Survey of Behavioral Indices of Welfare in Research Chimpanzees (*Pan troglodytes*) in the United States

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Chimpanzees demand specialized housing and care and the highest degree of attention to animal welfare. The current project used a survey method to collate information on chimpanzee housing and behavioral indices of welfare across all 6 of the chimpanzee research facilities in the United States. Data were compiled on 701 chimpanzees ranging from 2 to 62 y old (mean age, 26.0 y). All chimpanzees except for one were socially housed; the median group size was 7 animals, and group sizes ranged from 1 to 14. All of the subjects had access to outdoor spaces each day. Daily access to a natural substrate in the chimpanzee's enclosure was available for 63.8% of the subjects. Overall, 94.1% of the chimpanzees used tools to acquire food, 48.1% built nests, 75.8% copulated, and 83.3% initiated grooming bouts. The following atypical behaviors were reported most often: rocking (13.0%), coprophagy (10.0%), and stereotyped behaviors other than rocking (9.4%). There was widespread evidence of positive animal training techniques, with nearly all (97.7%) subjects reported to generally voluntarily cooperate with shifting in their enclosure, and 72.2% were reported to present for an injection of anesthetic. We include some comparison between these findings and data describing zoo-housed chimpanzees. In addition, we discuss survey findings in reference to recommendations made by the NIH Working Group on the Use of Chimpanzees in NIH-supported Research. The current survey assessed a larger sample of chimpanzees living under human care than has been published previously. This broad analysis can help to guide future improvements in behavioral management to address behavioral problems or deficits.

Abbreviations: HL, Hosmer and Lemeshow; MR, mother-reared; PRT, positive reinforcement training; WB, wild-born

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Chimpanzees living under human care in the United States live in 4 major settings: research centers, sanctuaries, zoos, and privately-owned facilities. For many years, the largest proportion of this chimpanzee population has lived in research centers, but with the on-going retirement of NIH-owned chimpanzees, there is a population shift toward sanctuaries.³² It is important that the welfare of chimpanzees is assessed objectively through behavioral science. For more than 3 decades, empirical research has been published regarding the welfare and psychologic wellbeing of captive chimpanzees. This research has focused on social housing, environmental enrichment, facility design, and animal training methods.¹⁷ Notably, the majority of these studies has been conducted in research facilities. It is laudable that similar research is becoming more widespread in zoos^{48,51,89} and has recently been published by some sanctuaries.^{45,55,56}

Here we provide information regarding the current state of chimpanzee care and management in research facilities in the United States, including assessment of some aspects of their care (for example social group size, outdoor access) as it

relates to recently proposed recommendations.⁷⁵ In addition, some data for zoo-living chimpanzees in the United States are provided as a point of reference for interpreting the information about research chimpanzees. Chimpanzees require specialized housing and care and the highest degree of attention to animal welfare. In addition, chimpanzees engender high degrees of public and political interest. For example, at the request of the NIH and in response to congressional inquiry, the Institute of Medicine conducted an analysis of the ongoing and future scientific necessity of chimpanzees for NIH-funded biomedical and behavioral research. In 2011, the Institute of Medicine committee issued a report that established criteria to guide current and future research use of chimpanzees; the Working Group on the Use of Chimpanzees in NIH-Supported Research (hereafter referred to as the Working Group) was then established to advise NIH on implementing recommendations from the Institute of Medicine report. The Working Group⁷⁵ defined a number of objectives for chimpanzee care and management. Because these objectives represent an expert consensus on issues important to chimpanzee welfare, they are useful benchmarks against which to compare the current status of research chimpanzees.

The current project used a survey method to collate fundamental information on chimpanzee housing and behavioral indices of welfare across all of the chimpanzee research facilities in the United States and encompasses a larger number of chimpanzees than has previously been published. The survey focused on topics considered central to chimpanzee welfare;

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most of these topics have broad support by experts in chimpanzee care as well as support by scientific data.

The survey included questions addressing outdoor access and enclosure substrate because the physical environment in which chimpanzees live influences their behavior. For example, providing chimpanzees with access to outside spaces leads to behavioral benefits, including less abnormal behavior, less tension-related behavior, more physical activity, and perhaps more use of enrichment materials.^{6,99} Providing chimpanzees with natural substrates such as grass, hay, and woodchips has been demonstrated to increase natural foraging behavior, activity, and play and to decrease abnormal behavior.^{3,26}

In addition, the survey contained questions on current social group size and early social environment. Scientists who study chimpanzee behavior in field, zoo, and research environments agree that social housing is the most critical aspect of captive chimpanzee welfare.^{2,14,15,42,84} Chimpanzees housed alone show increased levels of anxiety, aggression,⁴ and abnormal behavior as compared with those socially housed.²⁹ The early social environment is particularly influential, and rearing away from the mother (for example, nursery setting) leads to elevated levels of abnormal behavior compared with mother-reared counterparts^{66,93,94} as well as impaired sexual and maternal abilities^{15,30,57} and reduced problem-solving skills.²⁸ Indeed, even different methods of rearing by humans can have different, long-term effects on chimpanzee health and behavior measures.³³

Species-typical behaviors were assessed by the survey. Questions regarding chimpanzees' tool use, nesting, copulation, and grooming behavior were included. The presence of species-typical behaviors is one of the most commonly used metrics of welfare, and "an aim of many welfare assessments is to increase natural behaviors."⁶⁷ Although some natural behaviors do not indicate positive welfare (fear-related behaviors, for example), those we chose for this survey fall within the realm of positive natural behaviors, which are behaviors that animals tend to exhibit under natural conditions and because they are pleasurable or promote biologic functioning.²⁵ Behaviors with negative welfare value, in contrast, relate to stress, frustration, abnormal behavior, aggression, and reduced fitness.²⁵ Wild chimpanzees show many types of feeding-related tool use, including nut cracking, termite fishing, honey fishing, and spearing of mammalian prey.^{23,71,83,90} Because tool use is ubiquitous among wild chimpanzees,^{61,83} this is a desirable behavior to encourage in captive conditions.^{65,92}

Wild chimpanzees build nests made from branches and leaves and spend about 12 of every 24 h in their nests.⁸⁴ Some scientists have argued that nesting opportunities should be viewed as an important component of captive chimpanzee environments,⁸⁴ and the NIH Working Group likewise recommended daily provision of materials for nest construction.⁷⁵ Intense social interactions are a hallmark of chimpanzee life and thus were important to measure; grooming behavior is relatively easy to observe and to identify, as is copulation. Copulation has an obvious relationship to individual fitness, is typically shown by all adult chimpanzees, and is sensitive to perturbation by poor social conditions.^{57,86} Social grooming is important to chimpanzees as a primary mechanism for maintaining social relationships,⁴⁶ and active participation in grooming bouts is important for the formation and maintenance of close bonds.⁴² Grooming is negatively influenced by poor welfare conditions, such as early social and perceptual deprivation.^{41,97} Therefore, questions that addressed grooming and copulation were included in the survey.

A wide diversity of abnormal behaviors is well-documented among captive chimpanzees,¹⁰⁰ including stereotypical behaviors, abnormal appetitive behaviors, self-directed abnormal behaviors, and potentially self-injurious behaviors. Abnormal behaviors are those that are not typical of the species in the wild or that occur at very different frequencies in captivity than in the wild.³⁸ Abnormal behaviors are generally regarded as indicators of poor welfare because of their relationship to restrictive environments, deficiencies in the social environment, and insufficient management practices; notably, however, some experts have argued recently that coprophagy in chimpanzees should not be classified as an indicator of poor welfare because it is associated with desirable conditions, such as mother rearing.^{51,54} The survey included questions regarding the occurrence several types of abnormal behaviors in individual chimpanzees.

Positive reinforcement techniques (PRT) have been used to train chimpanzees to cooperate with a variety of husbandry, veterinary and research procedures.^{20,34,58,59} PRT relies on the voluntary participation of the animals, and they receive rewards, such as food, for offering a particular behavior. For example, if the desired behavior is for the chimpanzee to open his or her mouth when a cue is given, then the animal will receive a small piece of food after opening his or her mouth after the appropriate cue is presented.⁸¹ PRT reduces distress experienced by chimpanzees during veterinary-related procedures⁵⁸ and can have positive, generalized, and prolonged effects on behavior beyond the training sessions.⁸² Questions concerning the use of PRT were included in the survey because of these beneficial effects on welfare.

Because sex and early social rearing environments are known to affect behavioral measures of chimpanzee welfare,^{15,27,33,36} these factors were used as independent variables in some of the analyses. In addition, the age of the subjects was assessed as a possible factor, because age alone can affect some welfare-related behaviors.⁶⁶ Age also was considered relevant for this survey, because older research chimpanzees lived in conditions quite different from current conditions, and their prior environments might have altered their behavior long-term. The current size of each chimpanzee's social group was included as an independent variable to determine whether larger groups are associated with beneficial behavioral outcomes.

Materials and Methods

A written questionnaire was sent to each of the 6 research facilities in the United States that house chimpanzees (Yerkes National Primate Research Center, the Southwest National Primate Research Center, the Keeling Center, the New Iberia Research Center, the Alamogordo Primate Facility, and the Language Research Center at Georgia State University). All are AAALAC-accredited facilities. This survey-based research project complied with the appropriate IACUC approval requirements, the *Guide for the Care and Use of Laboratory Animals*,⁵² and the USDA Animal Welfare Regulations¹ assuring humane care and use of the animals. Questionnaires were sent between 2015 and 2017 in a staggered manner, and each facility completed the information for each chimpanzee in their care at that time (see Figure 1 for the survey questions). Individual chimpanzees were indicated as displaying a particular abnormal behavior when the behavior had been observed or recorded within the 2-y period prior to survey completion, thus giving a current assessment of the abnormal behavior profile of each subject.

The following predictors were entered into a logistic regression analysis by using a forward Wald stepwise procedure: sex (reference, female), age (reference, adult), rearing (reference,

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- 1) Provide the following information about your facility:
 - a) Name of facility:
 - b) Enter here the appropriate codes for all forms of information you provide (QBD, quantitative behavioral data; RBM, routine behavioral monitoring information; REC, records such as animal training records or other archived information; OBS, observations by behavioral staff or others; OTH, other [please describe]):
 - 2) List animals housed at your facility and, for each, provide the following information:
 - a) Age (as of 1/1/2016)
 - b) Sex
 - c) Rearing history (majority of the chimp's first 12 months of life):
 - i) MR, mother-reared; NR, nursery-reared; WB, wild-born; UNK, unknown; OTH, other [please describe]
 - ii) Comments on rearing history if needed:
 - d) Current group size (including subject):
 - e) Outdoor access:
 - i) Do they have outdoor access essentially all year (Y/N)?
 - ii) If not, how many months do they have essentially daily access to the outdoors?
 - f) Do they have daily access to a natural substrate (Y/N)?
 - i) List natural substrates they have access to (organic, pliable substrate such as grass, bark, soil, pea gravel):
 - ii) List 'unnatural' substrates they have access to (e.g., cement):
 - g) Behavior: Answer Y or N to the following questions. "Does this chimp ..."
 - i) Use tools to acquire food?
 - ii) Build a nest?
 - iii) Initiate grooming with others?
 - iv) Copulate (NA if not housed with member of opposite sex or if under 5 years of age)?
 - h) Abnormal behavior: Answer Y or N to the following questions. "In the last two years, has this chimp been seen to engage in ..."
 - i) Coprophagy?
 - ii) Regurgitation and reingestion of vomitus?
 - iii) Stereotyped behavior (other than rocking)?
 - iv) Rocking?
 - v) Hair-plucking (self-directed or socially directed)?
 - vi) Other self-directed, abnormal behavior (bizarre posturing, mouth movements, etc.)?
 - vii) Self-injurious behavior WITH wounding (the wounding does not need to be directly witnessed)?
 - i) Training: Answer Y or N to the following questions. "Does this chimp generally voluntarily cooperate with ..."
 - i) For the following, "yes" means the animal generally complies with shifting or separation but does not indicate anything about formal training for shifting or separation:
 - (1) Shifting (moving between different parts of his/her enclosure)?
 - (2) Separation from group members?
 - ii) For the following, "yes" means the animal is trained for this behavior and complies, and "no" means the animal is either not trained or has received training but does not comply:
 - (1) Body examination (e.g. show hands, feet, open mouth, etc.)?
 - (2) Urine collection?
 - (3) Blood withdrawal (using needle/syringe)?
 - (4) Capillary blood sampling or use of lancet (small amount of blood)?
 - iii) For the following, "yes" means the animal cooperated without any threat (e.g., showing dart gun); "no" means that the animal has not been trained for injection, was not offered the opportunity to hand-inject, refused to present for hand-injection or only presented for hand-injection after a threat (e.g., showing dart gun):
 - (1) During most recent attempt to inject this animal with anesthetic, did he/she cooperate?
 - (2) During the most recent attempt to inject this animal with a vaccination or other injectable medication, did he/she cooperate?
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Figure 1. Survey questions.

mother-reared or wild-born), and group size (reference, small groups). We also included all possible interactions in the analyses: sex×rearing, sex×age, sex×group size, rearing×group size, age×rearing, and age×group size. Animals were categorized as immature when they were 11 y or younger, adult when they were 12 to 39 y old, and elderly when they were 40 y or older. Small groups contained 3 to 6 animals; large groups contained 7 or more animals. The rest of the chimpanzees lived in pairs, with one singly housed animal who was included in the 'pair' category for analyses. Animals whose rearing history was unknown were not included in these analyses; this criterion resulted in the removal of 83 chimpanzees ($n = 618$). Each of the species-typical behaviors and each abnormal behavior was analyzed individually, as were

2 summary measures (presence of all 4 species-typical behaviors and presence of 3 or more abnormal behaviors). Of the models reported by each analysis, only models that were significant and passed a goodness-of-fit (Hosmer and Lemeshow [HL]) test were considered; we report the model that retained the most predictors or that accounted for the most variance in the data (according to Cox and Snell and Nagelkerke R^2 analysis). All predictors retained by the selected models are listed, but β values and associated statistics are reported for significant predictors only. Although some of our analyses required the removal of subjects, this study includes every chimpanzee living in a research facility in the United States and thus does not need many generalizations from sample to population.

Early rearing was defined in the survey as the predominant type of social setting during the subject's first 12 mo of life. For example, those animals identified as nursery-reared spent more than 6 of their first 12 mo in a nursery and being raised by humans; they may or may not have also lived with other infant chimpanzees. For many of the analyses, wild-born subjects were categorized with mother-reared subjects because chimpanzees that were captured in the wild and survived transport to the United States were typically older than 1 y (younger infants tended to not survive the experience) and therefore would have met the minimum requirement of at least 6-mo of mother-rearing while living in the wild. This category thus comprises mother-reared or wild-born (MR-WB) subjects. The category of 'not MR-WB' (NOTMR/WB) comprised nursery-reared subjects predominantly but also included a few animals with other, known, rearing backgrounds (for example, in a human home or in the entertainment industry). Many of the NOTMR/WB chimpanzees were nursery-reared because of maternal incompetence that would have led to the death of the infant had there been no intervention by those caring for the animals.

Because the type and amount of observation time was not specified for this project, it undoubtedly varied across facilities, thus potentially leading to variation in the identification of behaviors (that is, observing more would lead to the detection of more infrequent behaviors). Some of the behaviors evaluated required that the subjects had appropriate opportunities to display that behavior. For example, to assess whether a chimpanzee makes a nest, s/he must have been provided with appropriate materials. To assess whether a chimpanzee copulates, we determined that s/he must be at least 5 y old and housed with appropriate social partners. The assessment of tool use excluded those who were not observed with tools or did not have access to tools. Questions regarding PRT did not ask respondents to indicate whether each subject who did or did not perform the behavior had been trained, because this information would be impractical to complete for large numbers of subjects. Instead, the questions focused only on the outcome.

Results

The survey return rate was 100%. Each facility used archival animal records data, observational data, and animal training records to complete the survey. Methods of behavioral assessment varied across facilities (for example, 1–0 sampling of behavioral measures performed quarterly), but similar types of information were collected at all facilities. Data were compiled on 701 chimpanzees ranging from 2 to 62 y old, with a mean age of 26.0 y. Overall, 11.3% of the sample were immature animals, 78.2% were adult, and 10.6% were elderly (Table 1). In addition, 4 of the 49 wild-born animals were adults (3 female, 1 male), and the remaining 45 were elderly (27 female, 18 male); WB, and thus chiefly elderly, animals made up about 16% of the MR-WB group (Table 1).

Housing. Of 701 subjects, 11.1% lived in pairs, 51.9% in small groups, and 36.5% lived in large groups. The median group size was 7 chimpanzees, and the mean group size was 4.6 animals. Group size ranged from 1 to 14; one subject was housed individually. All of the subjects had daily access to outdoor spaces throughout the year (weather conditions permitting). Daily access to a natural substrate in the chimpanzee's enclosure was reported for 63.8% of the subjects. Grass was reported most commonly (43.8%), with soil (24.1%) and pea gravel (14.7%) reported also (some facilities reported multiple substrates). Postsurvey communication with each reporting facility confirmed that all chimpanzees lived in primary housing that was larger than the minimal allowable size.¹

Species-typical behaviors. Tool use. Data regarding tool use was not provided for 95 subjects, but among those for which data were provided ($n = 561$), 94.1% were reported to use tools to acquire food (Table 2). Regression analysis was conducted based on data from subjects with known rearing history and for which data were provided ($n = 523$; Figure 2). The selected model retained the predictors of sex×rearing and age×rearing. This model was significant ($\chi^2[3] = 43.94$, $P < 0.001$) and passed the goodness-of-fit test (HL $\chi^2[1] = 0.86$, $P = 0.354$). The model had a log likelihood of 150.85 and R^2 range of 8.1% (Cox and Snell) to 25.9% (Nagelkerke). According to the model, immature ($\beta = -2.77$, $SE = 0.47$, $Wald(1) = 35.26$, $P < 0.001$) and elderly ($\beta = -2.33$, $SE = 1.17$, $Wald(1) = 4.00$, $P < 0.05$) animals had a lower likelihood of exhibiting tool use than adults if they were also NOTMR/WB, and males also had a lower likelihood of exhibiting tool use than females if also NOTMR/WB ($\beta = -1.22$, $SE = 0.46$, $Wald(1) = 7.03$, $P < 0.01$).

Nesting. The 95 subjects that did not have data provided on nesting were removed from this analysis; of the remaining subjects ($n = 561$), about half (48.1%) were reported to build nests (Table 2). Regression analysis was conducted on all subjects for which data on nesting were provided and rearing history was known ($n = 523$; Figure 3). The selected model retained the predictors of age, sex, rearing, group size, age×sex, and group size×sex. This model was significant ($\chi^2[10] = 293.63$, $P < 0.001$) and passed the goodness-of-fit test (HL $\chi^2[8] = 5.83$, $P = 0.666$). The model had a log likelihood of 431.40 and R^2 range of 43.0% (Cox and Snell) to 57.3% (Nagelkerke). According to the model, immature animals had a lower likelihood of exhibiting nest-building than adults ($\beta = -3.73$, $SE = 0.76$, $Wald[1] = 24.39$, $P < 0.001$), male chimpanzees had a lower likelihood than female ($\beta = -1.71$, $SE = 0.30$, $Wald[1] = 32.14$, $P < 0.001$), NOTMR/WB subjects had a lower likelihood than MR-WB ($\beta = -1.65$, $SE = 0.25$, $Wald[1] = 44.24$, $P < 0.001$), and animals living in large groups were more likely to exhibit nest-building than those living in small groups ($\beta = 1.09$, $SE = 0.39$, $Wald[1] = 7.89$, $P < 0.01$). The retained interactions did not have any significant Wald values associated with predictors.

Initiating grooming. No subjects were missing data regarding grooming, so the prevalence of grooming was assessed for all 701 subjects. Grooming was initiated by 83.3% of the chimpanzees (Table 2). Logistic regression was conducted on the subset for which rearing history was known ($n = 618$; Figure 4). The selected model retained the predictors of sex, rearing, age×sex, and group size×sex. This model was significant ($\chi^2[6] = 94.14$, $P < 0.001$) and passed the goodness-of-fit test (HL $\chi^2[5] = 5.37$, $P = 0.372$). The model had a log likelihood of 400.85 and R^2 range of 14.1% (Cox and Snell) to 25.6% (Nagelkerke). According to the model, male chimpanzees had a lower likelihood than female to initiate grooming ($\beta = -0.96$, $SE = 0.28$, $Wald[1] = 12.15$, $P < 0.001$), and NOTMR/WB subjects had a lower likelihood than MR-WB ($\beta = -1.99$, $SE = 0.35$, $Wald[1] = 32.94$, $P < 0.001$); for elderly animals, being male further reduced the likelihood of grooming ($\beta = -1.35$, $SE = 0.54$, $Wald[1] = 6.21$, $P < 0.05$).

Copulating. Animals that had not had the opportunity to copulate (for example, those in same-sex groups) or who were young (5 y or younger) were not assessed for copulation, resulting in the removal of 162 animals from this analysis. Overall, 75.8% of the remaining chimpanzees ($n = 496$) copulated (Table 2). Regression was conducted on the subset of these animals for which rearing history was known, resulting in a sample size of 456 chimpanzees (Figure 5). The selected model retained the predictors of age, sex, rearing, group size, sex×rearing, and age×group size. This model was significant ($\chi^2[10] = 115.22$,

Table 1. Sex and early rearing status of chimpanzee subjects

	Mother-reared	Wild-born	Not mother-reared or wild-born	Other rearing or unknown	Total
Females	139	30	164	45	378
Males	118	19	148	38	323
Total	257 (36.7%)	49 (7%)	312 (44.6%)	83 (11.9%)	701

Table 2. Occurrence of species-typical behaviors

Group	Uses tools to acquire food	Makes nests	Copulates	Initiates grooming	Shows all 4 species-typical behaviors
Sex					
Female	291/301 (96.7%)	173/301 (57.5%)	227/269 (84.4%)	335/378 (88.6%)	150/268 (56.0%)
Male	237/260 (91.2%)	97/260 (37.3%)	149/227 (65.6%)	249/323 (77.1%)	75/226 (33.2%)
Early rearing					
Mother-reared and wild-born	275/278 (98.9%)	189/278 (68.0%)	229/263 (87.1%)	292/306 (95.4%)	171/263 (65.0%)
Nonmother-reared/wild-born	224/245 (91.4%)	73/245 (29.8%)	127/193 (65.8%)	241/312 (77.2%)	50/193 (25.9%)

Data are given as no. of animals showing behavior / no. of animals evaluated (percentage showing behavior)

Figure 2. Percentage of subjects that use tools, categorized (A) according to early rearing conditions by sex and (B) according to early rearing conditions by age. Categories graphed are those retained by a forward Wald regression.

$P < 0.001$) and passed the goodness-of-fit test (HL $\chi^2[7] = 7.63$, $P = 0.367$). The model had a log likelihood of 364.51 and R^2 range of 22.3% (Cox and Snell) to 34.3% (Nagelkerke). According to the model, immature animals had a lower likelihood of copulating than adults ($\beta = -1.66$, $SE = 0.42$, Wald[1] = 15.39, $P < 0.001$), NOTMR/WB animals had a lower likelihood than MR-WB ($\beta = -0.88$, $SE = 0.41$, Wald[1] = 4.63, $P < 0.05$), chimpanzees living in large groups had a higher likelihood of copulating than those in small groups ($\beta = 3.19$, $SE = 1.02$, Wald(1) = 9.68, $P < 0.01$), but immature animals living in large groups had a lower likelihood than adults ($\beta = -3.57$, $SE = 1.33$, Wald[1] = 7.23, $P < 0.01$).

All 4 species-typical behaviors. Only subjects that had data on all 4 species-typical behaviors were assessed for this summary measure. All 4 of the species-typical behaviors were shown by 45.5% of the 494 chimpanzees with appropriate data. Regression was conducted on the 456 subjects with appropriate data and known rearing history (Figure 6). The selected model retained the predictors of age, sex, rearing, group size, and age×rearing.

This model was significant ($\chi^2[8] = 242.62$, $P < 0.001$) and passed the goodness-of-fit test (HL $\chi^2[8] = 12.67$, $P = 0.124$). The model had a log likelihood of 389.10 and R^2 range of 41.3% (Cox and Snell) to 55.0% (Nagelkerke). According to the model, elderly animals had a higher likelihood of exhibiting all 4 species-typical behaviors than adults ($\beta = 1.19$, $SE = 0.50$, Wald[1] = 5.73, $P < 0.05$), male animals had a lower likelihood than female ($\beta = -1.12$, $SE = 0.26$, Wald[1] = 17.99, $P < 0.001$), NOTMR/WB animals had a lower likelihood than MR-WB ($\beta = -1.84$, $SE = 0.27$, Wald[1] = 45.92, $P < 0.001$), and animals living in large groups had a higher likelihood than those living in small groups ($\beta = 2.88$, $SE = 0.39$, Wald[1] = 54.53, $P < 0.001$).

Abnormal behaviors. General information. Overall, 37.1% of the chimpanzees ($n = 701$) showed one or more abnormal behaviors, and 5% exhibited 3 or more abnormal behaviors. Across the complete sample ($n = 701$), the prevalence of individual abnormal behaviors was: rocking, 13.0%; coprophagy, 10.0%; stereotyped behaviors other than rocking, 9.4%; hair plucking, 8.8%; regur-

Figure 3. Percentage of subjects that build nests, categorized (A) according to early rearing conditions, (B) to group size, (C) to age group and (D) to sex. Categories graphed are those retained by a forward Wald regression.

gitation and reingestion, 7.7%; self-directed abnormal behavior, 7.3%; and self-injurious behavior with wounding, 1.4% (Table 3).

Coprophagy. All subjects with rearing history provided ($n = 618$) were assessed for coprophagy. The selected model retained the predictors of sex, rearing, sex×rearing, and age×rearing (Figure 7). This model was significant ($\chi^2[5] = 73.73$, $P < 0.001$) and passed the goodness-of-fit test (HL $\chi^2[4] = 1.36$, $P = 0.852$). The model had a log likelihood of 362.94 and R^2 range of 11.2% (Cox and Snell) to 22.2% (Nagelkerke). According to the model, male chimpanzees were less likely to engage in coprophagy than female ($\beta = -2.85$, $SE = 0.61$, $Wald[1] = 21.87$, $P < 0.001$) and NOTMR/WB were less likely than MR–WB ($\beta = -1.32$, $SE = 0.34$, $Wald[1] = 14.59$, $P < 0.001$). However, NOTMR/WB male chimpanzees were more likely to show coprophagy than MR–WB males ($\beta = 1.94$, $SE = 0.79$, $Wald(1) = 5.98$, $P < 0.05$) and NOTMR/WB elderly animals were more likely than MR–WB elderly animals ($\beta = 1.65$, $SE = 0.74$, $Wald[1] = 5.06$, $P < 0.05$).

Regurgitation and reingestion. All subjects with rearing history provided ($n = 618$) were assessed for regurgitation and reingestion. The selected model retained the predictors of age and rearing×group size. This model was significant ($\chi^2[4] = 35.53$, $P < 0.001$) and passed the goodness-of-fit test (HL $\chi^2[5]$

$= 0.212$, $P = 0.900$). The model had a log likelihood of 296.98 and R^2 range of 5.6% (Cox and Snell) to 13.4% (Nagelkerke). According to the model, elderly animals had a higher likelihood of exhibiting regurgitation and reingestion than adults ($\beta = 1.21$, $SE = 0.37$, $Wald[1] = 10.64$, $P < 0.005$), and NOTMR/WB animals living in pairs had a higher likelihood than MR–WB animals living in pairs ($\beta = 1.68$, $SE = 0.45$, $Wald[1] = 14.12$, $P < 0.001$).

Stereotypy other than rocking. All subjects with rearing history provided ($n = 618$) were assessed for stereotypy other than rocking. The selected model retained the predictors of rearing and age×rearing. This model was significant ($\chi^2[3] = 36.87$, $P < 0.001$) and passed the goodness-of-fit test (HL $\chi^2[1] = 0.00$, $P = 1.00$). The model had a log likelihood of 334.19 and R^2 range of 5.8% (Cox and Snell) to 12.8% (Nagelkerke). According to the model, NOTMR/WB animals had a higher likelihood than MR–WB animals ($\beta = 1.30$, $SE = 0.35$, $Wald[1] = 13.84$, $P < 0.001$), and elderly NOTMR/WB subjects had a further increased likelihood of engaging in stereotypy as compared with MR–WB elderly chimpanzees ($\beta = 2.46$, $SE = 0.65$, $Wald[1] = 14.16$, $P < 0.001$).

Stereotyped rocking. All subjects with rearing history provided ($n = 618$) were assessed for stereotyped rocking. The selected model retained the predictors of rearing, age by rearing, and age

Figure 4. Percentage of subjects that initiate social grooming bouts, categorized according to (A) sex, (B) early rearing conditions, (C) sex by age and (D) sex by group size. Categories graphed are those retained by a forward Wald regression.

by group size. This model was significant ($\chi^2[7] = 88.17, P < 0.001$) and passed the goodness-of-fit test (HL $\chi^2[3] = 0.223, P = 0.974$). The model had a log likelihood of 417.71 and R^2 range of 13.3% (Cox and Snell) to 23.8% (Nagelkerke). According to the model, NOTMR/WB chimpanzees had a higher likelihood of rocking than MR-WB ($\beta = 1.59, SE = 0.34, Wald[1] = 22.14, P < 0.001$), and this likelihood was further increased for NOTMR/WB immature animals ($\beta = 2.06, SE = 0.38, Wald[1] = 30.01, P < 0.001$). Immature chimpanzees in large groups, however, had a reduced likelihood as compared with immature animals in small groups ($\beta = -1.78, SE = 0.86, Wald[1] = 4.27, P < 0.05$).

Hair plucking. All subjects with rearing history provided ($n = 618$) were assessed for hair plucking. The selected model retained only the predictor of sex×rearing. This model was significant ($\chi^2[1] = 5.35, P < 0.05$), but evaluation using the HL test for goodness of fit was not possible. The model had a log likelihood of 374.93 and R^2 range of 0.9% (Cox and Snell) to 1.9% (Nagelkerke). According to the model, NOTMR/WB male chimpanzees had a lower likelihood of engaging in hair plucking than MR-WB males ($\beta = -0.88, SE = 0.42, Wald[1] = 4.44, P < 0.05$).

Self-directed abnormal behavior. All subjects with rearing history provided ($n = 618$) were assessed for self-directed abnormal

behavior. The selected model retained the predictors of age, rearing, and rearing×group size. This model was significant ($\chi^2[5] = 47.27, P < 0.001$) and passed the goodness-of-fit test (HL $\chi^2[5] = 0.43, P = 0.994$). The model had a log likelihood of 275.15 and R^2 range of 7.4% (Cox and Snell) to 18.1% (Nagelkerke). According to the model, NOTMR/WB animals had a higher likelihood of exhibiting self-directed abnormal behavior than MR-WB ($\beta = 1.41, SE = 0.45, Wald[1] = 9.94, P < 0.005$), and this likelihood was further increased for NOTMR/WB animals living in pairs as compared with NOTMR/WB chimpanzees in small groups ($\beta = 1.56, SE = 0.45, Wald[1] = 11.74, P < 0.005$).

Self-injurious behavior with injury. All subjects with rearing history provided ($n = 618$) were assessed for this measure. The selected model retained only the predictor of sex×rearing. This model was significant ($\chi^2[1] = 9.40, P < 0.005$) but it was not possible to test for goodness of fit. The model had a log likelihood of 76.05 and R^2 range of 1.5% (Cox and Snell) to 11.7% (Nagelkerke). According to the model, NOTMR/WB animals had a higher likelihood than MR-WB of engaging in self-injurious behavior with injury if they were also male ($\beta = 2.29, SE = 0.82, Wald[1] = 7.77, P < 0.01$). Of the 10 cases during the 2-y period assessed for this study, only one required veteri-

Figure 5. Percentage of subjects that copulate, categorized according to (A) sex, (B) age, (C) sex by early rearing conditions and (D) age by group size. Categories graphed are those retained by a forward Wald regression.

nary intervention (for example, sutures, surgical intervention, surgical debridement).

One or more abnormal behaviors. Overall, 37.1% of the 701 subjects were reported to engage in at least one of the abnormal behaviors surveyed. All subjects with rearing history provided ($n = 618$) were assessed further for this summary measure (Figure 8). The selected regression model retained the predictors of sex, sex×rearing, group size×rearing, and age×rearing. This model was significant ($\chi^2[6] = 52.73$, $P < 0.001$) and passed a goodness-of-fit test (HL $\chi^2[4] = 1.07$, $P = 0.900$). The model had a log likelihood of 770.13 and R^2 range of 8.2% (Cox and Snell) to 11.1% (Nagelkerke). According to the model, male animals had a lower likelihood of exhibiting an abnormal behavior than female ($\beta = -1.11$, $SE = 0.25$, $Wald[1] = 19.92$, $P < 0.001$), NOTMR/WB males were more likely than MR-WB males ($\beta = 1.17$, $SE = 0.28$, $Wald[1] = 17.35$, $P < 0.001$), NOTMR/WB chimpanzees in large groups were less likely than NOTMR/WB animals in small groups ($\beta = -0.97$, $SE = 0.31$, $Wald[1] = 10.21$, $P < 0.005$), and NOTMR/WB immature chimpanzees were more likely than MR-WB immature animals ($\beta = 0.75$, $SE = 0.32$, $Wald[1] = 5.56$, $P < 0.05$).

Three or more abnormal behaviors. Only 5.0% of the subjects ($n = 701$) showed 3 or more abnormal behaviors. All subjects with rearing history provided ($n = 618$) were assessed through a regression procedure for this summary measure. The selected model retained the predictors of rearing×age and rearing×group size. This model was significant ($\chi^2[4] = 27.74$, $P < 0.001$) and passed the goodness-of-fit test (HL $\chi^2[2] = 0.006$, $P = 0.997$). The model had a log likelihood of 224.06 and R^2 range of 4.4% (Cox and Snell) to 13.1% (Nagelkerke). According to the model, elderly animals had a higher likelihood of exhibiting 3 or more abnormal behaviors than adult animals if they were also NOTMR/WB ($\beta = 1.77$, $SE = 0.72$, $Wald[1] = 6.08$, $P < 0.05$), and NOTMR/WB animals had a higher likelihood of exhibiting 3 or more abnormal behaviors if they were in either pairs ($\beta = 1.18$, $SE = 0.48$, $Wald[1] = 6.19$, $P < 0.05$) or large groups ($\beta = 1.79$, $SE = 0.53$, $Wald[1] = 11.54$, $P < 0.005$) rather than in small groups.

Positive reinforcement training. Nearly all (97.7%) of the 701 subjects generally voluntarily cooperate with shifting within their enclosure, and 95.4% cooperate with separating from their group members for brief periods ($n = 586$; data were not provided for some subjects). Cooperation with receiving an injection of anesthetic was reported for 72.2% ($n = 701$), and

Figure 6. Percentage of subjects that show all four STBs, categorized according to (A) sex, (B) age, (C) early rearing conditions, (D) group size, and (E) age by early rearing conditions. Categories graphed are those retained by a forward Wald regression.

69.5% ($n = 701$) have been trained to offer at least one body part for examination (that is, show hand or foot when asked). About 1/5 (19.5%, $n = 701$) of the chimpanzees were trained to provide a urine sample, 9.1% ($n = 701$) to cooperate with a capillary blood draw, 7.7% ($n = 561$; data were not provided

for some subjects) to cooperate with an injected vaccination or other medication, and 1.7% ($n = 701$) to cooperate with blood collection by using a syringe.

Table 3. Occurrence of abnormal behaviors (no. showing behavior [%])

Group	Rocking	Coprophagy	Stereotypy other than rocking	Hair pluck- ing	Regurgitation and reingestion	Self- directed	Self-injurious behavior with wounding	At least 1 behavior	3 or more behaviors
Sex									
Female (<i>n</i> = 378)	48 (12.7%)	61 (16.1%)	33 (8.7%)	38 (10.1%)	30 (7.9%)	27 (7.1%)	2 (0.5%)	148 (39.2%)	20 (5.3%)
Male (<i>n</i> = 323)	43 (13.3%)	9 (2.8%)	33 (10.2%)	24 (7.4%)	24 (7.4%)	24 (7.4%)	8 (2.5%)	112 (34.7%)	15 (4.6%)
Rearing									
Mother-reared and wild-born (<i>n</i> = 306)	14 (4.6%)	50 (16.3%)	12 (3.9%)	36 (11.8%)	19 (6.2%)	8 (2.6%)	1 (0.3%)	96 (31.4%)	10 (3.3%)
Nonmother- reared/ wild-born (<i>n</i> = 312)	74 (23.7%)	20 (6.4%)	43 (13.8%)	21 (6.7%)	28 (9.0%)	37 (11.9%)	7 (2.2%)	141 (45.2%)	22 (7.1%)

Discussion

The current study collated information on a variety of measures relevant to chimpanzee welfare and included all of the chimpanzees living in research laboratories in the United States. The survey assessed a larger sample of chimpanzees living under human care than has been published previously. Because of this comprehensive subject pool, many of the chimpanzees were undoubtedly subjects in published studies that were conducted at United States research facilities that we cited here as comparisons, so it is important to note that the subject pools are not independent.

Nearly every chimpanzee living in a research facility is socially housed. This finding is significant because social housing is such an important component of supporting chimpanzee wellbeing.^{14,74} There was a single exception to this rule, so 0.14% of the United States research chimpanzee population was individually housed at the time of survey completion. This figure represents a notable reduction in single housing since a previous survey, when 7.6% (*n* = 93) of the chimpanzees at research facilities were individually housed.¹⁷ One reason for this reduction is the cessation of biomedical research with chimpanzees,⁵³ which sometimes required periods of single housing. Other reasons may be an increase in research conducted on socially housed subjects, the retirement of singly housed chimpanzees to sanctuaries, and the development of methods to treat illnesses in chimpanzees while they are socially housed (for example, by training them to cooperate with treatment). However, it is worth noting that biomedical research was being conducted in 2004 when the previous survey was performed, and even then, more than 90% of the chimpanzees were socially housed.¹⁷ The NIH's Working Group Report recommended that "[u]nless dictated by clearly documented medical or social circumstances, no chimpanzee should be required to live alone for extended periods of time" (p 21).⁷⁵ With more than 99.0% of the research chimpanzee population currently socially housed, this objective seems to have been met.

Chimpanzees in United States research facilities are socially housed, but the size of their social groups is smaller than might be recommended. The mean group size was 4.6 animals, and the median was 7, with the largest group having 14 members. The Working Group Report (2013) recommended at least 7 animals per group. Only 36.5% of chimpanzees lived in groups of 7 or more, and the largest portion (51.9%) lived in groups of 3 to 6 animals. For comparison, in 2017, the 260 chimpanzees living in all 32 of the United States zoos accredited by the American

Zoological Association⁸⁷ had a mean group size of 6.8 animals, a median group size of 6, and a range of 2 to 15 group members. Only 2 of these zoo chimpanzees were housed in a pair. These group sizes are influenced by several zoos that used a 'fission-fusion' management approach, with fluid group membership that varied from day to day. These groups were coded as being 2 smaller groups rather than a single, larger one. The most notable difference between zoos and research facilities in terms of group size is the higher proportion of pairs housed in research facilities (11.1% compared with 0.8%). The median group sizes were quite similar across the 2 types of facilities, as was the range of group sizes. The mean group size in the research setting was smaller than in the zoo setting (4.6 animals compared with 6.8, respectively).

Wild chimpanzees live in large communities with 40 to more than 100 members.^{22,46} With a fission-fusion social structure, they spend most of their time in much smaller traveling parties with fluid membership, typically with 4 to 8 chimpanzees per party.²² Some authors have suggested that captive chimpanzee groups should mimic these traveling parties given that large, static groups are not species-typical for wild chimpanzees.⁸⁴ However, captive groups of 20 or more chimpanzees have successfully been managed in research facilities, zoos, and sanctuaries. The Chimpanzee Care Manual² recommends a group size of at least 3 adult male animals and 5 adult females and dependent offspring. The Working Group recommendation was that "[c]himpanzees must have the opportunity to live in sufficiently large, complex, multi-male, multi-female social groupings, ideally consisting of at least 7 individuals" (p 21).⁷⁵ These recommendations for group size are not based on published literature, because the relevant research projects have not been conducted. A recent conference presentation reported on behavioral differences between groups of different sizes (more or fewer than 7 members) and found that both affiliative and abnormal behaviors were higher in the larger groups and that other behaviors were unaffected by group size.⁸⁵ More data are needed to fully identify optimal or acceptable group sizes for chimpanzees and the needed characteristics of available space to support those groupings.

Research chimpanzees in the United States all have access to the outdoors on a daily basis. Our findings reflect an increase in the percentage of chimpanzees at research facilities housed with access to the outdoors since an earlier survey, which found that 7.6% of them lived indoors only.¹⁷ Some evidence suggests—albeit not strongly—that outdoor housing improves chimpanzee

Figure 7. Percentage of subjects that show coprophagy, categorized according to (A) sex, (B) early rearing conditions, (C) sex by early rearing and (D) age by early rearing. Categories graphed are those retained by a forward Wald regression.

wellbeing.^{6,99} In general, it is difficult to unambiguously evaluate the effect of living outdoors on primate behavior, given that outdoor access is typically confounded by size and complexity of the enclosure, complexity of the social group, and by husbandry routines and research procedures that may affect behavior.⁴⁰ One group⁶ assessed the behavior of 25 chimpanzees, only 13 of which were living indoors, so the sample size is modest, and the information is only available as a published abstract. Regardless, they found that chimpanzees with outdoor access showed less abnormal behavior, less yawning, more self-grooming, and more activity than those living indoors. These preliminary findings are promising, but a complete manuscript has not been published, and the type of enclosure and social group varied between the indoor and indoor-outdoor settings. Another study⁹⁹ found that chimpanzees housed indoors used enrichment less than those housed in indoor-outdoor enclosures. However, there was an age confound such that more of the chimpanzees housed indoors were older, and it has been demonstrated that age influences enrichment use.^{18,65} Studies of other NHP have found increases in species-typical behavior^{31,78} and reductions in abnormal behavior^{7,40} associated with outdoor housing, but again, confounding factors do not allow strict conclusions regarding the role that outdoor housing plays in promoting welfare. Despite the lack

of compelling scientific data, there is a common perception that outdoor housing is beneficial, and the Working Group Report indicates that “[c]himpanzees must be housed in environments that provide outdoor access year round” (p 22).⁷⁵ This recommendation is clearly met.

The Working Group further recommended that chimpanzees “should have access to natural substrates, such as grass, dirt, and mulch, to enhance environmental complexity” (p 22).⁷⁵ Approximately 2/3 of the research chimpanzees lived on such surfaces on a daily basis. This situation is beneficial, because these substrates provide environmental complexity; encourage foraging, activity, and play; and reduce abnormal behavior.^{3,26} Although the majority of research chimpanzees have this opportunity, not all do, and this provision should be encouraged as a future enhancement. It is notable that all of the research chimpanzees lived in primary housing that was larger than the minimal allowable size.

Two of the species-typical behaviors surveyed were tool use and nest building. Nearly all (94.1%) of the chimpanzees surveyed used tools to acquire food. Staff at chimpanzee research facilities have developed and used enrichment opportunities that facilitate tool use for many years,⁶⁵ and considerable research in tool use has been conducted with these chim-

Figure 8. Percentage of subjects that show some type of abnormal behavior, categorized according to (A) sex, (B) early rearing conditions by sex, (C) early rearing conditions by group size, and (D) early rearing by age. Categories graphed are those retained by a forward Wald regression.

panzees.⁵⁰ Both of these activities have probably contributed to the widespread tool capabilities in this population. Some rearing-associated effects were found for tool use, such that male chimpanzees were less likely than female animals to use tools when they were NOTMR/WB, and younger and elderly chimpanzees were less likely to use tools than adults when they were NOTMR/WB. These negative effects of nonmother rearing on tool use are consistent with other published literature.²⁸ Since tool use involves social learning or social facilitation,^{62,96} it is unsurprising that MR and WB subjects would be more likely to acquire this skill. Half (48.1%) of the research chimpanzees make nests, and females were more likely to make nests than males. This sex-associated difference is not species-appropriate, because essentially all wild adult chimpanzees make nests.⁸⁴ MR–WB subjects were more likely than NOTMR/WB to make nests, and immature chimpanzees were less likely to do so than adults. Finally, chimpanzees living in large groups were more likely to construct nests than those living in small groups. Previous studies found that adult chimpanzees who do not make nests and are then housed with or near others who do make nests still did not readily learn to do so themselves.^{9,10} Even when nesting materials were provided 25 times over several

months, none of the nonnest-builders learned to produce a nest.¹⁰ In one study, wild-born chimpanzees built and used nests significantly more than captive-born, and captive-born, mother-reared subjects spent more time building and using nests than nursery-reared animals.⁹⁸ Because experience with bedding materials as adults did not change this finding, the author concluded that nest building requires early experience and practice.⁹⁸ With less than half (44.5%) of the research chimpanzee population being mother-reared or wild-born, it is possible that NOTMR/WB animals will simply not learn to build nests, at least not through mere exposure to successful nest-builders and appropriate materials. Although the possibility has not been empirically tested, PRT techniques might be helpful, reinforcing chimpanzees as they manipulate nesting materials and thus shaping the behaviors required to successfully build a nest. Scaffolding the chimpanzees' behavior in this way could make it possible to 'teach' adult animals to successfully engage in some species-typical behaviors, assuming they are not entirely instinctive behaviors (see the discussion following). The Working Group Report recommendation that "[c]himpanzees must be provided with materials to construct new nests on a daily basis"⁷⁵ (p 23) cannot be fully evaluated through the current

study because the survey focused on individual behavior and did not ask about the provision of nesting materials.

The species-typical social behaviors that were queried were copulating and initiating grooming. A vast majority of the research subjects (83.3%) initiate grooming bouts with conspecifics. About 3/4 of the subjects older than 5 y and with access to an opposite sex partner ($n = 496$) copulate. In an archival study of a much smaller sample of zoo-housed chimpanzees, 75% of the subjects exhibited functional copulatory behavior,⁵⁷ mirroring the result in the research population. In one study,⁵⁷ 93% of zoo chimpanzees that lived with their mothers for at least their first year did copulate as adults, but only 50% of those separated from their mothers before 1 y of age copulated as adults. Of research chimpanzees that were mother-reared for at least 6 mo of their first year, 87.1% copulated compared with 65.8% who were not mother-reared. Again, research chimpanzees' copulation behavior shows a similar pattern to zoo-living chimpanzees.

MR-WB chimpanzees were more likely to initiate grooming and to copulate than NOTMR/WB animals. In addition, males were less likely than females to initiate grooming, and within males, age had an additional effect, such that elderly male chimpanzees were less likely than adult males to initiate grooming. Young animals were less likely to copulate than adults, but for immature chimpanzees, living in large social groups increased the likelihood of copulation over that of immature animals in small groups. Results of the current survey therefore parallel earlier findings,⁴¹ in which chimpanzees with less exposure to other chimpanzees during infancy showed a lower frequency of sexual behavior and grooming later in life. It is encouraging that the vast majority of research chimpanzees express these important social behaviors. However, given the substantial minority that does not, it is important to continue efforts to elicit these behaviors.

Ideally, all captive chimpanzees would show all 4 of the species-typical behaviors surveyed, but in the current population, only 45% ($n = 494$) did. The presence of all 4 behaviors was more likely for females (compared with males), elderly chimpanzees (compared with adults), MR-WB animals (compared with NOTMR/WB), and chimpanzees living in large groups (compared with small groups). Male animals, particularly those not reared by their mothers, are more negatively affected than females: only 14% of NOTMR/WB male chimpanzees for whom we had appropriate data ($n = 90$) exhibited all 4 behaviors, while 35.9% of NOTMR/WB females did. It is possible that this sex-associated difference is a result of differential social learning tendencies, given that females have been reported to develop socially learned skills at younger age than do males,⁶¹ to watch behavior being modeled more than males, and to copy models' techniques more conservatively,^{61,63} implying a less goal-directed style of learning. The mechanisms of social learning in chimpanzees, perhaps particularly for male animals, may be based on a more functional understanding of a demonstrated task's goal.⁷³ When the goal of a behavior is not obvious or not clearly desirable, this situation could interfere with learning behaviors such as copulation or nest-building. In other words, perhaps it is not that male, nursery-reared chimpanzees cannot learn to make nests or to copulate but rather that they are not sufficiently motivated to do so. PRT could perhaps address this gap by providing a clear, valued reward for engaging in the appropriate behavior (for example, nesting) until, ideally, the chimpanzee finds the well-built nest to be its own reward. Using PRT in this novel manner could contribute to improving welfare by facilitating the expression of a natural and positive behavioral pattern. This possibility may be worth investigation, because the

potential benefits are of high value and because prior research has shown that PRT can increase natural behaviors, such as social grooming, even outside of training sessions.⁹¹ Once the behavior is 'trained,' social grooming seems to be reinforced without external reward (such as food treats).

Identifying factors that underlie abnormal behaviors can improve our understanding of primate welfare and our ability to distinguish between abnormal behaviors that reflect poor welfare and those that may not.⁵¹ The measures of prevalence of abnormal behavior gathered in the current study do not reflect the frequency, duration, or intensity of these behaviors, and all of these features are important to consider when evaluating welfare.⁷⁷ In the current survey, about 1/3 (Table 3) of the research center chimpanzees showed some type of abnormal behavior in the 2 y prior to survey completion, and a small portion (5%) showed 3 or more abnormal behaviors.

The most common abnormal behavior was stereotyped rocking (13%), and early rearing effects were pronounced: only 4.6% of the MR-WB subjects rocked, whereas 23.7% of the NOTMR/WB subjects did. An effect of age was also evident, given that young chimpanzees who were NOTMR/WB were more likely to rock than adult NOTMR/WB animals, and young chimpanzees living in large groups were less likely to rock than young chimpanzees living in small groups. Stereotyped rocking has often been found to be associated with socially restrictive early rearing,^{8,36,68,69} although other factors also influence its expression.⁸⁰ Although stereotyped rocking typically develops at a young age, it may persist in adolescent and adult chimpanzees.^{35,37} Stereotypies such as rocking may serve to help an animal cope with environmental conditions that are suboptimal,⁷⁰ such as nursery-rearing and social restriction,⁶⁸ and once they have developed, they will persist as a response to encountered stressors.^{93,97}

In contrast to our findings, other studies identified coprophagy as the most common abnormal behavior in zoo-housed and research-facility-housed chimpanzees,^{12,54,68,74} and this behavior was much more prevalent in those samples than in the current sample (Table 4). Some of this difference is undoubtedly accounted for by the greater proportion of mother-reared animals in zoo populations^{12,54} (see following discussion), but a 1999 study of research chimpanzees also revealed higher rates.⁷⁴ The lower rate in the current study may be due to improved enrichment practices that reduce coprophagy.^{13,21,43} Although coprophagy may not be associated with poor welfare conditions such as nonmother-rearing, and thus is argued to be less reliable as a general welfare indicator than abnormal behaviors such as rocking or self-directed behaviors,⁵¹ it is still not a desirable behavior, particularly at high frequencies. Coprophagy or seed reingestion from feces has been reported in multiple wild communities of chimpanzees, although at much lower frequencies than are observed in captive chimpanzees. Coprophagy has been posited to be an adaptive strategy to maximize nutritional intake in certain conditions,^{11,79} but in captivity, where it is much more pervasive than in wild chimpanzee populations, it may be more likely to contribute to parasitic and bacterial disease transmission through a fecal-oral route of exposure with less benefit as from a nutritional deficiency.

The prevalence of hair plucking in the current study is lower than in others (Table 4), including a 2016 study⁵⁴ that used the same methodology. Other colleagues reported that 16.4% of the research chimpanzees they studied pulled their own hair, and 6.0% pulled from another animal.⁷⁴ Assuming none of the previous subjects did both, the sum would be 22.4%, showing a hair-pulling rate which is still lower than the rates reported

Table 4. Prevalence of various abnormal behaviors in chimpanzees in other published studies

	1 or more abnormal behaviors (including coprophagy)	1 or more abnormal behaviors (excluding coprophagy)	Coprophagy	Hair plucking (self or other)	Regurgitation and reingestion
Current data (research facilities)	37.1%	32.5%	10.0%	8.8%	7.7%
Reference 4 (research facilities)			33.2%	22.4% (maximum possible)	5.6%
Reference 12 (zoos)	100.0%		83.0%	78.0% (maximum possible)	30.0%
Reference 54 (zoos)	64.0%	48.0%	41.0%	32.0%	7.0%
Reference 56 (former research animals)			72.0%		
Reference 68 (former research animals)			37.7%		

in zoos. In addition, the previously cited study⁷⁴ reports higher numbers for this behavior than in the current study, and both studies defined hair-plucking in the same way. It is possible that, like coprophagy, the lower rates in the current study are due to improved enrichment and management practices, some of which have been shown to reduce hair plucking.¹³ Hair plucking directed toward oneself and toward others has been observed in many primate species across different settings.^{60,64}

The prevalence of regurgitation–reingestion was similar across several studies, including the current one, although higher rates were reported elsewhere¹² (Table 4). This finding may indicate that regurgitation–reingestion is not socially influenced, given that populations with more mother-reared subjects do not have higher prevalence rates of regurgitation. This contrasts with coprophagy which is affected by the social setting, as described earlier. Regurgitation–reingestion is related to feeding practices^{5,95} and animal training techniques have been applied to reduce it.⁷²

Self-directed abnormal behaviors (for example, bizarre posturing, self-clasping) did not vary with sex, but NOTMR/WB subjects were more likely to show these behaviors than MR–WB chimpanzees. This rearing effect is consistent with literature on other NHP.^{64,77} Previous research has found that self-directed abnormal behaviors were more widespread among chimpanzees that had been individually housed earlier in life as compared with those that were individually housed at later stages in their development,⁵⁶ generally corroborating our finding that early social environment affects self-directed behaviors.

Self-injurious behavior is a very concerning behavioral problem.⁷⁶ It has a strong relationship to early life stressors (for example, early removal from mother, indoor rearing), individual housing, and more chronic, stressful experiences, such as repeated room moves and blood withdrawals.^{47,76} With only 10 of 701 subjects showing this behavior, our findings are tentative, but did corroborate prior research. Across our subjects, we found that NOTMR/WB animals were more likely to show this behavior, but only if they were also male. This possible male bias had been noted previously.⁴² Unfortunately, self-injurious behavior may function to reduce arousal and is often resistant to treatment,⁷⁶ although comprehensive and intensive treatment may be successful.²⁴

Zoo-housed chimpanzees may have a higher prevalence of abnormal behavior than chimpanzees in United States research facilities. Higher rates of coprophagy in zoo populations account for some of this difference, but when those chimpanzees that showed only coprophagy were removed from the sample (reference 54 values in Table 4), there were still proportionally more zoo subjects showing abnormal behavior than in the current dataset. The “hypothetical average individual” in a 2011 zoo-based study¹² showed 5 different abnormal behaviors, and all subjects had at least 2, which again are higher values than the current findings (although see reference 88 for a critique of the methods in reference 12 study). Another possible explanation for reported differences between zoo and research facility behavioral patterns is that the facilities use different observational methods. Survey methods like the current study are susceptible to bias relating to the amount of behavioral observation that is done: facilities that conduct more observation of their chimpanzees would report more of the infrequently occurring behaviors. Although we are doubtful there is a systematic bias between the 2 facility types, it would be valuable to have more precise information regarding observational methods, the amount of time observing each individual, and staff training in behavior at each facility. The somewhat surprising result that more zoo chimpanzees show abnormal behavior than research chimpanzees will be addressed in an upcoming analysis (Bloomsmith and colleagues).¹⁶

Many abnormal behaviors in chimpanzees are influenced by early rearing history,^{41,55,74} and this was confirmed by the current analysis. In some cases, nonmother rearing seemed to have impact even within a particular subset of individuals, so, for example, males who were also NOTMR/WB might be more likely to engage in a particular behavior than males who were MR and WB, even if generally males were already more likely to engage in that behavior than females. Nonmother rearing was associated with more showing any abnormal behavior if subjects were males, with more stereotyped rocking, more nonrocking forms of stereotypy, more regurgitation/reingestion, more self-directed behaviors and more self-injurious behavior. Coprophagy was generally more common among MR and WB subjects, but the effects varied with sex, because NOTMR/WB male chimpanzees were more likely to engage in coprophagy than were MR–WB males, and with age, because

elderly NOTMR/WB animals were more likely than elderly MR and WB to do so. Other studies have likewise found that MR–WB chimpanzees are more likely to engage in coprophagy than NOTMR/WB,^{16,51,54,74} but the reverse effect of rearing on males' coprophagy has not been revealed in smaller samples. Hair-plucking was higher among MR and WB male chimpanzees than NOTMR/WB males, although the lack of goodness of fit of our model indicates that unmeasured influences may be present. One previous study⁷⁴ found that self-hairplucking was more prevalent in mother-reared subjects than nonmother-reared, which is somewhat consistent with our findings. When an abnormal behavior seems to be more prevalent in mother-reared animals, one possible explanation is that mother-reared chimpanzees have greater exposure to other chimpanzees that engage in coprophagy than nonmother reared chimpanzees and that the behavior is socially learned. Social learning has been implicated in the development of abnormal behavior in chimpanzees.⁴⁹ However, socially learned abnormal behaviors may not be indicators of negative welfare,⁵¹ thus complicating the usual assumption that when abnormal behavior of any kind is observed, it signals negative welfare, past or present.^{51,74} Environmental factors related to welfare, however, may be important in the origin of a potentially socially learned and socially transmitted abnormal behavior like coprophagy. These factors need to be understood, both to reduce currently expressed abnormal behavior and to prevent undesirable behaviors from appearing in the first place, from which point they may be socially transmitted. For example, methods of feeding captive apes have been shown to influence coprophagy and regurgitation–reingestion, and can be modified to reduce these behaviors.^{13,21,43,72}

Although male chimpanzees were more likely to show abnormal behavior than female animals, this effect appears to be driven only by females being more likely to show coprophagy than males. This female bias in coprophagy corroborates other findings^{54,56,74} and may be related to a female bias for social learning.⁶¹ Although male biases may have been reported for abnormal behavior in other primates,⁴⁷ this situation may not be the case for chimpanzees. For example, earlier studies^{80,93} found no sex-associated difference in stereotyped rocking in chimpanzees, and the current finding confirms that outcome. It is also possible that sex alone is insufficient to significantly affect abnormal behaviors except when combined with an additional factor, such as early rearing, and we did find such effects for hair-plucking and self-injurious behavior. However, in both of these cases, we were unable to find a good-fitting model that was based on our set of predictors, indicating that some mechanism other than sex, rearing, age, and group size influenced the behavior, or that the behavior itself may have more than one etiology and form.

Age affected the prevalence of abnormal behavior in a few situations. Elderly subjects were more likely to show regurgitation–reingestion than adult subjects, and early rearing had a significant effect within the elderly subset, such that NOTMR/WB elderly chimpanzees were more likely to show stereotypical behavior and coprophagy than MR and WB elderly animals. In addition, early rearing had a significant effect on immature subjects, such that NOTMR/WB immature subjects were more likely to exhibit any abnormal behavior and to exhibit rocking behavior than immature chimpanzees that were mother reared. Furthermore group size affected abnormal behavior in some cases. For example, within the category of immature animals, stereotyped rocking was more likely for those that also lived in small groups rather than large groups. Moreover, group size interacted with early rearing to influence abnormal behavior,

such that regurgitation–reingestion and self-directed abnormal behavior were more prevalent among pair-housed chimpanzees when they were also NOTMR/WB.

The voluntary cooperation of chimpanzees with routine husbandry activities, veterinary procedures, and research procedures has been greatly enhanced since the early 1990s,¹⁷ when the use of PRT techniques was implemented more widely. PRT is now a well-established refinement in chimpanzee care, and it has improved the ease and efficiency of captive chimpanzee management,²⁰ reduced chimpanzee distress related to research and veterinary procedures,⁵⁸ decreased abnormal and stress-related behaviors in captive chimpanzees,⁸² and, lastly, reduced aggressive behavior in captive chimpanzees.¹⁹ Findings from the current survey indicate that PRT is well-established at research facilities in the United States. The high percentage of chimpanzees that cooperate with receiving an injection of anesthetic (72.2%) and with presentation of body parts for examination (69.5%) is evidence that these approaches can be effective on a widespread basis. Biologic sample collection behaviors (for example, urine and blood collection) had been trained in far fewer subjects, perhaps reflecting an infrequent need for those samples. An earlier survey of 6 chimpanzee research facilities found that 5 of the 6 facilities had formal chimpanzee training programs that relied primarily on PRT and which had been established prior to 2004.¹⁷ Evidence from the current survey indicates that this sustained effort has been successful in enhancing chimpanzee welfare, given that the vast majority of research chimpanzees cooperate with receiving injections for veterinary care; with shifting, separating from group members, and other movements required to facilitate husbandry-related procedures; and with at least some body examination behaviors that facilitate veterinary care. This progress is relevant to the Working Group Report recommendation that “[p]ositive reinforcement training is the only acceptable method of modifying behaviors to facilitate animal care and fulfillment of management needs [...] and progress toward achieving established benchmarks should be documented” (p 24).⁷⁵ Although the current survey did not address this recommendation in detail (that is, did not ask about each subject's training history regarding queried behaviors), it is clear that PRT techniques are widely used and that a major effort has been directed toward gaining cooperation with a variety of husbandry and research-related procedures. It is probable that some of the chimpanzees that currently present for injection learned to do so prior to the establishment of PRT based programs and that they learned to present through negative reinforcement or coercion (for example, being ‘squeezed’ in a transfer box or shown a dart gun, respectively). However, it is highly unlikely that this situation accounts for the high percentage of animals (72.2%) reported to voluntarily present for anesthetic injection in this survey. Similarly, although it is possible that animals complying with requests to shift, separate, or present body parts have not been formally trained to do so, it is highly unlikely that they would comply with these requests at such high rates without positive reinforcement for doing so. So, although the data presented here may not reflect the results of only formal, PRT-based training, the high levels of compliant animals indicate that PRT is being widely used with chimpanzees in research facilities.

In conclusion, chimpanzees at research facilities in the United States are socially housed, have daily access to outdoor spaces, and have been trained using positive techniques to cooperate with a variety of procedures. Just under half of these chimpanzees show all 4 key species-typical behaviors recorded (tool use, nest building, copulating, initiating grooming bouts),

and about one-third of them show some type of abnormal behavior. This broad, survey-based analysis can help to guide future improvements in chimpanzee behavioral management to address behavioral problems or deficits. For instance, based on the finding that only half of the chimpanzees make nests, strategies should be developed to facilitate this behavior. Providing the remaining one-third of the population who does not have daily access to a natural substrate with this opportunity would be advantageous to their welfare. The mean group size was 4.6. Such small social groups are not species-typical and are not recommended by some experts because these group sizes do not facilitate important complexities in chimpanzee social interactions. Others have suggested that there may be a threshold for the number of chimpanzees that can live constantly together in compatible captive groups. Further study of group size and welfare is warranted, but reducing the number of research chimpanzees living in pairs or trios is a laudable goal for research chimpanzees. Each of the additional improvements suggested here will require additional resources and personnel effort. Although it is not possible to change the early rearing histories of the current population, the findings underscore the wide-ranging importance of providing early mother rearing for chimpanzees. Less than half of the population of research chimpanzees is mother-reared, and this characteristic affected the display of many behaviors. It is notable that early rearing had such substantial effects given that it was operationalized within the first year of life. That first year had profound and lasting influences on multiple behavioral measures of welfare. Comparing this type of welfare-related information for chimpanzees across settings (research centers, sanctuaries, zoos, privately owned facilities) will provide a more in-depth understanding of captive chimpanzee welfare in the United States, and we are working toward that goal.

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