SOCIAL HOUSING OF PREVIOUSLY SINGLE-CAGED MACAQUES: WHAT ARE THE OPTIONS AND THE RISKS?

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Abstract *Animal Welfare 1995, 4:* 307-328

A review of the scientific literature gives evidence that transferring previously single-caged adult macaques to permanent compatible pair-housing arrangements (isosexual pairs, adult/infant pairs) is associated with less risk of injury and morbidity than transferring them to permanent group-housing arrangements. Juvenile animals can readily be transferred to permanent group-housing situations without undue risks. Safe pair formation and subsequent pair-housing techniques have been developed for female and male rhesus (Macaca mulatta), *stump-tailed* (M. arctoides) *and pig-tailed macaques* (M. nemestrina) *as well as for female long-tailed macaques* (M. fascicularis). *Pair housing does not jeopardize the animals' physical health but it increases their behavioural health by providing them with an adequate environment to satisfy their need for social contact and social interaction.*

Keywords: *aggression, animal welfare, behavioural health, compatibility, distress, morbidity, primates, psychological well-being, social housing, undernourishment*

Introduction

The housing of non-human laboratory primates is a controversial issue. While the public argues that individual housing is not species-adequate and hence ethically not justifiable, some members of the primatological research community are reluctant to give up a housing system that is seemingly serving their scientific enterprise so well. A recent survey of North American primatological institutions showed that the most common laboratory primates, ie rhesus macaques *(Macaca mulatta)*, long-tailed macaques *(M. fascicularis)*, pig-tailed macaques *(M. nemestrina)*, and stump-tailed macaques *(M. arctoides)*, are being housed in appropriate social environments on average in only 38 per cent of cases (Reinhardt 1994a) despite the fact that published scientific information strongly supports guides and rules prescribing housing conditions that address the animals' social disposition.

The United States' Guide for the Care and Use of Laboratory Animals (National Institutes of Health 1985) states that group housing should be considered for communal animals. The British *Code of Practice for the Housing and Care of Animals Used in Scientific Procedures* (Home Office 1989) recommends that non-human primates be so housed that they have an opportunity for social interactions. The US Animal Welfare Act (US Department of Agriculture 1991) requires that institutions address the 'social needs' of social non-human

primates. An animal may be exempt from social housing for health reasons and approved scientific research reasons. The Swiss Animal Protection Law (Der Schweizerische Bundesrat 1981) explicitly restricts such exemptions for health reasons. The Canadian *Guide to the Care and Use of Experimental Animals* (Canadian Council on Animal Care 1993) stipulates that non-human primates should be provided with a social environment conducive to their well-being. The International Primatological Society's Guidelines (International Primatological Society 1993) propose that unless absolutely essential, primates should not be housed alone in a cage on a long-term basis, because a compatible conspecific probably provides more appropriate stimulation to a captive primate than any other potential environmental enrichment factor.

The intent of the guides and rules reflects frequently published notions of primatologists. Chance *et al* (1983) argue that except for some specialized cases the accepted practice of housing monkeys singly is completely unjustified, since primatologists are fully aware that monkeys are social animals and require companions for a healthy life. With sociality so central to the very survival of primates (Bernstein 1991), Bramblett (1989) points out that the most stimulating, diverse and biologically important addition to the welfare of a captive primate is a social companion (cf Bennett & Davis 1989; Fouts *et al* 1989; Pereira *et al* 1989; Segal 1989; Rümpler 1992). Social deprivation should not be considered any more normal than water or food deprivation (de Waal 1991). The assumption that non-human primates have social needs (US Department of Agriculture 1991) is echoed by Novak and Suomi (1991) who stated that social interaction is crucial for normal development in most primate species, and that having access to one or more companions may be the most effective way to foster their psychological well-being (cf Novak & Drewsen 1989).

Some primatologists warn against social housing, underscoring an increased potential for the transmission of contagious diseases, for wounding and for undernourishment (Novak & Suomi 1988; cf Vandenbergh 1989; Woolverton *et al* 1989). The concern for wounding has been expressed most strongly by Line (1987) arguing that any plan to increase social interaction also increases the risk of injury and death. Unless they have grown up in the same social group, primates are not likely to tolerate each other when placed together as adults (cf Line *et al* 1989a). The fear of risking injury is shared by Coe (1991) cautioning that especially when new pairs are formed 'veterinarians will be kept quite busy suturing wounds'. Novak and Suomi (1988) underscored that stress may be increased in pairs as a result of incompatibility or excessive aggression by the dominant member of the pair. Ruppenthal *et al* (1991) pointed out that pair rearing may lead to behavioural maladaptation.

Taking both, the social disposition of primates and the potential risk of social housing into account, the Association of Primate Veterinarians strongly recommends that a programme of social interaction be adopted by each institution (Keeling 1990). Contrary to this veterinary recommendation, only 12 per cent of primatologists (n = 105 respondents) indicated that if non-human primates should have rights, the provision of an appropriate social situation should be one of them (Petto 1994). Investigators at the National Institutes of Health suggest social housing of caged research primates less frequently (7.7%) as a modification of the cage environment, than provision of inanimate enrichment objects (27.8%) such as toys, swings, perches and shelves (National Institutes of Health 1991). Woolverton *et al* (1989) echoes this attitude by expecting only 'marginal benefits' of social housing for laboratory non-human primates.

The conflicting opinions of professionals working with laboratory primates warrant an evaluation of possible arguments used to justify individual housing (cf Visalberghi & Anderson 1993). The present review focuses on studies conducted in macaques *(Macaca* spp.), because comprehensive published information is available only for this genus.

Aggression

Group housing

Group housing is probably the biologically most appropriate housing condition for macaques (cf Bernstein 1991; Rolland 1991). Aggressive intolerance of strange conspecifics, however, distinguishes adult macaques; and the artificial formation of groups or the introduction of strangers into established groups is associated with considerable risks of trauma and death (rhesus macaques: Bernstein & Mason 1963; Southwick 1967; Bernstein *et al* 1974; Fairbanks *et al* 1977, pig-tailed macaques: Bernstein 1969; Tokuda & Jensen 1969; Erwin 1979, long-tailed macaques: Dollinger 1971, stump-tailed macaques: Rhine & Cox 1989). Kessler *et al* (1985), for example, routinely formed single male harems of 15–25 rhesus macaques and reported a 13 per cent trauma mortality rate per year.

Line *et al* (1990a) tried to circumvent the consequences of xenophobia in rhesus macaques. Future group members were therefore familiarized by placing two monkeys in wire-mesh cages at 7cm distance for 15 minutes. Fights were common during the first day of group formation. By day four, one male was depressed and withdrawn, and was regularly harassed by two of the other males. The victim was permanently removed for treatment of several bite wounds. Four days later, the top-ranking female was found dead in the cage from trauma. Within less than a month 77 per cent of the animals (10/13) had sustained injuries.

Assuming that adequate familiarization of potential group members cannot be achieved in the course of brief non-contact encounters, Reinhardt (1991a) formed two isosexual groups of six adult rhesus macaques each, after group members had been given the opportunity to physically interact with each other on a one-to-one basis for one week. In both instances, group incompatibility was heralded by certain subjects challenging other individuals to whom they had originally been subordinate. Aggressive harassment was intensive and persistent, but victims showed no resistance. Both groups were split up within less than one hour to avoid similar consequences as those described by Line *et al* (1990a).

Unlike adults, socially experienced juvenile and subadult macaques can readily be transferred from single-housing to group-housing arrangements with other peers. Bernstein and Draper (1964) released eight female and three male juvenile rhesus macaques into a compound and observed that the animals formed an organized social group without resorting to serious aggression. Schapiro *et al* (1994) reported no problems associated with aggression when moving 19 juvenile rhesus macaques from single cages into heterosexual peer groups and maintaining group membership until the animals reached sexual maturity. Wolff and Ruppert (1991) encountered no aggression-related problem when forming a heterosexual group of six formerly single-caged subadult rhesus macaques. Group members were compatible and showed no serious aggression during a nine-week follow-up period.

Vicious fighting among adult macaques is a frustrating management problem not only when groups are artificially formed, but also when excessive aggression develops

spontaneously in well-established troops (Chance *et al* 1977; Ehardt & Bernstein 1986; Samuels & Henrickson 1983; Reinhardt *et al* 1987a; Rolland 1991) and is likely to flare up in association with sexual competition (Judge *et al* 1994; Schapiro *et al* 1994) and whenever changes are being made in the troop's composition (Erwin 1977; Fairbanks *et al* 1978; Kaplan *et al* 1980; Kessler *et al* 1985; Rolland 1991).

Pair housing

Pair-housing techniques have been developed to avoid the risk of injury attendant on group housing. Reinhardt *et al* (1988a) and Eaton *et al* (1994) tested pairs of previously single-caged adult female rhesus macaques. Partners were first familiarized with each other in double cages with transparent barriers. Subsequent pair formation was successful in 89 per cent (16/18) and 90 per cent (19/21) of cases. In both studies two pairs were separated because of fighting. Eaton *et al* (1994) as well as Reinhardt *et al* (1988a) ascertained partner compatibility (cf Table 2) in 83 per cent of cases for 36 and 4 months respectively (Table 1).

In an attempt to minimize the typical fighting during the initial introduction of partners (cf Maxim 1976), Reinhardt (1989) paired adult male rhesus macaques after it was verified that partners had established clear dominance-subordination relationships during a five-day period of non-contact familiarization. It was hypothesized that the establishment of such rank relationships would make aggressive disputes rather unnecessary during pair formation (cf Bernstein & Gordon 1974), because partners would respect their relative dominance-subordination relationships. In order to form five pairs with clear relationships, seven different dyads had to be screened. No rank decisive interactions (cf Table 2) could be observed in two dyads. The partners of the other five dyads established rank relationships within the first day of familiarization. When those males were paired in a different double cage (a precaution against possible territorial antagonism: Reinhardt *et al* 1988a; Line *et al* 1990a) they confirmed their rank relationships within the first six minutes. No fighting, no biting and no signs of aggressive harassment or depression were observed during a five-day follow-up period. The males were strictly housed in male-only areas to exclude the risk of sexual competition possibly triggered by the sight of females (cf Coe & Rosenblum 1984; Coe 1991). Reinhardt (1994c, d) tested this technique again in other rhesus as well as in stump-tailed macaques of both sexes with the following results:

1 Male rhesus pairs were compatible in 80 per cent of cases throughout follow-up periods of one to five years (Table 1).

2 Female rhesus pairs were compatible in 88 per cent of cases during follow-up periods of one to seven years (Table 1).

3 All stump-tailed pairs were compatible during pair formation and during a six-month follow-up period (Table 1).

Crockett *et al* (1994) formed isosexual pairs of adult long-tailed macaques. Potential partners were also pre-familiarized, but no attempt was made to ascertain that they had established clear dominance-subordination relationships before introduction. During pair formation 13 per cent of the female pairs, and 67 per cent of the male pairs engaged in fighting. Two male dyads were split due to serious injuries. Unlike the above mentioned

studies, all newly paired subjects of the study by Crockett *et al* (1994) were separated after 90 minutes and reunited on the following day. On days 2–13 each pair was separated daily for 17 hours and re-introduced thereafter. All female pairs but only 40 per cent of the male pairs were compatible throughout the two-week study period (Table 1). Clarke *et al* (1986) also formed pairs of male long-tailed macaques, but allowed partners to continuously stay together as long as they did not fight excessively. Pairs were compatible in 58 per cent of cases for an eight-month follow-up period. Unfortunately, the authors did not elaborate on how partners were initially introduced to each other.

Table 1 Success rates of pairing techniques for previously single-caged adult macaques.

Pairing technique	Compatibility	Follow-up	Subject *Macaca*	Reference
prefamiliarization	83% (15/18)	4–6 months	female *mulatta*	Reinhardt *et al* 1988a
	92% (11/12)	36 months	female *mulatta*	Eaton *et al* 1994
	75% (3/4)	5–6 months	female *fascicularis*	Line *et al* 1990a
	100% (15/15)	2 weeks	female *fascicularis*	Crockett *et al* 1994
	40% (6/15)	2 weeks	male *fascicularis*	Crockett *et al* 1994
unknown	58% (7/12)	8 months	male *fascicularis*	Clarke *et al* 1986
rank relationships	100% (5/5)	5 days	male *mulatta*	Reinhardt 1989
established during	80% (16/20)	1–5 years	male *mulatta*	Reinhardt 1994d
prefamiliarization	88% (68/77)	1–7 years	female *mulatta*	Reinhardt 1994d
	100% (5/5)	6 months	female *arctoides*	Reinhardt 1994c
	100% (3/3)	6 months	male *arctoides*	Reinhardt 1994c
no familiarization	94% (16/17)	7–11 months	female/infant *mulatta*	Reinhardt *et al* 1987b
	94% (61/65)	1–8 years	female/infant *mulatta*	Reinhardt 1994d
	92% (11/12)	7–11 months	male/infant *mulatta*	Reinhardt *et al* 1987b
	92% (12/13)	1–4 year	male/infant *mulatta*	Reinhardt 1994d

Successful isosexual pair formation has been reported for male and for female pig-tailed macaques but the actual technique of partner introduction has not been published (Reinhardt 1994a).

As an alternative to adult-adult pairings, Reinhardt *et al* (1987b) socialized previously single-caged rhesus macaques with 1–1.5 year-old, naturally weaned infants from breeding troops. It was hypothesized that infants of this age would trigger parental responses rather than overt aggression in the adults (cf Lorenz 1971; Redican & Mitchell 1973; Gibber & Goy 1985; Schwind *et al* 1992). Infants were therefore directly placed into the cages of adults of both sexes. Pairs were compatible in 90 per cent of cases, with the adult subject huddling with the introduced infant, and the latter showing no signs of injury or depression. Compatibility was 94 per cent for female-infant pairs, 83 per cent for male-infant pairs (Table 1).

Adult males were as affectionate with juvenile companions as adult females (Figure 1). Pair incompatibility was due to non-injurious aggression in two cases, a non-bleeding injury in one case. In another study, Reinhardt (1994d) ascertained one to eight-year compatibility in 94 per cent of female-infant pairs, one to four-year compatibility in 92 per cent of male-infant pairs (Table 1).

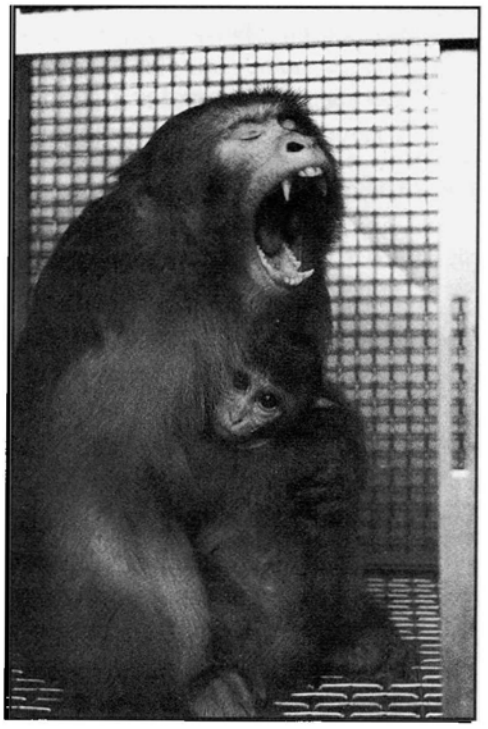

Figure 1 **Adult rhesus male protectively holding his juvenile companion three months after pair formation.**

There is little information about the risk of forming pairs of unfamiliar young macaques. Brandt and Mitchell (1973) paired eight pre-adolescent rhesus macaques with eight infants in isosexual and heterosexual dyads without encountering aggression related problems during a three-week follow-up period. Schapiro *et al* (1993) transferred 64 unfamiliarized juvenile rhesus macaques from single-housing to heterosexual pair-housing conditions for one year without noteworthy problems associated with aggression (cf Schapiro *et al* 1991; Schapiro & Bushong 1994). Weaned rhesus infants have been housed in isosexual pairs routinely at the Wisconsin Regional Primate Research Center without any aggression related problems. When this manuscript was written, the Center had 12 female and 4 male pairs. Partners had been directly introduced to each other with no incidence of serious aggression (cf Reinhardt 1994d), and they had lived together as compatible companions for up to three years (Figure 2).

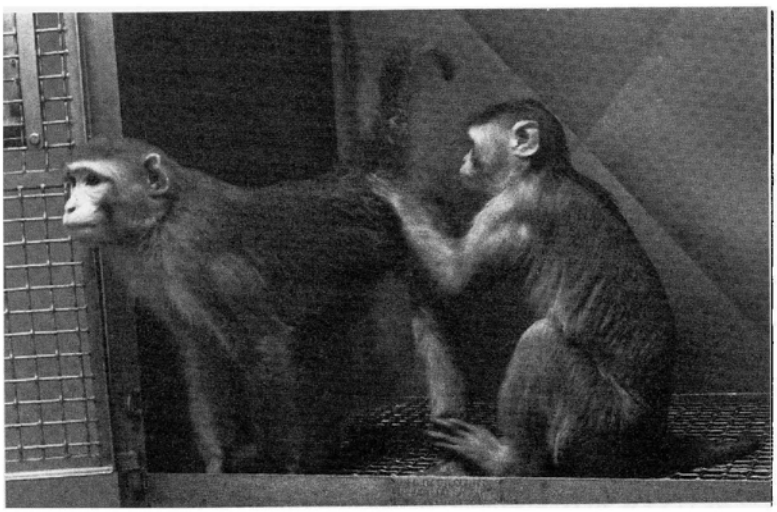

Figure 2 **Subadult rhesus females grooming each other three years after pair formation.**

Morbidity

Schapiro and Bushong (1994) assessed the rates of veterinary treatment in 98 rhesus macaques under the conditions of single, pair and group housing. Daily treatment per monkey was highest in the group condition, lowest in the pair condition, intermediate in the single condition. The authors underlined that there was relatively little intervention needed for pair-housed animals due to less diarrhoea and little trauma. Reinhardt (1990a) compared rates of veterinary treatment per year of 237 individually-housed with that of 382 pair-housed rhesus macaques that were kept in the same facility. Treatment was required by 23 per cent (54/237) of the single-housed, but only by 10 per cent (38/382) of the pair-housed subjects. Eaton *et al* (1994) found no significant difference in rates of clinical morbidity in 12 single-housed and 24 pair-housed female rhesus macaques.

Distress

There is no scientific evidence demonstrating that living in a group *per se* causes more distress than living alone. Living with conspecifics, however, may provide a buffer against environmental stress that the singly caged subject is lacking (cf Bovard 1959; Rowell & Hinde 1963; Epley 1974; Cubicciotti & Mason 1975; Cobb 1976; Arnone & Dantzer 1980; Gunnar *et al* 1980; Taylor 1981; Coe *et al* 1982; Gonzalez *et al* 1982; Hennessy 1984; Stanton *et al* 1985; Mendoza & Mason 1986; Lyons *et al* 1988; de Monte *et al* 1992). Gust *et al* (1994), for example, removed seven adult female rhesus macaques from their home group and housed them in a novel environment both alone or with a member of the group. Subjects experienced measurable distress (elevated cortisol concentrations and decrease in absolute number of lymphocyte subsets) in both conditions, but recovered from it significantly quicker in the presence of the companion. Shively *et al* (1989) noted in adult female long-tailed macaques that single housing may be a greater risk factor for atherogenesis than group housing. Thirty individually caged subjects had significantly more

https://doi.org/10.1017/S0962728600018017 Published online by Cambridge University Press

extensive atherosclerosis in the coronary arteries than 47 group-housed subjects. Atherosclerosis extent was four times greater in animals that were kept alone than in those that were living in groups. Coelho *et al* (1991) assessed the effect of companionship in four baboons (*Papio* spp.) during a distressing restraint situation. The animals were tested under traditional single housing, and under experimental social housing which implied that subjects had visual, tactile and auditory contact with compatible conspecifics. Being restrained in company with familiar social partners resulted in significantly lower resting blood pressure and lower heart rates than when being restrained alone, suggesting that familiar companionship ameliorated physiological stress responses.

Eaton *et al* (1994), Crockett *et al* (1994) and Reinhardt (1994c) emphasized that grooming is the salient social behaviour of compatible macaque pairs, and that companions show agonistic interactions only rarely but have a strong preference to stay in close proximity to one another (cf Washburn *et al* 1994). These observations indicate that compatible companionship is a source of comfort rather than distress.

Schapiro *et al* (1993) were unable to detect significant differences in cortisol response to single versus pair housing in 64 juvenile rhesus macaques. This finding supports results of Reinhardt *et al* (1991) who examined serum cortisol concentrations of single-housed and compatible pair-housed adult rhesus macaques. In both sexes, cortisol concentrations of isosexually paired animals (ten females, ten males) showed no significant differences with those of single animals (five females, five males). Both in female and in male pairs, dominant partners had cortisol concentrations that were equivalent to those of their subordinate counterparts (females: 19.5 $\mu g\ dl^{-1}$ vs 19.4 $\mu g\ dl^{-1}$; males: 17.5 $\mu g\ dl^{-1}$ vs 17.2 $\mu g\ dl^{-1}$). These data corroborate those of Crockett *et al* (1994) who found no evidence of elevated levels of urinary cortisol in response to compatible pair housing versus single housing in ten adult female long-tailed macaques.

Eaton *et al* (1994) assessed immune stress responses in adult female rhesus macaques when being single-housed (n = 45) versus pair-housed (n = 24) with a compatible partner. Lymphocyte proliferation response did not decline after pairing and showed no difference between dominant and subordinate members of pairs. The analysis of behavioural profiles complemented this finding, suggesting that subordinates were not stressed by the experience of pairing. Coe (1991) reported a decrease in lymphocyte proliferation response in old rhesus macaques when being transferred from single housing to pair or group housing with juveniles. These physiological observations are in line with ethological records by Reinhardt and Hurwitz (1993) showing that pair-housed aged rhesus macaques have to discipline their sometimes all too frisky young companions. The authors therefore recommended that pairs should be split in the event of excessive disturbance of the aged subjects by their young cagemates.

Taking the expression of gross behavioural disorders as signs of distress, compatible companionship may have a therapeutic effect (Harlow & Suomi 1971; Brandt & Mitchell 1973; Bushong *et al* 1992). Line *et al* (1990b) observed self-abusive behaviours in five female long-tailed macaques and noted cessation of this disorder in all cases after the animals had been transferred to compatible pair housing for five to six months. Reinhardt *et al* (1987b) noted bizarre stereotypical behaviour patterns in three singly-housed adult female rhesus macaques. All three animals were paired with infants and gradually abandoned their peculiar habits within four months of social housing. Bloomsmith and Schapiro (1994

personal communication) noted that pair housing previously single-caged juvenile rhesus macaques, significantly reduced the percentage of time that was spent by the subjects engaged in self-aggressive activities. Ruppenthal *et al* (1991) observed stereotypies in individually caged but not in pair-housed pig-tailed infants.

Social housing need not be distressing for laboratory non-human primates, however, involuntary separation from familiar companions for routine management or experimental reasons may be a disturbing experience (Redican & Mitchell 1973; Willott & McDaniel 1974; Suomi *et al* 1975; Reite *et al* 1981; Rasmussen & Reite 1982; Coe 1991; Mendoza 1991; Gordon *et al* 1992), as is the involuntary removal from the familiar home-cage (Mitchell & Gomber 1976; Holm 1979; Line *et al* 1989b; Line *et al* 1991). Allowing partners continually to keep visual and/or auditory contact during physical separation is likely to minimize their stress response (cf Gust *et al* 1994; Table 2).

Table 2 **Ethological guidelines to avoid aggression during and after pair formation of previously single-caged adult macaques of the same sex.**

1	Allow potential partners to establish clear dominance-subordination relationships during a non-contact familiarization period. This is a basic condition so that the animals will be able to live together in harmony.
2	Check for signs of an established rank relationship, such as unidirectional fear-grinning, withdrawing, looking away, threatening-away and absence of reciprocal threatening.
3	Pair partners only after they have established their rank relationship. This will give them no reason to fight over dominance.
4	Pair partners in a different double cage. This avoids possible territorial antagonism.
5	Do not force animals to live together when they are incompatible. Signs of incompatibility are serious injury, persistent fighting, aggressive harassment, depression and inadequate food sharing.
6	Keep male pairs in male-only areas. This avoids sexual competition possibly triggered by the sight of females.
7	Let a new pair live together continuously for at least one month. This allows them to establish a stable social relationship.
8	If partners have to be physically separated thereafter, allow them to keep continual visual and auditory contact. This minimizes the possible stress associated with separation.
9	If partners have to be housed in different rooms for more than one week, do not simply re-unite them in their home-cage thereafter, but give them the opportunity to briefly recognize each other across a temporary transparent cage divider. This is a safeguard that the animals will not treat each other as strangers, ready to fight over dominance.
10	Never threaten or scare the animals. This could excite them so much that they redirect the triggered aggressive tension toward each other.

Undernourishment

Eaton *et al* (1994) compared body weight developments of adult female rhesus macaques and found no differences between single-housed (n = 12) versus pair-housed subjects (n = 24), nor between dominant and subordinate partners of compatible pairs. Reinhardt *et al* (1988b) assessed body weight developments of 28 adult female rhesus macaques in the month before pairing, and in the first two months after formation of 14 compatible pairs. Compared with the pre-pairing situation, dominant partners showed no significant change in body weight during the first two months, while subordinates exhibited a significant increase in weight in the second month. Reinhardt and Hurwitz (1993) recorded body weights of eight aged rhesus macaques (six females, two males) one year prior to being paired with compatible companions, at the day of pairing, and again one year after pairing. The aged animals were so old (31-36 years) that they experienced a gradual loss in body weight. Living with a companion did not accelerate this biological process: average yearly body weight balances were -4.4 per cent in the year prior to pairing, -4.2 per cent in the year after pairing. Reinhardt *et al* (1987b, 1989) include food sharing between partners as one criterion of pair compatibility to guarantee that subjects obtain their adequate shares of the daily food ration (cf Table 2).

Maladaptation

Chamove *et al* (1973) examined eight rhesus infants raised without a mother and demonstrated that allowing them to interact with only each other precludes normal social behaviour development. Familiar peers exhibited a preponderance of mutual clinging because they had no opportunity to develop affectional ties with any other conspecifics (Chamove 1973). Ruppenthal *et al* (1991) tested infant pig-tailed macaques during play sessions scheduled throughout the first eight postnatal months. Play groups consisted each of two females and two males: four pair-housed versus four individually housed subjects. The animals had been separated from their mothers shortly after birth. They were artificially reared during 14–28 days and subsequently assigned to the experimental protocol. During the play sessions, pair-housed infants tried to maintain physical contact with their partners by clinging to each other. Individually housed infants spent significantly less time clinging to playmates and were less afraid to examine them. No significant difference in social play was found between rearing conditions. Unlike single subjects, paired subjects exhibited no rock/huddle/self clasp and stereotypic behaviour patterns, but instead spent significantly more time playing with toys. At the end of the study, all animals were placed in cages with seven to eight other monkeys. Informal observations suggested that the pair-reared subjects fared poorly in this social housing situation: they were submissive and appeared depressed. These reactions were not seen in the individually reared subjects. The authors concluded that pair rearing yields abnormal social development in pig-tailed macaques.

Unlike motherless peer rearing, mother rearing and subsequent pair housing with another peer is unlikely to produce developmental disorders. Schapiro *et al* (1994) separated 24 mother-reared rhesus infants from their natal group when they were a little over one-year-old and placed them in single cages for one year. The animals were subsequently paired with *another similarly reared peer* of the opposite sex. When they were three-years-old, subjects were placed into groups of six to eight other monkeys. The authors did not observe any social integration problems on these occasions.

Discussion

The present review leads to the conclusion that arguments justifying individual caging of laboratory non-human primates may often be based on assumptions rather than on facts. Rhesus macaques for example, are commonly single-housed because it is generally believed that the species is particularly aggressive and hence unsuitable for social housing. Disregarding this conventional wisdom, 295 adult rhesus macaques of both sexes assigned to research, were successfully transferred from single housing to permanent isosexual pair housing with each other (102 pairs) or to pair housing with infants (91 pairs). This socialization programme was associated with serious, yet not life threatening wounding in only less than 1 per cent (3/386) of animals (Reinhardt 1991b).

The available information indicates that transferring single-caged macaques to group housing is likely to be associated with a relatively high risk. The inherent socio-ethological advantages of group living, however, warrants carefully controlled and monitored attempts to provide compatible group housing, especially for young animals.

Scientific findings show that pair formation and subsequent permanent pair housing offers a safe alternative to unsuccessful group housing attempts. The relatively high degree of aggressive incompatibility found in male long-tailed macaques (Crockett *et al* 1994; cf Goosen *et al* 1984; Whitney & Wickings 1987) could probably be attenuated as in rhesus and stump-tailed males (Reinhardt 1994c,d), if partners were allowed: a) to establish rank relationships during prefamiliarization, and b) to stay together continuously rather than intermittently thereafter. Future studies will also have to examine if adult-infant pairing is equally successful in other macaque species as it is in rhesus macaques.

The information regarding the impact of social housing on morbidity is limited, but strongly suggests that the health risks associated with group living can effectively be minimized or even neutralized when non-human primates are housed in compatible pairs.

The literature reviewed offers no evidence that compatible social housing causes more distress than single housing. This does not imply that single housing is stressful. Compatible companionship, however, unlike solitary confinement, functions as a buffer against stress during fear-inducing events associated with routine management practices and experimental procedures. Housing gregarious non-human primates in compatible social conditions is also a safeguard against the pathological condition of behavioural disorders so commonly seen in single-caged subjects (cf Erwin *et al* 1973). Goosen *et al* (1984) recommend therefore that individual housing should be used only when strictly necessary for the well-being of the animals, eg during recovery from surgery.

To make social housing a successful management improvement:

a) partner compatibility must be ascertained on a daily basis (cf US Department of Agriculture 1991).
b) animals should not be forced to live with each other if observable and/or measurable evidence indicates that they are incompatible (cf US Department of Agriculture 1991).
c) companions should have the option of moving into temporary visual seclusion (Goosen *et al* 1984; Whitney & Wickings 1987; O'Neill 1989; Taff & Dolhinow 1989; Reinhardt & Reinhardt 1991).
d) male companions should be housed in male-only areas to prevent sexual competition (Reinhardt 1992a).

e) social relationships should not be disrupted to avoid possible distress triggered by involuntary separation from familiar conspecifics (cf Gordon *et al* 1992).

It has been shown that groups/pairs can be successfully trained to voluntarily separate for common procedures such as blood collection (Bunyak *et al* 1982; Vertein & Reinhardt 1989; Clarke *et al* 1990; Reinhardt & Cowley 1992), faeces collection (Phillippi-Falkenstein & Clarke 1992), systemic drug administration (Reinhardt 1992c), topical drug application (Reinhardt & Cowley 1990), vaginal swabbing (Bunyak *et al* 1982), tethering (Reinhardt 1991b), and headcap implantation (Reinhardt 1991b). Socially housed animals can readily be conditioned to allow capture in transport boxes (Smith 1981; Boccia *et al* 1992; Reinhardt 1992b; Luttrell *et al* 1994). If an animal has to be kept singly for a limited time period (ie metabolic studies, feeding studies, urine collection, post-operative recovery, experiments involving chair restraint) a compatible companion can be kept close by behind a transparent barrier allowing visual and/or acoustic social contact (cf Reinhardt *et al* 1989; Coelho *et al* 1991).

The normal social adjustability by pair-housed macaque infants that were naturally raised by their mothers, as opposed to the relatively poor social adjustment of pair-housed infants that were artificially reared without mother contact, endorses natural rather than artificial rearing conditions for non-human primates. The unnatural attachment of a mother-deprived infant to another infant inhibits rather than facilitates the devolvement of normal peer-peer interaction (Chamove *et al* 1973). The cause of this behavioural problem is obviously not the social peer-housing condition but the absence of the biological mother (cf Mason 1991). This notion is supported by findings of Alexander (1966) who reared infant rhesus macaques from birth for eight months with only their mothers. These animals did not show the typical together-together syndrome when separated from their mothers, and socialized with peers.

The present survey of the literature supports the regulatory recommendations of housing gregarious non-human primates, such as macaques, in an environment that allows them to express their social disposition. Keeping macaques under social rather than single housing conditions provides a simple way of approximating conditions that are normal. It makes the animals more valuable for unbiased scientific research because they are now truly what they are supposed to be: social animals. Partners of compatible macaque pairs spend approximately 1/5 of their time interacting with each other in affiliative ways typical for the species (Ranheim & Reinhardt 1989; Reinhardt 1990b; Line *et al* 1990a; Reinhardt & Hurwitz 1993; Crockett *et al* 1994; Eaton *et al* 1994; Reinhardt 1994c; Schapiro & Bloomsmith 1994). This is compatible with the situation in groups containing animals of both sexes and different ages (Rhine & Kronwetter 1972; Post & Baulu 1978; Bernstein 1980; Teas *et al* 1980; O'Keeffe & Lifshitz 1985; Chopra *et al* 1992; Leon *et al* 1993), and suggests that being transferred from single to pair housing improves the animals' behavioural health by providing them with an appropriate environment for the expression of their social disposition (Reinhardt 1987). Pair housing is likely to be one of the least expensive and most effective alternatives for improving the welfare of macaques in research facilities (Line *et al* 1990b).

It would defeat the purpose of the regulations to stubbornly force laboratory macaques to live together and possibly kill each other. Given the complexity of non-human primates and the inherent dynamics of their social relationships, it would be unrealistic to expect unvarying compatibility (Reinhardt 1994b). No strict rule can therefore be set which will

guarantee successful social housing in all instances. Attempts to transfer single-caged animals to compatible permanent group or pair housing have to be based on ethological principles (Table 2), common sense, some expertise, and also on good will in order to take variables into account that may directly affect the outcome. Such variables are: technique of partner introduction, sex, age, rearing history, social experience, health status, research protocol, animal caregiver/technician, feeding regime and physical environment.

The published data show that previously single-caged macaques can be transferred to social housing adequate for the species (group housing for juveniles, pair housing for adults) without undue risks to individual animals. Techniques that are currently applied successfully with macaques should be attempted with other appropriate species and modified if necessary. The work described in this review presents a justifiable plan of action to provide social non-human primates with a social rather than solitary housing environment.

Animal welfare implications

Scientific evidence shows that laboratory macaques can be permanently housed in a compatible social environment without unduly jeopardizing their safety. Providing them with a social rather than the traditional solitary environment, fosters their well-being by offering them means to satisfy their need for social interaction and social contact.

Acknowledgements

We are thankful to Mollie Bloomsmith, Gray Eaton, Catherine Reinhardt and Annie Reinhardt for reading the first draft of this manuscript and offering constructive criticism. The manuscript also benefited from very helpful suggestions of three anonymous referees.

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