Effects of changing housing conditions on mangabey behavior (Cercocebus atys): Spatial density, housing quality, and novelty effects

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Effects of changing housing conditions on mangabey behavior (*Cercocebus atys*): spatial density, housing quality, and novelty effects

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Abstract

The separate influences of spatial density and housing quality on the behavior of captive animals are difficult to measure because the two factors are often intrinsically linked. Here, we recorded affiliative and agonistic behavior in adult sooty mangabeys in various housing situations, testing spatial density and housing quality changes separately (N=26 experienced spatial density changes; N=12 experienced housing quality changes). We varied spatial density by 50% while holding housing quality constant and we varied housing quality while holding spatial density constant (achieved by comparing two types of run-housing that varied in the amount of visual privacy and outdoor access). Each housing condition was one month in duration. Prior to collecting data in each housing condition, we evaluated the subjects' initial responses to the change in housing environment during two-week novelty periods. Affiliative behavior did not change during the novelty periods. Agonistic behavior initially increased slightly when spatial density increased and it decreased significantly when spatial density decreased; it also decreased when subjects moved to housing that offered more visual privacy and outdoor space, indicating that the mangabeys were sensitive to these housing changes. After the novelty periods, affiliative behavior increased under higher spatial density, but remained unchanged across housing quality conditions; agonistic behavior remained unchanged across all conditions. Results suggest that a prolonged increase in spatial density led the mangabeys to adopt a tension-reduction coping strategy, in which the increase in affiliative behavior alleviates a presumed increase in social tension. Reducing visual privacy and choice did not affect the mangabeys' behavior, post-novelty period. Thus, like many other primates, the mangabeys managed tension by flexibly adapting to changes in their housing environment in ways that reduce the risk of severe aggression. This study highlights the importance of controlled behavioral studies in facilitating data-driven management decisions that promote animal welfare.

Keywords

spatial density; housing quality; novelty response; crowding; choice; visual privacy

INTRODUCTION

Spatial restriction is a common feature of the environment for all captive animals. To manage captive animals appropriately and conscientiously, it is important to understand how they respond to routine, temporary, and/or permanent changes in their housing environment, including changes in spatial density (the space available for a fixed number of animals), the physical complexity of the environment, and the novelty of the space. Such environmental features interact with the social context and other factors (e.g., individual temperament and past experiences, social relationships, group size and demographics, and species) to influence behavior [e.g., Judge and de Waal, 1997; Boyce et al, 1998; Ross et al, 2010; Duncan et al, 2013]. Spatial density studies often confound the physical quality and the novelty of a change in housing environment, making it difficult to disentangle their separate influences on behavior (e.g., [Alexander and Roth, 1971; Erwin, 1979; Boyce et al, 1998]). The purpose of this study was to investigate the behavioral responses of sooty mangabeys to these three factors separately.

Sooty mangabeys are a primarily terrestrial monkey species native to West Africa. They form large groups characterized by female philopatry and a linear dominance hierarchy that is less nepotistic and despotic than those of baboon and macaque social groups [Gust and Gordon, 1994; Range and Noë, 2002; Range, 2005]. The Yerkes National Primate Research Center houses a breeding colony of sooty mangabeys with a subset of the population living in run-housing. The mangabeys living in run-housing experience changes in their housing environment including the daily temporary reductions in available space during husbandry and the occasional move within or between run-housing buildings. Thus, this study has both theoretical and applied implications: 1) we investigated which theoretical model accounts for behavior under various housing conditions in a species which has not yet been investigated concerning this particular area of research and 2) we addressed how their behavior under various housing conditions informs their management and welfare in run-housing.

There are two theoretical models that explain how primates respond to increasing spatial density. The first is the density-aggression model, in which aggression is predicted to increase as spatial density increases [e.g., Elton and Anderson, 1977]. Few studies find evidence supporting the density-aggression model in the absence of other factors that might also influence aggression (e.g., physical complexity and/or sudden unfamiliarity with the housing environment [Alexander and Roth, 1971; Boyce et al, 1998]). The second is the coping model, which proposes that captive primates modify their behavior in ways that mitigate severe aggression when spatial density increases [de Waal, 1989]. There is an abundance of support for the coping model and many studies highlight behavioral flexibility in primates' response to increased spatial density depending on their particular social context and/or degree of crowding [e.g., Duncan et al, 2013].

Coping strategies generally take one of two forms: a conflict-avoidance strategy and a tension-reduction strategy. When primates adopt a conflict-avoidance strategy, all forms of social interaction decrease when spatial density increases (chimpanzees and gorillas, respectively [Aureli et al, 1995; Cordoni and Palagi, 2007]; rhesus and long-tail macaques,

respectively [Judge and de Waal, 1993; Aureli et al, 1995]; capuchins [van Wolkenten et al, 2006]). When primates adopt a tension-reduction strategy, affiliative and/or appeasement behaviors increase when spatial density increases, as a way to alleviate a presumed increase in tension and reduce the likelihood of severe aggression (chimpanzees, bonobos, and gorillas [Nieuwenhuijsen and de Waal, 1982; Caws and Aureli, 2003; Sannen et al, 2004; Cordoni and Palagi, 2007]; vervets [McGuire et al, 1978]). The coping strategy that is adopted by a group or individuals may be influenced by social factors [e.g., Erwin, 1979; Nash and Chilton, 1986; Novak and Drewsen, 1989; Duncan et al, 2013] and the duration of crowding: conflict-avoidance appears to be more prevalent in short-term crowding situations, which can last from hours to days, whereas tension-reduction develops over time in response to long-term crowding, which can last from several months to years [Aureli and de Waal, 1997; Videan and Fritz, 2007]. For either strategy, it is important to recognize that behavioral evidence for coping does not imply that animals are stress-free or content with a crowded situation [Erwin, 1979; de Waal, 1989].

Providing physical complexity and choice in a captive environment is at least as important as providing an adequate amount of space in promoting species-typical behavior, social stability, and psychological well-being in captive animals (goats and sheep [Anderson et al, 2002]; red deer [Whittington and Chamove, 1995]; polar bears [Ross, 2006]; giant pandas [Owen et al, 2005]; apes: [Wilson, 1982; Baker and Ross, 1998]; monkeys: [Badihi, 2006; Basile et al, 2007]). In environments that offer a choice to be inside or outside, primates show preferences for either location and/or preferences for specific areas within the indoor or outdoor space [Bettinger et al, 1994; Pines et al, 2007; Ross et al, 2009; Ross et al, 2011]. Primates also show differences in behavior and activity when housed outside compared to inside [Novak et al, 1992; Hoff et al, 1997; Fontenot et al, 2006], and just having the choice to be inside or outside may increase measures of psychological well-being, as has been shown for chimpanzees, giant pandas, and polar bears [Baker and Ross, 1998; Owen et al, 2005; Ross, 2006]. In addition, offering escape routes or simple visual barriers, such as walls and culverts, is usually associated with lower rates of aggression in nonhuman primates [Erwin and Erwin, 1976; Estep and Baker, 1991; Maninger et al, 1998; McCormack and Megna, 2001; Basile et al, 2007], as these features simultaneously increase physical complexity and choice.

Most spatial density studies make use of the subjects' familiar, existing space and the need to crowd animals into less space during husbandry, winter months, and/or construction of a new enclosure [e.g., Erwin, 1979; Novak and Drewsen, 1989; Judge and de Waal, 1993; Boyce et al, 1998; Sannen et al, 2004; Duncan et al, 2013]. However, novelty responses to changes in housing environment are rarely documented or systematically controlled. Those studies that included a period of time for animals to adjust to a housing change prior to data collection vary extensively in the duration provided, and most administered it prior to the crowded condition only (e.g., 30 minutes to several hours [Judge and de Waal, 1993; Aureli and de Waal, 1997; van Wolkenten et al, 2006]; 11 days to one month [McGuire et al, 1978; Sannen et al, 2004]). No explanation is provided regarding the adjustment period duration; however, one early study identified a period of 1–2 weeks in which subjects' behavior (baboons, in this case) changed in response to increased spatial density prior to returning to baseline levels [Elton and Anderson, 1977]. Thus, based on this and our experiences with

the mangabeys in run-housing, we administered a two-week adjustment period and evaluated whether the mangabeys exhibited a novelty response to initial changes in their housing environment. In this study, the term novelty does not refer to housing environments that are totally novel to subjects, but instead to the novelty of change in housing environments (e.g., the sudden reduction of available space by 50%).

Hypotheses and Predictions

To evaluate the mangabeys' response to changes in their housing environment according to the theoretical models described above, we recorded affiliative and agonistic behavior (including social wounding rate and severity) across high and low spatial density conditions and across housing quality conditions that varied in the degree of visual privacy and the choice to move indoors or outdoors. We hypothesized that both increased spatial density and decreased levels of privacy and choice would produce social tension in sooty mangabey groups and that they would modify their behavior under these housing conditions in accord with one of the theoretical models described above. If mangabeys responded according to the density-aggression model, we predicted wounding and agonistic behavior to increase with no change or a decrease in affiliative behavior under these conditions (Prediction 1). If they responded according to the conflict-avoidance coping strategy, we predicted affiliative and agonistic behavior to decrease (Prediction 2). If they responded with a tension-reduction coping strategy, we predicted affiliative behavior to increase while wounding and agonistic behavior remain relatively stable (Prediction 3). Finally, we predicted that when the mangabeys first experienced a change in housing environment, either in spatial density or housing quality, their behavior would not be uniform across all housing condition changes (for example, under conditions expected to stimulate social tension, affiliative and/or agonistic behavior would change in one direction and would change in a different direction when conditions were expected to reduce social tension). This would indicate a context-dependent novelty response (Prediction 4), as opposed to the same behavioral response to any change (for example, increased aggression regardless of whether the change was from low to high spatial density or vice versa; as in Nash and Chilton's novelty model [1986]).

METHODS

Subjects and Housing

Subjects were housed in runs at the Yerkes National Primate Research Center in Lawrenceville, GA USA and included a total of 31 adult sooty mangabeys (*Cercocebus atys*) living in seven groups (ages 11–31 years; mean age ± SE: 19 ± 1 years; 11 males, 20 females). Monkey chow was distributed twice daily, water was available *ad libitum*, and feeding enrichment (consisting of fresh fruits, vegetables, and seeds) was distributed daily. All runs were equipped with perches, plastic barrels, toys, a fire hose swing, and climbing apparatuses. This research was conducted within a protocol approved by the Emory University Institutional Animal Care and Use Committee, complied with U.S. laws and regulations regarding the care and use of animals in research, and adhered to the American Society of Primatologists principles for the ethical treatment of primates.

Table I provides detail on the group sizes and compositions, and the spatial density and number of runs available to each group in each housing condition that they experienced. Twenty-six subjects experienced spatial density changes (groups 1–6) and 12 subjects experienced housing quality changes (groups 4, 5, and 7). Thus, groups 4 and 5 (N=8 total) experienced both types of housing changes: group 4 experienced spatial density changes followed by the housing quality changes; group 5 experienced each type of housing change in the opposite order (each study period was separated by 1–2 months for both groups). All groups were tested between April 2012 and June 2013.

Each group began in one of two types of run-housing that were differentiated by the degree of visual privacy from group members and the choice of being indoors or outdoors (Fig. 1). Those that experienced spatial density changes remained in their respective run-housing type for the duration of testing, whereas those that experienced housing quality changes moved between the two types of run-housing. The high privacy/choice (P/C) housing consisted of 16 runs (eight interconnected runs on each side of a corridor), each with indoor and outdoor portions that were separated by a wall (indoors: 2.13×1.52 m; outdoors: 3.05×1.52 m; Fig. 1a). The runs were connected through doorways, one connecting the indoor and outdoor sections of each run and one connecting adjacent runs in both the indoor and outdoor sections (each doorway was approximately 30.48×30.48 cm). The low privacy/choice housing consisted of 24 indoor runs (two groups of six interconnected runs on each side of a corridor; 3.66×3.05 m) each connected through one doorway (approximately 30.48×30.48 cm) and through mesh tunnels connecting adjacent runs (Fig. 1b). Each group was given access to at least one run, depending on the size of the group and the housing condition (Table I). Solid metal panels were placed in the doorways between runs to separate groups. Garage doors ran the length of each side of the building so that one side of each run was exposed to the outdoors, but animals had no outdoor access (doors were closed in severe weather, but were generally left open for fresh air).

Experimental Design

To isolate the effects of spatial density, we compared behavior in high and low spatial density conditions (high density achieved by reducing available space by 50%), while keeping the physical features of the environment as constant as possible. To isolate the effects of housing quality, we compared behavior in two different types of housing environments that varied in the degree of visual privacy and the choice to move indoors or outdoors, while holding the space available to each group almost constant (within 1.5 square meters per animal). Each factor was tested using an ABA-style design with two-week testing phases: A1: baseline phase; B: experimental phase (change in housing environment); A2: return to baseline. Prior to collecting data in each phase, subjects were given a two-week period in which to adjust to any change in housing environment (referred to as the novelty periods: N1 and N2). Thus, testing for each group was completed over ten weeks: A1-N1-B-N2-A2.

The order of condition presentation was counterbalanced as much as possible across groups (Table II). For subjects experiencing spatial density changes, N=14 subjects in four groups experienced the low spatial density condition in phase A1, followed by the high spatial

density condition in phase B, then a return to low spatial density in phase A2. Twelve subjects in two groups experienced the conditions in the opposite order. Subjects remained in their respective housing type across ABA phases (Groups 3 and 4 were tested in the high privacy/choice housing throughout; Groups 1, 2, 5, and 6 were tested in the low privacy/ choice housing throughout). For subjects that experienced housing quality changes, N=8 subjects in two groups experienced the high privacy/choice condition in phase A1, followed by the low privacy/choice condition in phase B, then a return to the high privacy/choice condition in phase A2; N=4 subjects in one group experienced the conditions in the opposite order (Table II). All subjects that experienced housing quality changes had lived in both housing types at some point in their lives; thus we assessed how behavior differs in two qualitatively different housing environments, as opposed to environments that were completely novel to subjects.

Behavioral Data Collection

Although juvenile(s) and/or infant(s) were present in groups 4–6, we collected behavioral data on adult interactions only. For each group, we collected eight hours of behavioral data in each phase and novelty period. Each observation session was 30 minutes in duration and we conducted two per day (one each in the morning and afternoon, ranging between 0745– 1600 hours), four days per week for a total of 16 observation sessions per condition. For each 30-minute observation session, we recorded the occurrence of affiliative and agonistic behaviors among the subjects using instantaneous scan sampling on 30-second intervals (maximum total intervals 960 per phase; intervals were dropped if the observer had to end the session early or look away during the scan). Inter-rater reliability was maintained at or above 90% agreement between three observers prior to formal data collection.

Affiliative behavior involved gentle affiliative contact and tolerated close presence of another individual. Specific affiliative behaviors included grooming (using the hands or mouth to gently pick through another's fur), friendly body or manual contact (brief contact included touch, embrace, inspecting another's body/genitals; sustained contact included social play and resting in contact), and resting in arm's reach proximity. Agonistic behavior involved non-contact aggression and contact aggression. Specific non-contact aggression included threatening another (raising eyebrows and making direct eye contact), lunging at another (threat accompanied by a bluff charge), aggressive following and chasing another (both involving continued pursuit accompanied by threats and lunges). Specific contact aggression included brief manual aggressive contact (grabbing, slapping, or pushing another), pinning another to the ground, tail-biting (a ritualized behavior involving holding another's tail and repeated, non-injurious biting of the tail), biting (directed at body parts other than the tail), and grappling (escalating, full-contact fighting that usually results in severe injuries). We also recorded the number of wounds that subjects received from another monkey each day throughout their testing period. Wounds that occurred on weekends were recorded by trained research support staff (wounds were assessed by at least two people and the score agreed upon). Wounds were rated on a scale from 1 – 7 with 1 indicating a superficial scratch or scrape, 2 indicating a shallow cut with minimal bleeding, and ratings 3–7 indicating increasing levels of physical damage; however, we did not record any wounds in the 3–7 range of this scale in this study.

Data Analysis

We used non-parametric statistics due to small sample sizes (N=26 experienced spatial density changes and N=12 experienced housing quality changes), non-normal distributions (tested with Shapiro-Wilk tests with and without transformation), and violations of assumptions for homogeneity of variances required to conduct parametric tests (Box's M and Levene's tests). To compare behavior between housing conditions, we calculated the percent of total intervals each subject engaged in each behavioral category and each specific behavior per experimental phase and novelty period (summing the total number of intervals the subject engaged in affiliative behavior across sessions and dividing by the total number of intervals recorded for that subject in the phase, multiplied by 100). For each subject and behavioral category, this raw percent of intervals value was almost identical to the value calculated by averaging percent of intervals across sessions within phase, so we chose to use the former. Subject's behavior in phases A1 and A2 were averaged and we compared each behavioral category (affiliative and agonistic) across housing conditions using repeated-measures Wilcoxon signed-rank tests (high vs low spatial density; high vs low privacy/choice; $\alpha = 0.05$). Behavior in phases A1 and A2 did not differ significantly, with the following exceptions: for subjects that experienced changes in spatial density, agonistic behavior differed in A1 and A2 ($P < 0.03$).

To determine whether subjects displayed a novelty response, behavior during the novelty period was compared with behavior during the experimental phase that just preceded it using Wilcoxon signed-rank tests (N1 vs. A1; N2 vs. B). Because we used Wilcoxon signed-rank tests to compare behavior across experimental phases and between experimental and novelty phases, we report the median percent of intervals that subjects engaged in each behavior. We used Fisher's exact tests to compare the number of social wounds that occurred in each housing situation and Kruskal-Wallis tests and/or Mann Whitney U-tests to explore differences between social groups, males and females, and individuals of different dominance ranks, using Bonferroni corrections when performing multiple tests on the same dataset. Since the Mann Whitney U-test uses the sum of ranks within a sample to test differences in sample distributions, we present these data graphically using means (± 1 SEM error bars) to best display differences between groups and variation within groups of interest (i.e., social groups, sexes, ranks). We discuss within-group differences across conditions descriptively and used Wilcoxon signed-rank tests to assess within-group changes in behavior across conditions; however, these statistics should be interpreted cautiously due to very small sample sizes (as low as N=3 in some groups).

Assigning Dominance Rank—Prior to the start of the study, the dominance hierarchy of each group was determined through observation of the direction of displacements and non-contact aggression. The animals' ranks were corroborated by three additional staff members who were extensively familiar with the animals. We assigned the animals to one of three ranks (Highest = 1; Mid-rank = 2; Lowest = 3), which were determined by evaluating each animal's relative rank in their group. For example, in groups of three, each animal was assigned one of the three ranks; in groups of one male and three or more females, the alpha male and female were assigned Rank 1, Rank 2 was assigned to the 1–4 females that fell in the middle of the hierarchy, and Rank 3 was assigned to the lowest 1–3 females in the

hierarchy (the same procedure was used for Groups 1 and 3). Due to the natural social structure of mangabeys, dominance rank is closely associated with sex: adult males outrank all adult females [Gust and Gordon, 1994]; thus, Rank 1 is skewed toward males and Ranks 2 and 3 are skewed toward females (across all groups: Rank 1: 7 males, 3 females; Rank 2: 3 males, 9 females; Rank 3: 1 male, 8 females). Due to small sample sizes, we did not perform a rank analysis by sex (e.g., there was one male in Rank 3), so we acknowledge this association in our interpretations of results.

RESULTS

Behavioral Changes Across Housing Conditions

We hypothesized that the mangabeys would modify their behavior under conditions that were expected to stimulate social tension (i.e., under increased spatial density and reduced degrees of visual privacy and choice). Following the novelty period, the subjects showed a tension-reduction coping strategy under conditions of relatively higher spatial density, but not relatively lower levels of visual privacy and choice, thus partially supporting Prediction 3, in which we expected affiliative behavior to increase in both the high spatial density and low privacy/choice conditions and agonistic behavior to remain relatively stable across all housing conditions. Specifically, affiliative behavior increased and there was no change in agonistic behavior in the high spatial density condition, in which the available space was reduced by 50% compared to the low spatial density condition (affiliative behavior: $Z = -1.99$, $P = 0.046$; agonistic behavior: $P = 0.24$; Table III, Figure 2a). However, both affiliative and agonistic behavior remained stable across housing quality conditions, in which subjects experienced a change in the amount of visual privacy and choice (affiliative behavior: $P = 0.117$; agonistic behavior: $P = 0.38$; Table III, Fig. 2b). Thus, the subjects' behavior did not support Prediction 1, the density-aggression model, in which aggression was expected to increase under higher spatial density and lower privacy/choice; nor did their behavior support Prediction 2, the conflict-avoidance coping strategy, in which both affiliative and agonistic behavior was expected to decrease in those conditions.

In general, affiliative behavior was recorded significantly more frequently than agonistic behavior ($Z = -11.70$, $P < 0.001$), for all subjects and in all housing conditions. Grooming was the most commonly recorded form of affiliative behavior (grooming vs resting in arm's reach proximity to another: $Z = -8.55$, $P < 0.001$; grooming vs other affiliative contact: $Z = -11.51$, $P < 0.001$), followed by resting in arm's reach proximity, which occurred more frequently than other forms of affiliative contact (e.g., embrace; $Z = -10.58$, $P < 0.001$). Non-contact aggression was recorded more frequently than contact aggression ($Z = -7.92$, $P < 0.001$), for all subjects and in all housing conditions. There were very few socially-acquired injuries during the testing period for each group and all were rated a 1 or a 2 with no veterinary intervention. There were seven injuries altogether. Five injuries took place in groups that were experiencing changes in spatial density: three injuries took place in the high spatial density condition and two took place in the low spatial density condition (Fisher's exact tests showed no difference in the proportion of wounds that occurred during each condition: $P = 1.0$). Of the two injuries that took place in groups experiencing housing

quality changes, one took place in the low privacy/choice condition and the other took place in the high privacy/choice condition.

Initial Behavioral Responses to Change – Novelty Responses

When subjects first experienced a change in housing condition (i.e., during the two-week novelty period prior to collecting data in an experimental phase), behavioral changes were not uniform across housing conditions, supporting Prediction 4. Affiliative behavior did not undergo initial changes in response to a change in housing environment (Low to High SD: P = 0.78; High to Low SD: P = 0.40; High to Low P/C: P = 1.0; Low to High P/C: P = 0.58; Table III). However, agonistic behavior appeared to be context-dependent: when spatial density increased, the subjects' initial tendency was to increase aggression (marginally significantly; $Z = -1.71$, $P = 0.087$) and when spatial density decreased, the subjects' initial response was to decrease aggression ($Z = -2.91$, $P = 0.004$). While agonistic behavior did not undergo a significant initial change when the degree of privacy and choice declined ($P = 1.0$), it decreased significantly when the degree of privacy and choice increased ($Z = -2.43$, $P = 0.015$; Table III). Thus, the subjects' initial response to increased available space and increased visual privacy and choice was to reduce aggression.

Patterns of Behavioral Responses across Social Groups, Sexes, and Dominance Ranks

We investigated whether behavioral responses to housing changes varied according to social group membership, sex, and dominance rank. These data are presented in Figures 3–5 using means (± 1 SEM) to best display intragroup variation and intergroup differences (see Data Analysis). A Kruskal-Wallis test contrasting behavior between groups that experienced spatial density changes showed marginal group differences for affiliative behavior (χ^2 (5) = 9.56, P < 0.089). Overall, Groups 2 and 6 engaged in affiliative behavior more frequently than the other groups, though not significantly when comparing groups with follow-up Mann Whitney U-tests using an adjusted alpha level of 0.006 (for nine pairwise comparisons of Groups 2 and 6 with the other groups). Given the overall increase in affiliative behavior in the high spatial density condition (Fig. 2a), we looked descriptively at each group's pattern of behavioral change across spatial density conditions, despite the small within-group sample sizes. Although the Wilcoxon signed-rank tests were not significant (P > 0.05), five of the six groups demonstrated changes in affiliative behavior corresponding with the tension-reduction coping strategy by displaying more frequent affiliative behavior in the high spatial density condition compared to the low spatial density condition (Groups 2–6; Fig. 3a). A Kruskal-Wallis test showed significant group differences for agonistic behavior (χ^2 (5) = 24.08, P < 0.001). Group 5 engaged in significantly more agonistic behavior overall than Group 1 ($Z = -3.12$, P = 0.002), Group 3 ($Z = -3.26$, P = 0.001), and Group 4 ($Z = -2.85$, P = 0.004). Group 6 also engaged in significantly more agonistic behavior overall than Group 1 ($Z = -2.94$, P = 0.003). Also looking descriptively at within-group changes in behavior across conditions, Groups 2 and 5 increased agonistic behavior slightly in the high spatial density condition, however there were no significant within-group changes across conditions according to Wilcoxon signed-rank tests (P > 0.05; Fig. 3b).

A Kruskal-Wallis test contrasting behavior between groups that experienced housing quality changes showed marginal social group differences in affiliative behavior (χ^2 (2) = 5.77, P =

0.056) and no group differences in agonistic behavior (P = 0.35). Overall, Group 7 engaged in more affiliative behavior than Groups 4 and 5, both marginally significant differences when comparing groups using follow-up Mann Whitney U-tests at α = 0.0167 for three pairwise comparisons (Group 4 vs 7: Z = −1.95, P = 0.051; Group 5 vs 7: Z = −2.04, P = 0.041; Fig. 3c). The three groups were variable in their patterns of change across conditions in both affiliative and agonistic behavior. Group 7 decreased affiliative behavior in the low privacy/choice condition (Wilcoxon signed-rank test, P = 0.043), but there were no other significant within-group changes across conditions (Wilcoxon signed-rank tests, all P > 0.05; Fig. 3d).

Next we explored sex differences within each housing condition (Fig. 4a–d). A Mann Whitney U-test showed no differences in affiliative behavior between males and females that experienced spatial density changes (P > 0.05). Again, because of the overall increase in affiliative behavior in the high spatial density condition, we were interested in whether males and females differed in their pattern of behavioral change across conditions (10 males, 16 females). Thus, looking descriptively, it appears that males had a larger increase in affiliative behavior in the high spatial density condition than females (although both within-sex differences across conditions were not significant according to Wilcoxon signed-rank tests, P > 0.05; Fig. 4a). A Mann Whitney U-test showed a significant difference between males and females in agonistic behavior (Z = −3.57, P < 0.001). Females engaged in aggression more frequently than males in both spatial density conditions (Mann Whitney U-tests; low spatial density condition: Z = −2.40, P = 0.016; high spatial density condition: Z = −2.67, P = 0.008), however neither sex showed a significant change in agonistic behavior across spatial density conditions (Wilcoxon signed-rank tests; P > 0.05; Fig 4b). There were no differences in affiliative and agonistic behavior between the sexes in either housing quality condition (three males, nine females; Mann Whitney U tests, P > 0.05; Fig. 4c, d) and neither category of behavior changed significantly across conditions within sex (Wilcoxon signed-rank tests, all P > 0.05).

Finally, we explored how subjects of three different dominance rank categories differed within each housing condition (high-, mid-, and low-ranking; Fig. 5a–d). For subjects that experienced spatial density changes, a Kruskal-Wallis test showed marginal differences across dominance ranks in affiliative behavior (χ^2 (2) = 5.64, P = 0.06) and no differences across ranks in agonistic behavior (P = 0.35). Follow-up Mann Whitney U-tests at α = 0.0167 for three pairwise comparisons showed that high-ranking subjects engaged in affiliative behavior more frequently than low-ranking subjects, overall (marginally significantly at the conservative alpha level: Z = −2.26, P = 0.024). Looking within each housing condition, high- and mid-ranking subjects (high-ranking: six males, two females; mid-ranking: three males, seven females) engaged in affiliative behavior significantly more often than low ranking subjects (one male and seven females) in the high spatial density condition only (Mann Whitney U-tests; high vs mid rank: no difference, P = 0.18; high vs low rank: Z = −2.63, P = 0.009; mid vs low rank: Z = −2.49, P = 0.013; Fig. 5a). Although sex and rank are related, we looked descriptively at whether subjects in the three dominance rank categories differed in their patterns of change in behavior across conditions. High- and mid-ranking subjects increased affiliative behavior in the high spatial density condition (significantly for just high-ranking subjects, which were mostly males; Wilcoxon signed-

rank tests, $Z = -2.38$, $P = 0.017$). Agonistic behavior remained unchanged across spatial density conditions within rank categories (Wilcoxon signed-rank tests, all comparisons non-significant, $P > 0.05$; Fig. 5b). A Kruskal-Wallis test showed no overall differences across dominance ranks in affiliative and agonistic behavior across housing quality conditions ($P > 0.05$), and there were no within-rank differences in affiliative and agonistic behavior across conditions (high-ranking: three males, two females; mid-ranking: four females; low ranking: three females; Wilcoxon signed-rank tests, $P > 0.05$; Fig. 5c, d).

DISCUSSION

Effects of Changing Housing Conditions on Mangabey Behavior

As with other primates, including chimpanzees, bonobos, gorillas, and vervet monkeys [McGuire et al, 1978; Nieuwenhuijsen and de Waal, 1982; Caws and Aureli, 2003; Sannen et al, 2004; Cordoni and Palagi, 2007], sooty mangabeys' displayed a the tension-reduction coping strategy when spatial density increased (partially supporting Prediction 3; Fig 2a, b). Following the novelty periods, affiliative behavior increased while aggression remained unchanged under one condition predicted to stimulate social tension – higher spatial density. Although we also expected social tension to increase under relatively lower levels of visual privacy and choice, the mangabeys' behavior was unaffected. The degree to which visual privacy and choice was reduced in the Low P/C housing type in the present study may not have been enough to stimulate social tension; alternatively, mangabeys may not be as responsive to these features of the environment as they are to spatial density. Since evidence from the literature shows that providing visual privacy and choice are beneficial to primates [e.g., Baker and Ross, 1998; Badihi, 2006], the lack of a behavioral effect of changing housing quality post-novelty period is likely due to the former explanation, indicating that the housing types tested here both provide adequate levels of visual privacy and choice for sooty mangabeys.

The mangabeys' initial responses to housing changes (novelty responses) were context-dependent, supporting Prediction 4: while affiliative behavior did not undergo initial changes in housing conditions, there was a general tendency to initially increase aggression under conditions expected to stimulate social tension and reduce aggression when there was more space, visual privacy, and the choice to be indoors or outdoors. These initial responses appeared to dissipate over the two-week novelty period. During the spatial density experimental phases, their behavior shifted to reveal the coping strategy – the mangabeys adapted behaviorally, reducing the likelihood of conflict and wounding when living in the high spatial density condition for a prolonged period of time.

While overall differences in affiliative behavior between spatial density conditions was apparent, not all subjects demonstrated the same pattern of response. We explored differences in the pattern of responses across housing conditions between social groups, males and females, and three dominance rank categories (high-, mid-, and low-ranking). Most groups showed similar patterns of changes in affiliation across spatial density conditions – five of the six groups increased affiliation in the high spatial density condition (Fig. 3a). This effect appeared most dramatic for males, which were most often classified as high-ranking, as would be expected based on the natural social structure of mangabey

groups [Gust and Gordon, 1994] (Fig. 3–5a). While all groups showed little change in agonistic behavior across spatial density conditions, it appeared that females engaged in aggression more frequently than males (Fig. 4b). In contrast to the spatial density housing conditions, there were no consistent social group, sex, or dominance rank differences in affiliative or agonistic behavior across housing quality conditions.

For all subjects in all housing conditions, agonistic behavior remained relatively infrequent compared to affiliative behavior. Non-contact aggression was the predominant form of agonistic behavior overall, as opposed to contact aggression, which is a common pattern for Old World primates [see Bernstein et al, 1983; Gust and Gordon, 1993; Gust, 1994]. Thus it is not surprising that none of the changes in housing conditions stimulated severe aggression and wounding. In general, low ranking subjects (which were primarily female) had relatively low levels of social interaction, which may have been due to a general avoidance of more high-ranking group members, and/or a preference of the higher ranking group members to affiliate with one another, as opposed to low-ranking subjects. Because of the modest number of subjects in this study, further testing would help determine consistent behavioral effects of changing spatial density and -housing quality in sooty mangabeys living in run-housing.

Implications for management and welfare—It is important to use empirical data to guide management decisions regarding housing for captive animals and, indeed, the findings from the present study will assist in the management of the sooty mangabey colony. This study demonstrated that the mangabeys' welfare was not overtly compromised when they experienced relative crowding for a one-month period, as agonistic behavior and socially-acquired injuries remained low, and affiliative social interactions increased over time under relatively higher spatial density. The mangabeys coped with the housing changes without resorting to severe aggression or social wounding. This is important to understand as colony managers make decisions about housing mangabey groups in various types of available housing. Although visual privacy and choice to go inside or outside are desirable qualities for captive housing, the different levels of these features tested in the present study did not elicit a change in behavior, indicating that both housing types are suitable for the mangabeys. It is important to note, for management purposes, that the mangabeys may be more sensitive to prolonged spatial density changes than to housing quality changes. Overall, however, within the housing variation studied here, we found no evidence of concerning welfare issues (e.g., high rates of aggression, increased wounding) in any of the housing conditions we assessed.

Conclusions—We demonstrated that sooty mangabeys behave in a manner consistent with the tension-reduction coping strategy [de Waal, 1989] in response to increased spatial density. Thus, like many other captive primates, including chimpanzees, rhesus monkeys, and capuchin monkeys [Judge and de Waal, 1997; van Wolkenten et al, 2006; Videan and Fritz, 2007], the mangabeys in this study showed adaptive flexibility in response to changes in their housing situation. While the mangabeys themselves were not unique in this respect, this study was the first attempt to systematically disentangle the independent contributions of spatial density and housing quality to the behavior of captive primates while documenting

and removing the effects of initial behavioral responses to housing changes (i.e., novelty responses). We also incorporated housing quality (the physical characteristics of the space) into theoretical models accounting for behavior under varying spatial densities, expanding these models to consider the quality of the space to be as important in influencing social tension and animal welfare. We found that the mangabeys exhibited an initial behavioral response to a change in housing environments, in which aggression increased or decreased depending on the type of change they experienced. The initial novelty response (to changes within familiar housing environments) appeared to dissipate over the two-week novelty period, revealing a tension-reduction coping strategy under increased spatial density.

It is not surprising that there is so much variability in primates' behavioral responses to housing changes reported in the literature given the differences in the quantity and quality of captive housing across and within facilities, the durations of housing changes tested, and the data collection methods. Despite the variability, however, the common theme is that primates adapt to changes in their housing conditions. The specific ways in which they adapt are likely unique to their specific circumstances, underscoring the need to systematically evaluate captive animals' behavioral responses to various housing conditions before and after sustained housing changes. It is important to keep in mind that animals may not be content in a situation with increased spatial density or reduced visual privacy and choice just because they display increased affiliative behavior and/or reduced aggression [Erwin, 1979; de Waal, 1989]. Future research would be enhanced by also monitoring physiological measures of stress and tension-related behaviors (e.g., rough scratching and yawning) before and after changes in the housing environment.

Acknowledgments

References

Alexander BK, Roth EM. The effects of acute crowding on aggressive behavior of Japanese monkeys. Behaviour. 1971; 39:73–90. [PubMed: 4999798]

Anderson US, Benne M, Bloomsmith MA, Maple TL. Retreat space and human visitor density moderate undesirable behavior in petting zoo animals. Journal of Applied Animal Welfare Science. 2002; 5:125–137. [PubMed: 12738581]

Aureli F, de Waal FBM. Inhibition of social behavior in chimpanzees under high-density conditions. American Journal of Primatology. 1997; 41:213–228. [PubMed: 9057966]

Aureli F, van Panthaleon van Eck CJ, Veenema HC. Long-tailed macaques avoid conflicts during short-term crowding. Aggressive Behavior. 1995; 21:113–122.

Badihi, I. dissertation. University of Stirling; 2006. The effects of complexity, choice and control on the behaviour and the welfare of captive common marmosets (*Callithrix jacchus*).

Baker K, Ross S. Outdoor access: the behavioral benefits to chimpanzees. American Journal of Primatology. 1998; 45:166.

Basile B, Hampton R, Chaudry A, Murray E. Presence of a privacy divider increases proximity in pair-housed rhesus monkeys. Animal Welfare. 2007; 16:37–40.

Bernstein I, Williams L, Ramsay M. The expression of aggression in Old World monkeys. International Journal of Primatology. 1983; 4:113–125.

Bettinger T, Wallis J, Carter T. Spatial selection in captive adult female chimpanzees. Zoo Biology. 1994; 13:167–176.

Boyce WT, O'Neill-Wagner P, Price CS, Haines M, Suomi SJ. Crowding stress and violent injuries among behaviorally inhibited rhesus macaques. Health Psychology. 1998; 17:285. [PubMed: 9619479]

Caws C, Aureli F. Chimpanzees cope with temporary reduction of escape opportunities. International Journal of Primatology. 2003; 24:1077–1091.

Cordoni G, Palagi E. Response of captive lowland gorillas (*Gorilla gorilla gorilla*) to different housing conditions: Testing the aggression-density and coping models. Journal of Comparative Psychology. 2007; 121:171–180. [PubMed: 17516795]

de Waal FBM. The myth of a simple relation between space and aggression in captive primates. Zoo Biology. 1989; 8:141–148.

Duncan LM, Jones MA, van Lierop M, Pillay N. Chimpanzees use multiple strategies to limit aggression and stress during spatial density changes. Applied Animal Behaviour Science. 2013; 147:159–171.

Elton R, Anderson B. The social behavior of a group of baboons (*Papio anubis*) under artificial crowding. Primates. 1977; 18:225–234.

Erwin, J. Aggression in captive macaques: interaction of social and spatial factors. In: Erwin, J.; Maple, T.; Mitchell, G., editors. Captivity and behavior: Primates in breeding colonies, laboratories and zoos. New York: Van Nostrand Reinhold; 1979. p. 139-171.

Erwin N, Erwin J. Social density and aggression in captive groups of pigtail monkeys (*Macaca nemestrina*). Applied Animal Ethology. 1976; 2:265–269.

Estep DQ, Baker SC. The effects of temporary cover on the behavior of socially housed stumptailed macaques (*Macaca arctoides*). Zoo Biology. 1991; 10:465–472.

Fontenot BM, Wilkes MN, Lynch CS. Effects of outdoor housing on self-injurious and stereotypic behavior in adult male rhesus macaques (*Macaca mulatta*). Journal of the American Association for Laboratory Animal Science. 2006; 45:35–43. [PubMed: 16995645]

Gust DA. A brief report on the social behavior of the crested mangabey (*Cercocebus galeritus galeritus*) with a comparison to the sooty mangabey (*C. torquatus atys*). Primates. 1994; 35:375–383.

Gust DA, Gordon TP. Conflict resolution in sooty mangabeys. Animal Behaviour. 1993; 46:685–694.

Gust DA, Gordon TP. The absence of a matrilineally based dominance system in sooty mangabeys, *Cercocebus torquatus atys*. Animal Behaviour. 1994; 47:589–594.

Hoff MP, Powell DM, Lukas KE, Maple TL. Individual and social behavior of lowland gorillas in outdoor exhibits compared with indoor holding areas. Applied Animal Behaviour Science. 1997; 54:359–370.

Judge PG, de Waal FBM. Conflict avoidance among rhesus monkeys: coping with short-term crowding. Animal Behaviour. 1993; 46:221–232.

Judge PG, de Waal FBM. Rhesus monkey behaviour under diverse population densities: coping with long-term crowding. Animal Behaviour. 1997; 54:643–662. [PubMed: 9299049]

Maninger N, Kim J, Ruppenthal G. The presence of visual barriers decreases agonism in group housed pigtail macaques (*Macaca nemestrina*). American Journal of Primatology. 1998; 45:193–194.

McCormack K, Megna N. The effects of privacy walls on aggression in a captive group of rhesus macaques (*Macaca mulatta*). American Journal of Primatology. 2001; 54:50–51.

McGuire MT, Cole SR, Crookshank C. Effects of social and spatial density changes in *Cercopithecus aethiops sabaeus*. Primates. 1978; 19:615–631.

Nash LT, Chilton SM. Space or novelty?: Effects of altered cage size on Galago behavior. American Journal of Primatology. 1986; 10:37–49.

Nieuwenhuijsen K, de Waal FBM. Effects of spatial crowding on social behavior in a chimpanzee colony. Zoo Biology. 1982; 1:5–28.

Novak, MA.; Drewsen, KH. Enriching the lives of captive primates: Issues and problems. In: Segal, EF., editor. Housing, care and psychological wellbeing of captive and laboratory primates. Park Ridge, NJ: Noyes Publications; 1989. p. 161-182.

Novak MA, O'Neill P, Suomi SJ. Adjustments and adaptations to indoor and outdoor environments: continuity and change in young adult rhesus monkeys. American Journal of Primatology. 1992; 28:125–138.

Owen MA, Swaisgood RR, Czekala NM, Lindburg DG. Enclosure choice and well-being in giant pandas: is it all about control? Zoo Biology. 2005; 24:475–481.

Pines MK, Kaplan G, Rogers LJ. A note on indoor and outdoor housing preferences of common marmosets (*Callithrix jacchus*). Applied Animal Behaviour Science. 2007; 108:348–353.

Range F. Female sooty mangabeys (Cercocebus torquatus atys) respond differently to males depending on the male's residence status–preliminary data. American Journal of Primatology. 2005; 65:327–333. [PubMed: 15834893]

Range F, Noë R. Familiarity and dominance relations among female sooty mangabeys in the Taï National Park. American Journal of Primatology. 2002; 56:137–153. [PubMed: 11857651]

Ross SR. Issues of choice and control in the behaviour of a pair of captive polar bears. Behavioural processes. 2006; 73:117–120. [PubMed: 16687218]

Ross SR, Calcutt S, Schapiro S, Hau J. Space use selectivity by chimpanzees and gorillas in an indoor–outdoor enclosure. American Journal of Primatology. 2011; 73:197–208. [PubMed: 20938928]

Ross SR, Schapiro SJ, Hau J, Lukas KE. Space use as an indicator of enclosure appropriateness: A novel measure of captive animal welfare. Applied Animal Behaviour Science. 2009; 121:42–50.

Ross SR, Wagner KE, Schapiro SJ, Hau J. Ape behavior in two alternating environments: comparing exhibit and short-term holding areas. American Journal of Primatology. 2010; 72:951–959. [PubMed: 20623498]

Sannen A, Elsacker LV, Eens M. Effect of spatial crowding on aggressive behavior in a bonobo colony. Zoo Biology. 2004; 23:383–395.

van Wolkenten ML, Davis JM, Gong ML, de Waal FB. Coping with acute crowding by *Cebus apella*. International Journal of Primatology. 2006; 27:1241–1256.

Videan EN, Fritz J. Effects of short- and long-term changes in spatial density on the social behavior of captive chimpanzees (*Pan troglodytes*). Applied Animal Behaviour Science. 2007; 102:95–105.

Whittington C, Chamove A. Effects of visual cover on farmed red deer behaviour. Applied Animal Behaviour Science. 1995; 45:309–314.

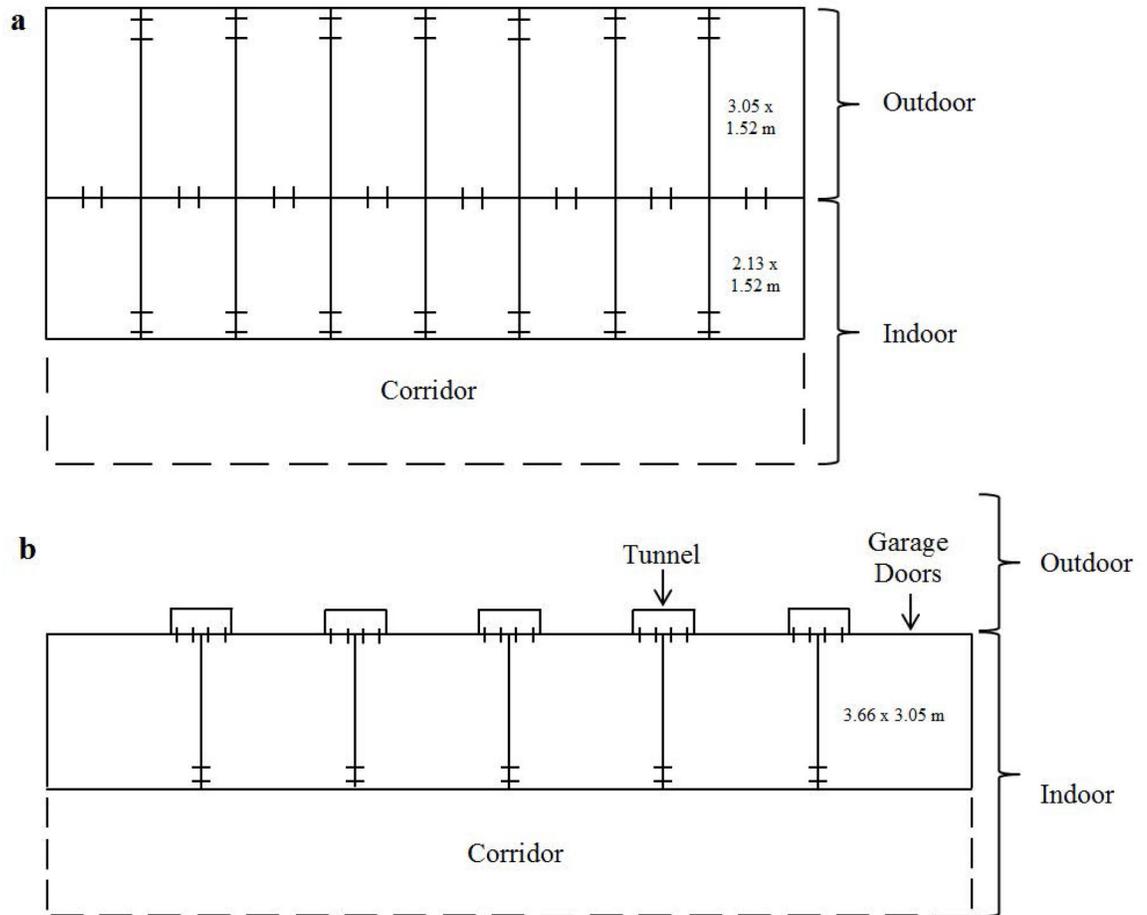Wilson SF. Environmental influences on the activity of captive apes. Zoo Biology. 1982; 1:201–209.

Figure 1.
a) Half of high privacy/choice housing; b) One quarter of low privacy/choice housing (runs are mirrored on the other side of the corridor; short parallel lines are small doorways). Not drawn to scale.
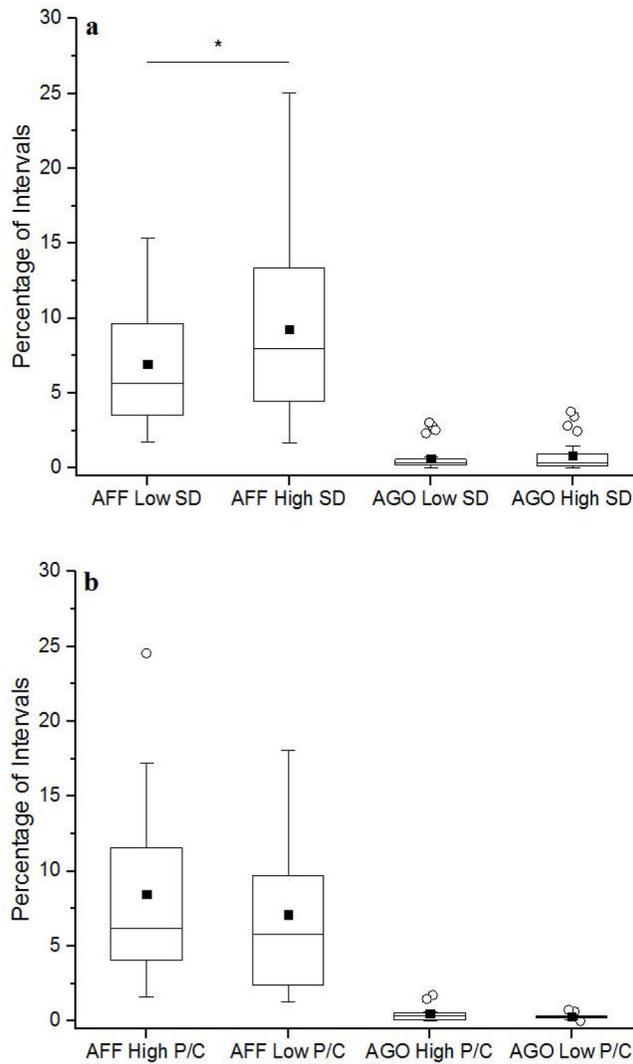
Figure 2.
Boxplots showing: a) Percentage of intervals subjects engaged in affiliative (AFF) and agonistic (AGO) behavior in each spatial density condition (Wilcoxon signed-rank tests: *P = 0.046); b) Percentage of intervals subjects engaged in affiliative (AFF) and agonistic (AGO) behavior in each housing quality condition. SD = spatial density; PC = privacy/choice. Central line of box indicates median; small square inside box indicates mean; upper and lower areas of box indicate upper and lower quartiles, respectively (i.e., the middle 50% of data points – the interquartile range); whiskers indicate maximum and minimum data points that are within 1.5 times the interquartile range; open circles indicate outliers.
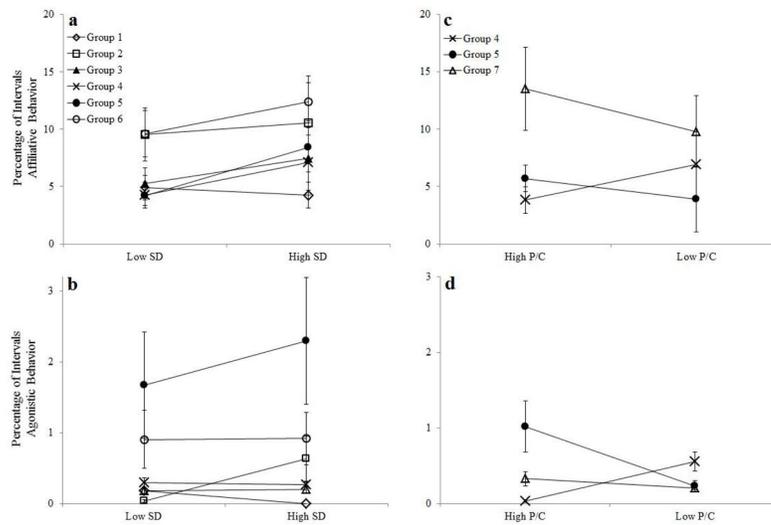
Figure 3.
Patterns of behavioral change across housing conditions in each social group: a) mean percentage of intervals each group engaged in affiliative behavior across spatial density conditions; b) mean percentage of intervals each group engaged in agonistic behavior across spatial density conditions; c) mean percentage of intervals each group engaged in affiliative behavior across housing quality conditions; d) mean percentage of intervals each group engaged in agonistic behavior across housing quality conditions. Note differing y-axis scales for affiliative and agonistic behavior. Error bars represent one standard error of the mean.

Figure 4.
Patterns of behavioral change across housing conditions in each sex: a) mean percentage of intervals each sex engaged in affiliative behavior across spatial density conditions; b) mean percentage of intervals each sex engaged in agonistic behavior across spatial density conditions; c) mean percentage of intervals each sex engaged in affiliative behavior across housing quality conditions; d) mean percentage of intervals each sex engaged in agonistic behavior across housing quality conditions. Note differing y-axis scales for affiliative and agonistic behavior. Error bars represent one standard error of the mean.
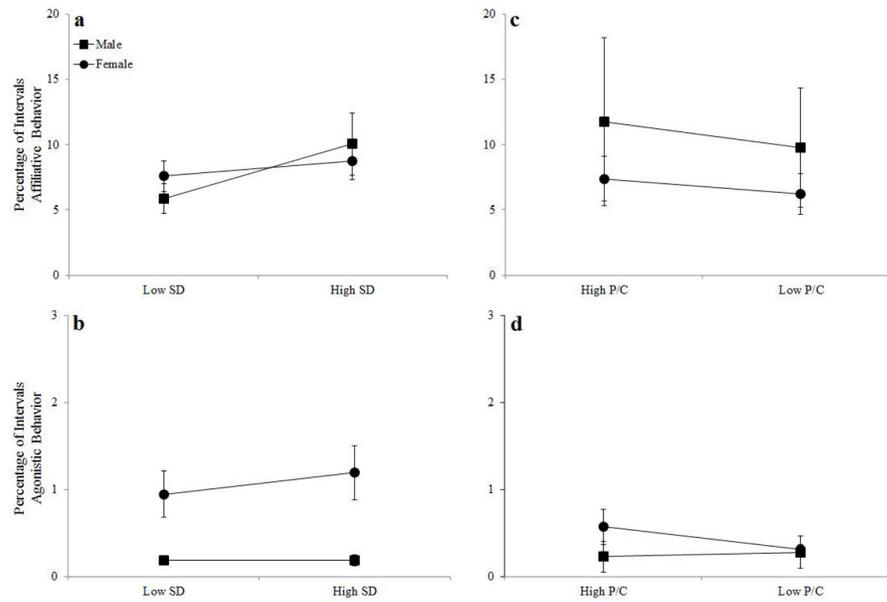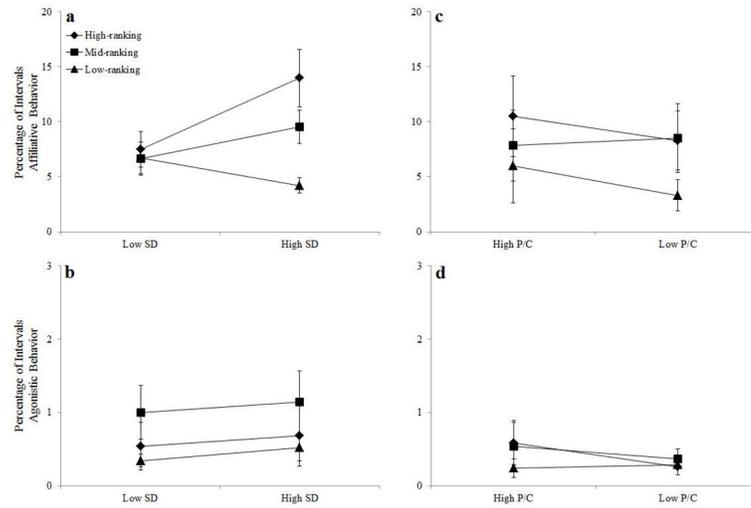
Figure 5.
Patterns of behavioral change across housing conditions in each dominance rank category (high-, mid-, and low-ranking): a) mean percentage of intervals each rank category engaged in affiliative behavior across spatial density conditions; b) mean percentage of intervals each rank category engaged in agonistic behavior across spatial density conditions; c) mean percentage of intervals each rank category engaged in affiliative behavior across housing quality conditions; d) mean percentage of intervals each rank category engaged in agonistic behavior across housing quality conditions. Note differing y-axis scales for affiliative and agonistic behavior. Error bars represent one standard error of the mean.

Table I

Group composition and housing condition details (spatial density – square meters per animal – and the number of runs available to each group in each condition).

Group N adults	Group Composition				Square Meters/Animal in Each Condition[1] Number of Runs Available			
	N Male	N Female	N Infant	Low SD	High SD	High P/C	Low P/C
Group 1 N = 3	2	1	0	24.38 2 runs	12.19 1 run		
Group 2 N = 3	1	2	0	24.38 2 runs	12.19 1 run		
Group 3 N = 4	4	0	0	25.91 4 runs	12.95 2 runs		
Group 4 N = 3	1	2	1	17.37 2 runs	8.53 1 run	25.91 3 runs	24.38 2 runs
Group 5 N = 4	1	3	1	18.29 2 runs	9.14 1 run	19.51 3 runs	18.29 2 runs
Group 6 N = 9	1	8	4	16.15 4 runs	8.23 2 runs		
Group 7 N = 5	1	4	0			12.95 3 runs	12.19 2 runs

[1] SD = Spatial Density; P/C = Privacy/Choice

Table II

Order of condition presentation for each group across each two-week phase.

Groups, Total N	Phase A1	Novelty 1	Phase B	Novelty 2	Phase A2
Spatial Density Changes[1]					
Groups 1, 2, 3, 5 Total N = 14	Low SD	High SD	High SD	Low SD	Low SD
Groups 4, 6 Total N = 12	High SD	Low SD	Low SD	High SD	High SD
Quality Housing Changes[1]					
Groups 4, 7 Total N = 8	High P/C	Low P/C	Low P/C	High P/C	High P/C
Group 5 Total N = 4	Low P/C	High P/C	High P/C	Low P/C	Low P/C

[1]SD = Spatial Density; P/C = Privacy/Choice

Table III

Median percentage of intervals that subjects engaged in affiliative and agonistic behavior in each housing condition across ABA experimental phases and novelty periods and the results of Wilcoxon signed-rank tests contrasting housing conditions (significant differences indicated with an asterisk, α = 0.05).

	Spatial Density Changes[1]			Housing Quality Changes[1]		
	Median % of Intervals			**Median % of Intervals**		
ABA Phases	**High SD**	**Low SD**	**Wilcoxon test**	**High P/C**	**Low P/C**	**Wilcoxon test**
Affiliative	7.98	5.65	Z = −1.99, P = 0.046*	6.22	5.79	Z = −1.57, P = 0.117
Agonistic	0.32	0.31	Z = −1.186 P = 0.24	0.37	0.27	Z = −0.86 P = 0.388
	Initial Increase in SD			**Initial Decrease in P/C**		
Novelty Periods	**Low SD → High SD**			**High P/C → Low P/C**		
Affiliative	5.78	6.51	Z = −0.28, P = 0.78	4.28	7.64	Z = 0.00, P = 1.000
Agonistic	0.27	0.44	Z = −1.71, P = 0.087	0.22	0.28	Z = −0.80, P = 0.42
	Initial Decrease in SD			**Initial Increase in P/C**		
	High SD → Low SD			**Low P/C → High P/C**		
Affiliative	8.71	7.54	Z = −0.84, P = 0.40	6.37	3.71	Z = −0.55, P = 0.58
Agonistic	0.37	0.21	Z = −2.91, P = 0.004*	0.31	0.19	Z = −2.43, P = 0.015*

[1] SD = Spatial Density; P/C = Privacy/Choice