



Published in final edited form as:

*Am J Primatol.* 2022 June ; 84(6): e23380. doi:10.1002/ajp.23380.

## Nonhuman Primate Abnormal Behavior: Etiology, Assessment, and Treatment

Corrine K. Lutz<sup>1,\*</sup>, Kristine Coleman<sup>2</sup>, Lydia M. Hopper<sup>3</sup>, Melinda A. Novak<sup>4</sup>, Jaine E. Perlman<sup>5</sup>, Ori Pomerantz<sup>6</sup>

<sup>1</sup>Institute for Laboratory Animal Research, The National Academies of Sciences, Engineering, and Medicine, Washington DC

<sup>2</sup>Oregon National Primate Research Center, Oregon Health and Science University, Beaverton, OR

<sup>3</sup>Department of Molecular and Comparative Pathobiology, Johns Hopkins University School of Medicine, Baltimore, MD

<sup>4</sup>Department of Psychological and Brain Sciences, University of Massachusetts, Amherst, MA

<sup>5</sup>Yerkes National Primate Research Center, Emory University, Atlanta, GA

<sup>6</sup>California National Primate Research Center, University of California, Davis, CA

### Abstract

Across captive settings, nonhuman primates may develop an array of abnormal behaviors including stereotypic and self-injurious behavior. Abnormal behavior can indicate a state of poor welfare, since it is often associated with a suboptimal environment. However, this may not always be the case as some behaviors can develop independently of any psychological distress, be triggered in environments known to promote welfare, and be part of an animal's coping mechanism. Furthermore, not all animals develop abnormal behavior, which has led researchers to assess risk factors that differentiate individuals in the display of these behaviors. Intrinsic risk factors that have been identified include the animal's species and genetics, age, sex, temperament, and clinical condition, while environmental risk factors include variables such as the animal's rearing, housing condition, husbandry procedures, and research experiences. To identify specific triggers and at-risk animals, the expression of abnormal behavior in captive nonhuman primates should be routinely addressed in a consistent manner by appropriately trained staff. Which behaviors to assess, what assessment methods to use, which primates to monitor, and the aims of data collection should all be identified before proceeding to an intervention and/or treatment. This

---

Corresponding Author: Corrine Lutz, Institute for Laboratory Animal Research, The National Academies of Sciences, Engineering, and Medicine, 500 Fifth Street NW, Washington, DC 20001, corrinelutz8@gmail.com.

\*This manuscript was initiated prior to the author's current affiliation. The views expressed in this manuscript are those of the author and do not necessarily reflect the views or policies of the Institute for Laboratory Animal Research or the National Academies of Sciences, Engineering, and Medicine.

Data Availability Statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

Conflict of Interest

Lydia M. Hopper and Corrine K. Lutz are members of the Editorial Board for this journal. Otherwise, the authors have no conflict of interest to report.

article provides guidance for this process, by presenting an overview of known triggers and risk factors that should be considered, steps to design a comprehensive evaluation plan, and strategies that might be used for prevention or treatment. It also outlines the tools and processes for assessing and evaluating behavior in an appendix. This process will lead to a better understanding of abnormal behavior in captive primate colonies and ultimately to improved welfare.

## Graphical Abstract



## Keywords

behavioral observation; intervention; risk factors; welfare; wellbeing

---

## 1. Introduction

Abnormal behavior in nonhuman primates (“primates” hereafter) is often broadly defined as behavior that deviates qualitatively or quantitatively from behaviors performed by conspecifics in their natural habitat (see Erwin, 1979 for an example). While commonly used, this definition can be somewhat misleading, as it implies that wild animals only engage in “normal” behavior. Further, there is not always a distinction between normal and abnormal behavior, as some abnormal behaviors may be repetitive or misdirected forms of normal behavior (Bayne, 1996; Mason, 1993; Mason, 1991). Abnormal behavior is a

heterogeneous group of behaviors that are often stereotypic and share certain characteristics, including a deviation from a standard such as species-typical behaviors shaped by natural selection or the average levels of the behavior exhibited by conspecifics maintained in captivity (see Novak and Meyer 2021). Importantly, these behaviors can indicate a state of poor welfare, since they are often associated with a suboptimal environment or atypical rearing (Gottlieb et al., 2015; Lutz, Well, & Novak, 2003; Vandeleeest et al., 2011), and thus are of concern to those caring for the animals.

Despite being widely used as indicator of poor welfare, abnormal behavior may be beneficial to the animal if it is a part of a coping strategy (Mason & Latham, 2004; Mason, 1991; Mason & Turner, 1993). However, the absence of abnormal behavior does not necessarily indicate good welfare (Mason & Latham, 2004). Abnormal behavior may also be a maladaptive response due to an underlying clinical disorder or psychopathology, resulting in conditions such as self-injury (Bayne & Novak, 1998; Novak et al., 2012; Novak & Suomi, 2008). Finally, abnormal behavior may be unrelated to the animal's current welfare state if it becomes habitual or an automatic response that persists long after the initial trigger has ended (for examples see: Lutz et al., 2004; Mason & Latham, 2004; Pomerantz, Paukner, et al., 2012). Therefore, abnormal behaviors may not be reliable welfare indicators and can be difficult to mitigate with simple alterations to the environment (Mason & Latham, 2004).

Abnormal behavior is displayed by many species of captive primates across various settings (Berkson et al., 1966; Bloomsmith et al., 2020; Capitanio, 1986; Lutz, Well, & Novak, 2003; McGrogan & King, 1982; Nash et al., 1999; Vandeleeest et al., 2011; Walsh et al., 1982). Given the aforementioned variation in their etiology and presentation, care should be taken in their interpretation. In this article we describe abnormal behaviors to aid in their identification, outline risk factors and triggers, present methods that can be used for monitoring and evaluation within individuals and populations, and suggest preventative measures and treatment. To provide practical advice, we also outline the tools and processes for assessing and evaluating behavior in an appendix.

## 2. Classification and Identification

Abnormal behaviors in primates are often idiosyncratic, varying in form, frequency, and context (Bayne & Novak, 1998; Mason, 1993). However, they can still be classified by type, comorbidity, and/or severity.

### 2.1 Classification by Type

When classifying by type, behaviors are often grouped into categories, such as motor stereotypes, self-directed behavior, appetitive behavior, self-injurious behavior (SIB), and withdrawn behavior (described below). For more detailed definitions of abnormal behaviors, see Baker et al., (2017).

**2.1.1 Motor stereotypes:** repetitive movements of either part or all of the body, which can include behaviors such as pacing, swinging, rocking, bouncing, or flipping (Bauer & Baker, 2016; Bayne & McCully, 1989; Capitanio, 1986; Crast et al., 2014; Gottlieb et al., 2015; Lutz, Well, & Novak, 2003; Lutz, 2018; Vandeleeest et al., 2011).

**2.1.2 Self-directed abnormal behaviors:** those that are focused on the animal's own body, such as hair plucking, periorbital contact (also called "saluting" or "eye poking"), self-clasping, or self-oral behaviors (Bauer & Baker, 2016; Crast et al., 2014; Lutz, Well, & Novak, 2003; Lutz, 2018; Thierry, 1984).

**2.1.3 Abnormal appetitive behaviors:** those associated with food, urine or feces, such as food smearing, regurgitation, urophagy, coprophagy, feces painting, or hair eating (Akers & Schildkraut, 1985; Capitanio, 1986; Crast et al., 2014; Gould & Bres, 1986; Lutz, 2018; Nevill & Lutz, 2015).

**2.1.4 SIB:** a behavior in which an individual either causes, or has the potential to cause, a self-inflicted injury that may require veterinary care; however, actual injury is relatively rare (Anderson & Chamove, 1980; Lutz, Well, & Novak, 2003; Novak, 2003; Novak, 2020). Examples of SIB include head banging, self-biting, self-hitting/slapping, and wounding due to aggressive hair plucking, and excessive wound picking (Bauer & Baker, 2016; Crast et al., 2014; Gottlieb, Capitanio, et al., 2013; Hosey & Skyner, 2007; Lutz, Well, & Novak, 2003; Lutz, 2018; Rommeck, Anderson, et al., 2009), with wounding severity differing markedly across individuals (Freeman, Krall, et al., 2015; Novak, 2020).

**2.1.5 Withdrawn behavior:** significantly reduced locomotor activity for a prolonged period and a lack of apparent interest in their environment. These animals tend to remain sitting with their heads tucked into their chest for much of the day. Taken together, these features are generally suggestive of depressive-like states (Ferdowsian et al., 2011; Hennessy et al., 2014; Lopresti-Goodman et al., 2013; Shively et al., 2008).

## 2.2 Classification Based on Comorbidity

This type of classification focuses on the co-occurrence of abnormal behaviors, rather than applying a phenotypic categorization approach (Hopper et al., 2016). A recent study with macaques reported four alternative categories of abnormal behaviors based on comorbidity between the behaviors (Polanco et al., 2021). The first category included self-biting, self-hitting, floating limb, leg lifting, and self-clasping. The second category included twirling, bouncing, rocking, swinging, and hanging. The third category included pacing and head-twisting, while the fourth category included flipping and eye poking. Additionally, self-sucking, hair-plucking, threat-biting, and withdrawn were considered to be individual behaviors and not included in any of the above categories (Polanco et al., 2021).

## 2.3 Classification by Degree of Severity

Abnormal behaviors can also be classified according to the severity of the behavior on a continuum ranging from mild (e.g., occurring at low levels or at discrete times), to moderate (e.g., occupying a greater portion of the animal's time, often interfering with the display of normal behavior), to severe (e.g., causing actual physical harm or injury to the animal; Bayne & Novak, 1998; Novak et al., 2006). Severe forms of abnormal behavior can be pathological as they are often disruptive, intense, and cause tissue damage (Bayne & Novak, 1998; Novak et al., 2012; Novak & Suomi, 2008). Even in settings where the percentage of animals exhibiting abnormal behavior is relatively high, abnormal behavior often only

constitutes a small portion of the animals' overall time budgets (Birkett & Newton-Fisher, 2011; Crast et al., 2014; Marriner & Drickamer, 1994). Therefore, understanding the severity of the behavior and its impact on the animal's health and wellbeing is key to determining the type of intervention to utilize and when to implement it.

### 3. Risk Factors

It is important to identify the intrinsic and extrinsic risk factors for abnormal behavior in order to determine appropriate management practices as well as intervention and prevention procedures. However, underlying causes of the development and expression of abnormal behaviors are not always known, and the cumulative effect of experiences, both positive and negative, can impact subsequent behavior (Polanco, 2021). Additionally, the presence of one or more risk factors does not mean that the animals will necessarily develop or exhibit abnormal behavior, but instead increase the probability that the behavior will occur. In the next section we consider the various risk factors known to increase the likelihood that captive primates will exhibit abnormal behaviors.

#### 3.1 Intrinsic

**3.1.1 Species**—Studies have revealed differences in the extent to which various primate species exhibit abnormal behaviors, as well as the form of the abnormal behaviors most likely to be expressed. For example, a survey of 108 zoos reported that 40% of apes, 14% of catarrhine monkeys, 6% of platyrrhine monkeys, and 7% of prosimians exhibited some form of abnormal behavior (Bollen & Novak, 2000). Similarly, a survey focusing on prosimians reported a significant effect of genus on abnormal behaviors presented; those in the genera *Varecia* and *Microcebus* were more likely to exhibit stereotypies than were those of other genera (Tarou et al., 2005). Similarly, when comparing three species of monkeys in research facilities, those in the genus *Macaca* exhibited higher overall levels and different patterns of abnormal behavior than those in the genus *Papio* (Lutz, 2018). There are also species differences in the type of abnormal behavior that is most commonly expressed. Coprophagy was reported to be the most common behavior in chimpanzees (*Pan troglodytes*; Birkett & Newton-Fisher, 2011; Jacobson et al., 2016; Nash et al., 1999), while regurgitation/reingestion was the most common in bonobos (*Pan paniscus*; Brand & Marchant, 2018). Further, motor stereotypies, such as pacing, were the most common in macaques, mangabeys, and prosimians (Bellanca & Crockett, 2002; Crast et al., 2014; Lutz, Well, & Novak, 2003; Lutz, 2018; Pomerantz, Paukner, et al., 2012; Tarou et al., 2005), but motor stereotypies and abnormal appetitive behavior were reported to occur at an equal level in baboons (*Papio hamadryas spp.*; Lutz, 2018). Thus, it appears that the species' natural biology plays a role in the ability to successfully cope with the challenges they encounter in captivity and the abnormal behaviors they express in response to such stressors.

**3.1.2 Age**—The form and frequency of expression of some abnormal behaviors may change as animals age (Mason, 1993). For example, self-sucking and rocking are commonly observed in nursery-reared infants, but these behaviors tend to decrease with age (Cross & Harlow, 1965; Pazol & Bloomsmith, 1993). More physically active motor stereotypies, such as pacing, body flipping, and swinging, also tend to be more common in younger than older

animals (Gottlieb, Capitanio, et al., 2013; Gottlieb et al., 2015; Lutz, Well, & Novak, 2003), while older animals typically exhibit self-directed behaviors that are less physically active, such as eye poking or covering, hair pulling, and SIB (Kroeker et al., 2014; Lutz, Well, & Novak, 2003; Thierry, 1984). However, although age-related patterns in abnormal behavior are common, they are not universal (Birkett & Newton-Fisher, 2011; Brand & Marchant, 2015; Hook et al., 2002; Less et al., 2013; Tarou et al., 2005).

**3.1.3 Sex**—As with age, some studies have found differences in the rate of expression of abnormal behavior between females and males. For example, male monkeys tend to display motor stereotypy (Gottlieb, Capitanio, et al., 2013; Lutz, Well, & Novak, 2003; Lutz, 2018; Vandeleest et al., 2011), abnormal appetitive behavior (Lutz et al., 2014), self-directed behavior (Lutz, Well, & Novak, 2003; Thierry, 1984), and SIB (Gottlieb, Capitanio, et al., 2013; Lutz, Well, & Novak, 2003) more often than females. Similarly, zoo-housed male bonobos were reported to be more likely to perform the poke anus abnormal behavior than females (Laméris et al., 2021). However, female mangabeys and chimpanzees were reported to exhibit greater levels of abnormal behavior than were males (Crast et al., 2014; Fritz et al., 1992; Hook et al., 2002; Jacobson et al., 2016; Nash et al., 1999) and in other studies, including those of prosimians, monkeys, and apes, no overall sex difference in abnormal behavior was reported (Birkett & Newton-Fisher, 2011; Hill, 2018; Less et al., 2013; Marriner & Drickamer, 1994; Tarou et al., 2005).

**3.1.4 Temperament**—An animal's temperament or personality can also play a role in the display of abnormal behavior. For example, bolder rhesus monkeys (*Macaca mulatta*, as tested via a novel-object test), were more likely to exhibit motor stereotyped behavior than those with an inhibited temperament (Gottlieb et al., 2015). Similarly, systematic biobehavioral assessment found that individuals scoring low on gentle temperament were also more likely to exhibit motor stereotypy (Gottlieb, Capitanio, et al., 2013). However, additional factors likely play a part as well. Another study reported that scoring high on gentle and nervous temperament during the same battery of tests was indeed a risk factor for motor stereotypy, but only in indoor-reared monkeys (Vandeleest et al., 2011). The different results obtained by these studies may be due to differences in the demographics of the study subjects, the variables chosen for analysis, or the way in which temperament was assessed (Gottlieb, Capitanio, et al., 2013). A more recent study with bonobos revealed a number of relationships between the expression of different abnormal behaviors and the apes' rating on four personality components (Laméris et al., 2021). For example, bonobos that scored low on "activity" and "sociability" performed coprophagy more frequently. In spite of the interest in individual differences for enhancing primate care, these studies reveal the paucity of research considering links between temperament and the presentation of abnormal behaviors and the importance of taking an individually tailored approach to primate care when possible (Coleman, 2012).

**3.1.5 Clinical Condition**—Abnormal behavior could also be a symptom of an underlying medical condition. In one case study of a chimpanzee who engaged in SIB, it was theorized that the behavior was, in part, associated with neuropathic pain because, in addition to other interventions, pharmacological treatment of the neuropathic pain reduced

the SIB (Bourgeois et al., 2007). Similarly, a rhesus monkey reported for self-injury was also diagnosed with neuropathy (Clemmons et al., 2015). Another example of clinical conditions being linked to abnormal behavior comes from rhesus macaques with retinal disease that were reported to exhibit eye poking and saluting behaviors, especially when in bright lighting conditions (Moshiri et al., 2019). Therefore, when evaluating behavioral expression, it is crucial to rule out any underlying clinical conditions that give rise to the behavior, prior to determining whether it reflects psychological distress.

## 3.2 Extrinsic

**3.2.1 Rearing history**—An animal's rearing condition plays a pivotal role in subsequent behavior. This has been conclusively demonstrated by early studies of total- and partial-isolation-rearing. In these studies, infant macaques were raised without any social contact and, as a result, developed an array of abnormal behaviors that lasted through adulthood (Baysinger et al., 1972; Berkson, 1968; Cross & Harlow, 1965; Davenport & Menzel, 1963; Mitchell et al., 1966; Suomi et al., 1971). In later studies of primates that included prosimians, monkeys, and apes, infants reared by humans in a nursery were shown to be at a significantly greater risk of developing and displaying higher levels of abnormal behavior than infants reared by their mother in social groups (Dettmer et al., 2012; Freeman & Ross, 2014; Jacobson et al., 2016; Mallapur & Choudhury, 2003; Marriner & Drickamer, 1994; Pirovino et al., 2011). Nursery-reared primates present a variety of abnormal behaviors, including self-directed behaviors, repetitive body movements, and SIB (Bauer & Baker, 2016; Bellanca & Crockett, 2002; Bloomsmith & Haberstroh, 1995; Conti et al., 2012; Dettmer et al., 2012; Dienske & Griffin, 1978; Fritz et al., 1992; Gottlieb, Capitanio, et al., 2013; Laméris et al., 2021, Marriner & Drickamer, 1994; Rommeck et al., 2006; Rommeck, Gottlieb, et al., 2009). Self-biting has been reported to occur as early as 32 days of age in nursery-reared rhesus macaques (Rommeck, Gottlieb, et al., 2009), and many of these abnormal behaviors often continue into adulthood (Bauer & Baker, 2016; Bourgeois et al., 2007). The type of nursery rearing can also play a role in subsequent behavior. For example, infant rhesus macaques housed in continuous full social contact with similar aged peers exhibited significantly less abnormal behavior than infants that were housed with only limited (intermittent) social contact with peers (Conti et al., 2012; Lutz et al., 2007); however, they also showed higher levels of partner clinging (Rommeck, Gottlieb, et al., 2009) and prolonged anxious behavior (Dettmer et al., 2012).

The relationship between early experience and later behavior may be explained by the Integrated Developmental-Neurochemical hypothesis which states that adverse early experiences followed by later stressful events can result in the dysregulation of neuropeptide and neuroendocrine systems. This dysregulation can then lead to heightened anxiety and the expression of abnormal behavior, which may serve as a coping mechanism (Tiefenbacher et al., 2005). Although the focus of this hypothesis is on self-biting, it provides a basis for better understanding the development and function of abnormal behavior in general. Similarly, chronic exposure of animals to unsuitable environments has been linked to long lasting neurological alterations that may be manifested in the expression of abnormal behaviors (Würbel, 2001). For example, Bogart and colleagues (2014) found that nursery-reared chimpanzees had significant anatomical differences in the development of cortical

organization compared to mother-reared conspecifics. Additional studies have demonstrated that the expression of stereotypic behavior may result from basal ganglia malfunction (e.g., Pomerantz, Paukner, et al., 2012).

While the relationship between nursery rearing and the development of abnormal behaviors is well established, in chimpanzees, coprophagy has been reported to be performed at higher rates by mother-reared individuals (Bloomsmith & Haberstroh, 1995; Freeman & Ross, 2014). Furthermore, a recent study with zoo-housed bonobos found that wild-born individuals exhibited a higher diversity of abnormal behaviors as compared to captive-born individuals (Laméris et al., 2021) and a previous study of sanctuary-housed orphaned bonobos and chimpanzees reported that these individuals had lower rates of abnormal behaviors as compared to mother-reared individuals in zoo settings (Wobber & Hare, 2011). It has, therefore, been posited that social learning may play a role in the expression of certain abnormal behaviors (Hopper et al., 2016; Less et al., 2013).

**3.2.2 Social Environment**—The percentage of animals exhibiting abnormal behavior is often notably high in singly-housed, as compared to socially-housed, primates (Camus et al., 2013; Crast et al., 2014; Lutz, Well, & Novak, 2003; Lutz, 2014). Moreover, such effects appear in both apes and monkeys (Brent et al., 1989; Gottlieb, Capitanio, et al., 2013; Gottlieb et al., 2015) and the same patterns are revealed across settings. For example, in a survey of 630 zoo-housed primates, 40% of the animals housed alone, 5% of paired animals, but none of the animals housed in groups of four or more exhibited abnormal behavior (Trollope, 1977). In addition, single housing at both an early age and for an extended period of time are risk factors for increased levels of abnormal behavior (Bellanca & Crockett, 2002; Crast et al., 2014; Lutz, Well, & Novak, 2003; Lutz, 2014).

**3.2.3 Physical Environment**—While both the macro and microenvironment have been shown to influence the animal's behavior and welfare (Morgan & Tromborg, 2007), in the following section we will focus on the microenvironment. With respect to cage size, it is typically thought that 'bigger is better.' When moved from standard research indoor housing to larger and more enriched play cages (Griffis et al., 2013) or semi-free ranging outdoor enclosures (Reamer et al., 2010), monkeys show increases in activity coupled with decreases in abnormal behaviors. The reduction in rates of motor stereotypy associated with increased cage sizes may well reflect that species-typical needs are better met, as research has shown a positive correlation between captive primates' pacing rates and their species' typical day journey lengths in the wild (Pomerantz et al., 2013). However, it appears, that relatively small changes in cage size have only minimal, if any, impacts on rates of abnormal behavior (Crockett et al., 1995; Draper & Bernstein, 1963; Line et al., 1990; Paulk et al., 1977). Furthermore, as outdoor cages are often larger than indoor cages, and larger cages typically offer more physically and socially complex environments, it can be challenging to tease apart the relative impact of cage size, location, and complexity on primates' behavior and welfare.

Specific characteristics of the space are also important to consider. For example, while motor stereotypies were shown to significantly decrease in common marmosets (*Callithrix jacchus*) when they were moved to larger enclosures (Yoshimoto et al., 2018), a previous



study had shown that simply providing these arboreal monkeys with increased vertical space also reduced motor stereotypies (Kitchen & Martin, 1996). Further, for primates living in research facilities, it has been demonstrated that the location of the cage within the room also plays a role in the likelihood to express abnormal behavior. Those individuals housed in bottom cages and/or near the room entry door (where animals are exposed to more activity) exhibited higher levels of stereotypic behavior and SIB (Gottlieb, Capitanio, et al., 2013). The amount of control afforded within that space can also influence the presentation of abnormal behaviors. Captive primates with no control over their environment express higher rates of abnormal behaviors (Buchanan-Smith, 1997; Maple & Finlay, 1986), while increased opportunities for control is associated with reductions in abnormal behavior (Bloomsmith et al., 1988; Videan et al., 2005).

**3.2.4 Clinical, Research, and Husbandry procedures**—Chronic exposure to common captive animal management practices can play a role in the development of abnormal behavior. Clinical procedures such as anesthesia events and blood draws were associated with an increase in motor stereotypies, self-directed behaviors, and SIB in rhesus macaques (Lutz, Well, & Novak, 2003; Vandeleest et al., 2011). Similarly, motor stereotypies increased by 5% for every research project to which an animal was assigned (Gottlieb, Capitanio, et al., 2013). However, invasiveness of the research projects was not a significant predictor for abnormal behavior in male pigtailed macaques (*Macaca nemestrina*; Bellanca & Crockett, 2002), and there was no association between the number of blood draws and abnormal behavior in sooty mangabeys (*Cercocebus atys*; Crast et al., 2014). Likewise, some studies have shown that husbandry practices such as relocation to new rooms within a facility, pair separations and cage sanitation have influenced the development of abnormal behavior (Gottlieb, Capitanio, et al., 2013). However, husbandry procedures may not always play a role (Lutz, Well, & Novak, 2003; Lutz, 2014).

## 4. Prevention

It is well established that once started, abnormal behaviors can be difficult to resolve (e.g., Novak et al., 2012), and thus, whenever possible, efforts should be aimed at improving primates' welfare and therefore preventing such behaviors from developing in the first place. Although few studies have explicitly examined prevention approaches, the studies mentioned above have identified intrinsic and environmental risk factors that can result in increased levels of abnormal behavior. By better understanding the environmental risk factors, we can work to improve captive conditions and ameliorate the impact of stressors. This can be achieved with a behavioral management program that prioritizes functionally appropriate environments (Bloomsmith, Hasenau, et al., 2017), a positive reinforcement training program, and continued staff education on the behavioral biology of each species. Additionally, husbandry practices similar to those previously described as risk factors for the *development* of abnormal behavior (e.g., relocation to a novel room, separation from cage mates, and routine husbandry procedures) can also serve as *triggers* for abnormal behavior in animals that have already developed the behavior (Cassidy et al., 2020; Davenport et al., 2008; Gottlieb, Coleman, et al., 2013; Lutz, Marinus, et al., 2003; Novak, 2003; Snyder et al., 1984; Suomi et al., 1975; Truelove et al., 2017; Waitt & Buchanan-Smith, 2001).

Therefore, recognizing potential risk factors and triggers and trying to reduce or eliminate them will help to improve environmental conditions, which will, in turn, enhance the primates' welfare and help to lessen or prevent the development of abnormal behavior.

## 5. Assessment

In instances in which an animal has already developed an abnormal behavior, the form and severity of that behavior must be assessed in order for an effective treatment strategy to be developed (see Appendix for a further description of assessment procedures). The measurement of abnormal behaviors not only allows for an assessment of welfare, but also serves as a tool to evaluate the efficacy of interventions and treatments and to better understand the underlying causes of such behaviors in order to help prevent them from occurring. These data can also be useful when addressing questions posed by accrediting and inspection agencies, identifying abnormal behavioral trends in certain sub-groups of populations (e.g., singly-housed primates or animals assigned to various research protocols), and following colony-wide management adjustments, such as increases in enrichment distribution (Perlman et al., 2018). Organization and review of these data may trigger follow up individual assessments and corresponding clinical and behavioral treatment. Additionally, such monitoring is demanded by, for example, the USDA's Animal Welfare Act (AWA) regulations (USDA, 2017), and the Association of Zoos and Aquariums (AZA), which require that facilities observe animals frequently and assess their health, behavior, and welfare. Demographic and life history events should also be documented to help determine different extrinsic and intrinsic risk factors that may contribute to the expression of the behavior (Rommeck et al., 2006).

### 5.1 Self-Injurious Behavior (SIB) With and Without Wounding

Because SIB typically occurs at low frequencies within a population, it may be especially difficult to identify and monitor. However, as SIB can result in self-inflicted wounds, in some cases it can be detected by observation of the resultant wounds as well as by direct observation of the behavior. Any injuries need to be reported in a timely manner to the veterinary team for clinical assessment, and to those responsible for behavioral care. Measurement of self-inflicted wounding should include the number of wounds, wound severity, wounding location on the body, and frequency of wounding. A wounding scale that standardizes ratings and definitions should be used (Baker et al., 2017; Cronin et al., 2020; Leeds et al., 2015). Measures of behavior should also be collected to assess self-biting behavior frequency and duration, triggers, and to evaluate the effectiveness of treatments. Some individuals that present with self-inflicted injuries may never be observed exhibiting self-injurious behavior, thus making it difficult to identify environmental triggers, if there are any. In such cases, the use of remote observations may be informative (Stanwicks et al., 2017).

### 5.2 Stereotypic and Repetitive Behaviors

Behavioral observations can be useful in detecting the type, duration, frequency, and triggers of stereotypic and repetitive behaviors. Some abnormal behavior, such as pacing, typically have a longer duration than others (e.g., head twirling), and therefore may be easier

to detect and monitor. Furthermore, such behaviors may represent anticipatory behaviors (Gottlieb, Coleman, et al., 2013; Watters, 2014) that are suppressed by the arrival of staff personnel, so remote monitoring may enable detection of these behaviors. In addition to direct observation, automated monitoring or the use of accelerometers may be used to detect full body movements (Papailiou et al., 2008).

### 5.3 Self-Directed Abnormal Behaviors

As with pacing, self-directed behaviors such as periorbital contact and self-sucking typically have longer durations and may be relatively easy to detect and monitor. In contrast, self-directed hair plucking can be more challenging to observe (Perlman et al., 2016). Hair-plucking can be monitored indirectly by measuring hair loss (alopecia), but Lutz and colleagues (2013) demonstrated that self-directed hair pulling played only a minor role in alopecia cases. Because a variety of factors are known to produce hair loss in primates (Beisner & Isbell, 2009; Novak & Meyer, 2009), behavioral observations are important to help determine the root cause of hair loss and the presence of hair plucking.

### 5.4 Abnormal Appetitive Behavior

Feces painting is not always directly observed, but the behavior can be indirectly monitored by the amount of feces spread on cage surfaces (Gottlieb et al., 2014). For socially-housed primates, individuals can be given different colored fecal dyes to help identify which group members perform the behavior (Fuller et al., 2011). In contrast, the detection of urine drinking and regurgitation and reingestion (R/R) is less obvious unless directly observed. Distinct postural movements provide visual detection of R/R in some great apes (Akers & Schildkraut, 1985). Regurgitate may also be found on the floor of the enclosure giving indirect evidence of the behavior. In cases of excessive urine drinking, a urine dipstick test may be needed to identify potential cases of glucosuria (Bayne et al., 1992).

### 5.5 Withdrawn Behavior

Withdrawn behavior includes a slumped body posture (head below shoulders), with open eyes, accompanied by a lack of responsiveness to environmental events (Shively et al., 2008). It should be noted that although this behavior can be long in duration, it can also be difficult to identify, because it looks like normal sleeping or rest behavior. Because the animal is typically not responsive to the environment, withdrawn behavior can be monitored in-person or via video.

## 6. Treatment Approaches

A wide range of treatment options are available, including, but not limited to, environmental enrichment, social housing, positive reinforcement training, and drug therapy, all of which are discussed below in relation to the type of abnormal behavior. Typically, the animals of greatest concern are those with severe forms of abnormal behavior. These animals likely require some intervention or treatment to alleviate their condition. The kind of treatment chosen depends on several factors, including the behavior of concern (e.g., SIB typically requires a different treatment modality than stereotypy), the needs of the animal, and the context in which the behavior arises (see Section 6.5 for more details). Treatment

elements may be prescribed singularly, in combination with other elements, during specific events, and times of day (Bourgeois et al., 2007; Whittaker, 2005). Targeted modifications of the animal's environment and operational procedures can further enhance treatment effectiveness (Whittaker et al., 2001). Importantly, too, the efficacy of any treatment should be evaluated. This can be done via behavioral observations and/or measures of physiological health and psychological wellbeing. Using the aforementioned observation and testing techniques described in the Appendix can provide a framework for such evaluations.

## 6.1 Environmental Enrichment

Enrichment items, such as bedding, puzzle feeders, forage trays, and toys, have all been found to be effective in reducing abnormal behavior in certain circumstances (e.g., Swaisgood & Shepherdson, 2005). Enrichment increases opportunities to engage in species typical behavior, thereby reducing boredom and frustration which can lead to the development of abnormal behaviors. Cognitive research can also offer enrichment opportunities (Clark, 2011; Ross, 2010). For example, cognitively challenging computer tasks have been found to reduce levels of stereotypies and other behavioral problems in macaques (Lincoln et al., 1995; Platt & Novak, 1997; Washburn & Rumbaugh, 1992) and baboons (Fagot et al., 2014), as well as promoting species typical activity budgets in chimpanzees (Yamanashi & Hayashi, 2011). Enrichment can also promote well-being by engaging multiple sensory systems and providing variation of stimuli (Coleman & Novak, 2017; Wallace et al., 2013; Wells et al., 2006). Moving animals from indoor to sensory complex outdoor environments has been found to reduce self-injurious behavior and stereotypy in both single and group-housed rhesus macaques (Fontenot et al., 2006). In indoor environments, porches or verandas, cage extensions that hang on the outside of the cage and provide enhanced visual access have been found to be highly effective in reducing feces painting (Gottlieb et al., 2014) and stereotypy (KC pers observation, although see Lutz & Brown, 2018).

While effective in certain situations, enrichment has limitations as a treatment for abnormal behavior. First, the benefits are often only effective while the enrichment is present (e.g., Lutz & Farrow, 1996), often because utilizing the enrichment item is incompatible with the abnormal behavior; an animal cannot simultaneously pace and eat from a puzzle ball secured to the front of the cage. Animals often resume the abnormal behavior after they have become habituated to the enrichment (in the case of toys) or after it has served its purpose (i.e., there is no more food present in the case of a puzzle ball). Further, while relatively useful for treating abnormal repetitive behaviors, at least in the short term, enrichment is less effective as a treatment for self-injurious behavior (Novak et al., 1998; see also Novak, 2020).

## 6.2 Social Enrichment

Although many studies examining the effects of social housing and abnormal behavior have been correlative, there have been some studies that have explicitly examined the role of social housing on abnormal behavior. In the laboratory environment, pair housing was found to reduce abnormal behaviors, including stereotypies, self-directed behavior, and SIB in macaques and baboons (Baker et al., 2012; Bourgeois & Brent, 2005). Social housing is not necessarily a panacea; in at least one study, the pair housing of rhesus macaques resulted

in only a temporary reduction in stereotypical behavior (Doyle et al., 2008). The benefits of social housing are likely dependent on several factors such as the tenure or cohesion of the social group or pair (e.g., Cassidy et al., 2020). Even in situations in which social housing does not significantly reduce the occurrence of abnormal behaviors, appropriate socialization may still help prevent the escalation of the behavior or the development of other, more concerning, abnormal behaviors. As stated above, the role inadequate socialization has in the development of abnormal behavior cannot be overstated.

Conspecific cage mates are not the only individuals that can promote social companionship for primates; captive primates are influenced by conspecific and heterospecific primates in adjacent cages as well as by humans (Hopper, 2021). Positive interactions with trusted care takers have been found to decrease abnormal oral behaviors such as regurgitation and reingestion in chimpanzees (Baker, 2004; although see Chelluri et al., 2013). Care must be taken, though, as the presence of unfamiliar or untrained people can lead to an increase in abnormal behavior in certain animals. Several studies have found that large numbers of visitors can lead to an increase in stereotypic behavior in zoo-housed primates (Mallapur et al., 2005; Wells, 2005), although the data are inconsistent and likely mediated by exhibit design, crowd behavior, and species (Bonnie et al., 2016; Hansen et al., 2020; For reviews see Fernandez et al., 2009; Sherwen & Hemsworth, 2019). Similarly, even individuals or small groups of unfamiliar people, such as regulatory inspectors or contractors, can lead to an increase in stereotypy in primates, highlighting the need for continued training of those working with or near captive primates (Rennie & Buchanan-Smith, 2006).

### 6.3 Positive Reinforcement Training

Another potential behavioral management strategy that can help reduce abnormal behavior is positive reinforcement training (PRT). PRT is a type of operant conditioning in which the trainer increases the expression of desired behaviors (e.g., presenting a body part) by rewarding the subject when it performs the behavior (e.g., Pryor, 2002). In addition to desensitizing animals to various procedures, and reducing the stress and fear associated with these procedures (Bassett et al., 2003; Clay et al., 2009; Lambeth et al., 2006; Schapiro et al., 2003), PRT also provides subjects with the choice to cooperate with the procedures, and thus provide some environmental control (Laule et al., 2003). There is evidence to suggest that PRT can reduce abnormal behavior in rhesus monkeys (Baker et al., 2010; Coleman & Maier, 2010), baboons (Bourgeois & Brent, 2005), and apes (Carrasco et al., 2009; Leeds et al., 2016; Pomerantz & Terkel, 2009), although other studies have not found this relationship (Baker et al., 2010). While PRT is often time consuming, and thus may not be feasible in all situations, it confers several other advantages to both humans and primates, including compliance with procedures, increased safety and decreased stress (e.g., Bliss-Moreau et al., 2013; Coleman et al., 2008; 2012; Graham et al., 2012; Veeder et al., 2009). Treatment success relies heavily on the working understanding of animal training techniques by the trainer and the provision of the time and tools from managers (Bloomsmith et al., 2007; Perlman et al., 2012). However, caution must be taken to ensure that staff do not inadvertently train the animal to engage in an undesired behavior (Hopper, 2021). If primates are rewarded, with either treats or human attention, for exhibiting abnormal

behaviors, they may be more likely to engage in that behavior going forward (see Dorey et al., 2009 for an example).

#### 6.4 Pharmacological Treatment

Pharmacotherapy is an additional form of treatment for abnormal behavior (As reviewed in Kummrow & Brüne, 2018). A wide range of drugs, including synthetic steroids (Eaton et al., 1999), GABA receptor agonists (Tiefenbacher et al., 2005), and those that target opioidergic (Kempf et al., 2012; Lee et al., 2015), serotonergic (Fontenot et al., 2005; Watson et al., 2009; Weld et al., 1998), or adrenergic (Freeman, Rice, et al., 2015; Macy et al., 2000) neurotransmitter systems, have been utilized as treatment options. This range of pharmacological treatments reflects the various trajectories by which abnormal behavior can develop. However, with drug therapy, abnormal behavior is typically reduced, rather than eliminated, and the effects are often not sustained beyond treatment duration (Kummrow & Brüne, 2018). Additionally, because of the potential for side effects, interactions with experimental treatments (e.g., difficulties in treating animals used in gut microbiota studies with antibiotics, Ramirez et al., 2020), and the ability to mask the effects of the studied variable(s) (McKinney et al., 1980), pharmacotherapy is typically used as a last resort. Because there is also a lack of standardized doses (Kummrow & Brüne, 2018) and the response to treatment can vary greatly across animals (Tiefenbacher et al., 2005), therapeutic strategies must be tailored to both the animal and the situation.

#### 6.5 When to Treat

The decision about whether or not to treat a primate exhibiting abnormal behavior should be based on several factors, including the behavioral issue, the context in which the behavior presents, the severity and duration of the behavior, and whether or not the behavior interferes with other functions, such as eating or socializing. Additionally, for severe cases, having clear endpoints in place is critical. For example, a monkey that paces a few minutes right before mealtime (Gottlieb, Coleman, et al., 2013) might not warrant intervention to the same extent as a monkey that exhibits SIB. When deciding whether or not to treat, and which treatment to use, it is important to look at the whole animal and not just at the behavior. Thus, a monkey that picks at a scab until it starts to bleed has caused an injury, and thus could be classified as wounding himself. However, this does not necessarily mean that it would benefit from treatment. Similarly, if a monkey has surgery on his upper arm and starts biting at that arm soon after, the biting may likely be a response to pain as opposed to a behavioral problem per se. Treatment may well be warranted in this case, but the monkey may benefit more from a pain medication than an anti-depressant (see Hutchinson et al., *In prep*). Overall, captive primate behavioral managers will want to make sure that the treatment fits the behavior and that they are only treating when necessary. However, there may be individual variability in responses to treatments. Therapeutic interventions that are effective in one individual are not necessarily effective in another, making the treatment of abnormal behavior quite challenging (Tiefenbacher et al., 2005).

## 7. Caveats and Considerations

The expression of abnormal behavior has traditionally been viewed as a result of a mismatch between environmental conditions and the set of behavioral tools that animals can employ to successfully address those conditions (Zala & Penn, 2004). Such failure to cope has been demonstrated to induce reductions in both fitness and welfare states. However, despite the wide use of this category of behaviors as measures of welfare, there are three major caveats that need to be considered when using abnormal behavior for this purpose.

First, there are many behaviors that fall into the category of abnormal behavior, with a vast heterogeneity of phenotypic expressions accompanied by a wide range of suggested etiologies (Nash et al., 1999). It would, therefore, be reasonable to ask whether all share a similar value as welfare indicators (e.g., Pomerantz, Paukner, et al., 2012), or if they should even be considered part of this category (Hopper et al., 2016), for example in cases when abnormal behaviors are socially learned (Hopper, 2017). Second, in the same way that the umbrella term abnormal behavior encompasses a vast array of behaviors, there is also significant variation across individuals in the rate at which they express certain abnormal behaviors, or the severity of those behaviors. Thus, those interested in understanding and characterizing primate welfare should not only consider the behavioral phenotype but also the rate of expression. Third, one needs to consider the role of behavioral plasticity and the ability to adapt to novel environmental conditions as fundamental elements of primates' coping mechanisms (Mason et al., 2013). Species-typical behaviors have been acquired through natural selection and enable animals to react to, and gain better control of, their environment. Can abnormal behaviors serve a similar purpose? It has been argued that those captive animals that express certain forms of abnormal behavior, such as motor stereotypies, may have superior levels of welfare compared to those that do not, due to their ability to cope with the challenges they face in that environment (Mason & Latham, 2004; but, see Broom, 2019 for an opposing view).

To date, only a few studies with a stated goal to tease apart the differential value of abnormal behaviors in welfare assessment have been published. In primates, some evidence suggests that certain types of abnormal behaviors are better indicators of the animals' welfare state than others. These suggestions resulted from the assessment of the relationships of specific types of abnormal behaviors and additional welfare indicators. For instance, tufted capuchins (*Cebus apella*) exhibiting higher levels of stereotypic head twirling were more likely to interpret ambiguous stimuli as signaling the arrival of an aversive experience, suggesting negative affect, while stereotypic pacing was not correlated with such measures of negative affective states (Pomerantz, Terkel, et al., 2012). Therefore, for this species, head-twirling was determined to be a more valid reflector of the animals' welfare than pacing. Additionally, rhesus macaques expressing higher levels of self-directed and fine-motor stereotypic behavior required more trials to extinguish a previously acquired response than animals that performed whole-body stereotypies, potentially indicating neurological malfunction of the basal ganglia (Pomerantz, Paukner, et al., 2012).

Not only do some abnormal behaviors appear to be more reliable indicators of welfare, but some may actually indicate an effective response to the environment. In particular, it has

been suggested that the expression of abnormal behavior serves a psychological function, enabling animals to better cope with stressors they encounter by employing a novel arousal reducing coping response (Crockett et al., 2007; Pomerantz, Paukner, et al., 2012). Further support for this notion comes from studies that have shown that preventing animals from expressing already developed abnormal behaviors reduces their welfare levels (Jones et al., 1989; McBride & Cuddeford, 2001). To add yet another layer of complexity, abnormal behavior may gradually become divorced from the original stimulus that triggered its development (i.e., emancipated, Vickery & Mason, 2004). Thus, it is important to recognize that abnormal behaviors may reflect a prior trauma, impoverished rearing, or previous housing in inappropriate conditions, and so may not represent a reliable reflection of an animal's current welfare state or the suitability of the housing and management program.

## 8. Conclusions and Future Directions

Abnormal behavior has strong links to conditions associated with poor welfare. While there is still much work to be done to better understand the value of abnormal behavior as a welfare assessment tool, it should additionally be acknowledged that, in light of the large body of literature that associates abnormal behaviors with unfitting environmental conditions, these behaviors should serve as a warning sign that warrants further investigation. The animal's quality of life should always be the central focus, and thus having clear endpoints in place is additionally critical. In this review, we have focused on the identification, risk factors, assessment, and treatment of abnormal behaviors. However, it is additionally clear that many factors prevent an unequivocal determination of an animal's wellbeing. Therefore, this review should also be utilized for addressing gaps in our knowledge. To undertake this challenge, further research into the specific significance and relative importance of particular abnormal behaviors is needed. Similarly, combining measurement of abnormal behavior with additional indicators is necessary to gain a more accurate understanding of the animal's welfare state. A better understanding of abnormal behavior overall will allow for improved captive conditions and welfare in primates.

## Acknowledgments

This article arose from a workshop on abnormal behavior identification and treatment that was hosted by the American Society of Primatologists' Primate Care Committee in 2019. From hosting that workshop it was clear that there was not a recent and comprehensive resource on how to identify, evaluate, monitor, and treat captive primates that exhibit abnormal behavior. Therefore, our aim with this article was to address this gap. We thank the organizers of the 2019 American Society of Primatologists Primate Care Committee workshop ("Identifying and Treating Abnormal Behaviors in Nonhuman Primates") that spurred us to write this review article.

Kristine Coleman was supported by National Institutes of Health grant number P51 OD011092 to the Oregon National Primate Research Center. Jaine Perlman was supported by National Institutes of Health grant number P51 OD011132 to the Yerkes National Primate Research Center. Ori Pomerantz was supported by National Institutes of Health grant number P51 OD011107 to the California National Primate Research Center.

## Appendix-Methods for Assessing Behavior

### Assessing Behavior

Programs monitoring primate behavior and welfare differ across institutions, depending on programmatic needs and staff constraints, but here we aim to describe universal methods



and tools to identify and assess behaviors of concern. Behavioral monitoring can be supplemented with other measures such as fecal hormones or hair cortisol (Davenport et al., 2006; Rimbach et al., 2013); as well as tests of mood and affect (Cassidy et al., 2021; Pomerantz et al., 2012); however, these methodologies are outside of the scope of this manuscript and will not be expanded upon here.

## 1. Staff Education

To ensure proper detection, monitoring, understanding, and treatment of abnormal behaviors, education about primate behavior to all personnel working with the animals is essential (Rennie & Buchanan-Smith, 2006), although the benefits depend on the quality and rigor of that training (reviewed in Glanville et al., 2020). Educational opportunities should be included as part of new employee orientation but should also be an on-going process. Such training should enable staff to identify and interpret common species-typical and abnormal behaviors, equip them to know how to appropriately interact with animals, and help them to identify, monitor, and report behaviors of concern with pertinent information relating to the animal and its environment (Bloomsmith, Perlman, et al., 2017).

## 2. Behavioral Assessment Methods

Systematic observations are essential in animal welfare assessment. Regular and reliable collection of both qualitative and quantitative data by trained staff should provide an adequate reflection of the animal's welfare state, and clear guidance on how to record such data appears in a number of publications (e.g., Altmann, 1974; Martin & Bateson, 2007; Teichroeb et al., 2021; Table 1).

**Table 1.**

Different approaches for collecting and recording observational data. The sampling methods describe which animals are observed and the recording methods describe how the data are documented. Sampling and recording methods can be used in combination.

Sampling Methods			
Method	Description	Advantages	Disadvantages
Focal sampling	Observing one animal or unit at a time via continuous, one-zero, or instantaneous recording.	Very detailed information can be recorded.	Can be time consuming to sequentially collect focal follows on all animals in a colony if whole groups are to be monitored at one time. Depending on the data recorded, focal sampling may obscure social interactions between group members.
Scan sampling	Observing a group of animals, each animal observed in turn.	Allows for a temporal understanding of how the behavior of each animal in a group may interact with others.	May lose track of individuals when the group is large.
Behavior sampling	Observations of every occurrence of specific behaviors whenever they are observed.	Useful for capturing rare behaviors or behaviors of specific concern.	Feasibility dictates that focus is limited to a small number of behaviors
Recording Methods			
Method	Description	Advantages	Disadvantages

Sampling Methods			
Method	Description	Advantages	Disadvantages
Continuous recording	Observations of all behaviors occurring within a specified amount of time	Effective for recording frequency and duration of behaviors. Offers a detailed understanding of the sequential presentation of behaviors that may be useful for identifying triggers and outcomes of behaviors.	A time-consuming and demanding approach that often requires the use of specialized software.
One-zero recording	Observations of the occurrence of a specified behavior within a set interval of time (e.g., whether behavior occurred or not within a 10-minute period).	Data collection is simple, leading to high interobserver reliability, and can be especially helpful to tracking rare behaviors or behaviors of concern.	True durations and rates are not calculated. Rare behaviors may be overemphasized in the dataset.
Instantaneous recording	Observations of specified behaviors at regular points in time (e.g., what behavior occurred at the end of each interval, for a set period of time).	Less demanding than continuous recording and can provide a good approximation of the proportion of time spent performing a given behavior. Less statistically biased than one-zero sampling (Brereton et al., 2022)	As data are only collected at intervals, rare behaviors may not be captured, and true rates and durations of behaviors are not calculated.

According to a recent survey, most (89%) research facilities that house primates in North America have personnel who monitor the animals for behavior problems and 52% use quantitative data collection measurements for this purpose (Baker, 2016). AZA-accredited zoos must also conduct regular welfare assessments that are recorded and evaluated, and across zoos standardized behavioral monitoring tools, such as ZooMonitor, have been widely adopted in recent years (Wark et al., 2019). The extent of behavioral monitoring depends upon several factors, including the number of personnel responsible for observations, as well as the size of the facility's primate population. Promisingly, between the years 2007 to 2016, the ratio of behavioral staff to the number of primates for which they are responsible has doubled in research facilities, reflecting the growing understanding of the critical role behavioral management has in maintaining healthy and stable populations (Baker, 2016; Baker et al., 2007).

When planning how best to monitor primates' behavior, a number of decisions need to be made: 1) which behaviors will be recorded? 2) what methods will be used to observe and monitor the primates? 3) what will be used to document the observed behaviors, and who will collect the data? 4) which primates will be monitored? and 5) what will be the sampling and recording rules of observation?

**2.1 Which behaviors will be recorded?**—Behavioral data systems capture the presence, absence, frequency, and durations of selected behaviors; therefore, the first step of any behavioral monitoring program is to develop an ethogram (a list of the behaviors of interest and their definitions). While many primates share similar behavioral profiles, there are also key species differences that must be acknowledged. For example, some species perform behaviors that others do not, or express similar behaviors that communicate different information. Therefore, when developing a new ethogram, it is important to be fully familiarized with the typical behavioral repertoire for the species. For commonly

studied species (e.g., rhesus macaques, baboons, chimpanzees), published ethograms may be available that can be adopted or adapted, which further allows for comparison across sites if needed. To facilitate the process of communicating about abnormal behavior across facilities, the National Institutes of Health's Behavior Management Consortium created an "Abnormal Behavior Ethogram" (Baker et al., 2017; see also The Macaque Website produced by NC3Rs <https://www.nc3rs.org.uk/macaques/>). In addition to selecting which behaviors to monitor, the intensity of the behavior should also be considered (see Baker et al., 2017 for an example).

**2.2 What methods will be used to observe and monitor the behavior of the primates?**—There are a number of methods that can be used to observe primates, the most common of which is direct observation. Following a recommended period of habituation to the human observer's presence, live, direct observations allow the observer to watch the animal(s) from different angles to get a clear view of their behavior. In some circumstances, when habituation is not possible or not appropriate, the presence of a person observing the primates may affect the animal's behavior (Iredale et al., 2010). To overcome this, animals can be monitored remotely in real time via live video feeds, although it is worth noting that real time observations cannot be reviewed. Consequently, fleeting, or cryptic behaviors, such as a head toss or brief self-bite, may be overlooked, particularly when a number of animals are housed together.

Video recording may be especially beneficial in cases when data need to be reviewed at a later time (Forrester, 2008) or during hours when staff are not present, such as nighttime (Anderson et al., 2019; Stanwicks et al., 2017). The use of video recording allows for more comprehensive, 24/7 welfare monitoring (Brando & Buchanan-Smith, 2018), and is also useful for staff education and identification of rare behaviors. Furthermore, video footage can be augmented to allow for thermal imaging data to be recorded (Ross et al., 2021). Scoring behavioral data from video can be time-consuming, although automated tools for coding video footage are being developed that can expedite the coding process (Labuguen et al., 2020). However, video is not without challenges; identifying subtle behaviors, such as hair plucking, may be difficult from video footage, whereas whole body, stereotyped behaviors are typically easier to detect, potentially biasing the results (Hansen et al., 2020). Identifying individuals in a group setting may also be more challenging via video and may require that the animals be clearly marked with tattoos, dyes, and/or shave patterns.

A third method to monitor captive primates' behavior is to use automated real-time video monitoring (Noldus et al., 2001) or via the use of wearable sensors (Gelardi et al., 2020). For such systems, the primates may need to wear different colored jackets, each of which is recognized and tracked separately by the monitoring system (Ballesta et al., 2014; Rose et al., 2012), although not all systems require this (Walton et al., 2006). Such automated systems reduce the need for staff time for observations or video coding and can often track detailed information about the primates' location and movement patterns (including pacing and stereotypic movement; Hayden et al., 2021). While such systems may not be sensitive enough to detect and record more subtle behaviors that may be of interest, such as self-directed or appetitive abnormal behaviors, software advances are continually being released that offer enhanced capacities (e.g., Bala et al., 2020). Additionally, such

an approach has inherent upfront costs in terms of time and money: time and care will be required to habituate the primates to wearing the jackets and tracking markers if required by the system, and costs associated with obtaining the necessary software and hardware may be prohibitive. However, these costs may be recovered in terms of personnel time savings.

**2.3 What will be used to document the observed behaviors, and who will collect the data?**—Beyond determining how best to observe and monitor primates, the hardware and software needed to record and collate behavioral data will need to be selected. The simplest approach to collect data is to use pen and paper. With this method, a pre-formatted table is typically printed on the paper for data collection (see Martin & Bateson, 2007 for an example) and a timer or stopwatch is utilized to keep track of time. Pen and paper can be used for a variety of data collection methods, including one-zero and instantaneous sampling (Altmann, 1974). While affordable, such an approach requires the transcription of data for analysis, which can be time consuming and may increase the likelihood of the introduction of errors. Alternatively, if using an electronic data collection system, specialized software can be used, or users can create their own ethogram and database via Microsoft Excel, Microsoft Access, Google Forms, or similar software. Choice of software may be driven by user needs and budget. Specialized systems can be used to enter data from real-time observations or when coding video footage, although some software are better suited for one approach than the other (reviewed in Hobson et al., 2020). In addition to selecting appropriate software, associated hardware will also need to be acquired, including a laptop or handheld device for entering data and, potentially, video cameras for remote observation.

All observers collecting the behavioral data need to be reliable with each other in correctly identifying the behaviors in the ethogram (Jansen et al., 2003). Appropriate training on the ethogram ensures consistency across observers. Specifically, inter-observer reliability measures (IORs) need to be achieved and maintained with all personnel collecting behavioral data. Repeated testing should also be conducted to ensure that there is no drift over time across or within observers in behavior identification from operational definitions. Typically, a new observer collects data simultaneously with a trained observer and their ratings are compared after the fact. Such tests can be run with live observations or from coding video footage and “blind” coding can further ensure that bias is minimized (Holman et al., 2015). Agreement between observers can be calculated manually by comparing ratings, creating a percent agreement, or via intra-class correlation coefficients or Cohen’s kappa scores, but some software packages (e.g., ZooMonitor, Observer XT) automatically calculate observer agreement. Given that some abnormal behaviors are only rarely seen, or may differ in their expression across different primates, IORs are key to ensuring reliable and meaningful datasets. Once data are collected, staff needs to be able to compile, analyze, and interpret the data in a timely manner to avoid overlooking opportunities to treat animals of concern or to evaluate interventions.

**2.4 Which primates will be monitored?**—Behavioral data may be collected on all animals at a facility to help assess the welfare of a population, identify overall abnormal behaviors expressed, and monitor trends in emergence of behaviors of concern, as well

as to monitor species appropriate behavior. Decisions about more focused monitoring of individuals within the population should be based on current expression of abnormal behavior (severity, frequency, duration), and/or intrinsic and extrinsic risk factors (rearing history, temperament, social environment, clinical health).

**2.5 What will be the sampling and recording rules of observations?**—The frequency and methods of data collection are first determined based on the goals of the behavioral monitoring program (e.g., identification of abnormal behaviors in a population or assessing treatment of an individual’s abnormal behavior). Based on these goals, there are three aspects of timing that must be determined: the frequency at which each animal/abnormal behavior type is observed (e.g., daily, weekly, monthly), the duration of each observation session, and the frequency with which data are recorded during each observation session (e.g., every 30 seconds, every minute, every five minutes, or continuously). Observations at different and/or targeted times of day help to identify triggers, such as loud noises, cage wash activities, research procedures, and staff or visitor behavior.

The frequency of formal data collection across North American primate research facilities varies widely from daily to annually, with monthly observations on primates being the most common (Baker, 2016). The regularity of observations may also differ within facilities, such that higher risk animals are observed more frequently, or observation rate may increase colony-wide at critical time points (e.g., during the breeding season or following transfer from another facility). Ideally, all animals should be observed on a regular basis as this allows a true understanding of colony health as well as an individual’s “baseline” behavior and activity budget. Such baseline data would allow a comparison point for situations that may trigger abnormal behaviors and would enable quick identification of when (and potentially why) an animal may begin to express abnormal behaviors, thus aiding treatment and care. In addition to the behavioral data, observers should also record pertinent independent variables and other correlative behavior that might provide insights to triggers of abnormal behaviors (e.g., time of day, weather, presence of staff or visitors, whether or not the animal is on study, time since last veterinary procedure etc.).

### 3. What to Measure

In the previous section we outlined the questions that must be addressed when planning a behavioral data collection and the different approaches that can be used to collect observational data. A key component of choosing the best method is identifying what the aims of the data collection are, which in turn will inform what methods are most appropriate and what behaviors should be recorded. For example, if the aim is to evaluate the prevalence of abnormal behaviors within a population, then a broad surveying approach, in which most or all of the population are observed on a regular basis and a broad array of behaviors are recorded, is needed. However, if the aim is to determine what environmental events may be triggering the presentation of a specific abnormal behavior in an individual or group, then a more targeted approach in terms of the number of animals observed and behaviors recorded, but with a more comprehensive list of independent variables and correlative events may suffice. Identifying the most appropriate methods will generate the most useful data set for answering the programmatic questions and, in turn, allow for the most detailed

understanding of the primates' welfare and the efficacy of any treatments or interventions that are deployed.

#### 4. Assessment Design

Once a behavioral concern has been identified, the next step is to decide how the primates' welfare will be assessed. As described above, observational data can be collected to assess behavior, potentially in conjunction with management changes or treatments (see Treatment Approaches in the main article). When collecting behavioral data, any changes in behavior can be examined against time or other independent variables and inferences drawn (although, it is important to remember that correlation does not equal causation).

In cases where an intervention is conducted, it is important to assess its efficacy. Experimental approaches to assess interventions can be roughly grouped into two types that describe how the animals are tested. In a between-subjects design, one group of animals is assigned to one condition while another group is assigned to a second condition. This might be a medication (test) versus a placebo (control), or it might be a comparison between two different test conditions (e.g., medication A versus medication B). Animals may either be randomly assigned to each condition (a true experiment) or assignments might be constrained/determined by facility needs (a quasi-experiment). In either case, the responses of individuals in one group are compared to those of individuals in the other group (e.g., Bloomsmith & Lambeth, 1995; Boinski et al., 1999; Buchanan-Smith & Badihi, 2012; Crockett et al., 2000). In contrast, in a within-subjects design, all animals experience a test condition and their responses are compared to themselves in another condition. For example, all animals in a colony might be monitored before an intervention (baseline condition) and once again after the intervention, such as the provision of new enrichment (test condition). Their behavior in the test condition is compared to their prior behavior in the baseline period (e.g., Wooddell et al., 2019). In some cases, their behavior is monitored again in a third phase in which the intervention is removed to assess the impact of removing the treatment, i.e., an A-B-A design (e.g., Lee et al., 2012). Such within-subject approaches are especially useful when only small sample sizes are being assessed, when there is high inter-individual variation, or if there is an expectation that the intervention will be beneficial and so all animals should receive it. Such interventions may also be unplanned but can still be documented if baseline data have been collected.

A more recent applied approach used to evaluate and treat behavioral problems in primates is functional behavior assessment. This is an applied behavior analysis approach originally developed for use with human patients (Hanley et al., 2003), but these techniques have proved successful in treating behavioral problems in nonhuman primates (Bloomsmith et al., 2007; Martin, 2017). A Functional Analysis is a single subject design with one control and several experimental conditions. The experimental conditions identify what purpose the problem behavior serves to the individual, such as to avoid an event or stimulus, gain human attention or access a stimulus. The findings are used to develop function-based treatments to weaken the relationship between a behavior and its reinforcer and also replace the abnormal/problem behavior with a more appropriate one (Iwata et al., 1994). In primates, this approach has proven successful for treating SIB in an olive baboon (*P. h. anubis*;

Dorey et al., 2009); human-directed feces throwing by a chimpanzee (Martin et al., 2011); and disruptive behavior in a rhesus monkey (Franklin et al., 2021). See Martin (2017) and Kummrow (2021) for more information on the application of Functional Analysis in primates to treat behavioral problems.

Other applied behavior analysis techniques, such as preference assessments and competing items assessments, are applied with primates to identify preferred foods which can increase desirable behavior responses (Martin et al., 2018) and preferred devices that increase the expression of targeted behaviors (Fernandez & Timberlake, 2019). The data from these techniques add more information to inform function-based therapeutic treatments and can be particularly effective in treating automatically reinforced behaviors by identifying an individual's preferred alternatives to destructive behavior (Piazza et al., 1998; Vollmer, 1994).

## References

- Akers JS, & Schildkraut DS (1985). Regurgitation/reingestion and coprophagy in captive gorillas. *Zoo Biology*, 4(2), 99–109. 10.1002/zoo.1430040203
- Altmann J (1974). Observational study of behavior: sampling methods. *Behaviour*, 49(3–4), 227–266. [PubMed: 4597405]
- Anderson JR, Ang MY, Lock LC, & Weiche I (2019). Nesting, sleeping, and nighttime behaviors in wild and captive great apes. *Primates*, 60(4), 321–332. doi: 10.1007/s10329-019-00723-2 [PubMed: 30972523]
- Anderson JR, & Chamove AS (1980). Self-aggression and social aggression in laboratory-reared macaques. *Journal of Abnormal Psychology*, 89(4), 539–550. 10.1037/0021-843X.89.4.539 [PubMed: 6772702]
- Baker KC (2004). Benefits of positive human interaction for socially-housed chimpanzees. *Animal Welfare*, 13(2), 239. [PubMed: 20505791]
- Baker KC (2016). Survey of 2014 behavioral management programs for laboratory primates in the United States. *American Journal of Primatology*, 78(7), 780–796. 10.1002/ajp.22543 [PubMed: 26971575]
- Baker KC, Bloomsmith MA, Coleman K, Crockett CM, Worlein J, Lutz CK, McCowan B, Pierre P, & Weed J (2017). The Behavioral Management Consortium: A partnership for promoting consensus and best practices. In Schapiro SJ (Ed.). *Handbook of Primate Behavioral Management* (pp. 9–23). Boca Raton, FL: CRC Press.
- Baker K, Bloomsmith M, Neu K, Griffis C, & Maloney M (2010). Positive reinforcement training as enrichment for singly housed rhesus macaques (*Macaca mulatta*). *Animal Welfare*, 19(3), 307. [PubMed: 25960611]
- Baker KC, Bloomsmith MA, Oettinger B, Neu K, Griffis C, Schoof V, & Maloney M (2012). Benefits of pair housing are consistent across a diverse population of rhesus macaques. *Applied Animal Behaviour Science*, 137(3), 148–156. 10.1016/j.applanim.2011.09.010 [PubMed: 25635151]
- Baker KC, Weed JL, Crockett CM, & Bloomsmith MA (2007). Survey of environmental enhancement programs for laboratory primates. *American Journal of Primatology*, 69(4), 377–394. 10.1002/ajp.20347 [PubMed: 17171695]
- Bala PC, Eisenreich BR, Yoo SBM, Hayden BY, Park HS, & Zimmermann J (2020). Automated markerless pose estimation in freely moving macaques with OpenMonkeyStudio. *Nature Communications*, 11(1), 1–12.
- Ballesta S, Reymond G, Pozzobon M, & Duhamel JR (2014). A real-time 3D video tracking system for monitoring primate groups. *Journal of Neuroscience Methods*, 234, 147–152. doi: 10.1016/j.jneumeth.2014.05.022. [PubMed: 24875622]
- Bassett L, Buchanan-Smith HM, McKinley J, & Smith TE (2003). Effects of training on stress-related behavior of the common marmoset (*Callithrix jacchus*) in relation to coping with routine

- husbandry procedures. *Journal of Applied Animal Welfare Science*, 6(3), 221–233. doi: 10.1207/S15327604JAWS0603\_07 [PubMed: 14612270]
- Bauer SA, & Baker KC (2016). Persistent effects of peer rearing on abnormal and species-appropriate activities but not social behavior in group-housed rhesus macaques (*Macaca mulatta*). *Comparative Medicine*, 66(2), 129–136. [PubMed: 27053567]
- Bayne K (1996). Normal and abnormal behaviors of laboratory animals: What do they mean? *Lab Animal*, 25, 21–24.
- Bayne K, Dexter S, & Suomi S (1992). A preliminary survey of the incidence of abnormal behavior in rhesus monkeys (*Macaca mulatta*) relative to housing condition. *Lab Animal*, 21, 38–46.
- Bayne K, & McCully C (1989). The effect of cage size on the behavior of individually housed rhesus monkeys. *Lab Animal*, 18, 25–28.
- Bayne K, & Novak M (1998). Behavioral disorders. In Bennett BT, Abee CR, & Henrickson R (Eds.) *Nonhuman Primates in Biomedical Research* (pp. 485–500). New York, NY: Elsevier.
- Baysinger C, Brandt E, & Mitchell G (1972). Development of infant social isolate monkeys (*Macaca mulatta*) in their isolation environments. *Primates*, 13(3), 257–270.
- Beisner BA, & Isbell LA (2009). Factors influencing hair loss among female captive rhesus macaques (*Macaca mulatta*). *Applied Animal Behaviour Science*, 119(1–2), 91–100.
- Bellanca RU, & Crockett CM (2002). Factors predicting increased incidence of abnormal behavior in male pigtailed macaques. *American Journal of Primatology*, 58(2), 57–69. doi: 10.1002/ajp.10052 [PubMed: 12386914]
- Berkson G (1968). Development of abnormal stereotyped behaviors. *Developmental Psychobiology*, 1(2), 118–132. 10.1002/dev.420010210
- Berkson G, Goodrich J, & Kraft I (1966). Abnormal stereotyped movements of marmosets. *Perceptual and Motor Skills*, 23(2), 491–198.
- Birkett LP, & Newton-Fisher NE (2011). How abnormal is the behaviour of captive, zoo-living chimpanzees? *PLoS One*, 6(6), e20101. 10.1371/journal.pone.0020101
- Bliss-Moreau E, Theil JH, & Moadab G (2013). Efficient cooperative restraint training with rhesus macaques. *Journal of Applied Animal Welfare Science*, 16(2), 98–117. 10.1080/10888705.2013.768897 [PubMed: 23544752]
- Bloomsmith M, Alford P, & Maple T (1988). Successful feeding enrichment for captive chimpanzees. *American Journal of Primatology*, 16(2), 155–164. doi: 10.1002/ajp.1350160206 [PubMed: 31968870]
- Bloomsmith M, Clay A, Ross S, Lambeth S, Lutz C, Breaux S, Pietsch R, Fultz A, Lammey M, & Jacobson S (2020). 21 Chimpanzees in US Zoos, Sanctuaries, and Research Facilities: A Survey-Based Comparison of Atypical Behaviors. In Hopper LM & Ross SR (Eds.). *Chimpanzees in Context* (pp. 481–508). Chicago, IL: University of Chicago Press.
- Bloomsmith MA, & Haberstroh MD (1995). Effect of early social experience on the expression of abnormal behavior among juvenile chimpanzees. *American Society of Primatology*, Scottsdale, AZ.
- Bloomsmith MA, Hasenau J, & Bohm RP (2017). Position Statement: “Functionally Appropriate Nonhuman Primate Environments” as an Alternative to the Term “Ethologically Appropriate Environments”. *Journal of the American Association for Laboratory Animal Science*, 56(1), 102–106. [PubMed: 28905724]
- Bloomsmith MA, & Lambeth SP (1995). Effects of predictable versus unpredictable feeding schedules on chimpanzee behavior. *Applied Animal Behaviour Science*, 44(1), 65–74.
- Bloomsmith MA, Marr MJ, & Maple TL (2007). Addressing nonhuman primate behavioral problems through the application of operant conditioning: Is the human treatment approach a useful model? *Applied Animal Behaviour Science*, 102(3–4), 205–222. 10.1016/j.applanim.2006.05.028
- Bloomsmith MA, Perlman JE, Hutchinson E, & Sharpless M (2017). Behavioral management programs to promote laboratory animal welfare. In: Weichbrod RH, Thompson GA, Norton JN (Eds). *Management of Animal Care and Use Programs in Research, Education, and Testing*, (pp. 63–82). Boca Raton, FL: CRC Press.



- Bogart SL, Bennett AJ, Schapiro SJ, Reamer LA, & Hopkins WD (2014). Different early rearing experiences have long-term effects on cortical organization in captive chimpanzees (*Pan troglodytes*). *Developmental Science*, 17(2), 161–174. 10.1111/desc.12106 [PubMed: 24206013]
- Boinski S, Swing SP, Gross TS, & Davis JK (1999). Environmental enrichment of brown capuchins (*Cebus apella*): Behavioral and plasma and fecal cortisol measures of effectiveness. *American Journal of Primatology*, 48(1), 49–68. doi: 10.1002/(SICI)1098-2345(1999)48:1<49::AID-AJP4>3.0.CO;2-6. [PubMed: 10326770]
- Bollen KS, & Novak MA (2000). A survey of abnormal behavior in captive zoo primates. *American Journal of Primatology*, 51 (S1), 47.
- Bonnie KE, Ang MY, & Ross SR (2016). Effects of crowd size on exhibit use by and behavior of chimpanzees (*Pan troglodytes*) and Western lowland gorillas (*Gorilla gorilla*) at a zoo. *Applied Animal Behaviour Science*, 178, 102–110. DOI:10.1016/J.APPLANIM.2016.03.003
- Bourgeois S, & Brent L (2005). Modifying the behaviour of singly caged baboons: evaluating the effectiveness of four enrichment techniques. *Animal Welfare*, 14(1), 71–81.
- Bourgeois SR, Vazquez M, & Brasky K (2007). Combination therapy reduces self-injurious behavior in a chimpanzee (*Pan troglodytes troglodytes*): A case report. *Journal of Applied Animal Welfare Science*, 10(2), 123–140. 10.1080/10888700701313454 [PubMed: 17559320]
- Brand CM, & Marchant LF (2015). Hair plucking in captive bonobos (*Pan paniscus*). *Applied Animal Behaviour Science*, 171, 192–196. DOI:10.1016/j.applanim.2015.08.002
- Brand CM, & Marchant LF (2018). Prevalence and characteristics of hair plucking in captive bonobos (*Pan paniscus*) in North American zoos. *American Journal of Primatology*, 80(4), e22751. doi: 10.1002/ajp.22751
- Brando S, & Buchanan-Smith HM (2018, 2018/11/01/). The 24/7 approach to promoting optimal welfare for captive wild animals. *Behavioural Processes*, 156, 83–95. 10.1016/j.beproc.2017.09.010 [PubMed: 29113925]
- Brent L, Lee DR, & Eichberg JW (1989). The effects of single caging on chimpanzee behavior. *Laboratory Animal Science*, 39, 345–346. [PubMed: 2761238]
- Brereton JE, Tuke J, Fernandez EJ (2022). A simulated comparison of behavioural observation sampling methods. *Scientific Reports*, 12, 3096. 10.1038/s41598-022-07169-5 [PubMed: 35197514]
- Broom DM (2019). Abnormal behavior and the self-regulation of motivational state. *Journal of Veterinary Behavior*, 29, 1–3. DOI:10.1016/j.jveb.2018.09.001
- Buchanan-Smith HM (1997). Environmental control: An important feature of good captive callitrichid environments. In Pryce C, Scott L, & Schnell C (Eds.), *Marmosets and Tamarins in Biological and Biomedical Research*. Salisbury (pp. 47–53). DSSD Imagery.
- Buchanan-Smith HM, & Badihi I (2012). The psychology of control: Effects of control over supplementary light on welfare of marmosets. *Applied Animal Behaviour Science*, 137(3–4), 166–174. 10.1016/j.applanim.2011.07.002
- Camus SM, Blois-Heulin C, Li Q, Hausberger M, & Bezard E (2013). Behavioural profiles in captive-bred cynomolgus macaques: Towards monkey models of mental disorders? *PLoS One*, 8(4), e62141. 10.1371/journal.pone.0062141
- Capitanio JP (1986). Behavioral pathology. In Mitchell G & Erwin J (Eds.), *Comparative Primate Biology* (Vol. 2A, pp. 411–454). New York, NY: Alan R. Liss, Inc.
- Carrasco L, Colell M, Calvo M, Abello MT, Velasco M, & Posada S (2009). Benefits of training/playing therapy in a group of captive lowland gorillas (*Gorilla gorilla gorilla*). *Animal Welfare*, 18(1), 9–19.
- Cassidy LC, Bethell EJ, Brockhausen RR, Boretius S, Treue S, & Pfefferle D (2021). The dot-probe attention bias task as a method to assess psychological well-being after anesthesia: a study with adult female long-tailed macaques (*Macaca fascicularis*). *European Surgical Research*. 10.1159/000521440
- Cassidy LC, Hannibal DL, Semple S, & McCowan B (2020). Improved behavioral indices of welfare in continuous compared to intermittent pair-housing in adult female rhesus macaques (*Macaca mulatta*). *American Journal of Primatology*, 82(10), e23189. 10.1002/ajp.23189

- Chelluri GI, Ross SR, & Wagner KE (2013). Behavioral correlates and welfare implications of informal interactions between caretakers and zoo-housed chimpanzees and gorillas. *Applied Animal Behaviour Science*, 147(3–4), 306–315.
- Clark FE (2011). Great ape cognition and captive care: Can cognitive challenges enhance well-being? *Applied Animal Behaviour Science*, 135(1), 1–12. 10.1016/j.applanim.2011.10.010
- Clay AW, Bloomsmith MA, Marr MJ, & Maple TL (2009). Habituation and desensitization as methods for reducing fearful behavior in singly housed rhesus macaques. *American Journal of Primatology*, 71(1), 30–39. doi: 10.1002/ajp.20622. [PubMed: 18850584]
- Clemmons EA, Gumber S, Strobert E, Bloomsmith MA, & Jean SM (2015). Self-injurious behavior secondary to cytomegalovirus-induced neuropathy in an SIV infected rhesus macaque (*Macaca mulatta*). *Comparative Medicine*, 65(3), 266–270. [PubMed: 26141451]
- Coleman K (2012). Individual differences in temperament and behavioral management practices for nonhuman primates. *Applied Animal Behaviour Science*, 137(3), 106–113. 10.1016/j.applanim.2011.08.002 [PubMed: 22518067]
- Coleman K, Bloomsmith MA, Crockett CM, Weed JL, & Schapiro SJ (2012). Behavioral management, enrichment, and psychological well-being of laboratory nonhuman primates. In Abee C, Mansfield K, Tardif S, & Morris T (Eds.). *Nonhuman Primates in Biomedical Research* (pp. 149–176). Waltham, MA: Elsevier Inc.
- Coleman K, & Maier A (2010). The use of positive reinforcement training to reduce stereotypic behavior in rhesus macaques. *Applied Animal Behaviour Science*, 124(3–4), 142–148. doi: 10.1016/j.applanim.2010.02.008 [PubMed: 20431691]
- Coleman K, & Novak MA (2017). Environmental enrichment in the 21st century. *ILAR Journal*, 58(2), 295–307. 10.1093/ilar/ilx008 [PubMed: 28444189]
- Coleman K, Pranger L, Maier A, Lambeth SP, Perlman JE, Thiele E, & Schapiro SJ (2008). Training rhesus macaques for venipuncture using positive reinforcement techniques: a comparison with chimpanzees. *Journal of the American Association for Laboratory Animal Science*, 47, 37–41.
- Conti G, Hansman C, Heckman JJ, Novak MF, Ruggiero A, & Suomi SJ (2012). Primate evidence on the late health effects of early-life adversity. *Proceedings of the National Academy of Sciences*, 109(23), 8866–8871. doi: 10.1073/pnas.1205340109
- Crast J, Bloomsmith MA, Perlman JE, Meeker TL, & Remillard CM (2014). Abnormal behaviour in captive sooty mangabeys. *Animal Welfare*, 23(2), 167–177. 10.7120/09627286.23.2.167
- Crockett CM, Bowers CL, Shimoji M, Leu M, Bowden DM, & Sackett GP (1995). Behavioral responses of longtailed macaques to different cage sizes and common laboratory experiences. *Journal of Comparative Psychology*, 109(4), 368. 10.1037/0735-7036.109.4.368 [PubMed: 7497695]
- Crockett CM, Sackett GP, Sandman CA, Chicz-DeMet A, & Bentson KL (2007). Beta-endorphin levels in longtailed and pigtailed macaques vary by abnormal behavior rating and sex. *Peptides*, 28(10), 1987–1997. 10.1016/j.peptides.2007.07.014 [PubMed: 17719139]
- Crockett CM, Shimoji M, & Bowden DM (2000). Behavior, appetite, and urinary cortisol responses by adult female pigtailed macaques to cage size, cage level, room change, and ketamine sedation. *American Journal of Primatology*, 52(2), 63–80. doi: 10.1002/1098-2345(200010)52:2<63::AID-AJP1>3.0.CO;2-K. [PubMed: 11051442]
- Cronin KA, Tank A, Ness T, Leahy M, & Ross SR (2020). Sex and season predict wounds in zoo-housed Japanese macaques (*Macaca fuscata*): A multi-institutional study. *Zoo Biology*, 39(3), 147–155. 10.1002/zoo.21533 [PubMed: 31990090]
- Cross HA, & Harlow HF (1965). Prolonged and progressive effects of partial isolation on the behavior of Macaque monkeys. *Journal of Experimental Research in Personality*. 1(1), 39–49.
- Davenport MD, Lutz CK, Tiefenbacher S, Novak MA, & Meyer JS (2008). A Rhesus Monkey Model of Self-Injury: Effects of Relocation Stress on Behavior and Neuroendocrine Function. *Biological Psychiatry*, 63(10), 990–996. 10.1016/j.biopsych.2007.10.025 [PubMed: 18164279]
- Davenport MD, Tiefenbacher S, Lutz CK, Novak MA, Meyer JS (2006). Analysis of endogenous cortisol concentrations in the hair of rhesus macaques. *General and Comparative Endocrinology* 147, 255–261. doi: 10.1016/j.ygcen.2006.01.005 [PubMed: 16483573]

- Davenport RK, & Menzel EW (1963). Stereotyped behavior of the infant chimpanzee. *Archives of General Psychiatry*, 8(1), 99–104. 10.1001/archpsyc.1963.01720070101013 [PubMed: 14025276]
- Dettmer AM, Novak MA, Suomi SJ, & Meyer JS (2012). Physiological and behavioral adaptation to relocation stress in differentially reared rhesus monkeys: Hair cortisol as a biomarker for anxiety-related responses. *Psychoneuroendocrinology*, 37(2), 191–199. 10.1016/j.psyneuen.2011.06.003 [PubMed: 21715101]
- Dienske H, & Griffin R (1978). Abnormal behaviour patterns developing in chimpanzee infants during nursery care—a note. *Journal of Child Psychology and Psychiatry*, 19(4), 387–391. 10.1111/j.1469-7610.1978.tb00485.x [PubMed: 568631]
- Dorey NR, Rosales-Ruiz J, Smith R, Lovelace B, & Roane H (2009). Functional analysis and treatment of self-injury in a captive olive baboon. *Journal of applied behavior analysis*, 42(4), 785–794. doi: 10.1901/jaba.2009.42-785 [PubMed: 20514183]
- Doyle LA, Baker KC, & Cox LD (2008). Physiological and behavioral effects of social introduction on adult male rhesus macaques. *American Journal of Primatology*, 70(6), 542–550. doi: 10.1002/ajp.20526 [PubMed: 18189243]
- Draper WA, & Bernstein IS (1963). Stereotyped behavior and cage size. *Perceptual and Motor Skills*, 16(1), 231–234. 10.2466/pms.1963.16.1.231
- Eaton G, Worlein J, Kelley S, Vijayaraghavan S, Hess D, Axthelm M, & Bethea C (1999). Self-injurious behavior is decreased by cyproterone acetate in adult male rhesus (*Macaca mulatta*). *Hormones and Behavior*, 35(2), 195–203. doi: 10.1006/hbeh.1999.1513. [PubMed: 10202127]
- Erwin J (1979). Strangers in a strange land: abnormal behaviors or abnormal environment? In Erwin J, Maple TL, & Mitchell G (Eds.), *Captivity and behavior* (pp. 1–28). New York, NY: Van Nostrand Reinhold.
- Fagot J, Gullstrand J, Kemp C, Defilles C, & Mekaouche M (2014). Effects of freely accessible computerized test systems on the spontaneous behaviors and stress level of Guinea baboons (*Papio papio*). *American Journal of Primatology*, 76(1), 56–64. doi: 10.1002/ajp.22193 [PubMed: 24038166]
- Ferdowsian HR, Durham DL, Kimwele C, Kranendonk G, Otali E, Akugizibwe T, Mulcahy J, Ajarova L, & Johnson CM (2011). Signs of mood and anxiety disorders in chimpanzees. *PLoS One*, 6(6), e19855. 10.1371/journal.pone.0019855
- Fernandez EJ, Tamborski MA, Pickens SR, & Timberlake W (2009). Animal–visitor interactions in the modern zoo: Conflicts and interventions. *Applied Animal Behaviour Science*, 120(1–2), 1–8. 10.1016/j.applanim.2009.06.002
- Fernandez EJ, & Timberlake W (2019). Selecting and testing environmental enrichment in lemurs. *Frontiers in Psychology*, 10, 2119. 10.3389/fpsyg.2019.02119 [PubMed: 31572280]
- Fontenot BM, Wilkes MN, & Lynch CS (2006). Effects of outdoor housing on self-injurious and stereotypic behavior in adult male rhesus macaques (*Macaca mulatta*). *Journal of the American Association for Laboratory Animal Science*, 45(5), 35–43.
- Fontenot MB, Padgett III EE, Dupuy AM, Lynch CR, De Petrillo PB, & Higley JD (2005). The effects of fluoxetine and buspirone on self-injurious and stereotypic behavior in adult male rhesus macaques. *Comparative Medicine*, 55(1), 67–74. [PubMed: 15766212]
- Forrester GS (2008). A multidimensional approach to investigations of behaviour: Revealing structure in animal communication signals. *Animal Behaviour*, 76(5), 1749–1760. 10.1016/j.anbehav.2008.05.026
- Franklin AN, Martin A, Perlman J, & Bloomsmith M (2021). Functional analysis and successful treatment of a captive rhesus macaque’s disruptive behavior. *Journal of Applied Animal Welfare Science*, 1–10. doi: 10.1080/10888705.2021.1931868
- Freeman HD, & Ross SR (2014). The impact of atypical early histories on pet or performer chimpanzees. *PeerJ*, 2, e579. doi: 10.7717/peerj.579 [PubMed: 25279262]
- Freeman ZT, Krall C, Rice KA, Adams RJ, Pate KMA, & Hutchinson EK (2015). Severity and distribution of wounds in rhesus macaques (*Macaca mulatta*) correlate with observed self-injurious behavior. *Journal of the American Association for Laboratory Animal Science*, 54(5), 516–520. [PubMed: 26424249]

- Freeman ZT, Rice KA, Soto PL, Pate KAM, Weed MR, Ator NA, DeLeon IG, Wong DF, Zhou Y, & Mankowski JL (2015). Neurocognitive dysfunction and pharmacological intervention using guanfacine in a rhesus macaque model of self-injurious behavior. *Translational Psychiatry*, 5(5), e567–e567. doi: 10.1038/tp.2015.61 [PubMed: 25989141]
- Fritz J, Nash L, Alford P, & Bowen J (1992). Abnormal behaviors, with a special focus on rocking, and reproductive competence in a large sample of captive chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, 27(3), 161–176. doi: 10.1002/ajp.1350270302 [PubMed: 31948132]
- Fuller G, Margulis SW, & Santymire R (2011). The effectiveness of indigestible markers for identifying individual animal feces and their prevalence of use in North American zoos. *Zoo Biology*, 30(4), 379–398. doi: 10.1002/zoo.20339 [PubMed: 20853410]
- Gelardi V, Godard J, Paleressompoulle D, Claidière N, & Barrat A (2020). Measuring social networks in primates: wearable sensors versus direct observations. *Proceedings of the Royal Society A*, 476(2236), 20190737. 10.1098/rspa.2019.0737
- Glanville C, Abraham C, & Coleman G (2020). Human behaviour change interventions in animal care and interactive settings: A review and framework for design and evaluation. *Animals*, 10(12), 2333. 10.3390/ani10122333
- Gottlieb DH, Capitanio JP, & McCowan B (2013). Risk factors for stereotypic behavior and self-biting in rhesus macaques (*Macaca mulatta*): Animal's history, current environment, and personality. *American Journal of Primatology*, 75(10), 995–1008. 10.1002/ajp.22161 [PubMed: 23640705]
- Gottlieb DH, Coleman K, & McCowan B (2013). The Effects of Predictability in Daily Husbandry Routines on Captive Rhesus Macaques (*Macaca mulatta*). *Applied Animal Behaviour Science*, 143(2–4), 117–127. 10.1016/j.applanim.2012.10.010 [PubMed: 23439920]
- Gottlieb DH, Maier A, & Coleman K (2015). Evaluation of environmental and intrinsic factors that contribute to stereotypic behavior in captive rhesus macaques (*Macaca mulatta*). *Applied Animal Behaviour Science*, 171, 184–191. doi: 10.1016/j.applanim.2015.08.005. [PubMed: 27034527]
- Gottlieb DH, O'Connor JR, & Coleman K (2014). Using porches to decrease feces painting in rhesus macaques (*Macaca mulatta*). *Journal of the American Association for Laboratory Animal Science*, 53(6), 653–656. [PubMed: 25650971]
- Gould E, & Bres M (1986). Regurgitation and reingestion in captive gorillas: description and intervention. *Zoo Biology*, 5(3), 241–250. 10.1002/zoo.1430050302
- Graham ML, Rieke EF, Mutch LA, Zolondek EK, Faig AW, DuFour TA, Munson JW, Kittredge JA, & Schuurman HJ (2012). Successful implementation of cooperative handling eliminates the need for restraint in a complex non-human primate disease model. *Journal of Medical Primatology*, 41(2), 89–106. doi: 10.1111/j.1600-0684.2011.00525.x [PubMed: 22150842]
- Griffis CM, Martin AL, Perlman JE, & Bloomsmith MA (2013). Play caging benefits the behavior of singly housed laboratory rhesus macaques (*Macaca mulatta*). *Journal of the American Association for Laboratory Animal Science*, 52(5), 534–540. [PubMed: 24041207]
- Hanley GP, Iwata BA, & McCord BE (2003). Functional analysis of problem behavior: A review. *Journal of Applied Behavior Analysis*, 36(2), 147–185. doi: 10.1901/jaba.2003.36-147 [PubMed: 12858983]
- Hansen BK, Hopper LM, Fultz AL, & Ross SR (2020). Understanding the behavior of sanctuary-housed chimpanzees during public programs. *Anthrozoös*, 33(4), 481–495. 10.1080/08927936.2020.1771055
- Hayden BY, Park HS, Zimmerman J (2021). Automated pose estimation in primates. *American Journal of Primatology*, 10.1002/ajp.23348
- Hennessy MB, McCowan B, Jiang J, & Capitanio JP (2014). Depressive-like behavioral response of adult male rhesus monkeys during routine animal husbandry procedure. *Front Behav Neurosci*, 8, 309. 10.3389/fnbeh.2014.00309 [PubMed: 25249954]
- Hill S (2018). 'Regurgitation and reingestion' (R/R) in great apes: a review of current knowledge. *International Zoo Yearbook*, 52(1), 62–78. 10.1111/izy.12204
- Hobson EA, Silk MJ, Fefferman NH, Larremore DB, Rombach P, Shai S, & Pinter-Wollman N (2020). A guide to choosing and implementing reference models for social network analysis. *arXiv preprint arXiv:2012.04720*. 10.48550/arXiv.2012.04720

- Holman L, Head ML, Lanfear R, & Jennions MD (2015). Evidence of experimental bias in the life sciences: why we need blind data recording. *PLOS Biology*, 13(7), e1002190. 10.1371/journal.pbio.1002190
- Hook MA, Lambeth S, Perlman JE, Stavisky R, Bloomsmith MA, & Schapiro S (2002). Inter-group variation in abnormal behavior in chimpanzees (*Pan troglodytes*) and rhesus macaques (*Macaca mulatta*). *Applied Animal Behaviour Science*, 76(2), 165–176. DOI:10.1016/S0168-1591(02)00005-9
- Hopper LM (2017). Social learning and decision making. In Schapiro SJ (Ed.) *Handbook of Primate Behavioral Management* (pp. 225–241). Boca Raton, FL: CRC Press.
- Hopper LM (2021). Leveraging Social Learning to Enhance Captive Animal Care and Welfare. *Journal of Zoological and Botanical Gardens*, 2(1), 21–40. <https://www.mdpi.com/2673-5636/2/1/3>
- Hopper LM, Freeman HD, & Ross SR (2016). Reconsidering coprophagy as an indicator of negative welfare for captive chimpanzees. *Applied Animal Behaviour Science*, 176, 112–119. 10.1016/j.applanim.2016.01.002
- Hosey GR, & Skyner LJ (2007). Self-injurious behavior in zoo primates. *International Journal of Primatology*, 28(6), 1431–1437. 10.1007/s10764-007-9203-z
- Hutchinson EK, Bellanca RU, Coleman K, Pomerantz O, Lutz C, Baker KC, Bloomsmith MA, & Pierre PJ (In prep). A Practitioner’s Guide to the Treatment of NHP Self-injurious Behaviors.
- Iredale SK, Nevill CH, & Lutz CK (2010). The influence of observer presence on baboon (*Papio spp.*) and rhesus macaque (*Macaca mulatta*) behavior. *Applied Animal Behaviour Science*, 122(1), 53–57. doi: 10.1016/j.applanim.2009.11.002 [PubMed: 20228948]
- Iwata BA, Dorsey MF, Slifer KJ, Bauman KE, & Richman GS (1994). Toward a functional analysis of self-injury. *Journal of Applied Behavior Analysis*, 27(2), 197–209. doi: 10.1901/jaba.1994.27-197 [PubMed: 8063622]
- Jacobson SL, Ross SR, & Bloomsmith MA (2016). Characterizing abnormal behavior in a large population of zoo-housed chimpanzees: Prevalence and potential influencing factors. *PeerJ*, 4, e2225. doi: 10.7717/peerj.2225 [PubMed: 27478710]
- Jansen RG, Wiertz LF, Meyer ES, & Noldus LP (2003). Reliability analysis of observational data: Problems, solutions, and software implementation. *Behavior Research Methods, Instruments, & Computers*, 35(3), 391–399. doi: 10.3758/bf03195516
- Jones GH, Mittleman G, & Robbins TW (1989). Attenuation of amphetamine-stereotypy by mesostriatal dopamine depletion enhances plasma corticosterone: implications for stereotypy as a coping response. *Behav Neural Biol*, 51(1), 80–91. 10.1016/s0163-1047(89)90686-9 [PubMed: 2705984]
- Kempf DJ, Baker KC, Gilbert MH, Blanchard JL, Dean RL, Deaver DR, & Bohm RP (2012). Effects of extended-release injectable naltrexone on self-injurious behavior in rhesus macaques (*Macaca mulatta*). *Comparative Medicine*, 62(3), 209–217. [PubMed: 22776054]
- Kitchen AM, & Martin AA (1996). The effects of cage size and complexity on the behaviour of captive common marmosets, *Callithrix jacchus jacchus*. *Laboratory Animals*, 30(4), 317–326. doi: 10.1258/002367796780739853 [PubMed: 8938618]
- Kroeker R, Bellanca R, Lee G, Thom J, & Worlein J (2014). Alopecia in three macaque species housed in a laboratory environment. *American Journal of Primatology*, 76(4), 325–334. doi: 10.1002/ajp.22236 [PubMed: 24243351]
- Kummrow M (2021). Diagnostic and therapeutic guidelines to abnormal behavior in captive nonhuman primates. *Veterinary Clinics: Exotic Animal Practice*, 24(1), 253–266. 10.1016/j.cvex.2020.09.012
- Kummrow MS, & Brüne M (2018). Review: Psychopathologies in captive nonhuman primates and approaches to diagnosis and treatment. *Journal of Zoo and Wildlife Medicine*, 49(2), 259–271. 10.1638/2017-0137.1 [PubMed: 29900784]
- Labuguen R, Matsumoto J, Negrete SB, Nishimaru H, Nishijo H, Takada M, Go Y, Inoue K. i., & Shibata T (2020). Macaque pose: A novel “in the wild” macaque monkey pose dataset for markerless motion capture. *Frontiers in behavioral neuroscience*, 14. 10.3389/fnbeh.2020.581154

- Lambeth SP, Hau J, Perlman JE, Martino M, & Schapiro SJ (2006). Positive reinforcement training affects hematologic and serum chemistry values in captive chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, 68(3), 245–256. doi: 10.1002/ajp.20148 [PubMed: 16477594]
- Laméris DW, Staes N, Salas M, Matthyssen S, Verspeek J, & Stevens JM (2021). The influence of sex, rearing history, and personality on abnormal behaviour in zoo-housed bonobos (*Pan paniscus*). *Applied Animal Behaviour Science*, 234, 105178. 10.1016/j.applanim.2020.105178
- Laule GE, Bloomsmith MA, & Schapiro SJ (2003). The use of positive reinforcement training techniques to enhance the care, management, and welfare of primates in the laboratory. *Journal of Applied Animal Welfare Science*, 6(3), 163–173. doi: 10.1207/S15327604JAWS0603\_02. [PubMed: 14612265]
- Lee GH, Thom JP, Chu KL, & Crockett CM (2012). Comparing the relative benefits of grooming-contact and full-contact pairing for laboratory-housed adult female *Macaca fascicularis*. *Applied Animal Behaviour Science*, 137(3–4), 157–165. 10.1016/j.applanim.2011.08.013 [PubMed: 22685366]
- Lee KM, Chiu KB, Didier PJ, Baker KC, & MacLean AG (2015). Naltrexone treatment reverses astrocyte atrophy and immune dysfunction in self-harming macaques. *Brain, Behavior, and Immunity*, 50, 288–297. doi: 10.1016/j.bbi.2015.07.017 [PubMed: 26191654]
- Leeds A, Elsner R, & Lukas KE (2016). The effect of positive reinforcement training on an adult female western lowland gorilla's (*Gorilla gorilla gorilla*) rate of abnormal and aggressive behavior. *Animal Behavior and Cognition*, 3, 78–87. DOI: 10.12966/abc.02.05.2016
- Leeds A, Boyer D, Ross SR, & Lukas KE (2015). The effects of group type and young silverbacks on wounding rates in western lowland gorilla (*Gorilla gorilla gorilla*) groups in North American zoos. *Zoo Biology*, 34(4), 296–304. doi: 10.1002/zoo.21218 [PubMed: 26094937]
- Less E, Kuhar C, & Lukas K (2013). Assessing the prevalence and characteristics of hair-plucking behaviour in captive western lowland gorillas (*Gorilla gorilla gorilla*). *Animal Welfare*, 22(2), 175–183(9). doi: 10.1002/ajp.22751
- Lincoln H, Andrews MW, & Rosenblum LA (1995). Pigtail macaque performance on a challenging joystick task has important implications for enrichment and anxiety within a captive environment. *Laboratory Animal Science*, 45(3), 264–268. <http://europepmc.org/abstract/MED/7650896> [PubMed: 7650896]
- Line SW, Morgan KN, Markowitz H, & Strong S (1990). Increased cage size does not alter heart rate or behavior in female rhesus monkeys. *American Journal of Primatology*, 20, 107–113. 10.1002/ajp.1350200205
- Lopresti-Goodman SM, Kameka M, & Dube A (2013). Stereotypical behaviors in chimpanzees rescued from the African bushmeat and pet trade. *Behavioral Sciences*, 3(1), 1–20. doi: 10.3390/bs3010001 [PubMed: 25379223]
- Lutz CK (2014). Stereotypic behavior in nonhuman primates as a model for the human condition. *ILAR Journal*, 55(2), 284–296. 10.1093/ilar/ilu016 [PubMed: 25225307]
- Lutz CK (2018). A cross-species comparison of abnormal behavior in three species of singly-housed old world monkeys. *Applied Animal Behaviour Science*, 199, 52–58. doi: 10.1016/j.applanim.2017.10.010 [PubMed: 29422700]
- Lutz CK, & Brown TA (2018). Porches as enrichment for singly housed cynomolgus macaques (*Macaca fascicularis*). *Journal of the American Association for Laboratory Animal Science*, 57(2), 134–137. [PubMed: 29555002]
- Lutz CK, Coleman K, Worlein J, & Novak MA (2013). Hair loss and hair-pulling in rhesus macaques (*Macaca mulatta*). *Journal of the American Association for Laboratory Animal Science*, 52(4), 454–457. [PubMed: 23849443]
- Lutz CK, Davis EB, Ruggiero AM, & Suomi SJ (2007). Early predictors of self-biting in socially-housed rhesus macaques (*Macaca mulatta*). *American Journal of Primatology*, 69(5), 584–590. doi: 10.1002/ajp.20370. [PubMed: 17216620]
- Lutz CK, & Farrow RA (1996). Foraging device for singly housed longtailed macaques does not reduce stereotypies. *Contemporary Topics*, 35, 75–78.

- Lutz C, Marinus L, Chase W, Meyer J, & Novak M (2003). Self-injurious behavior in male rhesus macaques does not reflect externally directed aggression. *Physiology & Behavior*, 78(1), 33–39. 10.1016/S0031-9384(02)00886-7 [PubMed: 12536008]
- Lutz C, Tiefenbacher S, Meyer J, & Novak M (2004). Extinction deficits in male rhesus macaques with a history of self-injurious behavior. *American Journal of Primatology*, 63(2), 41–48. 10.1002/ajp.20037 [PubMed: 15195326]
- Lutz C, Well A, & Novak M (2003). Stereotypic and self-injurious behavior in rhesus macaques: A survey and retrospective analysis of environment and early experience. *American Journal of Primatology*, 60(1), 1–15. 10.1002/ajp.10075
- Lutz CK, Williams PC, & Sharp RM (2014). Abnormal behavior and associated risk factors in captive baboons (*Papio hamadryas* spp.). *American Journal of Primatology*, 76(4), 355–361. 10.1002/ajp.22239 [PubMed: 24323406]
- Macy JD, Beattie TA, Morgenstern SE, & Arnsten AF (2000). Use of guanfacine to control self-injurious behavior in two rhesus macaques (*Macaca mulatta*) and one baboon (*Papio anubis*). *Comparative Medicine*, 50(4), 419–425. [PubMed: 11020162]
- Mallapur A, & Choudhury B (2003). Behavioral abnormalities in captive nonhuman primates. *Journal of Applied Animal Welfare Science*, 6(4), 275–284. 10.1207/s15327604jaws0604\_2 [PubMed: 14965782]
- Mallapur A, Sinha A, & Waran N (2005). Influence of visitor presence on the behaviour of captive lion-tailed macaques (*Macaca silenus*) housed in Indian zoos. *Applied Animal Behaviour Science*, 94(3–4), 341–352. DOI:10.1016/j.applanim.2005.02.012
- Maple TL, & Finlay TW (1986). Evaluating the environments of captive nonhuman primates. In Benirschke K (Ed.) *Primates. Proceedings in Life Sciences* (pp. 479–488). New York, NY: Springer. 10.1007/978-1-4612-4918-4\_38
- Marriner L, & Drickamer L (1994). Factors influencing stereotyped behavior of primates in a zoo. *Zoo Biology*, 13(3), 267–275. DOI: 10.1002/ZOO.1430130308
- Martin AL (2017). The primatologist as a behavioral engineer. *American Journal of Primatology*, 79(1), e22500. doi: 10.1002/ajp.22500
- Martin AL, Bloomsmith MA, Kelley ME, Marr MJ, & Maple TL (2011). Functional analysis and treatment of human-directed undesirable behavior exhibited by a captive chimpanzee. *Journal of Applied Behavior Analysis*, 44(1), 139–143. doi: 10.1901/jaba.2011.44-139 [PubMed: 21541106]
- Martin AL, Franklin AN, Perlman JE, & Bloomsmith MA (2018). Systematic assessment of food item preference and reinforcer effectiveness: Enhancements in training laboratory-housed rhesus macaques. *Behavioural Processes*, 157, 445–452. 10.1016/j.beproc.2018.07.002 [PubMed: 30003936]
- Martin P, & Bateson PPG (2007). *Measuring Behaviour: An Introductory Guide*. Cambridge, England: Cambridge University Press.
- Mason GJ (1991). Stereotypes: a critical review. *Animal Behaviour*, 41(6), 1015–1037. 10.1016/S0003-3472(05)80640-2
- Mason G (1993). Forms of stereotypic behaviour. In Lawrence AB & Rushen J (Eds.), *Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare* (pp. 7–40). Wallingford, UK: CAB International.
- Mason G, Burn CC, Dallaire JA, Kroshko J, Kinkaid HM, & Jeschke JM (2013). Plastic animals in cages: behavioural flexibility and responses to captivity. *Animal Behaviour*, 85(5), 1113–1126. 10.1016/j.anbehav.2013.02.002
- Mason, & Latham NR (2004). Can't stop, won't stop: is stereotypy a reliable animal welfare indicator? *Animal Welfare*, 13(Suppl), S57–S69.
- Mason GJ, & Turner MA (1993). Mechanisms involved in the development and control of stereotypies. In Bateson PPG, Klopfer PH, & Thompson NS (Eds.), *Perspectives in Ethology* (Vol. 10 - Behavior and Evolution, pp. 53–85). New York, NY: Plenum Press.
- McBride SD, & Cuddeford D (2001). The putative welfare-reducing effects of preventing equine stereotypic behaviour. *Animal Welfare*, 10(2), 173–189.

- McGrogan H, & King JE (1982). Repeated separations of 2-year-old squirrel monkeys from familiar mother surrogates. *American Journal of Primatology*, 3(1-4), 285–290. [PubMed: 31991991]
- McKinney WT, Moran E, Kraemer G, & Prange A (1980). Long-term chlorpromazine in rhesus monkeys: Production of dyskinesias and changes in social behavior. *Psychopharmacology*, 72(1), 35–39. doi: 10.1007/BF00433805 [PubMed: 6781005]
- Mitchell GD, Raymond E, Ruppenthal G, & Harlow H (1966). Long-term effects of total social isolation upon behavior of rhesus monkeys. *Psychological Reports*, 18(2), 567–580. 10.2466/pr0.1966.18.2.567
- Morgan KN, & Tromborg CT (2007). Sources of stress in captivity. *Applied Animal Behaviour Science*, 102(3), 262–302. 10.1016/j.applanim.2006.05.032
- Moshiri A, Chen R, Kim S, Harris RA, Li Y, Raveendran M, Davis S, Liang Q, Pomerantz O, & Wang J (2019). A nonhuman primate model of inherited retinal disease. *The Journal of Clinical Investigation*, 129(2), 863–874. [PubMed: 30667376]
- Nash LT, Fritz J, Alford P, & Brent L (1999). Variables influencing the origins of diverse abnormal behaviors in a large sample of captive chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, 48(1), 15–29. doi: 10.1002/(SICI)1098-2345(1999)48:1<15::AID-AJP2>3.0.CO;2-R. [PubMed: 10326768]
- Nevill CH, & Lutz CK (2015). The effect of a feeding schedule change and the provision of forage material on hair eating in a group of captive baboons (*Papio hamadryas* sp.). *Journal of Applied Animal Welfare Science*, 18(4), 319–331. doi: 10.1080/10888705.2014.980888 [PubMed: 25415057]
- Noldus LP, Spink AJ, & Tegelenbosch RA (2001). EthoVision: a versatile video tracking system for automation of behavioral experiments. *Behavior Research Methods, Instruments, & Computers*, 33(3), 398–414. 10.3758/BF03195394
- Novak MA (2003). Self-injurious behavior in rhesus monkeys: new insights into its etiology, physiology, and treatment. *American Journal of Primatology*, 59(1), 3–19. doi: 10.1002/ajp.10063. [PubMed: 12526035]
- Novak MA (2020). Self-Injurious behavior in rhesus macaques: Issues and challenges. *American Journal of Primatology*, e23222. 10.1002/ajp.23222
- Novak MA, Kelly BJ, Bayne K, & Meyer JS (2012). Behavioral disorders of nonhuman primates. In Abee C, Mansfield K, Tardif S, & Morris T (Eds.), *Nonhuman Primates in Biomedical Research Biology and Management* (Vol. 1, pp. 177–196). Waltham, MA: Elsevier.
- Novak M, Kinsey J, Jorgensen M, & Hazen T (1998). Effects of puzzle feeders on pathological behavior in individually housed rhesus monkeys. *American Journal of Primatology*, 46(3), 213–227. doi: 10.1002/(SICI)1098-2345(1998)46:3<213::AID-AJP3>3.0.CO;2-L. [PubMed: 9802512]
- Novak MA, & Meyer JS (2009). Alopecia: possible causes and treatments, particularly in captive nonhuman primates. *Comparative Medicine*, 59(1), 18–26. [PubMed: 19295051]
- Novak MA, & Meyer JS (2021). A rhesus monkey model of non-suicidal self-injury. *Frontiers in Behavioral Neuroscience*, 15:674127. doi: 10.3389/fnbeh.2021.674127
- Novak M, Meyer J, Lutz C, & Tiefenbacher S (2006). Deprived environments: Developmental insights from primatology. In Mason G & Rushen J (Eds.), *Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare* (pp. 153–189). Wallingford, UK: CAB International.
- Novak MA, & Suomi SJ (2008). Abnormal behavior in nonhuman primates and models of development. In Burbacher TM, Sackett GPGP, & Grant KS (Eds.), *Primate Models of Children's Health and Developmental Disabilities* (pp. 141–160). Waltham, MA: Elsevier.
- Papailiou A, Sullivan E, & Cameron JL (2008). Behaviors in rhesus monkeys (*Macaca mulatta*) associated with activity counts measured by accelerometer. *American Journal of Primatology*, 70(2), 185–190. doi: 10.1002/ajp.20476 [PubMed: 17854071]
- Paulk H, Dienske H, & Ribbens L (1977). Abnormal behavior in relation to cage size in rhesus monkeys. *Journal of Abnormal Psychology*, 86(1), 87–92. doi: 10.1037//0021-843x.86.1.87 [PubMed: 402405]
- Pazol K, & Bloomsmith M (1993). The development of stereotyped body rocking in chimpanzees (*Pan troglodytes*) reared in a variety of nursery settings. *Animal Welfare*, 2(2), 113–129.



- Perlman J, Martin A, & Bloomsmith M (2018). Increases in feeding and destructible enrichment distribution in caged rhesus macaques (*Macaca mulatta*) provide some behavioral benefits. *American Journal of Primatology*, 80(S1), 19.
- Perlman JE, Bloomsmith MA, Whittaker MA, McMillan JL, Minier DE, & McCowan B (2012). Implementing positive reinforcement animal training programs at primate laboratories. *Applied Animal Behaviour Science*, 137(3–4), 114–126. 10.1016/j.applanim.2011.11.003
- Perlman JE, Martin AL, Brennan CR, & Bloomsmith MA (2016). Optimizing behavior assessment programs: evaluation of frequency and duration of observation periods to detect abnormal behavior in caged rhesus macaques. IPS/ASP Joint Meeting, Chicago, IL.
- Piazza CC, Fisher WW, Hanley GP, LeBlanc LA, Worsdell AS, Lindauer SE, & Keeney KM (1998). Treatment of pica through multiple analyses of its reinforcing functions. *Journal of Applied Behavior Analysis*, 31(2), 165–189. doi: 10.1901/jaba.1998.31-165 [PubMed: 9652098]
- Pirovino M, Heistermann M, Zimmermann N, Zingg R, Clauss M, Codron D, Kaup F-J, & Steinmetz HW (2011). Fecal glucocorticoid measurements and their relation to rearing, behavior, and environmental factors in the population of pileated gibbons (*Hylobates pileatus*) held in European zoos. *International Journal of Primatology*, 32(5), 1161. 10.1007/s10764-011-9532-9
- Platt DM, & Novak MA (1997). Videostimulation as enrichment for captive rhesus monkeys (*Macaca mulatta*). *Applied Animal Behaviour Science*, 52(1–2), 139–155. 10.1016/S0168-1591(96)01093-3
- Polanco A (2021). Validating markers of cumulative experience in laboratory rhesus monkeys (*Macaca mulatta*) [Doctoral dissertation, University of Guelph]. The Atrium, University of Guelph. <https://hdl.handle.net/10214/26586>
- Polanco A, McCowan B, Niel L, Pearl DL, & Mason G (2021). Recommendations for Abnormal Behaviour Ethograms in Monkey Research. *Animals*, 11(5). 10.3390/ani11051461
- Pomerantz O, Meiri S, & Terkel J (2013). Socio-ecological factors correlate with levels of stereotypic behavior in zoo-housed primates. *Behavioural Processes*, 98, 85–91. 10.1016/j.beproc.2013.05.005 [PubMed: 23694743]
- Pomerantz O, Paukner A, & Terkel J (2012). Some stereotypic behaviors in rhesus macaques (*Macaca mulatta*) are correlated with both perseveration and the ability to cope with acute stressors. *Behavioural Brain Research*, 230(1), 274–280. 10.1016/j.bbr.2012.02.019 [PubMed: 22366267]
- Pomerantz O, & Terkel J (2009). Effects of positive reinforcement training techniques on the psychological welfare of zoo-housed chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, 71(8), 687–695. 10.1002/ajp.20703 [PubMed: 19434627]
- Pomerantz O, Terkel J, Suomi SJ, & Paukner A (2012). Stereotypic head twirls, but not pacing, are related to a ‘pessimistic’-like judgment bias among captive tufted capuchins (*Cebus apella*). *Animal Cognition*, 15(4), 689–698. 10.1007/s10071-012-0497-7 [PubMed: 22526692]
- Pryor K (2002). *Don’t Shoot the Dog!: The New Art of Teaching and Training*. Gloucestershire, UK: Ringpress Books Ltd.
- Ramirez J, Guarner F, Bustos Fernandez L, Maruy A, Sdepanian VL, & Cohen H (2020). Antibiotics as Major Disruptors of Gut Microbiota. *Frontiers in Cellular and Infection Microbiology*, 10(731). 10.3389/fcimb.2020.572912
- Reamer L, Tooze Z, Coulson C, & Semple S (2010). Correlates of self-directed and stereotypic behaviours in captive red-capped mangabeys (*Cercocebus torquatus torquatus*). *Applied Animal Behaviour Science*, 124(1–2), 68–74. 10.1016/j.applanim.2010.01.012
- Rennie A, & Buchanan-Smith H (2006). Refinement of the use of non-human primates in scientific research. Part I: the influence of humans. *Animal Welfare*, 15(3), 203–213.
- Rimbach R, Heymann EW, Link A, Heistermann M (2013). Validation of an enzyme immunoassay for assessing adrenocortical activity and evaluation of factors that affect levels of fecal glucocorticoid metabolites in two New World primates. *General and Comparative Endocrinology* 191,13–23. doi: 10.1016/j.ygcen.2013.05.010 [PubMed: 23707497]
- Rommeck I, Anderson K, Heagerty A, Cameron A, & McCowan B (2006). Risk factors and remediation of self-injurious and self-abuse behavior in rhesus macaques. *Journal of Applied Animal Welfare Science*, 9(4), 261–268. doi: 10.1207/s15327604jaws0904\_1 [PubMed: 17209750]

- Rommeck I, Anderson K, Heagerty A, Cameron A, & McCowan B (2009). Risk factors and remediation of self-Injurious and self-abuse behavior in rhesus macaques. *Journal of Applied Animal Welfare Science*, 12(1), 61–72. 10.1080/10888700802536798 [PubMed: 19107665]
- Rommeck I, Gottlieb DH, Strand SC, & McCowan B (2009). The effects of four nursery rearing strategies on infant behavioral development in rhesus macaques (*Macaca mulatta*). *Journal of the American Association for Laboratory Animal Science*, 48(4), 395–401. [PubMed: 19653949]
- Rose C, De Heer R, Korte S, Van der Harst J, Weinbauer G, & Spruijt B (2012). Quantified tracking and monitoring of diazepam treated socially housed cynomolgus monkeys. *Regulatory Toxicology and Pharmacology*, 62(2), 292–301. doi: 10.1016/j.yrtph.2011.10.008 [PubMed: 22051156]
- Ross SR (2010). How cognitive studies help shape our obligation for the ethical care of chimpanzees. In Lonsdorf EV, Ross SR, & Matsuzawa T (Eds.), *The Mind of the Chimpanzee: Ecological and Experimental Perspectives* (pp. 309–319). Chicago, IL: University of Chicago Press.
- Ross SR, Lake BR, Fultz AF, & Hopper LM (2021). An evaluation of thermal imaging as a welfare monitoring tool for captive chimpanzees. *Primates*, 62(6), 919–927. doi: 10.1007/s10329-021-00943-5. [PubMed: 34476667]
- Schapiro SJ, Bloomsmith MA, & Laule GE (2003). Positive reinforcement training as a technique to alter nonhuman primate behavior: quantitative assessments of effectiveness. *Journal of Applied Animal Welfare Science*, 6(3), 175–187. 10.1207/S15327604JAWS0603\_03 [PubMed: 14612266]
- Sherwen SL, & Hemsforth PH (2019). The visitor effect on zoo animals: Implications and opportunities for zoo animal welfare. *Animals*, 9(6), 366. doi: 10.3390/ani9060366
- Shively CA, Register TC, Adams MR, Golden DL, Willard SL, & Clarkson TB (2008). Depressive behavior and coronary artery atherogenesis in adult female cynomolgus monkeys. *Psychosomatic Medicine*, 70(6), 637–645. 10.1097/PSY.0b013e31817eaf0b [PubMed: 18596246]
- Snyder DS, Graham CE, Bowen JA, & Reite M (1984). Peer separation in infant chimpanzees, a pilot study. *Primates*, 25(1), 78–88.
- Stanwicks LL, Hamel AF, & Novak MA (2017). Rhesus macaques (*Macaca mulatta*) displaying self-injurious behavior show more sleep disruption than controls. *Applied Animal Behaviour Science*, 197, 62–67. doi: 10.1016/j.applanim.2017.09.002 [PubMed: 29276322]
- Suomi SJ, Eisele CD, Grady SA, & Harlow HF (1975). Depressive behavior in adult monkeys following separation from family environment. *Journal of Abnormal Psychology*, 84(5), 576–578. 10.1037/h0077066 [PubMed: 811700]
- Suomi SJ, Harlow HF, & Kimball SD (1971). Behavioral effects of prolonged partial social isolation in the rhesus monkey. *Psychological Reports*, 29(3\_suppl), 1171–1177. doi: 10.2466/pr0.1971.29.3f.1171 [PubMed: 5003142]
- Swaigood RR, & Shepherdson DJ (2005). Scientific approaches to enrichment and stereotypies in zoo animals: what's been done and where should we go next? *Zoo Biology*, 24(6), 499–518. 10.1002/zoo.20066
- Tarou LR, Bloomsmith MA, & Maple TL (2005). Survey of stereotypic behavior in prosimians. *American Journal of Primatology*, 65(2), 181–196. 10.1002/ajp.20107 [PubMed: 15706583]
- Teichroeb JA, Corewyn LC, & Paterson JD (2021). *Primate Behavior: An Exercise Workbook*. Long Grove, IL: Waveland Press.
- Thierry B (1984). Descriptive and contextual analysis of eye covering behavior in captive rhesus macaques (*Macaca mulatta*). *Primates*, 25(1), 62–77.
- Tiefenbacher S, Fahey MA, Rowlett JK, Meyer JS, Pouliot AL, Jones BM, & Novak MA (2005). The efficacy of diazepam treatment for the management of acute wounding episodes in captive rhesus macaques. *Comparative medicine*, 55(4), 387–392. [PubMed: 16158915]
- Trollope J (1977). A preliminary survey of behavioural stereotypes in captive primates. *Laboratory Animals*, 11(3), 195–196. 10.1258/00236777780936666 [PubMed: 560606]
- Truelove MA, Martin AL, Perlman JE, Wood JS, & Bloomsmith MA (2017). Pair housing of Macaques: A review of partner selection, introduction techniques, monitoring for compatibility, and methods for long-term maintenance of pairs. *American Journal of Primatology*, 79(1), 1–15. 10.1002/ajp.22485

- United States Department of Agriculture, & Animal and Plant Health Inspection Service, A. and Plant Health Inspection Service. (2017).
- Vandeleest JJ, McCowan B, & Capitanio JP (2011). Early rearing interacts with temperament and housing to influence the risk for motor stereotypy in rhesus monkeys (*Macaca mulatta*). *Applied Animal Behaviour Science*, 132(1–2), 81–89. doi: 10.1016/j.applanim.2011.02.010 [PubMed: 21537494]
- Veeder CL, Bloomsmith MA, McMillan JL, Perlman JE, & Martin AL (2009). Positive reinforcement training to enhance the voluntary movement of group-housed sooty mangabeys (*Cercocebus atys atys*). *Journal of the American Association for Laboratory Animal Science*, 48(2), 192–195. [PubMed: 19383217]
- Vickery S, & Mason G (2004). Stereotypic behavior in Asiatic black and Malayan sun bears. *Zoo Biology*, 23(5), 409–430. 10.1002/zoo.20027
- Videan EN, Fritz J, Schwandt ML, Smith HF, & Howell S (2005). Controllability in environmental enrichment for captive chimpanzees (*Pan troglodytes*). *Journal of Applied Animal Welfare Science*, 8(2), 117–130. 10.1207/s15327604jaws0802\_4 [PubMed: 16277595]
- Vollmer TR (1994). The concept of automatic reinforcement: Implications for behavioral research in developmental disabilities. *Research in Developmental Disabilities*, 15(3), 187–207. doi: 10.1016/0891-4222(94)90011-6 [PubMed: 7938787]
- Waïtt C, & Buchanan-Smith HM (2001). What time is feeding?: How delays and anticipation of feeding schedules affect stump-tailed macaque behavior. *Applied Animal Behaviour Science*, 75(1), 75–85. 10.1016/S0168-1591(01)00174-5
- Wallace EK, Kingston-Jones M, Ford M, & Semple S (2013). An investigation into the use of music as potential auditory enrichment for moloch gibbons (*Hylobates moloch*). *Zoo Biology*, 32(4), 423–426. doi: 10.1002/zoo.21074 [PubMed: 23733310]
- Walsh S, Bramblett CA, & Alford PL (1982). A vocabulary of abnormal behaviors in restrictively reared chimpanzees. *American Journal of Primatology*, 3(1-4), 315–319. 10.1002/ajp.1350030131 [PubMed: 31992005]
- Walton A, Branham A, Gash DM, & Grondin R (2006). Automated video analysis of age-related motor deficits in monkeys using EthoVision. *Neurobiology of Aging*, 27(10), 1477–1483. doi: 10.1016/j.neurobiolaging.2005.08.003. [PubMed: 16198447]
- Wark JD, Cronin KA, Niemann T, Shender M, Horrigan A, Kao A, & Ross MR (2019). Monitoring the behavior and habitat use of animals to enhance welfare using the ZooMonitor app. *Animal Behavior and Cognition*, 6, 158–167. 10.26451/abc.06.03.01.2019
- Washburn DA, & Rumbaugh DM (1992, Sep). Investigations of rhesus monkey video-task performance: evidence for enrichment. *Contemporary Topics in Laboratory Animal Science*, 31(5), 6–10. [PubMed: 11538195]
- Watson SL, McCoy JG, Fontenot MB, Hanbury DB, & Ward CP (2009). L-tryptophan and correlates of self-injurious behavior in small-eared bushbabies (*Otolemur garnettii*). *Journal of the American Association for Laboratory Animal Science*, 48(2), 185–191. [PubMed: 19383216]
- Watters JV (2014). Searching for behavioral indicators of welfare in zoos: Uncovering anticipatory behavior. *Zoo Biology*, 33(4), 251–256. 10.1002/zoo.21144 [PubMed: 25042907]
- Weld KP, Mench JA, Woodward RA, Bolesta MS, Suomi SJ, & Higley JD (1998). Effect of tryptophan treatment on self-biting and central nervous system serotonin metabolism in rhesus monkeys (*Macaca mulatta*). *Neuropsychopharmacology*, 19(4), 314–321. doi: 10.1016/S0893-133X(98)00026-8. [PubMed: 9718594]
- Wells DL (2005). A note on the influence of visitors on the behaviour and welfare of zoo-housed gorillas. *Applied Animal Behaviour Science*, 93(1–2), 13–17. 10.1016/j.applanim.2005.06.019
- Wells DL, Coleman D, & Challis MG (2006). A note on the effect of auditory stimulation on the behaviour and welfare of zoo-housed gorillas. *Applied Animal Behaviour Science*, 100(3–4), 327–332. 10.1016/j.applanim.2005.12.003
- Whittaker M (2005). Applied problem solving to diminish abnormal behavior. *Proceedings of the Seventh International Conference of Environmental Enrichment*,

- Whittaker M, Laule G, Perlman J, Shapiro S, & Keeling M (2001). A behavioral management approach to caring for great apes. *The apes: challenges for the 21st century*. Chicago, IL.: Brookfield Zoo, 131–134.
- Wobber V, & Hare B (2011). Psychological health of orphan bonobos and chimpanzees in African sanctuaries. *PLoS One*, 6(6), e17147. 10.1371/journal.pone.0017147
- Wooddell LJ, Beisner B, Hannibal DL, Nathman AC, & McCowan B (2019). Increased produce enrichment reduces trauma in socially-housed captive rhesus macaques (*Macaca mulatta*). *American Journal of Primatology*, 81(12), e23073. doi: 10.1002/ajp.23073
- Würbel H (2001). Ideal homes? Housing effects on rodent brain and behaviour. *Trends in Neurosciences*, 24(4), 207–211. 10.1016/S0166-2236(00)01718-5 [PubMed: 11250003]
- Yamanashi Y, & Hayashi M (2011). Assessing the effects of cognitive experiments on the welfare of captive chimpanzees (*Pan troglodytes*) by direct comparison of activity budget between wild and captive chimpanzees. *American Journal of Primatology*, 73(12), 1231–1238. 10.1002/ajp.20995 [PubMed: 21905060]
- Yoshimoto T, Takahashi E, Yamashita S, Ohara K, & Niimi K (2018). Larger cages with housing unit environment enrichment improve the welfare of marmosets. *Experimental Animals*, 67(1), 31–39. doi: 10.1538/expanim.17-0058 [PubMed: 28824049]
- Zala SM, & Penn DJ (2004). Abnormal behaviours induced by chemical pollution: a review of the evidence and new challenges. *Animal Behaviour*, 68(4), 649–664. 10.1016/j.anbehav.2004.01.005