AN ANALYSIS OF HUMAN INTERACTION AS ENVIRONMENTAL ENRICHMENT FOR CAPTIVE WOLVES AND WOLF-DOG HYBRIDS

By

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A THESIS PRESENTED TO THE GRADUATE SCHOOL
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To my Mom and Dad, for their enduring support,
to the sanctuaries, for their enduring trust,
and to Kobe, for his enduring companionship

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The benefits of environmental enrichment for captive mammals are well documented in the scientific literature. However, many facilities may have limited resources to implement traditional enrichment strategies. One possible solution is to provide socialized animals with positive interaction sessions with experienced volunteers. Although prior research has questioned whether human interaction alone may serve as enrichment, this topic has received little empirical attention to date. The present study aimed to evaluate whether human interaction could be enriching for socialized, pair-housed wolves and wolf-dog hybrids. Behavioral observations of each subject were conducted in a reversal design to measure species-typical affiliation, activity levels, and aberrant behaviors when volunteers were both present and absent. Results demonstrate high levels of human-directed affiliation and significantly higher levels of conspecific-directed affiliation when human interaction was made available to subjects relative to baseline conditions. Significantly higher activity levels were observed for two-thirds of replications during human interaction sessions compared to baselines. Individual data across conditions revealed reduced levels of pacing during

human interaction sessions for some subjects. One wolf-dog hybrid engaged in abnormal cage chewing in some baseline conditions following human interaction sessions. Social play also increased when caregivers were present, suggesting that play among conspecifics may be partially maintained by positive changes in an animal's environment. The potential for human interaction to be established as a scientifically validated, cost-effective enrichment strategy for captive animals is discussed, as well as the potential for play as an indicator of good welfare.

CHAPTER 1
INTRODUCTION

Human Interaction as Environmental Enrichment for Captive Animals

The benefits of environmental enrichment for zoo and laboratory mammals are widely documented in the empirical literature. Three acknowledged aims of environmental enrichment are to 1) promote opportunities for the occurrence of species-typical behaviors, 2) to promote novel sensory stimulation, and 3) to concurrently reduce the occurrence of aberrant behaviors that may be indicative of poor welfare (Shepherdson, 1998). Despite these benefits, enrichment strategies often cost time and resources to design, implement, and maintain. This suggests a need to establish cost-efficient enrichment methods that are equally effective in producing desired behavioral changes in captive animals. In addition, the evaluation of enrichment strategies is of great importance when determining if a particular strategy is satisfying these goals.

Enrichment practices that incorporate non-stressful stimuli and target the dominant sense for the species of interest are likely to result in the greatest benefits for animal welfare (Wells, 2009). However, stimuli specific to a species' natural habitat should not always be assumed to be meaningful to a captive individual of that species. In some cases, stimuli that do not occur naturally in the wild but are readily available in the captive environment may be more cost-effective in promoting overall welfare (Wells, 2009). Given that captive animals are provisioned with basic survival needs by human caretakers, the potential for human-animal interactions to be enriching has been proposed for captive animals that have positive relationships with humans (Claxton, 2011).

Comparing Training Versus Human Interaction Alone

Most empirical attention on human-animal interactions in this context has focused on the use of positive reinforcement training (PRT) to promote desirable behaviors while simultaneously providing an opportunity for positive interactions between animals and their caregivers (Laule, Bloomsmith, and Schapiro, 2003; Baker et al., 2010; Claxton, 2011;). Although PRT is clearly relevant to developing target behaviors that make aversive husbandry techniques obsolete (Laule et al., 2003), such methods generally cannot assess changes in behavioral welfare (e.g. species-typical behavior, activity levels) through observations (Baker, 2004). An additional limitation of PRT is that human-animal interaction during training sessions is often confounded with food reinforcement, thus obscuring the effects of human interaction alone on the behavioral welfare of captive animals.

What has perhaps been more seriously overlooked is the provision of free-contact interactions with captive animals and their human caregivers. Few studies have examined the benefits of positive human interaction for captive animals, mostly in non-human primates. For example, solitary and socially-housed laboratory chimpanzees (Waitt et al., 2002; Baker, 2004; Bloomsmith et al., 2004) showed reduced stereotypic behavior; macaques and socially housed common marmosets exhibited increased grooming when positive interactions with caretakers were available (Baker, 2003; Waitt et al., 2002; Manciocco et al., 2009). In addition, human interaction has been evaluated for shelter dogs (Coppola, Grandin, and Enns, 2006; Normando et al., 2009; Bergamasco et al., 2010).

However, the literature concerning the impacts of human interaction alone for captive animals is limited by restricted species generality, inconsistencies in the literature regarding the efficacy of such interactions, even within related species, and a lack a systematic evaluation of individual data. For example, Wood (1998) observed lower rates of positive species-typical behaviors in zoo-housed chimpanzees in the presence of larger crowds of visitors. Male rhesus macaques showed higher rates of abnormal behaviors during human interaction sessions (Maloney et al., 2007).

Limitations of Current Research

In addition, none of the prior studies were designed in a manner that would permit a direct analysis of cumulative behavior change, as a result of alternating conditions of caregiver presence and absence. Baker (2004) only examined changes when a caretaker was present but unresponsive to the chimpanzees' behavior; because of the restrictions on contact with subjects, her study could not examine the effect of free-contact interactions. This is problematic because important changes in behaviors of interest may occur not only when enrichment is available, but following its removal as well. Other limitations have been staff availability to provide interactions because of large group housings (Manciocco et al. 2009). Furthermore, replications were generally not conducted in these studies, which would allow for the assessment and reliability of enrichment effectiveness. Finally, because behavioral welfare is a property of individual animals, group designs and aggregate data are of only limited usefulness when evaluating enrichment efficacy.

Sanctuary Animals: An Ideal Population for Human Interaction Research

One population that may be ideal to implement and evaluate human interaction is that of privately-run sanctuaries for exotic animals. Many exotic animals that arrive at these sanctuaries have a unique history of extended contact with humans, as a result of being purchased by breeders from a young age, and subsequently hand-reared as companion animals in pet homes among humans. Yet this population of exotic animals still has direct application to enrichment evaluation for non-domesticated zoo animals. In addition, many such facilities are non-profit organizations that are run entirely on volunteer assistance and private donations, often making traditional environmental enrichment strategies both physically and financially difficult to implement. In this case, human interaction may serve as a financially feasible and readily accessible strategy to promote welfare of captive animals.

Wolf-Dog Hybrids as Scientific Subjects

A large proportion of the animals that exist in such facilities are wolves and wolf-dog hybrids. A wolf-dog hybrid is a cross between a wolf (*Canis lupus*) and a dog (*Canis familiaris*) or between animals where one or both parents contain recent wolf genes (Cusdin, 2000). At present, there are estimated to be anywhere from 300,000 to 1.5 million wolf-dog hybrids in captivity in the United States (Busch, 2007). In many cases, wolves and wolf-dog hybrids are relinquished voluntarily by their owners or confiscated by wildlife officials from situations in which the animals were illegally obtained and/or possessed or improperly cared for (e.g. in cases of abuse or neglect).

At present, however, no peer-reviewed publication presents data on the behavioral management of captive wolf-dog hybrids. Though objective information on this population is greatly needed, there are numerous limitations to the scientific literature on wolf-dog hybrids. First, the identification of wolf-dog hybrids is often a subject of primary concern and can be difficult when the hybridizing species are closely related and do not possess diagnostic genetic markers (Vilá et al. 2003). Second, legal ownership of wolf-dog hybrids varies by state, and even county, in the United States, contributing to substantial controversy. In addition, because wolf-dog hybrids are neither domestic nor exotic wildlife, studies proposing them as subjects of scientific inquiry are hard-pressed to find appropriate sources of funding to carry out objective behavioral evaluations.

Study Aims

The study of wolf-dog hybrids in particular has applications to both the management of exotic and domesticated species. Wolf-dog hybrids are often provided life-long care in sanctuaries, and in many cases, are not adopted out into the community. Thus, the need for effective environmental enrichment is central to the welfare of this population. Given the limitations of implementing traditional enrichment practices in these settings, human interaction seems an ideal strategy to evaluate with wolves and wolf-dog hybrids – a population that has not received empirical attention in this area of inquiry. Therefore, the objective of this study was to assess if human interaction could serve as enrichment for pair-housed wolves and wolf-dog hybrids at a sanctuary. It was predicted that contact with familiar caregivers would increase the occurrence of species-typical affiliative behavior, promote novel sensory stimulation (and thus, increase activity levels), and decrease the occurrence of any aberrant behaviors that were observed when human interaction was not provided.

CHAPTER 2
METHODS

Subjects

The subjects were two socialized wolves and six wolf-dog hybrids (Table 2-1). Wolf-dog hybrids were reportedly of varying wolf content; thus, each subject's relative wolf content was determined by recording physical similarities to a wolf phenotype (Cusdin, 2000). All wolf-dog hybrids in this study were identified as such by state officials prior to the onset of the study (Knight, 2011, personal communication), and were categorized either as high-content wolf-dogs (80-99% wolf phenotype), mid-content wolf-dogs (40-79% wolf phenotype), and low-content wolf-dogs (5-39% wolf phenotype) (Florida Lupine Association, 2011, personal communication).

All subjects were housed at Big Oak Wolf Sanctuary (Green Cove Springs, Florida, United States) at the time of this study. The sanctuary is a privately owned, non-profit organization that provides long-term residence and care to neglected and confiscated wolves and wolf-dog hybrids. The facility was not open to the general public, but all animals were accustomed to interaction sessions several times per week with sanctuary volunteers. All subjects were housed in similar enclosures (ranging from 2,286 to 3,048 m^2) surrounded by chain-link fencing (approximately 3.1 m in height) around the perimeter. All enclosures included a 2.6 kL pool, a wooden platform (3.1 m in height and 3.7 m by 3.7 m) above the pool, and an underground den (approximately 4.9 m by 2.4 m).

All subjects were adults that had been housed at the sanctuary for a minimum of 2 years at the time of the study. Each was housed with a conspecific of the opposite sex (e.g., wolf-dog hybrids were paired with another wolf-dog hybrid and wolves were paired with wolves). All pairs were housed together for a minimum of 1 continuous year prior to the study. All subjects remained in their original pairs throughout the study. One pair of wolf-dogs - Peter and Sara - was relocated to a different enclosure between the first and second replications for management reasons. Subjects were chosen for this study based on how well-socialized they were to familiar people and their ability to interact safely with a single person in the enclosure. All subjects were spayed or neutered prior to the onset of the study.

Sampson and Spirit were sibling hand-reared wolves purchased from a private breeder in Texas. Both had resided together at two other sanctuaries for approximately 5 months when they were under 1 year of age. They had resided at this sanctuary for 4 years prior to this study.

Sabbath and Ava were sibling, reportedly low-content, wolf-dog hybrids previously kept privately by separate owners. Reasons for relinquishment are unknown. Both Sabbath and Ava had been at the sanctuary for approximately 2 years.

Peace and Lea were reportedly high-content and low-content wolf-dog hybrids respectively, purchased from breeders for private ownership. Lea was reportedly surrendered for chasing livestock on her owner’s property. Peace reportedly had multiple owners before being relinquished. Peace and Lea had resided at the sanctuary for 2 and 3 years, respectively.

Peter and Sara were reportedly low-content wolf-dog hybrids. Sara was purchased from a breeder at 12 weeks of age and brought to the sanctuary 3 weeks later, after a neighbor reported physical abuse to Sara and another wolf-dog hybrid. Peter was adopted from an animal shelter, but subsequently surrendered when authorities informed owners that he was a wolf-dog hybrid. Peter had resided at the sanctuary for 3 years.

Procedure

An A-B-A-B-A reversal design was used to evaluate the effects of unstructured human interaction for pair-housed wolves and wolf-dog hybrids. A reversal design entails repeatedly alternating no treatment (baseline: A) conditions and treatment (intervention: B) conditions within each period of observation. Each pair was observed for 35 min., which consisted of an initial 5-min. baseline (A) condition, followed by a 10-min. treatment (B) condition, a subsequent 5-min. return-to-baseline (A) condition, a second 10-min. treatment (B) condition, and a final 5-min. baseline (A) condition, respectively. Three replications of observations were conducted for each pair, with 2 weeks between each replication. Replications were conducted in order to assess the reliability of the data obtained (Johnston and Pennypacker, 1993) for each pair.

Baseline conditions occurred in the absence of a person in the enclosure, but still in the presence of a conspecific, with which the subjects were always paired. However, because it was not always possible to ensure that volunteers were not visible or audible to the subjects during baseline conditions, volunteers were specifically instructed to avoid providing direct attention to the subjects during baseline conditions. During intervention conditions, a familiar female volunteer (with at least 3 months of experience of providing food and social interaction to subjects) was either instructed – either by the lead author or signaled by a pre-set timer – to enter the enclosure and interact with the subjects if they approached her. Social interactions included providing both tactile petting and verbal praise to subjects if the subjects engaged with or were in close proximity (within an arm’s length) to her. Volunteers were specifically instructed not to encourage play with the subjects (e.g. providing toys, grabbing onto any part of the animal's body) or solicit interactions (e.g. following subjects around the enclosure, calling subject's names) if the subjects did not engage with them at any point during the intervention condition. If interactions between conspecifics occurred during intervention conditions, volunteers were permitted to monitor the interaction, but were instructed to avoid responding in any way that could potentially interfere with the interaction (e.g., calling out subject's names, moving from a stationary position, emitting an audible nonverbal cue). Tangible items (e.g., edible treats, novel items, toys, training materials) were never present during either baseline or intervention conditions. All observations were subsequently viewed from videotape as a treatment integrity procedure.

All observations were collected between the hours of 17:00 h and 19:00 h between June and September. Observations were never conducted within 30 min. of a feeding or within 6 hours of volunteer interactions. Two female volunteers participated in each separate intervention condition per replication. The order of the volunteers within each session was held constant across all replications for all subjects. Volunteers had sufficient free-contact experience with all subjects, were knowledgeable about the temperament of the subjects and trained how to interact safely with each animal. In accordance with the sanctuary's protocols, volunteers were instructed to never restrain subjects, make quick or sudden movements, pet quickly or forcefully, stare at the subjects directly in the eyes for prolonged periods of time, or give reprimands. All observations were video-recorded using a high-definition camera (Kodak™ Zi6 HD Pocket Video Camera, Eastman Kodak Company, Rochester, NY, USA) that was positioned several meters from the front of the enclosure, or on an adjacent platform overlooking the subjects' enclosures. This was to minimize the impact of the camera on the subjects' behavior.

Ethogram

The following behaviors were measured: affiliation, proximity to human, proximity to conspecific, and inactivity (Table 2-2). All durations of conspecific, human, and other affiliation were recorded as measures of species-typical behaviors. Affiliation was defined as any of the following behaviors: tail-wagging, licking volunteer or conspecific, pawing, muzzle-grabbing, sitting in lap, or social play (Bekoff, 1974; Cools, Van-Hout, & Nelissen, 2008). Proximity measures were scored as either in contact, proximate (within an arm's length from volunteer, or within a body's length from conspecific), or distant (greater than an arm's length from volunteer, or greater than a body's length from conspecific) and were recorded instantaneously every 10 s in each condition. The percentage of time spent inactive for each condition was also calculated for each subject. Not visible was coded if subject was not visible for 30 s or more or for any duration in which the previous and subsequent behavior coded were not identical. All durations of aggression, scent-rolling or –rubbing, pacing, aberrant behavior (e.g. cage chewing), and vocalizations were also recorded. Other behaviors were defined as any other behavior not explicitly defined in the ethogram, and thus was mutually exclusive from all other behaviors in the ethogram. The requirement for recording a bout of behavior was that the behavior had to be observed for at least 3 s; similarly, the end of a bout required observation of at least 3 s in the absence of that behavior (with the exception of the not visible condition).

Video and Statistical Analyses

All observations were coded from digital video on computer for interobserver reliability (minimum of 90% agreement in all conditions). All behavior measures were recorded using Microsoft® Excel v.11.5.0. Durations of inactivity, affiliative behavior, pacing, and aberrant behaviors were calculated across all conditions and replications and subsequently converted to proportions for each condition to account for the differences in lengths of baseline and intervention conditions. Human affiliation and social play were recorded as durations. The duration of social play observed in each condition was recorded, and then divided by the total time elapsed in each condition and multiplied by 100% to obtain the percentage of each condition in which social play was observed. Human proximity and conspecific proximity measures were calculated as percentages per condition across all conditions and replications. Data for all behavioral measures was subsequently transformed to generate arcsine transformations of proportions of behavior observed for each condition within subjects.

For each replication, a t-test was used to compare proximity measures between intervention and baseline conditions, as well as between intervention conditions only, to determine if there was an effect of caregiver. As all subjects were pair-housed, each pair (not subject) was considered as an individual case for the purposes of statistical analyses on transformed data for all measures of social behavior. These measures included conspecific proximity, total affiliation, and conspecific affiliation. The mean raw durations of both total affiliation and conspecific affiliation between two pair members for each condition were used to calculate transformed data. Pair members' data for conspecific proximity was identical; as such, the actual raw duration data for each condition was transformed. Each subject was considered an independent sample for activity level data. A repeated measures Analysis of Variance (ANOVA) was subsequently used to compare arcsine transformations of proportions of behavior observed for each condition within subjects. Planned unpaired t-tests were also conducted to generate pair-wise comparisons between conditions for each replication. All statistical analyses were conducted using Microsoft® Excel v.11.5.0 or SPSS® v18 (SPSS, Inc., Chicago, IL, USA).

Table 2-1. Demographics of subjects at Big Oak Wolf Sanctuary

Pair/Names	Gender	Age (years)	Breed
Pair 1			
Sampson	Male	5	Alaskan gray wolf
Spirit	Female	5	Alaskan gray wolf
Pair 2			
Sabbath	Male	3	Wolf-dog hybrid
Ava	Female	3	Wolf-dog hybrid
Pair 3			
Peace	Male	3	Wolf-dog hybrid
Lea	Female	4	Wolf-dog hybrid
Pair 4			
Peter	Male	4	Wolf-dog hybrid
Sara	Female	5	Wolf-dog hybrid

Table 2-2. Ethogram of species-typical and abnormal behaviors for wolves and wolf-dog hybrids

Behavior	Definition
Conspecific affiliation	Tail-wagging, licking (usually face, but may be any part of body); or submission (may include crouching and licking while greeting, rolling on back or side and exposing underbelly) while oriented toward conspecific.
Human affiliation	Tail-wagging, licking (usually face, but may be any part of body); or submission (may include crouching and licking while greeting, rolling on back or side and exposing underbelly) and sniffing while oriented toward volunteer
Other affiliation	Tail-wagging, ears back, but not oriented toward any identifiable target
Aggression	Any aggressive response directed toward another animal or person; includes all non-contact aggression (e.g. growling, snarling, raised hackles, teeth baring) and contact aggression (e.g. inhibited biting, injurious biting, shoving, knocking over)
Inactive	Subject's body is stationary/immobile but not standing (e.g. sleeping, resting). Head may be erect or moving (e.g. looking around, panting).
Not visible	Any occurrence in which you cannot clearly see more than 50% of animal's body and/or such that you cannot identify the subject or its behavior with certainty. Recording "not visible" constitutes a 30-second period in which the subject meets the above criteria and in which the previously recorded and subsequently recorded behaviors are not identical.
Other	Subject is alert (eyes open). Record other anytime the subject is moving and not stationary (except while standing) (e.g. walking, grooming, digging)
Pacing	Subject repeatedly (>3 times, with no more than 3 seconds pause at any time) walks in a fixed route in enclosure (adapted from Hubrecht, Serpell & Poole, 1992).

Table 2-2. Continued

Behavior	Definition
Scent-rolling	Subject presses and subsequently rubs his or her body and/or head onto volunteer (can also be onto another object); may include rolling on back from side to side.
Social play	Any affiliative, non-aggressive interaction between two pair-housed animals occurring for at least 5 seconds; may include wrestling, relaxed body posture, reciprocal.
Vocalization	Any audible sound emitted from subject. May commonly include barking, howling, whining, or yelping.
Undesirable	May include cage chewing, tail-chasing, concentrated self-biting and/or self-licking that is compulsive (lasts for more than 15 seconds) and/or results in hair-removal, irritated skin, bleeding, etc.

Note: Definitions of all occurrences behaviors were recorded in durations (s). A minimum of 3s constituted the onset and offset of each behavior.

CHAPTER 3
RESULTS

Species-Typical Affiliative Behavior

Transformed proportions of conspecific-directed affiliation were significantly higher in intervention conditions relative to baselines for Replication 2 ($F = 4.97$, $P < 0.05$), and Replication 3 ($F = 74.0$, $P < 0.001$, where d.f. = 4, 12 for all F tests) (Fig. 3-1a & b). No significant difference in conspecific affiliation between conditions was observed for Replication 1 ($F = 2.89$, $P = 0.07$). For Replication 2, planned pair-wise comparisons revealed significant differences in conspecific affiliation between Baseline 1 and Intervention 2 ($t = -3.29$, $P < 0.05$) and Baseline 2 and Intervention 2 ($t = -3.29$, $P < 0.05$; d.f. = 3 for all t tests). In Replication 3, significant differences were found between Baseline 1 and Intervention 1 ($t = 18.0$, $P < 0.001$), Baseline 1 and Intervention 2 ($t = -3.86$, $P < 0.05$), Intervention 1 and Baseline 2 ($t = 30.5$, $P < 0.001$), Intervention 1 and Baseline 3 ($t = 9.51$, $P < 0.05$), and Intervention 2 and Baseline 3 ($t = 3.84$, $P < 0.05$, d.f. = 3 for all t tests). Transformed proportions of human-directed affiliation were also higher in intervention conditions relative to baselines in all replications, as human-directed affiliation was never observed during baselines (Fig. 3-1a & b).

Transformed proportions of total affiliation observed were significantly higher in intervention conditions than in baseline conditions for Replication 1($F = 24.8$, $P < 0.001$), Replication 2 ($F = 30.8$, $P < 0.001$), and Replication 3 ($F = 92.2$, $P < 0.001$, where d.f. = 4, 12 for all F tests). Planned pair-wise comparisons revealed significant differences in the first replication between Baseline 1 and Intervention 1 ($t = -10.8$, $P < 0.01$), Baseline 1 and Intervention 2 ($t = -4.04$, $P < 0.05$), Intervention 1 and Baseline 2 ($t = 8.34$, $P < 0.01$), Intervention 1 and Baseline 3 ($t = 6.30$; $P < 0.01$), Baseline 2 and

Intervention 2 ($t = -7.57$, $P < 0.01$), and Intervention 2 and Baseline 3 ($t = 7.46$, $P < 0.01$: d.f. = 3 for all t tests). In Replication 2, significant differences were found between Baseline 1 and Intervention 1 ($t = -10.8$, $P < 0.01$), Baseline 1 and Intervention 2 ($t = -11.6$, $P < 0.01$), Intervention 1 and Baseline 2 ($t = 7.50$, $P < 0.01$), Intervention 1 and Baseline 3 ($t = 4.80$; $P < 0.05$), Baseline 2 and Intervention 2 ($t = -10.7$, $P < 0.01$), and Intervention 2 and Baseline 3 ($t = 3.91$, $P < 0.05$: d.f. = 3 for all t tests). In Replication 3, significant differences were found between Baseline 1 and Intervention 1 ($t = -10.4$, $P < 0.01$), Baseline 1 and Intervention 2 ($t = -21.7$, $P < 0.001$), Intervention 1 and Baseline 2 ($t = 12.2$, $P < 0.01$), Intervention 1 and Baseline 3 ($t = 10.4$, $P < 0.01$), Baseline 2 and Intervention 2 ($t = -12.0$, $P < 0.01$), and Intervention 2 and Baseline 3 ($t = 21.7$, $P < 0.001$, where d.f. = 3 for all t tests).

There was no significant difference in total or conspecific affiliation between any baseline conditions across replications ($t = 1.8$, d.f. = 3, $P = 0.11$). In Replication 1 and Replication 2, no significant difference between intervention conditions was detected in total or conspecific affiliation. In Replication 3, a significant difference in conspecific affiliation ($t = 10.7$, d.f. = 3, $P < 0.01$) was found between the Intervention 1 and Intervention 2 conditions.

Durations and percentages of social play observed for each intervention condition for all pairs are reported in Table 3-2. Social play was never observed in baseline conditions.

Proximity Measures

The transformed proportion of proximity scans in which the subject was observed in contact, proximate to, or distant from both the other conspecific and human was calculated for all conditions. Proximity to conspecific is shown in Figure 3-2. No significant difference was found in the proportion of time conspecifics spent near one another when baseline and intervention conditions were compared in Replication 2 and Replication 3. A significant difference was found in the Replication 1 ($F = 3.8$, d.f. = 4, 12, $P < 0.05$); however, pair-wise comparisons did not reveal any significant differences in any comparison of baseline and intervention conditions. For three of the four pairs, higher proportions of time per condition that conspecifics spent in close proximity to one another were observed in baseline conditions following human interaction relative to the initial baseline (Fig. 3-2).

On average, subjects spent 66.03% of intervention conditions in close proximity (in contact or within an arm's length) of the volunteer. Peter spent the most time near the volunteer during interaction sessions (90.44% on average) and Spirit spent the least amount of time near the volunteer (53.55% on average). In addition, there was a significant difference in the proportions of time subjects spent near the volunteer between intervention conditions for Replication 2 ($t = 3.56$, d.f. = 7, $P < 0.001$) and Replication 3 ($t = 2.4$, d.f. = 7, $P < 0.05$). This effect was not observed for Replication 1.

Interactions were observed between human proximity data and conspecific proximity data for all individual subjects during intervention conditions. Mean percentages of scans in which subjects were observed near (defined as either in contact or proximate to) both the volunteer and conspecific during intervention conditions were as follows: 67.9% for Ava (Range: 21.4% to 94.8%), 76.4% for Sabbath (Range: 50.9% to 100%), 82.3% for Peace (Range: 37.2% to 100%), 74.0% for Lea (Range: 32.6% to 88.6%), 62.4% for Sampson (Range: 42.3% to 75.0%), 73.2% for

Spirit (Range: 19.2% to 89.3%), 91.7% for Peter (Range: 85% to 100%), and 77.0% for Sara (Range: 55.0% to 94.2%).

Activity Levels

Figure 3-3 shows the percentage of time (calculated from transformed proportions) observed in activity for all subjects on average in baseline and during human interaction. There was a significant difference in activity levels between baseline and intervention conditions in Replication 2 ($F = 7.45$, d.f. = 4, 28, $P < 0.001$) and Replication 3 ($F = 13.5$, d.f. = 4, 28, $P < 0.001$), such that duration of inactivity was significantly lower in baseline conditions than in intervention conditions. Planned pair-wise comparisons in Replication 2 further revealed an effect for Baseline 1 compared to Intervention 1 ($t = -3.25$, d.f. = 7, $P < 0.02$), Baseline 2 – Intervention 2 ($t = 3.2$, d.f.= 7, 28, $P < 0.01$), and Intervention 2 – Baseline 3 ($t = 2.95$, d.f. = 7, 28, $P < 0.02$) and in Replication 3 for Baseline 1 – Intervention 1 ($t = -8.74$, d.f. =7, 28, $P < 0.001$), Baseline 1 – Intervention 2 ($t =-8.40$, d.f = 7, 28, $P < 0.01$), and Intervention 2 – Baseline 3 ($t = 4.2$, d.f. = 7, 28, $P < 0.01$). This effect was not observed for Replication 1. In Replication 1, three subjects exhibited much higher rates of activity in intervention conditions relative to baselines, while the remaining five subjects did not (Fig. 3-3).

Durations of pacing observed per condition were also analyzed for all subjects that emitted this behavior. Three subjects exhibited significantly higher rates of pacing ($P < 0.05$) during baseline conditions relative to human interaction conditions in some replications (Fig. 3-4). One subject, Ava, exhibited increased rates of cage-chewing during baseline conditions following human interaction conditions for Replication 2 (Fig. 3-5).

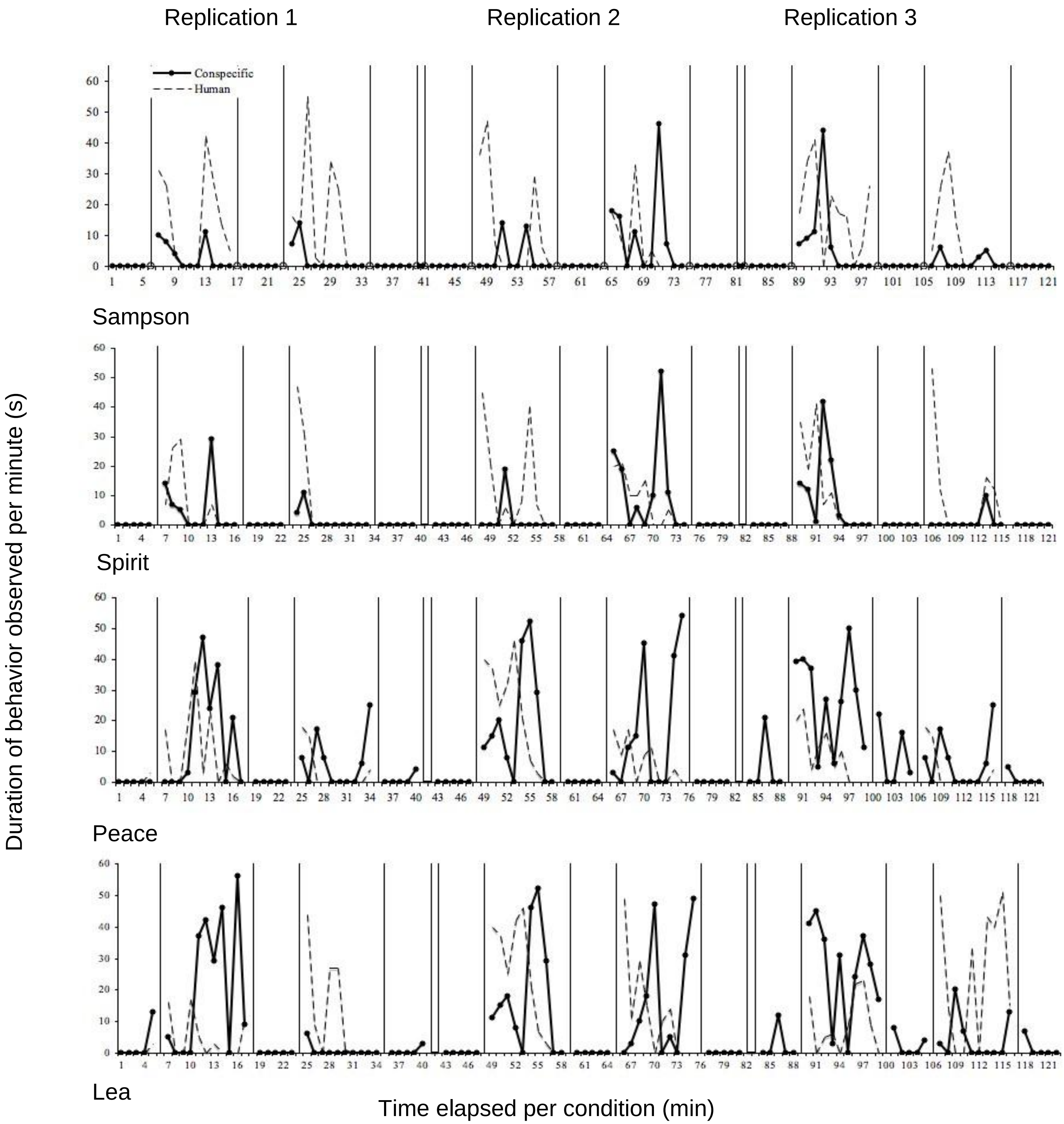

Figure 3-1.Duration of human and conspecific affiliation across replications for subjects in Pairs 1 & 2. Changes in conditions and replications are represented by single vertical lines and double vertical lines, respectively.

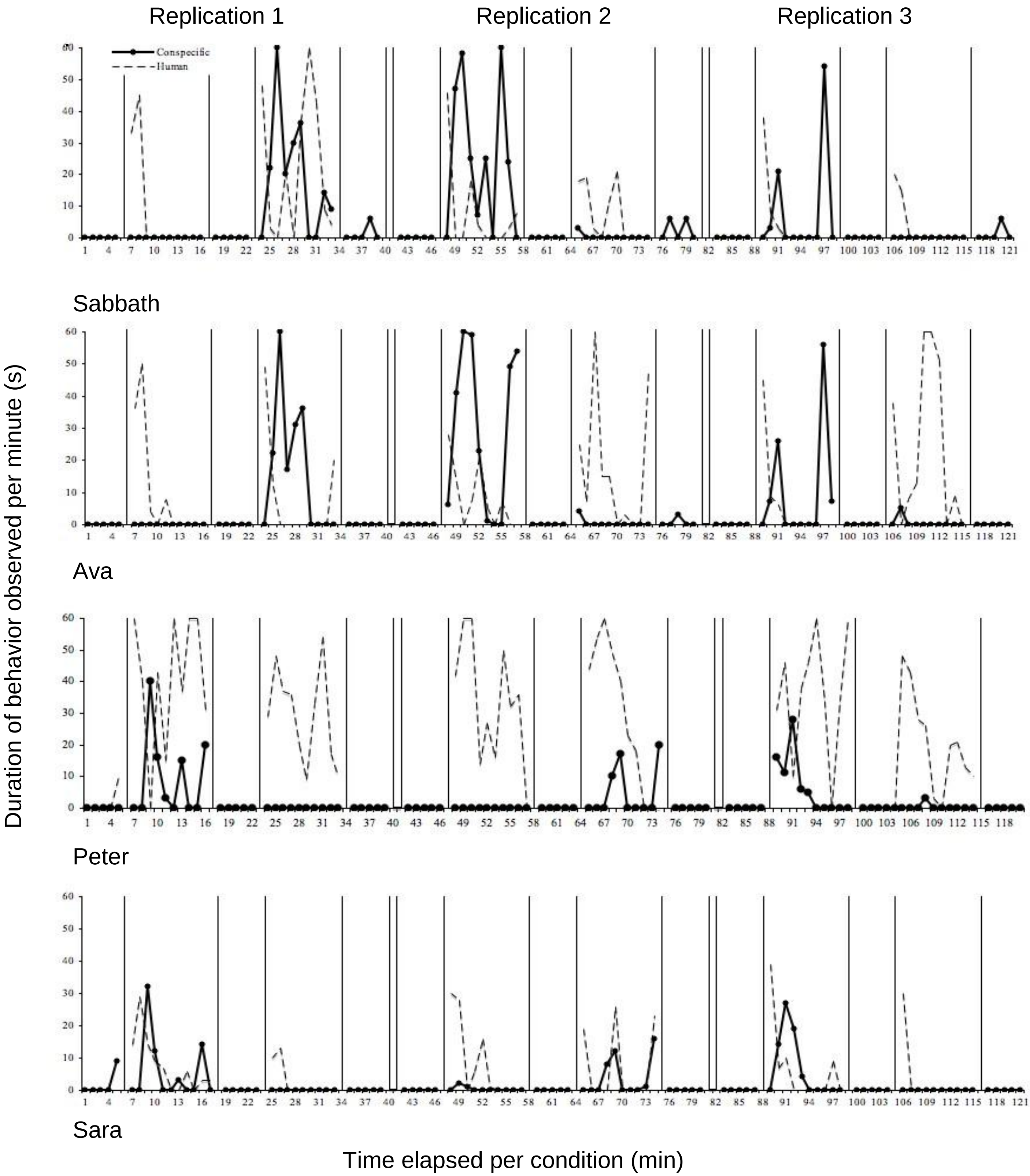

Figure 3-2. Duration of human and conspecific affiliation across replications for subjects in Pairs 3 & 4. Changes in conditions and replications are represented by single vertical lines and double vertical lines, respectively.

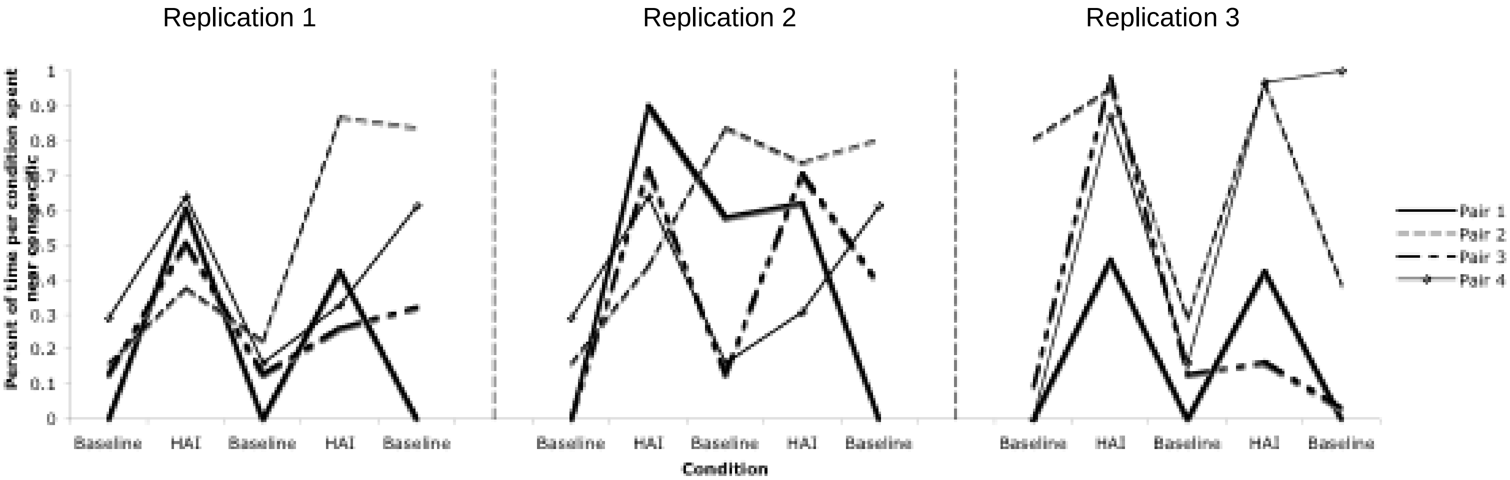

Figure 3-3. Proportions of scans per condition that pair-housed conspecifics were observed in close proximity to one another during baseline and human-animal interactions (HAI) across replications.

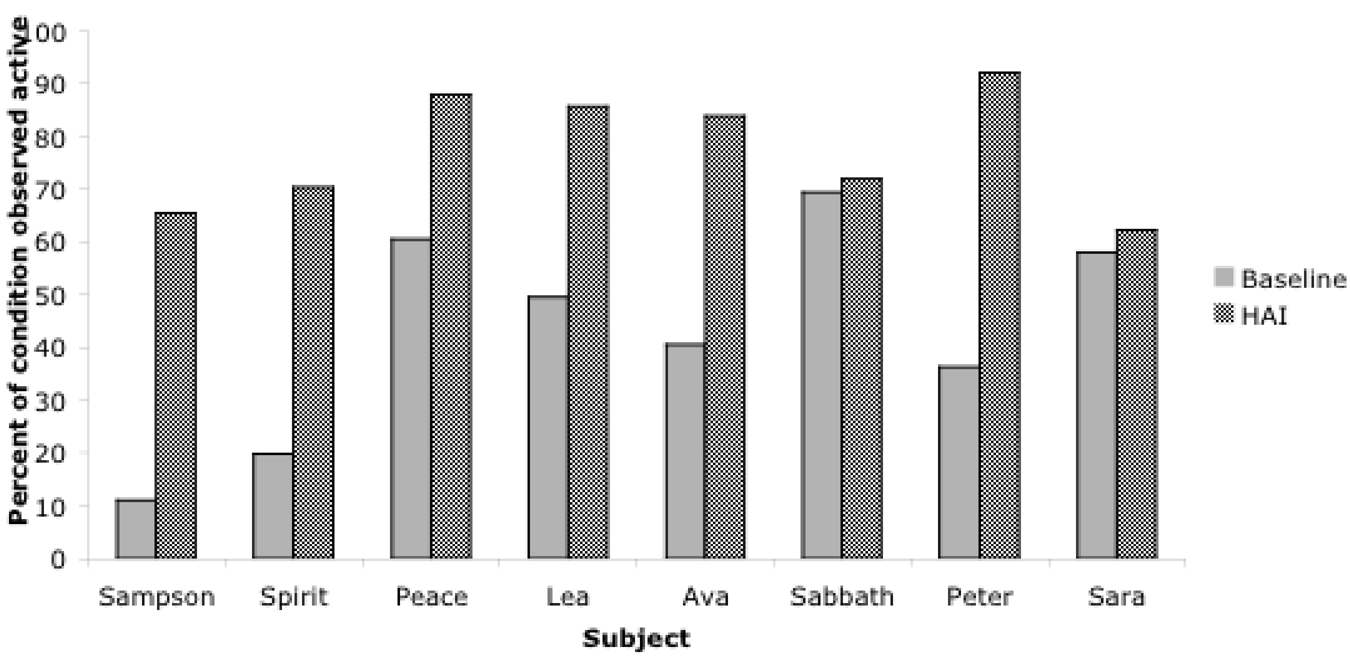

Figure 3-4. Activity levels for all subjects. Series represent mean percentage of baseline and human-animal interaction (HAI) conditions across replications that subjects were recorded as active.

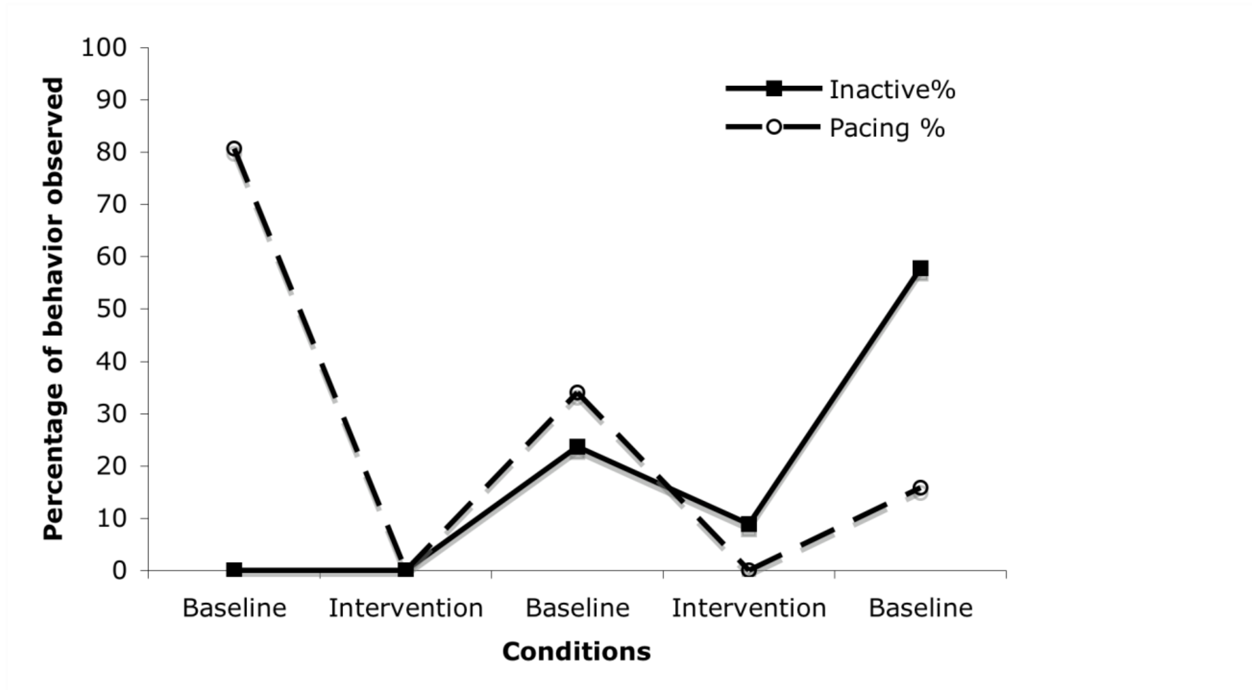

Figure 3-5. Activity and pacing levels for Peter in Replication 1. Peter displayed higher rates of inactivity during human interaction sessions; however, much of his activity during baselines was pacing, which decreased when a volunteer was present in the enclosure.

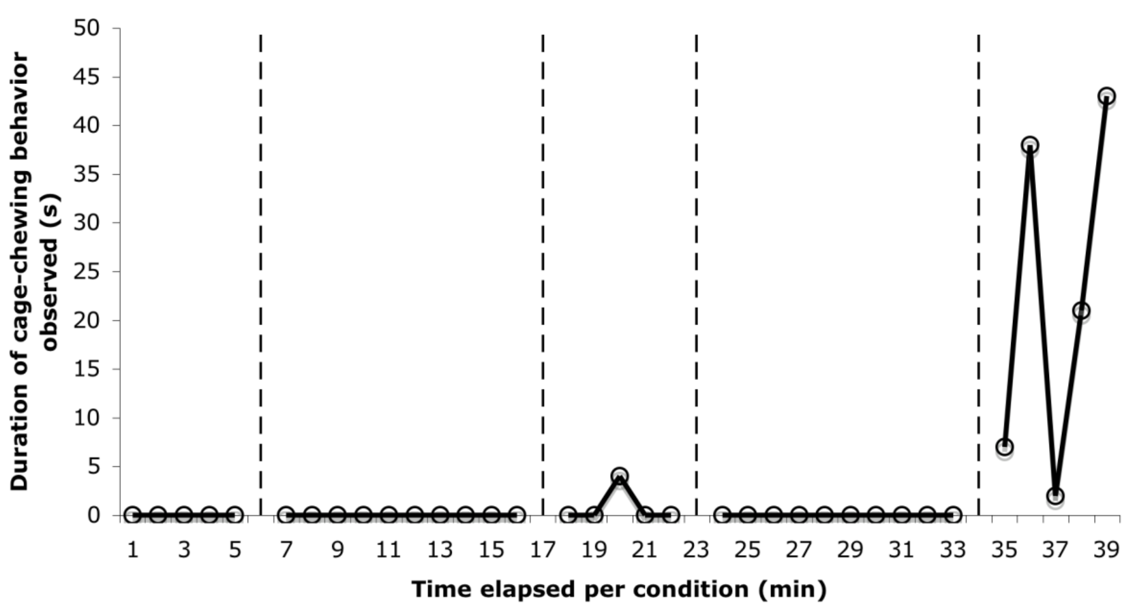

Figure 3-6. Duration of cage-chewing behavior emitted by Ava during Replication 2. Baseline (5-min) and intervention (10-min) conditions are separated by dashed lines.

Table 3-1. Percent of social play observed in human interaction conditions for wolves and wolf-dog hybrids

Pair	Replication 1		Replication 2		Replication 3	
	H 1	H 2	H1	H2	H1	H2
Sampson & Spirit	0%	0%	0%	3.7%	6.0%	0%
Peace & Lea	4.7%	0%	16.7%	9.3%	3.7%	4.2%
Sabbath & Ava	0%	21.5%	33%	0%	10.5%	0%
Peter & Sara	7.0%	0%	0%	4.3%	4.0%	0%

Note: First and second human interaction conditions are labeled H1 and H2, respectively across replications.

CHAPTER 4
DISCUSSION

Is Human Interaction Enriching for Wolves and Wolf-Dog Hybrids?

Enrichment is defined such that we cannot know if a strategy is "enriching" until we observe its effects on specific behaviors (Hoy et al., 2009); from these effects, assessments can be made with respect to an animal's well-being. Our results suggest that all subjects showed noticeably higher rates of positive species-typical affiliation – toward both humans and conspecifics – during human interaction sessions relative to baseline conditions. The presence of a familiar volunteer not only prompted greeting behavior and affiliative responses towards the human, but also promoted social interactions among each pair. This increase in social interaction among conspecifics is consistent with Baker's (2004) findings of human interaction on socially housed chimpanzees. Conspecifics also spent a significantly greater proportion of time in close proximity to one another when a volunteer was present in the enclosure in two-thirds of replications. Thus, free-contact interactions with familiar human caregivers appear to be an effective strategy for increasing species-typical social affiliation and enhancing conspecific interactions in socialized, pair-housed wolves and wolf-dog hybrids.

In addition, the results of this study provide an informative evaluation of a specific stimulus change to serve as environmental enrichment. Given the different histories of the subjects used in this study, the presentation of individual data allows one to examine the consistency and reliability of behavior patterns observed throughout intervention and baseline conditions across subjects. Individualized data presented cumulatively over time and replicated repeatedly also allow for the detection of unique changes in behavior within each individual subject that would otherwise be masked by group designs, averaging across conditions, and other forms of aggregate data treatment. Welfare is a property of the individual; thus, it is especially appropriate, instructive, and perhaps ideal, to study changes in behavior using a single-subject design when evaluating enrichment efficacy.

However, several limitations should be noted. First, the effects for conspecific proximity should be interpreted cautiously. In this study, enhanced conspecific proximity for all pairs appears to be related to human proximity for some intervention conditions. That is, our results suggest that in some interventions, the majority of scans in which conspecifics were scored as near one another, pair members were also scored as within an arm's reach of the volunteer. Thus, it should be noted that, at least sometimes, conspecific proximity was enhanced simply because both animals were engaging with the volunteer, and not necessarily with one another.

Although our results suggest that conspecific proximity is maintained for at least a brief time following human interaction, the dramatic increase observed in affiliative behaviors appears to be temporary. Most subjects, with the exception of Peace and Lea, exhibited affiliative responses only during the intervention conditions. This suggests that these high rates of increased social interaction may not be long lasting and possibly require the continued attention of a familiar volunteer to be maintained. This finding may be of interest both to theoretical questions about the function of play behavior (discussed below), as well as practical questions in applied settings. Many facilities that house captive animals seek ways to continuously promote positive, naturalistic social interactions among their animals, including at times that staff are not available to interact with the animals. Therefore, different schedules of social reinforcement should be explored for their ability to promote maintenance of positive intraspecific behavior in order to maximize welfare in captive canid populations.

Trends in activity levels were somewhat inconsistent across replications. Significant increases in activity levels were observed during intervention conditions in Replication 2 and Replication 3; however, no such effect was found in Replication 1. Upon closer examination of the data, it appears that activity levels were confounded with high rates of stereotypic behavior for two subjects in Replication 1. Five subjects exhibited significantly longer durations of inactivity during baseline conditions than in treatment conditions during Replication 1. The remaining three subjects – Sara, Peter, and Peace – showed higher levels of inactivity during treatment sessions relative to baselines. However, Peter and Peace exhibited a high frequency of pacing behavior in the initial baseline conditions, followed by a dramatic elimination of pacing in the first subsequent intervention condition.

Ava was the only other subject that exhibited an aberrant behavior (cage chewing) during observations. Interestingly, Ava's cage-chewing occreplurred only during baseline conditions following an intervention condition in Replication 2. Thus, increases in activity levels do not necessarily reflect an improvement in welfare. Future studies that evaluate enrichment in captive species should take steps to be sure that the type of activity emitted is being assessed, in addition to the general activity durations. In addition, Ava's increases in cage-chewing – which occurred in 22.2% of return-to-baseline conditions – further illustrates the importance of evaluating the effects of enrichment on an individual basis, replicating observations, and monitoring behavior following the removal of enrichment, and not solely while enrichment is being provided.

A recent study that surveyed over 200 personnel from 13 zoological institutions reported that less than half of all respondents reported collecting formal data on enrichment efficacy (Hoy et al., 2009).

Finally, one concern was that the presence of a single person in the enclosure would create an opportunity for increased aggression between the pairs. However, the low levels of aggression observed in all baseline conditions for all subjects were maintained throughout all human interactions sessions. Only one bout of aggression (3 s in duration) was recorded for one pair during human interaction. Thus, these data suggest that human interaction alone has the potential to be a highly enriching strategy for socialized wolves and wolf-dog hybrids who are pair-housed for an extended period of time. This is supported by higher rates of species-typical affiliation toward humans and conspecifics, higher activity levels for the majority of subjects, low levels of aggression, and decreased pacing for all subjects that exhibited this behavior in initial baselines.

Variables Influencing Enrichment Efficacy

A supplementary measure of conspecific interaction was subjects' proximity to their cage-mate (during both baselines and human interaction conditions) and to the volunteer (during human interaction conditions only). No difference was found in the proportion of time spent in close proximity to a conspecific across all conditions during Replication 1; however, there was an increase in the proportion of time conspecifics spent near one another from the initial baseline to the first intervention condition, but not between subsequent baselines and interventions. This is likely because pair-housed animals simply remained in close proximity to one another after human interaction was no longer available. Three out of four pairs remained in close proximity to one another in the final baseline condition (Fig. 3). In other words, the effects of human interaction on proximities appeared to be maintained through subsequent conditions.

All subjects spent, on average, more than half of each human interaction condition near the volunteer. In Replication 2 and Replication 3, there was a significant difference between the proportion of time spent in close proximity to the volunteer between the first and second intervention conditions, but this was not the case for Replication 1. There are several possible explanations for this. One possibility is that all subjects may have a preference for one volunteer over another. The volunteer that was present in all first interaction sessions was the co-owner of the facility, and thus more familiar to the subjects than the second volunteer, who had been with the sanctuary for 3 months. A second possibility is that the subjects satiate somewhat to human interaction at 10-min. session durations. It would thus be worthwhile to examine the effect of a longer inter-trial interval and return-to-baseline condition if there are limited volunteers or time to allocate to human-interaction sessions.

Another variable that may contribute to the efficacy of human interaction in evoking species-typical affiliation is the length of time since last feeding. An inverse relationship between length of time since last feeding and enrichment effectiveness has been suggested by Tarou and Bashaw (2007) and has also been reported with boomer balls in captive maned wolves (*Chrysocyon brachyurus*) (Cummings et al., 2007). Future studies should examine potential motivating operations – including proximity to feedings and length of time between caregiver interactions – that could influence the efficacy of human interactions.

Finally, the results in activity levels and affiliative behaviors presented here may be conservative estimates due to the high temperatures and humidity throughout the study. Although we only conducted observations during perhaps the coolest daylight hours, it may have still been to energetically expensive to exert much activity under such conditions for these species. Thus, future studies should examine the efficacy of human interactions for this population across seasonal variation.

Understanding Play and Welfare – Is Play Spontaneous?

The increases observed in conspecific affiliation during human interaction included multiple occurrences of social play across pairs. The presence of a familiar caregiver was also associated with increased levels of play among conspecifics. Furthermore, these increases in play were associated with concurrent decreases in stereotypic behavior during human interaction for subjects that exhibited pacing. Though the absence of social play in baseline conditions did not permit statistical analysis, it appears that a systematic trend emerged with respect to this behavior. All pair-housed subjects engaged in social play during human interaction sessions in every replication; within replications, however, social play repeatedly occurred only in one human interaction session for two pairs – Sabbath and Ava and Peter and Sara. Furthermore, this effect was not repeatedly observed solely in the presence of the same caregiver (although social play did occur more often when the first, more familiar caregiver was present). One possibility is that social play was too energetically expensive to engage in, given the seasonal time of the study, with a return-to-baseline interval of only five minutes in length. Peace and Lea, however, engaged in social play in both human interaction sessions in both Replication 2 and Replication 3. It may be the case that these subjects, being the youngest of all the subjects, were also the relative fittest and could thus physically engage in such behavior more often. These questions suggest that, in addition to examining seasonal variation, the schedules of human interaction should also be investigated; perhaps a longer interval between human interaction sessions would result in maximizing the efficacy of this strategy. This has also been proposed by Tarou and Bashaw (2007).

These findings support the notion play behavior is associated with the environmental context in which animals find themselves and thus may be a potential indicator of animal welfare (Held and Spinka, 2010). Previous research has claimed that animals will only play if they are well fed, healthy, and not subjected to stressful conditions (Burghardt, 2005; Fagen, 1981; Martin and Caro, 1985). This is also consistent with observational findings that social play in captive wolves occurs when conflict among group members is absent and stress is thus low or minimal (Cordoni, 2009).

However, the benefits of play behavior remain to be fully understood, as the task of defining welfare indicators experimentally is difficult. Furthermore, play has not been given much empirical attention in large part because of the premise that the behavior has no readily observable function; this implies that play does not contribute to the immediate survival of the organism (Burghardt, 2005). It may be argued, however, that failure to identify a function for a behavior may be due to a shortcoming of the observer rather than a true lack of function to the behavior. In this study, conspecific social play occurred only during human interaction conditions. As such, social play does not appear to be spontaneous nor independent of external stimulation, but rather, at least partially related to the presence of an interspecific social stimulus in this population.

An interesting observation is that social play did not occur in baselines – even if a volunteer was visible to the animals during that time. Prior to each observation, the lead author instructed all volunteers to ignore the subjects during baselines if the volunteer could not avoid being visible to the observed pair. It is possible that due to their extensive history of receiving reinforcement from human caregivers, subjects were sensitive to whether or not volunteers were attending to them. In contrast, volunteers were continuously providing attention to the subjects during human interaction conditions. It is thus possible that interspecific attention may be an environmental variable maintaining positive social interactions, including conspecific play. Dyadic play between domestic dogs was found to be directly correlated with conspecific attention, (Horowitz, 2009); however, the possibility that interspecific social attention could maintain social play among conspecifics has not previously been proposed. Perhaps in captive environments and households, where animals are dependent on human caretakers for survival essentials (e.g. food, shelter), play may function as an attention-maintained behavior.

Behavior Analysis as a Tool for Identifying Functional Relationships Between Play and the Environment

In applied behavior analysis, functional analysis is a highly effective tool in identifying variables that maintain self-injurious and other problematic behaviors in humans (e.g., Iwata et al., 1994) and non-human primates (Dorey et al., 2009; Martin and Bloomsmith, 2011). It has not yet been demonstrated whether functional analysis could also effectively identify environmental variables that maintain positive behaviors, including social play. Such findings would be useful in addressing both basic questions surrounding the theories of play, as well as addressing captive management issues in applied settings. Future studies may also examine ways to objectively test play as an indicator of good welfare and work toward determining a satisfactory and useful dependent measure of play for canids, and other species.

The functions and environmental variables affecting play behavior are not fully understood, and play itself does not have a universal definition. Because the focus of this study was to evaluate an extant husbandry strategy at a single facility, we had limited ability to manipulate variables that could have contributed to a more functional analysis of play behavior in this population. This is a valuable direction for future research. Our results here allow us to state that access to a familiar interspecific social stimulus evokes immediate, significant increases in positive species-typical behaviors, including social play, in socialized wolves and wolf-dog hybrids. Thus, it is possible that social play in this population is at least partially related to external stimulation in the captive environment.

A Note on Generality

While the results of this study suggest that human interaction can be a potent enrichment strategy for the present subjects, this is likely not the case for all wolves and wolf-dog hybrids housed in captivity. First, only socialized individuals were used in this study to ensure the safety of the human volunteers. However, many exotic animals arrive at sanctuaries through confiscation, often because they have been abused or neglected by their previous owners. Consequently, it is plausible that a substantial proportion of animals living in sanctuaries are not well socialized, but show fear or aggression to humans, as a result of prior experiences that make human presence aversive. Such animals are unlikely to respond as positively to human entrance into their enclosures, even if such a strategy were considered safe for the human volunteers involved.

Aggression can be treated as an operant behavior, and at least one unpublished study has successfully used distance from an aversive stimulus to reduce aggressive responses and shape desirable alternative behaviors in domestic dogs (Snider, unpublished, 2007). It would be interesting to determine whether such a negative reinforcement shaping procedure can effectively reduce fearful behaviors that occur in response to human volunteers (e.g., pacing, prolonged staring, tail-tucking, and crouching). To make human interaction an effective form of enrichment for more individuals, future research should explore such interventions that can reduce both fear and aggression, as well as promote affiliative behaviors in relatively non-socialized animals. This would be hugely beneficial for management purposes in any facility providing long-term residence to captive animals.

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BIOGRAPHICAL SKETCH

Lindsay Renee Mehrkam was born in 1987 in Allentown, Pennsylvania. She graduated summa cum laude from William Allen High School in 2005. She subsequently earned her Bachelor of Arts in animal behavior from Franklin and Marshall College in 2009, where she was also awarded the Roger and Elizabeth Thompson Award in Animal Behavior for her research on captive wolf-dog hybrids. Her study was conducted in collaboration with Dr. Roger Thompson, and was hosted at both the Wolf Sanctuary of Pennsylvania and the California Wolf Center.

Upon graduating in 2009, Lindsay was assigned a research internship at Animal Kingdom Theme Park at Walt Disney World, in Bay Lake, Florida. This position provided her with the opportunity to collect behavioral data on a wide range of non-human primates and avian species housed in captivity, to later be used for management and conservation purposes. In addition, Lindsay assisted with a project on Key Largo woodrats, a critically endangered species endemic to Florida. This field position allowed her to work temporarily with the U.S. Fish and Wildlife Service and the Florida Fish and Wildlife Commission, in conjunction with the Walt Disney Company®.

Lindsay's current assignment at the University of Florida in the Department of Psychology allows her the opportunity to study human-animal interactions with captive canids. In addition, Lindsay collaborates with the Santa Fe College Teaching Zoo on an evaluation study of environmental enrichment for Galapagos tortoises. Upon the completion of her Master of Science in psychology, Lindsay will continue in the doctoral program in psychology at the University of Florida, specializing in welfare research on captive wolf-dog hybrids and other exotic animals.