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SOCIALITY AND RECONCILIATION IN
MONK PARAKEETS (*MYIOPSITTA MONACHUS*)

by

Lynnsey Lee Morrison

A THESIS

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SOCIALITY AND RECONCILIATION IN
MONK PARAKEETS (*MYIOPSITTA MONACHUS*)

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University of Nebraska, 2009

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For animals living within socially complex groups, it is beneficial for all individuals to maintain group cohesion. Conflicts often arise in groups, which could potentially have high costs both to the subordinate and dominant members, and could lead to group instability. It has been shown numerous times that highly social group members participate in affiliative relationships with other group members discriminately. They also perform related behavior patterns such as reconciliation at a high rate, which could strengthen group stability. Reconciliation occurs when an affiliative interaction takes place between two individuals following an agonistic encounter. The rate of affiliation is higher after the conflict than had no conflict occurred. In several species, reconciliation appears to be shown more often between individuals with “mutually valuable relationships.” I tested the occurrence of reconciliation in a group of six individual monk parakeets. Monk parakeets likely live in complex societies and thus are good candidates for tests of reconciliation. First I developed an ethogram and quantified social behaviors. Multidimensional scaling of a hypergeometric similarity matrix allowed me to functionally define behaviors as affiliative or agonistic. A weighted score was assigned to each behavior based on these analyses. Each dyadic interaction between pairs of birds was then analyzed to see if they were significantly affiliative or agonistic. Among the 15

dyads, I found that six dyads showed behavior patterns that were primarily affiliative and four showed patterns that were primarily agonistic. In the reconciliation experiment, seven out of 13 dyads reconciled (54%), including five of the six dyads that were primarily affiliative. The results are consistent with the hypothesis that reconciliation occurs mainly in “mutually valuable relationships.” This is the first study to demonstrate reconciliation in an avian species.

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INTRODUCTION

RECONCILIATION REVIEW

Sociality is found in many different taxa; it can range from simple sociality in which group members are found in aggregations but are essentially strangers, to complex sociality where groups are permanent and stable with individualized relationships between group members. The relationships within complex groups span across years and even generations. Species living within socially complex groups spend the majority of their time with a known set of individuals with whom they forage, rest, breed and care for young. Not only do group members recognize other group members as individuals, but they remember past interactions with these individuals and modify future behavior based on these memories. The majority of socially complex groups have a dominance hierarchy, which regulates many behaviors within the group. Socially complex group members experience enhanced learning due to the social environment as individuals gather knowledge from interacting and observing group members (de Waal & Tyack 2003).

Within socially complex taxa, group members benefit from these individualized relationships in many ways. A major advantage to group living is cooperation between group members, where two or more individuals work together to gain higher benefits than they would acting alone (de Waal & Tyack 2003). Tai chimpanzees cooperate with one another to surround and attack prey. Everyone benefits from the hunt, as meat is of great nutritional value and is shared among the hunting party, females, and juvenile males

(Boesch 2003). Pinyon jays mob predators as a group and are successful at driving the predators away (Marzluff & Balda 1992). In spotted hyenas, group members will band together to defend their territory and carcasses from lions and other hyena groups (Drea & Frank 2003). A solitary individual would be unsuccessful at this defense, but within a group it is possible, due to individuals cooperating with one another. In many socially complex taxa, juveniles form crèches or nurseries. In spotted hyenas, allonursing actually takes place in these nurseries where mothers will nurse unrelated offspring (Drea & Frank 2003). This is seen in cooperative breeding birds as well where siblings will feed their parent's newly born young (Davies 1982). Thus, there are many fitness benefits to living in socially complex groups. Group members receive higher quality food, more food, lower predation risk and a lower cost to reproduction through cooperative breeding. These individualized relationships positively affect survival and reproduction of group members as participating in group tasks is more beneficial to the individual than solitary actions.

But with these benefits comes conflict over food, potential mates, and care of young, which is unavoidable in group situations as individuals must live and interact with each other at all times (Aureli & van Schaik 1991). These conflicts could have potentially high costs both to the subordinate and dominant individuals within the group. It has been shown numerous times that recipients of aggression are more likely to be reattacked (York & Rowell, 1988; Aureli & van Schaik 1991; Aureli 1992; Cords 1992; Watts 1995; Silk et al. 1996; Castles & Whiten 1998b; Das 1998; Schino 1998; Kutsukake & Castles 2001). They may also face negative ecological effects, such as reduced foraging time (Aureli 1992). Self-directed behaviors, like scratching, occur after

conflicts and some argue that this is an indication of higher anxiety levels (Maestriperi et al. 1992; Schino et al. 1996), but the traditional ethological view recognizes these behaviors as displacement behaviors, which are lower-priority behaviors that suggest conflicting motivational states. Long-tailed macaques, barbary macaques, japanese macaques and domestic goats all exhibit higher rates of scratching following a conflict (Aureli et al. 1989; Aureli & van Schaik 1991; Aureli 1992; Castles & Whiten 1998; Schino 1998; van den Bos 1998; Kutsukake & Castles 2001; Aureli 1997; Das et al. 1998). While these costs directly affect subordinates, they can also jeopardize group stability, which in turn can be of severe cost to the dominant individuals as well. Subordinate individuals might leave the group and thus reduce the fitness of dominant individuals, as all group members must work together in tasks and alliances. A dominant individual alone will have lowered fitness than one within a stable group, therefore it is beneficial for all members to minimize conflicts within the group and maintain cohesiveness (Aureli et al. 2002). Lorenz (1931) describes a situation in jackdaws, a highly social bird species, where a group of stranger jackdaws settled near his ‘tame’ jackdaws. When the strangers took flight, this elicited a flight response from juveniles in the ‘tame’ group; two adult males actually took flight and brought the juveniles back, suggesting a need for group cohesion.

One way to reduce conflicts within the group is through reconciliation. Reconciliation occurs when an affiliative interaction takes place between two individuals following an agonistic encounter. The rate of affiliation is higher after the conflict than had no conflict occurred. The term reconciliation was first defined by de Waal and Roosmalen (1979) as “a form of affiliative (friendly) interaction between former

antagonists which interact affinitively shortly after an agonistic event.” While this behavioral pattern is intriguing and could potentially be a widely evolved mechanism in socially living individuals, the mere term reconciliation is anthropomorphic and functional rather than descriptive, which has led to much confusion on how to actually test the function of these post-conflict affiliative behaviors and has greatly reduced how accessible the ideas have been to non-primatologists. It implies that a conflict causes the subsequent affiliation, but this causal relationship has never been demonstrated. Rowell (2000) recognized that primatologists have not approached reconciliation from an ethological standpoint. They are unfamiliar with the historical work on appeasement and social cohesion, and thus thought they ‘discovered’ reconciliation. Reconciliation, therefore, must be tested from an ethological standpoint taking into account all historical and current research in order to fully understand its function.

The most parsimonious explanation for reconciliation is that it is a process of appeasement. Tinbergen (1959) describes appeasement as an action pattern that is motivated by fear, a conflict between a tendency to escape and a tendency to stay put or approach. It is not an aggressive action, but rather one that functions to deter further attack from an opponent. Eibl-Eibesfeldt (1975) states that many behaviors found in courtship, such as allogrooming, can also function as appeasement behaviors.

Appeasement behaviors are the opposite of threat behaviors and they elicit affiliative behaviors in the opponent. Appeasement is different from submission in that submission indicates a dominance status between the individuals. The submissive display indicates that the individual will defer to his opponents in other conflicts as well. Aggression is reduced because the dominant individual won the conflict. Appeasement does not imply

a subordinate status, but indicates that the displaying animal is attempting to stop the conflict. It directly reduces the aggressive motivation of the attacker. In this light, the affiliative behaviors following conflict between individuals could be appeasement displays, which in turn would lower the probability of another attack. Many appeasement displays involve affiliation (Keltner & Potegal 1997). In a review by Silk (1996), she states that reconciliation behavior is a signal from the aggressor that he or she will not reattack. In baboons the signal is a grunt. Eibl-Eibesfeldt (1975) describes similar vocalizations as appeasement behaviors in polecats and rats. An appeasement account is, thus, the best established functional explanation for reconciliation.

The most widely cited functional explanation for reconciliation, however, is the “relationship repair hypothesis.” It states that reconciliation repairs damaged social bonds between individuals involved in a former aggressive interaction (de Waal & Aureli 1997; Wittig & Boesch 2005; Koski et al. 2007). This hypothesis implies that following a conflict the two animals are aware that their relationship has been damaged and that they must “make-up” with one another in order to keep the relationship intact and cooperate in the future. This could potentially be true, but it is extremely difficult to test, because individual relationships span years and generations. How would you experimentally determine whether a relationship has been repaired? If reconciliation consists of an exchange of appeasement displays to deter further attack or to signal that the attack will not be resumed, this would in itself reduce the probability of another conflict occurring without any anthropomorphic assumptions. Appeasement results in the same behavior pattern that is explained through the “relationship repair hypothesis.”

Silk (1996) argues that the “relationship repair hypothesis” is inherently flawed and will quickly lead to the evolutionary loss of reconciliation. Reconciliation would lose function quickly in a population because an aggressive interaction would occur, the aggressor would reconcile and then another aggressive interaction would occur, and reconciliation would happen and the cycle would continue, as dominant individuals are usually more aggressive in encounters, and conflicts would keep occurring. It would no longer mean the relationship was repaired after many conflicts, so the mechanism would be lost.

Therefore, I hypothesize that reconciliation functions as a signal that conflict has ended between two individuals. If there was not a signal from either partner that the conflict has subsided, it might continue on and on. The cost, especially to the subordinate individual, could be severe. He or she might end up leaving the group, which would then be costly to the dominant individual as well. So the dominant individual reconciles with the subordinate to maintain group cohesiveness and stability. Relationships within a group are important and individualized; if a group member leaves, there is no guarantee that he will be replaced with another who will cooperate at the same level. Thus, it is beneficial for dominants to reconcile with subordinates.

In pairs where reconciliation occurs, the two individuals involved in the conflict are less likely to engage in another subsequent conflict, compared to pairs in which reconciliation does not occur. This has been shown in long-tailed macaques, Japanese macaques, olive baboons and spotted hyenas (Aureli & van Schaik 1991; Cords 1992; de Waal 1993; Watts 1995; Silk et al. 1996; Castles & Whiten 1998b; Koyama 2001; Kutsukake & Castles 2001; Wahaj et al. 2001). This does not necessarily mean that

reconciliation causes a reduction in conflict. There are no studies, for example, comparing opponents who were physically separated after a conflict (preventing reconciliation) to dyads that were allowed to reconcile to see if reconciliation does in fact reduce conflict. In Japanese macaques individuals that did not reconcile decreased affiliation and increased aggression for 10 days after the initial conflict concluded. When reconciliation did occur no such changes in behavior were seen, but the comparisons were made between different individuals (Koyama 2001). Self-scratching, a behavior associated with anxiety and motivational conflict, was lowered post-reconciliation versus pre-reconciliation in long-tailed macaques, Japanese macaques, olive baboons and domestic goats (Aureli and van Schaik 1991; Das et al. 1998, Kutsukake and Castles 2001; Castles and Whitten 1998b; Schino 1998). A study on rhesus macaques showed that heart rates of opponents were also reduced after reconciliation (Smucny et al. 1997; Aureli & Smucny 2000). This is important because high levels of anxiety and stress are known to decrease fitness (von Holst 1998; von Holst et al. 1999).

In no species does every conflict lead to reconciliation. The percent of reconciled conflicts ranges from 7% to 55% in different studies (Aureli & de Waal 2000). De Waal and Aureli (1997) introduced the “valuable relationships hypothesis,” which states that the probability of reconciliation is higher when the individuals involved in the conflict have a mutually valuable relationship with one another. It would not be beneficial to either individual to reconcile if they do not, in general, both benefit from their interactions. A mutually valuable relationship, therefore, might be a mated pair which cooperates to raise offspring, two males which form alliances to defeat other males in contests, etc. In these terms, a valuable relationship is somewhat ambiguous and hard to

test as it must be shown that two individuals have both benefited in the past from their relationship. A more parsimonious approach would be to propose that individuals with strong affiliative bonds prior to testing should be more likely to reconcile, assuming that higher levels of affiliative behaviors indicate greater mutual value. Unless there is data showing cooperation between individuals and later showing that they reconcile and vice-versa with individuals that never cooperate and never reconcile, the only way to experimentally test the valuable relationships hypothesis is to look at prior affiliation rates between certain individuals and compare this to their likelihood of reconciliation. Using this method, one would predict that individuals with high affiliative bonds prior to testing are more likely to reconcile than those without any affiliative bond or with an agonistic relationship.

In many groups, the frequency of reconciliation varies greatly between conspecifics (Aureli et al. 2002). Several studies have shown that individuals differentially reconcile with others in their group. In macaques, reconciliation occurs at a higher rate after conflicts between kin than non-kin; in this species matrilineal kin cooperate closely, so kin relationships are more “valuable” than non-kin relationships (Demaria & Thierry 2001; Thierry 1990). In chimpanzees, reconciliation is seen at a higher rate between males involved in conflict than between females. In this species males form strong alliances with one another in competitions between and within groups, so these relationships may be more “valuable” than female-female relationships (Goodall 1986; de Waal 1986; Arnold & Whiten 2001). This evidence does not directly link pair bonds between individuals to their tendency to reconcile, but rather looks at characteristics of the group, correlates these characteristics with the probability of

reconciliation, and speculates that this could be due to “valuable relationships.” Looking at affiliation rates prior to testing and comparing this to the tendency to reconcile would still give evidence as to why some pairs reconcile and others do not without trying to speculate what a “valuable relationship” is within the group.

In 1983 de Waal and Yoshihara laid out three minimum requirements for reconciliation: that animals have individual recognition, a memory for past interactions, and conciliatory tendencies; since then scientists have stressed the importance of studying affiliation in species other than primates (Schino 2000; Aureli et al. 2002).

Reconciliation has been seen in 30 different primate groups with varying degrees of sociality, with only one negative study. Many of these studies occur in captive settings, which could artificially inflate the number of species shown to possess reconciliation. In captivity, relationships between group members become more pronounced as individuals are forced to live in close proximity. Complex relationships could, thus, emerge artificially in the captive setting, which would create a need for reconciliation. Therefore, when doing these experiments in captivity, the species has to be carefully studied and comparisons must be made to wild populations and other groups to show it is a species-wide phenomenon and not an artifact of captivity.

There are only five studies on reconciliation in non-primates, four of which are in mammals (Kutsukake & Castles 2004; Palagi et al. 2004; Cooper et al. 2005; Mason et al. 2005; Wittig & Boesch 2005; Koski & Sterck 2007; Koski et al. 2007). Reconciliation in non-primates has been documented in domestic goats (Schino 1998), bottlenosed dolphins (Samuels & Gifford 1997; Weaver 2003), and spotted hyenas (Wahaj et al. 2001). The study on goats induced aggressive interactions, while those on dolphins and

hyenas were taken from focal samples in the field over long periods of time. These studies illustrate that reconciliation is not only found in primates; thus it could be a much more widespread phenomenon occurring in similar social systems. A study on domestic cats and one on rooks did not find that reconciliation occurred after conflicts. Cats do not show reconciliation, but they do show high anxiety levels after aggression (van den Bos 1998). This species is not social, though, so this result is perhaps not surprising.

It is surprising, however, that rooks did not perform reconciliation, as they are highly social (Seed et al. 2007). Seed et al. (2007) asserted that mated pairs are never involved in conflict. This conclusion seems unwarranted, as the authors only looked at three aggressive behaviors and no submissive behaviors. All three aggressive behaviors are similar, in that one bird conspicuously attacks another bird from a distance. You would not expect mated pairs to perform these overt aggressive behaviors, but they are likely to perform more subtle agonistic behaviors. Mated pairs might be the only dyads that perform reconciliation, as they are the most likely candidates to show high affiliation prior to testing. Not looking at the behavior in finer detail could have meant that reconciliation was simply not recovered rather than that it did not occur.

Considering the limited number of reconciliation studies that have been conducted on non-primate groups and how few have tested the “valuable relationships hypothesis,” I designed a study testing reconciliation and the “valuable relationships hypothesis” on monk parakeets (*Myiopsitta monachus*). Monk parakeets are highly social, which is somewhat unusual for a parrot species. They live in permanent groups year-round. Monk parakeets are new world parrots and are unique in that they are colonial breeders

that build large nests where several pairs reside year round. Thus, testing questions of social complexity in monk parakeets is compelling.

SPECIES REVIEW

Monk parakeets are referred to by many different common names, including quaker parrots, quaker conures, quaker parakeets, monk parrots, and gray-headed or gray-breasted parakeets. They are found in the monotypic genus *Myiopsitta*, within the subfamily Arinae, in the family Psittacidae. A recent phylogenetic analysis based on combined nuclear and mitochondrial sequences found that *Brotogeris* was the closest relative of monk parakeets (Tavares et al. 2006). Four sub-species of monk parakeets are currently recognized based on phenotypic variation of wing length, bill size, body mass, and plumage coloration that is correlated with geographic variation (Spreyer & Bucher 1998).

Monk parakeets are native to Argentina, Brazil, Paraguay, Uruguay and Bolivia. They reside in open, dry lowland areas. They prefer to build nests in tall trees or man-made structures overlooking the landscape, possibly as a method to detect predators from far off distances. They are often found in areas densely populated with humans. Monk parakeets have expanded their habitat due to humans planting trees in urban areas. While most parrot populations are declining due to human exploitation of their habitats, monk parakeets are actually thriving in newly urbanized areas.

Due to the monk parakeets' popularity as a pet bird, large numbers have been exported to the United States. Within a four-year span in the late 1960s to early 1970s it

was reported that 64,225 monk parakeets were imported into the United States (Lever 1987). Many of these 'pet' birds were released by owners or escaped accidentally and were able to survive in the wild and breed. Starting in the 1960s people reported seeing feral free-flying monk parakeets living within North American cities (Spreyer & Bucher 1998). The majority of feral birds within the United States belong to the subspecies *M. m. monachus*, as these are found from Buenos Aires to Uruguay, which is where most of the imported birds come from. These parrots have become extremely successful as a feral species, colonizing areas of New York City (Brooklyn predominately), Chicago, Austin and many cities within Florida and Connecticut. There have been small numbers reported throughout the last 30 years in several other states as well, but these numbers have dwindled and in many cases, the parrots are no longer seen there. Florida has, by far, the largest population of monk parakeets, with 1,174 present in the Audubon Christmas Bird Count of 1994-1995 (LeBaron 1994, 1995). They adapt well to urban environments, taking advantage of tall telephone poles, stadium lights and similar man-made structures to build and sustain their large nests. Outside of the Americas, monk parakeets are found in Spain, Belgium, and Italy, where the populations are rapidly expanding. It would not be surprising if monk parakeet colonies were found in many other countries as well within the next few years.

Monk parakeets feed on several different types of food, including seeds, leaf buds, berries, nuts and blossoms, sometimes even consuming insects (Eberhard 1997; Spreyer & Bucher 1998). Some have been seen feeding on ripening crops as well, which has led South American farmers to consider monk parakeets pests. There are no systematic data showing crop loss due to their feeding habits, however, and farmers'

eradication attempts have been futile (Forshaw 2006). Their generalized food preferences could be one reason the species has easily adapted to life in the United States. Another probable reason this parrot species is so widely successful in the United States and other urban areas is due to its nesting structure. Monk parakeets are unique in that they are the only parrot species to build large, compartmentalized nests. All other parrot species are cavity nesters (Eberhard 1997) and only one other species of parrot, Patagonian conures (Eberhard 1997), nest colonially. Monk parakeets create their nests by weaving sticks together to form a large sphere. Eberhard (1998) and Bucher et al. (1990) have both described nest building behavior and have come up with differing reports. Bucher et al. (1990) asserts that all individuals, including juveniles, will cooperate with one another to enlarge the nests while Eberhard (1998) maintains that males actually do most of the work and focus mainly on their own hole within the nest (Eberhard 1998), so cooperation is less important. Both studies were carried out in the field in similar settings, so I cannot state which of these accounts is more accurate.

Several nests are often found clustered together in the same tree or man-made structure or on nearby structures to form colonies (Eberhard 1998). Monk parakeets are non-migratory; they live within these nests year round and perform maintenance year round (Eberhard 1996). An average nest contains one to four chambers (Bucher et al. 1990) with a mated pair and their nestlings occupying one chamber (Eberhard 1998; Bucher et al. 1990). These structures can grow extremely large; the largest on record weighed 1,200 kg and had over 200 pairs living within it simultaneously (Bucher et al. 1990). There have been reports that monk parakeets will actually exploit already constructed nest structures of other species and use these as a foundation for their own.

Eberhard (1996) found that 20 of 39 nest structures were actually remodeled brown cacholote nests. It also has been reported that monk parakeets use nests of firewood gatherers, jabiru storks, tree-ducks, guira cuckoo and bay-winged cowbirds. Their behavior, in this regard, is flexible.

The greatest cause of mortality in monk parakeets is predation on nestlings and eggs, which accounts for about a quarter of all deaths (Navarro et al. 1992). Predators include crested caracaras, spot-winged falconets, white-eared opossums, and grass snakes in their native habitats. Data are sparse on predation, so I would doubt these are the only predators of monk parakeets. When predators are seen near nests or while birds are foraging, monk parakeets will give alarm calls which increase in frequency as predators near. There are also suggestions that some individuals will act as sentinels during foraging, watching for predators while other individuals eat (Spreyer & Bucher 1998). When foraging, birds rarely travel alone (22.5% of the time), so this is a possibility (Eberhard 1998).

While a long-term study has not been completed, there is evidence that monk parakeets mate for life and are monogamous (Bucher et al. 1991). Extra-pair copulations have never been seen. Monk parakeets delay breeding: individuals are able to breed at two years of age but less than 50% actually do so (Martin & Bucher 1993). The majority of monk parakeets begin breeding at three years of age. It is unknown how long monk parakeets survive in the wild, but in captive settings they live for about 15 years (Alderton 1995). Juveniles begin to leave the parental nests at three months; by the next breeding season virtually all young are gone (Martin & Bucher 1993). On average, juveniles settle 503 m from their parental nests; this is considerably less than white-tailed

black-cockatoos (Saunders 1982), and galahs (Rowley 1983), which settle over 20 km away (Martin & Bucher 1993). Martin and Bucher (1993) suggest that this is because it is more energetically costly to build a new compound nest than to add on to one already present and close by.

Martella (1985) and Martin (1989) have suggested that the social organization of monk parakeets is complex. Reduced natal dispersal, high annual survival rates, delayed breeding and incidental helping at the nest in both the wild and captivity (Bucher et al. 1990; Emlen 1990) might have favored the further evolution of social cooperation in the monk parakeet (Bucher et al. 1990; Martin & Bucher 1993). The fact that several individuals live in close proximity throughout the year and that young have reduced dispersal suggests that relatedness within the group might be high and thus that relationships between individuals other than mates could be important. Also the fact that sentinels are present when foraging suggests that group members are dividing the labor and cooperating with one another to forage. Thus there are several reasons why monk parakeets should show signs of social complexity.

The first step in this research program was to develop an ethogram and to further the basic knowledge of sociality in monk parakeets by creating a behavioral index based on affiliation and aggression between individuals. This index was then used to quantify affiliation between dyads. The reconciliation experiment tested whether reconciliation occurs in monk parakeet societies and if so, whether the value of the relationship between two individuals influenced how readily they reconciled. I hypothesized that monk parakeets have strong individualized social bonds, that reconciliation does occur, and that

the probability of reconciling depends on the prior relationship between the two individuals.

ETHOGRAM

INTRODUCTION

An ethogram is a comprehensive description of the characteristic behavior patterns of a species (Lehner 1979). It is a starting-point for any animal behavior research. Each species exhibits its own unique suite of social behavior patterns, so there is not one unifying definition of what constitutes social behavior, and even closely related species can have vast behavioral differences (de Waal & van Roosmalen 1979; de Waal 1987, 1993; Hohmann & Fruth 2000). Subtle shifts in behavior can also have a large effect on the results. It is particularly important, therefore, to have a rigorous definition of social behavior in place for the species being studied before designing experiments testing sociality.

There are very few behavioral studies on monk parakeets, most of which are anecdotal. There is no comprehensive ethogram available. Alexandro (1978) attempted an ethogram of agonistic behaviors, but it was not complete and many of the descriptions are lacking or sketchy. Spreyer and Bucher (1998) refer to several behaviors, but, again, there is not a complete description. Nowhere in the literature is there an attempt at defining affiliative behaviors or non-social behaviors. To design experiments on the social structure of monk parakeets all behaviors must be understood fully. If a behavior is missed or not understood, the observations could be misinterpreted.

My first goal in putting together this research project was, therefore, to create an ethogram, to classify behaviors as affiliative or agonistic and to create an affiliation index

that would rank each dyad based on the degree of affiliation. Since very little information was available on monk parakeet behaviors it was important to compare behaviors seen in monk parakeets during observations to those of other psittaciforms and to conserve behavior names where appropriate. Behaviors were established through observations and comparisons to ethograms of lovebirds (*Agapornis*: Dilger 1960), budgerigars (*Melopsittacus undulatus*: Brockway 1964a; Brockway 1964b), spectacled parrotlets (*Forpus conspicillatus*: Garnetzke-Stollman & Franck 1991) and orange-fronted parakeets (*Aratinga canicularis*: Hardy 1963). All of these species except lovebirds are Neotropical parrots, so they are probably more closely related to monk parakeets than Australasian or African parrots. Their ethograms were very thorough, and many of the described behaviors were similar to those seen in monk parakeets.

METHODS

Seven monk parakeets were obtained commercially, four from a local breeder (Gems of the Jungle Aviary in Omaha, NE) and three from a pet store (Petco in Lincoln, NE); all individuals were less than a year old upon entering the lab. One individual developed fatty liver disease and was removed from the study. Of the remaining six individuals, four were females (Larry, Curly, Niko, Rosie) and two were males (Moe, Charlie). The genetic relationship between individuals was known: there were two pairs of siblings (Niko and Charlie; Moe and Curly) and the rest were unrelated.

Throughout these studies, the six parakeets were housed singly in separate cages in the same room. To maintain the psychological health and avoid artifacts of captivity,

the birds were given regular socialization sessions with one another either in dyads or triads. Pairs that were least aggressive towards one another were taken out of their cage and allowed to interact with one another for up to an hour three to five times per week for most of their first year in the facility.

A preliminary ethogram was developed based on initial direct observations of social interactions and comparisons to other parrot ethograms. Several behaviors proved similar in monk parakeets and other related species; names for action patterns were conserved where they were clearly homologous (Dilger 1960; Hardy 1963, Brockway 1964a; Brockway 1964b; Garnetzke-Stollman & Franck 1991). Any monk parakeet behaviors previously described in the literature were also taken into consideration (Alexandro 1978; Eberhard 1996; Eberhard 1998; Emlen 1990; Spreyer & Bucher 1998).

Systematic behavioral observations were made in an open room of approximately 4x2 m, containing an 'Avian Adventures Recreation Center' stand, a complex of perches that allowed the birds to be in close proximity, but provided space for them to separate themselves from one another if they so chose. One parrot toy – a rope with colored blocks attached – was available for the birds to manipulate on the stand.

Birds were observed both directly and through videotapes. During the direct observations, the experimenter was outside the room looking through an observation window of one-way glass. The window provided clear viewing of all areas of the room. Lights were off outside the room to ensure that the birds could not see the observer. Direct observations were only used during the first month of observations to develop an initial list of behaviors and to start taking notes. After this, all observations were taken from videotape. A color video surveillance camera was mounted on the wall near the

ceiling, angled down to capture the entire parrot stand. A microphone was present hanging from the ceiling to record any vocalizations. After initial descriptions of behaviors were made through preliminary observations, a controlled design was enacted to find the frequency of behaviors and to develop a behavioral index.

All observations were conducted in dyads to ensure as much precision and control over the interactions as possible. Each bird was paired with every other bird twice for a total of thirty sessions. Testing day and time was randomized for each pair. Birds were taken from their home cages individually and placed on the parrot stand within the open room to start an observation period. All dyads were videotaped while the birds freely interacted for up to an hour. Videotapes were scored using a 1-0 checksheet where presence or absence of behavior was recorded in 30 sec intervals. This method has been commonly used in primate behavioral studies (e.g. Kraemer 1979; Singh 1989) and is easily interpretable for cluster analysis (e.g. Cassini & Vila 1990; Diamond et al. 2006).

Because the frequency of behavioral events declined over time after the birds were introduced, only the first 13 min of each session was quantitatively analyzed (26 min of data per dyad). In most cases, the interaction was allowed to proceed without intervention from the observer. The only exception was when one or both birds flew off the stand and out of view of the camera. When this occurred, I interrupted the session and placed both birds back on the stand before restarting the camera. If the birds refused to remain on the stand after such interventions, however, the session was terminated. In most cases of early termination, I was able to increase the time sampled from the other session of the same dyad to compensate for the lost intervals. The final data set consisted

of 1290 30-sec records; 270 records were missing because of early termination of both sessions for a given dyad.

A rough comparison of the frequencies of occurrence of each of the described behaviors was calculated based on the percentage of 30-sec records in which the behavior was observed. (Note: Some behaviors in the ethogram have a frequency of 0.0% but are described nonetheless. This is because these behaviors were seen during other, initial observations but did not occur during the analyzed intervals.)

TABLE 1: ETHOGRAM**1. Bite (BB) (Freq = 0.1%)**

Bite occurs when one bird pecks or bites another bird's body. The bird opens its bill and closes it on the body of the other individual. This behavior usually occurs on the back or chest. In spectacled parrotlets and orange-fronted parakeets, this behavior was described as a peck (Hardy 1965; Garnetzke-Stollmann & Franck 1991). Dilger (1960) termed it a Bite in lovebirds.

2. Bill-Clasp (BC) (Freq = 0.1%)

Bill-Clasp occurs when two birds interlock their bills; the bills are slightly opened and then closed on one another during the interlock. This behavior is relatively slow when compared to Bill-Fencing and occurs in a different context, frequently with Allopreen. The birds keep their bills clasped for several seconds. Hardy (1963) described this behavior in orange-fronted parakeets, as well.

3. Allofeed (BCB) (Freq = 1.6%)

Allofeed occurs when one bird is in close contact with another individual (the recipient). The actor Head-Bobs while opening its bill. Then the actor clasps bills with the recipient and transfers food to the recipient's mouth. Usually the actor has its head raised higher than the recipient. The main components of Allofeed are Head-Bob with Bill-Clasp, which are two common behaviors; Allofeed is unique in that the sequence is put together to perform the act of food transfer. While the birds' bills are clasped, their heads are usually turned sideways towards each other with their bodies facing outward. Allofeed has been observed between siblings as well as in a female-female pair in the lab. It can be hard to tell if food is actually transferred. The only reliable indicator is when some food gets stuck to one of the bird's bills. Spreyer and Bucher (1998) have previously described this behavior in monk parakeets.

Occasionally, birds will display behaviors similar to those described in orange-fronted parakeets, in which the bird will raise its plumage, bill-snap and dilate its pupils rapidly prior to Allofeed, but this behavior is not consistently seen (Hardy 1963). Spectacled parrotlets and budgerigars perform this behavior in a similar manner (Brockway 1964b; Garnetzke-Stollmann & Franck 1991).

Monk parakeet Allofeed is similar to lovebirds in its appearance and in that it occurs throughout the year and is not just limited to the breeding season (Dilger 1960). Both Bucher (1990), in the wild, and Emlen (1990), in an aviary, observed helping at the nest where siblings fed nestlings. Emlen (1990) found that siblings fed the nestlings one-third of the time. The frequency in the wild is not known. Eberhard (1998) found that Allofeed in the wild was greatest before and during egg laying. The males increased Allofeed at this time due to increased begging from the females. Eberhard (1998) observed a female, male,

male trio in addition to her observations of mated dyads and found that both males Allofed the female.

4. Bill-Fence (BF)

(Freq = 2.5%)

Bill-Fence occurs when two individuals thrust their bills toward each other several times in a row, usually while vocalizing. Bill-Fence is much more rapid than Bill-Clasp and is seen in a different context, frequently with Bill-Thrust. In lovebirds and spectacled parrotlets this behavior has been interpreted as agonistic (Dilger 1960; Garnetzke-Stollmann & Franck 1991). Unlike lovebirds, however, monk parakeets do not direct Bill-Fence towards the opponent's toes (Dilger 1960). In orange-fronted parakeets, Bill-Fence is termed Bill-Spar and only occurs when Allofeed is being performed; sometimes if an individual's movement in Allofeed is too rapid, the partner will initiate Bill-Sparring momentarily. It is not seen in any other context in orange-fronted parakeets (Hardy 1963). In monk parakeets it is seen in contexts similar to all three species mentioned above.

5. Touch-Foot (BFT)

(Freq = 4.9%)

Touch-Foot occurs when a bird lowers its head and touches its own foot with its bill. Usually it nibbles on its foot as well, possibly to scratch or remove scales.

6. Bill-Gape (BG)

(Freq = 3.7%)

Bill-Gape occurs when the bird opens its bill wide. Usually the bird is sitting or leaning back slightly at an angle from the perch when performing this behavior. Bill-Gape does not appear to occur in an agonistic context in monk parakeets, unlike its described occurrence in lovebirds, budgerigars and orange-fronted parakeets. In these species the behavior referred to as Bill-Gape is more similar to Bill-Thrust in monk parakeets (Dilger 1960; Brockway 1964; Hardy 1965).

7. Honing-the-Tomium (BGR)

(Freq = 23.7%)

Monk parakeets, like many other parrots, have rasp-like ridges that run across the hard palate inside the upper bill. The birds hone the sharp edge or "tomium" of the lower bill by rubbing it back and forth against this rasp-like area. Dilger (1960) termed this behavior "honing the tomus."

8. Push (BP)

(Freq = 1.4%)

One bird directs its bill towards another, opens it, and gently pushes the other bird with it. This behavior is seen in spectacled parrotlets as well (Garnetzke-Stollmann & Franck 1991).

9. Allopreen (BPO & BPR)

(Freq = 5.8%)

Allopreen occurs when two birds are perched in close contact with one another. One bird will run its bill through the other bird's head and neck feathers, removing the white matter around the shaft. At times, a bird will direct Allopreening toward another area, such as the wing or back, but this usually lasts only a second or two, and it is infrequent. The bird being preened usually fluffs up all its head feathers. Occasionally, when a bird tries to Allopreen another individual, the recipient will Bill-Fence or move its head away. In monk parakeets Allopreen is common in the wild and in an aviary setting (Emlen 1990; Spreyer & Bucher 1998). In both cases, individuals will Allopreen other individuals in addition to their mates. Spreyer and Bucher (1998) described Allopreen as reciprocal and involving all members of the communal nests. The frequency of Allopreen increases when the young are hatched, continues to be frequent during the winter, and drops to a minimum during the breeding season (Spreyer and Bucher 1998). It is similarly performed in several other psittaciforms, including lovebirds, budgerigars, spectacled parrotlets, and orange-fronted parakeets (Dilger 1960; Hardy 1963; Brockway 1964; Garnetzke-Stollmann & Franck 1991). It is seen more frequently in monk parakeets than in lovebirds (Dilger 1960). BPR means Allopreen is being received and BPO means Allopreen is being given to another individual.

10. Self-Preen (BPS)

(Freq = 7.4%)

Self-Preen occurs when a bird runs its bill through its own feathers. The birds Self-Preen anywhere they can reach, though they are usually seen preening their wing and chest feathers. Occasionally they Self-Preen their back feathers including the tail feathers, which they run through their bills in long, continuous movements. Plumage-Ruffle usually occurs in conjunction with Self-Preen. Spreyer and Bucher (1998) found that preening occurs throughout the day, with a peak in afternoon, and that preening happens most often in May (early winter) and November (late spring). Preening is similar in lovebirds and budgerigars (Dilger 1960; Brockway 1964).

11. Body-Rigid (BRF)

(Freq = 1.1%)

Body-Rigid occurs in monk parakeets when a bird's feathers are slicked down as close to the body as possible and it stands rigid. Its body is angled forward with its head very forward. In other species, including lovebirds, spectacled parrotlets, and budgerigars this behavior is associated with attacks (Dilger 1960; Hardy 1963; Garnetzke-Stollmann & Franck 1991). Spreyer and Bucher (1998) termed this behavior a threat display. The Rigid-Forward-Posture, as Martella and Bucher (1990) refer to Body-Rigid, is assumed not only in conflicts with conspecifics but also when birds attack or mob other species (Martella and Bucher 1990).

12. Bill-Touch (BT)**(Freq = 0.1%)**

Bill-Touch occurs when one individual touches another individual's body or bill with a closed bill. This movement is not rapid. This behavior is seen in spectacled parrotlets as well (Garnetzke-Stollmann & Franck 1991).

13. Bill-Thrust (BTH)**(Freq = 3.4%)**

Bill-Thrust occurs when a bird lunges its head at its opponent with its bill open. If the bill actually touches the other individual during a Bill-Thrust, a bite has occurred after the thrust. In lovebirds this behavior occurs when one individual Bill-Thrusts toward another's toes (Dilger 1960). This differs from monk parakeets in that most Bill-Thrusts are directed towards the opponent's upper body rather than their toes. Occasionally an individual will bite another's toes, but a Bill-Thrust does not occur prior to this. In budgerigars this behavior was interpreted as agonistic (Brockway 1964). Brockway (1964) made a distinction between two different degrees of a similar behavior and termed them Bill-Gape and Bill-Thrust in budgerigars. In monk parakeets there is no distinction between these behaviors. Bill-Gape in monk parakeets refers to an entirely different behavior than Bill-Gape in budgerigars (Brockway 1964).

13. Body-Touch (BTO)**(Freq = 22.0%)**

Body-Touch occurs when two birds sit next to each other for an extended period of time with their bodies touching one another's. This occurs quite often in pairs as they perch in the wild, and it has been similarly described in spectacled parrotlets (Garnetzke-Stollmann & Franck 1991; Spreyer & Bucher 1998).

14. Bill-Wipe (BW)**(Freq = 2.6%)**

Bill-Wipe occurs when an individual lowers its head and wipes its bill across the perch.

15. Walk-Rigid (BWR)**(Freq = 0.7%)**

Walk-Rigid looks very similar to Body-Rigid, but the bird is walking at the same time. A bird will walk towards another individual with deliberate movement. Its head and body are tilted forward and rigid. This behavior is very similar to that described in lovebirds (Dilger 1960). In orange-fronted parakeets this behavior is referred to as Run-Rush, Chase and Slow-Advance (Hardy 1965). I made no distinction between these three behaviors in monk parakeets as the only difference was the speed with which the individual reached its opponent, and when scoring behavior, speed can sometimes be hard to quantify.

16. Climb (CL) (Freq = 0.0%)

Monk parakeets Climb in much the same way as lovebirds and budgerigars (Dilger 1960; Brockway 1964). To move upwards, the bird grabs a support above its head with its bill and then moves its feet upwards in the direction of its bill. The bird does this repeatedly until it reaches the desired height. To move downward, the bird moves its head to the side and grabs a support lower than its head. It then moves its feet below its head and does this repeatedly until it reaches the desired height.

17. Foot-Back (FBO) (Freq = 0.0%)

Foot-Back occurs when one individual will take the leg closest to the other individual, raise it off the perch and place it on the other individual's back. This behavior may be linked to copulation, though it was seen to occur when mounting did not. Foot-Back appears to be equivalent to clawing in orange-fronted parakeets (Hardy 1963).

18. Foot-Lift (FL) (Freq = 2.8%)

Foot-Lift occurs when an individual takes its foot off the perch, lifts it and it holds it in midair for more than a second. The foot is held parallel to the body.

19. Fly (FLY) (Freq = 2.8%)

Fly occurs when an individual flaps its wings and raises itself in the air. Spreyer and Bucher (1998) describe this behavior as swift and quick in the wild. The birds fly in small flocks where changes in direction and altitude are sudden and occur frequently. Their wings are level with their bodies and are never raised over the body. Wing beats are rapid (Forshaw 1989). (Note: in the lab birds only Fly from each other to terminate agonistic encounters.)

20. Scratch (FS) (Freq = 2.7%)

Scratching occurs on the head and the facial area. The bird lifts its leg over the wing and scratches its head with the longest toe. The bird either moves its head or foot in order to position its foot on the spot being scratched. Scratching in monk parakeets is common throughout the year (Spreyer & Bucher 1998) and is similar to lovebirds and budgerigars (Dilger 1960; Brockway 1964).

21. Grate-Walk (GW) (Freq = 0.0%)

Grate-Walk occurs when a bird walks along the grate on the stand.

22. Head-Bob (HB)**(Freq = 3.2%)**

In monk parakeets Head-Bob is performed by an individual repeatedly moving its head up and down vertically while its neck is conspicuously pumped up and down with the movements. The rapidity and frequency of Head-Bob varies greatly between individuals, with some individuals only performing Head-Bob once and others performing it over five times in a row. Some individuals move their head up and down slowly while others perform this movement quicker. A distinction is made between Head-Bob and Head-Quake, in that the movements in Head-Bob are slower and more pronounced, meaning the neck clearly is moving up and down, while in Head-Quake it is so rapid it might look as if only the head is moving. In several other parrot species (Dilger 1960; Hardy 1963; Brockway 1964) Head-Bob occurs only in the context of courtship feeding. While these descriptions of the behavior are very similar to that seen in monk parakeets, Head-Bob is frequently seen in monk parakeets outside of the courtship context.

23. Head-Crouch (HC)**(Freq = 9.5%)**

Head-Crouch occurs when an individual draws its head down. The scapulars are slightly raised as well. The bill does not touch the chest as with Head-Down, but the bird is still facing forward. This behavior frequently occurs with Fly and Body-Rigid whereas Head-Down frequently occurs with Allopreen.

24. Head-Down (HD)**(Freq = 4.1%)**

Head-Down is performed by a bird either cocking its head to the side or pushing its head straight down while in close contact with another individual. The bill is pulled in very close to the body and the feathers are usually fluffed up. This behavior differs from Head-Crouch as it often occurs with Allopreen while Head-Crouch occurs in a different context, mainly when Fly or Body-Rigid occur. This behavior has been inferred to function in soliciting Allopreen in lovebirds, budgerigars and spectacled parrotlets (Dilger 1960; Brockway 1964; Garnetzke-Stollmann & Franck 1991).

25. Head-Elongate (HE)**(Freq = 8.8%)**

Head-Elongate occurs when a bird raises its head up, fully extending its neck and holds it there for at least a second; This movement is slower than Head-Bob, as the individual is actually holding its head high, whereas in Head-Bob there is no pause between going up and going down.

26. Head-Jerk (HJ)**(Freq = 0.0%)**

Head-Jerk occurs after a bird performs Head-Elongate. The individual pulls its head backwards in a rapid movement. Usually a vocalization occurs. In orange-fronted parakeets this behavior is associated with Head-Bob as Head-Bob usually leads to

Head-Jerk and is associated with regurgitation during Allofeed (Hardy 1963). In monk parakeets, Head-Jerk does occur in this circumstance occasionally, but not always.

27. Head-Lower (HL) (Freq = 7.8%)

Head-Lower occurs when a bird lowers its head and then slowly and jerkily brings its head back up. The head is moved upward until the bird is standing very tall and erect. It will then put its head back down, sometimes touching the perch with its bill and bring it up again. It may bow in this fashion a number of times. Sometimes, it will not move its head down very far, so that it is only at chest level, but will bring it jerkily and slowly up until it is erect and tall. It appears to be equivalent to Bowing in orange-fronted parakeets (Hardy 1965) and Head-Pumping in budgerigars (Brockway 1964). Brockway's (1964) description of the behavior in budgerigar gives a clear image: "Pumping: This involves a series of up and down motions of the head and neck. Both are held horizontally throughout, giving the appearance of a 'hump-backed individual at the apex of the downward movement.'"

28. Head-Quake (HQ) (Freq = 1.9%)

This behavior looks similar to Head-Bob in that the head is pumped up and down. It is, however, a distinct behavior, in that the head is pumped much more rapidly than Head-Bob and the movements are much smaller. The neck is barely lifted or lowered. The individual performing the behavior is almost always looking at another individual. It is often seen with Walk-Rigid and Bill-Thrust.

29. Head-Shake (HS) (Freq = 1.9%)

Head-Shake occurs when a bird vigorously shakes its head from side to side. Eberhard (1998) describes Head-Shake as the beginning component of a copulation bout. Head-Shake occurs when food is stuck to the bill as well, which is similar to its occurrence in lovebirds, budgerigars and orange-fronted parakeets (Dilger 1960; Brockway 1964; Hardy 1963). It probably has many other functions as well.

30. Head-Tilt (HT) (Freq = 28.8%)

Head-Tilt occurs when an individual cocks or leans its head to one side. This behavior may be adjunct to listening, as it usually occurs when external noise is heard.

31. Look-Away (LA) (Freq = 8.4%)

Look-Away occurs when an individual that was previously looking at another individual looks away.

32. Look-Around (LR) (Freq = 7.8%)

Look-Around occurs when an individual moves its head around and surveys its surroundings. This sometimes occurs when an external noise is heard and after or before a Head-Tilt.

33. Look-Towards (LT) (Freq = 59.0%)

Look-Towards occurs when an individual looks at another individual or in that individual's direction.

34. Ladder-Walk (LW) (Freq = 0.0%)

Ladder-Walk occurs when an individual climbs a ladder.

35. Move-From (MF) (Freq = 8.7%)

Move-From occurs when an individual moves more than one body length away from another individual.

36. Move-Towards (MT) (Freq = 13.1%)

Move-Towards occurs when an individual moves in the direction of another individual.

37. Object-Manipulate-Solitary (OMS) (Freq = 2.2%)

Object-Manipulate-Solitary occurs when an individual manipulates the toy in the testing room alone.

38. Object-Manipulate-Other (OO) (Freq = 11.1%)

Object-Manipulate-Other occurs when an individual manipulates an object other than the toy with its bill, such as the perch or ladder.

39. Object-Manipulate-Together (OT) (Freq = 0.0%)

Object-Manipulate-Together occurs when two individuals manipulate the toy simultaneously. Object-Manipulate-Together is seen when two individuals were perched near the toy in close proximity and had been performing behaviors such as Allopreen and Bill-Clasp.

40. Plumage-Raised (PH) (Freq = 0.8%)

Plumage-Raised occurs when an individual lifts the feathers on its head only. This is different from Plumage-Ruffle as just the feathers on the very top of the head are

raised and the head is held high. This behavior is seen in a different context, occurring often with Body-Rigid and Head-Quake. In Plumage-Ruffle, when the head feathers are raised, so are the face and neck feathers.

41. Plumage-Fluff & Plumage-Ruffle (RP & PR) (Freq = 62.8% & 8.8%)

Plumage-Ruffle occurs when a bird fluffs up its feathers to the point where they are virtually perpendicular to its skin. Sometimes a bird will ruffle its feathers all at once and other times it gradually ruffles its entire plumage over several seconds. This behavior is performed in association with Self-Preen, but it also occurs in a great variety of other situations. Plumage-Ruffle is descriptively similar to that in lovebirds, budgerigars and orange-fronted parakeets, but it is not always seen in conjunction with the same behaviors as described in these three species (Dilger 1960; Brockway 1964; Hardy 1963). The distinction between Plumage-Ruffle and Plumage-Fluff is the duration of the behavior. In Plumage-Ruffle the feathers are quickly lowered again while in Plumage-Fluff the feathers stay raised for more than 30-sec and are gradually lowered.

42. Sit (S) (Freq = 0.2%)

Sit occurs when an individual is sitting and not performing any other behaviors within the time interval scored.

43. Tail-On (TO) (Freq = 1.8%)

Tail-On occurs when an individual's tail feathers are touching another individual's body for an extended period of time. This can occur when a bird walks past another individual and stops at a point where its tail feathers happen to be on top of another's tail feathers; this is quite common. It also occurs when two birds' bodies are touching.

44. Tail-Wag (TW) (Freq = 3.3%)

Tail-Wag occurs when a bird moves its tail feathers horizontally from side to side. Lovebirds perform Tail-Wag in a similar manner (Dilger 1960).

45. Vocalize (V) (Freq = 15.9%)

Vocalize occurs when an individual makes any sound or vocalization.

46. Walk (WA) (Freq = 13.1%)

Monk parakeets Walk on the ground in a forward motion, putting one foot in front of the other. They do not hop. When on a perch, the birds will either move sideways along the perch (sometimes referred to as Sidling in other species) or walk forward along it. Spreyer and Bucher (1998) classify their walk as a "slow, waddling gait."

47. Wing-Flap (WF)**(Freq = 0.0%)**

Wing-Flap occurs when an individual shrugs its scapulars, raises its wings slightly and beats them several times. This is different from Wing-Whir in that the wings are only partially raised, not fully raised and therefore a full extension of the wing does not occur.

48. Stretch (WS)**(Freq = 0.0%)**

Stretch occurs when one wing is extended sideways and the foot is pushed back simultaneously. The bird then repeats this behavior on the other wing. Stretch usually ends with both carpals being raised over the head. Sometimes wings are extended downward one at a time as well. This behavior is similar in lovebirds and budgerigars (Dilger 1960; Brockway 1964). It is usually associated with Self-Preen (Spreyer & Bucher 1998).

49. Wing-Whir (WW)**(Freq = 1.6%)**

Wing-Whir occurs when a bird rapidly flaps its wings while gripping the perch. Sometimes two individuals will Wing-Whir simultaneously or one will begin shortly after another has initiated the Wing-Whir and they will either continue simultaneously or alternate. This behavior is referred to as Wing-Flapping in orange-fronted parakeets (Hardy 1963). Wing-Whir in monk parakeets looks similar to the behavior in lovebirds and orange-fronted parakeets (Dilger 1960; Hardy 1963). In orange-fronted parakeets Wing-Flap is described as an intention movement of flight and as a component of aggression (Hardy 1963).

NON-BEHAVIORS RECORDED DURING TRIALS

50. Bird-Outside-of-View (OSI)

Bird-Outside-of-View is scored when an individual is outside of view on the video camera; this occurs if the bird flies off the stand in the room.

51. External-Noise (N)

External-Noise is scored when external noise is heard outside the testing room.

52. Observer-in-Room (OBS)

Observer-in-Room is scored when an observer is in the testing room. This only occurs when the birds are placed in the room at the beginning of the trial or when a bird has flown off the perch out of the viewing area of the video camera and has to put back on the stand.

53. Sign-Up (SN)

At the beginning of the trial, when a sign is up that says who the subjects are, trial number, date, time, etc.

BEHAVIORAL INDICES

INTRODUCTION

When studying sociality, it is necessary to go beyond the ethogram to determine which behaviors are social and, of these, which are affiliative or agonistic. Relationships between individuals can then be determined based on the frequency and timing of these behaviors. The most common method for testing reconciliation is by observing an agonistic encounter between two individuals and then scoring affiliation after this encounter. Most reconciliation studies do not present an ethogram or a classification of behaviors as affiliative or agonistic. They merely list the behaviors scored and classify these based on their assumptions of the function behind these behaviors. In primates, the affiliative behaviors most often used are sitting in close proximity, allogrooming, touching, embracing and kissing (de Waal 2000). These behaviors are most likely affiliative, but the researchers could be missing less obvious actions simply because there was no prior behavioral analysis. Agonistic behaviors can be missed quite often as well. Several displays look subtle to the human eye, and if the experimenter is only looking for conspicuous agonistic behaviors, such as a physical attack with injury, they may be missing the complex behavior patterns happening in these highly social species. In Seed et al.'s (2007) study on rooks, the behaviors classified as affiliative and agonistic were presented, but there was no explanation of how the experimenters chose those behaviors. It may be that they did not see reconciliation because they did not have a complete picture of all agonistic and affiliative behaviors. Seed et al. (2007) states that mated pairs

never perform agonistic behaviors towards one another, which is unlikely. They were not scoring subtle agonistic behaviors, however, and these might be the only ones mated pairs perform. Experimenters must classify behaviors to the fullest extent possible before experiments on reconciliation can be completed.

In order to classify behaviors as affiliative or agonistic and to determine the relationships between the birds, I did a cluster analysis of the similarity matrix of social behaviors from the initial sessions used in the ethogram study.

METHODS

After the ethogram was developed, I used the octave method to decide the correct interval to score behavior (Diamond and Bond 1999). Initially, the behavior was scored at 8 sec intervals, which are fairly short, but it was not known whether this was appropriate. If a time interval is too short you will lose all structure in your data because patterns will be dissected into different intervals and will not show up as associated. If a time interval is too long, the structure will be lost again as all behaviors will be meshed together and no patterns will show up. Therefore an initial short time period of 8 sec was used, because it can be lengthened by combining consecutive intervals. The 1-0 presence/absence checksheet method can provide information on both the frequency and duration of behaviors if the appropriate time interval is used (Suen and Ary 1984; Rhine and Linville 1980).

During each interval on the 1-0 checksheet, every behavior was marked as one if it occurred in that interval or zero if it did not. This event matrix, therefore, provided a

measure of how often one behavior appeared during the same time interval as another behavior. The checksheet was converted into a similarity matrix using a hypergeometric similarity analysis (Li and Dubes 1984; 1989), similar to Diamond and Bond (1999) and Diamond et al. (2006). All behaviors were run through a hypergeometric similarity analysis. This analysis calculates the probability of two behaviors occurring in the same sample under the assumption of randomness. It takes into account how many samples both behaviors occurred in, how many samples only one of the behaviors occurred in, the total number of samples and the proportion of ones in each column. Then it calculates how probable the observed similarities were if there was no relationship between the two behaviors by calculating the probability of association if the two columns were repeatedly, randomly permuted relative to one another.

The output provides similarity values from zero to one of the likelihood of two behaviors occurring in the same interval. These values give the statistical significance of the association between two behaviors across the time samples provided. In cases where the probability was 0.95 or higher the two behaviors can be considered significantly associated with one another. In cases where the probability was 0.05 or lower the two behaviors can be considered significantly unassociated with each other, meaning they have a negative relationship and rarely occur within the same interval. If the probability is in between these thresholds then the two behaviors' relationship is random with respect to one another, meaning they are not associated or similar to one another. This method has advantages over traditional hierarchical cluster analyses in that associations between behaviors are not changed depending on the behavior's association to other behaviors. The behaviors could be linked with several other behaviors and thus, the assumption that

each behavior fits on a “tree” in a certain place is false. Therefore, after analysis behaviors that are uninformative can be removed without affecting the entire analysis and having to rerun it.

To decide the appropriate time interval, the 8 sec intervals were successively merged together to create data sets of 16 sec intervals, 32 sec intervals, and 64 sec intervals. The 32 sec interval produced the highest amount of associations above 95% and was chosen to be the time interval used for further analysis. This yielded, at maximum, 52 samples per bird per dyad, but because some samples were missing due to shortened sessions, the total number of samples analyzed was 1291.

Several behaviors were deemed uninformative and were removed at this point. Behaviors that occurred in five or fewer samples were removed as the associations of such rare events are not reliable. The main focus of this analysis was to decide which behaviors were social, and of these, which could be classified as agonistic or affiliative based on their association with similar behaviors. Thus, behaviors that were deemed non-social from the initial hypergeometric similarity analysis, such as Foot-Scratch, Foot-Lift, Sit, etc. were also removed from further analysis. After removing these behaviors, an initial multidimensional scaling analysis (MDS) was completed on the 25 remaining behaviors.

MDS provides a graphical representation of the relationships between a set of points in space, which makes it a good technique to express the hypergeometric similarity matrix in an easily readable form. In this case, the MDS analysis took the hypergeometric similarity matrix and plotted each behavior as a point in space. These points or behaviors were then linked together with solid lines and dashed lines if the

association was significant. When a segment of points produce a closed polygon, it was considered a meaningful cluster (Diamond et al. 2006). The cluster is a graphical representation, which shows that each behavior within it is associated with every other behavior within that cluster. Tinbergen (1950) observed that behaviors are hierarchically organized meaning that neural units that control functionally related behaviors are more closely associated with one another in the nervous system than those behaviors that are not similar in function. These functionally related behaviors will, therefore, occur closer in time to one another than unrelated ones. So it can be assumed that behaviors closely associated in time are functionally similar, and thus clusters of associated behaviors will reflect similar functions.

Based on this analysis each behavior was assigned two weighted scores reflecting how well it linked to the affiliation and the agonistic clusters. The scores were obtained by calculating the average similarity between each behavior and all others (hereafter referred to as the total linkage score) and the average similarity for behaviors within each of the clusters. The affiliative weighting for each behavior was the difference between its total linkage and its affiliative similarity score, and likewise for its agonistic weighting. The weightings reflect the centrality or importance of that behavior as an indication of the bird's motivational state. The affiliative and agonistic weightings proved to be inversely correlated across the 25 behaviors ($r=-0.98$, $p<.0001$). In subsequent analyses, therefore, the affiliation score could be used alone to determine whether dyads were affiliative or agonistic and to determine whether reconciliation occurs.

These weightings allowed for a dyadic affiliation index to be created. Each occurrence of a behavior within the binary event matrix was replaced with its weighted

affiliation score. Then the affiliation scores were added across the sample interval, producing a summed affiliation score. For each dyad, the summed affiliation scores across all samples were added and then averaged to give one affiliation score for each dyad. This average affiliation score for each dyad was then compared to zero using a Wilcoxon signed-ranks test. Dyads with scores significantly greater than zero were considered affiliative, and dyads with scores significantly lower than zero were considered agonistic.

RESULTS

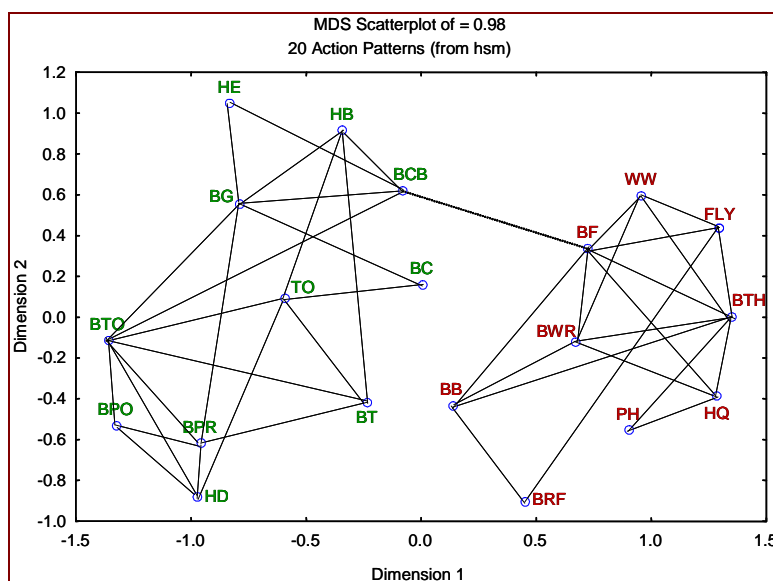
The MDS separated the behaviors into two distinct clusters based on significant similarity values. Initially the 25 behaviors that were common and thought to be social were run through the analysis. Three of the common behaviors (HC: Head-Crouch, RP: Plumage-Fluff, and LT: Look-Towards) did not link significantly with either of the clusters so they were removed from the analysis. Two behaviors (HL: Head-Lower and BP: Bill-Push) were linked equally with both clusters. They were removed because they were not differentially informative. 20 behaviors remained that were linked with at least two and as many as seven other behaviors within the cluster at the similarity value of 0.98. There was only one link remaining between the two clusters (between BF: Bill-Fence and BCB: Allofeed). From the original 54 behaviors scored, two distinct clusters emerged: 11 behaviors were linked to form an affiliation cluster and nine behaviors were linked to form an agonistic cluster (Fig. 1; Table 2).

TABLE 2: AGONISTIC AND AFFILIATIVE WEIGHTINGS

| Acronym | Behavior | Agonistic Weight | Affiliative Weight | Agonistic Weight – Affiliative Weight |
|---------|--------------------|------------------|--------------------|--|
| BTO | Body-Touch | -0.41919 | 0.28355 | -0.70274 |
| BPR | Allopreen Received | -0.25063 | 0.15281 | -0.40344 |
| HE | Head-Elongate | -0.19643 | 0.14988 | -0.34631 |
| BPO | Allopreen | -0.19678 | 0.11228 | -0.30906 |
| BG | Bill-Gape | -0.17796 | 0.12502 | -0.30298 |
| HD | Head-Down | -0.16853 | 0.09025 | -0.25878 |
| HB | Head-Bob | -0.07877 | 0.05198 | -0.13075 |
| TO | Tail-On | -0.07476 | 0.04550 | -0.12027 |
| BT | Bill-Touch | 0.01705 | -0.02283 | 0.03989 |
| BCB | Allofeed | 0.02702 | -0.02581 | 0.05283 |
| BC | Bill-Clasp | 0.05164 | -0.05044 | 0.10207 |
| BB | Bill-Bite | 0.10654 | -0.00116 | 0.10770 |
| BRF | Body-Rigid | 0.04696 | -0.06128 | 0.10824 |
| PH | Plumage- Raised | 0.08087 | -0.07765 | 0.15852 |
| BWR | Walk-Rigid | 0.08262 | -0.08123 | 0.16384 |
| FLY | Fly | 0.13178 | -0.11687 | 0.24865 |
| WW | Wing-Whir | 0.15157 | -0.12933 | 0.28090 |
| BF | Bill-Fence | 0.14938 | -0.13447 | 0.28385 |
| HQ | Head-Quake | 0.20470 | -0.17221 | 0.37691 |
| BTH | Bill-Thrust | 0.26835 | -0.23515 | 0.50350 |

The affiliative behaviors are indicated in green. The agonistic behaviors are indicated in red. The last column indicated the difference between the agonistic weight and the affiliative weight.

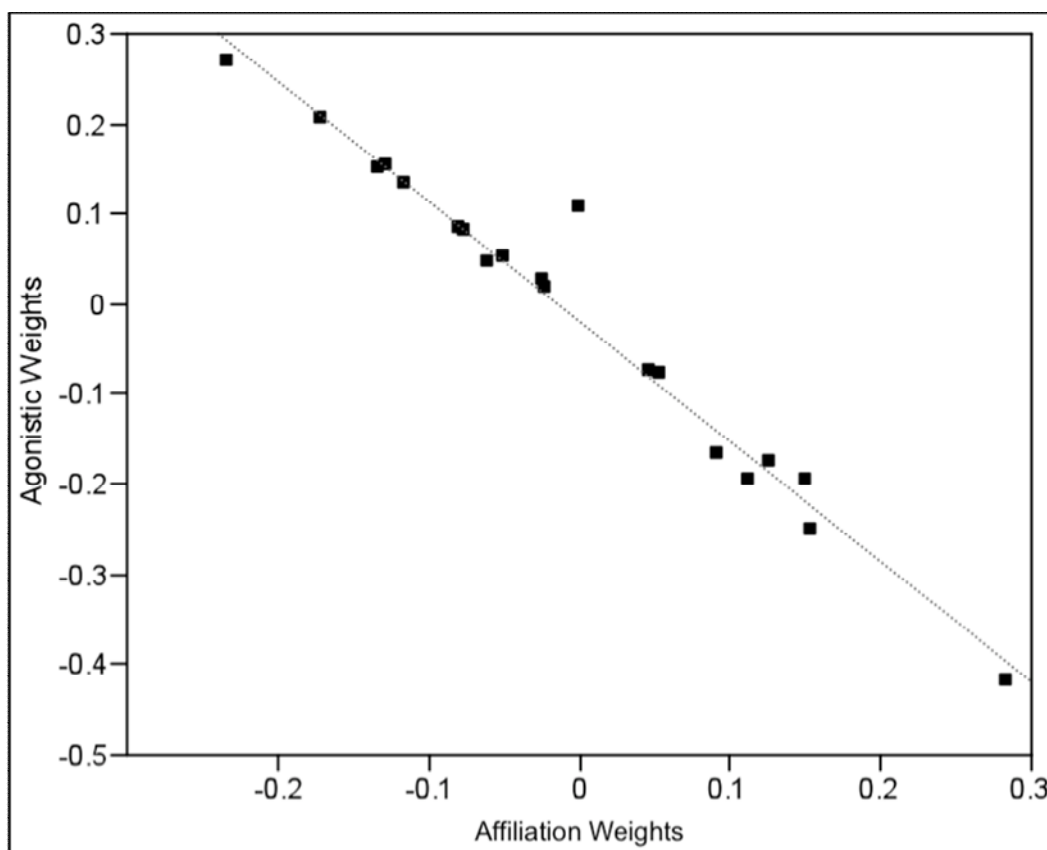
FIGURE 1: CLUSTER ANALYSIS OF AFFILIATIVE & AGONISTIC BEHAVIORS



Each line between behaviors indicates they have a similarity value ≥ 0.98 . Each behavior is linked to at least two other behaviors within the cluster and up to as many as seven other behaviors. The cluster on the left with behaviors in green is the affiliation cluster. The cluster on the right with behaviors in red is the agonistic cluster.

A Pearson correlation was performed on the 20 behaviors clustered within the MDS analysis. It showed that agonistic and affiliative weightings were significantly inversely correlated ($n=20$, $r=-0.98$, $p<.0001$; Fig. 2). In subsequent analyses, therefore, only the affiliation weightings were used based on these results.

FIGURE 2: LINEAR REGRESSION OF AGONISTIC & AFFILIATIVE WEIGHTINGS



A correlation analysis was performed comparing the agonistic weightings to the affiliative weightings. The Y-axis is the agonistic weighting and the X-axis is the affiliative weighting. A linear fit is represented by the dashed line. The weightings were significantly inversely correlated.

The dyadic affiliation index compared the average affiliation score for each dyad to zero. Each dyad was tested independently of every other dyad. Most of the dyads had a sample size of 104, but in the few cases, the sample size was less or more ranging from eight to 106. Based on a Wilcoxon signed-rank test, four of the 15 dyads tested had significantly negative affiliation scores and six had significantly positive affiliation scores.

FIGURE 3: DYADS

| | | | | | |
|-------|---------|-------|-------|-----|------|
| | Charlie | Curly | Larry | Moe | Niko |
| Curly | Ch-Cu | | | | |

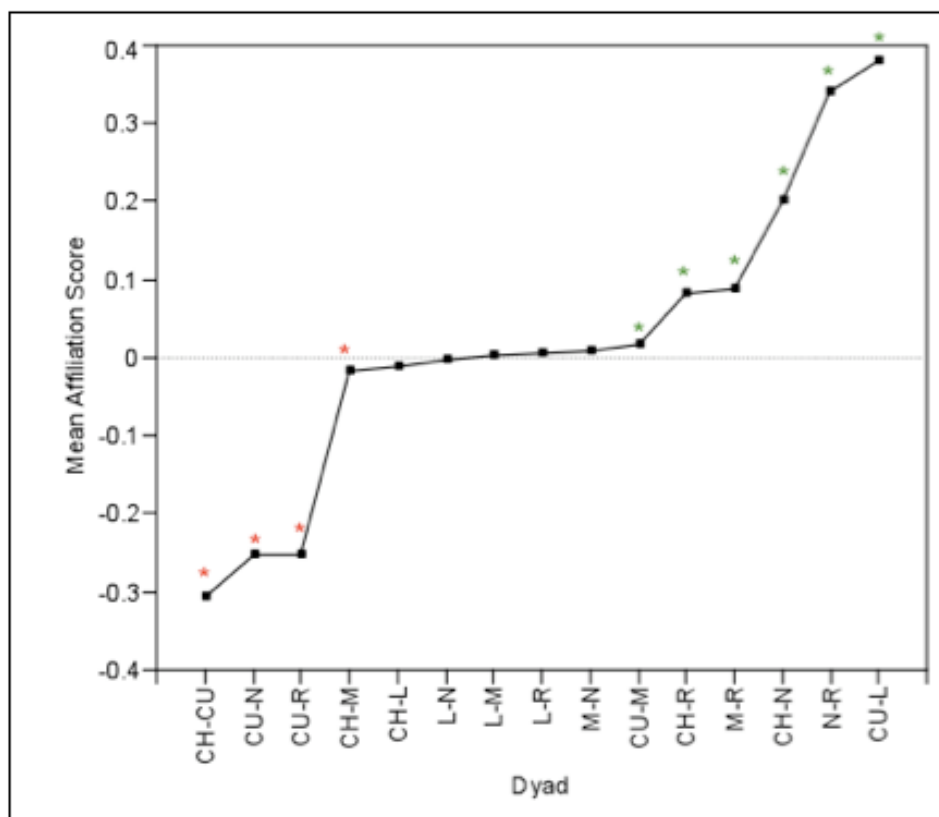
| | | | | | |
|-------|------|------|-----|-----|-----|
| Larry | Ch-L | Cu-L | | | |
| Moe | Ch-M | Cu-M | L-M | | |
| Niko | Ch-N | Cu-N | L-N | M-N | |
| Rosie | Ch-R | Cu-R | L-R | M-R | N-R |

Each dyad is shown above with its name. The dyads shown in red are agonistic; the solid red indicates a highly agonistic relationship. The dyads shown in green are affiliative; the dark green indicates a highly affiliative relationship.

TABLE 3: WILCOXON SIGNED-RANK TESTS RESULTS BY DYAD

| Dyad | Sample Size | Median | <i>T</i> | Probability | Significance |
|-------|-------------|---------|----------|-------------|--------------|
| Ch-Cu | 10 | -0.3520 | -18.0 | 0.008 | * |
| Cu-N | 8 | -0.2513 | -10.5 | 0.031 | * |
| Cu-R | 22 | -0.2352 | -52.5 | <0.001 | * |
| Ch-M | 104 | 0.0000 | -114.0 | 0.004 | * |
| Ch-L | 104 | 0.0000 | -14.5 | 0.090 | |
| L-N | 104 | 0.0000 | -1.5 | 0.500 | |
| L-M | 104 | 0.0000 | 3.0 | 0.250 | |
| L-R | 104 | 0.0000 | 84.0 | 0.243 | |
| M-N | 104 | 0.0000 | 25.5 | 0.234 | |
| Cu-M | 104 | 0.0000 | 74.5 | 0.006 | * |
| Ch-R | 104 | 0.0000 | 403.0 | <0.001 | * |
| M-R | 106 | 0.0000 | 492.5 | <0.001 | * |
| Ch-N | 104 | 0.2836 | 1958.0 | <0.001 | * |
| N-R | 104 | 0.3291 | 2376.5 | <0.001 | * |
| Cu-L | 104 | 0.3958 | 2576.5 | <0.001 | * |

FIGURE 4: DYAD AFFILIATION SCORES



The red asterisks denote a significantly agonistic relationship. The green asterisks denote a significantly affiliative relationship.

DISCUSSION

The behavioral weightings and the cluster analysis revealed which behaviors were associated with affiliative and which with agonistic interactions. Most of the social behaviors were either linked to one or the other cluster and their weights reflected the strength of this linkage.

In a typical affiliative interval, both birds will sit with Body-Touch. They might Allopreen one another. Occasionally an individual will Head-Down, which might be an indication that it is soliciting Allopreen from the other individual. Birds that are affiliative are often in close contact, which is why Tail-On happens quite regularly in

affiliative encounters. Head-Elongate, Bill-Gape and Head-Bob are displays one or both birds make often while sitting with Body-Touch, though functionally it is not known what these behaviors mean and why they are associated with affiliation.

In a typical agonistic encounter, one bird will have its Plumage-Raised and the other bird will have its Body-Rigid. One, apparently the dominant bird, will Head-Quake and Bill-Thrust in the direction of the other, apparently subordinate individual. Then it will Walk-Rigid towards the subordinate. The subordinate bird may respond with Body-Rigid. Once the dominant individual reaches the subordinate it will Bill-Bite, and the subordinate will counter with Bill-Fence. They will engage in Bill-Fence for a few seconds while the subordinate is Wing-Whirring. Usually, the subordinate will Fly to separate itself from the dominant and end the agonistic encounter.

Three behaviors (BT: Bill-Touch, BCB: Allofeed, and BC: Bill Clasp) were deemed affiliative based on their highly significant linkages to other affiliative behaviors, but their weightings revealed linkages to the agonistic cluster as well. Both Bill-Touch and Bill-Clasp happen quite often within the same interval as Allofeed, which retains a linkage to Bill-Fence in the agonistic cluster. In the majority of behavioral studies, Allofeed is considered an affiliative behavior, as one individual is giving food to another. In anthropomorphic terms, therefore, it “must” be affiliative because one animal is giving something up for another. This analysis has shown that behaviors such as Allofeed can have much more complex meanings than humans prescribe to them. It is extremely difficult to categorize motivational states in these animals; analyses such as this one are the only rigorous way to really test behaviors without putting anthropomorphic meanings

on them and even in these cases, there are anomalies showing how limited we are in our ability to test these things.

Usually Allofeed is only attempted between pairs that have a significant affiliative bond with one another. During a typical occurrence of Allofeed, one individual will stand next to the other individual with Body-Touch. It will then regurgitate food into its mouth, bend over the other individual and perform Bill-Touch, Bill-Clasp and then Allofeed. Many times the other individual moves its head away and will Bill-Bite. If the Allofeed attempt continues, the other individual will start a bout of Bill-Fence. It appears as though the other individual is rejecting the Allofeed attempt with agonistic behaviors. Once the Allofeed attempts have concluded, both individuals will discontinue the agonistic behaviors. Therefore Allofeed, while embedded in the affiliative cluster, is also linked to the agonistic cluster.

A Pearson's correlation analysis showed that the agonistic and affiliative weightings were significantly inversely correlated. This analysis allows for all subsequent analyses to be completed using only the affiliative weightings, as both provide the same information. The dyadic affiliation index provided a measure of the affiliative bond between individuals within a dyad. This analysis allowed me to test the "valuable relationships hypothesis" in the reconciliation experiment. It is important to know which individuals have positive affiliative relationships and which have negative affiliative relationships because if not all dyads reconcile, it allows a comparison of the results and an understanding of why this might happen. Reconciliation never happens 100% of the time, and knowing which relationships are positive or negative can shed light on why this is the case.

Out of these six birds, there were only two sibling dyads (Ch-N and Cu-M), both of which were male-female combinations. Both dyads had a significantly positive relationship, though Ch-N's average affiliation was much higher than Cu-M's. This could be a product of the age of these individuals: Charlie and Niko were approximately nine months younger than Curly and Moe. These tests were conducted while Charlie and Niko were one to two years old. Monk parakeets do not begin breeding until their second year, so Charlie and Niko could have a stronger bond than Curly and Moe because they had not reached breeding age yet, making sibling relationships still very important. In Curly and Moe the affiliative bond was less prominent, possibly because they were older and the importance of their relationship was fading as they started the mating portion of their lives.

Ch-M was the only male-male dyad, so it is not surprising they had a negative relationship. Probably the reason the relationship's mean affiliation score was only marginally low was because there was a big discrepancy in dominance. It appeared that Moe always dominated Charlie, which could be because of the age difference. If Moe was already into adulthood, but Charlie was still a juvenile, this could be a possible explanation. All three of the highly agonistic dyads involve Curly, and the sample sizes were low. The reason for low sample sizes was that Curly's opponent would always fly off the stand within the first minute or two of the encounter, which ended all interaction early. Besides Ch-N, the other two dyads with highly affiliative relationships were N-R and Cu-L, both of which were female-female pairs. Female-female bonds were not always affiliative, though: Cu-N and Cu-R were both female-female dyads, and they had highly agonistic relationships.

It is important to note that Charlie, Rosie and Niko all came from the same breeder, and Curly, Larry and Moe all came from the same pet store where their cages were in close contact. The social structure seems to have been affected by these previous relationships. The agonistic relationships all involve pairings of birds obtained from different locations. All but one of the affiliative relationships involve pairings obtained from the same place. These early life experiences seem to have a great effect on the overall social structure of the group. For the most part, Curly was the most aggressive individual in the group and Rosie was the most affiliative individual within the group.

These analyses have empirically shown which behaviors are affiliative and agonistic. Several studies (i.e. Castles et al. 1996; Das et al. 1998; Aureli & de Waal 2000; Koski et al. 2007) have classified behaviors as affiliative based on preconceived notions. For example, primatologists see chimpanzees kiss and embrace and have classified these as affiliative (de Waal 2000). While this interpretation may be correct, the behaviors were classified based on human analogies. Koski et al. (2007) define affiliative behaviors as contact sit, gentle touch, fingers/wrist to mouth, embrace (ventroventral or sideways), mount, genital touch or inspection, mate, kiss, kiss bite, groom, and contact play; yet, they never say how they concluded these behaviors were affiliative. This only leads the reader to interpret these behaviors as affiliative based on anthropomorphic assumptions. The same problem arises in Matsumura (1996), in which he defines affiliative behaviors as interactions that included grooming, clasping, playing, sitting in contact, mouthing, mouth approach, or approaching with lipsmacking or "staccato vocalization." He mentions other studies on affiliative behaviors in the

introduction, but never outlines how these behaviors were deemed affiliative. These are only a few examples of a widespread problem.

The dilemma with this definition of affiliation is that these primates might be performing several other behaviors that look neutral to the human eye but are actually affiliative; these behaviors are not scored and thus could have a potentially large impact on the results of social studies. And what happens in the case of non-primates, where behaviors are very dissimilar to those of humans? How do we classify affiliative and agonistic behaviors? The only way to empirically classify behaviors is to have a strong understanding of the species being studied and to do objective cluster analyses on the entire behavioral repertoire of the species. The clustering approach provided a reliable way to quantify motivation in a reconciliation context.

This study has shown the monk parakeet social behavior is as rich as that of primates and other socially complex species (de Waal and Tyack 2003). This is not surprising as there are many other similarities between monk parakeets and other socially complex species, including long life spans, delayed breeding, permanent individualized social groups, and advanced cognitive abilities. This behavioral study is only a starting point in testing larger questions about how complex monk parakeet societies are, but it is a very important starting point, and it is the only objective way to conduct detailed experiments dealing with sociality.

RECONCILIATION

INTRODUCTION

The main goal of this research project was to test whether reconciliation occurs in monk parakeets. My initial study involved the creation of an ethogram where behaviors were described, compared to those of similar species, and quantified. Next, behavioral indices were extracted, which provided the tools to test reconciliation and the “valuable relationships hypothesis.” A hypergeometric similarity analysis along with a MDS analysis allowed me to differentiate between affiliative behaviors and agonistic behaviors. Each behavior within the cluster analysis was given a weighted score based on how exclusively it was associated with the rest of the behaviors within the cluster. This allowed me to quantify not only the frequency of behaviors, but the importance of them with respect to affiliative and agonistic motivations. I could then determine which dyads were generally affiliative towards one another and which were generally agonistic. This criterion now allows a test of the “valuable relationships hypothesis,” determining whether dyads with an affiliative relationship were more likely to reconcile than those with a neutral or agonistic relationship during the reconciliation study. All these steps taken together provided independent, predictive variables for the reconciliation study and tools to quantify the intensity and motivational state of individuals during the agonistic encounters and the post-conflict affiliative behaviors.

EXPERIMENTAL METHODS

The experiment was conducted by placing pairs of birds in a transparent acrylic chamber (66x40x40 cm) with a clear plastic food dish mounted in the center. It has been suggested that reconciliation is less likely to occur if individuals can find other means of ending a conflict, such as increasing the distance between each other (Aureli et al. 2002). I therefore used this confined space to ensure that reconciliation would be the only option following the conflict. This chamber was placed on a rectangular table in the center of the same room in which the earlier dyad experiment had been conducted. A color video surveillance camera was mounted on the wall near the ceiling, angled down to capture the entire chamber. A microphone was present hanging from the ceiling to record vocalizations. All sessions were recorded on videotapes, though there was an observation window located outside the room from which the experimenter could monitor sessions. The window provided clear viewing of all areas of the room. Lights were off outside the room to ensure the birds could not see the observer.

Prior to testing, every individual was habituated to the testing apparatus with about 35, one hr familiarization periods. This was needed because monk parakeets are highly neophobic: in novel environments, they will freeze and not interact socially. It was therefore important to familiarize them with the experimental apparatus prior to beginning testing. During the habituation sessions there was food present (the parrot's normal daily diet, which consisted of pellets and a mixture of seeds) in the food dish, and the birds' food had been restricted to 1/8 cup the day before, making them slightly hungry. During the first few habituation sessions only one bird was present, but the bird

would stand still and not even attempt to go near the food dish. In subsequent habituation sessions, therefore, birds were placed in the chamber in pairs, with Ch-N, M-R and Cu-L being paired with one another. At this point the birds started to explore the chamber. When all birds were eating out of the food dish, habituation ended.

The testing methods were similar to those used during the previous study. The same six individuals were tested with every other bird in all 15 possible dyads. Each dyad received two sessions, an experimental session and a control session. The order was randomized, so some dyads received the control session first and the rest received the conflict session first. The day before testing, food was restricted to 2 tsp for each bird to ensure motivation. In the control session no food was provided. In the experimental session, food was present, consisting of $\frac{1}{4}$ tsp of the parrots' normal daily diet, the same food presented during habituation. This food was placed in the food dish prior to the birds entering the apparatus. They expected this food as it had been present during the previous habituation sessions. The birds were placed in the experimental apparatus and allowed to move freely throughout it for 30 min. The entire trial was videotaped.

Each 30 min videotape was scored in its entirety using my established 1-0 behavioral checksheet with 32 sec intervals. The 20 behaviors previously defined as affiliative and agonistic in the MDS analysis were scored.

ANALYSIS METHODS

There was a time gap of several months between the previous study and the reconciliation experiment, so I wanted to see whether the affiliation rates had changed

between dyads. The weighted affiliation scores in the control session were analyzed with a Wilcoxon signed-rank test, comparing the scores to zero. A dyad was said to be significantly different from zero if the p -value was less than 0.05. The dyad was considered affiliative if the T -value was positive or agonistic if the T -value was negative.

Before significance testing was conducted, a social relationships model was developed to determine how much of the variance in the behavioral scores was due to each opponent's independent behavior (actor and partner effects) or to the unique relationship between the two individuals (relationship effect) (Kenny et al. 2006). This analysis is important when using a round-robin design, as every individual is paired with every other individual, and there are no other ways to determine whether individuals or relationships are primary sources of behavioral variance. There are several possible outcomes. First, the identity of the partner might have no effect on the actor's behavior. Second, the identity of the partner might have some effect on the actor's behavior. Or, last, the relationship between the actor and partner might entirely determine both individuals' behavior. This model determines how much of the variance in the data is due to the specific relationship between two individuals and how much is due to individual level effects. It also addresses whether behavior is reciprocal in each dyad, i.e. how correlated the behavior between the two individuals is. The social relationships model takes into account the fact that the behavior of the two individuals might be correlated and thus each dyad might be independent from every other dyad depending on how much of the variance is due to the unique relationship between the two individuals.

This method has been used in several other experiments looking at dyadic interactions (Kenny et al. 2006; for animal behavior studies see Capitanio 1984; Dunlap

2002; Malloy et al. 2005). In order to run this analysis, the mean affiliation score for each individual within each dyad was used. This mean was taken from a post-conflict 10 min interval beginning when aggression ended. If aggression continued sporadically throughout the entire trial a cut-off point was used where the first affiliative behavior started the post-conflict period. The data were then converted from quantitative to interval data, as the social relationship model requires this format. This was accomplished by computing the entire range of the data and breaking this up into eight equal intervals. The intervals were labeled one through eight, consecutively increasing from the lowest to the highest affiliation score by roughly 0.046 (See Appendix A for conversions and post-conflict timing.) The data were then run through the SOREMO program, which resulted in variance measures for the actor, partner and relationship effects (Kenny et al. 2006). In the simplest terms, SOREMO performs a two-factor random-effects ANOVA with actor as one factor, partner as another factor and relationship as the interaction effect, modified for a round-robin design. See Kenny et al. (2006) for a complete description and formulas.

The reconciliation analysis was performed in the following manner. First a mean was taken from each dyad's control session. Then each dyad's conflict session was broken up into 3 time blocks: the initial 10 min, the middle 10 min, and the last 10 min. All blocks had a total of 38 samples. Because the birds were predicted to initially fight over access to the food, I predicted that the initial time block of a session should represent the agonistic component of the trial. By the last time block, affiliation should be apparent, if reconciliation occurred. As a control, the mean affiliation score from each corresponding dyad's control session was subtracted from each of the 38 samples within

a dyad's initial and last time block. If there was no difference between the affiliation scores in the conflict session and the control session then the result should be zero. A Wilcoxon signed-rank test was used to compare the differences. If the dyad's initial time block affiliation score was significantly less than zero, the pair had an initial agonistic interaction. If the dyad's last time block affiliation score was significantly higher than zero, the pair had a final affiliative interaction. If both of these criteria were met, the dyad reconciled, as the individuals performed affiliation at a higher rate after a conflict than when no conflict occurred.

RESULTS

The social relationships model demonstrated that all the variance within the data was due to the relationship (relative variance = 1.00) rather than the individuals (actor relative variance = 0.000, partner relative variance = 0.000) and that behavior was reciprocated between individuals (reciprocity correlation = 0.943). At a significance level of 0.05 any covariance above 0.95 can be considered significant. Therefore, in this analysis, a bird's behavior is significantly unique to the relationship with its partner. Individuals thus do not have stereotyped behavior patterns across all dyads. This analysis also shows that individuals perform a similar amount of affiliative behavior with one another in the dyad. This analysis outlined the appropriate level of independence: that each dyad is a unique sample and must be treated as such. Combining data from different dyads for each individual could lead to erroneous results, as each bird's data is not

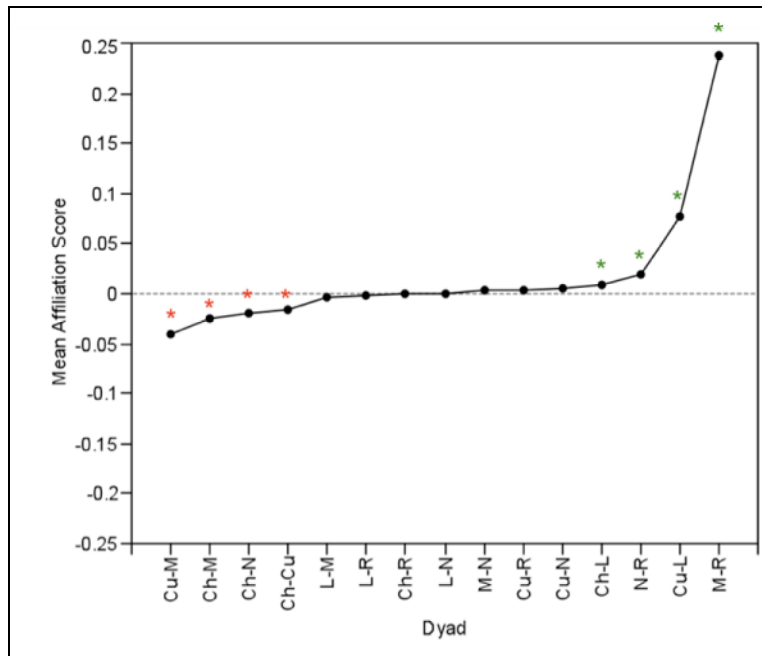
independent from the bird it interacted with. Therefore the following analyses were completed at the dyad level.

Each dyad was tested independently based on the social relationships model. The Wilcoxon signed-rank tests results for the control session showed that several dyads' affiliation scores had changed after the behavioral indices study was completed. All but one of the neutral relationships stayed neutral in the control session. Two of the highly negative relationships were neutral in the control session. One of the positive relationships changed to neutral in the control session, but the other three remained positive. Two of the positive relationships changed to negative in the control session. Two of the negative relationships stayed negative in the control.

TABLE 4: CONTROL SESSION WILCOXON SIGNED-RANK TESTS RESULTS

| Dyad | Sample Size | Median | <i>T</i> | Probability | Significance | Prior Relationship |
|-------|-------------|--------|----------|-------------|--------------|--------------------|
| Cu-M | 112 | 0.0000 | -240.0 | <0.001 | * | positive |
| Ch-M | 112 | 0.0000 | -68.0 | <0.001 | * | negative |
| Ch-N | 112 | 0.0000 | -40.5 | 0.002 | * | highly pos. |
| Ch-Cu | 112 | 0.0000 | -58.5 | 0.003 | * | highly neg. |
| L-M | 112 | 0.0000 | -17.5 | 0.769 | | neutral |
| L-R | 112 | 0.0000 | -0.5 | 1.000 | | neutral |
| L-N | 112 | 0.0000 | 0.0 | 1.000 | | neutral |
| Ch-R | 112 | 0.0000 | 0.0 | 1.000 | | positive |
| M-N | 112 | 0.0000 | 3.0 | 0.250 | | neutral |
| Cu-R | 112 | 0.0000 | 4.5 | 0.641 | | highly neg. |
| Cu-N | 112 | 0.0000 | 5.0 | 0.125 | | highly neg. |
| Ch-L | 112 | 0.0000 | 24.5 | 0.010 | * | neutral |
| N-R | 112 | 0.0000 | 264.0 | <0.001 | * | highly pos. |
| Cu-L | 112 | 0.0000 | 341.5 | <0.001 | * | highly pos. |
| M-R | 112 | 0.2836 | 1822.5 | <0.001 | * | positive |

The “prior relationship” column shows what the relationship was in the behavioral indices study and is color-coded to match the original study’s results. The significantly negative affiliation scores are in red, with solid being highly significant and the significantly positive affiliation scores are shown in green; the darker green indicates a highly affiliative score.

FIGURE 5: CONTROL SESSION MEAN AFFILIATION SCORES

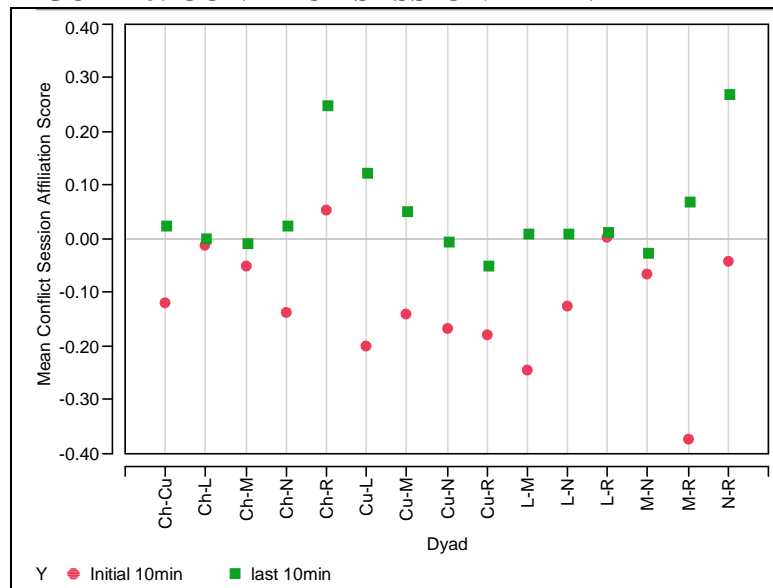
The red asterisks denote a significantly negative affiliation score during the control session. A green asterisk denotes a significantly positive affiliation score during the control session.

Seven out of 13 dyads reconciled (54%), meaning they had a significant agonistic encounter during the initial time block and a significant affiliative encounter during the last time block, both of which were different from the control session. Two dyads did not have a significantly agonistic encounter during the initial time block, so they could not be tested for reconciliation. Out of the seven dyads that reconciled, five had had a significantly affiliative relationship during the behavioral indices study. Only one of the dyads that reconciled had had a significantly agonistic relationship during the behavioral indices study. The other dyad that reconciled had a neutral relationship during the behavioral indices study. See Appendix B for time-course graphs of each dyad's sessions.

TABLE 5: RECONCILIATION WILCOXON SIGNED-RANK TESTS RESULTS

| Dyad | N | DURING CONFLICT | | | | POST-CONFLICT | | | | Rel. |
|-------|----|-----------------|--------|--------|---------|---------------|--------|--------|---------|--------|
| | | Median | T | Prob. | Signif. | Median | T | Prob. | Signif. | |
| Ch-Cu | 38 | 0.0156 | -139.5 | 0.019 | * | 0.0156 | 370.5 | <0.001 | * | agon. |
| Ch-L | 38 | -0.0091 | -333.5 | <0.001 | * | -0.0091 | -295.5 | 1.000 | | |
| Ch-M | 38 | 0.0246 | -87.5 | 0.100 | | 0.0246 | 73.5 | 0.136 | | agon. |
| Ch-N | 38 | 0.0196 | -117.5 | 0.040 | * | 0.0196 | 370.5 | <0.001 | * | affil. |
| Ch-R | 38 | 0.0000 | 30.5 | 0.973 | | 0.2836 | 297.5 | <0.001 | * | affil. |
| Cu-L | 38 | -0.2493 | -370.5 | <0.001 | * | 0.2065 | 293.5 | <0.001 | * | affil. |
| Cu-M | 38 | -0.1322 | -250.5 | <0.001 | * | 0.0400 | 305.5 | <0.001 | * | affil. |
| Cu-N | 38 | -0.1213 | -370.5 | <0.001 | * | -0.0045 | -370.5 | 1.000 | | agon. |
| Cu-R | 38 | -0.1568 | -370.5 | <0.001 | * | -0.0034 | -370.5 | 1.000 | | agon. |
| L-M | 38 | -0.1685 | -265.5 | <0.001 | * | 0.0037 | 370.5 | <0.001 | * | |
| L-N | 38 | 0.0000 | -68.0 | <0.001 | * | 0.0000 | 1.5 | 0.250 | | |
| L-R | 38 | 0.0021 | 236.5 | 1.000 | | 0.0021 | 370.5 | <0.001 | * | |
| M-N | 38 | -0.0033 | -270.5 | <0.001 | * | -0.0033 | -370.5 | 1.000 | | |
| M-R | 38 | -0.2369 | -370.5 | <0.001 | * | 0.0466 | 370.5 | <0.001 | * | affil. |
| N-R | 38 | -0.0190 | -307.5 | <0.001 | * | 0.2646 | 370.5 | <0.001 | * | affil. |

The orange rows designate dyads that both had a significant agonistic interaction in the first 10 min of the session and a significant affiliative interaction in the last 10 min of the session. These dyads reconciled. The column Rel. refers to the type of relationship resulting from the behavioral indices study and is color-coded to match this initial study.

FIGURE 6: CONFLICT SESSION MEAN AFFILIATION SCORE

The mean affiliation score is graphed on the Y-axis and the dyads are graphed on the X-axis. The initial 10 min of the conflict session is shown in red. The last 10 min of the conflict session is shown in green.

DISCUSSION

The control session results show that several changes in the relationship of individual dyads had occurred since the behavioral indices sessions. The simplest explanation for this is that these control sessions occurred in a different setting than the behavioral indices study. During the behavioral indices study, the birds were on a perch with a toy and could fly off or climb down. In the control sessions the birds were in an enclosed space, a plexiglass box. This seemed to have an effect on their behavior as all but one dyad's median behavior score was zero. They were not performing as many behaviors inside the box. Even though they went through hours of habituation to the box they still did not appear to behave normally when compared to their movements in their home cages and on the perch.

Another explanation for this change is that dominance had not been established prior to the behavioral indices study, but was actually still being determined. Affiliative or agonistic behaviors occurred at a higher rate during this time period, as the relationships were still being decided. This could also explain why Cu-R and Cu-N reversed their relationships from agonistic to neutral. Three affiliative relationships remained affiliative (N-R, Cu-L, and M-R) and two agonistic relationships remained agonistic (Ch-M and Ch-Cu). Charlie and Moe are both males, so I expected their relationship to remain agonistic. The two affiliative relationships that became agonistic in the control sessions were both sibling pairs (Cu-M and Ch-N). This suggests that sibling relationships may be transitory; the bonds are stronger when the individuals are younger but as they reach adulthood these relationships may become agonistic. This might be a mechanism to inhibit inbreeding once maturation is reached. It would be

worthwhile to do a study on how age affects an individual's dynamics within the social group.

The reconciliation results show that seven out of 13 dyads (54%) met the reconciliation criteria. Therefore I can conclude that reconciliation does happen in this species, at least in captivity. It would be very interesting to compare these results to a study on wild or feral monk parakeets to see whether they reconcile and if so, whether it is at a similar rate. There are several lines of evidence that suggests that reconciliation is not an artifact of captivity (for a review see Aureli et al. 2002). A study on long-tailed macaques showed that reconciliation occurred at a similar frequency in both wild and captive animals (Aureli 1992). Reconciliation never occurs 100% of the time following a conflict (for a review see Aureli & de Waal 2000). A reconciliation study on a wild population of spotted hyenas showed that reconciliation only occurred 15% of the time (Wahaj et al. 2001; Aureli et al. 2002). In the majority of studies on reconciliation, the percent of reconciled conflicts ranges from 7% to 55%. The rate of monk parakeet reconciliation is on the high end of that range, so I predict this to be a species wide phenomenon and not unique to the six captive individuals I tested.

As I defined it previously, a "valuable relationship" can be tested by comparing a prior affiliation score for each pair to the reconciliation results. It is predicted that dyads with significantly affiliative relationships will be more likely to reconcile than those with neutral or agonistic relationships. I found this to be the case. The results took into account the control session means, so a comparison can be made to the original behavioral indices study. Ch-R did not have a significant agonistic encounter during the initial time block and thus could not be tested for reconciliation. Out of the remaining

five dyads originally classified as affiliative in the behavioral indices study, all reconciled. Ch-Cu reconciled as well, which may be because neither is fully dominant to the other, making it necessary to find another means of ending the conflict. L-M reconciled as well, but their relationship was neutral in the previous analysis and during the control. This cannot be explained by the “valuable relationships hypothesis,” suggesting that reconciliation does not always depend on the nature of the prior relationship. The majority of dyads that reconciled had affiliative relationships prior to testing, which gives support to the “valuable relationships hypothesis” as I previously defined it.

In monk parakeets the “most valuable relationship” is the most affiliative one. Each individual within the group has another individual they prefer to spend all of their time interacting with. This could be their mate, their sibling, individuals of the same age, etc. Since this study only included six individuals, a broad generalization cannot be made as to why certain birds prefer some individuals to others, but we do see a pattern where all the affiliative dyads reconciled. These results provide support for the “valuable relationships hypothesis,” which has received little attention experimentally (Aureli et al. 2002). There are few clear cases where the social bonds of individuals were known prior to testing reconciliation. In a study on pig-tailed macaques it was found that the relationship level is the key level for understanding conciliatory patterns. Differences in reconciliation depend on the quality of relationship between members (Castles et al. 1996).

In the future it would be worthwhile to do a similar study with larger groups and between groups to see if there are any general relationships that are more “valuable” or

affiliative than others and thus where reconciliation happens more often. I suspect that a mated pair would have the most affiliative bond, but the monk parakeets in this study were not allowed to build nests or raise broods, so I cannot make assumptions in these six individuals about the strength of pair bonds.

These experiments have provided the basis for future work on social complexity in monk parakeets. There are several accessible feral populations in the United States, and it would be interesting to test reconciliation in naturalistic settings on these populations and compare the results across groups. Monk parakeets have a rich and complex society, much like primates, so it would also be valuable to look at other phenomena known to occur in complex societies, such as transitive inference, cultural transmission, social learning, etc. This is just the starting point when it comes to testing sociality in monk parakeets.

TABLE 6: POST-CONFLICT INTERVAL USED FOR THE SOCIAL RELATIONS MODEL

| Dyad | Start (min.sec) | End (min.sec) |
|-------------|------------------------|----------------------|
| Ch-Cu | 19.44 | 29.30 |
| Ch-L | 9.04 | 18.40 |
| Ch-M | 16.32 | 26.08 |
| Ch-N | 11.44 | 21.20 |
| Ch-R | 7.28 | 17.04 |
| Cu-L | 13.20 | 22.56 |
| Cu-M | 16.00 | 25.36 |
| Cu-N | 8.32 | 18.08 |
| Cu-R | 12.16 | 21.52 |
| L-M | 19.44 | 29.20 |
| L-N | 9.04 | 18.40 |
| L-R | 5.52 | 15.28 |
| M-N | 6.24 | 16.00 |
| M-R | 11.12 | 20.48 |
| N-R | 12.16 | 21.52 |

TABLE 7: EACH INDIVIDUAL WITHIN EACH DYAD'S MEAN AFFILIATION SCORE FOR THE CONFLICT SESSION AND CONVERSION FOR SOREMO

7a: mean affiliation score

PARTNER**ACTOR**

| | Charlie | Curly | Larry | Moe | Niko | Rosie |
|----------------|----------------|--------------|--------------|------------|-------------|--------------|
| Charlie | | 0.00274 | 0.01198 | 0.00932 | -0.0068 | 0.07494 |
| Curly | 0.00821 | | 0.22454 | 0.00701 | -0.0159 | -0.0229 |
| Larry | 0 | 0.2141 | | 0 | 0.00658 | 0.00789 |
| Moe | -0.0797 | -0.0194 | 0.00658 | | -0.0994 | 0.15410 |
| Niko | 0 | -0.0068 | 0 | 0.03264 | | 0.2686 |
| Rosie | 0.1595 | -0.0194 | 0.00789 | 0.17785 | 0.2686 | |

7b: conversion to intervals

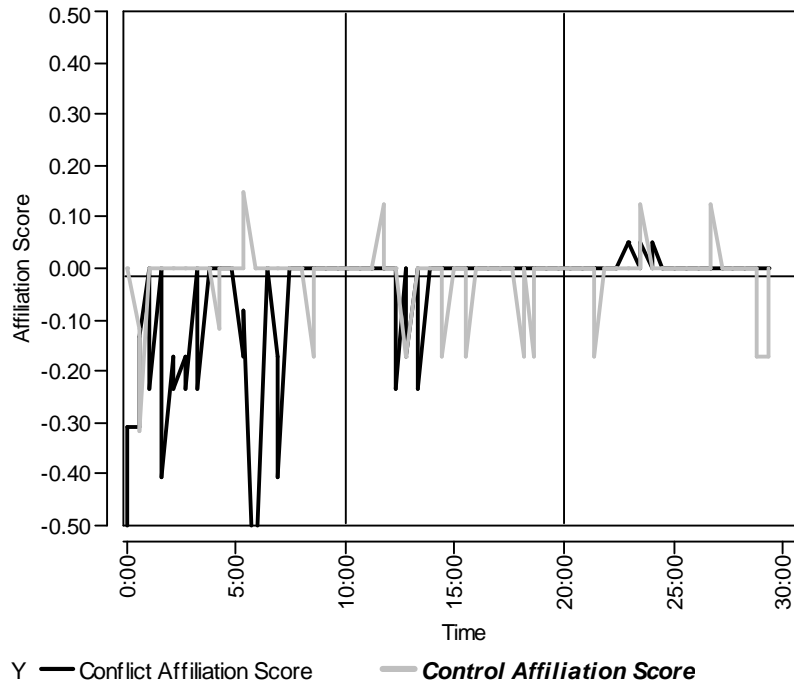
PARTNER**ACTOR**

| | Charlie | Curly | Larry | Moe | Niko | Rosie |
|----------------|----------------|--------------|--------------|------------|-------------|--------------|
| Charlie | | 3 | 3 | 3 | 2 | 4 |
| Curly | 3 | | 7 | 3 | 2 | 2 |
| Larry | 3 | 7 | | 3 | 3 | 2 |
| Moe | 1 | 2 | 3 | | 1 | 5 |
| Niko | 3 | 2 | 3 | 3 | | 8 |
| Rosie | 6 | 2 | 3 | 6 | 8 | |

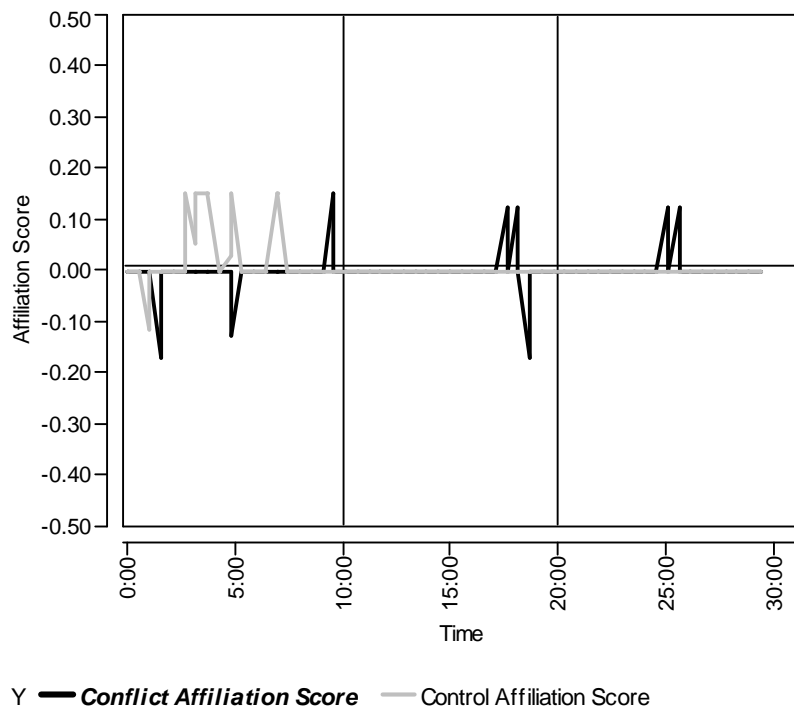
TIME-COURSE GRAPHS OF RECONCILIATION SESSIONS

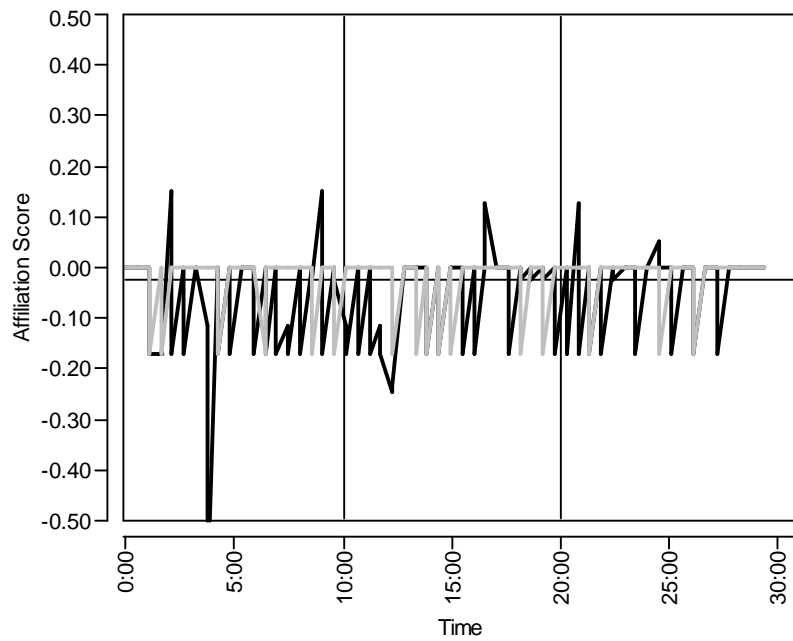
Note: The dashed line on each graph represents the control session mean

Dyad=Ch-Cu

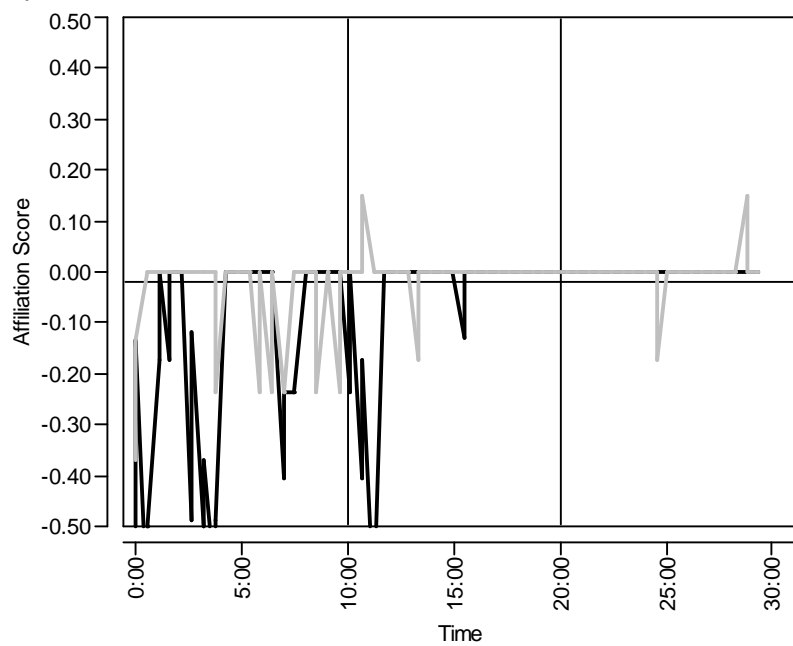


Dyad=Ch-L

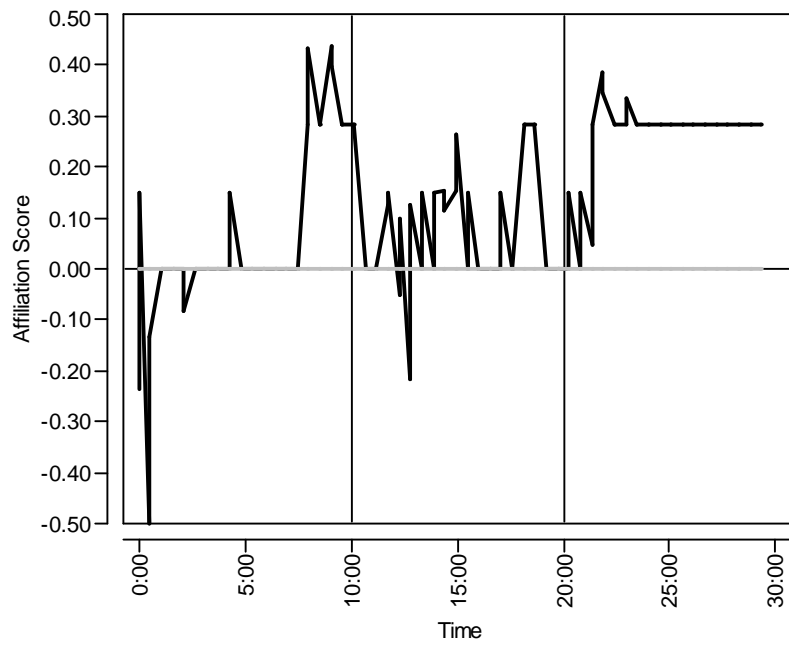
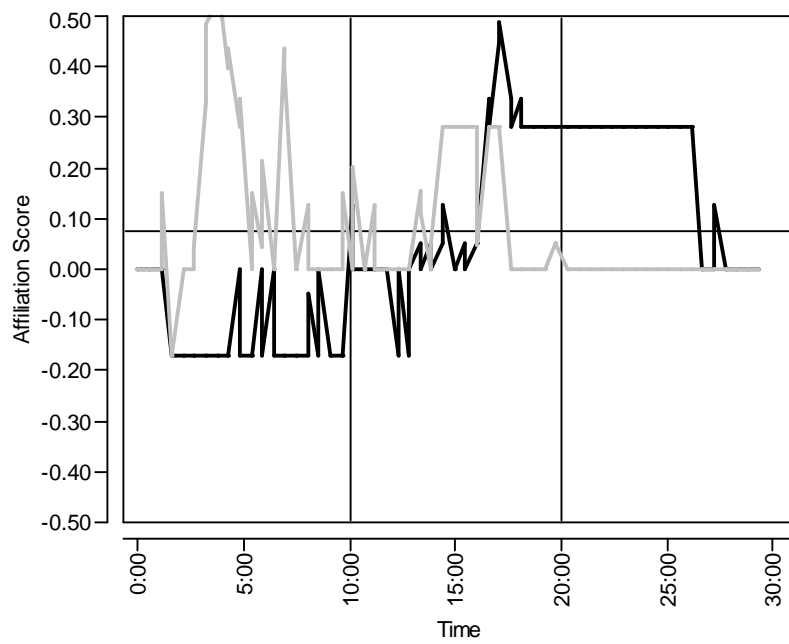


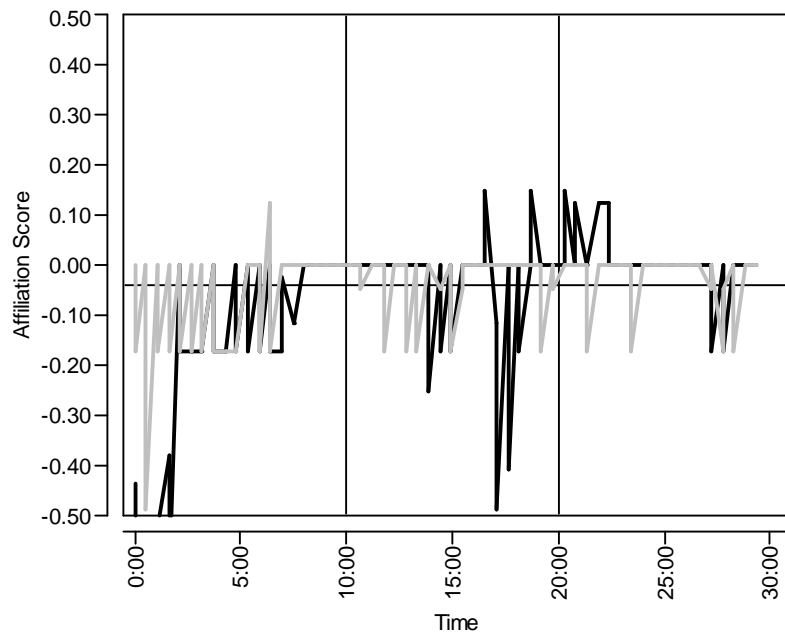
Dyad=Ch-M

Y — Conflict Affiliation Score — *Control Affiliation Score*

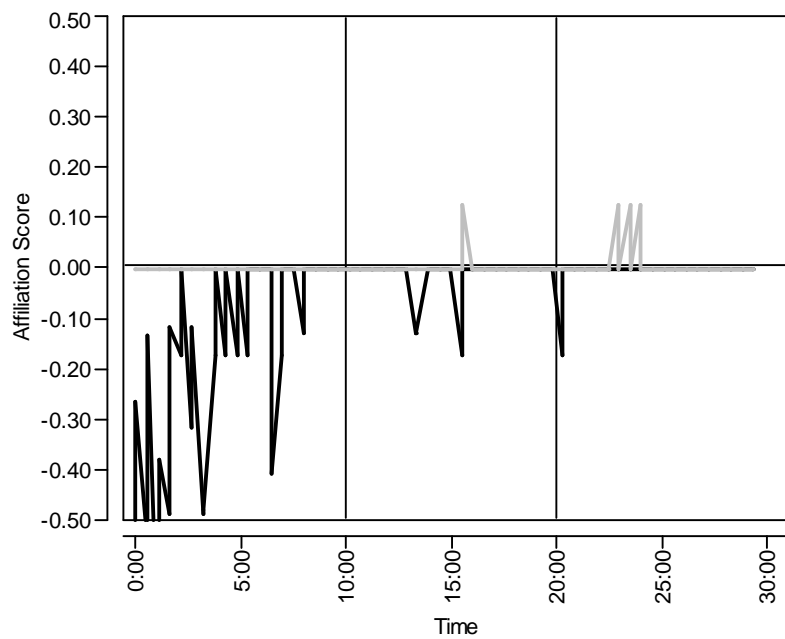
Dyad=Ch-N

Y — Conflict Affiliation Score — *Control Affiliation Score*

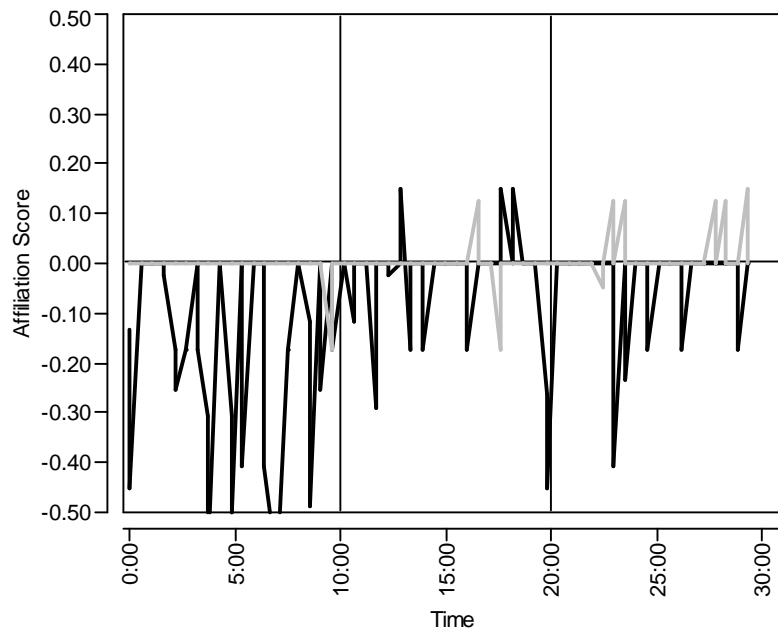
Dyad=Ch-R**Dyad=Cu-L**

Dyad=Cu-M

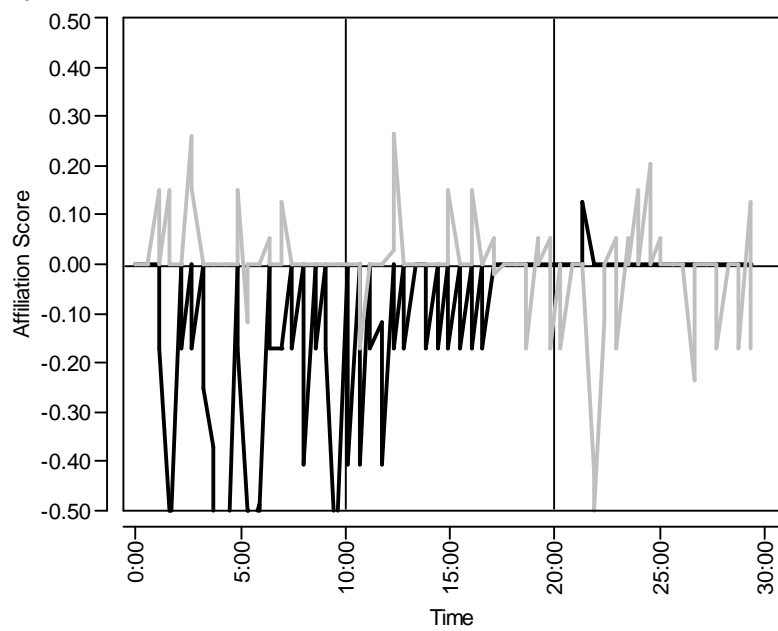
Y — Conflict Affiliation Score — Control Affiliation Score

Dyad=Cu-N

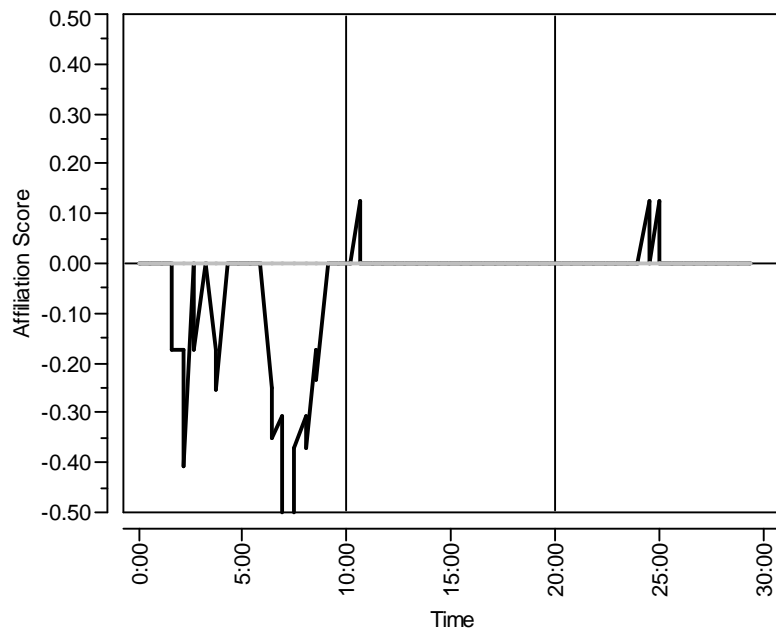
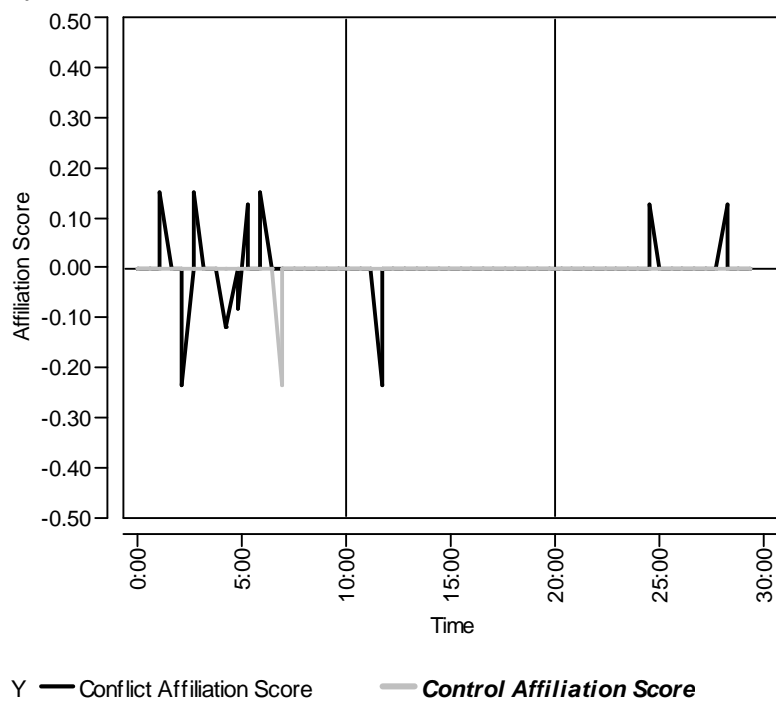
Y — Conflict Affiliation Score — Control Affiliation Score

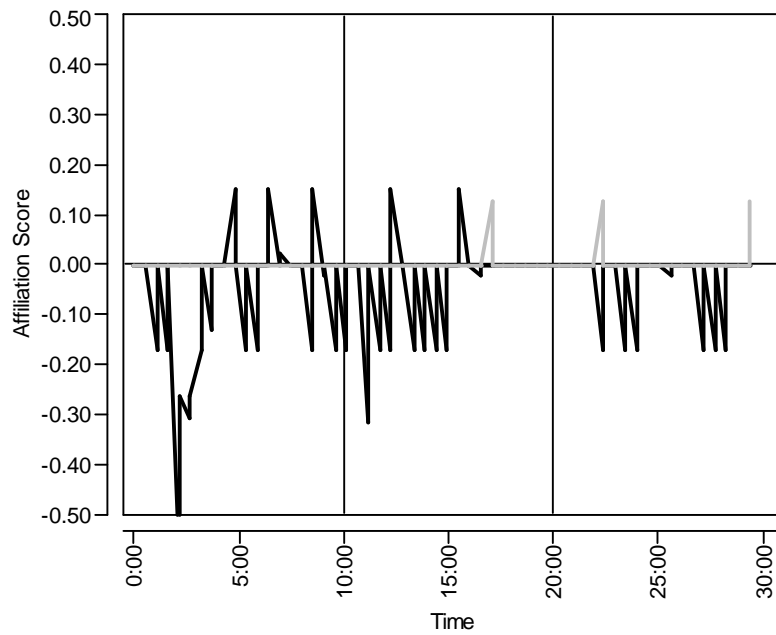
Dyad=Cu-R

Y — Conflict Affiliation Score — Control Affiliation Score

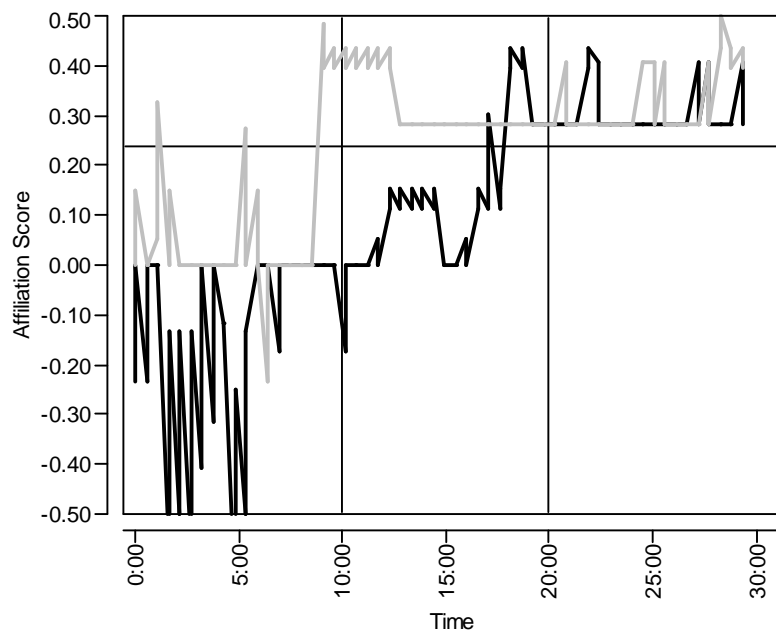
Dyad=L-M

Y — Conflict Affiliation Score — Control Affiliation Score

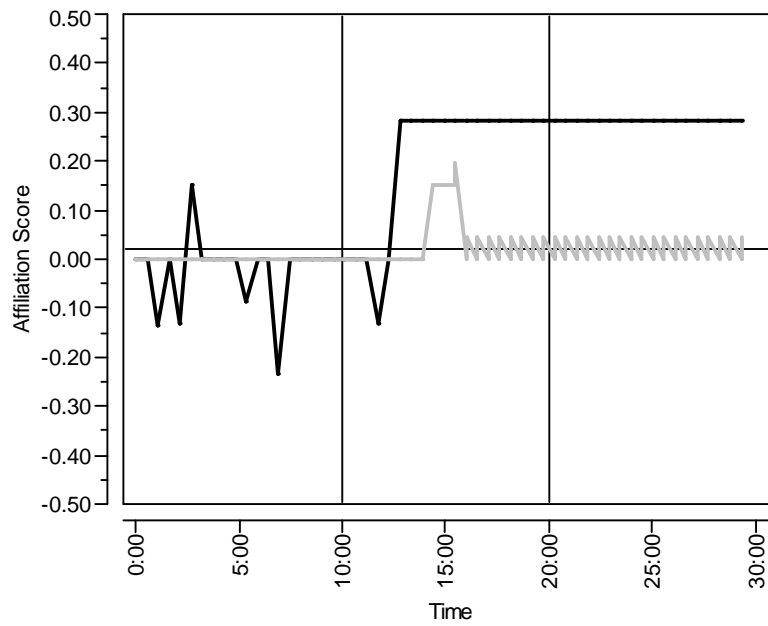
Dyad=L-N**Dyad=L-R**

Dyad=M-N

Y — Conflict Affiliation Score — Control Affiliation Score

Dyad=M-R

Y — Conflict Affiliation Score — Control Affiliation Score

Dyad=N-R

Y — Conflict Affiliation Score — *Control Affiliation Score*

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