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UNIVERSITY OF CALIFORNIA, SAN DIEGO

Social and Cognitive Complexity in Wild Bottlenose Dolphins (*Tursiops* sp.)

A dissertation submitted in partial satisfaction of the requirements
for the degree Doctor of Philosophy

in

Cognitive Science with a Specialization in Anthropogeny

by

Whitney Rachel Groves Friedman

Committee in charge:

Professor Douglas A. Nitz, Chair
Professor Andrea A. Chiba
Professor Richard C. Connor
Professor Pascal Gagneux
Professor James D. Hollan
Professor Federico Rossano

2017

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The Dissertation of Whitney Rachel Groves Friedman is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Chair

University of California, San Diego

2017

DEDICATION

To you. The inquiring soul who seeks to understand, communicate, and protect the incredible diversity of life on earth.

EPIGRAPH

“If we ascribe to individual minds in isolation the properties of systems that are actually composed of individual manipulating system of cultural artifacts, then we have attributed to individual minds a process that they do not necessarily have, and we have failed to ask about the process they actually must have in order to manipulate the artifacts”

E. Hutchins, Cognition in the Wild

“My view - and Defoe’s, as I understand him - is that it was the arrival of Man Friday on the scene which really made things difficult for Crusoe. If Monday and Tuesday, Wednesday and Thursday had turned up as well then Crusoe would have had every need to keep his wits about him... I propose that the chief role of creative intellect is to hold society together”

N. Humphrey, The Social Function of Intellect

“A thorough investigation will reveal that we need to conceive of natural processes (material, living, and mental) as unities or structured wholes rather than simply as multiplicities of events external to each other, bound together by efficient casual relations.”

E. Thompson, Mind in Life

“You cannot get through a single day without having an impact on the world around you. What you do makes a difference, and you have to decide what kind of difference you want to make.”

Jane Goodall

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ACKNOWLEDGEMENTS

This work would not have been possible without the commitment of many people and organizations.

I would like to acknowledge Professor Douglas Nitz for his support as the chair of my committee, and for helping me define and cross the finish line. Professor Richard Connor for sharing his incredible insights into dolphin behavior, and the world of the Shark Bay alliances. Richard Connor and Michael Krützen for their support and collaboration over many field seasons, and especially for their support in piloting technology and methods for this project. Professor Emeritus Edwin Hutchins for his countless words of wisdom, for carefully considering my ideas, for inspiring me to think beyond the boundaries of the light, for helping me to understand what it means to be a great scientist, and for teaching me an adage I repeat daily, “you always have time for the things you do first.” Professor James Hollan for his support from my undergraduate days through to my defense, and for teaching me to get feedback early and often. Professor Andrea Chiba for providing me with an early framework to think about networks, and for her continued support throughout my process. Professor Marta Kutas for her unfailing ability to provide poignant advice in critical moments, and for helping me to recognize that success is 90% grit. Professor Pascal Gagneux for inviting me into the world of CARTA and Anthropogeny, for sharing an incredibly rich knowledge from the symbiotic relationship between ants and acacia trees to evolutionary glycobiology, for taking me along on a journey of a lifetime to meet Ardi, Gaia, Douglas, the Hadza, to listen to the forest of Gombe from Jane’s Peak, and for his thoughtful feedback on of my dissertation. Professor Federico Rossano for his careful consideration of my work and helpful feedback.

I would also like to acknowledge John Hildebrand, Frank Chang, Greg Campbell and the Scripps Whale and Acoustics Lab for lending the hydrophone and recording equipment used in this study. UCSD undergraduates Ana Victoria Gil, Jeremy Schrader, Cindel Carballo and Daniel Kahl assisted with video analysis. Laurel C. Kistler, Deborah Ahn, Emon Shakoor and Leah Takahashi assisted with acoustic analysis.

Shark Bay field seasons were supported by the Krützen lab at the University of Zürich, Switzerland, a National Geographic Committee for Research and Exploration Grant (9301-13) awarded to WF, RCC and EH, and by two Dean of Social Science Travel Fellowships awarded to WF. Accommodation was generously provided by the Monkey Mia Dolphin Resort. Teresa Borcuch, Livia Gerber, Rebekah McLeod, Samuel Wittwer, Cory Jameson, and Cindel Carballo assisted in data collection, and Isabel Baker and Alex Brown helped to pilot aerial video methods. Stephen Potter provided technological advice.

I am grateful to have been supported by fellowships from the UCSD Department of Cognitive Science, Robert J. Glushko and Pamela Samuelson, and by Graduate Fellowships in Anthropogeny from the Mathers Foundation and Annette-Merle Smith.

Last, but certainly not least, I would like to acknowledge my village. My parents, Betsy and Mike Friedman, who fostered my imagination and inquisitions from an early age, never wavered in their support, and meant it when they taught me to follow my dreams. My incredible husband, Jonathan Hicken, who has been a sounding board, a lab-mate, an inspiration, and an unwavering pillar of support through distance and duration. My grandmother, whose spirit of determination and life-long pursuit of knowledge has always inspired me. The Friedman and Hicken clans, and my close friends, you are an incredible community. Thank you for your love and support.

Chapter 2, in part, is currently being prepared for submission for publication of the material. Friedman, W.R.; Krützen, M.; Connor, R.C. The dissertation author was the primary investigator and author of this material.

Chapter 3, in part, is currently being prepared for submission for publication of the material. Friedman, W.R.; Krützen, M.; Connor, R.C. The dissertation author was the primary investigator and author of this material.

Chapter 4, in part, is currently being prepared for submission for publication of the material. Friedman, W.R.; Krützen, M.; Connor, R.C. The dissertation author was the primary investigator and author of this material.

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Studies in Cetacean Biology

Professors Richard Connor, Christine Johnson, and John Hildebrand

Studies in Anthropogeny

Professor Pascal Gagneux

ABSTRACT OF THE DISSERTATION

Social and Cognitive Complexity in Wild Bottlenose Dolphins (*Tursiops* sp.)

by

Whitney Rachel Groves Friedman

Doctor of Philosophy in

Cognitive Science with a Specialization in Anthropogeny

University of California, San Diego, 2017

Professor Douglas A. Nitz, Chair

The Social Intelligence Hypothesis proposes that the kind of complex cognition observed in humans and other species co-evolved with complex societies. Research focusing on this topic has been conducted mostly on primates, with a significant body of work conducted under the Machiavellian Intelligence program. To further understand this relationship, there may be utility in looking beyond non-human primates to a species whose social complexity may be more similar to our own than any extant primate, with an updated methodological approach. Male bottlenose dolphins in Shark Bay, Western Australia, participate in up to three levels of alliance formation within a large society of resident dolphins. This nested structure of alliances may be the most complex outside of humans, but to date little is known

about third-order alliances, or how alliance relationships may be mediated through social interaction. This study focused on the relationships among 24 male allies within this system over a six-year period of time to address two principal questions: (1) how are third-order alliances structured, what are their dynamics, and how do they respond to change? (2) how do the particular kinds of behavioral interactions that allies engage in relate to the observed structure and dynamics of the alliance network? I found that the alliance network demonstrated features of complex systems including local segregation and global integration, dynamic (nonlinear) change, and the presence of social roles. The relationship between social complexity and social cognition was indicated by the range of interactions observed, as well as variability in when and with whom these interactions occurred. For example, second-order allies who frequently associated together engaged in higher rates of synchrony and affiliative contact. At a context hypothesized to have higher uncertainty (group joining events, or *fusions*), I found higher rates of social vocalizations, and higher rates affiliative interaction among third-order allies. This dissertation makes two kinds of contributions (a) toward the continued development of methodological practices for evaluating the proposed relationship between complex societies and complex cognition, and (b) toward further understanding of cetacean social organization, behavior, and cognition.

CHAPTER 1

INTRODUCTION

September 23, 2010

We departed heading north through the bay, encountering an adult male trio, a first-order alliance from the larger second-order PD alliance in the first channel. The trio, PRI WAB and NAT, were no longer with the female Phantom (or her weaning calf Opera), who they had been consorting just a few days prior.

Continuing north we encountered another first-order alliance from the second-order WC alliance, Wow, Pik, and Myrtle with the female Stetson. We started a focal follow to confirm the consortship. Within 10 minutes, another first-order trio from the WC alliance, Latch, Gripe and Vee, along with the popular female Phantom and her calf Opera fused (joined) with our focal group.

The two first-order WC alliances and female consorts travelled slowly northwest in two tight subgroups, the two consortship groups slightly separated from one another. During that hour the group maintained a low energy bout, slowly traveling and resting together, sometimes one breaking off to forage while another male stayed close by the female in his group. The two first-order WC alliances never strayed more than 100m from each other, and no other individuals were seen nearby.

Forty minutes after we began our follow another large group appeared on the horizon, moving rapidly toward the WC. Shoulder-to-shoulder, they moved in unison, white-water cresting as they charged at full-speed toward the WC. The two groups met in a wash of splashing, flukes flying. Immediately, a seventh member of the WC who we had not seen for the first forty minutes of observation joined the group. From the surface, we observed a mass of dolphins churning in towards each other, surging, charging, and chasing at times. Quick fin jerks at the surface indicated aggression below. Loud exhales called "chuffs" could be heard, and groups numbering two to five dove in synchrony.

The incoming group was a third-order alliance comprised of 6 adult males from the second-order AM alliance and 5 adult males from the second-order HG alliance.

After five minutes of intense fighting the groups split briefly - Phantom was still with the WC. Another minute of intense fighting - surging, tail hitting, and aggression and the groups split again. Some of the WC paused at the surface in a tight group, but the third-order AM-HG alliance were still in a excited churning

flurry, with WC males Latch and Gripe among them. The WC male Wow left the snagging group, charged into the fight, and surged with Latch and Gripe behind the AM male Orion. Someone was bodily pushed up to the surface from below, and we could hear loud whistles, even without a hydrophone in the water. The group continued surging, meeting head-to-head, with sub-groups surfacing in unison for another five minutes. 12 minutes after the AM-HG arrival, the WC separated with Stetson and Phantom in a tight pack, maintaining distance from the AM-HG. Screams, chuffs, and shrill chirps from the WC group were loud enough to be heard in the air. Immediately following this aural display, Latch returned to the snagging WC, then charged again to re-joining the AM-HG group, trailing at first behind an incredible surge.

Twenty-six minutes into the fight a new group appeared on the horizon - the AM-HG group moved towards them but no join was observed. These were offshore dolphins not well habituated to the research boat, but had been seen frequently enough with AM that we were starting to suspect a second- or third-order alliance between these “friends of AM” and AM. A few minutes later the incoming group disappeared completely without joining the competing group.

Intense fighting ensued for another 6 minutes - huge group surges accompanied tail hits, whistles in air, and a chase. Phantom and her calf Opera were now among the fighting males. The mass of dolphins surged in unison again as another six males from an in-shore second-order alliance (KS) approached the fighting group. It is unclear whether the six KS ever got closer than 10 meters to AM/HG, but coincident with their arrival (37 minutes after the arrival of AM-HG) the WC-KS and AM-HG groups split again, this time with AM-HG porpoising and leaping rapidly south - away from WC-KS. The KS excitedly socialized amongst themselves, but were no longer with the WC.

A hundred meters away the WC were traveling slowly in a tight pack. All 7 males and Stetson were present, but Phantom and Opera were not. The group moved slowly beside the boat and we observed petting between the males. We documented and verified the group membership before changing gears to chase down the still leaping AM-HG group. The group was still excited when we reached them again: As the group settled it became clear that three AM males had begun a new consortship with Phantom. The 5 HG males eventually departed, leaving the six male AMs in two subgroups, each consorting a female.

1.1 INTRODUCTION

The co-evolution of social and cognitive complexity has been a topic of scientific investigation since the 1960's and 70's, beginning with the Social Intelligence Hypothesis: the proposal that intelligence, rather than evolving in the context of increased foraging or technical skills, was linked in evolutionary ratchet with increasingly complex societies (Jolly,

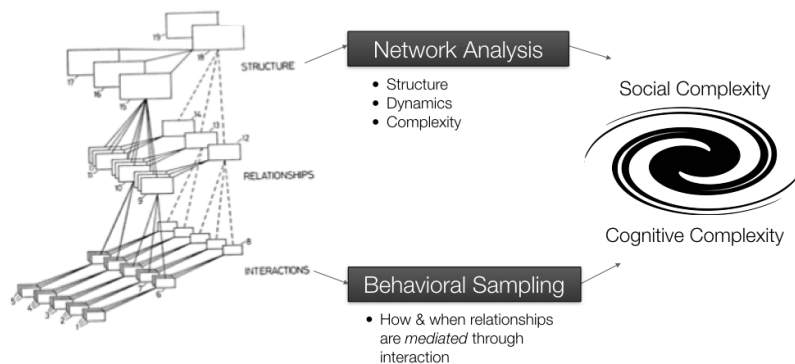
1966; Humphrey, 1976; Chance, 1961; Kummer, 1978). Research focusing on this topic has been conducted mostly on primates, with a significant body of work conducted under the Machiavellian Intelligence programme (Byrne and Whiten, 1988, 1997). The primate model provides important information for studies of human evolution: by using homology and divergence we can identify traits that humans share with close phylogenetic relatives, and those which have evolved uniquely in the hominid lineage. Another approach, the study of convergent evolution, explores the independent evolution of similar traits in more distantly related taxa; this approach can help us understand the context and mechanisms which may facilitate the evolution of similar biological phenomena, including those that exist in humans but are not shared by other primates. To further understand the co-evolution of complex societies and complex cognition, there may be utility in looking beyond non-human primates to a taxa where social structures may be more similar to our own than to any extant primate.

Male bottlenose dolphins in Shark Bay, Western Australia participate in up to three levels or *orders* of alliance formation within a large open society of resident dolphins. This nested structure of alliances may be the most complex mammalian society known outside of humans (Connor, 2007). In the Shark Bay alliance system, *First-order* alliances are comprised of pairs and trios of adult males who work together to sequester and consort estrus females (Connor et al., 1992a). Most adult males also belong to teams of 4-14 individuals, or *second-order* alliances, who work together to take females from other males and to defend against such attacks (Connor et al., 1992a,b). In 2011, a *third-order* of alliance formation was described in which two second-order alliances that exhibit less-frequent but consistent associations coordinated against other allied males during competitions over females (Connor et al., 2011).

Such nested structure where interactions among the same components at different scales result in functional differences meets the same formula for *complexity* used to describe the neural networks that constitute the human brain (Tononi et al., 1994). The nested structure of alliances in Shark Bay may be the most complex outside of humans (Connor, 2007), but while much work has been done to describe the function of first- and second-order alliances,

to date little is known about third-order alliances, how the structure of alliance networks are maintained, or how they respond to change.

In R.A. Hinde's classic scheme, a population's social structure is described by its pattern of social relationships, which, in turn, are comprised of a history of interactions among individuals (Hinde, 1976). In this dissertation I traverse Hinde's levels to examine the relationship between social complexity through quantitative analysis of a third-order alliance network, and social cognition through fine-scale observations of behavioral interactions among allies. I aim to make two kinds of contributions (A) to lay a few boards in the growing methodological bridge towards better understanding the relationship between, and co-evolution of, complex societies and complex cognition, and (B) to further our understanding of dolphin society and cognition. There are two principal questions that guide the research in this dissertation: (1) how are third-order alliances structured, what are their dynamics, and how do they respond to change? (2) How do the particular kinds of behavioral interactions that allies engage in relate to the observed structure and dynamics of the alliance network?



Hinde, R.A. 1976. Interactions, Relationships, and Social Structure. *Man* 11, 1-17.
 Humphrey, N. (1976). The social function of intellect. *Growing points in ethology*, pages 303-317.
 Jolly, A. (1966). Lemur social behavior and primate intelligence. *Science*, 153(3733):501-506.

Figure 1.1: The theory, methods, and big picture questions discussed in this dissertation

1.2 ORGANIZATION

This thesis is organized into two major sections of analysis. In Part A (Chapter 2), I use network analysis to describe the structure, dynamics, and complexity of third-order alliances. In Part B (Chapters 3 and 4), I use behavioral sampling to describe the context and production of interactions, and examine how such behaviors are used to mediate their social relationships. Chapter 5 investigates the relationship between findings in Part A and Part B, to explicitly address the links between social and cognitive complexity revealed by the undertaken analyses. Major claims for each chapter are summarized below.

Part A. Network Analysis & Social Complexity (Ch. 2)

This chapter examines the claim that the third-order alliance network is structurally complex. Evidence supporting this claim includes the following findings:

- Individual differences in association patterns indicate the presence of social roles
- Second-order alliances show structural variability and functional similarity.
- Temporal dynamics indicate the ability to adapt to change at all levels of alliance formation.
- Second-order alliances with more heterogeneous relationships are more resilient to change.
- Third-order alliances demonstrate the properties of local segregation and global integration.

Part B. Behavioral Analysis & Cognitive Complexity (Ch. 3, Ch 4)

These chapters examine the hypothesis that dolphins use social interactions and affiliative contact (SCC) to mediate alliance relationships. Evidence supporting this claim includes:

- During 1st-order consortship contexts, males who had stronger relationships engaged in higher rates of social affiliation and coordination (synchrony, formations, petting) than males who had weaker relationships. Males who had weaker relationships tended to engage in higher rates of display.

- Across both pre- and post- fusion sampling periods, second-order allies were found to engage in SCC at higher rates than third-order allies.
- At 3rd-order group fusions, 3rd-order allies engaged in higher rates of affiliative contact and coordinated behavior with a male recipient.
- Post fusion, third-order allies engaged in higher rates of synchrony and displays.

The Link Between Social and Cognitive Complexity (Ch. 5)

This chapter examines the claim that social and cognitive complexity are explicitly linked, and that link is brought to bear by what allies do when they interact, as well as when, with whom, and how such interactions occur. I review the evidence for the complexity of the social network, and describe how the patterns of interaction captured in Ch. 3 and Ch. 4 are related to those findings. Allies were found to differentiate between social context and social others. The non-random use of interaction suggests that these are semiotic resources in the alliance system, used to mediate and enact social relationships in particular contexts. Finally, I re-visit the social intelligence hypothesis, relating the findings of this study to the methodological development of this field of inquiry.

1.3 BACKGROUND

1.3.1 THE STUDY OF SOCIAL AND COGNITIVE COMPLEXITY

In the 1960's and 70's, advocates of the *Social Intelligence Hypothesis* proposed that intelligence, rather than evolving in the context of increased foraging or technical skills, was linked in evolutionary ratchet with increasingly complex societies (Jolly, 1966; Humphrey, 1976; Chance, 1961; Kummer, 1978). Jolly wrote, "since [social primates'] dependence on the troop both demands social learning and makes it possible, social integration and intelligence probably evolved together, reinforcing each other in an ever-increasing spiral" (Jolly, 1966, p 504).

In the late 1980's, the Social Intelligence hypothesis morphed into the Machiavellian Intelligence hypothesis, so called because individual success within complex so-

cieties appeared to be "...most effectively promoted by seeming altruistic, honest, and prosocial" (Byrne and Whiten, 1988; Byrne, 1997). While research conducted under this hypothesis has found a close relationship between social skills, group complexity, and brain size (Byrne and Whiten, 1997; Byrne, 1997), the theoretical framework within which these studies operated limited the degree to which behavioral studies could be used to derive 'hard' facts of animal cognition. Key questions focused on what mental representations individuals formed about others' relationships and perspectives, including whether they participated in deliberate deception of conspecifics, and whether they attributed and acted upon surmised belief states of others (Byrne and Whiten, 1988; Premack et al., 1978; Forster, 2012). The focus on using behavior as a "window into" the internal representational states of subjects was echoed throughout first generation cognitive science, but has since been abandoned by many researchers in favor of a more biological account of cognition.

Over the last thirty years, the field of cognitive science has seen a revolution of methodological approaches to the study of cognition. As more is understood about the continuity of brains, bodies, and worlds dynamically coupled in cognitive processes, researchers have been challenged to examine their units of cognitive analyses, question the absolute centrality of the individual mind in cognitive systems, and increasingly move towards an understanding of cognition as biological processes continuously produced by richly interdependent ecological webs.

A fundamental insight from this revolution is that social interactions are not simply *residua* of brain-bound cognitive events; but are themselves cognitive processes constituted by richly interconnected ecosystems spanning populations of cells, sensorimotor systems, bodies, and social interlocutors (Hutchins, 1995, 2006). On this view, social interactions are at least as descriptive of such distributed cognitive processes as the recordings we might take of an individual's neural activity. The careful description of such interactions constitute data points on cognitive events that can be taken in their own right, and may also be used to carefully generate hypotheses about the kinds of sensorimotor and perceptual capabilities a set of organisms must possess in order to produce the observed social interactions (Byrne

et al., 2001; Johnson, 2001; Johnson and Oswald, 2001; King and Shanker, 2003; Forster and Rodriguez, 2006; Forster, 2012).

Re-visiting Hinde's levels with this insight in mind, we find renewed methodological traction for the study of the relationship between social and cognitive complexity. Rather than the invisible box left off Hinde's handy diagram, we find that cognitive events are baked right in: they are the interactions. In this dissertation, my aim is to explore and explicate the relationship between social complexity, taken as a quantifiable property that describes a particular patterning of relationships of in an animal society, and cognitive complexity, taken as the context, process, and repertoire of social interaction. Rather than using behavior to infer the mental representations held by individuals, in this study I treat interactions between individuals as observable cognitive events that are the products of a socially distributed cognitive system: the alliance. This framework allows me to describe features of the cognitive system that might have otherwise gone ignored, or assumed to be a property of an individual rather than the larger system.

1.3.2 ALLIANCES, COALITIONS AND SOCIAL COMPLEXITY

Coalition and alliance formation fall within the larger class of cooperative behaviors studied by biologists and anthropologists (for a review, see Kappeler and Van Schaik, 2006), but are explicitly social and often political in nature. de Waal and Harcourt (1992) define a *coalition* as describing "a one-time cooperative action by at least two individuals or units against at least one other individual or unit." The difference between a coalition and an *alliance* is the persistence of the bond: de Waal and Harcourt (1992) write, "the term *alliance*...is reserved for long-term cooperative relationships, that is, partnerships that form coalitions on a regular basis."

While considered rare in nature, coalitional behavior under this definition has been documented in a wide range of taxa, though differing in function, longevity, party size, and demographic composition. Among platyrrhine primates including capuchins (*Cebus capucinus*), red howler monkeys (*Alouata seniculus*), and white-nosed coatis (*Nasua narica*),

as well as spotted hyenas (*Crocuta crocuta*), researchers have documented the formation of temporary coalitions of two or more individuals who jointly attack a third individual (Perry, 1998; Sekulic, 1983; Gompper et al., 1997; Engh et al., 2005). Male chimpanzees (*Pan troglodytes*) form short-term coalitions during rank-contests within the social unit (Goodall, 1986; Nishida, 1983; de Waal, 1984). Males of the same social unit also cooperate as a long-term alliance when they patrol and defend territory against incursions from neighboring males (Goodall, 1986; Wrangham, 1999). Long-term alliances have also been documented among related female prides of lions (*Panthera leo*) who coordinate to defend territory against other females, and offspring against infanticide attempts by over-taking males (Packer et al., 1991). Male lions (who are often but not always related) also form long-term alliances of up to 9 individuals who coordinate to take over and defend access to female prides (Packer et al., 1991; Heinsohn and Packer, 1995). There is also some evidence for long-term alliances within socially-bonded avian species: juvenile rooks (*Corvus frugilegus*) form long-term pairs who assist each other during agonistic encounters (Emery et al., 2007).

Among cetaceans, a number of studies have reported on the existence of multi-male groups, suggesting the possibility of coalitions and/or alliances, but in many cases lack behavioral evidence of such groups coordinating against a third party. Multi-male groups have been reported among spinner dolphins (*Stenella longirostris*, Östman, 1994), (*Stenella attenuata*, Pryor et al., 1991), resident killer whales (*Orcinus orcas*, Baird and Whitehead, 2000), northern bottlenose whales (*Hyperoodon ampullatus*, Gowans et al., 2001), sperm whales (*Physeter catadon*, Whitehead, 2003; Caldwell et al., 1966), and belugas (*Delphinapterus leucas*, Michaud, 2005). Male pairs have been observed in the context of mating (raising the possibility of cooperative mate-guarding) among humpback whales (*Megaptera novaeangliae*, Clapham, 1996), gray whales (*Eschrichtius robustus*, Samaras, 1974), and right whales (*Eubalaena australis*, Payne, 1995).

The most complete evidence for coalitions and alliances among cetaceans come from long term studies of spotted and bottlenose dolphins. Among Atlantic spotted dolphins (*Stenella frontalis*), groups of 2-3 males form stable associations for periods ranging less than

3 years up to at least 12 years (Elliser and Herzing, 2014). The presence of coalitions has been suggested due to limited observations of groups of 3-4 males chasing and surrounding a female prior to copulation (Herzing, 1996), as well as escorting behaviors that may last for multiple days (Elliser and Herzing, 2014). However, the best evidence for coalitionary behavior within this population comes from repeated observations of interspecific associations in which groups of up to 9 male spotted dolphins coordinate spatially and vocally to defend themselves against sympatric adult male bottlenose dolphins (Herzing and Johnson, 1997). Together, these observations suggest the possibility of two levels of coalition formation within this population, though this structure does not appear as ubiquitous as the patterns of male-male association among bottlenose dolphins in Shark Bay.

Bottlenose dolphins (*Tursiops sp.*) are by far the most well-studied of the cetaceans (Connor et al., 2000), and studies have shown a range of coalitional behavior across populations. In the Moray Firth, Scotland, studies have found no evidence of coalitional behavior (*Tursiops truncatus*, Wilson et al., 1992). Over thirty years of research in Sarasota Bay, Florida has found that adult males (*Tursiops truncatus*) either consort females singly, or form stable pair bonds among non-relatives (with some seen in association for as long as 20 years). Similarly, Möller et al. (2001) found stable associations between 2-4 unrelated adult males in Port Stephens, New South Wales, (*Tursiops aduncus*) that cooperated to consort females. In the northern Bahamas, Parsons et al. (2003) found frequently associated adult male dyads (*Tursiops truncatus*), suggestive of coalitions, with males sharing high maternal relatedness. None of these studies confirm the existence of coalitions or alliances as they do not include observations of multi-party groups coordinating *against* other groups or individuals. However, Lusseau (2007) found that while adult males (*Tursiops truncatus*) in Doubtful Sound, New Zealand engaged primarily in one-on-one agonistic interactions, there were instances of short-term coalitions during two-on-one "triadic head-butting bouts".

By far the most well-documented and conspicuous system of alliances among cetaceans is found among adult male bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia. Most adult males in this population belong to a 4 to 14 member "second-

order“ alliance who work together to steal and defend females from other adult male alliances. Over thirty years of research has found incredible persistence of second-order alliances: one group (WC) was first documented in 1989 and members are still found together at present (2016). This seems to be a general pattern for the population, though some changes in group membership appear to be precipitated by the loss (presumed death) of first- or second-order allies (Connor and Krützen, 2015). Within the second-order alliance, males form pairs or trios (“first-order“ alliances) who work together to consort females. First-order allies also work together during contests against other males over female consorts, with most competitions among males occurring outside their second-order alliance. First-order alliances vary in their longevity, with some exhibiting near-perfect stability, while others rotate membership over the course of a mating season (peaking Oct-Dec, Mann et al., 2000). In 2011, a “third-order“ of alliance formation was described in which two second-order alliances coordinated against other allied males during competitions over females (Connor et al., 2011).

Alliances between males are generally rare among mammals (Clutton-Brock, 1989). From an evolutionary perspective, males within a single population are assumed to be in reproductive competition with one-another. However, it seems there are some common ecological and social drivers for the formation of alliances, including high risk of predation and competition over limited resources, likely increased within areas with higher population density (Connor et al., 2000). Cooperation is considered more likely among relatives, as individual loss is mitigated by consanguineal success (kinship altruism, Hamilton, 1964). Among non-relatives, proposed mechanisms for the persistence of alliances include reciprocity, in which A directs costly beneficence towards B in expectation that B will subsequently invest in A (e.g. A engages in competitions with B in expectation that B will assist A in future competitions) (Trivers, 1971; Axelrod and Hamilton, 1981), pseudo-reciprocity, in which A directs beneficence towards B increasing the probability that B will perform acts which benefit B directly and A indirectly (e.g. A engages in competitions with alongside B to increase the chance of mating with the consorted female of B)] (Connor, 1986; Connor and

Smolker, 1995; Connor et al., 2000), and by-product mutualism in which the selfish behavior of B results in incidental benefit to A (West-Eberhard, 1975).

Chapais (1995) argued,

[the] ability to form alliances generates the most complex social structures in the animal world. In a social milieu in which organisms may influence others through the use of third-parties, relationships between individuals take on new dimensions of complexity. They cease to be relationships between two independent entities - that is, to be strictly dyadic - and become relationships between whole social networks.

In addition to the complexities implied by the polyadic nature of alliances, the dyadic relationship becomes more complex: rather than classifying a social other as simply 'friend' or 'foe', relationships among allies are *simultaneously* cooperative and competitive. The system of nested alliances in SB is considered to be among the most complex societies documented outside of humans (Connor, 2007). In SB, first-order allies engaged in consortship are in reproductive competition with the same individuals they rely on for success in intra-sexual competitions against other males (Connor et al., 2000; Connor, 2007). Given the functional requirement, long term stability, and evidence for preferred companions, it is clear that alliance membership is both critical and representative of substantial social investment. This conundrum predicts that males will behave in such a way as to maintain their alliance relationships, while at the same time competing just enough to insure (or increase) their own reproductive success.¹

This dissertation explores the relationship between the social complexities evidenced by the structure and dynamics of the nested alliance system found in SB, and the cognitive complexities apparent in the observable interactions that occur among allies as they maintain and recapitulate their complex multi-level society.

¹See Chapter 4 for more on this.

1.3.3 SOCIAL COORDINATION AND AFFILIATIVE CONTACT: INTERACTIONS AND COGNITION

1.3.3.1 Social Coordination

Connor, Smolker, and Bejder (2006) described the distribution of synchronous surfacing by pairs and trios of male dolphins in Shark Bay, finding that males were most likely to be synchronous with the same individuals with whom they spent the most time (e.g. their first order alliance affiliates), and that alliances varied significantly in their rates of synchrony. The authors suggest this variation might represent differences in alliance unity and/or age - the mature males demonstrated the highest percentage of "triple synchs" or synchronous surfacing between three individuals. Furthermore, the authors indicate a relationship between the long-term stability of an alliance and synchrony, and suggest that variation across trios in rates of triple synchs suggests that synchrony may be a more sensitive measure of alliance dynamics than is captured by the association coefficient.

A three-year study of the fourteen member second-order alliance (also called "super-alliance") WC found that individuals who formed more enduring alliances (higher individual alliance stability index) also showed higher consortship rates (Connor et al., 2001). This finding was later generalized to 12 second-order alliances (Connor and Krützen, 2015). Given that association predicts both synchronous interactions and consortship rate, Connor et al. (2006) predict that variation in synchrony may also predict a variation in reproductive success - perhaps at a finer level of discrimination than association coefficient.

Adult male dolphins in Shark Bay participate in an extraordinary range of coordinated, often synchronous displays, many of which have never been seen twice (Connor et al., 2000). Displays occur frequently in the context of mating consortships, often with the males performing coordinated behaviors around an individual female. For example, in a 'butterfly display', two males begin by tightly paralleling the female on either side, then move out in front of her before splitting in opposing directions and meeting again behind the female moving back toward her on either side (Connor et al., 2006). In 1992, Connor et al.

described a display that has not been seen since in which two males synchronously leapt towards each other in "reverse-parallel" formation on either side of a female, performing "belly-slaps" as they landed (Connor et al., 1992a, 2000). The distribution of display-types across alliances has not been quantified, but such observations suggests that such variation does occur.

1.3.3.2 Vocal Repertoire

Bottlenose dolphins produce a wide range of vocalizations that have been broadly classified into narrow-band whistles, and broad-band echolocation clicks and burst-pulse calls (Evans and Bastian, 1969; Caldwell and Caldwell, 1968; Caldwell et al., 1990; Ralston and Herman, 1989). Of these call types, both whistles and burst-pulse calls are consistently associated with social contexts, with the former studied much more intensively (e.g. Caldwell and Caldwell, 1968; Harley, 2008; Ralston and Herman, 1989; Tyack, 2000; Herzing, 2000). Of particular interest has been the study of repeated, individually-specific whistles termed "signature whistles", commonly recorded when individuals are separated from conspecifics and therefore considered to function in group cohesion (e.g. Caldwell and Caldwell, 1965; Janik and Slater, 1998; Harley, 2008; King et al., 2013). Recently, King et al. (2013) studied the phenomenon of signature-whistle copying (Watwood et al., 2005) in wild and captive bottlenose dolphins. The authors found that more frequent associates were more likely to engage in signature-whistle copying, and recorded such events in mother-calf pairs as well as 3 male-male pairs, including one known male alliance. Such signals may represent call convergence, but the possibility of referential use is also suggested (Janik, 2009; King et al., 2013). In an acoustic study on bottlenose dolphins in St. Andrews Bay, Scotland, Quick and Janik (2012) found that groups often produced stereotyped exchanges of whistles (signature whistles) prior to fusion events: that is, at fusions groups are likely to exchange identity information. A wide range of non-stereotyped whistles may also accompany such events. Such vocalizations may include alliance-specific whistles (Smolker and Pepper, 1999), and/or vocalizations which may convey information about the aggressive or affiliative

nature of the arrival, size, or demographic of individuals; though informational content of dolphin vocalizations is not yet well understood (Tyack, 2000).

1.3.4 FURTHER EVIDENCE FOR COGNITIVE SOPHISTICATION IN CETACEANS

1.3.4.1 Cetacean Neuroanatomy

The weighty brains of bottlenose dolphins exceed even that of humans in degree of fissurization and surface area, though many significant differences exist. Notably, cortical thickness is thinner than that of humans (1.3-1.8 mm, compared to 3.0 mm in humans), and the corpus callosum is much smaller comparatively. Auditory areas of the brain are significantly enlarged compared to the human brain (Ridgway, 1990). In terms of brain-to-body size, the general encephalization quotient (EQ) measure applied to terrestrial mammals (Jerison, 1955) is inappropriate for cetaceans whose bodies are adapted for an aquatic environment. When these differences were controlled for, Marino (1998) found that bottlenose (*T. truncatus*) and three other odontocetes possessed an EQ more similar to humans than to any other anthropoid primate (including chimpanzees) or odontocete.

Bottlenose dolphins (*Tursiops sp.*, "dolphins") have also been studied extensively in captivity, especially by experimental psychologists who have provided data on many traditional metrics of comparative cognition. Below is a short summary of some of the research highlights; for more extensive reviews see (Herman, 2002; Pack and Herman, 2006; Herman, 2010).

1.3.4.2 Cognitive Psychology

Short term memory in dolphins is well developed, with immediate memory for sounds heard and things seen (Herman and Gordon, 1974; Herman et al., 1989). Dolphins exhibit a recency effect, with memory best for the last item presented in a sequence of six sounds (Thompson and Herman, 1977).

In match-to-sample tasks, dolphins were visually presented with complex shapes (see, e.g. figure 1.2(a)), and tested on whether they could pick the "same" stimuli from a set

of two in either the visual or acoustic domain. Dolphins passed both tasks, demonstrating facility with "identity-matching" as well as the ability to apply this learned relationship across modalities (Herman et al., 1989; Pack and Herman, 2006, 2007, 1995). Dolphins can also distinguish between stimuli based on the learned relational concepts "same" and "different" (Herman et al., 1994, 1989), and can learn to associate trainers gestures or computer-generated acoustic signals with arbitrary (i.e. lacking morphological iconic resemblance) referents.

Extending on this ability, from 1980 to 2004 Louis Herman and collaborators constructed and trained dolphins on an artificial language that combined both semantic and syntactic features. Two to five word sentences, such as "speaker surfboard fetch"(bring the surfboard to the speaker) could be understood and acted upon with facility, and violations to the rules (e.g. "water speaker frisbee fetch") were acted upon flexibly - the dolphins would extract from this false construction one of two semantically and syntactically correct three-item sequences ("water frisbee fetch" or "speaker frisbee fetch"). If an object from a syntactically correct sentence was not present in the pool, the dolphins reliably selected a white paddle that indicated "no" (Herman, 1986, 2002).

Dolphins also exhibit both joint and triadic attention: they can comprehend the referents of human pointing (Herman et al., 1999; Tschudin et al., 2001) and even spontaneously point and monitor human divers using alternations of gaze and body position (with rostrum oriented at a potential food location, see Figure 1.2) (Xitco et al., 2001).

Dolphins engage in vocal mimicry (Caldwell and Caldwell, 1972; Richards et al., 1984), and have also demonstrated the ability to mimic the movements of human trainers using analogous body parts (see figure 1.2) (Herman et al., 2001). In addition to mimicking the behavior of others, dolphins can self-mimic when asked to repeat their own previous activities (Mercado III et al., 1999). Dolphins have also been tested on the mirror-self-recognition task (Gallup Jr, 1970; Reiss and Marino, 2001). In the latter study, two captive dolphins were found to spend more time in front of a mirror when marked than when sham-marked or not touched. This evidence has been used to suggest that dolphins have

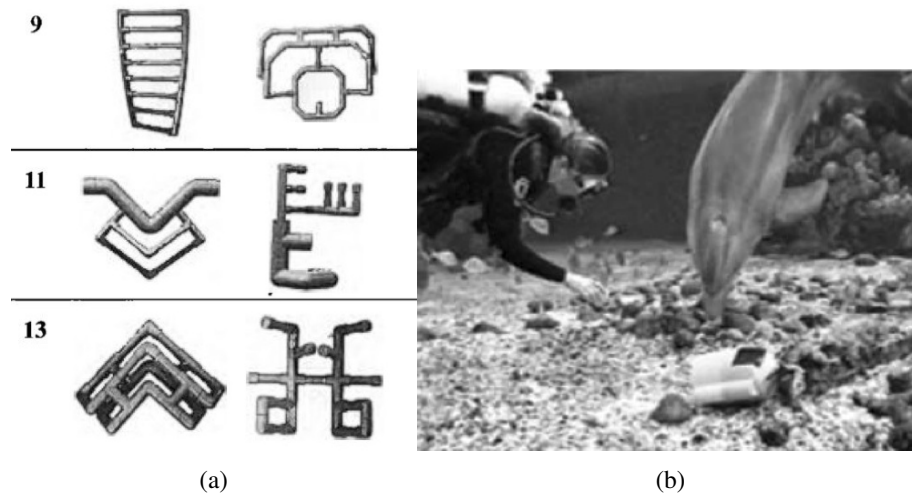


Figure 1.2: (a) Stimuli used in Match-to-Sample tasks (Pack and Herman, 1995). (b) Dolphin pointing with rostrum to an opaque container of food that cannot be opened by the dolphin and must be opened by a trainer (Xitco et al., 2001)

an objective notion of self, perhaps allowing for the sort of meta-representation sometimes experienced by humans. It occurs to me that the context and use of signature whistles (Caldwell and Caldwell, 1965) might provide more convincing evidence on this topic.

1.4 ADDENDUM

1.4.1 NOTES ABOUT THE 23 SEPTEMBER 2010 OBSERVATION

This event is compelling because it illustrates and otherwise suggests the nature of the social and cognitive complexities that exist in a radically different species than our own. Attributes of all three levels of alliance formation among the adult male bottlenose dolphin in Shark Bay are discernible in this event:

- The first-order PD alliance PRI WAB NAT were seen together in the absence of a female consort.
- The first-order WC alliances WOW PIK MYR and LAT GRI VEE were both consorting females at the start of the observation, as well demonstrating the fission-fusion dynamic typical of second-order alliances during the peak mating season, where close

proximity allows the males to join together to defend their consortships readily, as happened in this event.

- A seventh WC male, AJA, who was not involved in either consortship, joined his group as soon as it was under attack, with no indication (in this event or in long-term project records of other similar events) of immediate benefit.
- The second-order WC moved both in unison, as sub-groups, and as individuals during the fight against AM-HG, and all seven males were present from start to finish.
- Midway through the fight, the WC separated, made extremely unusual vocalizations, and re-grouped before re-engaging with AM-HG. Might this represent a kind of tactic among males with a very long history of working together in such encounters?
- The petting we observed among the WC after the fight was likely conciliatory in nature, and may be a mechanism for maintaining alliance relationships in periods of instability.
- AM and HG moved in unison as a third-order alliance to successfully attack the WC, arriving and departing as a coherent group, and with all males engaged in physically intense and potentially dangerous encounter. For the HG there were no immediate benefits, and the AM trio who did not end up with PHA risked the loss of their consortship.
- In all, five second-order alliances were present for this event. Two second-order alliances (Friends of AM, KS) were observed near the fight, perhaps ready to join, or even playing a role that went un-detected by boat-based human observers. Long-term project records suggests one of these alliances is a likely third-order ally to AM. Additionally, in an open and dynamic social network such as this one, there are likely benefits to keeping track of relationships among second-order alliances, similar to the manner in which other species keep track of a changing dominance hierarchy within their group.

- Structural and functional indications of social complexity are explicitly present in this observation: WC first-order alliances were participating in consortships, fissioning and fusing in these sub-groups prior to and during the fight. The original six WC were joined by a seventh WC during a reproductive competition in which all WC males fought against the AM-HG alliance. The second-order AM-HG groups formed a temporary coalition, moving and fighting in unison against the WC. During the fight itself the consorting WC males played 3-4 roles each: a consort proximal to and defending his mate, a first-order ally coordinating with the other two males in his consortship trio, a second-order ally coordinating activity among the other six males in the WC group, and perhaps even a third-order ally when engaged with the KS. Eventually, the AM males would play all these roles as well: a third-order ally coordinating his behavior with the other 11 AM-HG males, a second-order ally when (possibly precipitating) the AM and HG split, a first-order ally when coordinating with two other males to establish a new consortship with Phantom, and a consort to Phantom. These examples naturally separate into temporal and functional units, but during the fight we observed individuals moving fluidly between roles, existing in multiple roles in a single instance.

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CHAPTER 2

THE STRUCTURE AND DYNAMICS OF THIRD-ORDER ALLIANCES

2.1 INTRODUCTION

Male bottlenose dolphins in Shark Bay, Western Australia participate in up to three levels or *orders* of alliance formation within a large open society of resident dolphins. *First-order* alliances are comprised of pairs and trios of adult males who work together to sequester and consort estrus females (Connor et al., 1992a). Most adult males also belong to teams of 4-14 individuals, or *second-order* alliances, who work together to take females from other males and to defend against such attacks (Connor et al., 1992a,b). In 2011, a *third-order* of alliance formation was described in which two second-order alliances coordinate against other males during competitions over females (Connor et al., 2011).

Such nested structure where interactions among the same components at different scales result in functional differences meets the same organizational criteria for *complexity* described for the organization among neural networks in the the human brain (Tononi et al., 1994). The network of alliances in Shark Bay may represent the most structurally complex mammalian society described outside of humans. While much work has been done to describe the function of first- and second-order alliances, to date little is known about third-order alliances, how the structure of alliance networks are maintained, or how they respond to change.

In R.A. Hinde's classic scheme, a population's social structure is described by its pattern of social relationships, which, in turn, are comprised of a history of interactions among individuals (Hinde, 1976). In this dissertation I traverse Hinde's levels to examine the relationship between social complexity through quantitative analysis of social networks,

and social cognition through fine scale observations of behavioral interactions. In doing so, I aim to lay a few boards in the growing methodological bridge towards better understanding the relationship between, and co-evolution of, complex societies and complex cognition ¹.

In this chapter, I describe the relationships among three second-order alliances over a six-year period of time. During the study period, four of the original twenty-four males in the study group 'disappeared', and are presumed to have died, and new third-order relationships were forged. Coincident with the observed shifts in social relationships, the larger Shark Bay ecosystem experienced a cascade of changes including widespread seagrass die-off associated with one of the strongest *La Niña* events ever recorded in the region (Pearce and Feng, 2011; Thomson et al., 2014). I use network analysis to describe the *structure* and *dynamics* of second- and third-order alliances, and discuss the implications of my results in terms of the function of third-order alliances. I test which features of the alliance network best predict the shifts observed between time periods. Finally, I use our findings to evaluate the complexity of third-order alliances and discuss how the kinds of social complexity exhibited by this population may arise in through social interaction, which I evaluate further in chapters 3, 4, and 5.

In addition to furthering our understanding of cetacean sociality and the relationship between social and cognitive complexity, such data can increase our understanding of how complex natural systems are organized, and inform management strategies through a better understanding the response of such systems to ecological disturbances, as well as implications for the removal of particular individuals in societies exhibiting social differentiation of roles. As well as benefiting species and demographic-based management strategies, shifts in patterns of sociality among high trophic level species such as bottlenose dolphins may reflect, and therefore be used to monitor, ecosystem-wide change (Anthony et al., 2000; Lusseau and Newman, 2004; Estes et al., 2010; New et al., 2013). For example, long-term monitoring of the health, behavior, and population dynamics of keystone species such as gray whales (Moore, 2008) and sea otters (Estes et al., 2010) has allowed researchers to

¹These concepts further elaborated in Ch. 1

detect ecosystem-wide shifts, leading to the appointment of such long-lived and well-studied populations as “sentinels of change.”

2.1.1 BACKGROUND

Terminology

Relationships and Alliances I use the word *relationship* to describe the frequency of two individuals associating over time (§2.2.3). A relationship is always dyadic, and may exist among any two individuals in the study population. An *alliance* is a particular set of dyadic relationships cut at functional boundaries (§2.1.1.1). For example, a third-order *alliance* is the complete set of dyadic relationships within and between two second-order alliances. Third-order *relationships* are just those dyadic relationships that include one individual from each of the two second-order alliances that comprise a third-order alliance.

Networks Networks are comprised of sets of individuals within a population, and are defined by patterns of association over periods of time. In this study networks are comprised of the members of three second-order alliances (KS,PD, and RR). I use two kinds of time periods: the six-year period from 2009-14, and 'discrete-snapshots' of the network in two-year intervals.

Node Nodes represent individuals. In this study I have used node size to display various measures corresponding the individual's patterns of association within the network.

Edge An edge, or line, represents a relationship between two individuals. In this study I use the half-weight index (hwi), which ranges from 0 to 1, to describe the differential patterns of association observed among dyads. Lines are scaled so that thicker lines represent allies who associate more frequently.

2.1.1.1 Function

Alliances are defined in terms of function: first-order alliances are comprised of pairs and trios of adult males who work together to sequester and consort estrus females (Connor et al., 1992a), and both second- and third-order alliances work together during large scale mate-competitions to steal and defend females from other groups (Connor and Krützen, 2015). Participation in alliances is the predominant strategy governing male reproductive success in this population (Krützen et al., 2004). However, alliances are also found together

outside of the mating context, traveling, foraging, and resting together, suggesting that the function of alliances may extend beyond the mating context.²

It is curious that the second- and third- level of alliance formation should have the same functional role. Connor and Krützen (2015) hypothesize that third-order alliances benefit smaller second-order alliances through increased numbers and proximity of allies when competitions occur, and reported observations of surviving 'lone trios' from older second-order alliances that formed third-order relationships with other lone trios or second-order alliances. These observations suggest that in addition to their function in mate-competition, third-order alliances may function as "back-up" alliances that allow for prolonged reproductive success when second-order alliances deteriorate. However, in the limited cases reported thus far, the possibility of a third-order alliance relationship preceding the observed switch was unknown.

In this study I examined the shifting relationships among three second-order alliances, including the formation of new third-order alliance relationships. During the shift, the opportunity to form new first-order relationships from within the third-order alliance network was present, but not observed. Further evidence for the function of third-order alliances is provided through analysis of the kinds of general activity states observed outside of competitive context.

2.1.1.2 Structure

The second-order alliance is considered the 'core-unit' in Shark Bay: most mature males belong to a second-order alliance, and membership remains stable for years to decades. Second order alliances vary in size from as few as 4 to as many as 14 individuals (Connor et al., 2011). Males in smaller second-order alliances tend to be more related than expected

²Though coordinated group foraging strategies are rare in this population, one alliance foraging strategy called "lateral line" foraging may be an exception. This behavior has only been seen among allied males, and as the name suggests, describes two or more individuals dispersed 50-100m moving in parallel to one another, all exhibiting a diving and breathing pattern consistent with individual foraging. In this formation, alliances should be able to scan a greater area, potentially encountering higher rates of patchy prey and achieving higher foraging success together (though at the risk of increased resource competition). Resting in groups is seen widely among cetaceans, and is assumed to provide increased detection of and defense against predators (Connor, 2000).

by chance, but this pattern does not hold in the largest second order alliances (Krützen et al., 2003). In addition to belonging to a second-order alliance, males form first-order alliances with members of their second-order alliance. First-order alliances vary in (1) size: from two to three individuals, and (2) stability: some first-order alliances are stable over decades (Connor et al., 2006), and others are more labile, with membership that may shift between or even within a particular mating season (Connor et al., 2001). Third-order alliances are larger groups containing members of two second-order alliances. The nature of the relationships that constitute third-order alliances is not well-understood.

In this study, I am particularly interested in the global structure of third-order alliances, as well as the relationships that mediate third-order alliances (see §2.1.1.4)

2.1.1.3 Dynamics

Differences in the stability of first-order alliances have been reported since the earliest papers on alliances in Shark Bay (Connor et al., 1992a; Smolker et al., 1992). A spectrum of labile and stable first-alliances have been observed, with evidence for a positive relationship between first-order alliance stability and consortship rate (Connor et al., 2001). Second-order alliance membership is remarkably stable, with groups forming around the age of sexual maturity and persisting through adulthood (Connor and Krützen, 2015). Little is known about the stability of third-order alliances over time, or how the local and global structure of alliance relationships respond to loss of individuals or major ecological events.

Though the dynamics of social systems has long been recognized, the tools to describe change in these systems over time has been limited. Recently, the potential to make progress on this front using social network analysis has been recognized (Krause et al., 2007; Croft et al., 2008), and researchers are actively developing methods to describe change in such networks over time (Pinter-Wollman et al., 2013; Hobson et al., 2013).

Although methods vary widely, many studies use a “snapshots” approach to study the change in network structure by comparing discrete time intervals (Pinter-Wollman et al., 2013). The challenge for analyses focusing on structural change in social relationships

is that the measures describing individual roles and dyadic relationships are based on repeated observations of polyadic events, and as such are inherently non-independent, and not amenable to standard statistical analyses (Farine and Whitehead, 2015). The current best solutions use matrix permutation procedures to test for correlations among discrete time intervals, and to examine how those correlations change through time (Henzi et al., 2009; Hobson et al., 2013; Farine and Whitehead, 2015).

In this study, I employ matrix permutation procedures to address the question of how different the three time periods in our study are, and follow with a detailed descriptive analysis of what changed in these social networks in terms of alliance relationships and related network attributes.

2.1.1.4 Social Roles

The presence of individual *roles* in the formation or maintenance of the Shark Bay alliance system has not been investigated. In their study of bottlenose dolphins in Doubtful Sound, New Zealand, Lusseau and Newman (2004) used social network analysis to identify “brokers” as individuals located at the boundaries between communities, and whose temporary disappearance suggested their role in maintaining cohesion of the population. Flack et al. (2005, 2006) used social network analysis and a perturbation / knockout approach to identify the structural effects of “policers” (high-ranking individuals found to intervene and terminate conflicts between others) within a captive breeding group of pigtailed macaques. They found that when policers were present, group members had greater partner diversity and therefore larger social networks. In the absence of policers, there were higher rates of conflict, more “conservative” social interactions, and a less integrated society. Various studies of non-human primates have reported on the use of infants (and sometimes adult females) as “buffers” used by adult males to reduce the intensity of received aggression during encounters with other adult males (e.g Kummer, 1971; Packer, 1980; Silk and Samuels, 1984). Related to this effect, use of infants as a social “passport” has also been observed among non-human primates: e.g. Itani (1959) reported on the use of an infant by an adult male Japanese

macaque to gain access to the center of the troop where group leaders and higher ranking females congregate. Primates, typically sub-adult males, also make use of social “passports” when they immigrate to new social groups: Cheney and Seyfarth (1983) found that a majority of subadult males transferred to groups that included members of their previous groups, likely reducing the amount of aggression received from resident adults. Boelkins and Wilson (1972) found that immigrating subadult Rhesus macaques were accepted into new groups by forming an affiliative relationship (demonstrated by mutual grooming) with a resident male. Other important social roles found in mammalian societies include “leaders” (including matriarchs) who initiate food and route planning, migration patterns, or social fusions (e.g. Kummer (hamadrayas baboons; 1971), McComb et al. (african elephants; 2001), Bigg et al. (orcas; 1990), Lewis et al. (bottlenose dolphins; 2011)).

In this study, I am interested in how individual roles influence the structure of the tiered alliance network. I replicate the analysis of Lusseau and Newman (2004) to investigate the role of “brokers”, but find the role as previously defined insufficient for understanding which individuals play the greatest role in maintaining third-order alliances in this system. I introduce a metric to better quantify this network position (“bStrength”), and call individuals with maximal bStrength values “liaisons”. I also identify individuals who maximize within-group associations as “facilitators.” Finally, I apply the concept of “passports” where evidence suggests that certain association patterns may result from individuals gaining admission into social groups through its associations with another individual.

All individuals in this study are mature adult males in their reproductive prime. According to life history theory, all males should be working hard to increase their reproductive success, which in this population means forming and maintaining alliances. In this study I investigate the variation in the degree to which males participate in different levels of alliance formation in relation to their consortship rate (a proxy for reproductive success).

2.1.1.5 Social Complexity

The complexity of human and non-human societies has been a subject of discussion and investigation for centuries, yet there is no consistent definition for social complexity (Whiten, 2000). However, there are rich descriptions of the features of complex societies, both in terms of their global structure, trends in life history, and the behaviors and challenges entailed for individuals. Here I'm focusing only on those identified features which describe the *structure* of complex societies. Group size is often cited, though later works have argued that group size alone is not sufficient to describe social complexity (Dunbar, 1993; Byrne, 1997). Other features include: population density, group stability, social turnover, social hierarchies, levels of social structure, cooperative groups, individual roles, division of labor, relationship stability, encounter variability, fission-fusion grouping patterns, combinatoric richness, and the existence of alliances (Richerson and Boyd, 1999; de Waal and Harcourt, 1992; Kummer et al., 1997; Barrett et al., 2007; Whiten, 2000). The existence of alliances is considered a mark of social complexity because they upset linear rank hierarchies by challenging the relationship between rank and power (De Waal, 1982).

Complexity has been more formally defined in other fields, and some researchers have adapted these definitions to provide a more formal definition for social systems. Strum and Latour (1987) state the that definition of complexity is “to simultaneously embrace a multitude of objects”, and apply this to the social sphere of baboons. While useful for other projects, this definition does not satisfy a structural definition of complexity. Sambrook and Whiten (1997); Whiten (2000) draw from algorithmic information theory to derive their position that “one system is *more complex* than another if it contains more elements and, even more importantly, more combinations or links between the elements.” This definition fails to discern between *complex* systems from *complicated* or random systems: a complicated system is one made of many simple relationships; e.g. a network where each node has only a few connections (Strum and Latour, 1987, Hutchins, pers comm). (Tononi et al., 1998) found this measure to be appropriately low for completely regular strings, it is highest for random strings.

The development of the study of complexity in neural systems has resulted in other useful advances: Tononi et al. (1994) recognized “functional segregation and global integration” as a hallmark of complexity in the neurological organization of higher vertebrates, where functional segregation occurs when small subsets of the system behave independently, and global integration is achieved when large subsets behave coherently (Sporns and Tononi, 2002). Building from Shannon entropy (Shannon and Weaver, 1949), Tononi et al. (1994) introduced a measure for complexity (C_N) “shown to be high when functional segregation coexists with global integration, and to be low when the components of a system are either completely independent (segregated) or completely dependent (integrated).” This contribution has been used widely in the neurosciences, and has more recently been applied to the study of complex networks (Sporns and Tononi, 2002; Sporns, 2006).

Research into social, computational, and cellular networks have independently found that across research domains, complex networks share similar features, many of which relate and help to quantify the local segregation and global integration of such systems. Complex networks show a *small-world topology* in which there are highly connected communities, but each node can reach all other nodes in the network within a small number of steps. Left-skewed degree distributions with fat tails (approaching power-law distributions in the case of scale-free networks) indicate that as the network gets larger, the likelihood of a single node having full connectivity is increasingly low, but the probability of strongly connected local networks is high. Highly connected hubs indicate the presence of social differentiation, with some individuals providing a link between otherwise less densely connected parts of the network. Distinct structural levels also exist in these more complex networks, and are indicated by various network measures (e.g. modularity, multi-layeredness, functional motifs, high average clustering coefficients) (Bullmore and Sporns, 2009; Rubinov and Sporns, 2010; Boccaletti et al., 2006, 2014).

In this study, I apply measures developed in network analysis to quantify and describe the complexity evidenced by the Shark Bay alliance network in terms of functional segregation and global integration (Tononi et al., 1994). Additionally, I describe the dynamics

of the system over time, and discuss the relationship between temporal dynamics, resilience, and social complexity.

2.1.2 RESEARCH QUESTIONS AND SPECIFIC HYPOTHESES

The particular research questions and hypotheses address in this chapter are as follows:

1. What is the structure of second- and third-order alliance?
 - 1.1. I describe the global structure of the second- and third- order alliance using hierarchical clustering analysis and network analysis metrics.
 - 1.2. I evaluate the different kinds of social roles exhibited in the alliance network, and test the hypothesis that some individuals play a greater role in mediating third-order alliance relationships.
2. What are the dynamics of second- and third-order alliances?
 - 2.1. I describe the change in social networks from one time period to the next using the same metrics for describing global structure and roles indicated in (1).
 - 2.2. I use a permutation analysis to test the hypothesis that the alliance network significantly changed from one two-year time period to the next.
 - 2.3. I treat the loss of individuals as a natural perturbation study and describe the observed versus expected changes in the alliance network
 - 2.4. I use the quantitative metrics above in combination with observational data to provide a detailed descriptive analysis of the observed change in alliance relationships.
3. What features of alliance relationships best predict the observed patterns?
 - 3.1. Life history theory predicts that similarly aged males should be investing resources into increased reproductive success. In this population, the predominant strategy for increasing reproductive success is through alliance formation, so all males should be trying equally hard to form and maintain alliance relationships. I test the hypothesis males who have the highest consortship rates are also the most 'central' in terms of their within- and between- group relationships.

3.2. I test the hypothesis that second-order alliances that have more redundant relationships (higher entropy) exhibit more resilience to change.

4. How *complex* are 3rd order alliances?

4.1. I use the data collected in this study to evaluate the hypothesis that third-order alliances are qualitatively and quantitatively complex, and discuss how the kind of social complexity exhibited by this population may arise in through social interaction, which I evaluate further in Chapters 3-5.

2.2 METHODS

2.2.1 DATA COLLECTION

Data for this study were collected as part of a longitudinal study of bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia, in which procedural five-minute surveys of group membership, activity, and location are taken for all groups encountered during normal research operations (Smolker et al., 1992; Mann et al., 2000). An individual is considered to be a member of a group if it is within 10 meters of any other member (Smolker et al., 1992). For this study I restricted the analysis to completed 5-min surveys collected from 2009 to 2014, and to activity contexts that do not include foraging (when aggregations are likely to form), including:

- Socializing: physical contact, splashing, little directional progress
- Resting: very slow travel or hanging still at the surface
- Traveling: slow to moderate speed swimming (1-3.9 mph) with consistent directional progress

Additionally, surveys were eliminated from analysis if they were a repeat observation of the same group in the same day, if the predominant distance between individuals was estimated by observers to be greater than 5-meters, or if the survey had been taken while the group was in the process of a large-scale competition (because these survey data would not have distinguished competing from cooperating sub-groups).

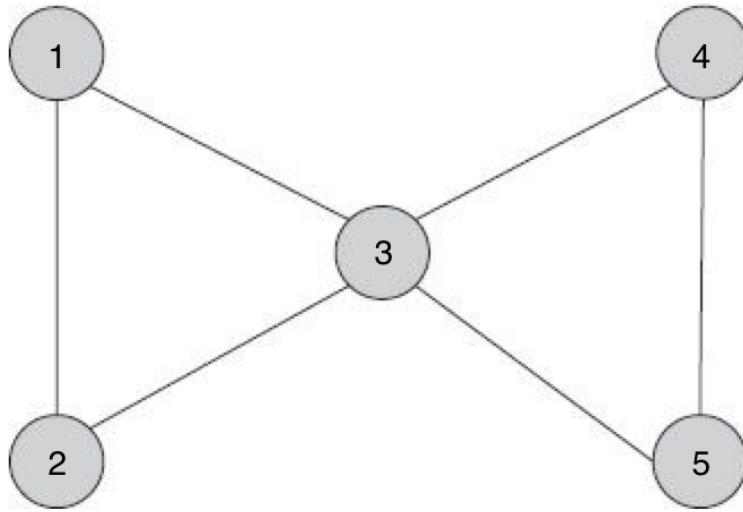


Figure 2.1: A basic “bow-tie” network graph. Individuals (nodes) are represented as circles. Relationships between individuals (edges), are represented by lines. Image modified from (Borgatti et al., 2013).

2.2.2 FOCAL GROUPS

This study focuses on the relationships among three well-studied and frequently-sighted “second-order” alliances, KS, PD, and RR. At start of this study all focal males were reproductively mature and full grown (aged 19 - 37 in 2009). The PD alliance had ‘crystallized’ by 1997, when their within-alliance HWI values rose from 26-73 in 1994-1995 to 75-91. The KS alliance had reached coherence by 2001, and the RR alliance by 2004. These three alliances represent the most frequently sighted alliances in the study site: with core home ranges overlapping the protected bay directly offshore of the research camp (Randić et al., 2012), it is often possible to find and observe these group even when conditions are poor in other parts of the study site.

2.2.3 MEASURING ASSOCIATION

Associations among individuals were estimated by calculating pairwise half-weight indices (HWI) for all individuals in the study (Cairns and Schwager, 1987; Whitehead, 2008). In the equation below (Eqn. 2.1), x is the number of days containing a survey with individuals A and B together, y is the number of days in which both A and B were found in

separate surveys, y_A is the number of days in which A was found but not B, and y_B is the number of days in which B was found but not A.

$$\text{Half-Weight Index (HWI)} = \frac{x}{x + y_{AB} + \frac{1}{2}(y_A + y_B)} \quad (2.1)$$

2.2.4 COMMUNITY STRUCTURE

Hierarchical clustering analysis is a commonly used method in which clusters are formed either by division or agglomeration of subjects. For this analysis, I use the “average-linkage” agglomerative method which begins with each individual in its own cluster, then iteratively combines clusters that share the smallest euclidean distance, defined by a similarity matrix of dyadic association indices. The nature of this method imposes a hierarchical model onto a social group, and the appropriateness of this model can be tested by calculating a cophenetic clustering coefficient (CCC), which is the correlation between the dyadic association indices and the level at which the dyads are joined on the dendrogram. A CCC greater than 0.8 indicates that the hierarchical model provides a good representation of the social network (Whitehead, 2008). Significant groupings within the hierarchical model are detected by calculating a modularity score (Q) for each partition of the network. Modularity compares the number of internal links in the groups to how many one would expect to see if they were distributed at random. The peak modularity value for a hierarchical model is considered to represent a good community partition (Borgatti et al., 2013; Newman, 2004). In this study hierarchical clustering analysis was performed using the software programs SOCPROG (Whitehead, 2009) and UCINET (Borgatti et al., 2002).

Network graphs, in which individuals are represented by *nodes* and relationships among individuals are represented by *edges* (or lines), provide an informative representation of a network (see Figure 2.1). In this paper, edges represent dyadic half-weight indices, with thicker line widths corresponding to higher HWI values. Different algorithms can be used to influence the structure (i.e. circular, unstructured, etc) and spatial parameters of a network graph, with the goal of providing objective summaries of observed data. In this paper, I

use the scale-free, force-directed *ForceAtlas2* algorithm implemented in the program Gephi (Jacomy et al., 2014; Bastian et al., 2009), to produce graphs where distances among nodes represent the strength of relationships (stronger associates and communities of associates are located closer together, in addition to having thicker connecting lines). To generate each network graph, I started from a randomized spatial layout and ran the forceAtlas2 algorithm until it converged on a solution (~ 20 minutes). I repeated this process a minimum of three times per graph to ensure that the resulting graphs represented global solutions.

2.2.5 CENTRALITY OF MEMBERS

There is an extensive set of measures for determining an individual's *centrality*, or importance, in a social network (e.g. Wey et al., 2008; Whitehead, 2008; Borgatti et al., 2013; Gazda et al., 2015). Many of the measures are related, and the choice of a measure should be made carefully to ensure that it addresses the particular research question. In this study, I am interested in the question, "are there individuals who are playing a greater role in maintaining third-order alliances?" This question requires a method for determining an individual's centrality relative to the different levels of social organization present in this social network (§2.3.2). Below I introduce some of the more commonly cited measures of centrality, focusing on those most relevant to the question at hand which I evaluate against other measures in this paper.

- Degree centrality: the number of edges (connections) an individual (i) has (Borgatti et al., 2013). In the formula below, A is the adjacency matrix describing all associations in the network, with a_{ij} equal to 1 if the nodes i and j are joined by an edge, and 0 if not. In figure 2.1, $d_1 = 2$, and $d_3 = 4$.

$$d_i = \sum_j a_{ij}$$

- Strength (a.k.a weighted degree centrality): the sum of the weighted edges connected to an individual. For a weighted network of association indices, this is the sum of

all dyadic association indices for each individual (Whitehead, 2008, ch. 5). In the formula below, HWI is the matrix of all association indices for pairs of individuals in the network, with hwi_{ij} equal to the specific half-weight association index of nodes i and j :

$$s_i = \sum_j hwi_{ij}$$

- **Betweenness centrality:** quantifies the frequency that a node falls along the shortest path between two other nodes. This measure has been used to identify social “brokers”, or nodes who link communities, among other populations of free-ranging bottlenose dolphins (Lusseau and Newman, 2004). In the formula below, g_{ijk} is the number of shortest paths (geodesics) connecting j and k through i , and g_{jk} is the total number of shortest paths connecting j and k (Borgatti et al., 2013). In figure 2.1, node 3 lies on the shortest path between nodes $\{1,5\}$ and $\{2,4\}$, and would have the highest betweenness value within that network.

$$b_i = \sum_{j < k} \frac{g_{ijk}}{g_{jk}}$$

- **Eigenvector centrality:** this value is high for nodes that are either (a) connected to many other nodes, or (b) connected to others who are themselves connected to many other nodes. It has been used to explain the likelihood of calf survival among bottlenose dolphins (Mann et al., 2012). In the formula below, A is the adjacency matrix of associations, a_{ij} is the binary value indicating association among i and j , E is the eigenvector of A , with eigenvalues e_j calculated for each vector (individual associations). λ is the characteristic value (eigenvalue) of the adjacency matrix A , required so that the equations have a nonzero solution (Bonacich, 1987; Spizzirri, 2011; Borgatti et al., 2013).

$$e_i = \lambda \sum_j a_{ij} e_j$$

To provide the most direct assessment of the research question posed above, I utilized the results of our hierarchical clustering analysis to assign individuals to groups and subsequently calculate within- and between-group strength values, $wStrength$ and $bStrength$ accordingly, for all individuals in the social network. In the formulas below (Eqns. 2.2,2.3), HWI is the matrix of all association indices for pairs of individuals in the network, with hwi_{im} equal to the specific half-weight association index of nodes i and m , where m represents i 's external connections, and n represent i 's internal connections.

$$bStrength_i = \sum_m hwi_{im} \quad (2.2)$$

$$wStrength_i = \sum_n hwi_{in} \quad (2.3)$$

Because of the influence of network size on these two measures, I also created relativized formulas for each of these measures by dividing by the number of possible associates (N) in each category. In the equations below (Eqns. 2.4,2.5), N_m is the total number of possible KS, PD, or RR associates outside the individual's second-order alliance, and N_n is the total number of possible KS, PD, or RR associates within the individual's second-order alliance (e.g. their second-order alliance size -1).

$$bStrengthR_i = (\sum_m hwi_{im})/N_m \quad (2.4)$$

$$wStrengthR_i = (\sum_n hwi_{in})/N_n \quad (2.5)$$

These measures are related to the "E-I index" proposed by Krackhardt and Stern (Krackhardt and Stern, 1988), which describes how homo- or hetero-philic an individual is.

In the formula below, (E) is the number of external connections to individual i , and (I) is the number of internal connections to i . In weighted networks (as are used here), E and I are the sums of weighted connections (HWI) for the external and internal networks. The E-I index ranges from -1 (all connections internal) to +1 (all connections external) (Crossley et al., 2015; Krackhardt and Stern, 1988).

$$EI_i = \frac{E - I}{E + I} \quad (2.6)$$

Though I report both measures, I have chosen to focus on *bStrengthR* in this paper for two reasons. (1) The E-I index has been criticized because it does not account for the variable number of internal or external connections an individual has to choose from (Crossley et al., 2015). (2) The E-I index folds two kinds of relationships into one measure, and therefore masks the phenomenon of interest in this study.

Finally, I used the program UCINET (Borgatti et al., 2002) to analyze the alliance network for *blocks* and *cut-points*. A *cut-point* is a node whose removal would lead to the fractionation of a network into independent (non-connected) *blocks* (Croft et al., 2008). In figure 2.1, node 3 is a cut-point because its removal would lead to two network blocks comprised of nodes {1,2} and {4,5}. In my analyses, I was specifically interested in whether there were any cut-points positioned between two second-order alliances (e.g. individuals entirely responsible for the third-order phenomenon).

2.2.6 DYNAMICS THROUGH TIME

During the course of the six-year study, four of the focal males who had been regularly sighted for 10-15 years disappeared from all surveys and are presumed to have died. Two males from the 'KS' alliance disappeared between the end of the 2010 field season and the start of the 2011 season. The other two males from the 'PD' alliance both disappeared between the end of the 2012 field season and the start of the 2013 field season. Males are presumed dead due to the regularity with which they were sighted for the prior 10-15 years

and their consistent occurrence in the most well-sampled area of the study region. This study uses a discrete “snapshots” approach (de Silva et al., 2011; Pinter-Wollman et al., 2013) to examine the changing dynamics among members of this social network in two-year intervals. This method is well-suited to the seasonal nature of our data collection, and the two-year intervals correspond with the timing of the observed disappearances.

Restricting the association matrix to only those individuals that survived through subsequent time periods, I used a quadratic assignment procedure (QAP) to test the null hypothesis that each time period and the next following were not any more correlated than expected by chance (Borgatti et al., 2013; Crossley et al., 2015). QAP calculates a correlation measure (I use Pearson’s r) between two matrices, then compares the observed correlation to the correlations between thousands of pairs of permuted matrices constructed from one of the input matrices. The resulting p-value indicates the proportion of correlations among these matrices that were as large as the observed correlation (Borgatti et al., 2013, p.128). I used 50,000 permutations to ensure the p-value had stabilized.

The manipulated association matrices described above constitute null, or “artificial knockout” models of the types of association patterns one would observe if the removal of individuals had no perceivable effect on the associations among those remaining. In addition to the QAP analysis, I contrast the null 2011-2012 model with the observed 2013-2014 model, focusing on the predicted versus observed change in within, between, and total Strength scores.

2.2.7 SOCIAL ROLES AND REPRODUCTIVE SUCCESS

In this study I used individual *consortship rate* as a proxy for reproductive success, where consortship rate (CSR) is defined as the number of peak mating season days (September 1 - Jan 1) in which each male was found in a consortship (dCSR), divided by the total number of days that male was sighted (dOBS) (Connor et al., 1996; Connor and Krützen, 2015)

$$CSR_i = \frac{dCSR_i}{dOBS_i}$$

This variable was used to test the null hypothesis that there is no linear relationship between bStrength and CSR for the 2013-2014 period (where I have complete data for both variables).

2.2.8 COMPLEXITY

The complexity of the 2009-2014 alliance network is described in terms of functional segregation (local clustering) and global integration (coherence), using measures developed in the network analysis literature. Functional segregation is described in terms of modularity and clustering coefficients. Global integration is described in terms of the network's global characteristic path length and hierarchical clustering (Boccaletti et al., 2006; Bullmore and Sporns, 2009; Rubinov and Sporns, 2010). Definitions for each of these measures is given below:

- *Modularity*. This measure indicates the degree to which a network may be sub-divided into non-overlapping groups (clusters), and is quantified by the modularity index Q (§2.2.4) (Newman, 2004).
- *Clustering Coefficient*. The clustering coefficient of node c_i describes the likelihood any two neighbors of i to be associated, and is calculated on a binary network of associations. The global clustering coefficient C of a graph is the average of c_i over all the nodes in the network, and ranges from 0 to 1 (Watts and Strogatz, 1998; Boccaletti et al., 2006). The clustering coefficient is high for complex networks and low for random networks (Bullmore and Sporns, 2009).
- *Characteristic Path Length*. As defined in §2.2.5, geodesics are the pathways with the fewest number of edges between two nodes in a network. The diameter of a network is the maximum geodesic distance in a network. The average shortest path length, or characteristic path length, is the mean geodesic distance between all pairs of nodes in the network (Boccaletti et al., 2006). It is considered to be a good measure of a network's *integration*. However, both complex and random networks show a short

mean path lengths (Bullmore and Sporns, 2009).

- *Hierarchical clustering*. Related to modularity, hierarchical clustering (§2.2.4) also reveals the global integration of networks and provides metrics for how regularly distributed or nested relationships are.

In addition, the complexity indicated by the alliance network is discussed in terms of the temporal dynamics, robustness, and social roles described in this chapter.

2.3 RESULTS

2.3.1 WHAT IS A THIRD-ORDER ALLIANCE?

Third-order alliances were first described in the context of mate-competitions and associations (Connor et al., 2011). Here I've restricted the sighting data I use to describe third-order alliances to explicitly *exclude* these kinds of events (§2.2.1). As a consequence, the results I report here are on those associations among third-order alliances that occur in non-competition contexts. Detailed descriptions of the interactions that occur among third-order associates will be described in Chapter 3, here I describe some of the basics of these types of associations.

Of the 1314 5-minute surveys that met the criteria for inclusion in this analysis, there were 138 surveys that included any KS males, 85 that included any PD males, and 98 that included any RR males (282 surveys included any KS or PD or RR males). Surveys were considered “third-order associations” if they contained individuals from two second-order alliances (KS and PD = 26, KS and RR = 11, PD and RR = 2). The third-order KS-PD alliance was persistent throughout the study period; 11.66% of all surveys in which any KS or PD males were present were third-order associations between the KS and PD males (26/223). Ratios of primary activities recorded among third-order groups were broadly similar to that of second-order groups. However, third-order groups spent less time resting and traveling and more time socializing than second-order groups (Table 2.1).

Table 2.1: Activities of 2nd and 3rd order alliances (KS, PD, RR combined)

Primary Activity	2nd-Order	3rd-Order
Rest	49.2 %	43.6%
Travel	33.8 %	25.6%
Socialize	14.6 %	20.5%
Unknown	2.4 %	10.3%

2.3.2 COMMUNITY STRUCTURE

Hierarchical clustering analysis of half-weight association indices (HWI) among the 22 males present for more than two years out of the six-year study period detected the same three communities (max $Q = 0.40$ at $HWI = 0.20$), that had been identified as second-order alliances by field teams and in previous work (Connor et al., 2011). Figure 2.2 shows the second-order alliances in blue (PD), green (KS), and red (RR). The dendrogram also shows a distribution of first-order HWI, with some individuals nearing 1 (e.g. $HWI \{NAT, WAB\} = 0.97$). The model has a very high CCC (0.98) indicating that the hierarchical model provides a good representation of the the relationships among these individuals. One individual, BAR, is indicated as a peripheral member to the PD alliance, consistent with field observations.³

The graph in Figure 2.4 is another representation of the same data. In this graph, we can readily identify the most stable first-order alliances as those trios with the thickest connecting lines (“edges”), second-order alliances as those with stronger within- than between-group associations (and who share a color assigned by the modularity analysis), and third-order alliances as weakly connected second-order alliances.

2.3.3 CENTRAL MEMBERS

2.3.3.1 Degree

The number of connections per individual ranged from 10 to 21 (the maximum number of possible connections in the KS-PD-RR network). Individuals with the highest degree values were from the PD and KS alliances, however within all three groups there was

³It is important to note that while these metrics *describe* first-, second-, and third-order alliances, levels of alliances are *defined* functionally (§2.1.1.1).

at least one trio that showed a higher number of connections relative to other individuals within the same second-order alliance (Table 2.2, Figure 2.8a).

2.3.3.2 Strength (weighted degree)

Strength was highest for individuals in the KS alliance: members of the KS alliance had the highest combined association values. This finding is consistent with the large size of the KS alliance, and the tendency for all males in the second-order alliance to associate together, especially during the peak mating season (Table 2.2, Figure 2.8b).

2.3.3.3 Betweenness

Males with the highest betweenness were also the individuals with the most connections in the network (those with highest degree). This measure indicates members of the KS alliances as most central because they fall along the highest number of geodesic paths in the network. A trio in each of the PD and RR alliances also show relatively higher betweenness centrality values compared to the other members of their group (Table 2.2, Figure 2.8c). Prior studies have labeled individuals showing high betweenness “brokers”, and suggest these individuals play a crucial role in maintaining the cohesion of a community (Lusseau and Newman, 2004). In addition, such individuals may confer a social advantage to the peripherally connected individuals by acting as a ‘passport’ (Itani, 1959) to allow peripheral individuals to join groups to which they are not otherwise connected (such events were not captured in the survey data). A shortcoming of this measure is that it does not take into account any information about the position of the individuals connected in by those with the resulting high betweenness scores. For example, when BAR, a peripheral male who has low centrality scores across the board, was removed from the 2009-14 network, the already low betweenness scores for PRI WAB NAT NOG drop to zero, and those for FRE RID BIG DNG decline dramatically (Table 2.3). Thus ‘centrality’ indicated by an individual’s betweenness score should be treated with caution as it may also indicate a failure to participate in relationships with more influential individuals.

2.3.3.4 Eigenvector

Eigenvector centrality emphasizes the members of the KS alliances as being the most 'well-connected' individuals in the network, and is highly correlated with strength (see Figure 2.6). Because this is a small network with most individuals participating in a large number of relationships, eigenvector centrality does not show strong discrimination among individuals (Table 2.2, Figure 2.8d).

2.3.3.5 Within and Between Group Strength

Figure 2.9 shows the proportion of each individual's total strength that is within-group (darker color) versus between-group (lighter color). Nodes are sized based on an individual's relativized between-group strength value (*bStrengthR*). This graph and the associated values for bStrength and bStrengthR in Table 2.2 indicate that in each alliance, there is one trio who more frequently participates in between-group associations. In this study I call these individuals *liaisons*. Consistent with this role, in the network graph, these same individuals are found on the borders of their second-order alliance space closest to other second-order alliances.

The distribution of bStrengthR is relatively normal (Figure 2.7). All individuals in this social network participated in some third-order associations, although two individuals (REA, LAN) show particularly low bStrength values ($z < -1.5$). The individuals with the highest bStrength values for the entire 6-year period were PON, QUA and PAS ($z > 1$).

2.3.4 DYNAMICS THROUGH TIME

To examine the change in alliance relationships through time, I divided the six-year dataset into three two-year periods: 2009-2010 (T1), 2011-2012 (T2), and 2013-2014 (T3).

2.3.4.1 T1: 2009-2010

Figure 2.14 summarizes the group relationships in 2009-2010. The third-order alliance relationship between PD and KS was already present ($Q = 0.3522$ at $HWI = 0.2788$;

CCC = 0.9657), and no cut-points were found. RR males were not found in associations with PD or KS males during this period. Three males within the PD group (PRI WAB NAT) showed highest between-group strength values (bStrength = 2.93 to 3.06, bStrengthR = 0.17 to 0.18), indicating their increased role in maintaining this third-order alliance (Table 2.4). Among the KS, another trio (MID PON QUA) showed the highest between-group strength values (bStrength = 1.63 to 1.80, bStrengthR = 0.14 to 0.15). Both trios were stable 1st-order alliances, and both were positioned on the border between the two second-order alliances in the network graph (Figure 2.14).

2.3.4.2 T2: 2011-2012

After the end of the 2010 field season two of the KS males (BOL and MID) were no longer sighted and are assumed to have died⁴. Figure 2.15 shows the network graph for this period. There were still no indications of a relationship between either group and the RR alliance during this period. The third-order alliance relationship between KS and PD was maintained (Q = 0.4617 at HWI = 0.21341, CCC = 0.9855). BAR had a low number of sightings (n=4) with either KS or PD. No cut-points were detected. The same three PD as in the prior period showed high between-group strength values (PRI WAB NAT: bStrength = 1.72, bStrengthR = 0.11, Table 2.4). Within the KS, two of the high bStrength males from the prior period (PON QUA) were again among the trio with the highest between group strength values (bStrength = 1.35, bStrengthR = 0.11). Interestingly, during this period PAS moved in to the *liaison* role previously assumed by MID: his between group strength value was the highest observed in KS in the period (bStrength = 1.50, bStrengthR = 0.12) and his node replaced MID's in a border-position in the social network.

Could we have predicted these shifts? Possibly: In 2009-2010 (Figure 2.14, Table 2.4), PON QUA MID formed a stable trio within KS. The strongest KS associates to either PON and QUA other than MID included BOL, CEB, DEE and PAS (HWI 0.45 to 0.54;

⁴It is very unlikely that these males were still alive but have since gone undetected by observers, (a) because their long-term alliance, KS, was frequently sighted without them, and (b) because their core range fell within the most often-surveyed portion of the research area.

Table 2.6). BOL disappeared, and CEB and DEE were among the males with the lowest bStrength values for the T1 period. PAS and NOG had the next highest bStrength values (1.2 and 1.33, respectively), but PAS had the stronger relationship to both PON and QUA, and was not part of a stable trio. Based on these qualifications, he may have been the best candidate to fill MID's vacant role.

In 2009-2010, BOL had among the lowest values for bStrength (0.91), but was in the highest end of the distribution for wStrength values (5.3) (Table 2.4). He was not in a stable trio; instead he belonged to the subset of KS males who formed more stable pairs and rotated individuals to form a trio during consortships (Figure 2.21). His high wStrength value is due to a larger set of relationships at mid-range HWI's, rather than a limited set of relationships with very high HWIs (Table 2.6). Thus, rather than acting as a liaison to other groups, BOL's association pattern seems to have provided some of the social webbing that may facilitate coherence within large second-order alliances. This role (here called "provincial hub" (c.f. Bullmore and Sporns, 2009)) seems to be important within the larger KS alliance: after his disappearance, all KS males except the three T2 liaisons showed increased wStrength, with the highest values belonging to DNG and NOG, followed by MOG IMP and KRO (Table 2.4). DNG NOG KRO were a stable trio in T1, and continued in this capacity through the T2 period. In T2 MOG formed a stable trio with CEB DEE. In T1, CEB's closest associate had been BOL, and DEE's had been PAS. Given the outcomes for BOL and PAS, it may have been natural for CEB and DEE to form a pair in T2. Their inclusion of MOG required the disintegration of the formerly strong MOG-IMP pair, but allowed the KS alliance to form three trios, a more stable state for these trio-consorting males. Though the tenth member of a now stable group, IMP showed increased, rather than decreased, wStrength values from T1-T2 with a broad distribution of mid- to high-level HWI's, filling BOL's role as the *provincial hub* that helped this larger second-order group to maintain its coherence during the T2 period (Tables 2.4 and 2.7).

2.3.4.3 T3: 2013-2014

The most notable shift in alliance relationships happened between the 2011-12 and 2013-14 periods. The peripheral PD male “BAR” and the central PD male “PRI” were not sighted during any surveys after November 2012 and are presumed to have died. In addition to the survey data used in this analysis, in 2013 and 2014 we were conducting intensive focal follows on the KS and PD groups. From July through mid-November 2013, there were no surveys or follows that included RR males with KS or PD males other than in a foraging capacity, similar to the prior periods. In mid-November 2013 we observed a sudden inclusion of the RR, with KS most frequently, though also with PD, in all contexts (Figure 2.16). This association has continued through the most recent (2016) field season. Modularity and hierarchical clustering analysis of this period assigns individuals to three clusters, corresponding to the KS, PD, and RR groups identified by observers ($Q = 0.3112$ at $HWI = 0.1296$, $CCC = 0.9601$). No cut-points were detected. Interesting shifts occurred in terms of bStrength centrality: the three RR males observed most commonly with the KS and PD groups showed the highest overall bStrength values (bStrength = 1.83 to 1.96, bStrengthR = 0.12 to 0.13), and the highest proportion of between to within-group strength observed in any period. During this period we observed the RR alliance shift from a five-member group, to a 'lone' trio, with LAN at first associating and participating in consortships, though eventually the most prevalent RR trio was SMO URC COO. Within the KS alliance, the same three individuals as in the prior period showed the highest values of bStrength within their group (bStrength = 1.45 to 1.69, bStrengthR = 0.14 to 0.17), increased from the T2 period. Among PD males, NAT and WAB, first-order associates of PRI, showed a notable decrease in bStrength (bStrength = 1.09 to 1.12, bStrengthR = 0.07), while the remaining three males in the PD alliance increased bStrength relative to T2 (bStrength = 1.25 to 1.39, bStrengthR = 0.08 to 0.09) (Figure 2.10, Tables 2.4,2.5). Within the PD alliance additional shifts are apparent: wStrength declined for all PD males (Figure 2.11), and the average HWI between the two first-order PD alliances declined precipitously from 0.717 in T2 to 0.132 in T3 (Figures 2.22 and 2.23).

The loss of BAR was unlikely to have precipitated these changes: with the lowest bStrength and wStrength values among all PD males during both T1 and T2 (Table 2.4), and a betweenness value of 0 (Table 2.2) there is no indication of that BAR engaged in either the *liaison* or *provincial hub* roles within the PD alliance. However, some of the observed changes may be attributable to the loss of PRI.

In T1 and T2 PRI WAB NAT were the most stable first-order alliance in the KPR network ($HWI = 0.97$ to 1.00 ; Figures 2.21, 2.22). All three males, including PRI, had the highest bStrength values for the PD alliance in T1 and T2, indicating their role as *liaisons* to the KS alliance. After PRI's disappearance bStrength for WAB and NAT declined, suggesting that PRI may have been mediating their third-order associations. One prediction stemming from these observations is that the HWI between the KS and PD alliances would have decreased with the loss of PRI. Instead, very little change was recorded ($HWI_{T2} = 0.126$, $HWI_{T3} = 0.124$), owing to the simultaneous increase in bStrength for the remaining PD trio (Figures 2.21, 2.22, Table 2.4). The same is not true for the observed change in wStrength; as previously noted all males decreased in wStrength after the loss of PRI, suggesting that he was also playing an important role as a *provincial hub* of the PD alliance.

2.3.5 QAP & THE THEORETICAL 'KNOCKOUT' MODEL

QAP analysis of the T1 knockout model ($T1_{ko}$) and T2 showed high correlation between the two time periods ($r = 0.8275$, $p < 0.001$). The correlation between the T2 knockout model ($T2_{ko}$) and T3 showed a lower, though still significant correlation ($r = 0.7569$, $p < 0.001$). In both cases I reject the null hypothesis that there is no correlation between time periods. Despite the disappearance of individuals and observable re-organization, the overall structure of the KS-PD network persisted over time.

At the individual level, we see that there is some significant change. Figure 2.17 shows the expected versus observed change in within-group strength values. The $T2_{ko}$ model predicted that only PD males would show a decrease in within-group strength, as both removed males were part of the PD alliance. The observed change shows that all males in

the social network decreased their within-group strength values. A Wilcoxon signed-ranks test indicated that the change we saw from T2-T3 differed significantly from the expected change from $T2_{ko}$ to T3 ($Z = 3.296$, $p < .001$, $r = 0.623$).

In figure 2.18 we see the expected versus observed change in between-group strength values. Here, the $T2_{ko}$ model predicted that all KS males would show a decrease in bStrength values, reflecting the loss of their third-order PD associates. PD males were not expected to show a change in bStrength. The observed change shows a global *increase* in between-group associations, with the exception of the first-order associates of the lost PD male PRI, who showed a large *decrease* in between-group associations. The Wilcoxon signed-ranks test does not show that the change we saw from T2-T1 differed significantly from the expected change from T1-KO, likely because of the two outliers ($Z = -1.9147$, $p = 0.058$, $r = -0.362$).

Figure 2.19 shows the expected versus observed change in between-group strength, but this time taking into account the wider adult male alliance network to examine the possibility that males had increased between-group associations outside the KPR network. The pattern is largely similar to the KPR network, though accentuated in both directions for the members of the PD alliance.

2.3.6 SOCIAL ROLES AND REPRODUCTIVE SUCCESS

For the 2013-2014 period there was a significant positive correlation ($r = 0.722$, $p < .001$) between individual consortship rate (CSR) and bStrengthR (see Figure 2.20). Individuals who participated in higher rates of third-order association also had a higher consortship rate.

2.3.7 COMPLEXITY

The complexity of the alliance network is indicated by the degree to which it demonstrates functional segregation and global integration. In addition, network complexity may be indicated by the existence and nature of social roles, and the manner in which it responds to change.

The 2009-14 alliance network showed a peak modularity Q at 0.40, splitting the network into three communities where HWI values were greater than 0.20 for each community member. These three communities corresponded to the three second-order alliances KS, PD, and RR. This structural segregation is also functional, as we know alliances work together during competitions over female consorts. This network also shows high clustering coefficients (mean = 0.896, sd = 0.075), indicating that most individuals are found within densely connected sub-networks.

Global integration is indicated by the existence of a short characteristic (mean) path length (1.195), and a small network diameter (2.0). All nodes in the network are within two steps of one-another. Functional integration is provided again by the biological function of the male alliance network (competitions). Hierarchical clustering indicates both structural segregation of communities and global integration, showing the average association value between the most minimally connected communities (RR and PD) is low but above zero ($hwi = 0.008$), with higher average association values for KS and PD ($hwi = 0.124$), and increasing values for second-order and first-order alliances (Figure 2.2).

In order to achieve the structural pattern indicated by local functional segregation and global integration, there must exist individuals who act to bind areas of the network that would otherwise lead to a total fractionation. These “connector hubs” may be detected by a number of measures depending on the network under investigation. Here those individuals are best described by $bStrength$ and $bStrengthR$, high for individuals who, in addition to having strong within-community connections, also have strong extra-community ties. At least this level of social differentiation should be present in complex networks. In addition, this study found individuals who had higher with-group connections (sometimes the same individual). Such individuals have been referred to in the literature as “provincial hubs” (Bullmore and Sporns, 2009).

The network’s response to the temporal dynamics described in this study are another indication of social complexity. Given the presence of social roles, the removal of more or less central individuals may affect the organization of relationships in a social network

differently. The disappearance of MID and BOL (from the KS alliance) after T1 corresponded to local re-organization in T2, but the disappearance of PRI and BAR (from the PD alliance) after T2 corresponded to global and unexpected shifts in the alliance network. The difference between these two disappearances were explained in terms of the individuals' network position, as well as the structure of the second order alliance. The KS alliance was larger than the PD alliance, with less regular sub-groups. The PD alliance was comprised of two very strong trios (and the peripheral male BAR). Such structures likely contribute to a network's resilience to change.

2.4 DISCUSSION

2.4.1 COMMUNITY STRUCTURE

The community structure of the KS-PD-RR network fits a hierarchical model in which individuals are modularly organized at three levels of association, in agreement with prior studies (Connor et al., 2011). The representation of pairwise associations as a network graph allows for an informative visualization of all three levels of alliance.

2.4.2 FUNCTION

Previous reports of third-order alliances focused on their role in mate-competition (Connor et al., 2011; Connor and Krützen, 2015). In this study I excluded mate-competition from my analyses to focus on the relationships among third-order allies outside this primary competition. I found that ratios of primary activities recorded among third-order groups were broadly similar to that of second-order groups. However, third-order groups spent less time resting and traveling and more time socializing than second-order groups. This increased rate of socialization is likely important for establishing and maintaining the third-order associations; this topic is further examined in Chapter 4. Prior observations (Connor and Krützen, 2015) suggest that in addition to their function in mate-competition, third-order alliances may function as 'back-up' alliances that allow for prolonged reproductive success when second-order alliances deteriorate. In this study I examined the shifting relationships

among three second-order alliances, including the formation of new third-order alliance relationships. During the shift, the opportunity to form new first-order relationships from within the third-order alliance network was present, but not observed.

2.4.3 CENTRAL MEMBERS

I reported on several metrics used to identify central members of social networks, and concluded that *bStrength*, the sum of the half-weight association indices between an individual and associates external to their 2nd-order alliance, provided the most informative metric when addresses the question of whether certain individuals played a greater role in maintaining third-order relationships. I found that within each second-order alliance, there was one trio who participated in higher rates of third-order association than their fellow group members, while maintaining similar levels of within-group associations. By participating in higher-levels of between-group associations, these individuals appear to be playing a critical social role in mediating third-order alliances. Interestingly, these individuals also constituted the strongest first-order alliances in the study group.

2.4.4 DYNAMICS THROUGH TIME

I used a discrete “snapshot” approach to examine the changes in this social network over three two-year intervals. QAP analysis indicated that each time period was significantly correlated to the preceding period, but that the T2-T3 periods were less correlated than the T1-T2 periods. Visual analysis of the network graphs for these associated periods highlights just how different the T3 period was: the RR alliance, previously not associated with either KS or PD, became a close associate of both alliances. Major fractionation is apparent in the PD alliance. I used an artificial “knockout” approach (Flack et al., 2006) to predict change in between- and within- group associations from one time period to the next. When these models were compared to the observed networks, I found systemic shifts in the T3 period that were not predicted by the knockout models.

I offer two explanations for why the T3 period showed such differences: (1) Given

the strength of the third-order relationship between PRI WAB and NAT, and the radical decrease in bStrength values for WAB and NAT, it is possible that PRI was initiating the observed between-group associations, and may have acted as a passport (Itani, 1959) for WAB and NAT. However, this explanation fails to account for the widespread changes in both within and between-group associations across all members of the social network. (2) For 10 weeks in the Austral Summer of 2010/2011 the Western Coast of Australia experienced a marine heat wave associated with one of the strongest *La Niña* events ever recorded (Pearce and Feng, 2011), with sea-surface temperature in Shark Bay reaching its peak at $\sim 4^{\circ}\text{C}$ above average in February 2011. High temperatures were sustained at $\sim 2^{\circ}\text{C}$ above average in February 2012 and 2013 (Caputi et al., 2014). Coincident with this event, the median coverage for the most common seagrass (*A. antarctica*) experienced a 97% dieback, green turtle health status declined precipitously from 2011-2013, and abundances for scallops and blue swimmer crabs were sufficiently low to necessitate fisheries closures in 2012 (Thomson et al., 2014; Caputi et al., 2014). Given the ecosystem-wide nature of these shifts, an effect on the bottlenose dolphin population in Shark Bay would seem inevitable, and as secondary/tertiary consumers such effects are likely to have been delayed. It is quite possible that the network-wide shifts documented in T3 were a by-product of the temperature anomalies experienced in Shark Bay just prior to that period, however further data will be required to evaluate this hypothesis.

This study highlights the importance of long-term studies capable of documenting change in individual's life histories: in order to manage populations as they continue to experience more frequent and/or intense climatic events, we need to be able to predict their response to such events. Here we see a substantial re-organization of social relationships coincident with the loss of key members and an extreme climatic event, suggesting some resilience for the bottlenose dolphins at this point in time. However, further research is required to fully understand the effect of this event on the dolphin population.

2.4.5 SOCIAL ROLES AND REPRODUCTIVE SUCCESS

For the 2013-14 period, I found that individuals who participated in high combined rates of association (total Strength) also had high consortship rates, and that similar (though slightly weaker) correlations existed for within-group Strength and consortship rate as well as between-group Strength and consortship rate. The most gregarious males in terms of their alliance relationships had the highest consortship rates, suggesting either that gregariousness is directly related to consortships, or that males who invest more heavily in alliance relationships reap the benefits of higher consortship rate. This may occur via increased odds of inclusion in a consortship group or by increased ability to attract allies during competitions. A prior study (Connor et al., 2001) found a significant relationship between consortship rate and alliance stability; this variable, as well as first-order alliance strength (e.g. maximum half-weight index found for each sub-group using the hierarchical clustering procedure) may provide further insight into the correlations found here.

2.4.6 COMPLEXITY

The alliance network showed features of local functional segregation and global integration. Communities of individuals are evidenced within a larger network with closely linked members. This criteria is the same used to define the “small-world topologies” seen across a range of networks, and considered a hallmark of complexity (Bullmore and Sporns, 2009). The existence of social roles (connector hubs / liaisons and provincial hubs) and the particular ways in which the network responded to change over time are further descriptions of the complexity of the alliance network. Future work will continue to assess this network’s complexity through application of the measure for complexity C_N developed by Sporns, Tononi and colleagues (e.g. Sporns and Tononi, 2002), and application of the multi-layered analysis framework to take into account different categories of connections such as relatedness, behavioral interactions, and consortship frequency.

2.5 ACKNOWLEDGEMENTS

Chapter 2, in part, is currently being prepared for submission for publication of the material. Friedman, W.R.; Krützen, M.; Connor, R.C. The dissertation author was the primary investigator and author of this material.

2.6 FIGURES AND TABLES

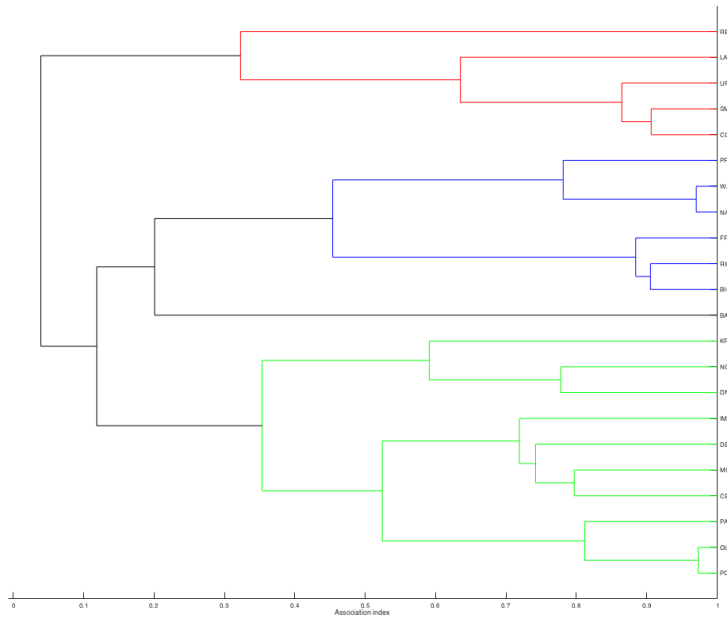


Figure 2.2: Results of hierarchical cluster analysis / cluster dendrogram. Distance = euclidean. Clustering method = average

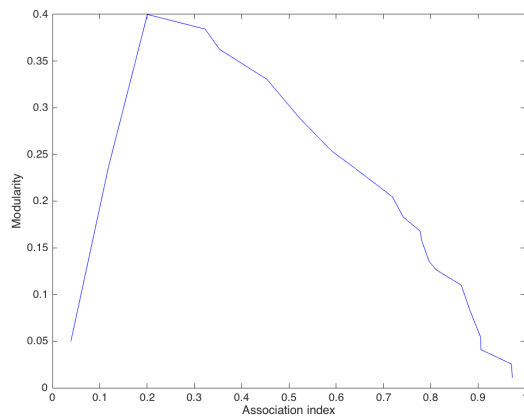


Figure 2.3: Modularity graph. The peak modularity value for a hierarchical model is considered to represent a good community partition. Here $\max Q = 0.40$ and $\text{HWI} = 0.20$, dividing the set of males into three alliances. This aligns to the breaks in the dendrogram in Figure 2.

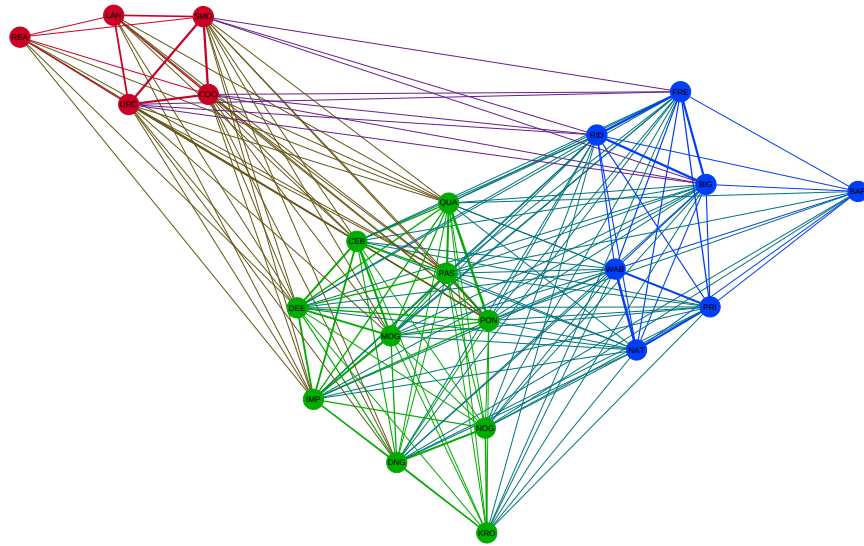


Figure 2.4: Network graph of HWI association data. Nodes are individuals, edges (lines) are dyadic associations. Edge width and node distance indicate the strength of relationships. Second-order alliances are colored based on the result of the hierarchical clustering analysis.

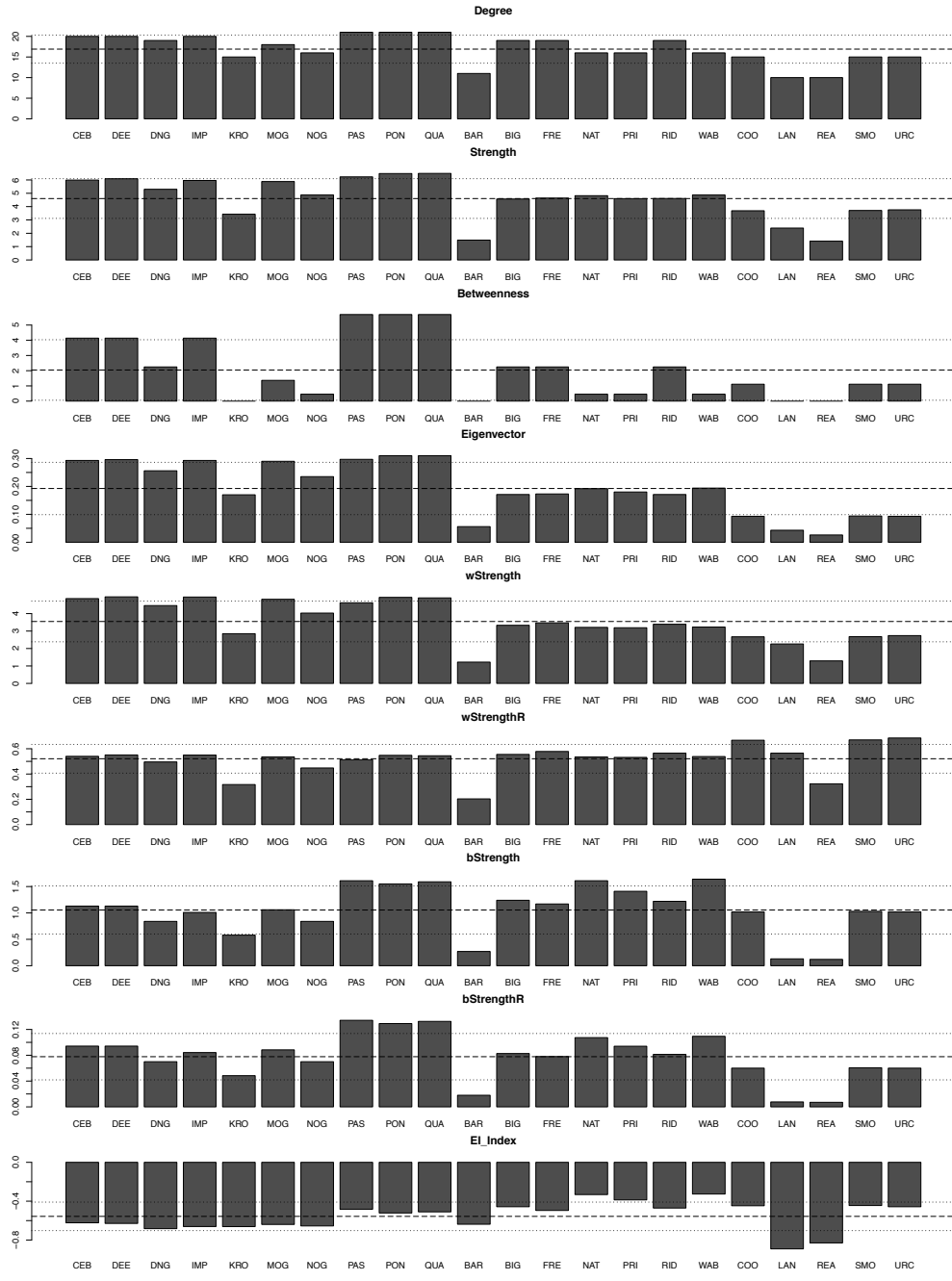


Figure 2.5: Barplots of centrality measures (2009-14). Lines represent mean (long dash) and mean +/- 1SD (dotted). Very few values are 2 or more SD from the mean.

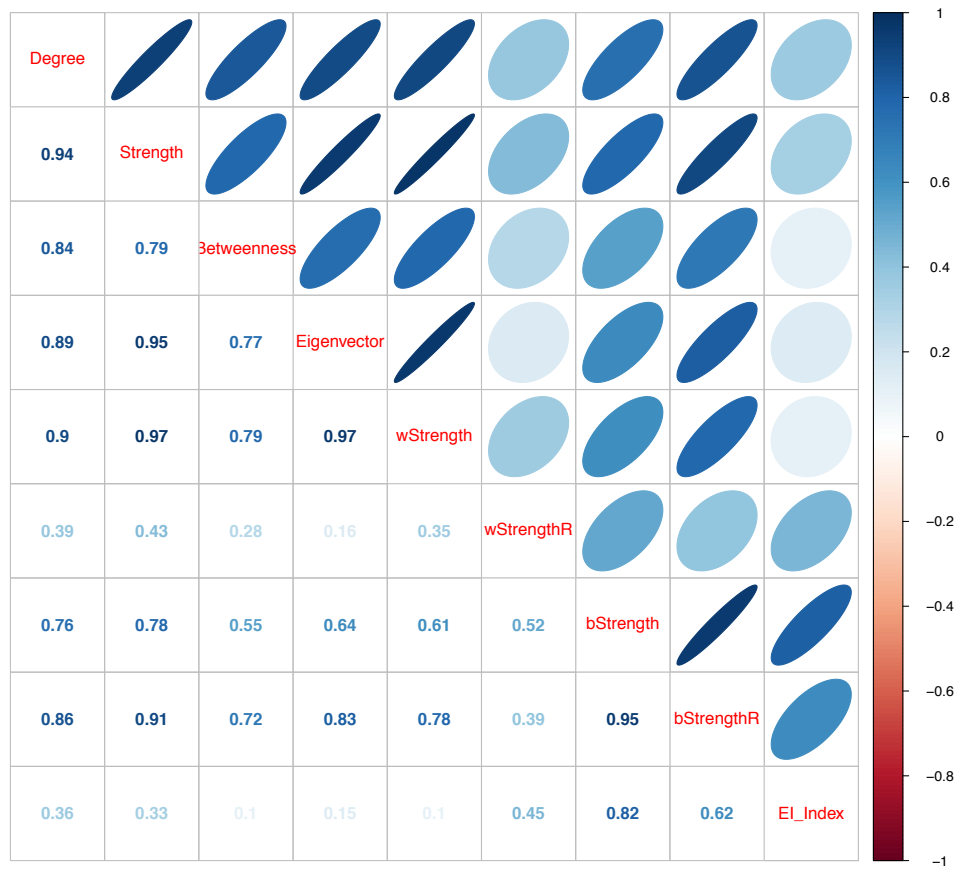


Figure 2.6: Correlation plot of centrality measures (2009-14)

Table 2.2: Centrality measures for the 09-14 network

	Alliance	Degree	Strength	Betweenness	Eigenvector	wStrength	wStrengthR	bStrength	bStrengthR	ELIndex
CEB	KS	20	5.99	4.14	0.29	4.86	0.54	1.13	0.09	-0.62
DEE	KS	20	6.09	4.14	0.30	4.96	0.55	1.13	0.09	-0.63
DNG	KS	19	5.30	2.25	0.26	4.46	0.50	0.84	0.07	-0.68
IMP	KS	20	5.96	4.14	0.29	4.95	0.55	1.01	0.08	-0.66
KRO	KS	15	3.43	0.00	0.17	2.85	0.32	0.58	0.05	-0.66
MOG	KS	18	5.88	1.36	0.29	4.82	0.54	1.06	0.09	-0.64
NOG	KS	16	4.87	0.46	0.23	4.03	0.45	0.84	0.07	-0.66
PAS	KS	21	6.23	5.69	0.30	4.62	0.51	1.61	0.13	-0.48
PON	KS	21	6.48	5.69	0.31	4.93	0.55	1.55	0.13	-0.52
QUA	KS	21	6.49	5.69	0.31	4.90	0.54	1.59	0.13	-0.51
BAR	PD	11	1.49	0.00	0.06	1.22	0.20	0.27	0.02	-0.64
BIG	PD	19	4.57	2.25	0.17	3.33	0.56	1.24	0.08	-0.46
FRE	PD	19	4.64	2.25	0.17	3.47	0.58	1.17	0.08	-0.50
NAT	PD	16	4.82	0.46	0.19	3.21	0.54	1.61	0.11	-0.33
PRI	PD	16	4.60	0.46	0.18	3.19	0.53	1.41	0.09	-0.39
RID	PD	19	4.61	2.25	0.17	3.39	0.56	1.22	0.08	-0.47
WAB	PD	16	4.87	0.46	0.19	3.23	0.54	1.64	0.11	-0.33
COO	RR	15	3.69	1.11	0.09	2.67	0.67	1.02	0.06	-0.45
LAN	RR	10	2.39	0.00	0.04	2.26	0.56	0.13	0.01	-0.89
REA	RR	10	1.41	0.00	0.03	1.29	0.32	0.12	0.01	-0.83
SMO	RR	15	3.71	1.11	0.09	2.68	0.67	1.03	0.06	-0.44
URC	RR	15	3.76	1.11	0.09	2.74	0.69	1.02	0.06	-0.46

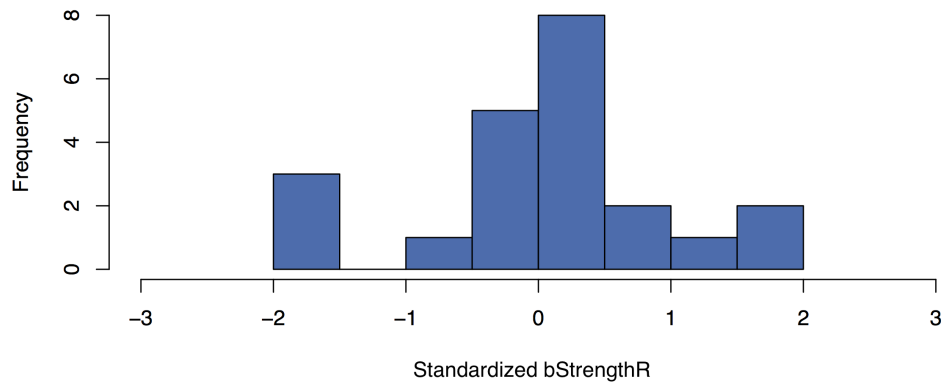
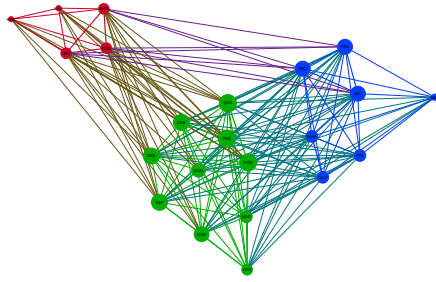
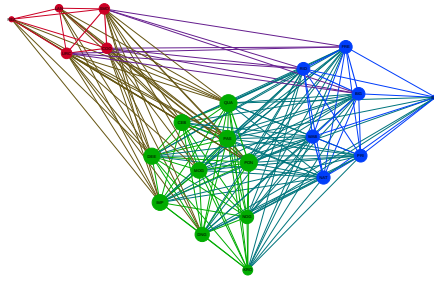
**Figure 2.7:** Standardized distribution of bStrengthR 2009-14

Table 2.3: Betweenness comparison with and without BAR

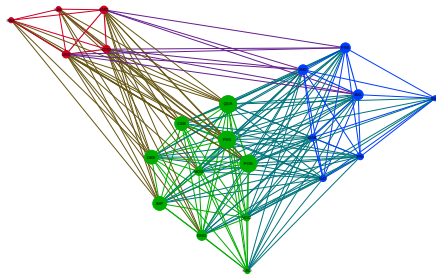
ID	Betweenness-wBAR	Betweenness-woBAR
PAS	5.691	4.141
PON	5.691	4.141
QUA	5.691	4.141
CEB	4.141	4.141
DEE	4.141	4.141
IMP	4.141	4.141
BIG	2.247	1.364
DNG	2.247	1.364
FRE	2.247	1.364
RID	2.247	1.364
MOG	1.364	1.364
COO	1.111	1.111
SMO	1.111	1.111
URC	1.111	1.111
NAT	0.455	0
NOG	0.455	0
PRI	0.455	0
WAB	0.455	0
BAR	0	NA
KRO	0	0
LAN	0	0
REA	0	0



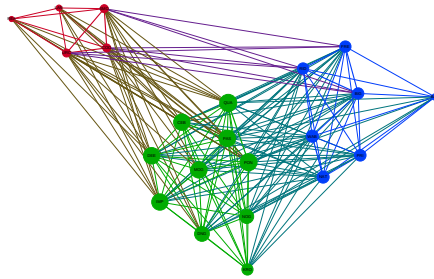
(a) Degree



(b) Strength



(c) Betweenness



(c) Eigenvector

Figure 2.8: Centrality measures, 2009-14. Nodes sized based on the value of each measure

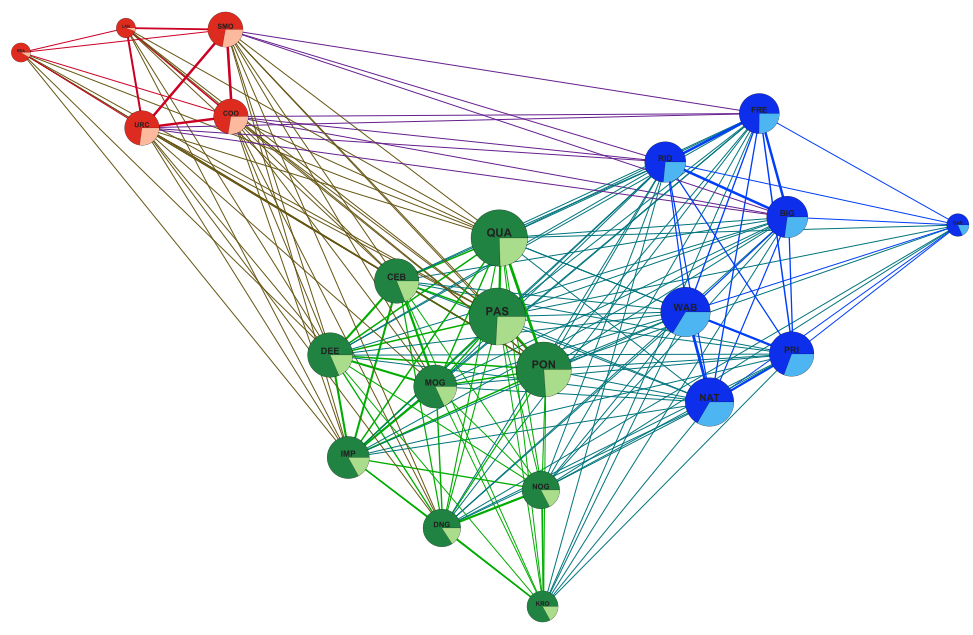
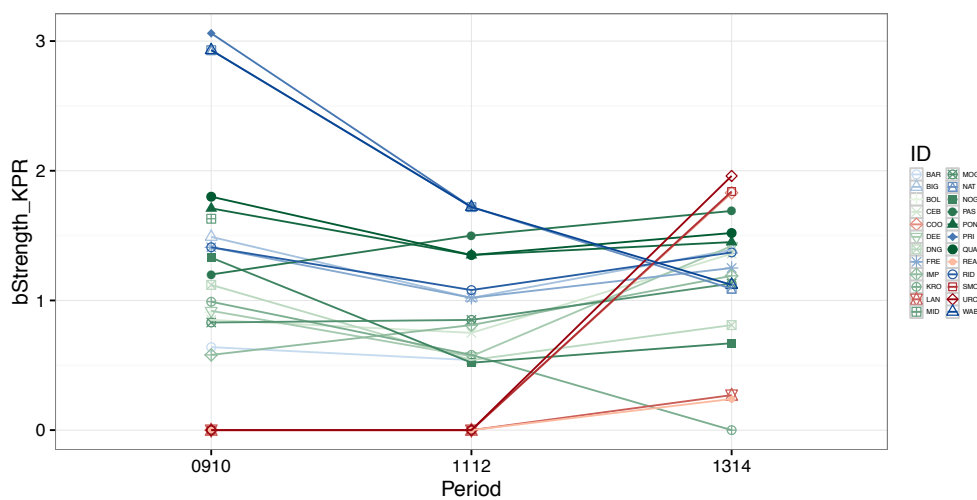


Figure 2.9: Inter/Intra- group strength. 2009-2014. Nodes are sized based on each individuals bStrengthR value. Pie charts depict the ratio between absolute wStrength (dark color) and bStrength (light color). Each alliance has one trio with higher overall and relative bStrengthR values.

Table 2.4: bStrength and wStrength, 2y intervals

ID	Alliance	bStrength			wStrength		
		0910	1112	1314	0910	1112	1314
BOL	KS	0.91	-	-	5.3	-	-
CEB	KS	0.85	0.75	1.36	5.28	5.88	4.6
DEE	KS	0.92	0.57	1.42	5.17	5.7	4.81
DNG	KS	1.12	0.54	0.81	4.35	5.97	3.57
IMP	KS	0.58	0.81	1.19	4.74	5.9	4.6
KRO	KS	0.99	0.58	0	4.12	5.28	0.25
MID	KS	1.63	-	-	4.82	-	-
MOG	KS	0.83	0.85	1.13	4.75	6	4.42
NOG	KS	1.33	0.52	0.67	4.14	5.62	2.72
PAS	KS	1.2	1.5	1.69	5.08	4.87	4.59
PON	KS	1.71	1.35	1.45	5.6	5.38	4.84
QUA	KS	1.8	1.35	1.52	5.55	5.38	4.8
BAR	PD	0.64	0.54	-	2.22	1.28	-
BIG	PD	1.49	1.02	1.39	3.86	4.48	1.79
FRE	PD	1.41	1.02	1.25	3.84	4.48	1.82
NAT	PD	2.93	1.72	1.09	3.89	4.24	1.29
PRI	PD	3.06	1.72	-	3.79	4.24	-
RID	PD	1.41	1.08	1.37	3.81	4.34	1.98
WAB	PD	2.93	1.72	1.12	3.89	4.24	1.3
COO	RR	0	0	1.83	2.15	3.05	2.47
LAN	RR	0	0	0.27	2.66	2.58	1.93
REA	RR	0	0	0.24	0.15	2.03	0.96
SMO	RR	0	0	1.84	2.6	2.95	2.49
URC	RR	0	0	1.96	2.6	2.99	2.55

**Figure 2.10:** Change in bStrength over 3 time periods

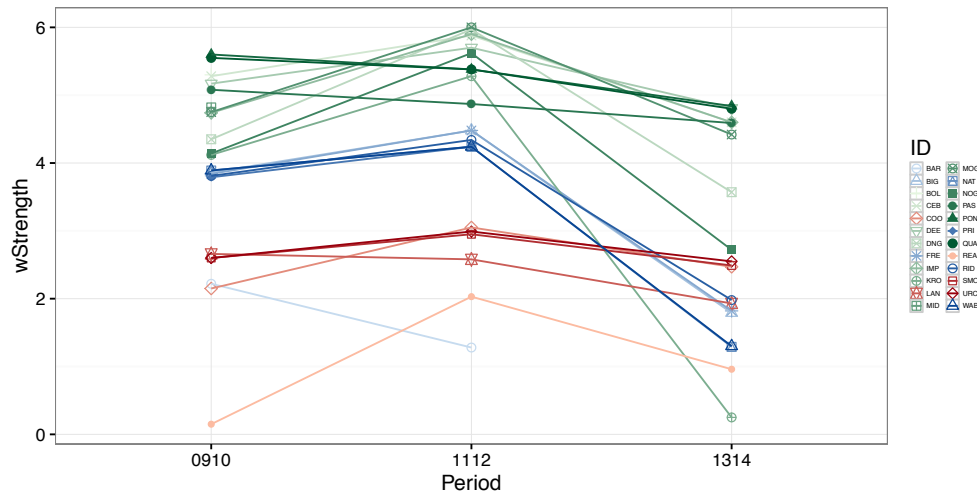


Figure 2.11: Change in wStrength over 3 time periods

Table 2.5: bStrengthR and wStrengthR, 2y intervals

ID	Alliance	bStrengthR			wStrengthR		
		0910	1112	1314	0910	1112	1314
BOL	KS	0.08	-	-	0.48	-	-
CEB	KS	0.07	0.06	0.14	0.48	0.65	0.51
DEE	KS	0.08	0.05	0.14	0.47	0.63	0.53
DNG	KS	0.09	0.04	0.08	0.40	0.66	0.40
IMP	KS	0.05	0.07	0.12	0.43	0.66	0.51
KRO	KS	0.08	0.05	0.00	0.37	0.59	0.03
MID	KS	0.14	-	-	0.44	-	-
MOG	KS	0.07	0.07	0.11	0.43	0.67	0.49
NOG	KS	0.11	0.04	0.07	0.38	0.62	0.30
PAS	KS	0.10	0.12	0.17	0.46	0.54	0.51
PON	KS	0.14	0.11	0.14	0.51	0.60	0.54
QUA	KS	0.15	0.11	0.15	0.50	0.60	0.53
BAR	PD	0.04	0.04	-	0.37	0.21	-
BIG	PD	0.09	0.07	0.09	0.64	0.75	0.45
FRE	PD	0.08	0.07	0.08	0.64	0.75	0.46
NAT	PD	0.17	0.11	0.07	0.65	0.71	0.32
PRI	PD	0.18	0.11	-	0.63	0.71	-
RID	PD	0.08	0.07	0.09	0.64	0.72	0.49
WAB	PD	0.17	0.11	0.07	0.65	0.71	0.33
COO	RR	0.00	0.00	0.12	0.54	0.76	0.62
LAN	RR	0.00	0.00	0.02	0.67	0.65	0.48
REA	RR	0.00	0.00	0.02	0.04	0.51	0.24
SMO	RR	0.00	0.00	0.12	0.65	0.74	0.62
URC	RR	0.00	0.00	0.13	0.65	0.75	0.64

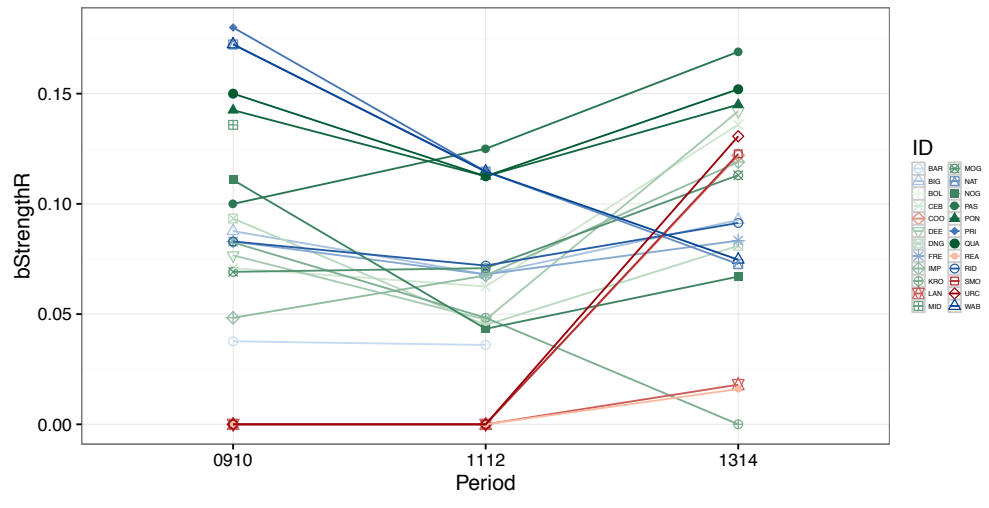


Figure 2.12: Change in bStrengthR over 3 time periods

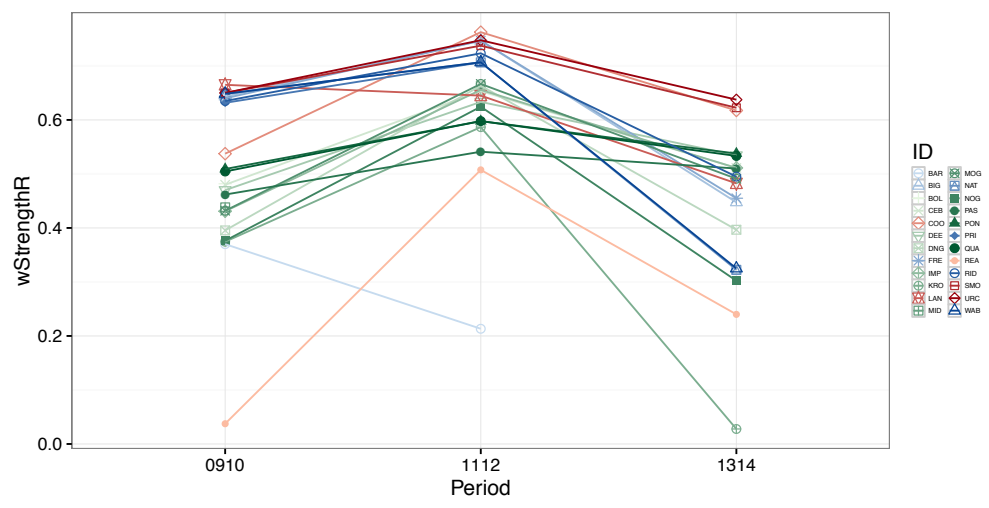


Figure 2.13: Change in wStrengthR over 3 time periods

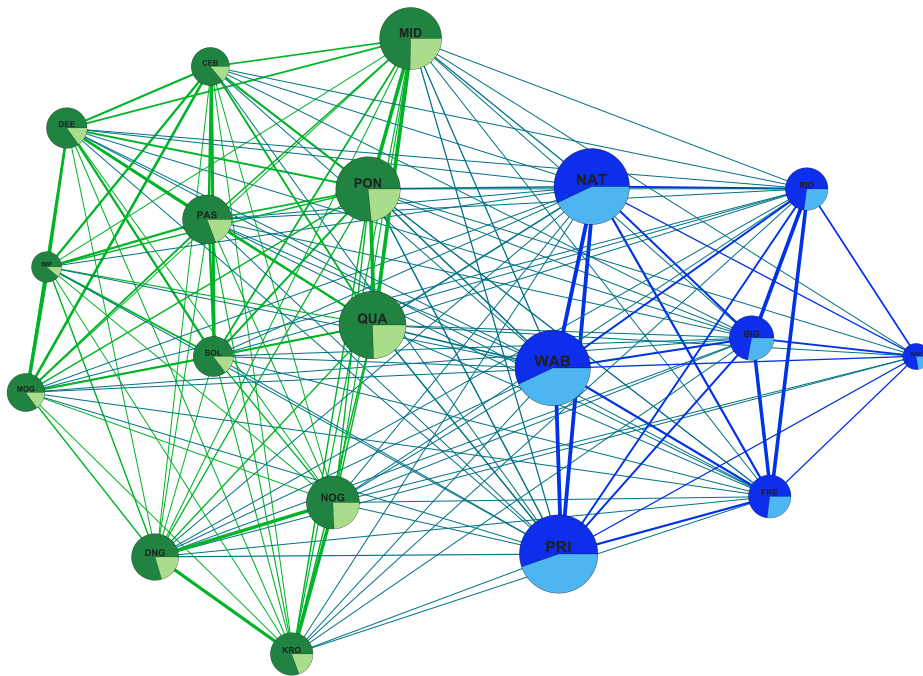


Figure 2.14: Inter/Intra- group strength. 2009-2010. Node size based on bStrengthR

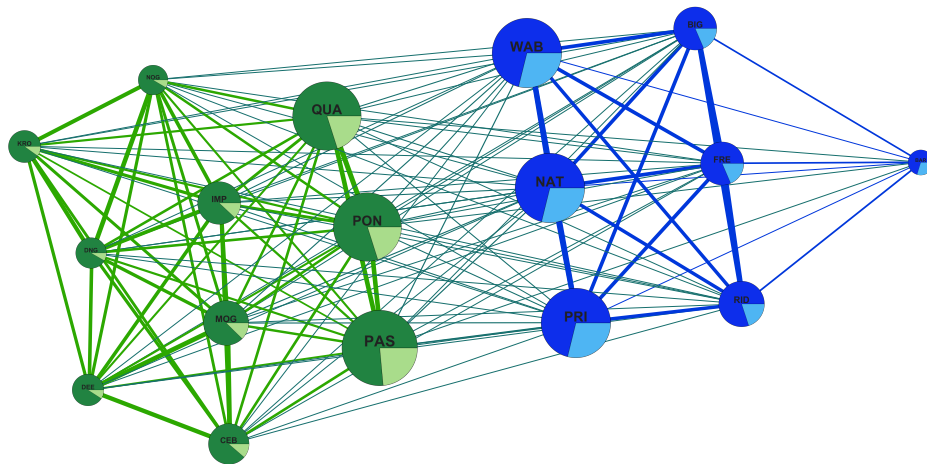


Figure 2.15: Inter/Intra- group strength. 2011-2012. Node size based on bStrengthR

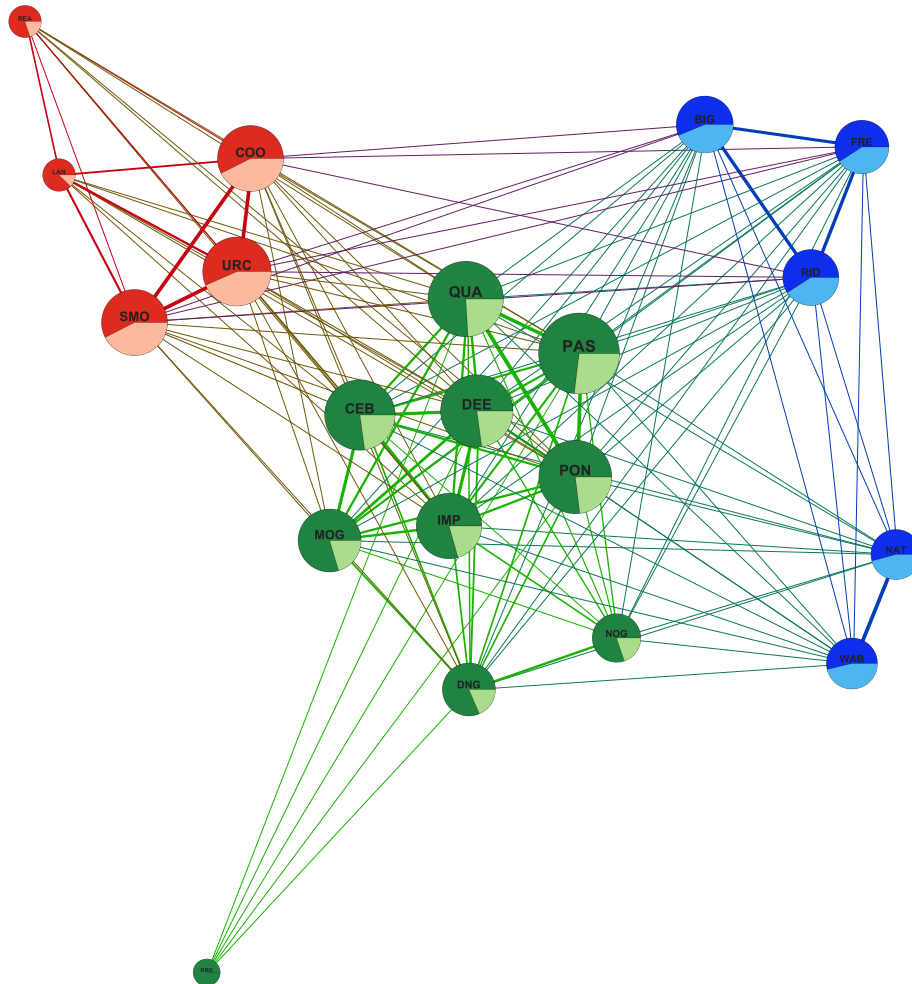


Figure 2.16: Inter/Intra- group strength. 2013-2014. Node size based on bStrengthR

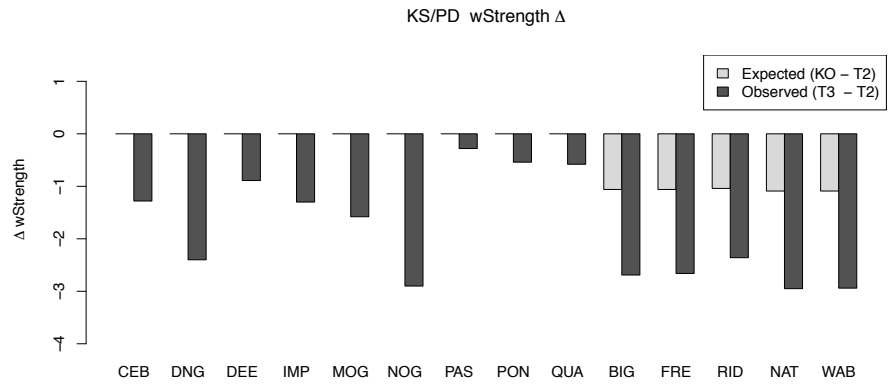


Figure 2.17: Expected vs. observed change in wStrength corresponding to the loss of two PD males between T2 and T3.

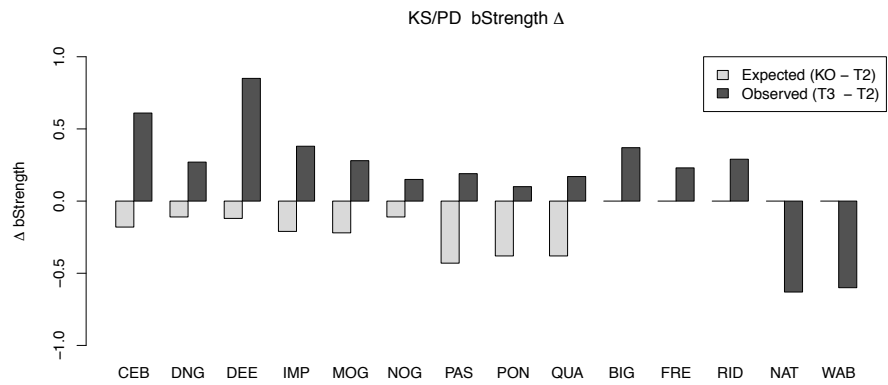


Figure 2.18: Expected vs. observed change in bStrength corresponding to the loss of two PD males between T2 and T3.

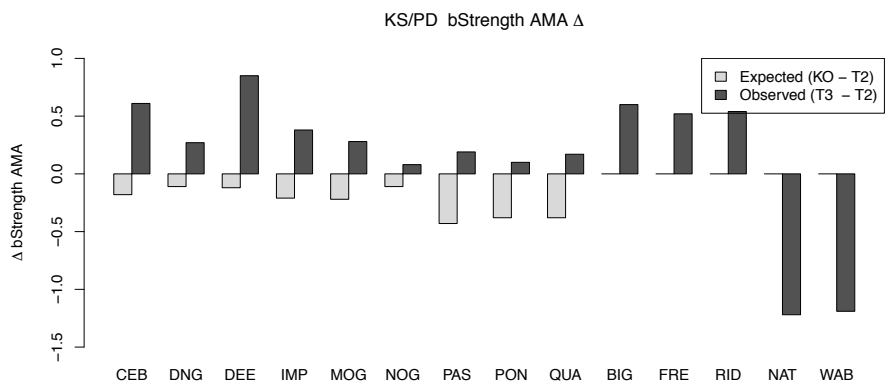


Figure 2.19: Expected vs. observed change in bStrength for the larger all male allies network corresponding to the loss of two PD males between T2 and T3.

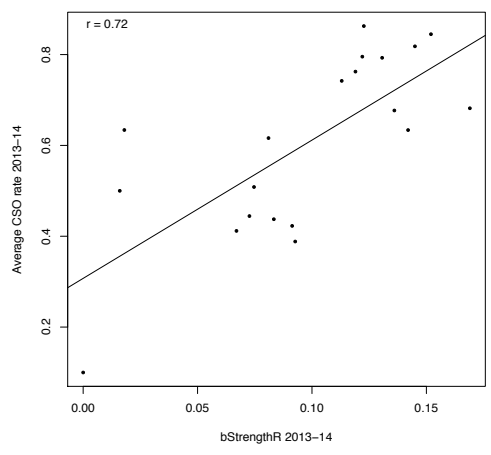


Figure 2.20: Correlation between bStrengthR and individual consortship rate for 2013-2014

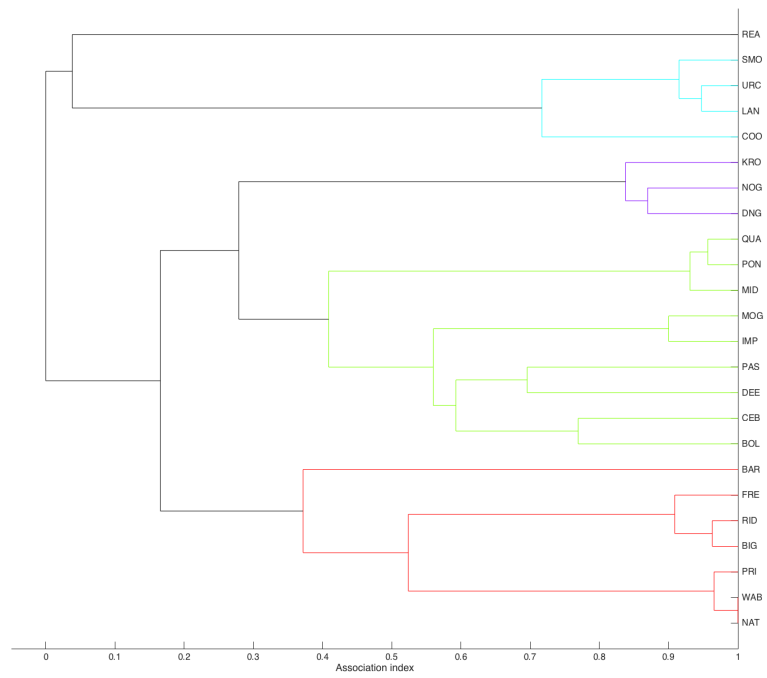


Figure 2.21: Dendrogram for T1

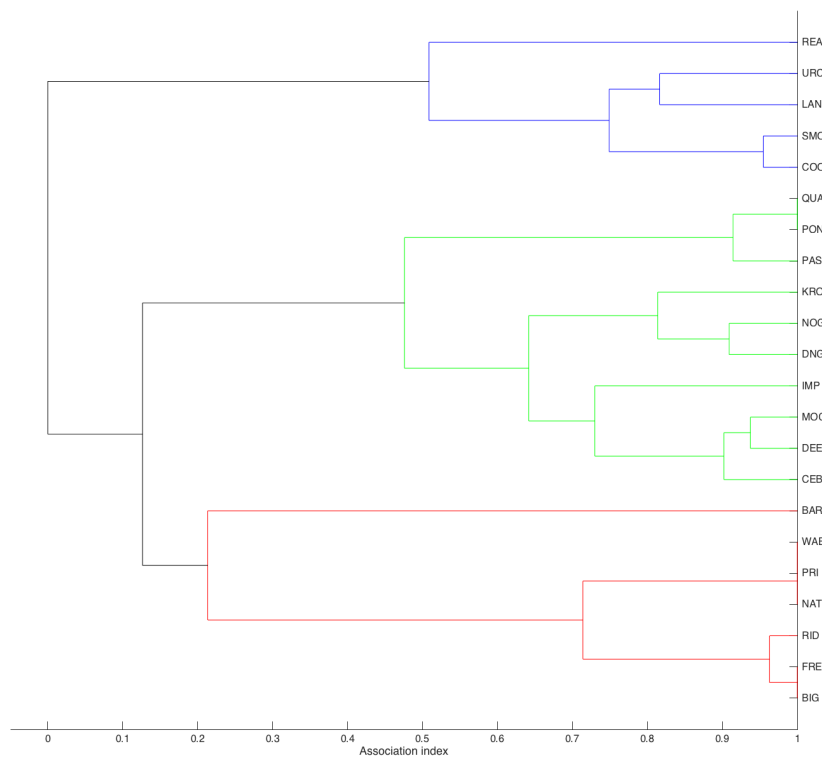


Figure 2.22: Dendrogram for T2

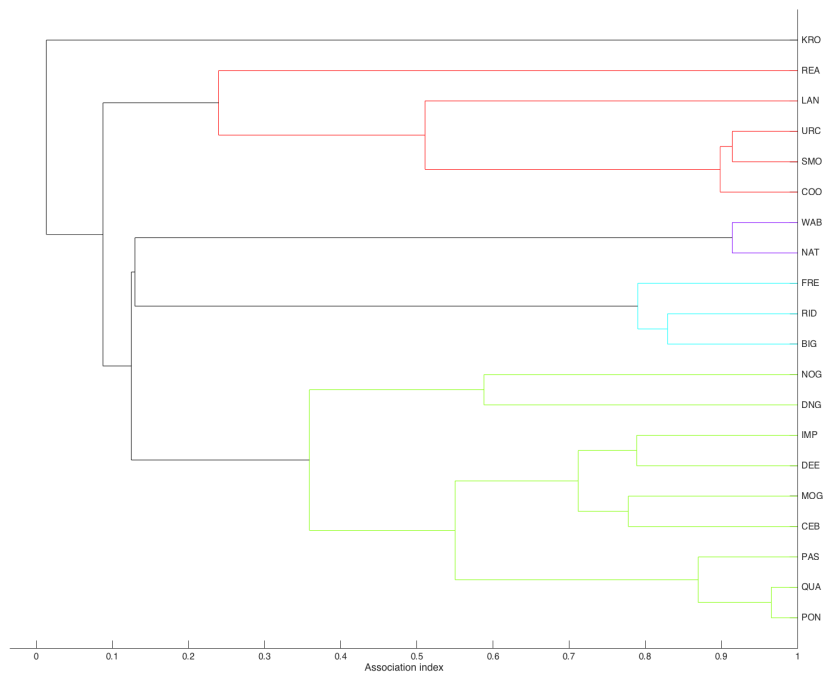


Figure 2.23: Dendrogram for T3

Table 2.6: 2009-2010 Association Matrix

	BAR	BIG	BOL	CEB	COO	DEE	DNG	FRE	IMP	KRO	LAN	MID	MOG	NAT	NOG	PAS	PON	PRI	QUA	REA	RID	SMO	URC	WAB
BAR	0.00	0.47	0.00	0.00	0.00	0.00	0.12	0.33	0.00	0.00	0.00	0.14	0.00	0.33	0.13	0.00	0.12	0.32	0.13	0.00	0.44	0.00	0.00	0.33
BIG	0.47	0.00	0.16	0.15	0.00	0.08	0.08	0.89	0.00	0.09	0.00	0.17	0.09	0.52	0.17	0.17	0.16	0.50	0.17	0.00	0.96	0.00	0.00	0.52
BOL	0.00	0.16	0.00	0.77	0.00	0.58	0.25	0.15	0.45	0.27	0.00	0.45	0.55	0.15	0.35	0.61	0.50	0.15	0.52	0.00	0.15	0.00	0.00	0.15
CEB	0.00	0.00	0.77	0.00	0.00	0.54	0.23	0.14	0.58	0.17	0.00	0.42	0.67	0.14	0.24	0.64	0.54	0.14	0.48	0.00	0.14	0.00	0.00	0.14
COO	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.77	0.00	0.00
DEE	0.00	0.08	0.58	0.54	0.00	0.00	0.25	0.08	0.64	0.27	0.00	0.45	0.55	0.23	0.17	0.70	0.50	0.22	0.52	0.00	0.08	0.00	0.00	0.23
DNG	0.12	0.08	0.25	0.23	0.00	0.00	0.08	0.36	0.82	0.00	0.00	0.17	0.36	0.23	0.08	0.87	0.16	0.30	0.35	0.00	0.08	0.00	0.00	0.23
FRE	0.33	0.89	0.15	0.14	0.00	0.08	0.08	0.00	0.00	0.08	0.00	0.17	0.36	0.23	0.08	0.57	0.16	0.55	0.16	0.00	0.93	0.00	0.00	0.57
IMP	0.00	0.00	0.45	0.58	0.00	0.64	0.36	0.00	0.00	0.20	0.00	0.30	0.20	0.25	0.19	0.57	0.36	0.24	0.29	0.00	0.00	0.00	0.00	0.17
KRO	0.00	0.09	0.27	0.17	0.00	0.27	0.82	0.08	0.20	0.00	0.00	0.30	0.20	0.25	0.86	0.29	0.36	0.24	0.38	0.00	0.08	0.00	0.00	0.25
LAN	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.89	0.00	0.00
MID	0.14	0.17	0.45	0.42	0.00	0.45	0.27	0.17	0.20	0.30	0.00	0.00	0.20	0.33	0.29	0.38	0.91	0.32	0.95	0.00	0.17	0.00	0.00	0.33
MOG	0.00	0.09	0.55	0.67	0.00	0.55	0.36	0.08	0.90	0.20	0.00	0.20	0.00	0.17	0.19	0.44	0.36	0.24	0.29	0.00	0.08	0.00	0.00	0.17
NAT	0.33	0.52	0.15	0.14	0.00	0.23	0.23	0.57	0.17	0.25	0.00	0.33	0.17	0.00	0.24	0.48	0.38	0.97	0.40	0.00	0.50	0.00	0.00	1.00
NOG	0.13	0.17	0.35	0.24	0.00	0.17	0.87	0.16	0.19	0.86	0.00	0.29	0.19	0.24	0.00	0.27	0.35	0.23	0.36	0.00	0.16	0.00	0.00	0.24
PAS	0.00	0.17	0.61	0.64	0.00	0.70	0.26	0.16	0.57	0.29	0.00	0.38	0.48	0.24	0.27	0.00	0.43	0.23	0.45	0.00	0.16	0.00	0.00	0.24
PON	0.12	0.16	0.50	0.54	0.00	0.50	0.33	0.15	0.36	0.36	0.00	0.91	0.36	0.38	0.35	0.43	0.00	0.37	0.96	0.00	0.15	0.00	0.00	0.38
PRI	0.32	0.50	0.15	0.14	0.00	0.22	0.30	0.55	0.24	0.24	0.00	0.32	0.24	0.97	0.23	0.23	0.37	0.00	0.38	0.00	0.48	0.00	0.00	0.97
QUA	0.13	0.17	0.52	0.48	0.00	0.52	0.35	0.16	0.29	0.38	0.00	0.95	0.29	0.40	0.36	0.45	0.96	0.38	0.00	0.00	0.16	0.00	0.00	0.40
REA	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
RID	0.44	0.96	0.15	0.14	0.00	0.08	0.08	0.93	0.00	0.08	0.00	0.17	0.08	0.50	0.16	0.16	0.15	0.48	0.16	0.00	0.00	0.00	0.00	0.50
SMO	0.00	0.00	0.00	0.00	0.71	0.00	0.00	0.00	0.00	0.00	0.89	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.94
URC	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
WAB	0.33	0.52	0.15	0.14	0.00	0.23	0.23	0.57	0.17	0.25	0.00	0.33	0.17	1.00	0.24	0.24	0.38	0.97	0.40	0.00	0.50	0.00	0.00	0.00

Table 2.7: 2011-2012 Association Matrix

	BAR	BIG	CEB	COO	DEE	DNG	FRE	IMP	KRO	LAN	MOG	NAT	NOG	PAS	PON	PRI	QUA	REA	RID	SMO	URC	WAB	
BAR	0.00	0.33	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.09	0.00	0.20	0.17	0.09	0.17	0.00	0.35	0.00	0.00	0.00	0.09
BIG	0.33	0.00	0.07	0.00	0.07	0.07	1.00	0.06	0.07	0.00	0.06	0.73	0.06	0.20	0.18	0.73	0.18	0.00	0.96	0.00	0.00	0.00	0.73
CEB	0.00	0.07	0.00	0.00	0.87	0.65	0.07	0.71	0.57	0.00	0.94	0.18	0.56	0.52	0.53	0.18	0.53	0.00	0.07	0.00	0.00	0.00	0.18
COO	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.59	0.00	0.95	0.84	0.00	0.00
DEE	0.00	0.07	0.87	0.00	0.00	0.71	0.07	0.71	0.64	0.00	0.94	0.12	0.62	0.39	0.41	0.12	0.41	0.00	0.07	0.00	0.00	0.00	0.12
DNG	0.00	0.07	0.65	0.00	0.71	0.00	0.07	0.74	0.83	0.00	0.67	0.11	0.91	0.44	0.51	0.11	0.51	0.00	0.07	0.00	0.00	0.00	0.11
FRE	0.33	1.00	0.07	0.00	0.07	0.00	0.06	0.07	0.00	0.06	0.73	0.06	0.73	0.06	0.20	0.18	0.73	0.00	0.96	0.00	0.00	0.00	0.73
IMP	0.00	0.06	0.71	0.00	0.71	0.74	0.06	0.00	0.62	0.00	0.78	0.21	0.72	0.46	0.38	0.21	0.58	0.00	0.06	0.00	0.00	0.00	0.21
KRO	0.00	0.07	0.57	0.00	0.64	0.83	0.07	0.62	0.00	0.00	0.60	0.12	0.80	0.34	0.44	0.12	0.44	0.00	0.08	0.00	0.00	0.00	0.12
LAN	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.39	0.00	0.70	0.82	0.00	0.00
MOG	0.00	0.06	0.94	0.00	0.94	0.67	0.06	0.78	0.60	0.00	0.00	0.22	0.59	0.48	0.50	0.22	0.50	0.00	0.07	0.00	0.00	0.00	0.22
NAT	0.09	0.73	0.18	0.00	0.12	0.11	0.73	0.21	0.12	0.00	0.22	0.00	0.11	0.00	0.23	1.00	0.21	0.00	0.69	0.00	0.00	0.00	0.11
NOG	0.00	0.06	0.56	0.00	0.62	0.91	0.06	0.72	0.80	0.00	0.59	0.11	0.00	0.42	0.50	0.11	0.50	0.00	0.07	0.00	0.00	0.00	0.23
PAS	0.20	0.20	0.52	0.00	0.39	0.44	0.20	0.46	0.34	0.00	0.48	0.23	0.42	0.00	0.91	0.21	0.91	0.00	0.21	0.00	0.00	0.00	0.23
PON	0.17	0.18	0.53	0.00	0.41	0.51	0.18	0.58	0.44	0.00	0.50	0.21	0.50	0.91	0.00	0.21	1.00	0.00	0.19	0.00	0.00	0.00	0.21
PRI	0.09	0.73	0.18	0.00	0.12	0.11	0.73	0.21	0.12	0.00	0.22	1.00	0.11	0.23	0.21	0.00	0.21	0.00	0.69	0.00	0.00	0.00	1.00
QUA	0.17	0.18	0.53	0.00	0.41	0.51	0.18	0.58	0.44	0.00	0.50	0.21	0.50	0.91	0.00	0.21	1.00	0.00	0.19	0.00	0.00	0.00	0.21
REA	0.00	0.00	0.00	0.59	0.00	0.00	0.00	0.00	0.00	0.39	0.00	0.00	0.00	0.00	1.00	0.21	0.00	0.00	0.69	0.00	0.00	0.00	1.00
RID	0.35	0.96	0.07	0.00	0.07	0.07	0.96	0.06	0.08	0.00	0.07	0.69	0.07	0.21	0.19	0.69	0.19	0.00	0.00	0.51	0.00	0.00	0.69
SMO	0.00	0.00	0.00	0.95	0.00	0.00	0.00	0.00	0.00	0.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
URC	0.00	0.00	0.00	0.84	0.00	0.00	0.00	0.00	0.00	0.82	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.54	0.00	0.79	0.00	0.00	0.00
WAB	0.09	0.73	0.18	0.00	0.12	0.11	0.73	0.21	0.12	0.00	0.22	1.00	0.11	0.23	0.21	0.00	0.21	0.00	0.69	0.00	0.00	0.00	0.00

Table 2.8: 2013–2014 Association Matrix

	BIG	CEB	COO	DEE	DNG	FRE	IMP	KRO	LAN	MOG	NAT	NOG	PAS	PON	QUA	REA	RID	SMO	URC	WAB
BIG	0.00	0.14	0.07	0.14	0.09	0.76	0.11	0.00	0.00	0.14	0.10	0.12	0.17	0.12	0.15	0.00	0.83	0.07	0.07	0.10
CEB	0.14	0.00	0.25	0.78	0.41	0.12	0.76	0.00	0.06	0.78	0.04	0.24	0.51	0.55	0.57	0.04	0.11	0.27	0.29	0.04
COO	0.07	0.25	0.00	0.23	0.07	0.04	0.18	0.00	0.45	0.20	0.00	0.00	0.25	0.23	0.23	0.22	0.08	0.90	0.90	0.00
DEE	0.14	0.78	0.23	0.00	0.44	0.12	0.79	0.05	0.06	0.69	0.11	0.33	0.54	0.60	0.59	0.04	0.11	0.24	0.26	0.11
DNG	0.09	0.41	0.07	0.44	0.00	0.11	0.43	0.07	0.00	0.46	0.15	0.39	0.41	0.40	0.36	0.00	0.10	0.07	0.07	0.15
FRE	0.76	0.12	0.04	0.12	0.11	0.00	0.12	0.00	0.00	0.12	0.12	0.15	0.15	0.10	0.14	0.00	0.82	0.04	0.04	0.12
IMP	0.11	0.76	0.18	0.79	0.43	0.12	0.00	0.00	0.06	0.61	0.08	0.39	0.51	0.35	0.56	0.04	0.11	0.20	0.21	0.08
KRO	0.00	0.00	0.00	0.05	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.04	0.04	0.00	0.00	0.00	0.00	0.00
LAN	0.00	0.06	0.45	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.03	0.03	0.40	0.00	0.52	0.56	0.00
MOG	0.14	0.78	0.20	0.69	0.46	0.12	0.61	0.00	0.00	0.00	0.08	0.26	0.50	0.56	0.56	0.00	0.11	0.19	0.21	0.08
NAT	0.10	0.04	0.00	0.11	0.15	0.12	0.08	0.00	0.00	0.08	0.13	0.13	0.18	0.16	0.16	0.00	0.16	0.00	0.00	0.91
NOG	0.12	0.24	0.00	0.33	0.59	0.15	0.39	0.00	0.00	0.26	0.13	0.33	0.33	0.29	0.29	0.00	0.13	0.00	0.00	0.14
PAS	0.17	0.51	0.25	0.54	0.41	0.15	0.51	0.05	0.03	0.50	0.18	0.33	0.33	0.88	0.86	0.04	0.18	0.24	0.26	0.19
PON	0.12	0.55	0.23	0.60	0.40	0.10	0.55	0.04	0.03	0.56	0.16	0.29	0.88	0.88	0.86	0.04	0.13	0.23	0.24	0.17
QUA	0.15	0.57	0.23	0.59	0.36	0.14	0.56	0.04	0.03	0.56	0.16	0.29	0.86	0.97	0.97	0.04	0.16	0.22	0.23	0.16
REA	0.00	0.04	0.22	0.04	0.00	0.00	0.04	0.00	0.40	0.00	0.00	0.00	0.04	0.04	0.04	0.04	0.00	0.16	0.18	0.00
RID	0.83	0.11	0.08	0.11	0.10	0.82	0.11	0.00	0.00	0.11	0.16	0.13	0.18	0.13	0.16	0.00	0.00	0.07	0.08	0.17
SMO	0.07	0.27	0.90	0.24	0.07	0.04	0.20	0.00	0.52	0.19	0.00	0.00	0.24	0.23	0.22	0.16	0.07	0.00	0.91	0.00
URC	0.07	0.29	0.90	0.26	0.07	0.04	0.21	0.00	0.56	0.21	0.00	0.00	0.26	0.24	0.23	0.18	0.08	0.91	0.00	0.00
WAB	0.10	0.04	0.00	0.11	0.15	0.12	0.08	0.00	0.00	0.08	0.91	0.14	0.19	0.17	0.16	0.00	0.17	0.00	0.00	0.00

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CHAPTER 3

BEHAVIORAL INTERACTIONS AMONG FIRST-ORDER MALE ALLIES

3.1 INTRODUCTION

Among primates, extensive research has revealed the importance of social interactions for understanding the dynamics of animal societies. Interactions can have immediate consequences, as in unrelated female vervet monkeys for whom grooming prior to a call for help increased affiliates response duration (Seyfarth and Cheney, 1984), or among male chimpanzees who directed grooming towards potential allies in moments of intense social conflict (Nishida, 1983), but see (de Waal, 1984). In other contexts, interactions may be used to test or strengthen bonds between individuals (Zahavi, 1977). For example, eye-poking between capuchins (Perry, 2011) or sexual greetings among adult male baboons (Smuts and Watanabe, 1990) may be a test of the strength of the relationship between individuals. In the latter study, the strongest male alliance was also the only dyad that showed complete symmetry in their exchange of sexual greetings (*ibid*). Finally, certain kinds of interactions among individuals have been shown to relate to the eventual reproductive success of the actors. For example, in adult female savannah baboons, increased time spent grooming and associating with other adult females is positively correlated with increased reproductive success (Silk et al., 2003). Studies relating interactions to social relationships are rare among cetaceans, but the observed similarities in social complexity suggest that dolphins may use similar mechanisms as primates to mediate their relationships.

In this chapter I examine the degree to which adult male bottlenose dolphins in Shark Bay (SB), WA, use social coordination and contact behavior (SCC) to mediate their alliance relationships, and whether such behaviors relate to their reproductive success. I use

a common context (first-order male allies with a female consort) to capture variability in the production of SCC among allies, and relate this to the rate at which each dyad associates and consorts together.

Behavioral observation of alliances *in situ* suggests that coordinated social behavior is a common behavior found during mate competition and consortship; activities principal to the SB alliances. During intense contests between second-order alliances, males can be observed coordinating in both space and time as they engage in behaviors such as charging to attack a group or chase a single individual. During consortships, allies can be observed coordinating in space and time as they maintain a side-by-side abreast “formation” behind a female dolphin, produce intricate sequences of mirrored synchronous displays, or surface and dive in synchrony. Parsimony suggests that males should enact (communicate) their relationships via the same mechanisms critical to their success as allies. That is, even outside the context of mate-competitions, males are likely to be enacting their relationships via similar kinds of coordinated social behavior that they use during high-stakes but less frequent contests. Additionally, male allies have been observed engaging in affiliative contact behavior such as petting using their pectoral fins, and rubbing bodies alongside one-another. These behaviors are likely to have a similar function as grooming among primates, and may similarly relate to increased association frequency and possibly increased reproductive success. Of these behaviors, only synchrony, which has a reliable surface component, has been quantified for the SB alliances due to the inherent challenge of reliably quantifying the many other kinds of behavior that often occur underwater and out of the sight of boat-based observers. We surmounted this challenge by using aerial videography paired with boat-based data collection to collect detailed records of sub-surface behaviors (Nowacek et al., 2001; Hodgson, 2007; Friedman et al., 2014).

Connor et al. (2006) described the distribution of synchronous surfacing by pairs and trios of male dolphins in Shark Bay, finding that males were most likely to be synchronous with the same individuals with whom they spent the most time (e.g. their first order alliance affiliates), and that alliances varied significantly in the proportions of “triple synchs”, or

synchronous surfacing between three individuals. The authors suggest this variation might represent differences in alliance unity and/or age, as mature males demonstrated the highest percentage of triple synchs. Furthermore, the authors indicate a relationship between the stability of an alliance and synchrony, and suggest that variation across trios in rates of triple synchs suggests that synchrony may be a more sensitive measure of alliance dynamics than is captured by the association coefficient.

A three-year study of the fourteen member second-order alliance WC found that individuals who showed higher alliance stability also engaged in higher consortship rates (Connor et al., 2001). Given that association predicts both synchronous interactions and consortship rate, Connor et al. (2006) predicted that variation in synchrony may also predict a variation in reproductive success, perhaps at a finer level of discrimination than association coefficient.

Adult males in SB participate in an extraordinary range of coordinated, often synchronous displays, many of which have never been seen twice (Connor et al., 2000). Displays occur frequently in the context of mating consortships, often with the males performing coordinated behaviors around an individual female. For example, in a 'butterfly display', two males begin by tightly paralleling the female on either side, then move out in front of her before splitting in opposing directions and meeting again behind the female moving back toward her on either side (Connor et al., 2006). In 1992, Connor et al. described a display that has not been seen since in which two males synchronously leapt towards each other in "reverse-parallel" formation on either side of a female, performing "belly-slaps" as they landed (Connor et al., 1992a, 2000). The frequency of displays among alliances has not been quantified, but such observations suggest that variation is likely.

If social coordination and affiliative contact (SCC) behaviors are used to mediate alliance relationships, we should expect to see differences in the rate that SCC behaviors are produced among allies of differing relationship strengths, as well as differences in the kinds of SCC produced, when SCC is produced, and how it is achieved among different kinds of allies. This chapter focuses on *with whom* and *what kinds* of SCC behaviors are

produced among second-order allies of differing relationship strengths, as measured by their overall social association rate and their rate of consortship association. Further, I examine the prediction that beyond the simple act of association, what individuals do when they're together (i.e. the *quality* of their associations), mediates their relationships. The analyses in this chapter are restricted to a common context, first-order allies with a female consort, in attempt to limit some of the variation inherent to natural observation. Four predictions are examined to evaluate the claim that dolphins use SCC to mediate alliance relationships:

- H1: There are differences in the production of coordinated behavior among male allies.
- H2: Males with higher dyadic *association* indices (those who associate together most frequently) engage in coordinated social behavior more frequently than males with lower dyadic association indices
- H3: Males with higher dyadic *consortship* indices (those who consort together most frequently) engage in coordinated social behavior more frequently than males with lower dyadic consortship indices
- H4: SCC is a stronger predictor of dyadic consortship index than non-consortship association rate alone.

3.2 METHODS

3.2.1 SITE

Data for this study were collected as part of a longitudinal study of bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia. Research at this site has been conducted since the early 1980's, and individuals are well-habituated to boat-based researchers. Data analyzed for this study were collected during the peak mating season in the the austral spring (September - December) in 2013 and 2014.

3.2.2 SUBJECTS

The subjects of this study were fifteen males found within two “second-order” alliances (10 KS and 5 PD). Both groups were highly accessible as they frequented the waters nearest the field station in Monkey Mia (Figure 3.2). They are among the most intensively observed alliances so there is an extensive database on past associations and the composition of 1st order-alliances within these groups. Males in all groups form trios to consort females, almost exclusively. However, due to the disappearance (probable death) of one PD male, included in study is the reduced pair from that first order alliance (NAT WAB).

3.2.3 FOCAL FOLLOWS

One-hour boat-based focal follows were conducted on each of the fifteen males in the KS and PD alliances. Focal males were selected using a daily randomized list of individuals from each alliance. Since we were at the mercy of encounter to find the individuals, when we did encounter a KS or PD subgroup, we followed the first individual from the list who was present, and who we had followed least frequently. In effort to reduce autocorrelation, in the case that we finished a focal follow with another KS or PD subgroup in sight, we switched to a new KS or PD subgroup, and selected the next focal in the same manner as described above. If no new subgroup was in sight, we waited twenty minutes before beginning the next focal follow on the next individual in the randomized list from within our group.

During each one-hour focal follow, behavioral and ecological data were recorded simultaneously using a range of sensors:

1. *Aerial video* was collected using a tethered helium aerostat. A 2.3m diameter Allsopp “Helikite” was tied to the boat, Tethered helium aerostats have been used to record foraging behavior of bottlenose dolphins *Tursiops truncatus* off the Florida coast (Nowacek, 2002), activity budgets of free-ranging dugongs *Dugong dugong* and their responses to anthropogenic noise (Hodgson, 2004), and leadership among bottlenose dolphins in the Lower Florida Keys (Lewis et al., 2011).

2. *Side-angle video* was collected using a hand-held Canon Vixia HF11 camcorder to capture the surface behavior of the dolphins (mostly synchronous surfacing and dives) as well as the dorsal fins, used to identify individuals.
3. *Acoustic recordings* were collected using a towed hydrophone fabricated at the Scripps Whale Acoustics lab at SIO. It was equipped with one low-frequency transducer (P190) and one high-frequency transducer (HS150). The frequency response curve for this hydrophone is shown in Figure §4.1. Acoustic data were recorded using a Fostex FR-2 Memory Recorder
4. *Vocal annotations* were used to continuously record the identities of individuals in order to later verify the identify of individuals on video records.
5. *5-minute behavioral and ecological instantaneous scan samples* (Altmann, 1974) were collected by trained boat-based observers. Appendix C shows a completed focal follow sheet. The columns, labelled 1-8, correspond to the following kinds of data:
 - 5.1. (a) Time of 5-minute scan. (b) Number of dolphins within the group (using 10-meter chain rule; (Smolker et al., 1992) (c) The nearest male neighbor (NN) of the focal individual. (d) The category of notes being recorded (e.g. '5' means 5-minute scan, 'FIZ' refers to a departure, 'FUZ' refers to an arrival), or frame number of photo with notes.
 - 5.2. The activity pattern of the focal and his nearest neighbor, including the distance ('dist') between them.
 - 5.3. Dive synchrony - whether the focal and NN made their last dive of the bout synchronously ('Y'), not synchronously ('N') or almost synchronously ('al') (see ethogram in Appendix A).
 - 5.4. The relative orientation of focal and NN at the time of the beep (e.g. parallel, converging, diverging, staggered)
 - 5.5. The focal's position within the group (L=leading third, M=middle third, T=trailing third).

- 5.6. General characteristics of group activity (Gr Act) including: traveling, resting, socializing, foraging, or unknown. Movement (Mvmt) = straight (whole group maintains same heading), meander (individuals move in parallel but change direction often), mill (individuals move in different directions with respect to other group members). Heading (Hdg) = cardinal direction of the group. Speed (Spd) = very slow (<1mph), slow (1-2mph), cruise (2-3mph), moderate (3-4mph), fast (4-6mph), and blasting (>6mph).
- 5.7. Ecological data: depth, bottom substrate (sandy or seagrass 1-4), habitat (1=beach, 2=offshore shallows, 3=embayment plain, 4=channel, 5=edge of channel, 6=flats), beaufort.
- 5.8. Group composition/Notes: qualitative description of activity and social coordination events.
6. *Positional* data were continuously recorded using a Magellan eXplorist 610 GPS unit.
7. *Depth* data were recorded at 5 or 15 minute intervals on the ethogram. The depth sounder was turned off between point samples to reduce the amount of additional noise captured on the hydrophone.

All signals were aligned at the start of each focal session using a film clapperboard. Data were synchronized for review using ChronoViz (Fouse et al., 2011), a software tool for visualization and analysis of multi-modal data (Figure 3.3).

3.2.4 CONSORTSHIP DATA

Consortships were recorded using an all-occurrence protocol (Altmann, 1974). Years used for this analysis were 2009-2014. These events take precedence over other sampling methods as they are of critical import for defining the relationships among allies. A 'consortship' is defined by any single occurrence or combination of the following events (Connor et al., 2001):

1. A female is captured by an alliance of males

2. A female attempts to escape by rapidly swimming ('bolting') from an alliance of males
3. At least one of the males produces a vocal threat called a 'pop' that induces the female to remain close. These are often produced when the male has his head at the surface of the water and the pops can be heard in air by observers (Connor and Smolker, 1996)
4. At least one of the males directs physical threats or aggression toward the female
5. Teams of two alliances attempting to take the female from the focal alliance (Connor et al., 1992a,b)
6. A clear pair or trio of males maintain association with a female for at least one hour, or across multiple surveys (total time longer than 1hr)

3.2.5 BEHAVIORAL SAMPLING OF VIDEO DATA

A group instantaneous-sampling method (Altmann, 1974) was developed and employed to capture rates of interactions among male dyads. The interval between point-samples was 5-seconds: this interval is longer than the length of the shortest event sampled (synchrony, 3s) and therefore allows for the capture of changing behavior over time, but is short enough to consistently track the movement of individuals relative to one-another. In addition to the benefits of interval over all-occurrence and one-zero sampling, this method is particularly well-suited to the aerial video dataset. At each sampling point, all dolphins who are present for observation (see below) are recorded, and only the behaviors among those visible individuals are scored.

Video sampling began at the first five-minute point after the start of the focal follow in which 2+ group members were present for observation, and group behavior was scored as social, rest, or travel (but not foraging) during the boat based focal follow. The context for this analysis were male trios from the same second-order alliance with a confirmed female consort, while any other dolphins were at a distance greater than 10-meters. All males were in one of two focal second-order alliances (KS or PD). A group was defined

by a “10-meter-chain rule” (Smolker et al., 1992) where individuals were considered part of the focal group as long as they were within 10-meters of another dolphin. Distance was estimated by body-lengths, where one-body length is estimated to be approximately 2-meters, and was measured on the aerial video frame when in question. Video data were sampled from 1.58 to 24.42 minutes (mean = 10.50 min, std = 5.38 min) from which daily *rates* of interaction were calculated for each dyad. Figure 3.5 shows the total number of five-second points samples scored for each of 19 dyads who were sampled for at least 20 point samples, with the number of sample days listed at the base of each bar.

At each five-second point sample, the identity of all individuals who were “present for observation” were recorded. To be present for observation, an individual had to be distinguishable on the aerial video data as an “identifiable dolphin-like shape”, including resolution of flukes, rostrum, and/or pectoral fins, within two frames (0.067s) of the sample frame to allow video or glare to resolve (this is much shorter than any event). Limiting factors to observation include the vertical visibility through the water, moving surface sun glare, and the framing of the group on the aerial video.

Behaviors were scored within five categories (see Figure 3.4 and ethogram in Appendix A for further detail on categories, behaviors scored, mutual exclusivity rules, and differentiating actors and recipients). IRR for identifying behavior in the above categories was 0.73 (Cohen’s Kappa; 0.82 using basic percent agreement) between the primary analyst (WF) and three trained observers.

1. *Synchrony* was scored if 2+ dolphins broke the surface / dove within 9 frames (0.033 seconds) of each other. Frames were counted between the first emergence / total disappearance of dorsal fins, or heads if dorsal fins were not visible or of the same size / shape (Connor et al., 2006). This behavior was primarily scored using the deck video, but could be scored by counting frames between the first evidence of exhalation (spray) if visible only on the aerial video. Finally, the defining part of the event (breaking surface / disappearing) must have occurred within 1-second of the sample frame in order to be recorded.

2. *Polyadic Displays* were scored if 2+ dolphins engaged in a spatially and temporally coordinated sequence of movements. The simplest display is a “tango” where two individuals in parallel engage in two or more quick turns in unison while maintaining their parallel orientation. More complicated displays include mirrored activity, and mirrored or parallel activity around a third individual. Displays often included, but were not limited to synchronous surfacing or diving. Synchrony (as described above) and displays are mutually exclusive. Records indicate whether the display included individuals coordinating their movements with each-other, or individuals coordinating their movements around a passive third individual, as well as whether the display included contact.
3. *Non-agonistic Contact* events were scored if 2+ dolphins contacted via petting (using pectoral fins) or rubbing of other appendages. Events in which dolphins were overlapping spatially but petting or rubbing could not be confirmed were scored as “distance-zero” (D0). Behaviors were distinguished by the body parts in contact, including ventral-ventral rubbing or mounting, either of which may indicate copulation. Records indicate actor and recipient when distinguishable. This analysis uses only confirmed contact events, not D0.
4. *Formations* are salient patterns of spatial orientation that are often held for periods of time. Four types of formations were scored: individuals positioned in parallel ($< 5^\circ$), less than 1/2 of a body-length offset and within one body-length’s distance from their neighbor (“abreast”), individuals positioned in parallel ($< 5^\circ$), less than 1 body-length offset and greater than two body-length’s distance from their neighbor (“lateral line”), individuals positioned in parallel but around another individual (“formation”), and individuals returning from a distance to a position around a single individual (“converging”). Records indicate actors and recipient if applicable. This analysis uses only formations among males with a female recipient (FRM, COF); abreast and lateral line events were not included.

5. *Agonistic* interactions are forceful, directed events that produce a salient reaction from the recipient. Reactions including rapidly swimming away, fluking up, or lying passively at the surface. Records indicate actors and recipients, as well as whether the event was dyadic or polyadic.

3.2.6 INTERACTION RATES

Each five-second point sample contained the identities (or unknown codes when identities could not be verified) of all individuals visible for observation §(B.2.5). On-going behavior was sampled in the categories of contact, synchrony, displays, formations, and agonism (see detailed ethogram in §B: Appendix A).

From these point samples, a mean *Interaction Rate* (*IR*) was calculated as follows for each each dyad (AB) and behavioral category (β):¹

$$IR(AB, \beta) = \frac{\# \text{ Points AB in Behavioral Category } \beta}{\text{Total } \# \text{ Points AB Present for Observation}} \quad (3.1)$$

3.2.7 ASSOCIATION INDICES

Three kinds of association indices from the 2009-2014 survey and consortship records were calculated for each dyad. A standard half-weight index (HWI) of association (Cairns and Schwager, 1987; Whitehead, 2008) was calculated using the formula in Eqn. 3.2, where x is the number of days containing a survey with individuals A and B together, y is the number of days in which both A and B were found in separate surveys, y_A is the number of days in which A was found but not B, and y_B is the number of days in which B was found but not A.

$$\text{Half-Weight Index (HWI)} = \frac{x}{x + y_{AB} + \frac{1}{2}(y_A + y_B)} \quad (3.2)$$

¹The use of a daily mean interaction rate was also considered, but due to the varying number of points each dyad was able to be sampled in per sample period, I concluded that this method provided a more accurate representation of the data. The concern either method attempts to address is whether one very active (or lethargic) day is overly represented in the analysis.

The standard HWI formula was adapted to calculate a *consortship* half-weight index (cHWI) for each dyad, which describes the propensity for A and B to participate in consortships together. In Eqn. 3.3, x_c is the number of days containing a confirmed consortship observation with individuals A and B together, y_c is the number of days in which both A and B were found in separate confirmed consortships, y_{cA} is the number of days in which A was found in a confirmed consortship but not B, and y_{cB} is the number of days in which B was found in a confirmed consortship but not A.

$$\text{Consortship Half-Weight Index (cHWI)} = \frac{x_c}{x_c + y_{cAB} + \frac{1}{2}(y_{cA} + y_{cB})} \quad (3.3)$$

A *non-consortship* half-weight index (ncHWI) was calculated for each dyad, which describes the co-occurrence of A and B when there was no confirmed or probable consortship recorded. In Eqn. 3.4, x_{nc} is the number of days in which A and B were found together in a survey, but no consortship was suspected or confirmed. All other variables are the same as in the original equation (Eqn. 3.2)

$$\text{Non-consortship Half-Weight Index (ncHWI)} = \frac{x_{nc}}{x_{nc} + y_{AB} + \frac{1}{2}(y_A + y_B)} \quad (3.4)$$

Finally, for each individual, a consortship rate (CSR) was calculated by dividing the total number of days that individual was observed in a confirmed or probable consortship by the total number of days that individual was observed, with all sightings limited to the peak mating season (September 1 - December 31) (Connor and Krützen, 2015).

$$\text{Consortship Rate (CSR)} = \frac{\text{days individual in consortship}}{\text{days individual observed}} \quad (3.5)$$

3.2.8 STATISTICAL ANALYSIS

Correlation analyses were used to examine the linear relationship between the four SCC variables and association indices. Statistical significance of the observed r -value was tested using a matrix permutation analysis (QAP, equivalent to the Mantel Permutation), used to control for the issue of social autocorrelation, which arises in this dataset because dyadic data were taken on polyadic groups of interacting individuals (the behavior of A-B has the potential to influence the behavior of B-C and A-C). Mantel permutation tests work by calculating a matrix correlation between observed and randomized matrices, testing for significance by comparing the observed r -values to that of the randomized matrices. Given a pair of $N \times N$ matrices, where N is the set of individuals in the study population, the Mantel test randomly permutes the identities of the individuals in one matrix many (in this case 50,000) times, so that the values in the matrix remain the same but the dyad linked to that value changes, and calculates a correlation statistic (Pearson's r) at each iteration. The observed value of r is then compared to the distribution of randomized r 's to assess the statistical significance of the observed relationship (Whitehead, 2008) Mantel tests were conducted using the "QAP" method in the program UCINET (Borgatti et al., 2002). This method is able to handle missing values from one matrix, which occurs in this dataset because not all possible pairs of dyads were recorded in the first-order consortship context (considered to be acceptable using this QAP test (Borgatti et al., 2013)). Though widely used, it is worth noting that there is debate in the literature about the propensity for Mantel / QAP analyses to give Type I errors, though this concern appears to be relative to the partial Mantel test, which is not used here (Guillot and Rousset, 2013; Farine and Whitehead, 2015; Legendre, 2000; Dekker et al., 2007)

An alternative to the Mantel permutation is to use generalized linear mixed models with association variables as predictors of SCC variables, including 'random' effects of individual and sample to resolve issues of non-independence. However, the SCC data are zero-inflated, and proper application of these models require further investigation.

Linear regression analysis was used to test the hypothesis that SCC interaction

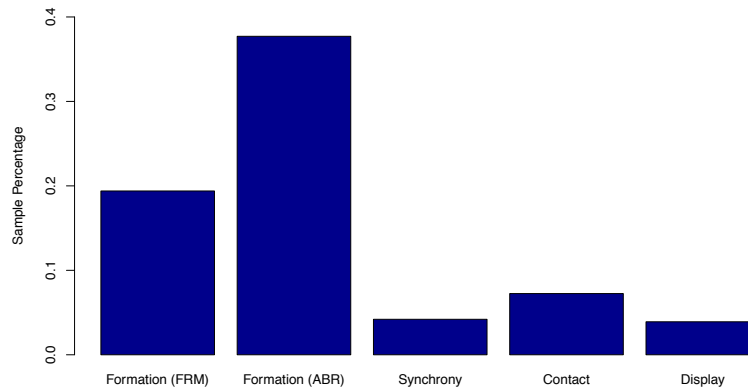


Figure 3.1: Percentage of point samples including at least one male-male dyad engaged in interaction type, out of the number of points in which it was possible to observe that interaction type.

rates provide a more sensitive measure of dyadic consortship index than non-consortship association rate alone. This analysis might be improved further by using an MR-QAP linear regression (a matrix permutation method similar to the one used above, modified for multiple regression analyses) using R package “asnipe” by D. Farine.²

3.3 RESULTS

A total of 18 dyads were used in the analysis, with each dyad meeting the sampling criteria outline above. Dyads were sampled for as many points as possible up to 250 five-second point samples. Total points sampled ranged from 21 to 207, over 1 to 7 days (Figure 3.5).

3.3.1 BEHAVIORAL VARIATION (H1)

First order allies vary in their production of social coordination. Figure 3.7 shows the mean IR observed for each behavioral category and each dyad. Figure 3.6 is a within-dyad comparison that shows, for each dyad, the proportion of total activity recorded that fell into each behavioral category. These figures indicate that each dyad may have a distinct profile of

²This requires some further study, and I’m not convinced the results will be any different from those reported.

interaction, however results are not conclusive on this since each dyad was sampled within a triad.

3.3.2 FREQUENT AND INFREQUENT ASSOCIATES (H2)

Correlation analysis and mantel permutations were used to test the hypothesis of a positive linear relationship between SCC behaviors and frequency of general association (HWI). Frequent associates tended to participate in higher rates of contact ($r = 0.35$) and synchrony ($r = 0.70$). A slight negative relationship was found between both formation ($r = -0.19$) and display rates ($r = -0.18$), with both types of interaction occurring at somewhat higher rates among infrequent associates. The QAP (Mantel) permutation showed that the observed correlation between synchrony and HWI was significant ($p < 0.05$) against 50,000 random permutations of the dyadic interaction rate matrix (Fig. 3.8).

To engage this question with more specificity, the same method was used to test the hypothesis of a positive linear relationship between SCC behaviors and frequency of non-consortship association (ncHWI). The findings were very similar: frequent associates tended to participate in higher rates of contact ($r = 0.32$) and significantly higher rates of synchrony ($r = 0.67$). A slight negative relationship was again found for display rates ($r = -0.18$), though very little relationship was found between rate of formation and ncHWI ($r = -0.07$). The mantel permutation showed that the observed correlation between synchrony and ncHWI was significant ($p < 0.01$) against 50,000 random permutations of the dyadic interaction rate matrix (Fig. 3.9).

3.3.3 FREQUENT AND INFREQUENT CONSORTING PAIRS (H3)

The same analysis procedure was used to test the hypothesis of a positive linear relationship between SCC behaviors and frequency of consortship association (cHWI). Again, positive trends were found for both synchrony ($r = 0.54$) and contact ($r = 0.43$), while formation rate was higher for males who consorted together less frequently ($r = -0.31$). No trend was found between display ratio and cHWI ($r = 0.02$). However, the trends

Table 3.1: Linear regression results. Model results describe the performance of each model. Model comparison shows the results of a general linear F-test between H_0 and each of the alternative models H_1 and H_2 .

Model	Variables	Model Results	AICc	Model Comparison
H_0	ncHWI	$F(1,16) = 25.44, p = 0.00012^*, R^2 \text{ adj} = 0.5898$	1.17	
H_1	ncHWI + Contact Ratio	$F(2,15) = 13.81, p = 0.0004^*, R^2 \text{ adj} = 0.601$	2.87	$F(1,15) = 1.46, p = 0.246$
H_2	ncHWI + Synchrony Ratio	$F(2,15) = 11.97, p = 0.0008^*, R^2 \text{ adj} = 0.5633$	4.50	$F(1,15) = 0.031, p = 0.863$

found between synchrony, contact and cHWI were not found to be significant in the Mantel permutation. (Fig. 3.10)

3.3.4 IS SCC IS A STRONGER PREDICTOR OF DYADIC CONSORTSHIP INDEX THAN NON-CONSORTSHIP ASSOCIATION RATE ALONE? (H4)

To further examine the question of whether interactions predict consortship associations (cHWI) better than non-consortship association (ncHWI) alone, I compared the performance of a null (restricted) model (H_0) that describes the linear relationship between cHWI (y_i) and ncHWI (X_1) (Eqn. 3.6), against two candidate models that included ncHWI plus contact ratio (H_1) and synchrony ratio (H_2) as predictors (Eqn. 3.7). The correlations among model variables are shown in Figure 3.11.

Significant regression equations were found for all three models. However, AICc comparison showed the null model, H_0 , as the preferable model with the lowest AICc value. General linear F-tests between H_0 and H_1 , and between H_0 and H_2 did not indicate that inclusion of either interaction measure provided a significant improvement over the null model (Table 3.1). Overall results show that adding synchrony to the model did not offer a significant improvement as it was already highly correlated with ncHWI ($r = 0.67$, fig. 3.11). Adding affiliative contact did improve the model, but not significantly.

$$y_i = \beta_0 + \beta_1 X_1 + \epsilon \quad (3.6)$$

$$y_i = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \epsilon \quad (3.7)$$

3.3.5 DESCRIPTIVE ANALYSIS

3.3.5.1 Contact

Non-agonistic contact between two males occurred in 7.2% (n=69) of 952 point samples in which there were at least two males visible on the aerial footage.

So far, I have focused on rates of interaction (point samples which dyads were engaged in a particular behavior / total samples in which it would have been possible to observe each dyad in that state). Here I will also be discussing independent contact *events*. An *event* was counted only for the first point in which definite affiliative contact (excluding 'distance-0' events) occurred between two or more individuals, and only if it occurred at least five minutes after the end of a prior petting bout between the same individuals. 49 independent contact events fit this criteria. In 9 events, no actor or recipient could be determined and the event was scored as 'mutual'. 8 of the 9 'mutual' events were between 2 males and 1 'mutual' event included three males. 23 of the 49 events occurred between an individual male and the consorted female, with 5 events directed from the female to the male, and 18 events directed from the male to the female. 2 of the 23 the directed male-female events could be categorized as "socio-sexual". These two events occurred on the same day, once from the consorted female to male consort (VRB, cFEB to CEB), and 22 minutes later from the same male consort to the same consorted female (VRB, CEB to cFEM). A 'VRB' is ventral-ventral contact, alluding to the increased likelihood (but not confirmation) of sexual behavior. All other male-female contact events were general affiliative contact behaviors (PET or RUB). 1 directed event involved two males doing a "side-press", orienting their bodies parallel alongside to "sandwich" a third male between them (SDP, IMP NOG to DNG; see ethogram in Appendix A). The three males involved were the members of a consorting trio (first-order alliance). The remaining 16 directed contact events occurred between two consorting first-order male allies. 12 of the 16 events were initiated by a male with a lower consortship rate (CSR) towards a male with a higher consortship rate. Two events could be categorized as "socio-sexual". Both events were directed from CEB to DEE, but occurred in

different years. One event was a VRB, and the second was one of the few occurrences of mounting (MNT) observed in the dataset. All other male-male directed contact events were general affiliative contact behaviors (PET or RUB). Within the events already described, switching actor-recipient roles within prolonged bouts occurred four times:

- 20-Nov-13: MNT, CEB to DEE; switch to KRB, DEE to CEB; then KRB, CEB to DEE; then RUB, DEE to CEB
- 20-Nov-13: RUB, DNG to NOG; switch RUB, NOG to DNG
- 7-Oct-14: RUB, QUA to PON; switch to KRB, PON to QUA; then RUB, QUA to PON. During this bout QUA and PON were joined distance-0 by PAS, consorted female PIC, and calf PPR. Within the same bout another (non-independent) switching event occurred: RUB, QUA to PAS and switch to RUB, PAS to QUA.³
- 18-Oct-14: VRB, HOW to CEB; switch GSE, CEB to HOW

3.3.5.2 Synchrony

Synchrony between two males occurred in 4.2% (n=40) of 952 point samples in which there were at least two males visible.

Like contact, synchrony can also occur in bouts. While short in duration (a continuous synchronous surface and dive takes an average of 3 seconds), multiple synchronous events between two individuals can occur in series. Therefore, as with contact, I am limiting this analysis to synchronous events separated by at least five minutes. 40 independent synchronous events were found (excluding “almost-sync” events). 13 events including the female consort and at least one other male, with 2 events occurring as part of a triple sync (two males and female consort) and one as part of a quadruple sync (three males and female consort). The remaining 27 events were between first-order consorting male allies, including 4 triple syncs. A preliminary analysis of the 23 dyadic male-male syncs showed a positive

³This is a good example of what was counted as ‘independent’ in this analysis: in this bout, only the first RUB, from QUA to PON was scored as ‘independent’ and counted as one of the 49 events

trend in the data between number of sync events and the dyadic cHWI and HWI values. However, I believe that the quantitative analysis above better addresses this relationship as it takes into account the proportion of activity observed and observable per dyad, while this analysis does not.⁴

3.3.5.3 Formations

Two classes of formations exist within this dataset. In the statistical analysis above, I have used only formations in which two or three males organized their behavior (FRM or COF) around a female consort. The second category of formation (which has otherwise been left out of the analysis) occurred when at least two males were observed in a side-by-side parallel orientation (ABR or LL). Overall, at least two males were scored as “actors” in any type of formation (FRM, COF, ABR, LL) in 41.7% (n = 512) of 952 point samples in which at least two males were visible on the aerial footage.

Formations in which two or three males organized around a third individual (FRM or COF) occurred during 19.4% (n = 154) of 794 point samples in which there was one male dyad plus at least one other individual observable. Predominantly, formations occurred with the males organizing around the female consort (n=145 point samples), however in 9 point samples (7 independent events), the individual being followed was male. 6 point samples (5 independent events) included the consorted female with the consorting males in formation behind another male. The remaining 3 point samples included two males in formation behind a third male.

ABR or LL formations occurred during 37.7% (n = 359) of 952 point samples in which there was at least one male dyad observable. LL was very rare, occurring in only 4 samples, comprising 2 independent events. The first event include two males, and the second event included two males plus the consorted female. Overall, ABR occurred frequently, and very often included the consorted female with males. In the total set of 814 point samples in

⁴This is in fact the reason I chose, after much trial and error, to focus on rates of interaction rather than events. Given the surface and dive patterns of the subjects and the imperfect aerial coverage, it was more reliable to score point samples of states and observability for each individual as a point sample than to keep a continuous record.

which ABR was scored (not limited to points including at least 2 males, as above), 390 point samples (47.9%) included the consorted female.

3.3.5.4 Displays

Displays in which at least two males were scored as 'actors' occurred in 3.4 % (n=32) of 952 point samples in which there was at least one male dyad observable. 14 point samples (6 independent events) included two males coordinating around the consorted female. Continuous events ranged in length from 1 to 4 point samples (< 5 seconds up to 19 seconds). Examples include:

- 8-Oct-13: IMP and NOG synchronously surface on either side of VBE (consorted female) with slight tilt-head-in.
- 4-Nov-13: DNG and IMP sweep alongside SUR (consorted female). IMP turns out at end, while DNG continues forward.
- 10-Sep-14: PAS cross-parallel with PON as they porpoise synchronously and split on either side of EED (consorted female).

18 point samples (4 independent events) included two males engaged in a sequence of coordinated behavior that was not organized around a third individual. Continuous events ranged in length from 1 to 14 point samples. Events included:

- 23-Nov-13: BIG RID engage in a short series of coordinated back and forth turns (TGO)
- 9-Sep-14: NAT and WAB engage in a series of slow synchronous turns (TGO); 14 point samples.
- 18-Oct-14: QUA and DNG turn in towards each other synchronously (no recipient).
- 21-Oct-14: IMP DEE do a coordinated turn, ending up belly-up towards the surface.

3.3.5.5 Aggression

Male-male aggression was extremely rare overall, occurring in only two of the total 952 point samples that contained at least two males. Both observed events occurred on the same day. One instance involved one male pushing up another male from below (PUP, CEB to IMP), and the second event involved two males pushing up another male from below (PUP, IMP DEE to CEB).

Coordinated aggression, instances of at least two males coordinating to direct aggression towards a third individual, was also extremely rare, also occurring in only two of the total 956 sample points that contained at least three males. One case has already been noted above (PUP, IMP DEE to CEB), though in this case the phenomenon of interest is the coordination between IMP DEE, toward a third individual, CEB. Another case involved a PUP from three males to the dependent calf of a consorted female (PUP, NOG DNG IMP to SON).

Three other instances of directed aggression were scored: a tail whack (TW) from adult male to consorted female (TW, DEE to HOW), and two PUP from individual adult males to the dependent calf of a consorted female, both occurring during the same focal follow (PUP, DNG to SON; PUP, NOG to SON)

3.3.5.6 Displacement

One behavior I noticed during the analysis was the presence of occasional displacements between the males as they moved into a position nearest to the female consort. This behavior was noted on 4 of the 952 sample points that contained at least two males, and all occurred among different individuals or on different days. Table 3.2 details one of the observed events in which the male RID is displaced from a position proximal to the consorted female FUF twice by first-order ally BIG.

Similarly, other events were observed that involved an extended contact bout among all three males as they maintained close positioning to the female consort. These events appear generally affiliative, and are interesting because in a mating context, an observer

might expect all males to be attending to the female consort rather than other males. However, these events raise the question of whether the males are in fact engaged in a type of displacement activity, negotiating amongst themselves for access to the consorted female. See supplementary video file “V1-2013-09-01-0805-QUA-59m-triadicpet.mov” for an example of this type of behavior.

Both displacement and these otherwise suggestive events allude to the delicate nature of the first-order alliance relationship as males work together to maintain a consortship while simultaneously engaging in low-levels of competitive behavior (and very little aggression).

3.4 DISCUSSION

This study aims to further our understanding of how alliance relationships are mediated by social interaction. Here’s what I found: (A) Alliance relationships are diverse. First-order allies exhibited variation in the rate at which they engage in different types of social coordination and affiliative contact (SCC). The dyadic interaction profiles (Figure 3.6) indicate that each relationship may be characterized by a distinct “fingerprint” of interaction. I characterized relationships using two measures: a basic index of overall association (HWI) and an index of association during consortship (cHWI). (B) I found that first-order allies who frequently associated across social contexts (higher HWI) tended to engage in higher rates of synchrony and contact during consortships. Allies who associate less frequently tended to engage in higher rates of displays and formations, though these relationships were not as strong. (C) First-order allies who frequently consorted together (higher cHWI) also engaged in higher rates of affiliative contact and synchrony. Males who consorted together less frequently (lower cHWI) tended to engage in higher rates of formation during the consortship context. (D) A comparison of the simple linear relationship between cHWI and ncHWI (restricted model) was compared with multivariate (full) models that included synchrony and contact in addition to ncHWI for each dyad. While all models were significant, the models including SCC behaviors were not significantly more explanatory than model of the simple linear relationship between ncHWI and cHWI.

In sum, first-order allies who were commonly found together both in and out of the consortship context tended to engage in high rates of synchrony. A higher correlation was found between synchrony and non-consortship association (ncHWI) than synchrony and consortship association (cHWI), suggesting that synchrony may be a feature of common associates across contexts. A stronger relationship was found between contact and consortship association (cHWI) than between contact and non-consortship association (ncHWI), suggesting that affiliative contact may be related to specific social contexts, including that of consortship. In these contexts, contact may be used to continually recruit, maintain, or enact cooperative engagement among allies. Both synchrony and contact behavior play a role in the mediation of alliance relationships, although the lack of correlation between the two behaviors (Pearson's $r = 0.16$, Figure 3.11) suggests that they do not share an identical function.

Behavioral synchrony has been described in many species, with different suggested functions. Behaviors such as the synchronous movements of schooling fish (Shaw, 1978), flashing of fireflies (Buck and Buck, 1968), and even schooling of cetaceans may function in anti-predator avoidance (Norris and Schilt, 1988). Moving as a synchronous, cohesive group also has energetic advantages. Coordinated flocking and schooling behavior among birds and fish is known to confer energetic advantages to both drafter and draftee who take advantage of low-pressure zones and eddies caused by movement through both air and liquid. Norris and Prescott (1961) suggest the same principle is likely to be at play in the often observed positioning of a dolphin calf next to its mother.

Other studies have suggested that synchrony may function to enact or signal alliance unity (Fellner, 2000; Connor et al., 2006). In this study I found that synchrony occurred among allies who frequently associated across contexts. Synchrony is a short duration, highly salient, and potentially inexpensive way to enact or advertise a relationship. The positive relationship between frequent associates and synchrony suggests that this indeed may function as a relatively 'cheap' signal of alliance unity.

The duration and range of movement required to initiate and sustain a bout of

petting, in which principles such as the slipstream are not likely to apply, suggest that this is a more energetically 'expensive' behavior, and therefore should be used somewhat more conservatively than synchrony. Affiliative contact was found to occur more often among individuals who commonly consorted together over the six year period between 2009-2014. If contact behavior was only a feature of consortships, no relationship would have been captured since all data in this chapter were collected during the context of a first-order consortship. Holding context and group size constant then, it appears as though affiliative contact may be an interaction that occurs between alliances that are more consistent in their interactions. It may function to recruit and maintain participation in the shared activity of a consortship. The descriptive analysis of petting events revealed that directed petting events were commonly initiated by a male with a lower consortship rate (CSR) towards a male with a higher consortship rate, again suggesting its role in recruitment. Additionally, I found that directed male-female contact behavior was commonly directed from the male to the female consort.

Perhaps playing a similar function to affiliative contact behavior, grooming among primates has been extensively studied and findings suggest that this behavior may function as a social 'commodity' used to modulate social relationships. Evidence is summarized briefly here, but see Barrett et al. (1999) for an excellent review. Both Goodall (1968) and Nishida (1970) observed asymmetric patterns grooming among pairs of adult male chimpanzees with the direction of grooming favoring the more dominant individual. Seyfarth (1980) found a significant, positive correlation between high rates of grooming among vervet monkeys and coalitionary support. Seyfarth and Cheney (1984) conducted a playback study and found that grooming prior to a call for help increased the duration of subject's responses. Silk et al. (2003) found that female savannah baboons who spent more time grooming and associating with others were more likely to rear their infants successfully. In addition the relationship between grooming and coalitionary or social support, other studies have shown a relationship between grooming and increased tolerance and access to scarce resources (Barrett et al., 1999, reviewed in).

The occurrence of affiliative contact behavior has been reported in a variety of cetacean species in captivity and in the wild, including spinner dolphins (Johnson and Norris, 1994), spotted dolphins (Dudzinski, 1998; Daisy Kaplan and Connor, 2007), bottlenose dolphins (Tavolga and Essapian., 1957; Mann and Smuts, 1998; Connor et al., 2000; Sakai et al., 2006; Connor et al., 2006), sperm whales (Whitehead and Weilgart, 2000), and long-finned pilot whales (Aoki et al., 2013). Documentation across this range of species suggests this behavior may be prevalent among odontocetes, though functions may vary across demographic classes, as indicated by the variation in the demographic composition and context of affiliative contact. For example, Mann and Smuts (1999) found that calves often initiated petting bouts with their mothers, and also reported a high rate of male-female petting. Tamaki et al. (2006) reported anabolic increase in the rate of affiliative contact after agonistic encounters among a captive group of three bottlenose dolphins *T. truncatus* including one juvenile male and two adult females. Though previous reports have suggested that affiliative contact may function as grooming among primates (Johnson and Norris, 1994; Dudzinski, 1998), only two studies have described patterns of affiliative contact behavior beyonds its occurrence in different demographic classes; one has already been discussed (Tamaki et al., 2006). The other, Connor et al. (2006) described a tendency for petting to occur among allied males, and found a positive correlation between petting and synchrony. In this study, we were able to observe the use of affiliative contact among 14 first-order allies (18 dyads). Males who frequently consort together also engaged in the highest rates of contact behavior.

This study also contributed further descriptions of the displays used by male allies, though I did not find that displays were related to any of the association indices tested. I differentiated between two kinds of displays: those that are organized around a third party, which may be taken as a form of triadic attention, and those which were organized with respect to each other (dyadic). Both are more elaborate cases of synchrony, taking more time and requiring more energetic investment by the individuals.

Overt cases of male-male agonism were extremely rare, occurring only twice and on

the same day. However, the descriptive analysis indicates that first-order allies may engage in low-level displacement activities as they vie for proximity to the consorted female. It is not necessarily the case that proximity will be correlated with increased reproductive success, but it seems reasonable to suggest that this may be the case. The absence of overt aggression and presence of displacement activity favors the hypothesis that males maintain a tenuous balance between coordinating as an alliance and competing for reproductive success during the consortship association.

3.5 ACKNOWLEDGEMENTS

Chapter 3, in part, is currently being prepared for submission for publication of the material. Friedman, W.R.; Krützen, M.; Connor, R.C. The dissertation author was the primary investigator and author of this material.

3.6 FIGURES

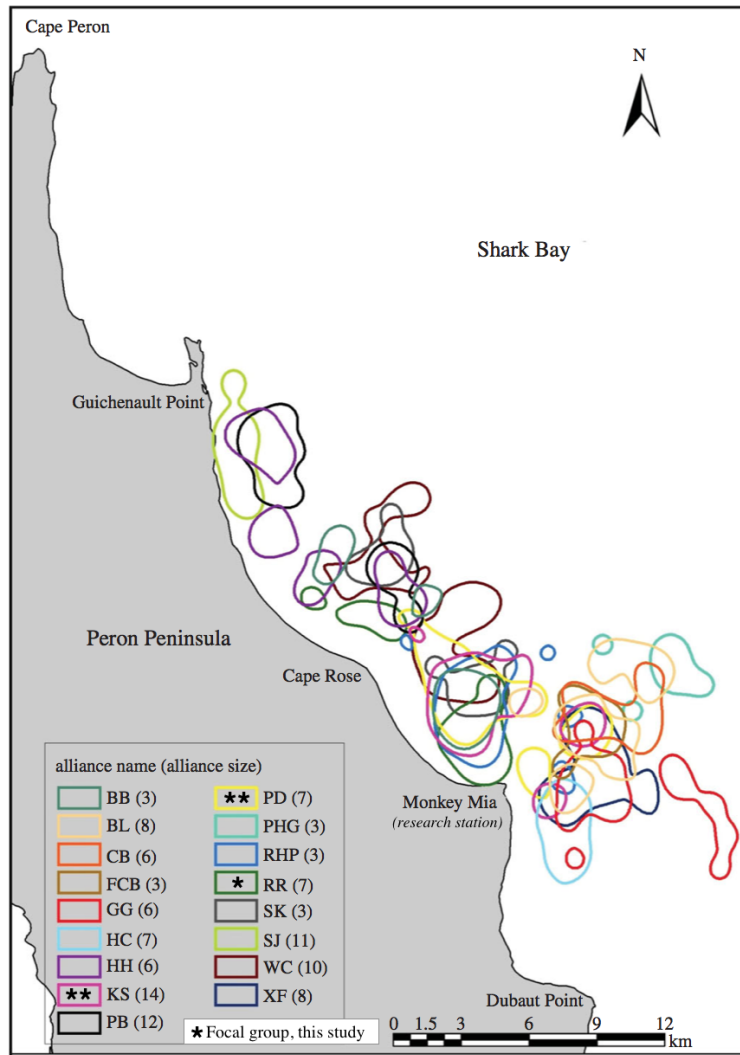


Figure 3.2: Ranges, fixed kernel density, reproduced from Randić et al. (2012)



Figure 3.3: Analysis window. Deck camera (left), aerial view (right). Video was analyzed using ChronoViz (Fouse et al., 2011).

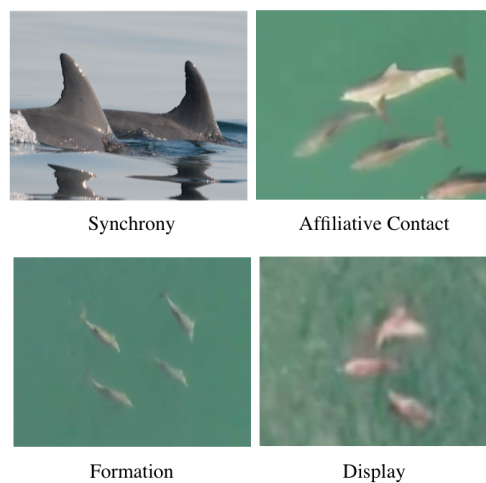


Figure 3.4: Social coordination and affiliative contact behaviors were grouped into four main categories for analysis: synchrony, affiliative contact, formations, and displays

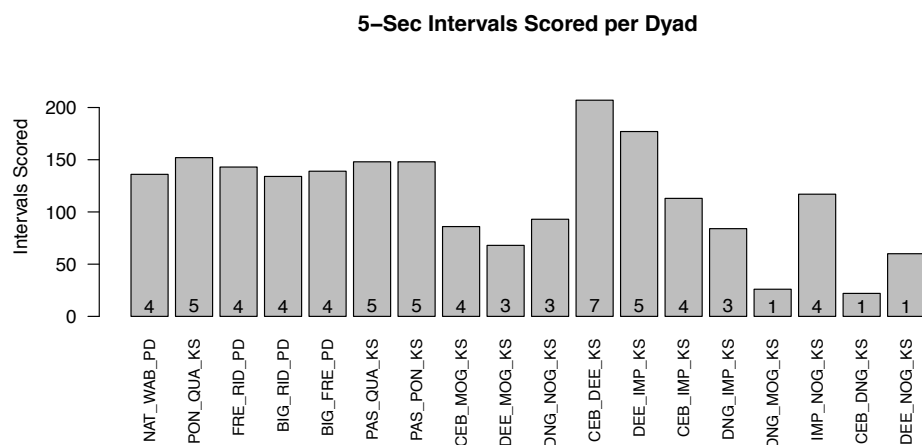


Figure 3.5: Five-second points samples scored for each dyad. Number of days sampled listed at the bottom of each bar. Each bar is labelled with the individual IDs as well as the second-order alliance in which they associate. Bars are ordered by HWI, with most frequent associates are on the left.

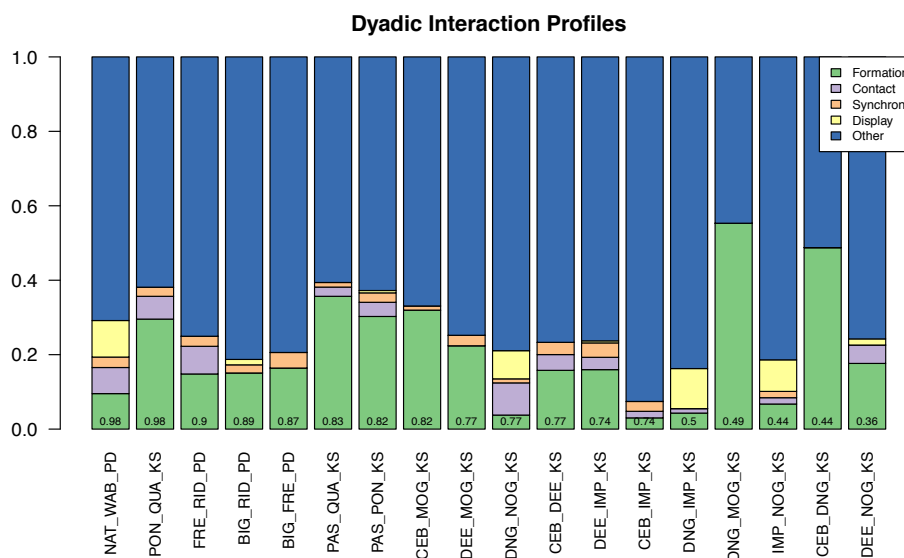


Figure 3.6: Dyadic interaction profiles. The relative proportion of behavioral interaction rates observed by dyad, $IR(\beta_x, AB) / \text{sum of all } IR(\beta_x; \beta_y, AB) + \text{rate of non-interaction (or other)}$. Informs the question “when they interact, what does each dyad do?”. Bars are ordered by HWI, with most frequent associates are on the left. Green = formation, purple = contact, orange = synchrony, yellow = display.

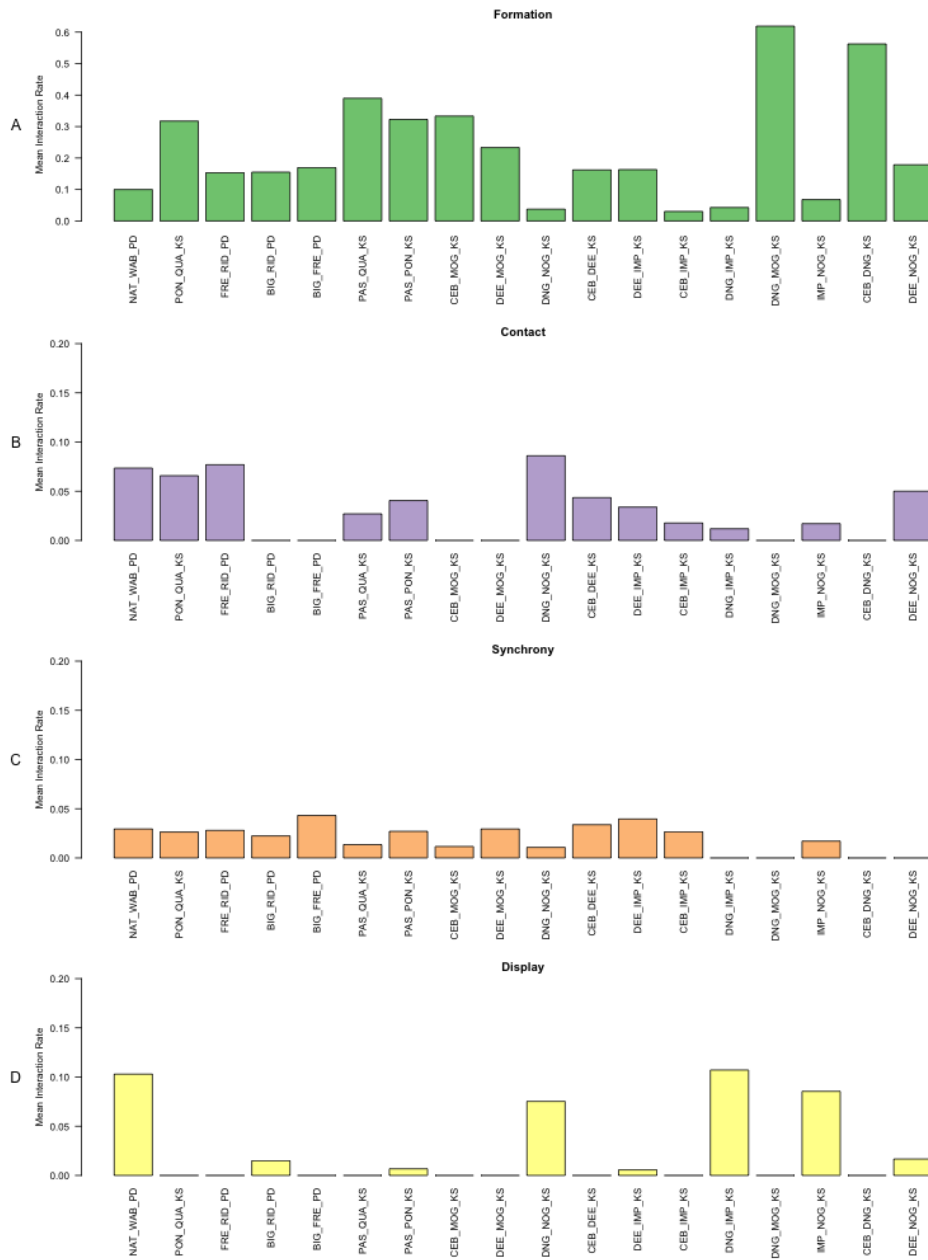


Figure 3.7: Mean interaction rates for each dyad and each behavioral category

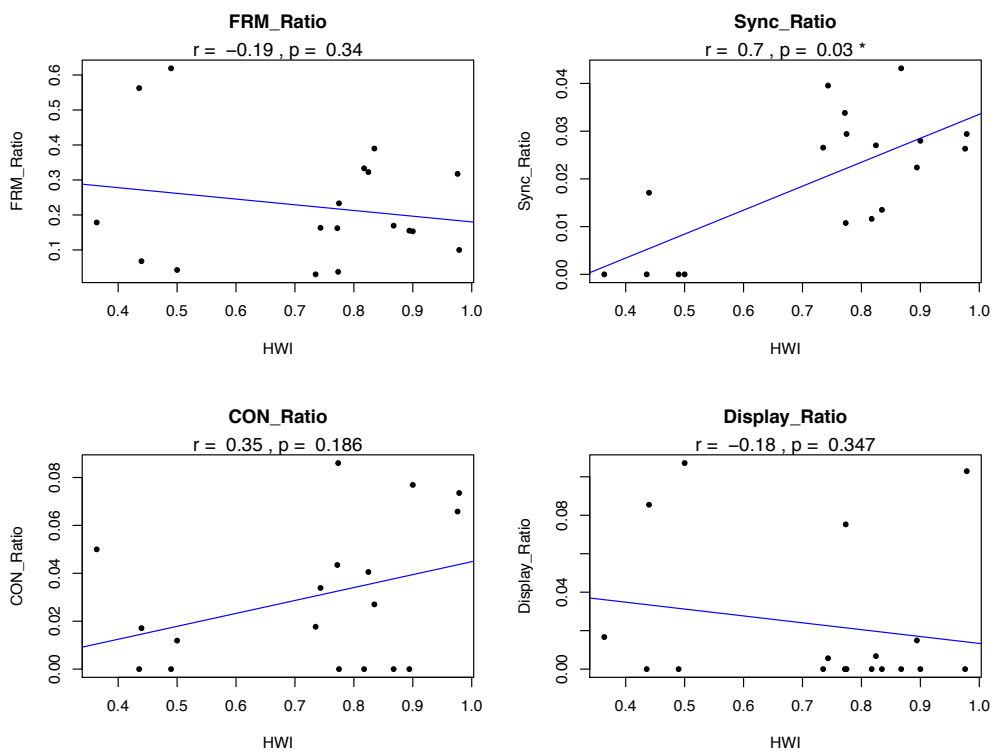


Figure 3.8: Correlation plots of dyadic HWI and dyadic SCC ratio. Statistics reported are Pearson's r, p-value obtained by testing whether observed r was significant against 50,000 permutations (QAP/Mantel test, performed in UCINET)

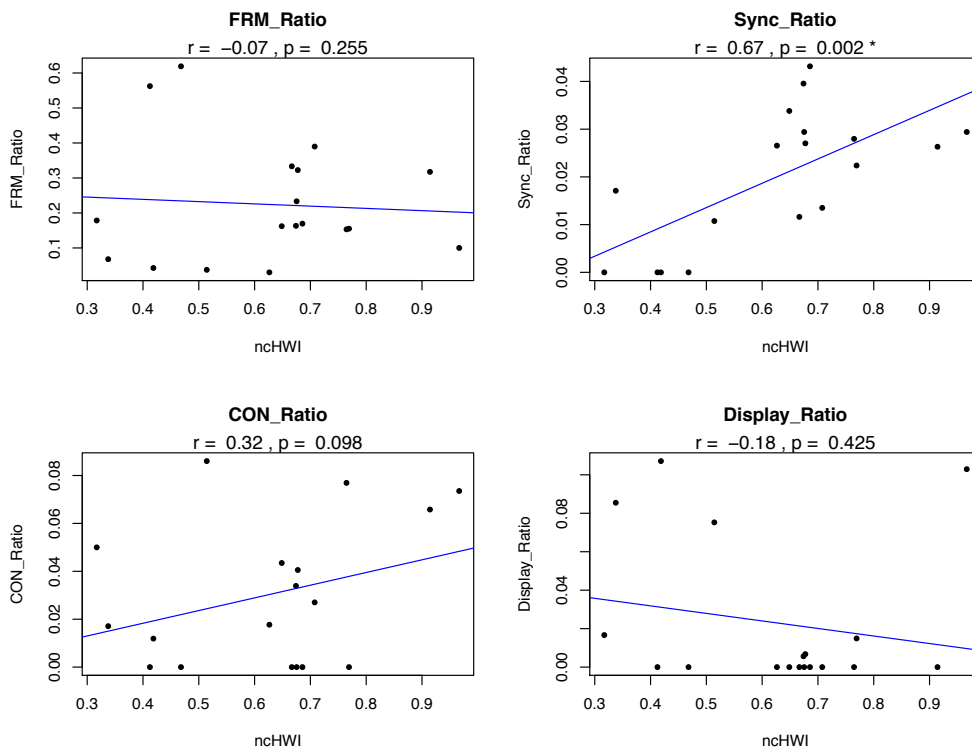


Figure 3.9: Correlation plots of dyadic ncHWI and dyadic SCC ratio. Statistics reported are Pearson's r , p-value obtained by testing whether observed r was significant against 50,000 permutations (QAP/Mantel test, performed in UCINET)

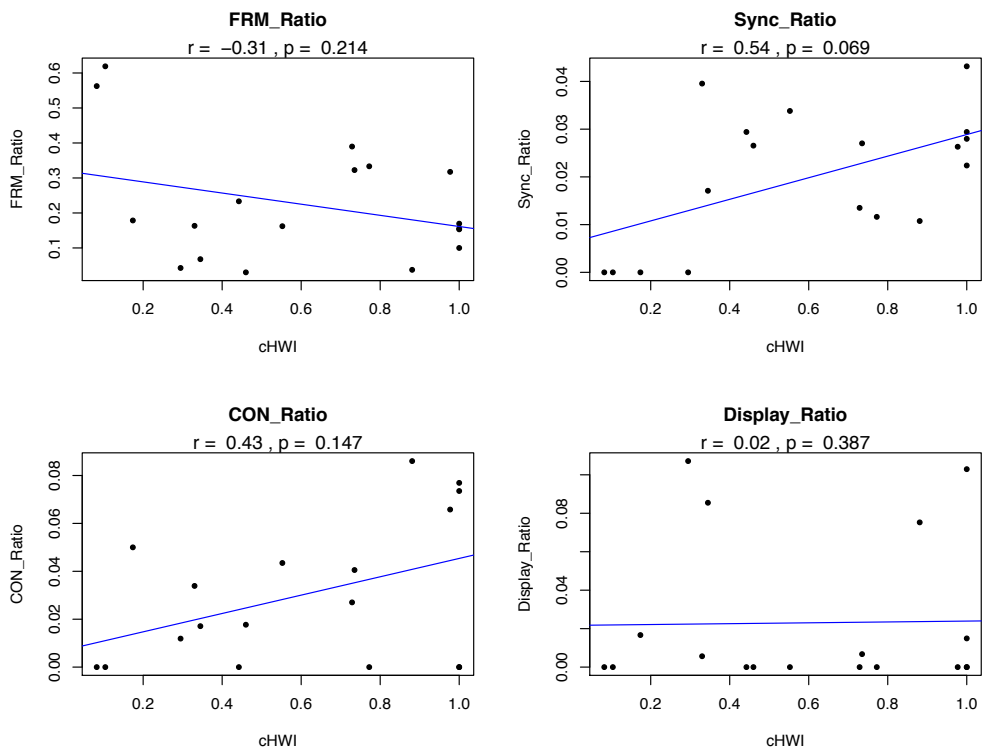


Figure 3.10: Correlation plots of dyadic cHWI and dyadic SCC ratio. Statistics reported are Pearson's r , p -value obtained by testing whether observed r was significant against 50,000 permutations (QAP/Mantel test, performed in UCINET)

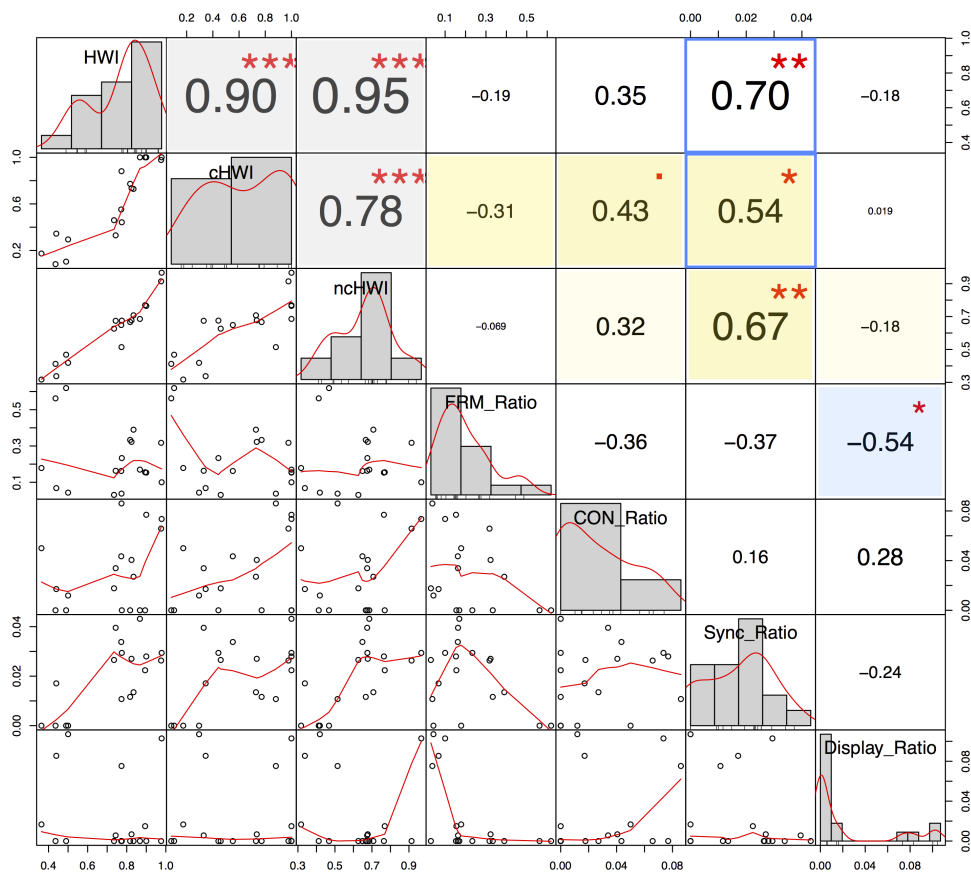


Figure 3.11: Correlations among SCC variables (formation = FRM Ratio, contact = CON Ratio, synchrony = SYN Ratio, displays = DSP Ratio) and association indices (half weight index = HWI, consortship index = cHWI, non-consortship half-weight index = nchWI). Filled boxes indicate correlations with Pearson's $r \geq 0.4$ or ≤ -0.4 . Red stars indicate significance of Pearson's r . Blue outlined boxes indicate significant relationships found using Mantel permutations. GAMM and GLMM models did not show any relationship between the SCC variables and association indices as significant after controlling for the effects of dyad ID and sample ID.

Table 3.2: Displacement event. Males vie for position closest to consorted female (FUF). BIG displaces RID.





Image	Frame	Description
	19.48.1	BIG RID sync-up (SSU-1), then dive.
	19.55.3	RID surfaces first, turning towards FUF (emerging)
	19.57.4	RID moves under FUF, distance-0.
	19.59.6	RID, still distance-0 to FUF, turns slightly away as FRE emerges parallel (ABR-1) to FUF. BIG angles slightly towards the group

Table 3.2: Displacement event. Males vie for position closest to consorted female (cont'd)





Image	Frame	Description
	20.01.4	FUF turns to and approaches FRE distance=0. RID drops back as BIG approaches.
	20.02.8	FUF rubs alongside FRE. RID re-approaches.
	20.06.0	BIG angles in towards FUF, moving between RID and FUF (Displace)
	20.07.9	BIG moves into the center position as all three males engage in formation (FRM-1) behind FUF. BIG is slightly closer to FUF than FRE.

Table 3.2: Displacement event. Males vie for position closest to consorted female (cont'd)





Image	Frame	Description
	20.11.8	BIG breaks formation and moves alongside then away from the group. RID FRE stay in formation behind FUF.
	20.13.3	As BIG moves away, RID moves closer to FUF. RID FRE are still in formation behind FUF (FRM-1)
	20.14.6	RID and FRE orient their heads towards FUF's peduncle (TLH-0)
	20.17.5	FRE dives below RID (away from FUF), rubbing under RID's peduncle, as BIG surfaces and again angles in towards the group. RID FUF are parallel (ABR-1).

Table 3.2: Displacement event. Males vie for position closest to consorted female (cont'd)







Image	Frame	Description
	20.19.3	RID and FUF are parallel (ABR-1) briefly as BIG approaches.
	20.21.8	BIG and FRE approach FUF in parallel (ABR-1), displacing RID.
	20.24.3	BIG and FRE are in formation (FRM-1) behind FUF. RID is trailing
	20.26.6	FRE FUF and BIG are parallel (ABR-1) with FUF in the middle. RID is still trailing (odd-male-out, OMO)

Table 3.2: Displacement event. Males vie for position closest to consorted female (cont'd)

Image	Frame	Description
	20.28.4	RID approaches FUF again. FRE FUF RID are still ABR-1
	20.31.4	BIG FRE maintain close proximity to FUF as RID moves away (OMO)

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CHAPTER 4

THIRD-ORDER FUSIONS

4.1 INTRODUCTION

Though varying in population size and social structure, bottlenose dolphins world-wide demonstrate a grouping pattern in which sub-groups disperse and aggregate throughout the day according to activity and distribution of resources (Connor et al., 2000). Such “fission-fusion” dynamics (Kummer, 1971; Aureli et al., 2008) are characteristic of the Shark Bay (SB) dolphin population, including among male alliances (Smolker et al., 1992). For example, in a typical follow we may encounter an individual in a group with 1-2 other first-order allies, who then join (“fuse”) with 6-8 other second-order allies and any female consorts, before fusing with another second-order alliance of 10-12 males (third-order allies) and female consorts, and later departing from that group (“fizzing”) either individually or with his first- or second-order allies.

Such dynamics in group membership introduces uncertainty into “third party” relationships (Connor, 2007): e.g. if individuals A, B, and C are co-present all the time, as is the case with many [new world primates; cercopithecines cite. e.g. macaques], then information about their relationships (A-B, B-C, A-C) is always available. However, in higher fission-fusion systems like we see in SB, the relationship between B and C may change outside of the association with A. Information about third-party relationships should be at a premium to the degree that the functions of a social system are contingent on a balance of social relationships, and the probability of a change in relationships is substantial.

In the SB alliance system the preponderance of evidence suggests this is the case. The majority of consortships involve two to three males who coordinate their activities

in space and time around and with the consorted female, sometimes for months at a time (Connor et al., 1992a,b). The composition of such consortship groups are non-random: they are based on long-term association (Connor et al., 1999). Thus one function of the alliance system (consortship and associated reproductive success) is contingent on social relationships. However, while the composition of second-order alliances is almost perfectly stable once males reach prime reproductive age, the composition of first-order alliances is more variable, with some groups maintaining stability over many years, and others rotating members within seasons (Connor et al., 1999). Another primary function of alliances, mate competition, requires the participation of multiple alliance partners (Connor et al., 1992a,b). However, it is likely that variation in relationships among second-order allies affects participation in these events. Relationships among third-order allies introduce further uncertainty, as two second-order alliances may at times work together during competitions (thus forming a third-order alliance), or compete against one-another during such contests (Connor, 2010).

The combination of variability in relationships (uncertainty in the system) and functional reliance suggests that allies are likely to engage in behaviors that maximize information about the status of their relationships, especially when reuniting after periods of separation - that is, upon fusion. Aureli et al. (2008) argued that “members of higher [fission-fusion] groups must have ways to reestablish relationships and resolve uncertainties (e.g., concerning alliances, dominance status, and each individual’s relationship to third parties), depending on the frequency and patterns of spatial and temporal separations.”

Thus, we predict that individuals should engage in *informative acts* during fusion events - but what form might such behavior take? The animal behavior literature provides some possibilities: (a) Individuals may engage in stressful behaviors, considered to function to test the quality of a bond (Zahavi, 1977; Kummer, 1978). For example, Perry (2011) described the behavior of pairs of white-faced capuchins (*Cebus capucinus*) who inserted their “partner’s finger into their own eye socket up to the first knuckle.” Similarly, Smuts and Watanabe (1990) described the greeting rituals of male olive baboons (*Papio cynocephalus*

anubis), including the presentation of hindquarters to another male which may be followed by genital touching, an act in which the individual is “literally placing his future reproductive success in the palm of a potential rival’s hand.” In the latter study, the strongest male alliance was also the only dyad that showed complete symmetry in their exchange of sexual greetings (*ibid*). (b) Individuals may engage in affiliative behaviors such as grooming which may increase the probability or duration of coalitional support (Seyfarth, 1977). For example, among unrelated female vervet monkeys (*Cercopithecus aethiops*), grooming prior to a call for help increased affiliates response duration (Seyfarth and Cheney, 1984). Similarly, (Nishida, 1983) found that male chimpanzees (*Pan troglodytes*) directed grooming towards potential allies in moments of intense social conflict. (c) Individuals may engage in ritualized dominant / sub-ordinate behaviors, whose function is likely to establish or reinforce social hierarchies. For example, Kummer (1978) observed that among captive gelada baboons (*Theropithecus gelada*), “presenting and mounting appear as an acknowledgement of rank and as a reduction of agonistic tendencies that finally permits the intimate interaction of grooming.” (d) Another class of behaviors, known as *derived*, *allochthonous*, or *intention movements*, were described in detail by many of the mid-century ethologists (e.g. Daanje, 1950; Hinde, 1952; Tinbergen, 1952). In these studies, ethologists noticed a class of behaviors which bore structural resemblance to those occurring in longer sequences, especially in contexts of heightened aggression. For example, Hinde (1952) observed that a “head-up aggressive posture, which normally appears in reproductive fighting, occurs occasionally in food disputes between Great Tits during the period before the break-up of the flocks.” Similarly, threat-postures used by social mammals (canines, primates, felines) such as pilo-erection and bared teeth are known to preempt the escalation of contests. In each case the observed behavior is a *synecdoche*: a physical part of a behavior or behavioral sequence common to more intense interactions.

Behavioral observations of alliances *in situ*, as well as past studies (Connor et al., 2000), suggest that coordinated social behavior is a fundamental aspect of mate competition and consortship, two principal functions of male alliances. During intense contests between

second-order alliances, males can be observed coordinating in both space and time as they engage in behaviors such as charging to attack a group, chasing a single individual, or pushing another's body out of the water (effectively demobilizing the opponent, if briefly). During consortships, allies can be observed coordinating in space and time as they maintain a side-by-side abreast "formation" while herding a female consort, produce intricate sequences of mirrored synchronous displays, or simply surface and dive in synchrony.

Parsimony suggests that allies should enact ¹ (communicate) their relationships via the same mechanisms critical to their success as allies. That is, even outside the context of mate-competitions, males are likely to engage in informative acts that bear structural resemblance to the kinds of coordinated social behavior that they use during high-stakes but less frequent contests (e.g. allochthonous behaviors).

Male allies have also been observed engaging in affiliative contact behavior: petting using their pectoral fins, and rubbing bodies alongside one-another. These behaviors are likely to have a similar function as grooming among primates, and may similarly relate to improving the strength of alliance relationships and the likelihood that an ally will participate in consortships or intra-specific competitions.

Finally, bottlenose dolphins produce a wide range of vocalizations that have been broadly classified into narrow-band whistles, and broad-band echolocation clicks and burst-pulse calls (Evans and Bastian, 1969; Caldwell and Caldwell, 1968; Caldwell et al., 1990; Ralston and Herman, 1989). Of these call types, both whistles and burst-pulse calls are consistently associated with social contexts, with the former studied much more intensively (Caldwell and Caldwell, 1968; Harley, 2008; Ralston and Herman, 1989; Tyack, 2000). Of particular interest has been the study of repeated, individually-specific whistles termed "signature whistles", commonly recorded when individuals are separated from conspecifics and therefore considered to function in group cohesion (Caldwell and Caldwell, 1965; Janik and Slater, 1998; Harley, 2008). In an acoustic study on bottlenose dolphins in St. Andrews Bay, Scotland, Quick and Janik (2012) found that groups often produced stereotyped ex-

¹VRT...

changes of whistles (signature whistles) prior to fusion events: that is, at fusions groups are likely to exchange identity information. A wide range of non-stereotyped whistles may also accompany such events. Such vocalizations may include alliance-specific whistles (Smolker and Pepper, 1999), and/or vocalizations which may convey information about the aggressive or affiliative nature of the arrival, size, or demographic of individuals; though informational content of dolphin vocalizations is not yet well understood (Tyack, 2000). For instance, Connor et al. (1996) described a low-frequency vocalization train called “pops” used by consorting males preceding a return of the consorted female to a more proximal position. This may be a threat vocalization, and appears to function in the maintenance of a consortship. (Vollmer et al., 2015) found that the “pop” vocalization occurred at significantly higher rates during consortships than in non-consortship associations among male allies. The informational content of dolphin vocalizations is not yet well understood. However, if allies are exchanging information about the status of their relationships during fusion events, we should expect some (if not most) of that information to be conveyed via the primary sensory modality of this species. In this study, I test whether the rate of whistle activity is higher at fusion versus post-fusion, and provide a description of the types of whistles and other call types recorded.

In this chapter I examine the context of two first-order male trios with female consorts from different second-order alliances joining together (“third-order fusions”) to examine how third-order alliances are mediated through social interaction. I test the hypotheses that males participate in social coordination, contact, and vocalizations at higher rates at the time of fusion than later periods during their time together, and provide a descriptive analysis further detailing the kinds of behaviors and vocalizations recorded at and post-fusion. Additionally, I describe the difference in interaction rates between second- and third-order allies, as well as differences pre- and post- fusion in female- directed behaviors. To explicitly describe the process of fusion interactions, I use a limited set of the scored behaviors (displays or synchrony), to conduct a fine-scale descriptive analysis of the coordination of visible sensorimotor resources through space and time. The following hypotheses are tested:

- H4 The production of SCC among third-order allies will be higher at fusion events than post-fusion
- H5 Third-order fusions will be accompanied by higher rates of acoustic vocalizations (whistling) than post-fusion

4.2 METHODS

4.2.1 SUBJECTS

The subjects for this analysis were groups containing two first-order male trios from two different second-order alliances and at least one female consort. All males were in one of the three focal second-order alliances (KS, PD, or RR).²

4.2.2 FUSION EVENTS

From 2013-2014 we recorded 26 fusion events between two trios from different second-order alliances with at least one consorted female. Of these, fusion events were analyzed only if (1) the exact time of fusion was known, (2) the data were recorded in a sea state of Beaufort 3 (winds less than 12mph) or less. If multiple fusion events were recorded for the same subgroup in a single day, I used the first fusion recorded.³ Fusion events were sampled during two periods: 0-5 minutes (“at fusion”), and from 5-10 minutes (“post-fusion”). Up to five minutes were sampled in each period, but scoring was stopped 1 minute prior to any of the following events: (a) if the group split apart (“fizzed”) to a distance greater than 10-meters (3 at-fusion samples, 1 post-fusion sample) (b) if another group fused (1 at-fusion sample), (c) the predominant group activity shifted to foraging (2 at-fusion samples). The number of five-second points scored during each sample was also limited by the presence of focal individuals near the surface and visible for observation on the aerial

²Since a first-order alliance is a subset of a second-order alliance, but no additional second-order allies were included in this analysis, in this chapter “first-order allies” are synonymous with “second-order allies”. “Third-order allies” refers to groups comprised of males from two different second-order alliances.

³Observations *in situ* suggest that first-fusions may differ in quality from fusion events involving the same subgroups that occur closer in space or time throughout the day, though it is not possible to address this hypothesis with the current dataset.

video. Events are described in terms of rates of activity over the set of points possible to score for each event (§4.2.3.2). Due to varying lengths of encounters and limited data, it was not always possible to score the same event during the at- and post- fusion period. 13 fusion events were used in this analysis, including 10 at-fusion samples and 5 post-fusion samples. At-fusion samples included 7 unique combinations of male allies. 2 groups were KS-PD, 7 groups were KS-RR, and 1 group was PD-RR. Samples ranged in length from 1m25s to 5m0s. Post-fusion samples included 5 unique combinations of male allies. 3 groups were KS-PD and 2 groups were KS-RR. Samples ranged in length from 4m30s to 5m0s. One at-fusion event was the first fusion recorded, but not the first fusion observed between the two groups that day. No group was sampled more than once for pre- or post- fusion in a single day. Audio data were matched to the exact time of fusion for all 10 at-fusion events, and for 4 of 5 post-fusion events. 4 additional post-fusion periods were scored where data was available for acoustic but not video analysis. In these samples, it was possible to verify the group in the recording through scans and side-angle video records. In total 10 at-fusion events and 8 post-fusion events were sampled for acoustic events.

4.2.3 BEHAVIORAL INTERACTIONS

4.2.3.1 Sampling

Aerial and side-angle video data were sampled using a five-second group instantaneous sampling method (Altmann, 1974). Sampling began at the first evidence of fusion, defined as either (A) the first frame of aerial video in which at least one individual from each of the two subgroups were visible for observation and within 10-meters, or (B) if the fusion was not captured on the aerial video, the exact time that observers identified the fusion event. A “fused” group was defined by a “10-meter-chain rule” (Smolker et al., 1992) where individuals were considered part of the focal group as long as they were within 10-meters of another dolphin. Distance was estimated by body-lengths, where one-body length is estimated to be approximately 2-meters, and was measured on the aerial video frame when in question.

At each five-second point, the identity of all individuals who were “present for observation” were recorded. To be present for observation, an individual had to be distinguishable on the aerial video data as an “identifiable dolphin-like shape”, including resolution of flukes, rostrum, and/or pectoral fins, within two frames (0.067s) of the point sample frame to allow video or glare to resolve (this is much shorter than any event). Limiting factors to observation include the vertical visibility through the water, moving surface sun glare, and the framing of the group on the aerial video.

Behaviors were scored within five categories (see Figure 4.1 and ethogram in Appendix A for further detail on categories, behaviors scored, mutual exclusivity rules, and differentiating actors and recipients):

1. *Synchrony* was scored if 2+ dolphins broke the surface / dove within 9 frames (0.033 seconds) of each other. Frames were counted between the first emergence / total disappearance of dorsal fins, or heads if dorsal fins were not visible or of the same size / shape (Connor et al., 2006). This behavior was primarily scored using the deck video, but could be scored by counting frames between the first evidence of exhalation (spray) if visible only on the aerial video. Finally, the defining part of the event (breaking surface / disappearing) must have occurred within 1-second of the point sample frame in order to be recorded.
2. *Polyadic Displays* were scored if 2+ dolphins engaged in a spatially and temporally coordinated sequence of movements. The simplest display is a “tango” where two individuals in parallel engage in two or more quick turns in unison while maintaining their parallel orientation. More complicated displays include mirrored activity, and mirrored or parallel activity around a third individual. Displays often included, but were not limited to synchronous surfacing or diving. Synchrony (as described above) and displays are mutually exclusive. Records indicate whether the display included individuals coordinating their movements with each-other, or individuals coordinating their movements around a passive third individual, as well as whether the display included contact.

3. *Non-agonistic Contact* events were scored if 2+ dolphins contacted via petting (using pectoral fins) or rubbing of other appendages. Events in which dolphins were overlapping spatially but petting or rubbing could not be confirmed were scored as “distance-zero” (D0). Behaviors were distinguished by the body parts in contact, including ventral-ventral rubbing or mounting, either of which may indicate copulation. Records indicate actor and recipient when distinguishable.
4. *Formations* are salient patterns of spatial orientation that are often held for periods of time. Four types of formations were scored: individuals positioned in parallel ($< 5^\circ$), less than 1/2 of a body-length offset and within one body-length’s distance from their neighbor (“abreast”), individuals positioned in parallel ($< 5^\circ$), less than 1 body-length offset and greater than two body-length’s distance from their neighbor (“lateral line”), individuals positioned in parallel but around another individual (“formation”), and individuals returning from a distance to a position around a single individual (“converging”). Records indicate actors and recipient if applicable.
5. *Agonistic* interactions are forceful, directed events that produce a salient reaction from the recipient. Reactions including rapidly swimming away, fluking up, or lying passively at the surface. Records indicate actors and recipients, as well as whether the event was dyadic or polyadic.

Inter-rater reliability for classifying behavior in the above categories was substantial ($\kappa = 0.73$, percent agreement = 0.82) between the primary analyst (WF) and three trained observers.

4.2.3.2 Analysis

Each five-second point sample contained the identities (or unknown codes when identities could not be verified) of all individuals visible for observation, as well as their on-going behavior in the categories of contact, synchrony, displays, formations, and agonism (see detailed ethogram in §B: Figure 4) From these point samples, *Interaction Rates (IR)*

were calculated as follows for each sampling period:

$$IR = \frac{\text{nDyads in Behavioral Category } (\beta) \text{ in Period } \tau}{\text{nDyads Present for Observation } (\Theta) \text{ in Period } \tau} = \frac{\sum_{i \in \tau} \beta Dyads_i}{\sum_{i \in \tau} \Theta Dyads_i}, \quad (4.1)$$

Where τ refers to the complete set of 5s point samples in a sampling period at fusion (minutes 0-4.99) or post-fusion (minutes 5-9.99), and i refers to a single point sample within the set τ . Only one period at- and post- fusion was sampled per third-order group, per day. If multiple fusion events between the same subgroups were captured in a day, only the first fusion event captured on that day was sampled. Because fusion events were of differing lengths, and because not all events were captured on aerial video for the entire length of the interaction, it was not possible to construct paired samples for each event (i.e. not all “at-fusions” have a paired “post-fusion” sample, and vice versa).

Equation 4.1 was modified for interaction rates among second-order allies (Eqn. 4.2) or third-order allies (Eqn. 4.3) as follows:

$$IR_2 = \frac{\sum_{i \in \tau} \beta_2 Dyads_i}{\sum_{i \in \tau} \Theta_2 Dyads_i}, \quad (4.2)$$

$$IR_3 = \frac{\sum_{i \in \tau} \beta_3 Dyads_i}{\sum_{i \in \tau} \Theta_3 Dyads_i}, \quad (4.3)$$

Where $\beta_2 Dyads$ is the number of second-order dyads and $\beta_3 Dyads$ is the number of third-order dyads in behavioral category β , and where $\Theta_2 Dyads$ is the number of second-order dyads and $\Theta_3 Dyads$ is the number of third-order dyads visible for observation in the set of all point samples τ .

In addition to the sampled behavioral categories, data were re-classified into the categories following for further analysis. Each pair was counted only once per point sample.

- Any Interaction (AnyIxn): male pairs engaged in any type of interaction (contact, displays, formations, synchrony, or agonism). Pairs could be both actors, both recipients,

or actor-recipient pairs.

- Any Coordination (AnyCoord): male pairs engaged in any spatially and/or temporally coordinated activity (display, formation, synchrony, or agonism), where both males are actors.
- Coordinated Male-Male Agonism (AgPairs): male pairs engaged in potentially agonistic activities (display, formation, agonism) where the recipient is another male. Both males are actors.
- Actor-Recipient Agonism (AgAR): male pairs engaged in potentially agonistic activities (display, formation, agonism) where one male from the pair is an actor and the other is a recipient.
- Coordinated together (CoordTog): male pairs engaged in coordinated activity (contact, displays, formations, and synchrony) without a recipient.
- Coordinated around (CoordAround): male pairs engaged in coordinated activity (contact, displays, formations, and agonism) directed towards or around a recipient.
- Out-male-approach (OMA): Male-female pairs where the male is actor and female is the recipient in contact, displays, formations, or agonism, or both are actors in synchrony. The female is the consorted female of the third-order male allies of the male actor (not the female that he is consorting with his first-order allies). Equation 4.4 is used for this category.
- Male-to-Consorted Female (CSO): Male-female pairs where the male is actor and female is the recipient of contact, displays, formations, or agonism, and both are actors in synchrony. The female is the same female that he is consorting with his first-order allies. Equation 4.5 is used for this category.

$$IR_{oma} = \frac{\sum_{i \in \tau} \beta_{oma} Dyads_i}{\sum_{i \in \tau} \Theta_{oma} Dyads_i}, \quad (4.4)$$

Where $\beta_{oma}Dyads$ is the number of male-female OMA pairs engaging in OMA behavior, and where $\Theta_{oma}Dyads$ is the number of possible OMA dyads visible for observation in the set of point samples τ .

$$IR_{cso} = \frac{\sum_{i \in \tau} \beta_{cso}Dyads_i}{\sum_{i \in \tau} \Theta_{cso}Dyads_i}, \quad (4.5)$$

Where i is a five-second point sample, $\beta_{cso}Dyads$ is the number of male-female pairs engaging in CSO behavior, and $\Theta_{cso}Dyads$ is the number of possible CSO dyads visible for observation in the set of point samples τ .

4.2.4 ACOUSTIC PRODUCTION

Acoustic recordings were collected during focal follows using a towed hydrophone fabricated at the Scripps Whale Acoustics lab at SIO. It was equipped with one low-frequency transducer (P190) and one high-frequency transducer (HS150). The frequency response curve for this hydrophone is shown in Figure 4.2. Acoustic data were recorded using a Fostex FR-2 Memory Recorder

Whistle production was sampled over the same periods as third-order fusions and post-fusions, ensuring that the dolphins were near enough to the boat to have their whistles captured by the towed hydrophone. Acoustic data were reviewed using spectrographic displays (Fast Fourier Transform size: 1024, weighting function: Hanning window, time resolution: 3s, sampling rate: 192 kHz) using the free, open-source *Audacity* software. Those recording segments in which engine noise exceeded 2 kHz were discarded from the analysis (King and Janik, 2014). Whistles were sampled by a human observer (WF), using an all-occurrence sampling method. Each whistle was labeled to mark the onset, offset, and duration of the vocalization. Independent whistles were defined by temporal breaks in the vocalization. Whistles that overlapped in time were marked separately, therefore a single point sample might include up to four separate whistles. Additionally, the presence/absence of burst-pulse, pops, and echolocation were noted for each at- and post-fusion event sampled.

Inter-rater reliability between the primary analyst (WF) and three trained observers on categorizing whistles was almost perfect ($\kappa = 0.979$, percent agreement = 0.991).

Two metrics were used to compare whistle activity during and post-fusion events: (1) a *whistle rate* was defined as the number of independent whistles scored divided by the total duration of the sampling period, and again divided by the number of individuals present (Eqn. 4.6). (2) a *whistle activity index* was defined as the number of 0.01 second point samples, derived from the all-occurrence dataset, in which a whistle was marked as occurring, divided by the total number of 0.01 second point samples scored, again divided by the number of individuals present (Eqn. 4.7). The latter metric was developed to account for variations in the duration and overlap of calls, and to provide a general index of 'acoustic activity'. A sensitivity analysis of sampling rates revealed that re-sampling the data at 0.01-seconds provided an accurate representation of the data (Martin and Bateson, 1994).

$$WhistleRate(WR) = \left(\frac{nWhistles}{SamplingDuration(sec)} \right) * \left(\frac{1}{nDolphins} \right), \quad (4.6)$$

$$WhistleIndex(WI) = \left(\frac{nWhistlePointSamples}{TotalPointSamples} \right) * \left(\frac{1}{nDolphins} \right), \quad (4.7)$$

4.2.5 STATISTICAL ANALYSIS

After rates of interaction per dyad were tallied (as described above), the data was transformed to a binary matrix to provide a more conservative analysis that reduces the risk of social autocorrelation in the data. Though each interaction type could be and was frequently observed occurring among two individuals (three in the case of interactions around a third individual), interactions may also be polyadic. For example, a typical 'formation' occurs when three males line up side-by-side abreast behind a consorted female. In the raw counts, this interaction would be counted once for each male dyad observed (3 times), and a rate of interaction would be calculated as the number of males dyads in interaction (3) out of the total number of males observed (3), extended over the entire sampling period. If there were only two males in formation behind the female, the rate of interaction would be 1/3,

providing a more accurate overall estimate of the density of interaction, but at the risk of inflating estimates for dyads through social association.⁴

The binary form of the data asks the question, “for each point sample in which it was possible to observe interaction X (e.g. affiliative contact), was that interaction observed?”. In the above example, if any males were in formation the score for that sample period would be 11, whether the formation occurred with two males or three“. The resulting rates of interaction are temporal rates, but do not represent the fraction of pairs interacting at a particular point sample. Over the course of a 5 minute long sampling period, the maximum number of point samples is 60 (12 5-sec point samples minute), and the maximum rate of interaction ranges from 0 (060) to 1 (6060).

Welch two-sample t-tests were used to test the hypotheses that the means of each sample grouping (1. rates of second vs third order interaction, 2. rates of third-order interaction at vs. post fusion, 3. rates of second-order interaction at vs. post fusion, 4. rates of whistles at vs. post fusion) were the same. Directionality of tests are reported with the results. Welch’s t-test are used to test for differences between two data sets with unequal variances and sample sizes.

4.2.6 DESCRIPTIVE ANALYSIS

A fine-scale descriptive analysis was conducted for the third-order fusion event on 07-October-2014, 09:23:53. During this event, three males from the KS alliance (PAS PON QUA), along with their consorted female (PIC) and her calf (PPR) fused with three males from the RR alliance (SMO COO URC), along with their consorted female (NIR). The descriptive analysis includes the five-second sampling frames supplemented by key events falling between the sample points. Behaviors were described by their corresponding name in the ethogram (Section B, Figure 4). Also noted are examples of behavioral patterns that are starting to emerge through observation of the aerial video and of the alliances *in situ*, and may be the subjects of future study.

⁴Arguments might be made either way here, but I have decided after much thought that this is the more conservative approach.

4.3 RESULTS

4.3.1 BEHAVIORAL INTERACTIONS

4.3.1.1 Second vs. Third Order Allies

Before noting *how* third order allies use interactions to mediate their social relationships, it is useful to first note that they *do* interact with one another, though at a reduced rate when compared to second-order allies. Figure 4.3A shows the interaction rates for second- and third- order male dyads engaged in any type of interaction (AnyIxn), where males were either actor or recipient in any of the behavioral categories sampled. Figure 4.3B shows the interaction rates for second- and third- order male dyads engaged in any type of coordinated interaction (AnyCoord), where both males were actors in the behavioral categories display, formation, agonism, or synchrony. Second-order allies interacted at a higher rate than third-order allies for both AnyIxn (Welch two-sample $t(27.9) = 2.60$, $p < .001$), and AnyCoord (Welch two-sample $t(26.6) = 4.28$, $p < .001$).

In particular, I found that second-order allies engaged in significantly higher rates of display (Welch two-sample $t(18.0) = 1.92$, $p < .05$) and abreast (ABR) formations (Welch two-sample $t(23.5) = 3.56$, $p < .001$) than third-order allies (Figure 4.4). Second-order allies also engaged in significantly higher rates of CoordTog (Welch two-sample $t(24.7) = 2.77$, $p < .01$) and CoordAround (Welch two-sample $t(24.9) = 2.04$, $p < .05$), with both second- and third-order allies engaging less frequently in CoordAround than CoordTog (Figure 4.4).

4.3.1.2 At vs. Post Fusion (H5)

The primary hypothesis I stated at the beginning of this chapter is that third-order allies engage in higher rates of social coordination at fusion events compared to 5-10 minutes post-fusion. In fact the two general indicator AnyCoord (but not AnyIxn), indicates the opposite relationship, but does not show a significant difference between contexts (Figure 4.6). However, a closer look at the behavioral categories shows that certain kinds of behavior occurred at a higher rate at fusion, while other kinds of behavior occurred at a higher rate

post-fusion. In particular, third-order allies engaged in significantly more contact behavior (Welch two-sample $t(11.35) = 2.19, p < .05$; Figure 4.7 A) and coordinated agonism towards another male (Welch two-sample $t(9) = 1.93, p < .05$; Figure 4.7 F) at fusion. Post-fusion, third-order allies tended to engage in higher rates of classic formation and abreast (ABR) formation (Fig 4.7 D,E). A moving window average (window size = 60s) over the fusion data shows a declining trend in rates of contact among third-order allies (Fig 4.9). Interestingly, the same analysis does not show an obvious trend for second order allies (Fig 4.10). Out-male-approaching behavior (OMA) tended to occur at higher rates post-fusion than at fusion (Fig 4.14). Interactions between first-order males and the female they were consorting occurred at significantly higher rates post-fusion than at fusion (Welch two-sample $t(11.9) = -1.78, p < .05$).

I also tested the hypothesis that second-order allies engage in higher rates of social coordination at vs. post fusion. Rates of AnyIxn and AnyCoord among second-order allies were similar across contexts, with no significant differences. However, second-order allies did show slightly increased rates of AnyCoord at fusion (Figure 4.11). Again, the behavioral categories showed a more complicated pattern: second-order allies engaged in significantly higher rates of displays (Welch two-sample $t(9) = 2.93, p < .01$), and male-male agonism amongst themselves (Welch two-sample $t(9) = 2.2, p < .05$) at fusion (Fig 4.12 C,G). Second-order allies also tended to engage in higher rates of coordinated agonism towards other males during fusions, as well as higher rates of contact, and formation post-fusion (Fig 4.12 A,D,E).

4.3.2 DESCRIPTIVE ANALYSIS: AT VS. POST FUSION SCC

This section takes a closer look at contact and synchrony among third order allies. Rather than relying on rates of interaction (as above), this analyses focuses on independent events. Events among the same individuals were considered independent if they were separated by at least five-minutes Events with differing group compositions were also considered independent. An event in which members joined or ceased interacting were not

considered independent if two or more members of the interacting group remained the same.

4.3.2.1 Affiliative Contact

A total of 22 independent contact events occurred among third-order allies over the range of time sampled during and post fusions. 19 events occurred within five minutes of a group fusion, and 3 events occurred at least five-minutes post fusion.⁵ All events described located during this restrictive search were dyadic. Dyads from all three possible third-order associations (KS-PD, KS-RR, and PD-RR) were observed engaging in contact behavior. Dyad composition was unique in all 22 event (22 different dyads engaged in the 22 events), and the events occurred on 8 different days between Sept-Dec 2013 and 2014. 19 events were body to body "rubs", including 3 ventral rubs. Two events were pectoral fin to body "pets", and one event was a (rarely observed) mount. 17 of the 22 events were directed from an actor to a recipient, while only 5 were 'mutual'. The ratio of directed to mutual events was similar to that reported among 2nd order males (16 directed, 9 mutual; Ch 3).

4.3.2.2 Synchrony

20 independent synchrony events were scored at and post fusions. Only 5 of those events were among third-order allies. Events occurred on 4 days between Sept-Dec 2013 and 2014. The 5 events occurred among 5 different sets of individuals, including four male-male pairs, and one all male trio (FRE RID PON). Members of all three possible third-order alliances (KS-PD, KS-RR, and PD-RR) were represented in the synchronous groups. 4 events occurred at fusion and 1 event occurred post-fusion.

The remaining 15 independent synchrony events occurred among pairs of first-order allies, and in two cases (on two different days) included two males and the female being consorted (PAS QUA NIR). Males from all three second-order alliances participated in these synchronous events, and 10 different sets of individuals were observed.

⁵Note, this is a subset of the total data used for the interaction rates analysis above

4.3.2.3 Displays

13 independent displays were recorded during the fusion analysis, with all events occurring at- fusion. 9 of the 13 events involved a coordinated second-order male pair. 5 of those events were coordinated displays around a third-order male recipient. For example on 23-Oct-14: BIG FRE coordinated side-press to PAS, ending in a double roll out (CDC, BIG FRE to PAS). 1 event involved a coordinated second-order male pair (URC SMO, RR alliance) around the consorted female of the other 2nd order group (an "XCO" event). In this event, URC SMO were stacked vertically and coordinated such that URC stayed almost entirely underneath SMO as they approached and contact PIC. The remaining 3 second-order displays did not include an obvious recipient (e.g. 10-Sept-14: SMO COO surfaced in parallel and split in opposing directions; ended up both distance-zero to others but display is not obviously around anyone). 3 events occurred among third-order dyads (e.g. 28-Nov-13: URC PON converge in coordinated cross-parallel orientation. URC tilts away from PON, turning belly-up as they pass each other). The last event occurred between a male and the female his group was consorting (28-Nov-13, ZIP and IMP approach from a distance and do a cross-parallel turn-out).

4.3.3 WHISTLE PRODUCTION AT VS. POST FUSION (H6)

Higher rates of whistles, as described by both whistle rate (WR) and whistle activity index (WI), were observed at fusion compared to post-fusion (WR: Welch two-sample $t(9.10) = 1.98$, $p < .05$, WI: Welch two-sample $t(9.11) = 2.12$, $p < .05$) (Fig 4.15).

At fusion whistles included both repeated and overlapping types, with repeated whistles occurring in 8 of the 10 samples. Burst pulse calls occurred in 5 of the 10 at-fusion samples, and pops were observed in 4 of 10 at-fusion samples. In comparison, only 1 of 5 post-fusion samples included repeated whistles, 2 included burst-pulse, and 1 sample (the same that had repeated whistles) also included pops. In a detailed analysis of a maturing first-order male trio over four years, Smolker and Pepper (1999) found that as the males increased their time together and consortship behavior, they converged on a set of closely

related whistles, and suggested the possibility that alliances converge on a set of 'alliance specific' calls. In the analysis of fusion events in this study I came across an interesting set of repeated whistles that may further relate to alliance specific calls. This call (Figure 4.16) starts with three overlapping flat whistles before diverging into 2-4 distinct vocalizations in series. Like previously described signature whistles, this series was repeated within a short (493 ms) interval. This call was emitted 31s after the fusion of a male trio from the PD alliance with female consort and a male trio from the KS alliance with female consort. This limited observation suggests the possibility that an alliance can use a converged call to identify themselves as an alliance, while potentially retaining individual information, in a way similar to the use of signature whistles. I leave this here as a note to future investigators, and, as far as I can tell, the first report of this particular usage of calls.

4.3.4 THE PROCESS OF FUSION

A full descriptive analysis can be found in Table 1. The event begins when three males from the KS alliance (PAS PON QUA), along with their consorted female (PIC) and her calf (PPR) fuse with three males from the RR alliance (SMO COO URC), along with their consorted female (NIR). The groups fuse along a head-to-head trajectory, with individuals from both alliance engaging in an side-by-side abreast formation (ABR). One male (COO) precedes the rest of the RR group, positioned first mid-way between then groups, then joining singly before the rest of his group joined. This behavior, tentatively labelled "ambassador" was observed in two additional fusion events of the 10 scored "at fusion". COO changed from a head-to-head trajectory to finally fuse with the group along the outside, closest to the consorted female of the KS males (PIC) and her calf (PPR). The pattern of the "out-male" approaching or interacting with the consorted female of another group was described earlier in this chapter (OMA); I found that OMA occurred at higher rates post-fusion than at-fusion. COO continued his approach diving under at distance-0 to PPR. This was not an overtly agonistic or affiliative kind of contact, but rather suggests the possible use of calves as "buffers" or "passports" to decrease the probability of agonism

among males (e.g. Itani, 1959; Hrdy, 1976; Silk and Samuels, 1984). COO continues around the rear of the group, a possible submissive act (R. Connor, pers com), and initiates a rub alongside QUA, before re-approaching PIC and PPR. COO "gooses" PPR, orienting his rostrum towards the calf's peduncle / genital region, and moves again towards the outside of the group nearest PIC and PPR. When PPR dives COO is closest to PIC but appears to be displaced by PON who moves between COO and PIC, briefly, until PON is displaced by COO moving between PON and PIC.⁶ When SMO and URC join, they approach the opposite side of the group, moving together between QUA and PIC and then in unison behind the group. The males form pairs of third-order allies, engaging in contact behaviors rubbing sides, ventrally, and fluke-to-body. Two KS males, PON and PAS approach URC, and NIR rubs under URC⁷.

Five-minutes post-fusion, the groups have settled into a mostly abreast orientation relative to one-another, but there are still third-order interactions. PAS and PON are positioned between the PIC PPR pair and the rest of the KS-RR group. PPR stays in infant-position except to come up to baby-position for a breath. QUA (KS) is actively engaged with RR. He moves above the group as they dive, and when they come up SMO and COO do a spatially and temporally coordinated side-press which starts out around QUA and URC, but as the display continues URC remains at the center and QUA falls behind. Similar to the event described in the "at-fusion" bout, NIR again moves towards URC to rub underneath. QUA then initiates a rub to URC, which turns into mutual pec-to-pec petting between the pair. As the groups begin to separate, QUA remains with the RR a bit longer before rubbing under URC as he returns to his group. The RR dive and when they surface again the two groups are greater than 10 meters apart and have "fizzed".

⁶Such displacements may represent a kind of 'low-level agonism' among male allies that could act as mechanism for establishing relationships, possibly even dominance, without jeopardizing the critical relationship as second or third-order allies

⁷In the post-fusion bout documented, URC continues to receive a lot of attention. Why?

4.4 DISCUSSION

This study found differences in the type and rate of interaction among second- and third-order allies, as well between third-order allies as at- and post- fusion. Across both pre- and post- fusion sampling periods, second-order allies were found to engage in SCC at higher rates than third-order allies (Figure 4.3). In particular, second-order allies were found to engage in higher rates of synchrony, displays, formations, as well as in the aggregate categories of coordinated activity without a recipient, coordinated activity organized around a male or female recipient, and coordinated activity organized around another male, than third-order allies (Figures 4.4,4.5). Third-order allies tended to engage in more agonistic behavior where one was the recipient, than second-order allies.

I found differences in the type and rate of interactions produced among third-order allies at-fusion compared to post-fusion. At fusion, third-order allies engaged in significantly higher rates of contact and coordinated activity around another male recipient compared to post-fusion. Post-fusion, third-order allies engaged in higher rates of formation, as well as in the aggregate category of coordinated activity without a recipient.

Interactions between second-order allies also differed at- compared to post- fusion, but in different ways than the activities among third-order allies. At fusion, second-order allies engaged in significantly higher rates of displays, but engaged in similar rates of contact, formation, and synchrony as post-fusion. Second-order allies also tended to engage in higher rates of coordinated activity with a male recipient, as well as male-male agonism amongst themselves at fusion. The latter finding is interesting as it shows an occasional lack of unity within the second-order alliance during fusions.

The focal groups engaged in significantly higher rates of whistles at fusions compared to post-fusion. This finding is similar to that of Quick and Janik (2012), although the time period sampled in this study is at-fusion, whereas Quick and Janik studied the period leading up to fusion events. Quick and Janik suggested that increased whistles during fusions may be likely to contain information about the identity, size, and/or demographic of the individuals joining, and possibly the affiliative or aggressive nature of the encounter. The

presence of repeated, stereotyped whistles suggests the use of signature whistles at fusions. These whistles may include individual and alliance specific whistles (Smolker and Pepper, 1999). The whistle sequence I described suggests a possible alliance-specific whistle that may also contain individual information. Pops and burst-pulse calls were also observed more frequently at fusion than post-fusion, though these calls were not quantified. If their function is maintained in this context, pops at fusion indicate a closely maintained interaction with female consorts at the same time that third-order allies are engaged in other kinds of social mediation.

The observed differences in the range of behaviors examined suggest a differentiation between (a) social context and (b) type of ally. The instance of a fusion between two second-order groups simultaneously involved two kinds of social contexts: a consortship maintained by second-order allies, and a union between two social units. This overlap an example of contextual embeddedness (Johnson, 2010), and relates to the social complexity described in Ch 2. Third-order allies can act cooperatively one day and compete the next. The volatile nature of third-order alliances suggests that a fusion event is a moment of high uncertainty, and that allies may act to resolve such uncertainty by establishing the state of the relationship. At fusion, I found that third-order allies participated in increased rates of affiliative contact and coordinated behavior around male recipients. As in primates, affiliative contact may serve to reduce tension between two individuals. The act of petting requires physical coordination in space and time as individuals align their bodies in positions to give and receive affiliative contact (e.g. pectoral fin petting, body-body rubbing). Such positioning puts individuals in a position of physical vulnerability, but this is quickly resolved through the act of affiliative contact, likely triggering the pleasure and reward system of each individual, and initiating a positive feedback loop that may sustain an affiliative state of interaction unless it is otherwise perturbed. The production of affiliative contact is an informational act. It involves some degree of risk by both participants, but is highly information of the nature of the interaction. Such acts are similar, to a degree, to the sexual greetings described among male baboons, and other such 'stressful' behaviors thought to test the quality of a

bond. Among humans, we find such behaviors as hand-shakes and hugs that may play a similar role.

At fusion, I also found evidence for increased rates of social coordination produced by third-order allies around another (second- or third- order) male. I am fascinated by this finding, as it suggests not only that males do engage in allochthonous activity during periods of uncertainty, but that they do so in a way that goes beyond what was expected (e.g. by orienting around another male, rather than or in addition to the females present) and that reduces uncertainty over the possibility of a competitive encounter (e.g. theft of female consort). While I cannot discount the possibility of an immediate proximate function of two third-order allies coordinating their behavior around another male, I also cannot ignore the similarity between this behavior and that which is required of males during competitions. At fusion, third-order allies enact their relationship by engaging in allochthonous activity.

Post fusion, I found that third-order allies participated in higher rates of synchrony and formations. These behaviors are both instances of social coordination, and are also considered allochthonous activities. However, they differ from the behaviors seen more frequently at-fusion in important ways: (a) They do not require contact. These behaviors were produced between dyads at a distance greater than $1/3$ body-length and less than 5 body-lengths apart, most commonly occurring between $1/3$ and 2 body-lengths distance. While still close, these behaviors were produced at a distance that affords a lower risk of bodily aggression. (b) They are likely to require less energy than contact or coordinated activity around another male. While still requiring energy expenditure to maintain spatial and temporal cohesion, synchrony requires less deviation from a normal swimming pattern than either of the significant at-fusion behaviors, and does not require contact or organization 'around' another individual. Similarly, the specific kind of formation that was likely produced at the highest rates during this encounter was an abreast side-by-side positioning, which requires spatial but not temporal coordination. Synchrony and formations are less risky and less 'expensive' energetically, but are still instances of allochthonous activities.

This study reports on a behavior not previously described called 'out-male-approach'

(OMA). OMA occurs when a male ally outside of a consortship group approaches the consorted female of that group. I found that rates of OMA were higher post-fusion compared to at-fusion. At-fusion third-order allies organize around other males, and not around the consorted female of the opposite group; post-fusion they engage in OMA. This again suggests that at-fusion, the allies establish the nature of the encounter as friendly or competitive. Post-fusion, it may be possible to approach the female of another consortship group without challenging this relationship. The fact that this activity is not met with overt aggression by the consorting group suggests one of two things (a) the admission of OMA activity functions to re-enforce their social relationship by enacting a state in which the coordination of the larger group allows for the possibility of increased reproductive success of allies (b) low-level of competition is tolerated among allies against the risk of jeopardizing the critically important alliance relationship.

This analysis also reported on the possibility of a new role, an 'ambassador' who initiates fusion events and/or is the last to leave another group during a fission. Future analyses will focus on whether such individuals interact differently, or occupy different social roles, than others.

In this discussion I have argued that allies differentiate among social others (second, third-order allies) and between contexts (at, post fusion). I have also argued that they act to resolve uncertainty by engaging in 'informative acts' at fusion. Important questions for cognitive science are *who* differentiates, and *who* is uncertain? Rather than leap too quickly to infer the mental state of the dolphins, let's instead build from the outside-in. It has previously been established that alliances are comprised of different types of relationships: strong and weak allies (Connor and Krützen, 2015, Ch. 2), first-, second-, and third- order allies, related and un-related individuals (Krützen et al., 2003), provincial hubs and liaisons (Ch. 2). The alliance system is diverse. That allies act in accord with this diversity suggests that these relationships are not just products of analysis but are recognized within the system. The system is diverse, and individuals differentiate among social others and social contexts. Uncertainty is the emergent property of a system that shows variability. Here that variability

is the type of encounter that two groups will have when they come together. The uncertainty is demonstrated and resolved by the system through informative acts; here petting and coordinated social behavior.

4.5 ACKNOWLEDGEMENTS

Chapter 4, in part, is currently being prepared for submission for publication of the material. Friedman, W.R.; Krützen, M.; Connor, R.C. The dissertation author was the primary investigator and author of this material.

4.6 FIGURES

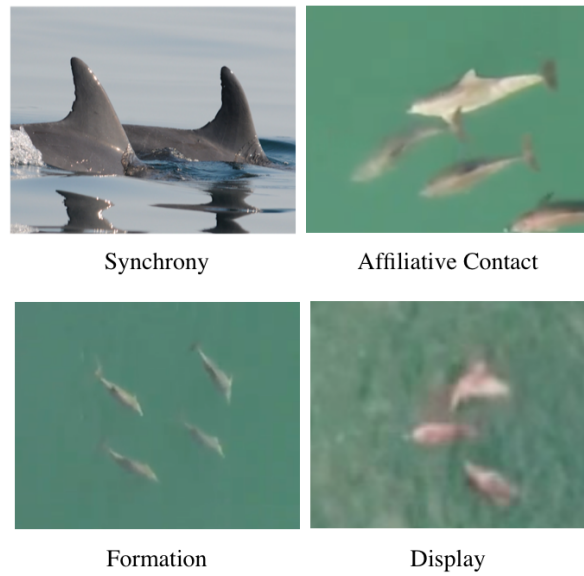


Figure 4.1: Behavioral categories of social coordination and affiliative contact used in the analysis.

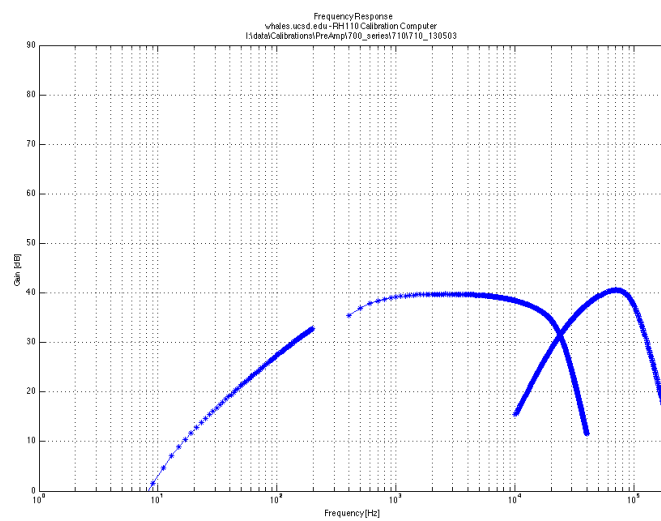


Figure 4.2: Hydrophone response curve

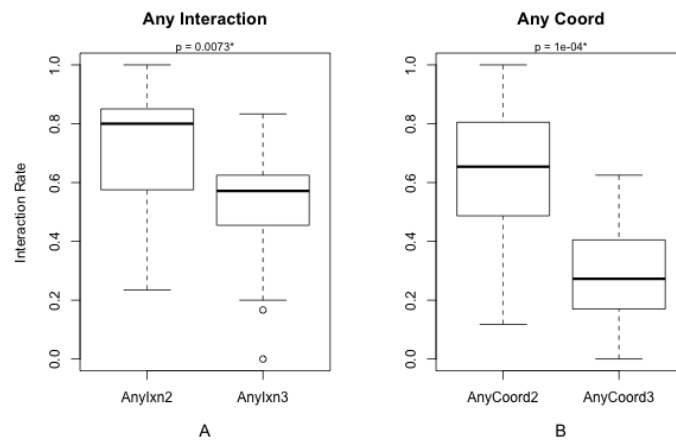


Figure 4.3: Rates of AnyIxn(A) and AnyCoord (B) recorded among second-order allies and third-order allies any time after fusion. Second-order allies engage in significantly higher rates of both categories.

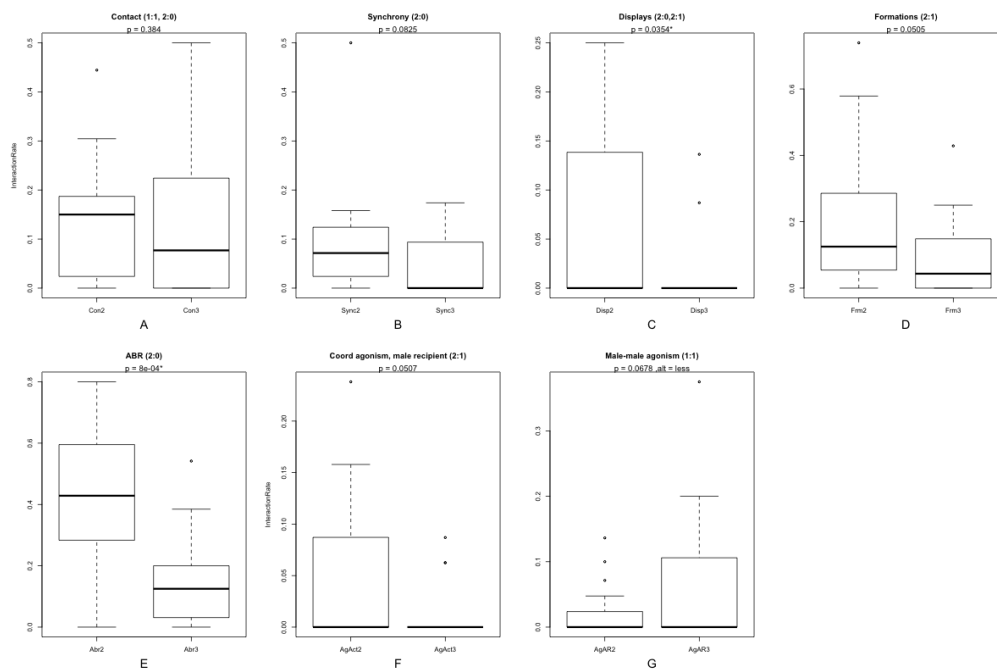


Figure 4.4: Interaction rates (A-G) recorded among second-order allies and third-order allies any time after fusion. Second order allies engage in significantly higher rates of displays and parallel swimming (ABR).

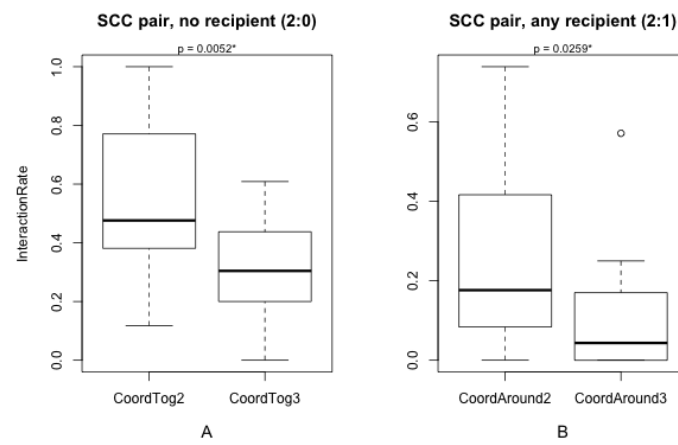


Figure 4.5: Interaction rates recorded among second-order allies and third-order allies any time after fusion. Second-order allies engage in significantly higher rates of dyadic and polyadic SCC.

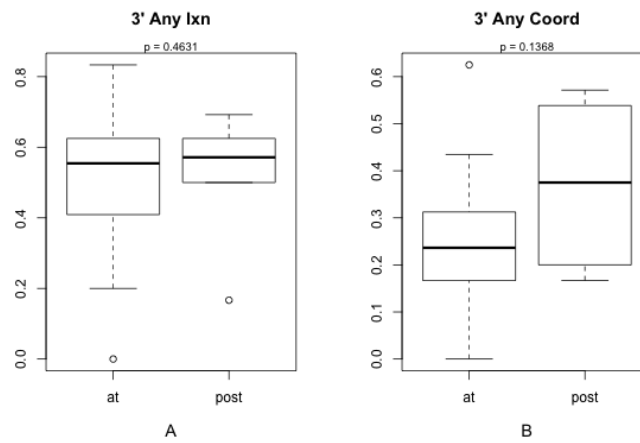


Figure 4.6: Rates of interaction between third-order allies at vs. post fusion. No significant differences were found in the summary categories. (N at-fusion = 10, N post-fusion = 5).

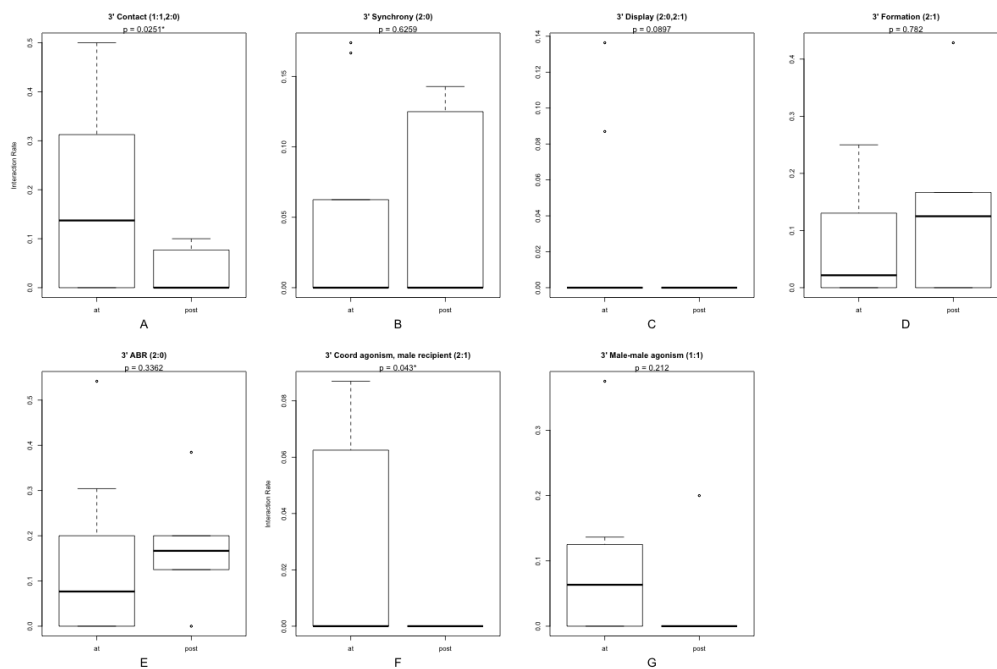


Figure 4.7: Rates of 3rd order affiliative contact, as well as coordinated agonistic interactions towards a male recipient were higher at fusion. Post fusion, third-order allies tended to engage in higher rates of formation and parallel swimming (ABR). (N at-fusion = 10, N post-fusion = 5).

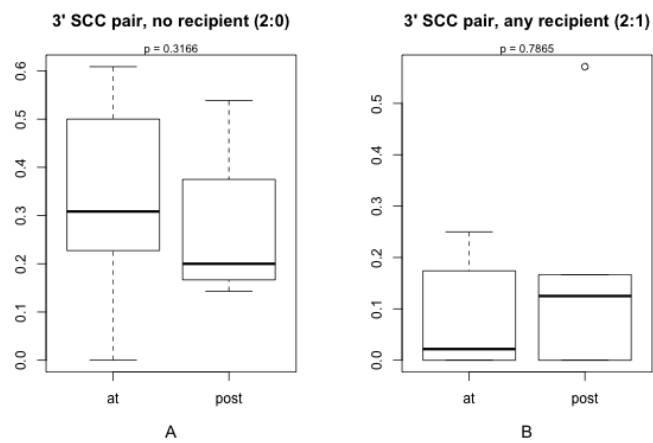


Figure 4.8: Rates of interaction between third-order allies at vs. post fusion. No significant differences were found in rates of dyadic or polyadic SCC at vs. post fusion. (N at-fusion = 10, N post-fusion = 5).

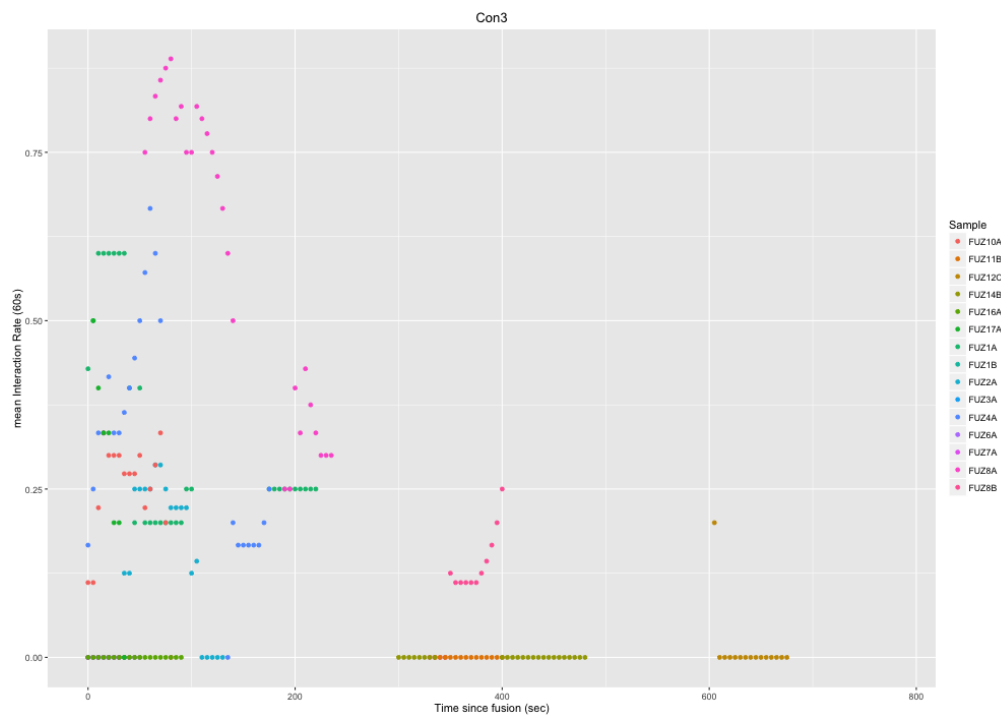


Figure 4.9: Moving window analysis of rates of affiliative contact among third-order allies during fusion events. Each color represents a different sampling period. Rates of affiliative contact decline as time from fusion increases.

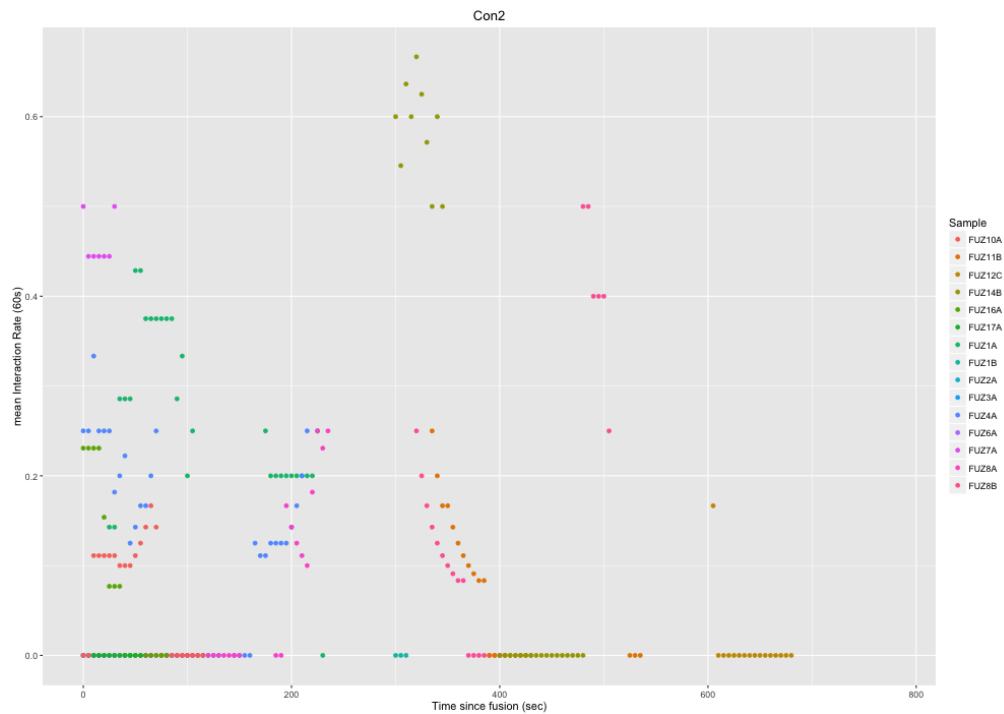


Figure 4.10: Moving window analysis of rates of affiliative contact among second-order allies during fusion events. Each color represents a different sampling period. Rates of affiliative contact remain variable throughout sampling period.

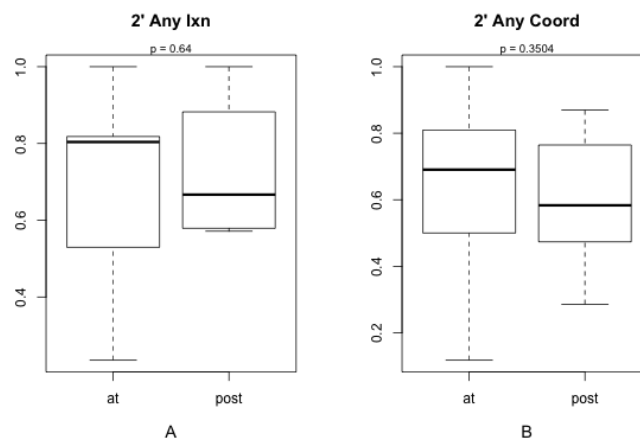


Figure 4.11: Rates of second-order interaction at and post fusion. No significant differences were found in the general categories of any interaction and any coordinated interaction.

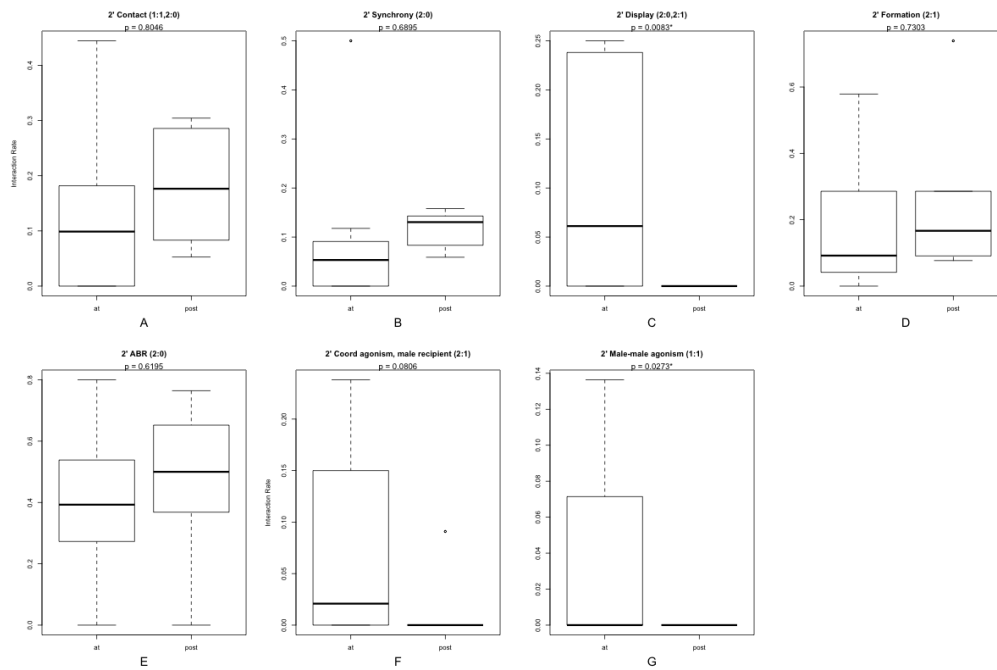


Figure 4.12: Rates of second-order interaction at and post fusion. Second-order allies engaged in significantly higher rates of displays and within-group male-male agonism at fusion. Post-fusion, second-order allies tended to engage in higher rates of affiliative contact, synchrony, and formation. (N at-fusion = 10, N post-fusion = 5).

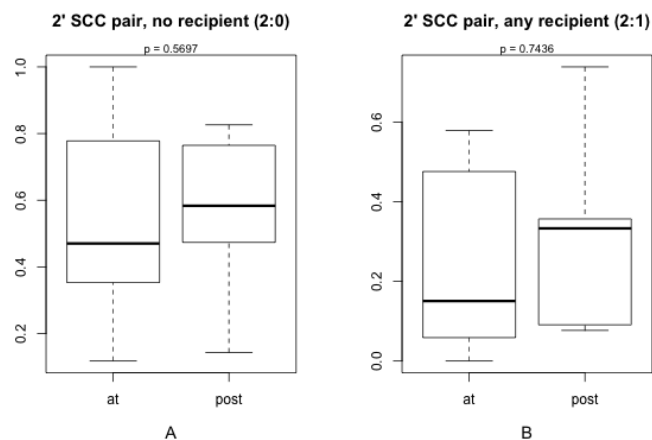


Figure 4.13: Rates of second-order interaction at and post fusion. No significant differences were found in the rates of dyadic or polyadic SCC at vs. post fusion. (N at-fusion = 10, N post-fusion = 5).

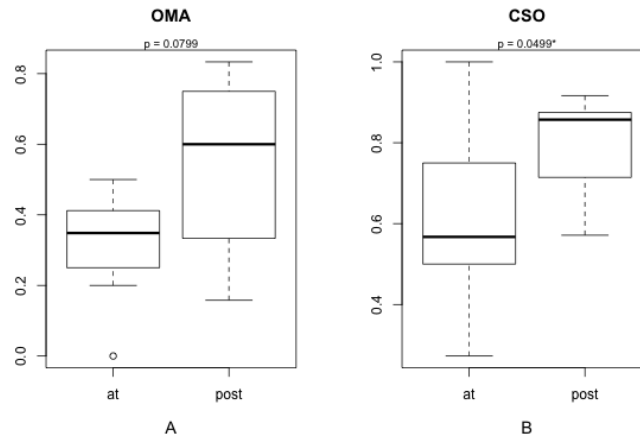


Figure 4.14: Higher rates of out-male-approach were found post fusion. Significantly higher rates of behavior towards a female consort was observed post-fusion. (N at-fusion = 10, N post-fusion = 5).

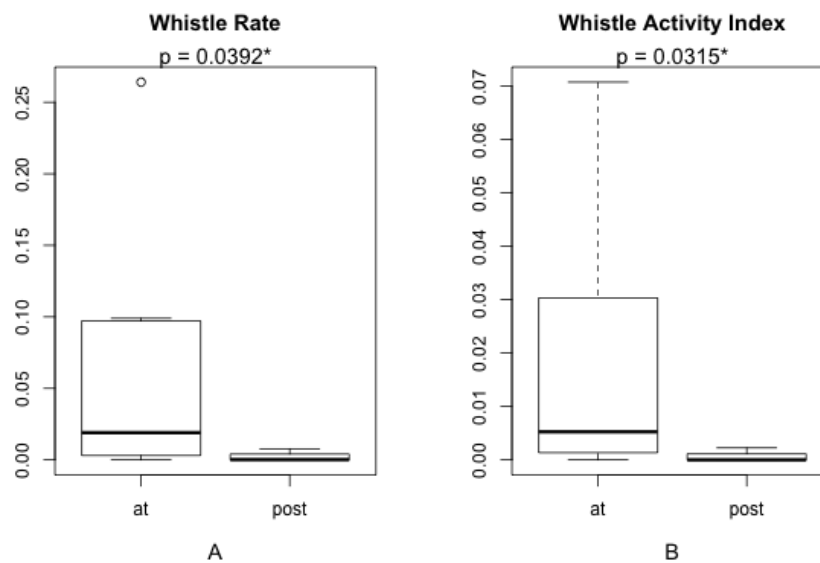


Figure 4.15: Significantly higher rates of whistle behavior, as described by both whistle rate and whistle activity index, were recorded at fusion. (N at-fusion = 10, N post-fusion = 8).

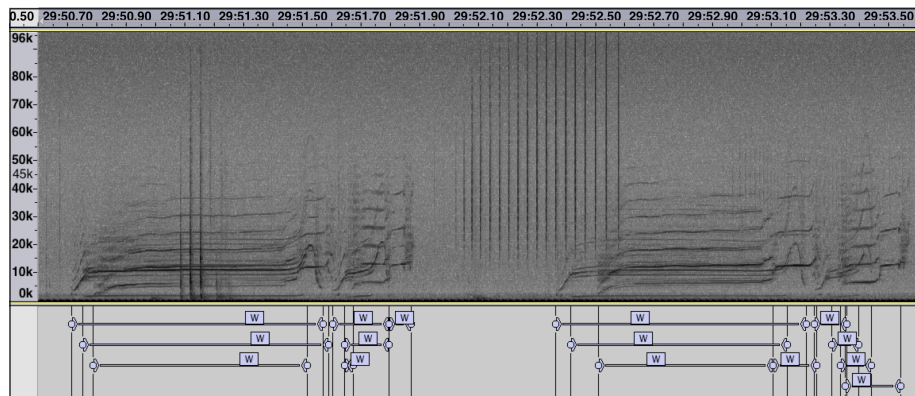


Figure 4.16: A potential alliance whistle recorded during a fusion event. A long, unmodulated call appears to have three sources which diverge at the end of the call before the pattern is repeated.

Table 4.1 Third-order fusion event. Three males from the KS alliance (PAS PON QUA), along with the female they are consorting (PIC) and her calf (PPR) fuz with three males from the RR alliance (SMO COO URC), along with the female they are consorting (NIR). 07-October-2014, 09:23:53 (recording time 0:53:59.0). Below is a description of the fusion event with five-second sampling frames supplemented when key events fall between the interval sample. Behaviors are described by their corresponding name in the ethogram (Section B, Figure 4). Italics indicate examples of behavioral patterns that are starting to emerge through observation of the aerial video and of the alliances *in situ*, and may be the subjects of future study.

At Fusion


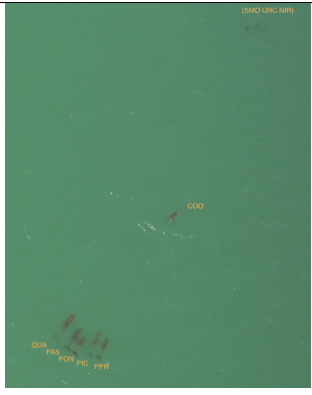

Frame	Time	Description
	53:59.0	The KS group, all abreast (ABR), move to fuse head-to-head with COO from the RR group. <i>COO fuses ahead of the rest of his group, possibly acting as an 'ambassador'</i>
	54:04.0	COO is clearly positioned between the abreast KS group and the rest of the RR group. The abreast RR group follow. PAS and PON are distance-zero.
	54:09.0	COO approaches the KS group, heading towards the consorted female of the KS group (PIC) and her calf (PPR). PAS and PON rub (no clear actor/recipient).

Table 4.1: Third-order fusion event (cont'd).




Frame	Time	Description
	54:12.1	COO joins the group diving under, distance-zero, to PPR. The KS are distance-zero and abreast. <i>Possible use of PPR as a passport by COO.</i>
	54:14.0	COO joins at the rear of the group, approaching PON then PAS distance-zero. The rest of the RR group lingers outside of 10-meters, not yet fused. <i>Approaching to the rear of the group may precede amicable encounters</i>
	54:16.4	COO approaches and rubs alongside QUA. PAS PON and COO are all distance-zero. PON approaches PIC to distance-zero.

Table 4.1: Third-order fusion event (cont'd).



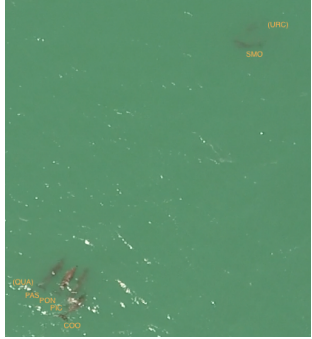
Frame	Time	Description
	54:19.0	COO continues to rub while turning away from QUA, and approaching PIC to distance-zero. PON and PIC are still distance-zero, as are PIC and PPR. The rest of the RR group are still outside of 10-meters but two are abreast behind SMO, approaching the KS group in a group formation. COO's interactions with PIC are instances of out-male-approach (OMA).
	54:24.0	COO gooses PPR, orienting his rostrum to the calf's genital region. PPR reacts moving peduncle upwards out of the water. QUA approaches to rub alongside PAS. COO's interaction with the calf again suggests the possible use of PPR as a passport.
	54:29.0	QUA and PPR dive down out of sight. PAS PON PIC are abreast. COO is staggered behind PIC. COO has returned to his original position closest to the female being consorted by his third-order allies.

Table 4.1: Third-order fusion event (cont'd).




Frame	Time	Description
	54:34.0	SMO URC, almost abreast, fuse with KS and COO (now within 10-meters). PON moves over the top of PIC, distance-zero. COO is still distance-zero alongside PIC on the outside of the group.
	54:34.5	PON turns towards COO (all other behavior remains constant from the previous frame). <i>PON has moved from his position towards COO, possibly to start to move him away from PIC</i>
	54:39.0	PON moves between PIC and COO. COO is briefly ABR (54:38.1) before beginning to move back towards PIC (54:38.9). The KS and remaining RR continue to move towards a head-to-head fuse, and are now within two body-lengths (distance-2). <i>PON displaces COO.</i>

Table 4.1: Third-order fusion event (cont'd).





Frame	Time	Description
	54:42.0	COO moves between PIC and PON. <i>COO displaces PON</i>
	54:44.0	COO and PAS dive down. The remaining RR and KS close to within one body-length (distance-1). The approach is still head-to-head, with SMO URC abreast, and QUA PIC PON abreast.
	54:46.0	The remaining RR and KS meet head-to-head, with SMO nearest to QUA and URC nearest to PIC.
	54:46.9	URC passes close by PIC in cross-parallel orientation. SMO moves over QUA towards URC and PIC. <i>URC and SMO drive a separation and converge on the open space closest to PIC. Another examples of OMA.</i>

Table 4.1: Third-order fusion event (cont'd).





Frame	Time	Description
	54:49.0	URC and SMO (stacked vertically with SMO above URC) pass through the KS to the rear of the group, distance-0 with PIC. URC and SMO are temporally and spatially coordinated in a <i>CDC</i> display around PIC.
	54:54.0	COO emerges again distance-1 and abreast with PIC. PON crosses over COO distance-0 towards the outside of the group. <i>OMA</i> .
	54:59.0	NOG emerges, rubbing under COO as he approaches PIC. PPR is in infant-position below PIC. PON remains on the outside of the group. <i>OMA</i> .
	55:04.0	SMO initiates a ventral-ventral rub (VRB) with QUA, and both males are distance-0 to COO. URC and PON are distance-0. PPR is in infant-position below PIC. <i>The third-order allies have paired off and are engaging in contact behavior, which may seem affiliative. However, notice that in both dyads, the RR male is closer to PIC than the KS males who have been consorting her.</i>

Table 4.1: Third-order fusion event (cont'd).







Frame	Time	Description
	55:09.0	SMO rubs alongside QUA, while QUA approaches and rubs PON. PON and URC are abreast with URC now on the outside of the group. COO is approaching PIC. <i>OMA</i> .
	55:14.0	PON and PAS orient rostrum-towards to contact URC. PIC and COO are abreast. SMO QUA and NIR are staggered, with NIR abreast to URC.
	55:19.0	NIR and URC rub. URC rubs PON with his flukes as PON moves alongside. SMO rubs QUA with his flukes as QUA moves alongside. <i>Third-order contact behavior</i>
	55:24.0	NIR rubs under URC. PON and URC are still distance-0. SMO and QUA are abreast. <i>Third-order contact and formation.</i>

Table 4.1: Third-order fusion event (cont'd).

Frame	Time	Description
	55:29.0	URC and NIR remain at the surface, almost abreast and almost in contact.
	55:34.0	URC and NIR dive down distance-zero, asynchronously.

5-minutes Post-Fusion


Frame	Time	Description
	59:24.0	PPR is in infant-position under PIC. PAS and PON are the closest males to PIC and are distance-0. Others are emerging.

Table 4.1: Third-order fusion event (cont'd).




Frame	Time	Description
	59:29.0	The group has become mostly parallel and abreast. PPR is in infant-position under PIC. PAS and PON are abreast. QUA and URC are abreast. SMO reaches out with his flukes to rub URC. COO and NIR are abreast.
	59:34.0	PAS QUA NIR are abreast. PPR is in baby-position next to PIC
	59:39.0	PAS PON QUA are abreast. PPR is in infant-position below PIC Others are below QUA with some white flashes indicating ventral turns but individuals can't be distinguished or scored.

Table 4.1: Third-order fusion event (cont'd).





Frame	Time	Description
	59:44.0	PIC and NIR are on the outer edges of the group. PPR is in infant-position below PIC. PAS and PON are abreast. SMO and COO do a spatially and temporally coordinated side-press which starts out around QUA and URC.
	59:46.7	SMO and COO continue the coordinated side-press display now just around URC.
	59:49.0	SMO and COO finish the coordinated side-press display around URC. QUA and NIR are abreast in formation (FRM) behind URC. QUA and URC are distance-0. PAS and PON are abreast. PIC and NIR are still on the outside of the group, with PPR in infant-position below PIC.
	59:54.0	PIC is still on the outside of the group with PAS PON closest and abreast. NIR does a ventral-rub (VRB) to URC.

Table 4.1: Third-order fusion event (cont'd).







Frame	Time	Description
	59:59.0	NIR continues to rub under URC. QUA and URC are abreast.
	1:00:04.0	QUA rubs URC. <i>Lots of attention is being paid to URC in this bout. Why?</i>
	1:00:09.0	QUA and URC engage in mutual pec-to-pec petting.
	1:00:14.0	PIC PPR PAS PON surface again, abreast, with PAS PON between PIC and the rest of the group. PIC and NIR are on the outer edges of the group again, with PPR in baby-position next to PIC. QUA rubs under URC. Groups are starting to separate, but QUA continues to interact with the RR group. <i>QUA remains interacting affiliatively with the RR while PAS PON maintain a position separating PIC from the RR. Simultaneously offensive and affiliative roles within the same group. QUA's position is similar to that of COO's in the beginning, marking QUA as a potential 'ambassador'</i>

Table 4.1: Third-order fusion event (cont'd).

Frame	Time	Description
	1:00:19.0	PIC PAS PON are abreast with PIC on the outer edge of the group, and all three trailing behind the RR group. QUA rubs under URC before turning away to return to his group.
	1:00:24.0	PIC PAS PON are abreast trailing the RR. PPR is in infant-position beneath PIC. QUA is returning to his group, and the RR are diving. The KS and RR continue to separate. After this, SMO dives and the next time the RR group surfaces they have fizzed / are greater than 10-meters from KS.

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CHAPTER 5

SOCIAL AND COGNITIVE COMPLEXITY: TRAVERSING THE LADDER

5.1 INTRODUCTION

The Social Intelligence Hypothesis (SIH) proposes that higher intelligence is linked in evolutionary ratchet with increasingly complex societies (Jolly, 1966; Humphrey, 1976; Chance, 1961; Kummer, 1978). The bottlenose dolphins in Shark Bay, WA, form one of the most complex societies known outside of humans (Connor, 2007): the levels of alliance formation among male-allies surpass in complexity that of any known primate or other mammalian society. The study of this system provides the opportunity to inform the SIH model by providing an additional point along the scale of complex societies between non-human primates and ourselves. In R.A. Hinde's classic scheme, a population's social structure is described by its pattern of social relationships, which, in turn, are comprised of a history of interactions among individuals (Hinde, 1976). In this dissertation I traverse Hinde's levels to examine the relationship between social complexity through quantitative analysis of a third-order alliance network, and social cognition through fine-scale observations of behavioral interactions among allies. The two general questions that I aimed to address in this dissertation were: (1) how are third-order alliances structured, what are their dynamics, and how do they respond to change? (2) How do the particular kinds of behavioral interactions that allies engage in relate to the observed structure and dynamics of the alliance network?

The structure of the networks described in Chapter 2 are determined by the patterning of association among male allies: each link between nodes represents the existence and strength of the HWI between each pair of individuals. What I proposed in this dissertation is that the linkages and types of relationships observed are built and reinforced not only

through the simple act of association, but by the nature and frequency of interaction. We can imagine this as the character (perhaps squigglyness, loopy-ness) of the link, or even as an overlay of each dyadic interaction profile as the character of the link. In this dissertation, I was interested not only in the content of social interactions, but in whether and how the social interactions observed among individuals related to the social structure described in Chapter 2. Chapters 3 and 4 explore these relationships. In Chapter 3, I focused on the frequency and nature of interactions produced by first-order allies in the context of a consortship. The goal of Chapter 3 was to generate 'baseline' data on the range and frequency of interactions among male allies during a context primary to the nature of their relationship and frequently observed during the study period. In Chapter 4, I examined the interactions among third order allies during and after group fusions. To maintain consistency with the analysis in Chapter 3, I specifically studied third order fusions that occurred between two first-order consortship groups from different second order alliances. Later in this chapter I present results from a comparison of rates of interaction across both contexts examined. This chapter summarizes the findings of this dissertation, and through these findings examines the claim that social and cognitive complexity are explicitly linked, and that link is brought to bear by what allies do when they interact, as well as when, with whom, and how such interactions occur.

5.2 SUMMARY OF FINDINGS

5.2.1 THE STRUCTURE OF THE ALLIANCE NETWORK (CH. 2)

The third order alliance network examined in this study showed features of social complexity in its global structure, dynamic change, and social differentiation. A system shows structural complexity if it demonstrates both local segregation and global integration (Tononi et al., 1994). Figure 5.1 shows the patterns of association among the KS, PD, and RR second-order alliances over a six-year period. The nested, hierarchical organization of allies into three orders of association demonstrate both local segregation and global integration. The orders of alliance relationships are both functional and structural. As

previously described, first-order allies work together to consort individual females during the mating season, and tend to share the highest association values (Connor et al., 1992; Connor and Krützen, 2015). Both second- and third- order allies work together to steal or defend females during competitions with other alliances (Connor et al., 1992; Connor, 2010; Connor and Krützen, 2015), however second-order allies associate more frequently than third order allies, and instances of consortships comprised of third-order allies is exceedingly rare (Connor, 2010; Connor and Krützen, 2015, this study). Local segregation is demonstrated by the organization of the population into the structural and functional units of first, second, and third order alliances. Global integration is demonstrated by the coordination of sub-units into larger functional units, as is seen when second and third order alliances coordinate spatially during a competition.

Dynamic change was demonstrated in the shifts in the alliance network coincident with the loss of individuals, and an extreme warming event implicated in the ecosystem-wide shifts documented in Shark Bay. Each of the three two-year networks showed structural differences, with the largest shift occurring between T2 and T3. In T3, we documented the formation of a new third-order relationship between the RR males and each of the KS and PD alliances. Additionally, the changes in the relationships between KS and PD males showed that rather than fractionating, the overall organization of the network showed re-organization in response to the observed disturbance.

Figure 5.1 also shows differences between individuals in terms of their inter-group associations (“bStrength”). In each of the three second-order alliances, there was one trio who participated in higher rates of third-order association. These individuals (“liaisons”) are constituting a critical social role in the structure of the alliance network, by acting to bind areas of the network that would be otherwise weakly connected. Other individuals (“provincial hubs”, re: Bullmore and Sporns (2009)) engaged in higher rates of intra-group association, constituting a role as a cohesive agent within their second-order alliance.

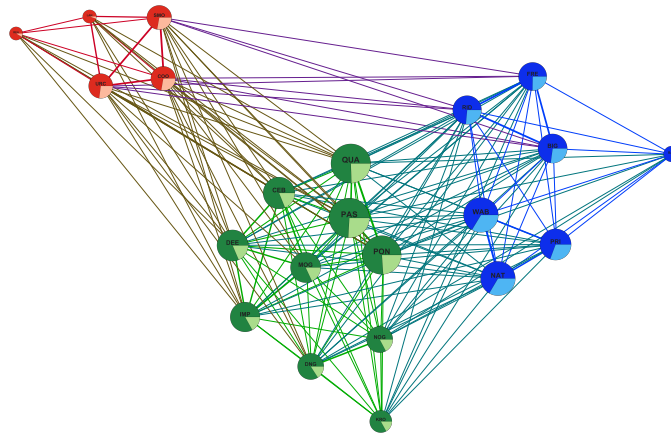


Figure 5.1: KPR Network 2009-2014. Nodes are sized based on each individuals intra-group strength (bStrengthR) value. Pie charts depict the ratio between absolute wStrength (dark color) and bStrength (light color). Each alliance has one trio with higher overall and relative bStrengthR values

5.2.2 INTERACTIONS THAT MEDIATE ALLIANCE RELATIONSHIPS (CH. 3, CH. 4)

In Chapter 3, I described rates of social coordination and affiliative contact that male allies engaged in during the consortship context, and related those findings to metrics of social relationships. I hypothesized that social coordination and affiliative contact behaviors are used by allies to enact or mediate their social relationships. The context of consortship means that the observed interactions may relate both to maintaining the alliance and maintaining the consortship, though these relationships are themselves intertwined.

Figure 5.2 shows the overall rates of interactions observed during the consortship context, with each bar representing the number of point samples in which at least one male dyad was engaged in a particular SCC interaction, divided by the number of point samples in which it was possible to observe that kind of interaction. Though generally non-overlapping, event types were not mutually exclusive, and are analyzed independently of one another. The most common type of interactions observed during the consortship context were formations. Two types of formations were distinguished, those that included 2-3 males side-by-side following behind (FRM) or converging on (COF) a consorted female, and those that simply included at least two males swimming in a parallel orientation (ABR, LL). Fewer intervals

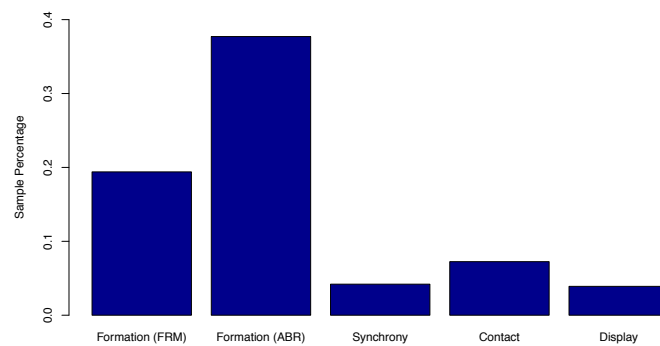


Figure 5.2: Percentage of point samples including at least one male-male dyad engaged in a particular interaction type, divided by the number of intervals in which it was possible to observe that interaction type.

included synchrony, contact, or displays among male allies, though these interactions tend to be shorter in time.

Dyadic interaction profiles indicated different 'fingerprints' of interaction rates for each pair of allied males observed (Figure 5.9). This suggests that social differentiation exists within the alliance system: different relationships were enacted through different suites of interaction.

Do the observed rates of social interaction relate to the observed patterning of the social structure? In Chapter 3, I used two metrics of social relationships to address this question: general non-foraging association (HWI) and consortship association (cHWI). The strongest relationships observed were between synchrony and general association ($r = 0.70$), and between contact and consortship association ($r = 0.43$). Individuals who associated across contexts engaged in higher rates of synchrony, while individuals who frequently engaged in consortships in particular engaged in higher rates of contact. These relationships were significant when tested by Mantel Permutation, however GAMM models controlling for the effect of dyad and sample were not significant.¹ In Chapter 3, I also described the relationship between the directionality of male-male contact events and consortship rate

¹Due to limited, and sometimes small samples, the mantel permutation computed using pairwise averages of interaction across sample periods was considered a more appropriate test of the data than the GAMM

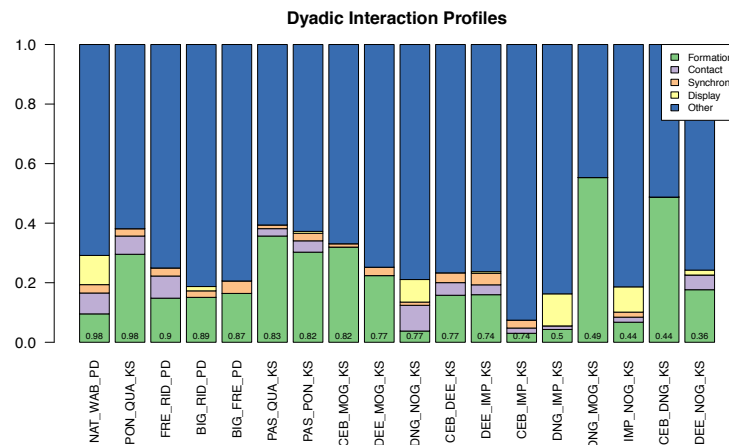


Figure 5.3: Dyadic interaction profiles. The relative proportion of behavioral interaction rates observed by dyad, $IR(\beta_x, AB) / \text{sum of all } IR(\beta_x: \beta_y, AB)$. Informs the question “when they interact, what does each dyad do?”. Bars are ordered by HWI, with most frequent associates are on the left. HWI values are at the base of each bar.

(CSR). 16 independent directed contact events occurred between two first-order male allies. 12 of the 16 events were initiated by a male with a lower consortship rate (CSR) towards a male with a higher consortship rate. Despite the small sample size, this suggests that, as with grooming among primates (Seyfarth, 1977), contact may be directed *up* a social hierarchy, to the degree that individual consortship rate captures social hierarchy.

Chapter 4 focused on fusion events between two first-order consortship groups from different second-order alliances, e.g. third order fusion events. Fusion events between third-order allies represent a period of potential *uncertainty*: relationships within groups may have changed in the period between encounters, and the capricious nature of third-order alliances means that the union could be affiliative or competitive. If males use SCC to enact or mediate their social relationships, they should show increased engagement in these behaviors at the time of fusion relative to other periods during their association. To test this hypothesis, I compared the interaction rates among third-order allies during two contexts: at-fusion and five-plus minutes post-fusion. I found that at fusions, third-order allies engaged in significantly higher rates of affiliative contact behavior than post-fusion (Figure 5.4a). A moving window analysis showed that the rate of contact between third-order allies declined

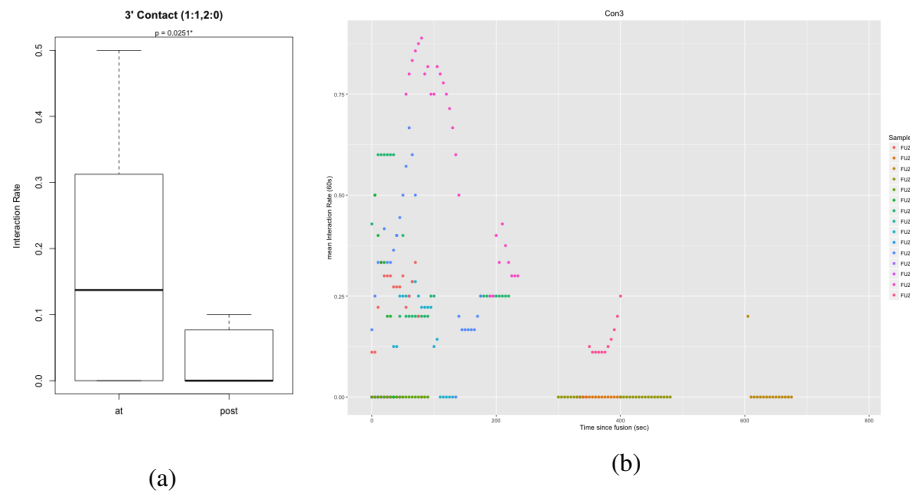


Figure 5.4: Rates of contact among third-order allies are higher at fusion compared to post-fusion.

as time from fusion increased (Figure 5.4b). Coordinated agonism, in which two third-order allies coordinated their behavior around another male recipient, was only observed at fusion. I reported a new behavior, “out-male-approach” (OMA), in which a male interacts with the consorted-female of his third-order associates. Rates of OMA were higher post-fusion. If the period at fusion is a critical period for enacting / re-establishing relationships, it follows that OMA may only be tolerated once a non-agonistic period of association has been established. Post-fusion, males also engaged in significantly higher rates of interaction with the females they were in consortship with (Chapter 4, Figure 13).

Acoustic data were analyzed over the same periods (at and post-fusion), and revealed that groups showed significantly higher rates of whistling at fusion. This finding is similar to that found by a previous study that showed increased rates of whistle behavior among bottlenose dolphins in St. Andrews Bay, Scotland just prior to group fusions. Vocalizations included stereotyped, repeated whistles, suggesting the use of signature whistles (Caldwell and Caldwell, 1965; Janik and Slater, 1998; Harley, 2008) carrying identifying information at fusions. I described a series of overlapping whistles that diverged towards the end of the call, and suggested that this may be an alliance specific whistle, perhaps propagating the identifying information “we’re us” in the synchronous phase, and “I’m me” in the

asynchronous phase (Chapter 4, Figure 15). This contributes to the previous finding of Smolker and Pepper (1999) of whistle convergence among three males as they formed an alliance.

Again relating the rates of interaction to features of the alliance social network, Chapter 4 also compared rates of SCC between second-order allies and third-order allies at and post-fusion. Across both contexts, second-order allies engaged in higher rates of interaction. In particular, second-order allies engaged in significantly higher rates of displays ($p < 0.05$) and parallel abreast formations ($p < 0.001$), as well as in the aggregate categories of coordinated behavior without recipient ($p < 0.01$) and coordinated behavior around a recipient ($p < 0.05$), than third-order allies. In contrast to third-order allies, second-order allies did not show much difference in their rates of contact at- and post-fusion. However, they did engage in significantly higher rates of displays ($p < 0.01$) at fusion (Ch. 4, Figures 11 and 12).

Using the same methods as in Chapter 4, I examined the mean rates of SCC behaviors among second-order allies across all three contexts sampled. In general, second-order allies engaged in higher rates of contact and synchrony post-fusion, and in higher rates of displays at-fusion. Mean rates of synchrony among second-order allies differed significantly across contexts (Welch's ANOVA, $F(2,9) = 6.68$, $p < 0.05$, Figure 5.8), with the highest rates of synchrony observed between second-order allies occurring post-fusion.

Based on these results, I have concluded that of the four SCC behaviors examined in this study, the most informative behaviors were synchrony, and contact, but that they are likely serving different functions.

Higher rates of synchrony occurred across contexts among the second-order allies who were most frequently associated. Thus, as suggested originally by Smolker and Pepper (1999), synchrony may function as a signal of alliance unity. Interestingly, the highest rate of synchrony among second-order allies was observed post-fusion, suggesting that the time following a shift in social dynamics may be a period of social reinforcement for second-order allies (e.g. "they're here, but we're still strong"). At fusion, second-order allies engaged in

higher rates of displays, including both displays without a recipient, and displays in which the recipient was a third-order male ally.

Affiliative contact behavior requires prolonged and intimate coordination in space and time, and is therefore more risky, more energetically expensive, and likely more rewarding than synchrony. Higher rates of affiliative contact was found among frequent second-order consortship associates and among third-order allies at-fusion. Both findings suggest that males may be using contact behavior in these contexts to sustain their association, or even to recruit one another in continued co-ordinated activity, as in the consortship context.

5.3 LINKS BETWEEN SOCIAL AND COGNITIVE COMPLEXITY

The third order alliance network examined in this study showed features of social complexity in its modular structure, dynamic change, and social differentiation.

The nested, hierarchical organization of allies into three orders of association demonstrate both local segregation and global integration. The orders of alliance relationships are both functional and structural. Local segregation is demonstrated by the organization of the population into the structural and functional units of first, second, and third order alliances. Global integration is demonstrated by the coordination of sub-units into larger functional units, as is seen when second and third order alliances coordinate spatially during a competition.

Adaptive change was demonstrated in the shifts in the alliance network coincident with the loss of individuals, and an extreme warming event implicated in the ecosystem-wide shifts documented in Shark Bay. Each of the three two-year networks showed structural differences, with the largest shift occurring between T2 and T3. In T3, we documented the formation of a new third-order relationship between the RR males and each of the KS and PD alliances. Additionally, the changes in the relationships between KS and PD males showed that rather than fractionating, the network re-organized in response to the observed disturbance.

In each of the three second-order alliances, there was one trio who participated in higher rates of third-order association. These individuals (“liaisons”) are constituting a critical social role in the structure of the alliance network, by acting to bind areas of the network that would be otherwise weakly connected. Other individuals (“provincial hubs”, re: Bullmore and Sporns (2009)) engaged in higher rates of intra-group association, constituting a role as a cohesive agent within their second-order alliance.

The degree to which this complex structure is realized within the alliance network is demonstrated by when, with whom, and how allies interact.

When. This study contributed evidence that allies differentiate between social context. Comparison of rates of social coordination and affiliative contact (SCC) among 3rd order allies at and post fusion shows that third order allies engage in higher rates of affiliative contact at fusion. Comparison of rates of SCC among 2nd order allies across 3 contexts shows that second-order allies engage in higher rates of displays at fusion, and higher rates of synchrony and affiliative contact post-fusion.

Who. This study also contributed evidence suggesting that allies differentiate between social others. Figures 5.9 and 5.10 show the interaction profiles of all dyads observed in this study. I cannot claim to have explained all the variation that exists in these profiles. However some of the variation observed can be attributed to the nature of their relationship. Second-order male allies who commonly associate throughout contexts engage in significantly higher rates of synchrony. Second-order allies who commonly consort together engage in higher rates of affiliative contact (Ch. 3). When both second- and third- order allies are present, second-order allies are more likely to be engaging in any kind of social interaction than third-order allies (Ch. 4). In particular, second-order allies engaged in higher mean rates of all behaviors measured, including significantly higher rates of displays and parallel swimming (Ch. 4).

How. The process of achieving, modulating, and sustaining an activity is a cognitive process that is affected both by the who is present and the social context. Second-order allies engaged in consortships while separate from other groups engaged in all four categories of

SCC. Swimming in parallel or in formation behind the consorted female were frequently observed behaviors. Synchrony occurred most frequently among frequent associates, and contact behavior occurred most frequently among frequent consortship associates. I suggested that there may be a functional difference between synchrony and contact: synchrony appears to be a lower-energy signal of alliance unity, whereas contact may function to modulate or sustain an interaction. Indeed, in the fusion context, I observed higher rates of contact behavior among third order associates during the first five minutes of group fusion than at later times (Ch.4, also here Fig. 5.6). This again suggests that contact behavior may be used by allies to reinforce their relationships and / or sustain an activity. A future study might address whether fusions in which allies engage in affiliative contact behavior are longer than those in which allies do not engage in this type of interaction.

Displays are also likely to signal alliance unity, though require a higher energetic investment than synchrony as they require sustained coordinated behavior over a longer period and are often organized around a shared target. Higher rates of displays among second-order allies occurred during the first five minutes of third-order fusion than during the other two contexts (Fig. 5.8), suggesting third-order allies as a potential (though not exclusive) audience of these interactions. Post-fusion, both second- and third-order allies returned to more regular pattern of swimming in parallel or in formation. During this time of lower-intensity interactions, second order allies showed the highest rates of synchrony observed among all three contexts, suggesting that post-fusion they return to a lower-energy behavior that may contribute to reinforcing their social bond. Interestingly, third-order allies engaged in very little synchrony, suggesting that synchrony may be a low-energy solution that re-enforces established relationships, but is not sufficient to modulate relationships that are less well-established or more variable over time. The different kinds of interactions that dolphins engage in require differential use of haptic, temporal, visual, and aural resources. The non-random use of interaction suggests that these are semiotic resources in the alliance system.

The distributed cognition methodology suggests breaking down cognitive systems

into elements, relations, and processes. In this framework, “the boundaries of the unit of analysis for distributed cognition are not fixed in advance; they depend on the scale of the system under investigation...[and] within a particular scale, the boundary of the cognitive unit of analysis may shift dynamically during the course of activity.” (Hutchins, 2014).

Within the alliance network, cognitive processes can be observed at multiple scales. One of the simplest processes described in this study is parallel swimming. The elements of parallel swimming are two individuals, each equipped with bodies of a particular form and their coupled sensorimotor systems (constituting many embedded cognitive systems), as well as space, time, and a fluid environment. Add these 4 elements together in a particular way and we arrive at parallel swimming. The relation between two bodies and space is orientation. The relation between two bodies and time is relative speed. Parallel swimming (indeed, most dolphin activity) occurs in a fluid environment with some useful properties. Fluid dynamics can be modulated by the movement of bodies, which in turn is perceived through sensorimotor systems, and can facilitate the sustained perception-action loop of coordinated movement.

Synchrony is a form of parallel swimming in which relative timing and space are tightly modulated. A property of a synchronous surface between two individuals is often a synchronous breath, which likely acts to perpetuate the activity by affecting the time each dolphin requires before surfacing again.

Parallel swimming is embedded within the process of a formation. Let’s consider a formation that includes two male allies following behind a third individual (usually the consorted female). There are three pair-wise processes occurring simultaneously: (1) the two males parallel swimming, and (2,3) staggered swimming between each male and the consorted female. Simulations of flight behavior between flocking birds has revealed that simple rules governing cohesion, alignment, and separation, can produce many of the observed formations (Reynolds, 1987). Indeed, similar sorts of processes may explain the general form of group swimming among dolphins. The formations described in this study consistently occur as two males behind the consorted female, suggesting that something more

is going on. In this process, elements include three individuals, three sustained processes (males in parallel, and each staggered behind the consorted female), and four new relations: the males to each other (alliance, also competitors), two male-female relationships (mates), and one polyadic relationship (consortship). I have suggested elsewhere in this dissertation that males may be vying for proximity to the consorted female, while avoiding overt agonism with each-other. The formations observed during consortship may be an emergent property of these two processes.

Displays between two males around a female consort involve the same set of elements, nested processes, and relations, but like synchrony, requires a tighter modulation of timing, space, and feedback. Arguably, both displays and formations may constitute forms of joint triadic attention (Bakeman and Adamson, 1984). Group fusions and competitions involve many embedded forms of the processes described above, and are themselves cognitive processes with different sets of elements (e.g. alliances) and relations (e.g. length of association, competition). Left out of these descriptions is the element of vocalizations and acoustic coordination, both of which are likely to play a role in coordinated activity among cetaceans. Further descriptions and dedicated analyses of these processes may be the subject of future study.

5.4 IMPLICATIONS FOR THE STUDY OF SOCIAL AND COGNITIVE COMPLEXITY

The Social Intelligence Hypothesis (SIH) proposes that the kind of complex cognition observed in humans and other species co-evolved with complex societies (Jolly, 1966; Humphrey, 1976; Chance, 1961; Kummer, 1978). It is possible to evaluate this hypothesis by comparing these properties in extant species. However, it requires a means of measuring *social complexity* across species, and a means of measuring *cognitive complexity* relative to the organization of a society.

In the first major wave of research conducted around this hypothesis, which took place largely under the “Machiavellian Hypothesis” program, studies focused on a range of

behaviors suggested to indicate complex psychological processes such as 'tactical deception' and 'theory of mind' as evidence of cognitive complexity (Whiten and Byrne, 1988; Premack and Woodruff, 1978; Byrne and Whiten, 1988; Byrne, 1997). Social complexity was less well defined, but properties such as group size, dominance relationships, variability, fission-fusion, and the existence of alliances were all considered (Dunbar, 1993; Kummer et al., 1997).

Since then, theoretical and methodological advances have been made in the study of complexity, social network analysis, and cognitive science. The burgeoning field of social network analysis is continuing to develop tools and methods for measuring different aspects of a society, many of which may contribute to the analysis of social complexity. The field of cognitive science has extended its scope of investigation, realizing the scientific value in extending the scope of our investigations to include the ways in which cognitive systems are distributed, from neural communities to social and technological communities (Hutchins, 2014). With these advances in mind, it is possible to recalibrate the analytical approach taken to address the SIH in new and productive ways. Strum et al. (1997) laid the foundation for doing just this, advocating a situated, distributed, co-ordination based approach for the study of social cognition *in situ*. This methodology was further refined by Johnson (2001) and Forster (2012). This study builds on the theoretical re-framing suggested by (Strum et al., 1997). The same principles advocated by these authors guides my approach to the study of cognitive complexity, but I have advocated a more standardized approach to the analysis of social complexity.

Social Complexity

This study uses a definition of *complexity* derived from research in systems neuroscience: a system is considered complex if it demonstrates the features of local segregation and global integration (Tononi et al., 1994) at both structural and functional levels. Dynamic (non-linear) change and individual differentiation appear to be features of complex societies. Other definitions of complexity are reviewed in Chapter 2 §1.1.5. Alliances and coalitions

are frequently recognized as features of complex societies (Chapais, 1995). The Tononi et al. (1994) principles of complex systems allows us to formalize that relationship. For example, pairs of male chimpanzees form temporary coalitions in which they work together to overthrow an alpha (Nishida, 1983; de Waal, 1984; Goodall, 1986) (an instance of *local segregation*), but those same males may also join together to form a cohesive unit in 'boundary patrols' who work together during territory defense (Goodall, 1986; Wrangham, 1999) (an instance of *global integration*). Further up the scale, all individuals are found within a troop that share resources such as territory and food (Goodall, 1968, e.g.).

In human societies, the properties of local segregation and global integration have been observed from hunter-gatherer and pastoral societies to modern post-industrial societies. For example, the social organization of Iñupiaq Eskimos of Northwest Alaska (ca 1800-1850), a traditional hunter-gatherer society, was organized into three major levels: groups of close relatives formed *family groups*, *nations* were comprised of multiple related family groups who shared a common dialect, and *multi-nation alliances* comprised of 2-4 nations came together to trade, feast, and to cooperatively attack other nations. An intermediate level of the Iñupiaq society was the *settlement*, consisting of one or more family groups, contingent on the availability of resources. (Burch, 1980, 2006).

The residential and social affiliations of the US post-industrial society includes familial networks, professional networks, friendship networks, political networks, and geographic networks. Locally, each of these social networks engages in activities (e.g. playing soccer, co-authoring a publication) that are often distinct from the accomplishments of the larger network (e.g. electing a politician, or uniting in protest). Organizations also show the property of local segregation and global integration: e.g. members of congress form temporary political alliances while engaging in an activity such as proposing legislation. The same members participate in a chamber of congress which participates in activities such as confirming political nominations, and in larger political parties that work together to engage in activities such as forming policy agendas and electing leaders.

As Strum et al. (1997) points out, computational models demonstrate that social

complexity can arise from simple rules and or simple agents and thus, social complexity does not necessitate or guarantee cognitive complexity. They must be separately assessed, and their relationship substantiated by evidence.

Cognitive Complexity

Social interactions, once considered only a “window in to cognition” are recognized more recently as cognitive activities in their own right, largely because they often produce the representational states once thought to exist only within individual minds (Hutchins, 1995). The Vygotskian stance that representations occur first and foremost in the world, before (if) within the individual (Vygotsky, 1978), is complementary with this approach (Johnson, 2001). Descriptions of social interactions are descriptions of the cognitive system that are necessarily complementary to but are non-redundant with with neural activity and internal psychological processes (Hutchins, 2006, 2014). This shift in perspective within cognitive science has important entailments for the study of animal cognition (Johnson, 2001) and for evaluation of the SIH: rather than using behavior to infer certain kinds of complex mentalizing, we can instead focus on the ways in which social interactions themselves relate to social complexity (Strum et al., 1997; Forster, 2012).

This dissertation is intended as an example of the kinds of analyses that can be done under this ‘second wave’ approach for evaluating the SIH. I use social network analysis to describe the complexity of the dolphin alliance network, and methods derived from ethology and behavioral ecology to describe how social interactions relate to the observed social structure. My results contribute to the understanding of social and cognitive complexity among cetaceans, and provide an example of how much of the previous and current work in behavioral ecology and animal behavior might be used in a comparative approach to evaluate the SIH among extant species. For example, many studies of primates have found that individuals direct grooming ‘up’ the social hierarchy (e.g. towards individuals who are more more dominant or have higher reproductive success) (reviewed in Schino, 2001). Grooming is a socially distributed cognitive process that requires (at minimum)

the coordination of space and sensorimotor resources among two individuals within the social context of the group. The finding that primates often direct grooming 'up' the social hierarchy indicates that information about the social structure is represented within the group. The next question is critical: *where* is that information represented? Is it within each individual? Or somewhere else? Playback studies conducted among free-ranging female baboons (*Papio cynocephalus ursinus*) suggest that individuals are aware of, and respond to changing relationships within their social group (Cheney and Seyfarth, 1999). This finding might lead us to surmise that in small groups with constant association and relatively stable relationships, all individuals maintain and update a mental representation of the social hierarchy, perhaps most importantly as it relates to them (their *egonet* in network analysis terms). But update it with what? Again, we have to ask, where is the information? By taking the distributed cognition approach, it is possible to observe that the information is first and foremost in the interaction. Interactions enact relationships: a grooming interaction enacts an affiliative relationship. The directionality of grooming enacts, represents, modulates the social structure. The grooming interaction is an informative act to the social system. The relationships that comprise social structures are represented first and foremost in the social group.

Perhaps in small groups with constant association it is possible for each individual to maintain an updated representation of the social system. But what of larger fission-fusion societies? Coupled with relevant findings from neuroscience, we can generally expect that social mammals are able to maintain representations of their own histories of social interaction. Perhaps these are in the form of episodic memories (requiring an advanced memory system) or simply a positive valence of association (modulated primarily by the reward system). But in larger societies when changing group composition, fission-fusion dynamics, and variability in relationships introduce sufficient uncertainty in a social system (Connor, 2007), we should expect that no single individual maintains a representation of the entire system. Where are those representations? Here again, by broadening our unit of cognitive analysis we can observe that the interactions themselves are where relationships

are enacted, modulated, and *represented* within the social group. Interactions are informative acts. Social relationships are represented by interactions among individuals, and those interactions are socially distributed cognitive events.

We can assess the relationship between social and cognitive complexity by describing the range of interactions produced, relative to variability in when and with whom these interactions occur. If the social system is represented in the cognitive system, then the patterns of interactions among individuals should relate to the structure and dynamics of the social system. A very basic prediction is that individuals who engage in higher rates of affiliative interactions will associate more frequently. Not only should we expect that affiliative interactions modulate relationships, they also enact the state of a relationship. The representation of the relationship is the interaction itself. Other dimensions of social complexity such as variability in group composition, reconfigurations of the social structure, and variability in the nature of encounters (such as seen in fission-fusion societies) should also be represented in interactions. These features indicate uncertainty in the system. We should expect that at times of high uncertainty (e.g. at group fusions after sufficient separation), social groups will *enact* their relationships. Finally, if social roles are represented within the system, then individuals who fill those roles should show different profiles of interaction than those who occupy different social roles.

This level of analysis may be sufficient for assessing social and (socio-)cognitive complexity across taxa, but certainly other levels of description of the cognitive system may be undertaken, indeed are facilitated by this approach. Observing social interactions constrains our hypotheses about the kinds of processes (e.g. psychological, neurobiological, sensori-motor), that might be required to complement the kinds of activity observed. For example, Johnson and Oswald (2001) used the distributed framework to the study of “social tool use” among eight captive bonobos. Rather than using their data to make inferences about intentionality, deception, theory of mind in her subjects, Johnson and Oswald draw from their fine-scale data on shifts in social attention among bonobo triads to make the observationally grounded and qualitatively different conclusion that these interactions demonstrate

a rudimentary capacity for multitasking.

In this dissertation, social complexity was evaluated using network analysis. The alliance network showed the features of local segregation, global integration, dynamic (non-linear) change, and the presence of social roles. Socio-cognitive complexity was indicated by a range of interactions, as well as variability in when and with whom interactions occurred. Association frequency was related to affiliative interactions: more frequent second-order associates engaged in higher rates of synchrony and petting. At a context hypothesized to have higher uncertainty (fusion), those joining one another (3rd-order allies) engaged in higher rates of petting when compared to their post-fusion rates. A conservative list of hypotheses about the nature of the individual systems involved in these interactions includes: a sensorimotor system capable of sustaining these interactions, a memory system capable of representing a history of interactions, a reward system responsive to social stimuli, and the ability to differentiate social others and changes in social contexts. Perhaps most important to the evaluation of the SIH, the conclusion of this author is that social interactions are cognitive events that represent aspects of social complexity; these cognitive representations occur first and foremost in the social world, and can therefore be captured and compared by classic ethological methods. I propose a simple approach to studying the relationship between social and cognitive complexity across taxa: patterns of association can be used to describe social complexity using network analysis, and the range and patterning of social interactions can be used to describe and compare the relationship between social and cognitive complexity.

5.5 FIGURES

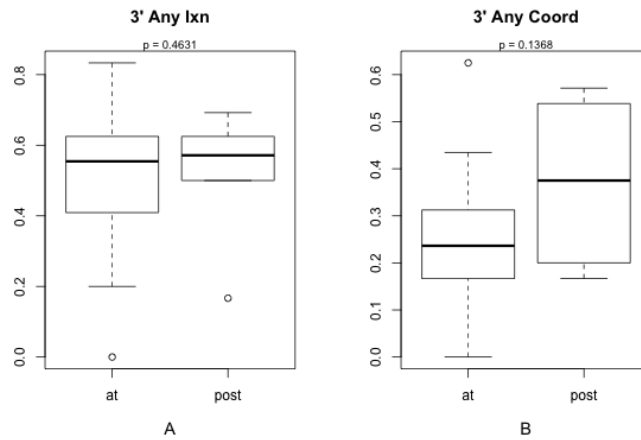


Figure 5.5: Rates of interaction between third-order allies at vs. post fusion.

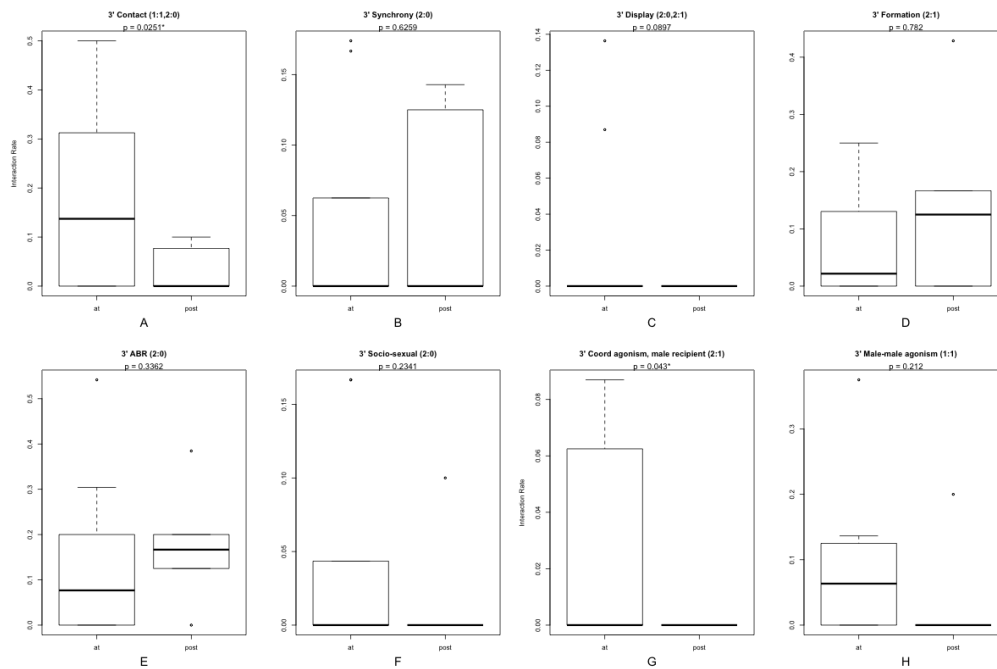


Figure 5.6: Rates of 3rd order affiliative contact, as well as coordinated agonistic interactions towards a male recipient were higher at fusion. Post fusion, third-order allies tended to engage in higher rates of formation and parallel swimming (ABR).

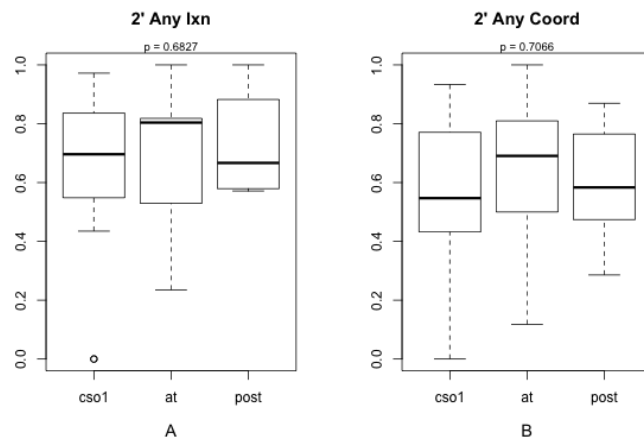


Figure 5.7: Comparison of rates of SCC among 2nd order allies across 3 contexts shows that second-order allies do not show differences in their general rates of interaction (Welch's ANOVA).

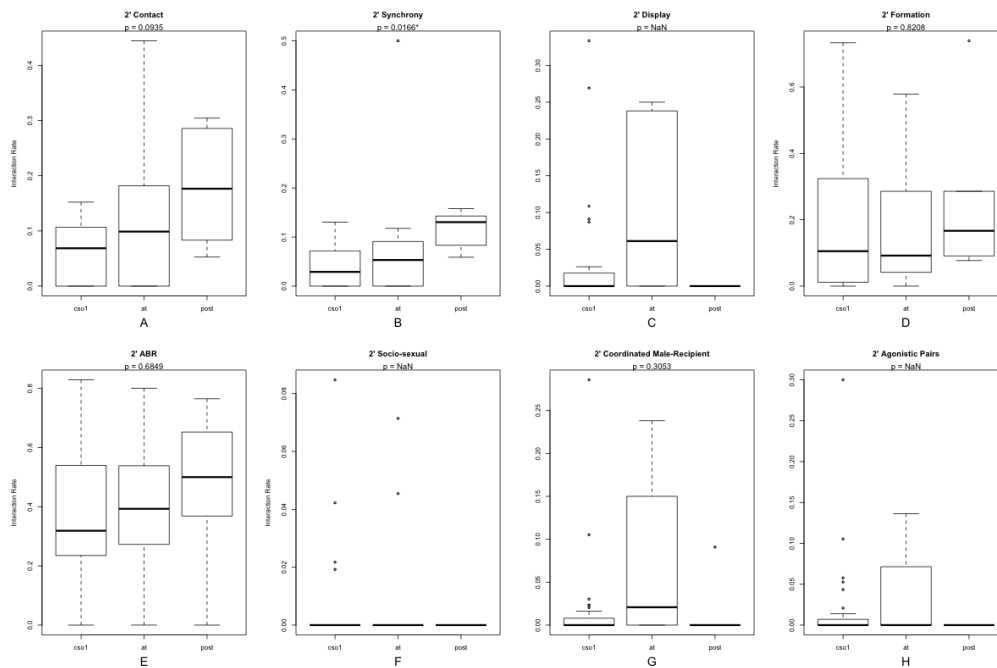


Figure 5.8: Comparison of rates of SCC among 2nd order allies across 3 contexts. Rates of synchrony varied significantly by context (Welch's ANOVA, $F(2,9) = 6.68$, $p < 0.05$). In general, second-order allies engaged in higher rates of contact and synchrony post-fusion, and in higher rates of displays at-fusion (results of Welch's ANOVA are null for variables without observations in one of the contexts).

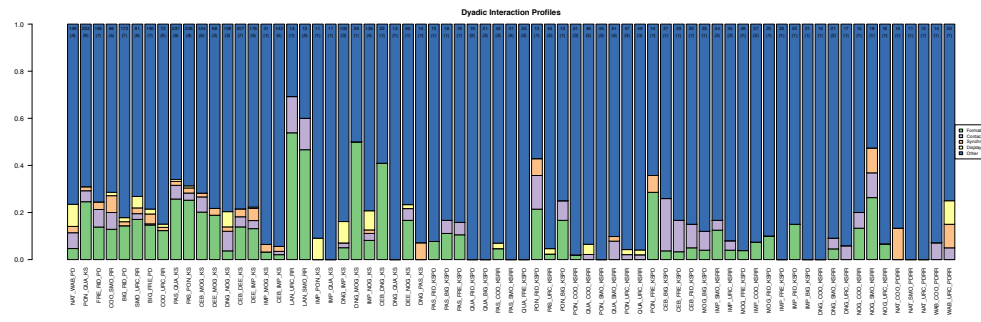


Figure 5.9: Dyadic interaction profiles summarizing rates of interaction across all 3 contexts (consortship group, fusion, and post-fusion)

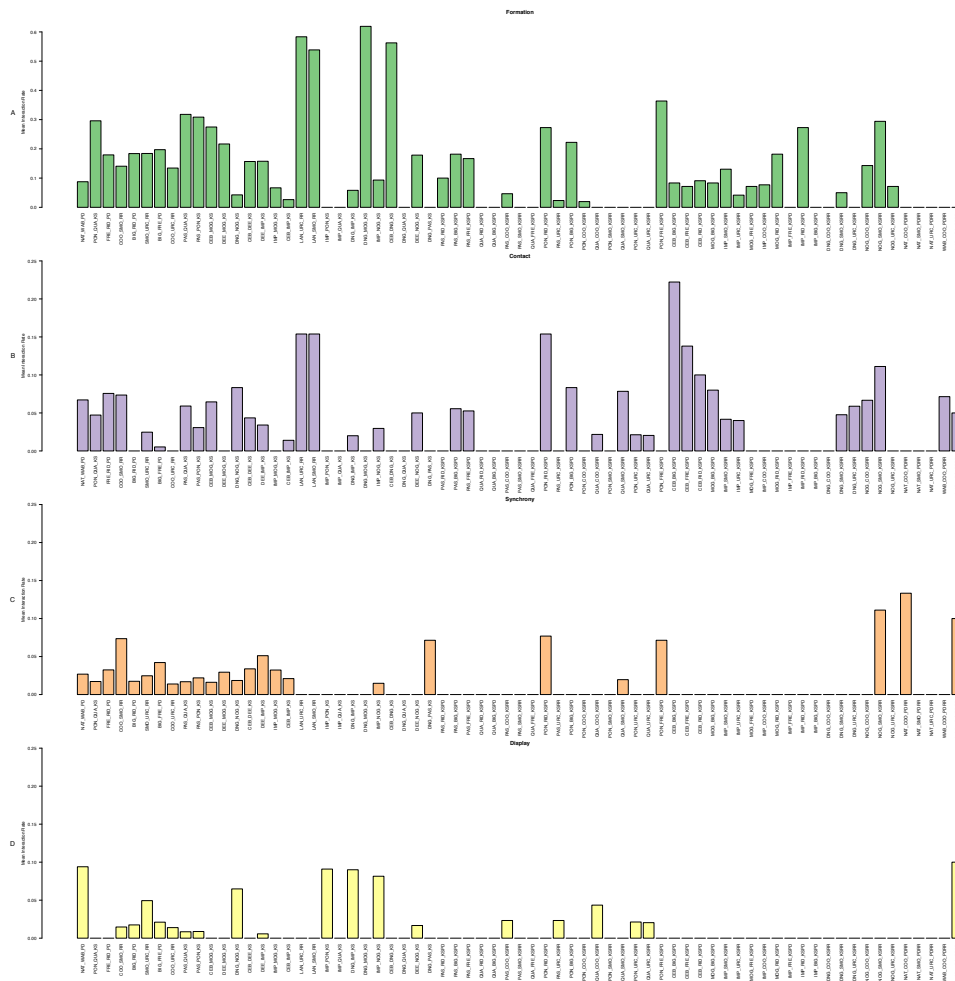


Figure 5.10: Rates of SCC by dyad across all 3 contexts (consortship group, fusion, and post-fusion)

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Appendix A

Behavioral ethogram for sampling aerial and deck video data

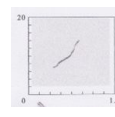
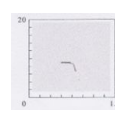
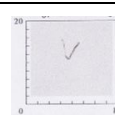
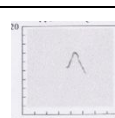
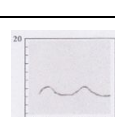
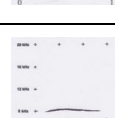
-- Synchrony (SYN) --				* RULE 1: 9 frames. "Synchrony" occurs if dolphins surface/dive within 9 frames of each other. 9 frames can be counted between (a) dorsal fins (deck only), melons (deck only), or bubble clouds (aerial only), whichever is best visible, but MUST be counted by the same body part for both animals. Default is dorsal fins. * RULE 2: Only synchronous events between individuals <1BLD are counted. * RULE 3: Defining part of event (breaking surface / disappearing) MUST OCCUR within 1s of interval.			
SSU	D/P	BEH, Actors, Dist	SSU, NAT WAB, 2	2+ dolphins break the surface OR dive "almost" synchronously - within 10 to 20 frames			
SSA	D/P	BEH, Actors, Dist	SSA, NAT WAB, 2	2+ dolphins dive synchronously			
SSD	D/P	BEH, Actors, Dist	SSD, FRE EED, 1	2+ dolphins synchronously break the surface to a leap			
LPO	D/P	BEH, Actors, Dist	LPO, NAT WAB, 1	2+ dolphins synchronously break the surface to a porpoise			
PPO	D/P	BEH, Actors, Dist	PPO, NAT WAB, 1				
-- Contact Behavior (CON) (non-Agonistic) --				Events are mutually exclusive, but possible for one individual to be involved in >1 event (e.g. in center of 2 with pec fin on both others). Synchronous polyadic events should be scored using the general display code "CDC" with further behavioral code written as a "tag"			
D0	D/P	BEH, Actors	D0, PAS QUA	* If events are mutual, recipient field = "M". If recipient cannot be determined but the event is directional, recipient field = "U". Distance 0 (could be touching, but not 100% sure, contact event such as pet/rub can't be clearly distinguished) FN - Body Contact. Gentle contact involving movement between the pectoral fin, dorsal fin, or flukes of one individual with any part of the body of another individual. Petting triplets, with two individuals petting another positioned between them, are sometimes seen. Actors pec is resting on the body of the recipient. If petting is mutual, both IDs should be listed as actors with "M" written in "recipients" column			
PET	D/P	BEH, Actor(s), Recipient(s)M	PET, PAS, QUA	Body-Body Contact. Note if ventral to ventral (use "VV" tag) "VV" tag outstated; using VRB			
RUB	D/P	BEH, Actor(s), Recipient(s)M	RUB, PAS, QUA	Mutual face-genital petting. Recipient receives petting around genitals, Actor receives petting around faec.			
MFG	D	BEH, Actor, Recipient	MFG, PAS, QUA	One dolphin rubs ventral aspect of flukes and/or keel of peduncle against (typically) the leading edge of another dolphin's pec. Female to male but may also occur male-male (female-female?). The pec often knee-jerks. One individual may knee-rub to two others simultaneously who are side-by-side at distance 0.			
KRB	D/P	BEH, Actor, Recipient	KRB, LIT, PAS	Ventral-ventral contact (possible mount)			
VRB	D/P	BEH, Actor, Recipient	VRB, PAS, LIT	A dolphin approaches another and rubs, head first, under the chin of the other dolphin. Often observed female to male. The rubbing dolphin may be right side up, or belly up but more typically is on its side.			
CRB	D/P	BEH, Actor, Recipient	CR, VBE, WAB	Bonding. One d (actor) rests its pec against the flank of another d, behind the other's pec and just below or posterior to dorsal fin. The actor is positioned at a distance 0 behind the tip of the other's rostrum.			
BND	D	BEH, Actor, Recipient	BND, PAS QUA	One or more dolphin(s) approaches another from the side and slides its ventrum up over the dorsum of the other dolphin at a 5-30 degree angle with respect to the anterior-posterior axis of the other dolphin. An erection may be seen if the mounting individual is male.			
MNT	D/P	BEH, Actor(s), Recipient	MNT, FRE RID, EED	A dolphin approaches another as though to mount but instead of angling up over the back of the other it presses against its side in parallel orientation. May simply be another variation of mounting. Often occurs with two dolphins "sandwiching" a third between them.			
SDP	D/P	BEH, Actor(s), Recipient	SDP, PAS QUA, WHN	A dolphin moves its rostrum into the genital area of another dolphin. May be performed slowly and gently in affiliative interactions and violently in aggressive interactions. The goosed dolphin often avoids by rolling belly up and tail-slapping at the goosing dolphin. A tail-slap, rub, or belly-present may also precede a goose in affiliative interactions.			
GSE	D/P	BEH, Actor(s), Recipient	GS, WAB, EED				
-- Displays (DSP) --				Scored if 2+ dolphins engaged in a spatially and temporally coordinated sequence of movements. Displays may include synchronous surfacing or diving but such event types are mutually exclusive. Polyadic behavior, sometimes organized around or in presence of another individual. Can be individual, dyadic, or triadic.			
RST	I	BEH, Actor	RST, CEB	Rooster strut as performed by 1 dolphin			
CNS	I	BEH, Actor	CNS, PAS	A dolphin raises its head out of the water and slaps its rostrum against the water surface. May be light or hard; general class of coordinated display with contact. May occur as 2+ side-by-side performing same action, or 2+ performing same action around third (recipient)			
CDC	D/P	BEH, Actors (, Recipient)	CDC, PAS PON, LIT	general class of coordinated display withOUT contact. May occur as 2+ side-by-side performing same action, or 2+ performing same action around third (recipient)			
CDO	D/P	BEH, Actors (, Recipient)	CDO, PAS PON, LIT				
-- Displays Tags --				Two dolphins approach another from either side and contact the central dolphin's pecs with the same body part and perform synchronous movements against the pecs and/or are petted by both pecs of the central dolphin synchronously.			
SPT	P	BEH, Actors, Recipient	SPT, PAS QUA, LIT	Tilt-belly-in. A dolphin tilts its belly toward another dolphin while positioned beside "OR" just behind the dolphin. Often performed by two dolphins in formation behind another. (as soon as this involves contact, it is a petrub, not a TLB)			
TLB	D/P	BEH, Actor(s), Recipient	TLB, PON PAS, LIT	Tilt-head-in TLH: A dolphin, from tilt-in position, angles its head into the vicinity of the other dolphin's genital slit. (AKA "Genital Inspect")			
TLH	D/P	BEH, Actor(s), Recipient	TLH, QUA, LIT	Surf-out. From formation, 2-3 dolphins surface, porpoise, or leap synchronously at a 30-60 degree angle out from the center dolphin.			
SFO	P	BEH, Actors, Recipient	SFO, KRO DNG, EED	Two dolphins synchronously leap toward each other from distance 2 and cross at the apex of their leaps.			
XLO	P	BEH, Actors	XLO, KRO DNG	Two or three dolphins, SBS, make synchronous abrupt turns from side to side. May be very brief. A minimum of two turns is required for a tango.			
TGO	P	BEH, Actors	TGO, KRO DNG	A general class of displays that begin in formation position. The flanking dolphins move past the center dolphin, turning in our out, then swim past the center dolphin in the other direction and repeat the process. Different "patterns" of circles and circle-eightings forming "butterfly wings" are formed by the movements depending on 1) the type of turn (in or out), 2) the size of the turn (wide or narrow) and, 3) the location of the turn relative to the female (just behind, beside or in front). May be accompanied by chin and/or tail slaps.			
BTD	P	BEH, Actors, Recipient	BTD, KRO DNG, CRV				
-- Formations (FRM) --				Salient patterns of spatial orientation that are often held for periods of time. Generally a male-specific behavior but females are scored the same as males if they are "actors" in these formations			
with leader // organizing "around" another. Requires the coordination of all individuals simultaneously							
FRM	P	BEH, Actors, Recipient	FRM, IMP DNG DEE, SUR	* For triads, note who is in CENTER position using tag "MID" after SEMICOLON			
LL	P	BEH, Actors, Distance	LL, PAS PON QUA, WSP	Males trailing behind female (>1/2 BLD & < SBLD) STG or ABR to one another.			
ABR	D/P	BEH, Actors	ABR, FRE EED BIG	Lateral Line. Individuals ABR or STG but distance is >5m/2BLD			
COF	P	BEH, Actors, Recipient	COF, IMP DNG DEE, SUR	Individuals are parallel (<5) side-by-side abreast, each staggered less than 1/2 BLD to their NN ("rostrum is at or in front of NN's pectoral and/or dorsal fin") & <=1BLD distance			
-- Agonistic Behavior (AGR) --				Forceful, directed events that produce a salient reaction from the recipient. Reactions including rapidly swimming away, fluking up, or lying entirely passively on-side			
TF	D/P	BEH, Actors	TF, BIG FRE	Tiff. A head to head in which at least one individual is bobbing his head up and down. Accompanied by Donald Duck vocalizations.			
HJ	I/D/P	BEH, Actors, Recipient	HJ, BIG	Head Jerk. A sharp lateral or vertical jerk of the rostrum. Often accompanied by a sharp band sound. Note "recipient" if there is a clear party the behavior is directed towards			
JC	I/D/P	BEH, Actors, Recipient	JC, RID	Jaw clap. An exaggerated opening and closing of the mouth. Note "recipient" if there is a clear party the behavior is directed towards			
CHS	D/P	BEH, Actors, Recipient	CHS, NAT, DNG	Chase. 2+ individuals fast swimming, one behind the other. The individual in the aft position is the chaser (actor)			
CHG	D/P	BEH, Actors, Recipient	CHG, NAT, DNG	Charge. A dolphin rapidly accelerates and swims fast directly at another dolphin approaching to within two meters. Includes circle charge			
THT	D/P	BEH, Actors, Recipient	THT, NAT, EED	Tail Hit. A dolphin strikes another violently with its flukes / peduncle			
RHT	D/P	BEH, Actors, Recipient	RHT, NAT, EED	Rostrum Hit. A dolphin strikes another with a sharp lateral jerk of its rostrum.			
BSL	D/P	BEH, Actors, Recipient	BSL, NAT, COO	Body slam. A charging dolphin slams into another with any part of its body other than its rostrum or tail. (Note, may include pec hit or fin hit)			
RAM	D/P	BEH, Actors, Recipient	RAM, NAT, COO	Ram. A dolphin charges into another dolphin with its rostrum			
BTE	D/P	BEH, Actors, Recipient	BTE, NAT, COO	Bite. A dolphin bites another with a rapid motion of the head and jaws			
PUP	D/P	BEH, Actor(s), Recipient	PUP, FRE RID, EED	One or more dolphins push up under another dolphin's midsection forcing it up out of the water. The dolphin being pushed is typically on its side or belly-up			
-- Other Behaviors to Note in 5-min scans (OTH) --				Guarding. 1-2 males stay close by the side of the consorted female while other male(s) from the consorting group forage			
QUA	P	BEH, Actors, Recipient	QUA, RID, LIT	Salient change in direction made by a group of 2+ individuals			
DIR	P	BEH, Actors	DIR, PAS PON QUA				
Other Definitions of Note							

Distances		* Dist noted for >2 individuals is smallest dist between any two individuals	
Vit	0		0 - 1/3 BLD (0 - 67m)
Tig	1		1/3 - 1 BLD (67 - 2m)
Mod	2 (*or 3)		1-2 BLD (2 - 4m)
Spr	5		3-5 BLD (5 - 10m)
Wsp	9		>5BLD (>10m)
TAGS			
Tag	Tag_ID		
OMA	BEH, Actor > Recipient	OMA, BIG > PIC	Out-male-approach. A male approaches or interacts with the consorted female of another 1' group.
HTH	BEH, Actors	HTH, PAS PON, FRE RID	Head-to-head
XCO	BEH, Actors	XCO, FRE QUA	Cross coalitional Petting / contact behavior
MID	BEH, Actors	MID, PAS	Male in center position of a formation "mid"
DSP	BEH, Actor > Recipient	DSP, FRE > BIG	Displace
TRI	BEH, Actors	TRI, FRE RID BIG	Triple sync
TTO	BEH, Actor(s), Recipient(s)	TTO, CEB IMP, DEE HOW	Turn-to. 1+ individual makes salient turn to the other. Can be 2+ & coord
FRO	BEH, Actor(s), Recipient(s)	FRO, CEB IMP, DEE HOW	Turn-to. 1+ individual makes salient turn FROM another. Can be 2+ & coord
TLH	BEH, Actor(s), Recipient(s)	TLH, CEB, HOW	Tilt head in AKA genital inspect. A dolphin, from tilt-in position, angles its head into the vicinity of the other dolphin's genital slit.
CMA	BEH, Actors	CMA, DEE	Call-male association (e.g. pet)
BND	D, BEH, Actors	BND, QUA PON	Two adults swimming dist-0 in parallel. One is in "echelon" with the other. Usually between consorted females
AMB	I, BEH, Actor	AMB, PAS	Ambassador. During fuz, one individual joins group first before the rest of his group
FFF	P, BEH, Actors, Recipient(s)	FFF, QUA PAS PON, NIR	Following the foraging female. Female forages, males trail behind within 10m
Actors & Recipients			
Actor			If the converging path of the two individuals is projected onto a line, the ACTOR is the one who would have travelled a GREATER distance to the start of the interaction
Recipient			If the converging path of the two individuals is projected onto a line, the RECIPIENT is the one who would have travelled a SHORTER distance to the start of the interaction
* Mutual			If the converging path of the two individuals is projected onto a line, both individuals would have travelled the same distance to the start of the interaction
RULES FOR DATA ENTRY			
* If ID is unknown, use code UNK			
* Any IDs that are unsure should be indicated in NOTES only, otherwise written as UNK			
* All "rows" of data are separated by a COMMA (,) (ChronoViz only)			
* Any notes should be written after the behavioral code, separated by a SEMICOLON (;) (ChronoViz only)			
* An individual can be scored if it can be justified that it is an "identifiable dolphin shape" whose behavior could be observed. Blurs are treated as though the dolphin is fully submerged, and therefore not visible.			
* If partially off-aerial, body must be visible from dorsal fin to rostrum			
* If an interval suggests evidence of foraging (fish chase, fish catch, wsp foraging) note in the "FOR?" column. These data will not be used.			
* Polyadics are by chain: 4 ABR means each individual is ABR to the next. Polyadics should be counted differently than dyadics			
* NM to CSO fem: should only count when >1 male are visible at surface? (otherwise by default, and other males could be elsewhere?)			
* UNK = INDIVIDUAL WITHIN FOCAL GROUP BUT ID UNKNOWABLE. XXX/ADD = ADDITIONAL UNKNOWN INDIVIDUAL. STARTS ON LINE 3494			
Mutually exclusive events			
ABR & Contact		ABR is dist 1, contact is dist 0	
CDC & ANY Group Contact		CDC is the event; not pet/rub/ possible version of these.	
SS & Display		Sync's that happen during a display should not be double counted.	
Non-mutually exclusive events			
FRM / ABR & dyadic contact within POLYADIC group			
Formations & synchrony (synchrony is not inherent to a formation)			

Appendix B
Acoustic Categories

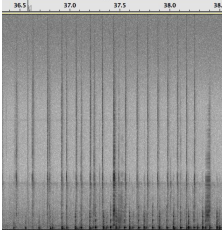
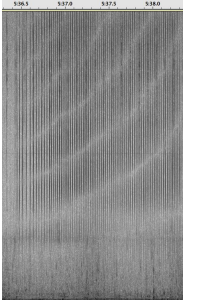
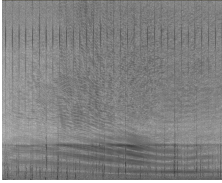
TONAL CALLS (Whistles)

Whistles are narrow-band tonal vocalizations whose primary frequency is often modulated. These vocalization may occur with or without equally spaced harmonics.

Name	Code	Description	Image
Upsweep / Rise	W	Frequency is lower at the start of the call than at the end of the call (LO to HI)	
Fall	W	Frequency is higher at the start of the call than at the end of the call (HI to LO)	
U-shape	W	Frequency shifts during the call from HI to LO to HI again	
Wave	W	Frequency shifts during the call from LO to HI to LO again	
Sine	W	Frequency shows at least 2 HI peaks & 2 LO frequency valleys during a single call (e.g. LO-HI-LO-HI)	
Flat	W	Frequency shows no salient variation	
Other	W	Frequency-modulated tonal calls that are not captured by the above categories	

* Images from Janik and Slater 1998

PULSED CALLS (B,E,C,P)

Name	Code	Description	Image
Pops	P	Narrow-band, low frequency pulses with peak energy <3000Hz. Typically produced in trains of 3-30 pops at a rate of 6-12 pops/s. Sound like coconuts knocking together.	 <p>A spectrogram showing a series of vertical, narrow-band pulses. The x-axis represents time with markers at 36.5, 37.0, 37.5, 38.0, and 38.5. The y-axis represents frequency. The pulses are concentrated in the lower frequency range, appearing as thin vertical lines.</p>
Echolocation	E	A pattern of clicks in which the inter-pulse-interval is always short, though increases or decreases over time. Visually, you may notice a variation in which frequencies are produced with the highest amplitude.	 <p>A spectrogram showing a series of vertical pulses. The x-axis represents time with markers at 3.063, 3.378, 3.373, and 3.360. The y-axis represents frequency. The pulses are concentrated in the lower frequency range, appearing as thin vertical lines.</p>
Burst Pulse	B	Burst-pulse calls are actually a closely grouped series of clicks, which we hear as 'growls' or 'screams' or 'squawks'. Visually, the clicks are often less broad-band than in echolocation, and do not have salient periods of silence between pulses. These calls may have a social function but much less is understood about this category than the others preceding.	 <p>A spectrogram showing a series of vertical pulses. The x-axis represents time with markers at 3.063, 3.378, 3.373, and 3.360. The y-axis represents frequency. The pulses are concentrated in the lower frequency range, appearing as thin vertical lines.</p>

Appendix C
Focal Follow Datasheet

Date:	12 Oct 12	Focal:	QUA	All ID:	SCA, COX, PAS, PON	Follow #:	1	Wind Dir:	East	Wind Speed:	20%	Cloud Cover:	20%	Hydrophone:	Deck:			
Start Time:	8:45	WPT:	26	Wind Dir:	East	Wind Speed:	27	Cloud Cover:	10%	Hydrophone:		Deck:						
End Time:	9:45	WPT:	27	Wind Dir:	East	Wind Speed:	27	Cloud Cover:	10%	Hydrophone:		Deck:						
Time	# Ds	NN	beh/pic	Focal Activity 2	Focus	Dist	Orientation	Dive Sync	Group Activity 8	Group Composition / Notes 8								
				Foc Act	NN Act	Dist	Foc/NN	(Y/N/all)	U/M/T	Gr Act	Hab	Bft	Leader on L	Proximal 1st	// # > 50m			
8:45	5	SCA	5	Rest	Rest	tg	N	→	T	Rest	N	Slo	9.9	UN	4	1	Rest included in formation snagg ing	
8:50	5	PON	5	Snagg	Snagg	tg	N	→	T	Rest	Mill	S	Velow	9.6	UN	4	1	Direction change to S @ record time
				Increased speed				change to SE,										activity - possibly towards offc
				KROKERS near														
8:55	5	PON	5	Rest	Snagg	tg	N	→	T	Rest	SE	Velow	9.0	UN	4	1	PAS, SCA, COX then PON, QUA behind COX in BP	
9:00	5	SCA	5	Trav	Rest	tg	N	→	T	Trav	SE	Velow	8.5	UN	4	1	QUA slightly behind rest of group by ~0.5 m.	
				Direction change														
				QUA & PON dive				period										
9:05	5	PON	5	Trav	Trav	tg	Y	→	L	Trav	S	Slo	8.0	UN	4	1	Single surface with NN Petting / belly up - Petting blue	
9:10	5	SCA	5	Snagg	Snagg	tg	N	→	M	Rest	E	Vel	3.8	Sand	6	1	PON; QUA, SCA, COX; PAS	
9:15	5	SCA	5	Snagg	Snagg	mod	N	→	M	Rest	S	E	Vel	6.0	Sand	5	1	PON & QUA sync divc - Pa PON; QUA, SCA, COX; PAS
9:20	5	PAS	5	Trav	Trav	tg	N	→	NA	Rest	S	Vel	7.0	Sand	4	1	All as gp - no leader - COX in infant pose? maybe feeding	
				POPs - not sure				who from - Right after										Direction change to E after POPs
9:25	5	SCA	5	Trav	Trav	tg	N	→	M	Trav	Mill	E	Vel	6.4	Sand	5	1	Individuals turning towards each other just after record
9:30	5	SCA	5	Trav	Trav	tg	Y*	→	T	Trav	SW	Slo	2.4	UN	6	1	PON, PAS; QUA, SCA, COX PON belly up next to PAS	
				*Dive Sync by				whole gp /										Another animal ~ 30m behind heading towards out of group. Not sure if dolphin or ray or fish
9:35	5	PON	5	Trav	Trav	tg	NA	→	M	Trav	S	Slo	6.1	UN	4	1	PON; QUA; SCA, COX, PAS	