Journal of Applied Animal Welfare Science

sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

Routledge
Taylor & Francis Group

Pair Housing for Female Longtailed and Rhesus Macaques in the Laboratory: Behavior in Protected Contact Versus Full Contact

Kate C. Baker,[1] Carolyn M. Crockett,[2] Grace H. Lee,[2]
Brooke C. Oettinger,[2] Valérie Schoof,[1] and Jinhee P. Thom[2]
[1]*Tulane National Primate Research Center, Tulane University*
[2]*Washington National Primate Research Center, University of Washington*

Pair housing for caged macaques in the laboratory generally allows unrestricted tactile contact but, less commonly, may involve limited contact via grooming-contact bars or perforated panels. The purpose of using this protected contact housing, which prevents entry into pair-mates' cages, typically is to accommodate research and management requirements. The study used behavioral data collected on 12 pairs of female longtailed macaques (*Macaca fascicularis*) at the Washington National Primate Research Center and 7 pairs of female rhesus macaques (*Macaca mulatta*) housed at the Tulane National Primate Research Center to assess the relative benefits of protected versus full protected contact. The study collected data in stable pairs housed first in protected contact followed by full contact. Species combined, the study found the presence of the panel was associated with lower levels of social grooming and higher levels of self-grooming, abnormal behavior, and tension-related behavior. Within species, only the protected- versus full-contact contrasts for abnormal and tension were statistically significant—and only for rhesus macaques. Results suggest that for female rhesus macaques, potential disadvantages or inconveniences of full contact should be balanced against the improved behavioral profile in comparison to protected contact. The use of protected contact among female longtailed macaques does not appear to require the same cost-benefit analysis.

Correspondence should be sent to Kate C. Baker, Tulane National Primate Research Center, Tulane University, 18703 Three Rivers Road, Covington, LA 70433. Email: kbaker1@tulane.edu

Social housing is widely held to be the most effective form of environmental enrichment for macaques in the laboratory, permitting species-appropriate social behaviors and reducing the development and expression of abnormal behaviors (Bayne, Dexter, & Suomi, 1992; Bellanca & Crockett, 2002; Doyle, Baker, & Cox, 2008; Eaton, Kelley, Axthelm, Iliff-Sizemore, & Shiigi, 1994; Lutz & Novak, 2005; Lutz, Well, & Novak, 2003; Reinhardt, 1989; Reinhardt, Houser, Eisele, Cowley, & Vertein, 1988; Roberts & Platt, 2005; Schapiro, Bloomsmith, Porter, & Suarez, 1996). Behavioral and physiological responses suggest that pair-housed macaques also cope better with routine changes in their environment (Doyle et al., 2008; Gilbert & Baker, 2011; Roberts & Platt, 2005). These effects are not surprising given that macaques are by nature highly social nonhuman animals (Melnick & Pearl, 1987). Their social needs must be addressed under U.S. federal regulations (U.S. Department of Agriculture, 1991) and the *Guide for the Care and Use of Laboratory Animals* (National Research Council, 1996, 2011). Adequate socialization is an important element in refinements in husbandry of nonhuman primates (Jennings & Prescott, 2009).

Pair housing in laboratory macaques usually involves cohousing in connected adjacent cages (hereafter termed "full contact"). Crockett, Bellanca, Bowers, and Bowden (1997) were among the first to promote the idea of providing tactile contact through a "grooming-contact" panel that prevents entry into neighboring cages. From unpublished data in a 2007 survey, Baker, Weed, Crockett, and Bloomsmith (2007) found tactile contact through a barrier (hereafter termed "protected contact") is less common than providing full contact. In comparison to full contact, protected contact housing has the potential to ameliorate possible stress from the inability to control proximity in a restricted space and may also protect subordinate individuals from possible food monopolization and unwanted social interaction. It also may increase implementation of social housing by accommodating research requirements for different diets or feeding and watering schedules (Thom & Crockett, 2008). In some configurations, protected contact housing can prevent breeding in male-female pairs (Crockett et al., 1997). Protected contact has been the prevalent method for pairing macaques and baboons at the Washington National Primate Research Center (WaNPRC) and is associated with generally high success rates for pair introductions (Crockett et al., 1997; Crockett, Lee, & Thom, 2006; Lee, Thom, Chu, & Crockett, 2012).

However, evidence is emerging that species differences and style of pair housing interact to influence success and benefits of pair housing. For example, at the WaNPRC the success rate of introductions of longtailed macaques (*Macaca fascicularis*) is more than twice that of rhesus macaques (*Macaca mulatta;* Crockett et al., 2006; Lee et al., 2012). Research at Tulane National Primate Research Center (TNPRC) and Yerkes NPRC found that for both males and females, long-term protected contact housing provided to individually housed rhesus macaques produced fewer behavioral benefits than housing them in full

contact. Protected contact did not reduce levels of abnormal or anxiety-related behavior as did full contact in the same pairs; these pairs also socially groomed significantly less in protected contact (Baker et al., 2008).

Longtailed and rhesus macaques are among the most prevalent nonhuman primate species held in laboratories in the United States (Carlsson, Schapiro, Farah, & Hau, 2004; Conlee, Hoffeld, & Stephens, 2004). It is important to tailor their behavioral management to species differences. Although closely related, longtailed macaques and rhesus macaques shared a last common ancestor 1 to 2 million years ago (Delson, 1980; Hayasaka, Fujii, & Horai, 1996; Morales & Melnick, 1998; Thierry, Iwaniuk, & Pellis, 2000; Tosi, Morales, & Melnick, 2003). In the laboratory environment, the two species respond differently to a variety of environmental stressors, with longtailed macaques consistently found to be more reactive (Bowers, Crockett, & Bowden, 1998; Clark, Mason, & Mendoza, 1994; Clark, Mason, & Moberg, 1988). Both in the wild and in naturalistic captive social settings, longtailed macaques are more tolerant of strangers, less aggressive, more affiliative, and show more frequent behaviors associated with tension reduction (Angst, 1973; Southwick, Siddiqi, Farooqui, & Pal, 1974; Thierry, 1986; Thierry et al., 2000). It is therefore not surprising that in pairing laboratory macaques, longtailed macaque introductions are successful in higher proportion than rhesus macaque introductions (Crockett et al., 2006). Research is needed to identify how to tailor the social management of these two species in the laboratory environment. This study sets out to compare protected contact and full contact housing for paired macaques and to examine the interaction between species and housing. We analyzed subsets of behavioral data from larger research projects (Baker et al., 2008; Lee et al., 2012). The data were collected during comparable social settings and housing conditions: pairs already compatibly housed in protected contact and the same pairs 1 month after conversion to full contact.

METHOD

Subjects and Housing

Subjects comprised 36 adult female macaques, including 24 longtailed macaques and 14 rhesus macaques of Indian origin. Longtailed macaque subjects were mother-reared in Indonesia and imported to WaNPRC in 2001 and 2002. They ranged in age from 8.9 to 15.2 years during data collection (2007–2008). For much of the time at WaNPRC, they were housed in protected contact with another female; most subjects had experienced more than one social partner and periods of separation owing to incompatibility or changing protocol assignment. Rhesus subjects had been mother-reared in field cages (in most cases well into adulthood) at the TNPRC breeding colony and housed in its research facility.

Prior to being transferred to protected contact housing, they had been singly housed indoors for at least 6 months after having been removed from the outdoor field cages. They ranged in age from 4.7 to 13.6 years during data collection (2004–2005).

Both facilities were fully accredited by the Association for the Assessment and Accreditation of Laboratory Animal Care, International. All aspects of housing, care, and research conformed to the U.S. Department of Agriculture's Animal Welfare Regulations (U.S. Department of Agriculture, 1991) and the *Guide for the Care and Use of Laboratory Animals* (National Research Council, 1996).

Subjects were housed in rooms containing 12–27 individuals of the same species. Each room included rows of two-tiered caging facing each other; consequently, animals had visual access to other monkeys at all times. Subjects were fed commercial biscuits once or twice daily (*M. fascicularis* always twice) and had access to fresh, clean water ad libitum. Rooms were maintained on a 12:12 hr light:dark cycle. The ambient temperature in longtailed macaques' rooms was $75° \pm 3°$F ($24° \pm 1°$C) with 30%–50% humidity; rhesus room temperatures ranged from $64°$ to $72°$F ($18°$ to $22°$C) with a relative humidity of 30% to 70%. Each animal was provided a portable toy and an enrichment object or foraging device hanging on the outside of cages and was fed fresh produce and/or a foraging mix at least five times per week. Each cage contained a perch running parallel to the cage side.

For both species, cage floor area was 4.3 square feet, with a height of 30 in. for longtailed macaques and 36 in. for rhesus macaques. Longtailed macaques' cages consisted of mesh ceilings, mesh floors, and barred fronts. Cage sides included mesh side gates in the front portion to permit visual and tactile access while restricting each animal to the animal's own cage. Sides also included a solid metal area in the back of the cage in order to provide a visual barrier (Bielitzki, Susor, Elias, & Bowden, 1990). Opening mesh side gates revealed three vertical grooming-contact bars spaced to provide four 2-in. by 15-in. openings, as shown in Figures 1, 2, and 3 (Crockett et al., 1997; Lee et al., 2012). Full contact was achieved by reversing the cages, left-right, such that opening the mesh side gates revealed unobstructed openings between the two cages.

Rhesus cages were similar but had one solid side wall and another consisting of a removable panel between adjacent cages. Solid stainless steel panels were inserted between cages to create single housing and removed for full contact. Protected contact housing for rhesus macaques was provided by substituting for the solid panel a panel perforated with 12 oblong openings (2 in. in height × 1 in. in width) arranged in a grid pattern toward the front of the cages, four holes vertically and three holes horizontally, with holes separated by a half in. of panel material. To provide a visual barrier, the back half of the panel was not perforated. Full contact housing resulted from removal of these panels and did not include a visual barrier.
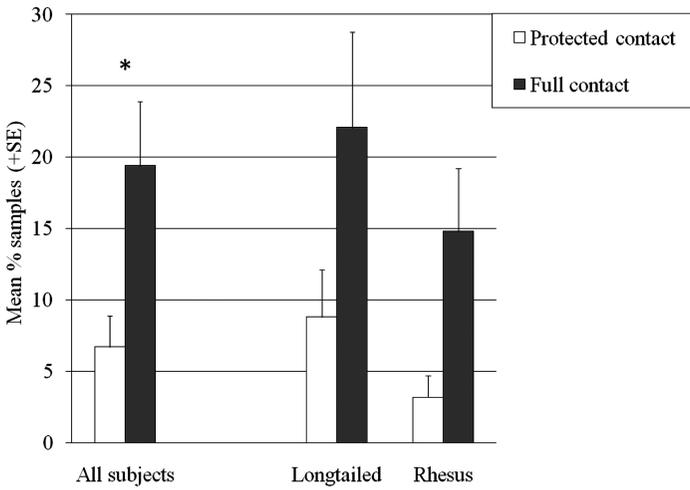
FIGURE 1   Levels of social grooming across study conditions (* = $p \leq .05$ for pairwise comparisons between housing conditions).
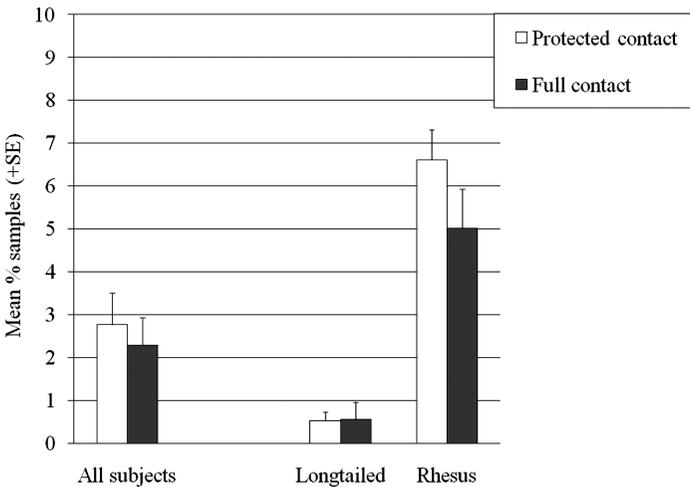

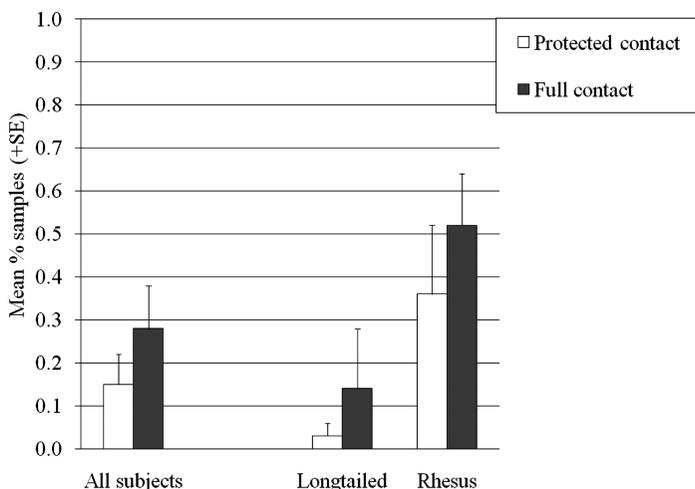FIGURE 2   Levels of noncontact partner affiliation.

FIGURE 3 Levels of agonism directed toward social partners.

Data Collection and Analysis

This study consisted of two phases: protected contact followed by full contact. We combined comparable data sets extracted from larger studies as described in Lee et al. (2012) and Baker et al. (2008). The former also included a second protected contact phase, and the latter included subsequent phases involving other styles of pair housing. At the WaNPRC, longtailed macaque pairs had been introduced compatibly in grooming-contact cages for 0.63–4.72 years ($M = 2.1$ years, $SD = 1.6$) before the onset of protected contact data collection (Lee et al., 2012). In no case was protected contact housing for a pair preceded by full contact housing. Full contact data included in this analysis were collected over a 2-week period beginning 1 month after the transition to this form of housing. The data contributing to this study were derived from 12 pairs who successfully transitioned from protected contact to full contact; data from 2 additional pairs with unsuccessful full contact introductions are excluded (Lee et al., 2012).

At the TNPRC, all rhesus macaque subjects were introduced into protected contact 4 months prior to the onset of data collection and transitioned to full contact 2–6 months after the onset of data collection. In no case was the protected contact phase preceded by a full contact phase, and there were no social separations following introduction into protected contact. In addition to the subjects included in the current study, 4 pairs failed to make this transition successfully due to aggression and did not contribute data to the study. Data were collected in the full contact condition beginning 1 month after the transition from protected contact to full contact.

At both facilities, data were collected via videorecordings scheduled to avoid daily feedings, routine husbandry, and research procedures and commenced at the same time of day for both phases. At TNPRC, each subject was video-taped for a total of 6 hr per phase. Recordings were coded using Observer 5.0 software (Noldus Information Technology Inc., Leesburg, VA). At WaNPRC, videorecordings approximately 50 min long were recorded on each of 3 days over 2 weeks per phase per pair. Two or three 10-min segments per day were coded (1–1.5 hr per phase) not using the Observer program (Lee et al., 2012).

Instantaneous sampling quantified the behavioral data (30-s interval at TNPRC and 15-s interval at WaNPRC). The data from *M. fascicularis* at WaNPRC were collected after discussions with the first author at TNPRC to establish clearly defined and mutually distinguishable behavioral definitions to match those at TNPRC. Data were coded for the two species by different individuals, but each study subject's data were coded by the same individual in both study phases. Data were coded using an ethogram of mutually exclusive behaviors. Behaviors of interest were categorized into six measures for analysis (Table 1).

In each study condition, the percentage of point samples in which each behavioral category occurred was calculated across observations for each subject. Mean values across the 2 members of each pair were then calculated. The unit of analysis was the mean percentage of samples per pair during which a given behavior occurred for each housing phase. The *M. mulatta* data were based on a longer sampling duration, but the *M. fascicularis* data sample points were twice as frequent. Because the data were converted to percentages per pair per housing condition phase, the two species data were equivalent for statistical testing purposes.

The primary comparison of interest was the style of pair housing. Two-tailed Wilcoxon matched pairs tests were performed to compare pairs' be-havior in full contact and protected contact housing. Significant results ($p <$ .05) were followed by separate Wilcoxon matched pairs tests for each species. Because of the confound of species with facility differences and the lack of interobserver reliability testing, species differences in behavior were explored only as potential explanatory variables using the Mann-Whitney U statistic. In preliminary analyses of the data, we discovered some discrepancies between statistical testing programs. Our investigation led us to reports of differences in accepting or refuting null hypotheses based on inappropriate use of the "asymptotic" rather than the "exact" variant of a nonparametric test with small sample sizes (Bergman, Ludbrook, & Spooren, 2000; Mundry & Fischer, 1998). For the Wilcoxon test (Siegel, 1956), matched pairs with zero difference are discarded and the *n* correspondingly reduced. Following the statistical test eval-uation guidelines of Mundry and Fischer (1998), we used an online website to calculate Wilcoxon exact probabilities. The website (http://www.fon.hum.uva.nl/Service/Statistics/Signed_Rank_Test.html) calculates exact probabilities for

TABLE 1
Behavioral Categories and Social Behaviors

Social Groom

Pick, stroke, and/or lick partner's hair
Receive groom

Noncontact Partner Affiliation

Lip-smack, present body part for grooming, attempt to touch in a nonaggressive manner

---

Agonistic

Contact aggression
Push, pull, grab, scratch, bite
Noncontact aggression
Cage shake, crook tail, ear flick, grab at, jaw snap, lunge, open-mouth stare, stare, teeth grinding,
    attempt to bite
Submissive behavior
Fear grimace, rapid glances, cringe, crouch, retreat, screech vocalization, rump present

---

Nonsocial Behaviors

Abnormal behavior
Locomotor stereotypy (flip, head toss, jump, pace, rock, spin) and self-directed hair pluck, deposit
    and reingest food, self-mouth, self-clasp, eye poke, floating limb, bizarre posture
Tension-related
Body shake, head bob, lid flash, scratch, teeth chomp or grind, yawn
Self-groom
Pick, stroke, and/or lick one's own hair

$n \leq 20$, with which our samples sizes conformed. For the Mann-Whitney U
tests, we used the U calculated with ties-included option (Data Desk; Velleman,
1997) and consulted the critical values (Siegel, 1956) for $n_1 = 7$ and $n_2 = 12$
(two-tailed, $p \leq .05$, $U = 18$). Outcomes of statistical tests are summarized in
Table 2.

RESULTS

Effects of Housing

In protected contact, pairs groomed each other at lower levels. Although descrip-
tively this was the case in both species, this contrast was not significant within

TABLE 2
Summary of Statistical Tests Comparing Protected Contact (PC) Versus Full Contact (FC) for Longtailed Macaques
and Rhesus Macaques

Behavior	PC vs. FC: All Subjects	PC vs. FC: Longtailed Macaques	PC vs. FC: Rhesus Macaques	Longtailed vs. Rhesus Macaques: PC	Longtailed vs. Rhesus Macaques: FC
Test	Wilcoxon[a]	Wilcoxon[a]	Wilcoxon[a]	Mann-Whitney[b]	Mann-Whitney[b]
Social grooming	**W+ = 28, W− = 143,** **n = 18, p ≤ .01**	W+ = 12, W− = 54, n = 11, NS	W+ = 5, W− = 23, n = 7, NS	U = 42, NS	U = 43, NS
Affiliative to partner (noncontact)	W+ = 90, W− = 46, n = 16, NS	Not tested	Not tested	**U = 0, p ≤ .05**	**U = 3, p ≤ .05**
Affiliative to other (noncontact)	W+ = 30.5, W− = 35.5, n = 11, NS	Not tested	Not tested	U = 51, NS	U = 52, NS
Agonism to partner	W+ = 14, W− = 31, n = 9, NS	Not tested	Not tested	**U = 10.5, p ≤ .05**	**U = 7, p ≤ .05**
Agonism to other	W+ = 9, W− = 46, n = 10, NS	Not tested	Not tested	**U = 17, p ≤ .05**	U = 23.5, NS
Abnormal	**W+ = 80, W− = 11,** **n = 13, p ≤ .013**	W+ = 22, W− = 6, n = 7, NS	**W+ = 21, W− = 0,** **n = 6, p ≤ .031**	U = 25.5, NS	U = 31.5, NS
Tension	**W+ = 128, W− = 25,** **n = 17, p ≤ .013**	W+ = 44, W− = 11, n = 10, NS	**W+ = 28, W− = 0,** **n = 7, p ≤ .016**	U = 32, NS	U = 26, NS
Self-grooming	**W+ = 151, W− = 39,** **n = 19, p ≤ .023**	W+ = 60, W− = 18, n = 12, NS	W+ = 25, W− = 3, n = 7, NS	**U = 8, p ≤ .05**	**U = 5, p ≤ .05**

Note. p ≤ .05 in bold; p > .05 listed as NS.
[a]Wilcoxon tests from web page: http://www.fon.hum.uva.nl/Service/Statistics/Signed_Rank_Test.html; W is equivalent to T of Siegel (1956). [b]Mann-Whitney U values (including ties) from Data Desk (Velleman, 1997); significance ≤ .05 from Table K, Siegel (1956), for $n_1 = 7$ and $n_2 = 12$, $U = 18$. Does not include any adjustment for tied ranks between groups.
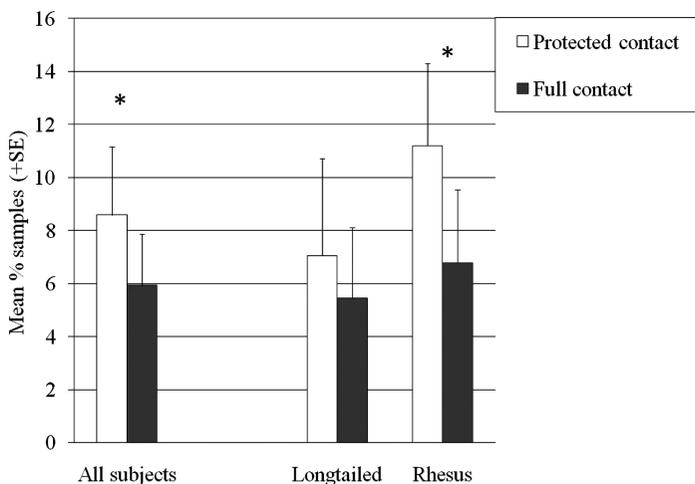
FIGURE 4   Levels of abnormal behavior across study conditions (* = $p \leq .05$ for pairwise comparisons between housing conditions).

either species alone (Figure 1). Pairs did not differ across housing conditions with respect to noncontact partner affiliation (Figure 2).

Agonism toward the partner did not differ significantly between housing conditions (Figure 3). No contact aggression was recorded in longtailed macaque pairs. Noncontact agonism toward other monkeys in the room averaged 0.1% versus 0.3% of scan samples and did not differ significantly between housing conditions.

Across both species, levels of abnormal behavior were significantly higher in protected contact than in full contact. This pattern was statistically significant in the rhesus macaques but not in the longtailed macaques (Figure 4). Pairs displayed higher levels of tension-related behaviors in protected contact. This contrast was significant among rhesus macaques but not among longtailed macaques (Figure 5). Pairs self-groomed at higher levels in protected contact, but within-species comparisons were not significant although they differed in the same direction as the overall pattern (Figure 6).

Species Differences

The species did not differ in levels of social grooming in either housing condition (Figure 1). However, they did with respect to noncontact, affiliative behaviors directed toward their partners; longtailed macaques showed lower levels in both housing conditions (Figure 2). In both conditions, longtailed macaques
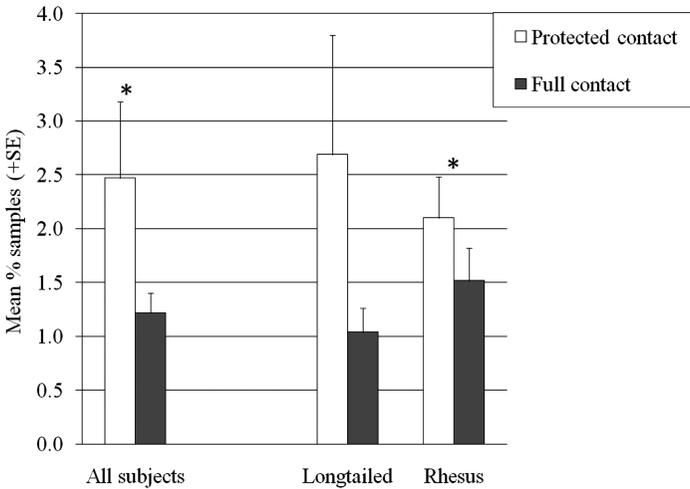
FIGURE 5   Levels of tension-related behavior across study conditions (* = $p \leq .05$).

were less agonistic toward partners than were rhesus macaques (Figure 3). No species differences in levels of abnormal behaviors were found for either housing condition (Table 1). Tension-related behavior did not vary between species in either housing condition (Figure 5). Longtailed macaques showed higher levels of self-grooming in both housing conditions (Figure 6).

FIGURE 6   Levels of self-grooming across study conditions (* = $p \leq .05$).

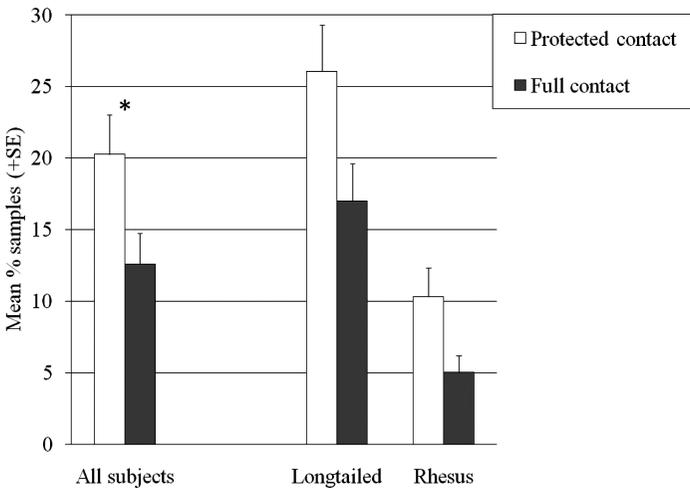## DISCUSSION

This study found no behavioral evidence suggesting that long-term protected contact housing, the style of pair housing employing a barrier allowing limited tactile contact between partners, was superior in its behavioral effects to full contact for adult female macaques. In fact, a few unfavorable effects were detected. Across both species, presence of the panel was associated with higher levels of abnormal and tension-related behavior. The panel appeared to restrict the expression of social grooming between partners with a correspondingly higher level of self-grooming during the protected contact phase. However, when species were examined separately, only abnormal behavior and tension-related behavior were statistically significantly higher in protected contact and only among the rhesus macaques.

Conclusions regarding these results must be tempered by two aspects of the study design that may have contributed to response to the housing change in the two species. First, data were collected on the longtailed macaque pairs after a longer tenure in protected contact (averaging 2 years) than on rhesus macaques (4 months), who had also been previously singly housed. Although unlikely, it is possible that relationships among the rhesus macaque pairs had not been fully established by the onset of data collection and became more stabilized over the course of the study, as did acclimation to a pair-caged setting.

In other words, the differences in abnormal and anxiety-related behavior could have related to the elapsed time since introduction rather than the type of pair housing. The consistency in elapsed time across pairs unfortunately prevents an assessment of any correlation with levels of behavior. However, the finding that neither noncontact partner affiliation nor agonism differed between pair housing style supports the notion that social uncertainty was not the cause of elevated abnormal and anxiety-related behavior. In addition, there were no species differences in tension behavior in either housing condition. The previous single housing of rhesus macaque subjects is unlikely to be a confound within subjects; if anything, individuals could be expected to interact at relatively high levels soon after a period of single housing; this could only hamper the detection of the differences in social grooming between housing styles. In addition, for the longtailed macaques, differing durations in prior contact among pairs had little relation to behavior during the study. Correlations between duration of protected contact before the onset of data collection found almost no significant correlations (Lee et al., 2012); a positive correlation with social grooming during the protected contact phase disappeared during the full contact phase.

Second, the design of the panels separating neighbors at the two facilities differed considerably. The "grooming-contact" barred panels provided the long-tailed macaques much better visual and tactile access than the rhesus's perforated

panels, and contact social interactions may have been less physically awkward because the entire vertical space was available for positioning the hands for grooming or withdrawing quickly if warranted. This style of caging was not available at the time that the rhesus subjects were being observed. The more restricted physical contact in the protected contact phase for rhesus may have contributed to the increased tension and abnormal behavior compared with full contact. However, the levels of social grooming did not differ significantly within species across the housing conditions; the direction of change (more social grooming in full contact) was the same in both species.

This study suggests that, for female longtailed macaques, full contact does not confer conspicuous long-term benefits over protected contact. Additional support is provided by examining their behavior sooner after transition from protected contact to full contact than the 1-month, posttransition data used in the current study. Even in the early weeks after this transition, no ephemeral benefits of full contact were detected save a short-term increase in social grooming (Lee et al., 2012), which also occurs in the transition from single housing to full contact in this species (Crockett, Bowers, Bowden, & Sackett, 1994). Self-grooming showed the opposite effect (a short-term reduction in full contact), but no undesirable behaviors varied across the two phases of full contact (Lee et al., 2012). Furthermore, when the longtailed macaque subjects in the current study were subsequently returned to protected contact after full contact, no significant behavioral changes were detected (Lee et al., 2012). For the current study, rhesus macaque subjects were not returned to protected contact but rather to other forms of housing under investigation in the larger study from which subjects were drawn. Conclusions of the current study could be tested in future studies by employing an ABA design.

It is not particularly surprising that the patterns of social grooming (Figure 1) and self-grooming (Figure 6) were approximately opposite. Grooming is associated with reduced heart rate (Aureli, Preston, & de Waal, 1999), opioids (Graves, Wallen, & Maestripieri, 2002; Keverne, Martensz, & Tuite, 1989; Martel, Nevison, Simpson, & Keverne, 1995), and oxytocin (Snowden et al., 2010). Monkeys who are positively reinforced by the sensation of grooming are likely to direct this activity toward a partner when more access is provided. An earlier study of longtailed macaques in grooming contact found that self-grooming significantly predicted the amount of time spent grooming the partner (Crockett et al., 1997). In both phases of the current study, the female longtailed macaques groomed themselves at significantly higher levels than rhesus. The levels of social- and self-grooming combined, 35% in protected contact and 39% in full contact, are very similar to the 37% of the time budget spent in self-grooming reported for female longtailed macaques when singly housed (Crockett et al., 1995). It is also worth noting that the average of 37% self-grooming in the 1995 study was based on considerably more hours of data collection than

the present values for longtailed macaques and was scored using a continuous sampling method rather than scan sampling.

It is important to note that the behavioral profile of long-term compatible pairs is not the only measure of interest when comparing the benefits of the two forms of pair housing. For example, differences in success of social introductions and the risks during both introductions and sustained cohousing are important variables to consider. If protected contact housing showed a relatively higher introduction success rate, a larger number of singly housed animals could be provided social contact within a finite amount of time and effort. Among potential female rhesus macaque subjects for this study, 4 pairs did not transition successfully from protected contact to full contact, a failure rate of 36%. Withdrawal of the panel resulted in aggression, wounding, or persistent fearful behavior that terminated the experiment with those animals. The initial sample of WaNPRC pairs in long-term protected contact included 2 pairs who did not transition successfully to full contact, a failure rate of 14% (Lee et al., 2012). These findings are consistent both with prior research (Crockett et al., 2006) and with the documented species differences in tolerance, aggressiveness, and affiliation (Angst, 1973; Southwick et al., 1974; Thierry, 1986; Thierry et al., 2000). Although initially surprising that levels of noncontact partner affiliation were higher in rhesus than in longtailed macaques, summing contact and noncontact yielded levels that were numerically identical in protected contact (10%) and very similar in full contact (23% in longtailed macaques and 20% in rhesus macaques), demonstrated that the longtailed macaque pairs were at least as affiliative as rhesus macaques.

Although there were some differences in data collection schedules and details of protected contact panels, this type of collaborative study between facilities is of great value in enlarging the available pool of data for analysis and for understanding of behavioral management of nonhuman primates. Rhesus and longtailed macaques are the predominant laboratory monkey species in the United States. A direct comparison of behavioral management techniques between the species, even though housed at another facility, provides an important perspective. Indeed, many species comparisons are not possible within individual facilities that do not house substantial populations of more than one species.

The results of this study should be generalized to other monkey species (particularly to males) with great caution. Findings are likely to vary among male-male pairs. Longtailed macaque males are more difficult to pair than are females (Crockett et al., 1997; Crockett et al., 1994). In addition, behavioral benefits of moving from single housing to full contact in rhesus macaques may vary with sex (e.g., the degree of reduction [Baker et al., 2008] and persistence of reduction in abnormal behavior [e.g., Eaton et al., 1994 versus Doyle et al., 2008]). The rhesus subjects of this study were of Indian origin; therefore, these

results may not fully apply to Chinese origin females (Baker et al., 2009). It should also be emphasized that adult male-female pairs can be very compatibly housed in appropriately configured cages (i.e., with two sets of grooming-contact bars) without the need for chemical or surgical contraception or sterilization (Crockett et al., 1997; Crockett et al., 2006). Lee et al. (2012) review other potential positive aspects of grooming-contact, such as increased control and choice. Simply because female rhesus macaques appear to benefit more from full contact, protected contact should not be abandoned as a behavioral management strategy or be considered inferior to full contact in broader application. It is another tool in the behavioral management chest of techniques to improve the psychological well being of laboratory primates.

CONCLUSION

The results of this study speak only to the behavior of compatible pairs of female longtailed and rhesus macaques but not to the benefits of either form of pair housing over single housing. Many studies reviewed support the provision of social contact to nonhuman primates whenever possible. This study suggests that in choosing which style of pair housing to use for female rhesus macaques, potential disadvantages or inconveniences of full contact should be balanced against the improved behavioral profile in comparison to protected contact. On the other hand, the use of protected contact among female longtailed macaques does not appear to require this cost-benefit analysis. The risks and benefits of both options must be measured in order to determine which best provides for well being in a caged setting.

ACKNOWLEDGMENTS

REFERENCES

Angst, W. (1973). Pilot experiments to test group tolerance to a stranger in wild *Macaca fascicularis*. *American Journal of Physical Anthropology, 38*, 625–630.

Aureli, F., Preston, S. D., & de Waal, F. B. M. (1999). Heart rate responses to social interactions in free-moving rhesus macaques (*Macaca mulatta*): A pilot study. *Journal of Comparative Psychology, 113*, 59–65.

Baker, K. C., Bellanca, R. U., Bloomsmith, M. A., Coleman, K., Crockett, C. M., Maier A., . . . Perlman, J. E. (2009). Behavioral contrasts between Chinese-origin and Indian-origin rhesus macaques (*Macaca mulatta*) in a caged laboratory setting. *American Society of Primatology, 71*, 32.

Baker, K. C., Bloomsmith, M., Neu, K., Griffis, C., Oettinger, B., Schoof, V., . . . Maloney, M. (2008). Benefits of isosexual pairing of rhesus macaques (*Macaca mulatta*) vary with sex and are limited by protected contact but not by frequent separation. *American Journal of Primatology, 70*, 44.

Baker, K. C., Weed, J. L., Crockett, C. C., & Bloomsmith, M. A. (2007). Survey of environmental enhancement programs for laboratory primates. *American Journal of Primatology, 69*, 377–394.

Bayne, K., Dexter, S., & Suomi, S. (1992). A preliminary survey of the incidence of abnormal behavior in rhesus monkeys (*Macaca mulatta*) relative to housing condition. *Lab Animal, 21*, 38–46.

Bellanca, R. U., & Crockett, C. M. (2002). Factors predicting increased incidence of abnormal behavior in male pigtailed macaques. *American Journal of Primatology, 58*, 57–69.

Bergmann, R., Ludbrook, J., & Spooren, W. P. J. M. (2000). Different outcomes of the Wilcoxon-Mann-Whitney test from different statistics packages. *The American Statistician, 54*(1), 72–77.

Bielitzki, J., Susor, T. G., Elias, K., & Bowden, D. M. (1990). Improved cage design for single housing of social nonhuman primates. *Laboratory Animal Science, 40*, 428–431.

Bowers, C. L., Crockett C. M., & Bowden, D. M. (1998). Differences in stress reactivity of laboratory macaques measured by heart period and respiratory sinus arrhythmia. *American Journal of Primatology, 45*, 245–261.

Carlsson, H. E., Schapiro, S. J., Farah, I., & Hau, J. (2004). Use of primates in research: A global overview. *American Journal of Primatology, 63*, 225–237.

Clarke, A. S., Mason, W. A., & Mendoza, S. P. (1994). Heart rate patterns under stress in three species of macaques. *American Journal of Primatology, 33*, 133–148.

Clarke, A. S., Mason, W. A., & Moberg, G. P. (1988). Differential behavior and adrenocortical responses to stress among three macaque species. *American Journal of Primatology, 14*, 37–52.

Conlee, K. M., Hoffeld, E. H., & Stephens, M. L. (2004). A demographic analysis of primate research in the United States. *Alternatives to Laboratory Animals, 32*(Suppl. 1A), 315–322.

Crockett, C. M., Bellanca, R. U., Bowers, C. L., & Bowden, D. M. (1997). Grooming-contact bars provide social contact for individually caged laboratory macaques. *Contemporary Topics in Laboratory Animal Science, 36*, 53–60.

Crockett, C. M., Bowers, C. L., Bowden, D. M., & Sackett, G. P. (1994). Sex differences in compatibility of pair-housed adult longtailed macaques. *American Journal of Primatology, 32*, 73–94.

Crockett, C. M., Bowers, C. L., Shimoji, M., Leu, M., Bowden, D. M., & Sackett, G. P. (1995). Behavioral responses of longtailed macaques to different cage sizes and common laboratory experiences. *Journal of Comparative Psychology, 109*, 368–383.

Crockett, C. M., Lee, G. H., & Thom, J. P. (2006). Sex and age predictors of compatibility in grooming-contact caging vary by species of laboratory monkey. *International Journal of Primatology, 27*, Abstract No. 417.

Delson, E. (1980). Fossil macaques, phyletic relationships and a scenario of development. In D. G. Lindburg (Ed.), *The macaques: Studies in ecology, behavior and evolution* (pp. 10–30). New York, NY: Van Nostrand Reinhold.

Doyle, L. A., Baker, K. C., & Cox. L. D. (2008). Physiological and behavioral effects of social introduction on adult male rhesus macaques. *American Journal of Primatology, 70*, 542–550.

Eaton, G. G., Kelley, S. T., Axthelm, M. K., Iliff-Sizemore, S. A., & Shiigi, S. M. (1994). Psychological well-being in paired adult female rhesus (*Macaca mulatta*). *American Journal of Primatology, 33*, 89–99.

Gilbert, M. H., & Baker, K. C. (2011). Social buffering in adult male rhesus macaques (*Macaca mulatta*): Effects of stressful events in single versus pair housing. *Journal of Medical Primatology, 40*, 71–78.

Graves, F. C., Wallen, K., & Maestripieri, D. (2002). Opioids and attachment in rhesus macaque (*Macaca mulatta*) abusive mothers. *Behavioral Neuroscience*, *116*, 489–493.

Hayasaka, K., Fujii, K., & Horai, S. (1996). Molecular phylogeny of macaques: Implications of nucleotide sequences from an 896-base pair region of mitochondrial DNA. *Molecular Biology and Evolution, 13*, 1044–1053.

Jennings, M., & Prescott, M. J. (2009). Refinements in husbandry, care and common procedures for non-human primates: Ninth report of the BVA/AWF/FRAME/RSPCA/UFAW Joint Working Group on Refinement. *Laboratory Animals, 43*(Suppl. 1), 1–7.

Keverne, E. B., Martensz, N. D., & Tuite, B. (1989). Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology, 4*, 155–161.

Lee, G. H., Thom, J. P., Chu, K., & Crockett, C. M. (2012). Comparing the relative benefits of grooming-contact and full-contact pairing in laboratory-housed adult female *Macaca fascicularis*. *Applied Animal Behaviour Science*. Retrieved from http://dx.doi.org/10.1016/j.applanim.2011.08.013

Lutz, C. K., & Novak, M. A. (2005). Environmental enrichment for nonhuman primates: Theory and application. *Institute for Laboratory Animal Research Journal, 46*, 178–191.

Lutz, C., Well, A., & Novak, M. (2003). Stereotypic and self-injurious behavior in rhesus macaques: A survey and retrospective analysis of environment and early experience. *American Journal of Primatology, 160*, 1–15.

Martel, F. L., Nevison, C. M., Simpson, M. J. A., & Keverne, E. B. (1995). Effects of opioid receptor blockade on the social behavior of rhesus monkeys living in large family groups. *Developmental Psychobiology, 28*, 71–84.

Melnick, D. J., & Pearl, M. J. (1987). Cercopithecines in multimale groups: Genetic diversity and population structure. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 121–134). Chicago, IL: University of Chicago Press.

Morales, J. C., & Melnick, D. J. (1998). Phylogenetic relationships of the macaques (*Cercopithecidae: Macaca*), as revealed by high resolution restriction site mapping of mitochondrial ribosomal genes. *Journal of Human Evolution, 34*, 1–23.

Mundry, R., & Fischer, J. (1998). Use of statistical programs for nonparametric tests of small samples often leads to incorrect *p* values: Examples. *Animal Behaviour, 56*, 256–259.

National Research Council (Institute of Laboratory Animal Resources). (1996). *Guide for the care and use of laboratory animals*. Washington, DC: National Academy Press.

National Research Council (Institute of Laboratory Animal Resources). (2011). *Guide for the care and use of laboratory animals*. Washington, DC: National Academy Press.

Reinhardt, V. (1989). Behavioral responses of unrelated adult male rhesus monkeys familiarized and paired for the purpose of environmental enrichment. *American Journal of Primatology, 17*, 243–248.

Reinhardt, V., Houser, D., Eisele, S., Cowley, D., & Vertein, R. (1988). Behavioral responses of unrelated rhesus monkey females paired for the purpose of environmental enrichment. *American Journal of Primatology, 14*, 135–140.

Roberts, S. J., & Platt, M. L. (2005). Effects of isosexual pair-housing on biomedical implants and study participation in male macaques. *Contemporary Topics in Laboratory Animal Science, 44*, 13–48.

Schapiro, S. J., Bloomsmith, M. A., Porter, L. M., & Suarez, S. A. (1996). Enrichment effects on rhesus monkeys successively housed singly, in pairs, and in groups. *Applied Animal Behaviour Science, 48*, 159–171.

Siegel, S. (1956). *Nonparametric statistics for the behavioral sciences*. New York, NY: McGraw-Hill.

Snowdon, C. T., Pieper, B. A., Boe, C. Y., Cronin, K. A., Kuriana, A. V., & Ziegler, T. E. (2010). Variation in oxytocin is related to variation in affiliative behavior in monogamous, pair-bonded tamarins. *Hormones and Behavior, 58*, 614–618.

Southwick, C. H., Siddiqi, M. F., Farooqui, M. Y., & Pal, B. C. (1974). Xenophobia among free-ranging rhesus groups in India. In R. L. Holloway (Ed.), *Primate aggression, territoriality, and xenophobia* (pp. 185–209). New York, NY: Academic.

Thierry, B. (1986). A comparative study of aggression and response to aggression in three species of macaque. In J. G. Else & P C. Lee (Eds.), *Primate ontogeny, cognition and social behaviour* (pp. 307–313). New York, NY: Cambridge University Press.

Thierry, B., Iwaniuk, A. N., & Pellis, S. M. (2000). The influence of phylogeny on the social behaviour of macaques (Primates: *Cercopithecidae*, genus *Macaca*). *Ethology, 106*, 713–728.

Thom, J., & Crockett, C. M. (2008). Managing environmental enhancement plans for individual research projects at a National Primate Research Center. *Journal of the American Association for Laboratory Animal Science, 47*, 51–57.

Tosi, A. J., Morales, J. C., & Melnick, D. J. (2003). Paternal, maternal, and biparental molecular markers provide unique windows onto the evolutionary history of macaque monkeys. *Evolution, 57*, 1419–1435.

U.S. Department of Agriculture. (1991). Final rules: Code of federal regulations, title 9, part 3. *Federal Register, 55*, 6426–6505.

Vellman, P. F. (1997). *Learning data analysis with Datadesk for Windows 6.0.* San Francisco, CA: Addison Wesley Benjamin-Cummings.