

Use of Introduction Enclosures to Integrate Multimale Cohorts into Groups of Female Rhesus Macaques (*Macaca mulatta*)

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Integrating animals into a new group is a challenge for both free-ranging and captive adult male rhesus monkeys (*Macaca mulatta*), and for females in groups receiving new males. To ensure the genetic viability of the population, however, male transfers must occur in both natural and captive settings. To facilitate the introduction of groups of adult males to adult females, we designed a new enclosure that is attached to the outdoor compound where females are housed. Here we describe the construction of 3 introduction enclosures, their use during 4 introductions of groups of adult males to adult females, a brief comparison of introduction success rates associated with the new introduction enclosures with those of our traditional male introduction method, and a critique by the various groups of staff members working with the new enclosures. Overall, the introduction enclosures benefitted both the macaques and the facility personnel and appear to be a useful enhancement to our process of integrating breeding groups.

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Integrating into a new group is a challenge for both free-ranging and captive adult male rhesus monkeys (*Macaca mulatta*) as well as for the females in groups receiving new males. To ensure the genetic viability of the population, however, male transfers occur in both natural and captive settings. In wild groups of rhesus monkeys, male migration facilitates inbreeding avoidance.^{14,16,19,23} Typically, males transfer out of their natal groups between 3 and 5.5 y of age (median, 4.5 y).⁶ These males often move into groups that occupy areas adjacent to those of their natal groups,¹⁶ and they generally transfer individually or in small bachelor groups.¹⁰ This process results in varying levels of aggression from resident group members. Because males often join new groups as low-ranking members,^{7,24} they face aggression from higher-ranking females and subadult males, who sometimes band together to prevent new males from entering their group.¹⁷ Even when the transferring males are successful in copulating with resident females, they still experience harassment from other group members and threats from resident males, often resulting in severe wounding.¹⁴

In captive settings, breeding groups of macaques must be regulated to avoid inbreeding. Managing breeding groups can be accomplished by different means (for example, removing related group members before breeding can occur, cross-fostering of infant males into other groups near birth, disbanding groups before female offspring of males are old enough to reproduce), and a common approach is to rotate adult males from one group of females to another every few years so that those males cannot breed with their maturing daughters.¹⁸ There is no standard procedure for male introductions. Resident males in a group are generally removed for a period of time, ranging from a few days or weeks to a year, prior to introducing novel

males.¹⁸ Introductions of adult males are socially disruptive and may result in severe aggression directed toward the new males.^{4,5} Minimizing aggression is a primary objective during introductions. Gradual introduction with visual barriers in the enclosure reduced traumatic wounding rates for rhesus macaques involved in introductions when compared with more rapid introductions in enclosures without visual barriers,²⁵ so that an approach using visual barriers may be useful.

The long-term goal of conducting male introductions is to efficiently and safely integrate males into groups of females such that the resulting breeding groups are socially stable and produce a satisfactory number of offspring that can be reared safely in the group. Empirical evidence indicates that nonnatal adult males provide a stabilizing role by reducing severe aggression and wounding and increasing affiliative social behavior within a group.^{2,8,9} Specifically, nonnatal adult males, particularly high-ranking ones, intervene most frequently and most successfully in conflict among their group members, leading to lower rates of aggression and trauma as well as improved social network stability and integration.^{2,3,8,9} Consequently, group stability can be enhanced by increasing the proportion of nonnatal adult males in breeding groups. Macaques in socially unstable situations may experience stress and have an increased risk of injuries.¹⁸ Therefore, male introductions serve the dual purpose of maintaining genetic diversity in the colony and improving group stability.

The rhesus macaque breeding colony at our facility (Yerkes National Primate Research Center) is primarily maintained in large breeding groups (18 to 170 animals), comprising multiple, multigenerational matrilineal and housed in 0.06- to 0.38-acre outdoor compounds with attached indoor enclosures. For many decades, we have conducted male introductions into established groups of females. Over time, we have had increasing difficulty in completing these introductions with groups of males, such that we now have fewer adult males per female in the breeding

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groups than in the past. As described earlier, these increasingly skewed sex ratios are undesirable for group stability.² For this reason, we wanted to develop a different introduction process that might help to integrate larger numbers of adult males into groups successfully and to compare that new method with our traditional introduction method.

Traditional Method for Introducing Males into Female Groups

The traditional approach to multimale (3 or more) introductions at our facility involves moving the male group from their run housing into the larger part of the indoor enclosure, which is attached to a compound containing females. The males are moved during the day and are returned to their run housing each afternoon, such that females have full access to the indoor space overnight. This process requires personnel to move each male from the run into an individual transport box, take the transport boxes to the indoor portion of the compound, and release each male there; this process is repeated in reverse later in the day. The traditional transport process typically took 3 or 4 staff members working together for 60 to 90 min to complete each way and was done twice daily. This process computes to a minimum of 4.5 h of personnel effort (and in some cases, considerably more) just for moving the males each day of these traditional introductions. In addition, the transport process can be stressful, sometimes triggering male fighting and wounding. While housed in this area, the males have visual access to the females that can enter an adjacent, indoor compound space, as well as limited physical contact with the females through chain-link fencing. As positive interactions increase between males and females, males are given full access to the females for increasing periods of time while being monitored by colony management staff members, and the male macaques are removed from the females when not being monitored. Eventually, the males are allowed to stay overnight with the females, dependent upon positive social interactions, and to live full time with the females. The total duration of an introduction varies depending on the behavior of the animals, staffing, and weather. This method limits the amount of time that males can interact with the female group (typically about 5 h daily [maximum of 7 h]), and the moves may not be possible when staffing is low. In addition, the males are exposed only to the females that venture inside, giving the males a limited view of the female group dynamics.

New Method for Introducing Males into Female Groups

To improve the ease of introductions and accommodate larger groups of males, we designed a new introduction enclosure that is permanently attached to the outdoor compound where females are housed. This introduction enclosure can house multimale groups 24-h a day, for indefinite periods of time. This process allows protected contact interactions between the new males and the females through chain-link fencing, compared with the 5- to 7-h maximum in the traditional introduction system. This procedure eliminates the personnel time and the stress of repeatedly transferring macaques between run housing and indoor compound spaces. Both males and females have the choice to interact through the chain-link fence or distance themselves from others by moving behind privacy panels or elsewhere throughout the compound. As with the traditional method, interactions between the males and females were monitored by colony management staff, and as positive

interactions increased, males were released into the outdoor compound space with full access to the females. These periods of monitored full access were extended over time, and the males could still be brought back into the introduction enclosure at any time to be separated from females when deemed necessary. Eventually, the males were allowed to stay overnight with the females, as in the traditional approach. We believe this new procedure may better simulate the natural integration process of wild rhesus macaques, which involves immigrant males joining a new group with space to distance themselves from aggressive group members.⁷

The objectives of this report are to (1) describe the construction of 3 introduction enclosures at our facility, (2) describe their use during 4 introductions of groups of adult males to adult females, (3) briefly compare the success of male introductions using the introduction enclosures with those using our traditional technique, and (4) report a critique of the introduction enclosures by the various groups of staff members working with them. The introduction enclosures were constructed as part of a grant-funded project we are conducting to fully evaluate their use and their effect on behavioral and stress measures; these results will be published in coming months.

Materials and Methods

This work was conducted at the Yerkes National Primate Research Center Field Station (Lawrenceville, GA). The facility and its programs are fully AAALAC-accredited. Procedures involving animals were approved by the Emory University IACUC and were conducted in accordance with the USDA Animal Welfare Regulations,¹ the *Guide for the Care and Use of Laboratory Animals*,¹² and institutional policies. All animals were free of SIV, simian T-lymphotropic virus, simian type D retroviruses, and herpes simian B virus. All animals had continuous access to fresh drinking water and unrestricted access to food. Routine enrichment provided to all animals included fresh produce, climbing and play structures, foraging devices with a variety of foods, and manipulanda. The introduction enclosures were used during the breeding seasons of 2017 through 2019 (late September through early January).

Design features and goals. The new enclosures were intended to enable larger groups of males to be introduced to female groups while increasing group stability and decreasing trauma. All of the introduction enclosures were designed to be cost-effective additions to outdoor enclosures that could be constructed inhouse and that would facilitate increasing the exposure of multimale groups to females during the introduction process in a less stressful manner. The enclosures were intended to allow staff to gain quick access to the macaques in case of injury or illness, to require few alterations to the existing outdoor compound, and to give the animals continuous protected contact access to one another throughout the introduction process. We anticipated that the use of the introduction enclosures might improve the success rate of introductions, helping us to achieve our goal of improving the sex ratio in rhesus macaque breeding groups.

Initially, we considered building a portable introduction enclosure that could be moved to different compounds as introductions were being conducted. As we carefully examined the variation in space available at each compound, the varied terrain, visibility concerns, differing compound fixtures, and other permanent roads and structures, we determined that each unit would need to be customized and permanent. However, in a different context, portable introduction enclosures may be a viable option.



Figure 1. Original introduction enclosure retrofitted with heaters (hanging under the solid roof).

Construction. The Facilities Management team constructed 2 new introduction enclosures and modified an existing space to create a 3rd introduction enclosure. A committee composed of personnel with a range of expertise (facilities, veterinary, colony management, animal care, and behavioral management staff members) provided input from numerous perspectives before the construction of each enclosure.¹³ Broad input was needed to ensure that we optimized the design for cleaning, veterinarian care, social management, and animal welfare. In addition, this collaboration led to a smooth transition for all staff working with this new type of animal enclosure.

Each of the introduction enclosures was permanently attached to the outdoor portion of a large compound that housed macaque groups. The 2 new introduction enclosures were built on concrete slabs to provide a level and dry foundation. The posts were 5.08-cm galvanized steel square tubing, and the fencing was 9-gauge galvanized chain-link. We routinely use these materials for primate run housing, large social compounds, and indoor housing areas. The macaque doors were 0.47-cm aluminum sheet plates, and the perching was 5.08-cm-diameter polyvinyl chloride pipe. In addition, human-access doors were made from 5.08-cm galvanized steel square tubing and 9-gauge galvanized chain-link (Figure 1). Each introduction enclosure contained a small capture area for separating individual males or moving them into a transfer box when needed (Figure 2). The introduction enclosures shared a single chain-link barrier with the compound, which eliminated the risk of animals getting an arm stuck between 2 fences and allowed males and females to observe and interact with each other with limited physical contact prior to full introduction (Figure 3 A and B). Structural enrichment items, including privacy panels for separation from

each other or females, milk crates and perches, manzanita wood, forage boards, and toys were placed in the enclosure, allowing the macaques to engage in species-typical behaviors.¹³ Finally, watering lines and feed bins were added to ensure that the males had access to drinking water and food.

The 2 newly constructed enclosures were built a year apart, so we tested the first model and made adjustments before the second was built. After we used the first enclosure, limitations related to weather and functionality became apparent, so 3 changes were made. First, Dayton infrared gas tube heaters (length, 660.4 cm; width, 46.04 cm; height, 21.59 cm) and removable hanging polypropylene panels (91.44 to 121.92 cm × 182.88 cm) that served as wind blocks were added to allow the animals to safely and comfortably stay in the introduction enclosure during colder conditions²⁶ (Figure 4). Second, an animal door was added to the compound to give direct access from the enclosure to the compound (Figure 5). This extra door facilitated direct movement of males between the enclosure and compound, thus increasing the ease and speed of moving them (especially as compared with the alternative of moving them into transport boxes and releasing them into the compound). Third, the second enclosure was designed to be larger than the first in order to accommodate larger groups of males (Figure 6).

For the third introduction enclosure, we modified a vacant indoor area that already had many of the necessary components (Figure 7). As a result, each of the 3 introduction enclosures differed in dimensions and construction cost (Figure 8).

Use of introduction enclosures. Four introductions of adult males to adult female groups were accomplished successfully with the introduction enclosures. In each situation, a stable cohort of breeder males was identified, with 3 to 5 males per



Figure 2. Capture unit inside the introduction enclosure. The capture unit is a 1.16 m × 2.87 m enclosed space behind the enclosure proper. The locked sliding door here separates the 2 areas.

cohort. The males were moved into the introduction enclosure early in the breeding season, between 1 and 48 d after the previous males were removed from the female group. The duration of time without males varied based on the stability of the female groups when they were without males; if considerable fighting occurred among the females, the introduction of new males began more quickly. The males had protected contact interactions (through chain-link fencing) with the females 24 h a day. The male cohorts were introduced to female-offspring groups with 38 to 75 members. The length of time each male cohort stayed entirely in the introduction enclosure varied depending on interactions among the monkeys, staff availability, weather, and receptivity of the female group and ranged from 9 to 41 d. Colony managers evaluated the groups for stable dominance relationships among the males in the presence of the females and for females to appear interested in the males while in the introduction enclosure. Colony managers decided when to release the cohort into the group's large outdoor compound and gradually increased the length of time males spent in the compound each day but returned the males to the enclosure for the night. This process was accomplished by opening the animal door to the introduction enclosure and encouraging the males to go inside, by using verbal cues from outside the compound. When needed, staff entered the compound area and corralled the males into the enclosure. When colony managers were able to leave the area for several hours during the day with few or no severe conflicts or injuries among the macaques, they allowed the males to spend the night with the females. Technicians checked on the groups throughout the

night for the first week that the males were fully integrated into the breeding groups. The duration of these entire introduction processes ranged from 10 to 128 d (including the 9 to 41 d in the introduction enclosures). In some cases, the males were in the hospital or other temporary housing for substantial amounts of time, thus considerably lengthening the process. In the first year, males were removed from the introduction enclosure when the temperature dropped below freezing, but after weatherizing was complete, the males were able to remain despite the colder conditions. Temperatures inside the introduction enclosures remained comfortable (over 70 °F [21 °C]) even when ambient temperatures were below 32 °F (0 °C).

Traditional introductions documented for comparison. To determine a general success rate for our traditional introduction method in order to compare it with the new introduction enclosure method, we used a random sample of 4 female groups that had experienced multimale (3 or more males) traditional introductions between 2003 and 2013. These 4 groups experienced a total of 8 introductions. In addition, we assessed the traditional introduction method in another 4 multimale introductions to female groups. Male groups with 3 to 7 members were introduced to female-offspring groups with 26 to 177 members. Total introduction durations ranged from 6 to 36 d.

Survey methods. We consulted with representatives from the Animal Care, Colony Management, and Veterinary groups at our facility throughout the process of enclosure design and construction. Because each of these groups was involved with the use and maintenance of the enclosures, we collected feedback



Figure 3. (A) Male and female macaques interacting through the introduction enclosure. (B) Males observing females in compound.

from them after the introduction enclosures were used for 3 groups of males. A combination of in-person and email surveys were completed over 1 wk. Respondents were selected based

on their experience interacting with the enclosures. Two people from each department were asked the same open-ended survey questions (Figure 9). The goal of this survey was to use general



Figure 4. Enclosure with infrared gas tube heaters and hanging polypropylene panels.

feedback from a variety of perspectives to improve the introduction enclosure design.

Results

Of the 12 traditional method introductions, 7 (58%) failed (no males integrated into the breeding group), 4 (33%) were partially successful (at least one male integrated into the breeding group), and one (8%) was successful (all males integrated into the breeding group). Of the 4 introductions using the introduction enclosures, 3 were successful (75%) and one was partially successful (25%). The males stayed entirely in the introduction enclosures for 9 to 41 d, depending on the number of behavioral interactions that we observed. The new enclosures allowed extended exposure of the new males to the resident females, as we had hoped. The entire duration of the introduction processes, from initial exposure to living full-time in the same space, ranged from 10 to 128 d. Although the traditional introductions required fewer days (average 15.75 days) than those using introduction enclosures (average 55.5 days), most of the traditional introductions were terminated due to severe aggression and were considered failures.

Our second objective was to improve the skewed sex ratios in the rhesus groups. Among the traditional method groups over an 11-y period, we found that the mean sex ratio was 18:1 (females:male). In comparison, our successful male introductions using the new introduction enclosures resulted in more

balanced sex ratios (3.5:1, 5:1, and 8:1), which are more similar to what is seen in wild populations.^{11,15,20-22}

We collected feedback from staff members from each department that interacted with the introduction enclosures. Colony managers reported that using the introduction enclosures saved them a considerable amount of time and physical effort because the males did not have to be moved to and from the social group's indoor housing area in transport boxes each day during the introduction process. They thought that the male macaques benefited from having a longer period of time to learn the female social dynamics. Veterinary staff expressed the benefits of using the capture area of the introduction enclosure to easily give oral medication or supplemental food to individual males without competition from other animals, as could occur when trying to do the same in a compound or run housing. They also believed that additional uses were possible for the cages outside of breeding season. Animal Care staff appreciated the fact that the enclosure can accommodate absorbent bedding material (for example, aspen wood chips) with a lower animal density than our typical housing, thereby requiring less-frequent cleaning (about 3 cleanings per week) than typical housing areas (about 5 cleanings per week). Each department also offered constructive feedback on the enclosures' design and use. The Animal Care department suggested adding a drainage mechanism so that rainwater and water from cleaning would not collect in the enclosure. The Colony Management department recommended that the enclosures be 7 feet tall so that taller staff members could



Figure 5. Enclosure with sliding animal door to the female compound. The arrow indicates the door that opens directly to the compound.

comfortably move around inside the enclosure when needed but not so high that people would struggle to access animals that cling to the ceiling, out of reach. Colony Management staff suggested we change the door to the capture area so that it could be operated from the outside of the enclosure.

Discussion

Three new introduction enclosures were constructed inhouse by our Facilities Management staff in a cost-effective manner by using materials we routinely use for other monkey housing. Heaters and wind blocks were added to the original design to adequately weatherize the spaces so the males could live in them overnight and during various weather conditions. We also increased the size of the later enclosures and added a door so the macaques could move directly into the compound from the introduction enclosures. We consider the cost of these units (\$20,350 to \$25,000) to be reasonable.

The introduction enclosures functioned well for their intended purpose. Four different groups of breeder males, with 3 to 5 males per group, were introduced to large female groups. The additional time for visual access and limited interactions between males and females with use of the introduction enclosures may be more like the natural process of young male transfer, when they gradually work their way into new groups by staying on the periphery as they attempt to join, and therefore may avoid attacks long enough to establish firm ties with group members.⁷

We accessed archival data on multimale introduction success rates to allow a comparison of the new introduction enclosures with our traditional introduction procedures. Of the 12 traditional, multimale introductions evaluated, only one was fully

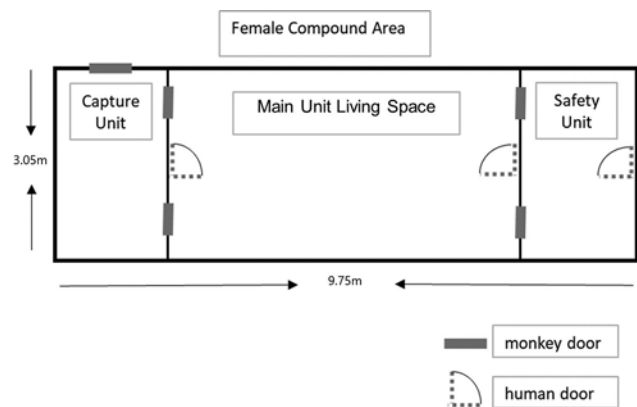


Figure 6. Diagram of introduction enclosure 2, illustrating the safety unit for animal release, main unit living space, and capture unit for animal capture.

successful (8%), and 4 were partially successful (33%), with at least one male integrated into the group. In contrast, of the 4 multimale introductions using the introduction enclosures, 3 were successful (75%), and one was partially successful (25%). Although we have a small sample of groups that used the new introduction enclosures, the new method appears to increase the successful integration of male groups into established female groups, thus meeting the intended purpose of the new enclosures.

The long-term reason for forming multimale breeding groups of rhesus macaques is to create breeding groups that are socially stable and productive. The introduction enclosures may facilitate



Figure 7. Modified introduction enclosure 3.

Introduction enclosures	Dimensions	Total cost (labor and materials)
Introduction enclosure 1	3.05m × 6.71m × 1.83m	\$20,350 (including retrofitting)
Introduction enclosure 2	3.05m × 9.75m × 2.44m	\$25,000
Introduction enclosure 3	9.14m × 1.83m × 2.13m	\$1,400

Figure 8. Dimensions and cost of introduction enclosures.

1. What do you like about the introduction enclosure and how do you think they benefit the animals and your staff?
2. Do you have any constructive feedback about the introduction enclosures?
3. Is there anything we can do to improve future design?
4. Do you have ideas for other ways the introduction enclosures can be used outside of breeding season?

Figure 9. Introduction enclosure survey.

that process. Because nonnatal adult males contribute to reducing aggression and wounding and to increasing affiliative social behavior,^{2,8,9} it is important to identify strategies to safely add more males into groups. The introduction enclosure may be such a strategy. Wild groups of rhesus monkeys are reported to have female:male sex ratios of 1.4:1 to 3.8:1.^{11,15,20-22} In our archival sample of groups, the mean ratio was 18:1. In comparison, our successful multimale introductions using the new enclosures resulted in more balanced sex ratios, with a mean of 5.5:1, which is a more natural social group composition for rhesus macaques.

The introduction enclosures provided several benefits over our traditional introduction methods. Our informal survey of users of the introduction enclosures indicated a consensus that the units functioned well for the intended purposes and that the monkeys benefitted from their use. They believed that the males benefited from having an extended time to observe the female group's social dynamics. When males were housed in an introduction enclosure during their initial exposure to females,

they could see the entire female group, compared with the traditional method in which the males were housed in the indoor portion of the compound building, limiting the male and female interactions. With the enhanced visual, olfactory, auditory, and tactile exposure, the males may be able to learn more about the matrilineal structure, dominance, and estrous states of more of the females before fully joining the group themselves. The introduction enclosures provided more and better-quality space (for example, outdoors, accommodation of more enrichment, privacy) for the males than the indoor units. The larger size facilitates the introduction of larger cohorts of males than was feasible using our traditional introduction system.

Notable advantages of the new strategy included reduced time for colony management (because macaques did not have to be moved back and forth to the compound space each day) and a reduced requirement for cage cleanings (because the enclosure can accommodate bedding material such as aspen wood chips, generally 3 cleanings per week were sufficient rather than 5).

Veterinary staff liked being able to use the capture area of the introduction enclosure to easily give medication or food to individual males without interference from other animals. Some personnel also suggested that these enclosures could be used year-round for a variety of purposes. For instance, they could serve as temporary housing for an injured or sick monkey that requires daily medication; housing in the introduction enclosure would allow that monkey to be near his/her group and to interact through the fencing while receiving the needed clinical support. The enclosures could also be used to house individuals or entire matriline being reintroduced to their group after temporary removals for research procedures, veterinary care, or social unrest. This adaptation may allow colony managers to gauge the behavior of the individual better or the group to minimize conflict during reunions.

Suggested alterations to the introduction cages included adding a drainage mechanism, setting the height at 7 feet, and allowing the capture unit door to be operated from outside of the enclosure. Although the cost for each unit is reasonable, our facility has 19 more compounds that could use introduction enclosures, and constructing them all would be costly. In addition, there is no-one-size-fits-all introduction enclosure, so each must be designed individually given available space, terrain, and weather requirements. Despite these few shortcomings, the introduction enclosures were well-received by all groups working with the macaques at our facility. Overall, the introduction enclosures benefitted both the animals and the facility personnel and appear to be an effective enhancement to our process of integrating breeding groups.

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References

1. **Animal Welfare Regulations.** 2008. 9 CFR § 3.129.
2. **Beisner BA, Jackson ME, Cameron A, McCowan B.** 2012. Sex ratio, conflict dynamics, and wounding in rhesus macaques (*Macaca mulatta*). *Appl Anim Behav Sci* **137**:137–147. <https://doi.org/10.1016/j.applanim.2011.07.008>.
3. **Beisner BA, McCowan B.** 2013. Policing in nonhuman primates: partial interventions serve a prosocial conflict management function in rhesus macaques. *PLoS One* **8**:1–13. <https://doi.org/10.1371/journal.pone.0077369>.
4. **Bernstein IS, Draper WA.** 1964. The behaviour of juvenile rhesus monkeys in groups. *Anim Behav* **12**:84–91. [https://doi.org/10.1016/0003-3472\(64\)90107-1](https://doi.org/10.1016/0003-3472(64)90107-1).
5. **Bernstein IS.** 1964. The integration of rhesus monkeys introduced to a group. *Folia Primatol (Basel)* **2**:50–63. <https://doi.org/10.1159/000155003>.
6. **Colvin JD.** 1986. Proximate causes of male emigration at puberty in rhesus monkeys, p 132–157. In: Rawlins RG, Kessler MJ, editors. *The Cayo Santiago Macaques: History, Behavior, and Biology*. Albany (NY): State University of New York Press.
7. **Drickamer LC, Vessey SH.** 1973. Group changing in free-ranging male rhesus monkeys. *Primates* **14**:359–368. <https://doi.org/10.1007/BF01731357>.
8. **Flack JC, Girvan M, Waal FBMD, Krakauer DC.** 2006. Policing stabilizes construction of social niches in primates. *Nature* **439**:426–429. <https://doi.org/10.1038/nature04326>.
9. **Flack JC, Krakauer DC, Waal FBMD.** 2005. Robustness mechanisms in primate societies: a perturbation study. *Proc Biol Sci* **272**:1091–1099. <https://doi.org/10.1098/rspb.2004.3019>.
10. **Gacho-Neveu H, Ménard N.** 2004. Gene flow, dispersal patterns, and social organization, p 117–134. In: Thierry B, Singh M, Kammann W, editors. *Macaque societies: a model for the study of social organization*. New York (NY): Cambridge University Press.
11. **Goldstein SJ, Richard AF.** 1989. Ecology of rhesus macaques (*Macaca mulatta*) in northwest Pakistan. *Int J Primatol* **10**:531–567. <https://doi.org/10.1007/BF02739364>.
12. **Institute for Laboratory Animal Research.** 2011. *Guide for the care and use of laboratory animals*. Washington (DC): National Academies Press.
13. **Kelley ST, Crockett CM.** 2012. Laboratory housing of nonhuman primates, p 251–268. Chapter 9. In: Abee CR, Mansfield K, Tardif S, Morris T, editors. *Nonhuman primates in biomedical research: biology and management, vol 1*. San Diego (CA): Elsevier. <https://doi.org/10.1016/B978-0-12-381365-7.00009-1>
14. **Lindburg DG.** 1969. Rhesus monkeys: mating season mobility of adult males. *Science* **166**:1176–1178. <https://doi.org/10.1126/science.166.3909.1176>.
15. **Makwana SC.** 1978. Field ecology and behaviour of the rhesus macaque (*Macaca mulatta*): I. Group composition, home range, roosting sites, and foraging routes in the Asarori Forest. *Primates* **19**:483–492. <https://doi.org/10.1007/BF02373310>.
16. **Melnick DJ, Pearl MC, Richard AF.** 1984. Male migration and inbreeding avoidance in wild rhesus monkeys. *Am J Primatol* **7**:229–243. <https://doi.org/10.1002/ajp.1350070303>.
17. **Neville MK.** 1968. A free-ranging rhesus monkey troop lacking adult males. *J Mammal* **49**:771–773. <https://doi.org/10.2307/1378749>.
18. **Rox A, Vliet AHV, Sterck EHM, Langermans JAM, Louwse AL.** 2019. Factors determining male introduction success and long-term stability in captive rhesus macaques. *PLoS One* **14**:1–20. <https://doi.org/10.1371/journal.pone.0219972>.
19. **Sade DS.** 2017. A longitudinal study of social behavior of rhesus monkeys, p 378–398. Chapter 17. In: Tuttle R, editor. *The functional and evolutionary biology of primates*. New York (NY): Routledge. doi: <https://doi.org/10.4324/9781315132129-17>
20. **Seth PK, Seth S.** 1985. Ecology and feeding behavior of the free ranging rhesus monkeys in India. *Indian Anthropologist* **15**: 51–62. Cited [16 September 2020]. Available at: <https://www.jstor.org/stable/41919505>
21. **Southwick CH, Beg MA, Siddiqi MR.** 1961. A population survey of rhesus monkeys in villages, towns and temples of northern India. *Ecology* **42**:538–547. <https://doi.org/10.2307/1932240>.
22. **Southwick CH, Siddiqi MF.** 1977. Population dynamics of rhesus monkeys in northern India, p 339–362. Chapter 10. In: Rainier III, Bourne GH, editors. *Primate conservation*. New York (NY): Academic Press. <https://doi.org/10.1016/B978-0-12-576150-5.50015-7>.
23. **Southwick CH, Richie T, Taylor H, Teas HJ, Siddiqi MF.** 1980. Rhesus monkey populations in India and Nepal: Patterns of growth, decline, and natural regulation, p 151–170. In: Cohen MN, Malpass RS, Klein HG, editors. *Biosocial mechanisms of population regulation*. London (United Kingdom): New Haven Yale University Press.
24. **Vessey SH, Meikle DB.** 1987. Factors affecting social behavior and reproductive success of male rhesus monkeys. *Int J Primatol* **8**:281–292. <https://doi.org/10.1007/BF02735177>.
25. **Westergaard GC, Izard MK, Drake JH, Suomi SJ, Higley JD.** 1999. Rhesus macaque (*Macaca mulatta*) group formation and housing: Wounding and reproduction in a specific pathogen free (SPF) colony. *Am J Primatol* **49**:339–347.
26. **Wolfensohn S, Honess P.** 2005. *The physical environment*, p 15–31. In: *Handbook of primate husbandry and welfare*. Ames (IA): Blackwell Publishing. <https://doi.org/10.1002/9780470752951.ch2>