNeilage, 2013). We are excited about the future of research on social interactions and hope that it will continue to advance in the years to come with less emphasis on war and more on love and reproduction!

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