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Animal Pointing: Changing Trends and Findings from 30 Years of Research

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Abstract

The past 30 years have witnessed a continued and growing interest in the production and comprehension of manual pointing gestures in nonhuman animals. Captive primates with diverse rearing histories have shown evidence of both pointing production and comprehension, though there certainly are individual and species differences, as well as substantive critiques of how to interpret pointing or “pointing-like” gestures in animals. Early literature primarily addressed basic questions about whether captive apes point, understand pointing, and use the gesture in a way that communicates intent (declarative) rather than motivational states (imperative). Interest in these questions continues, but more recently there has been a dramatic increase in the number of papers examining pointing in a diverse array of species, with an especially large literature on canids. This proliferation of research on pointing and the diversification of species studied has brought new and exciting questions about the evolution of social cognition, and the effects of rearing history and domestication on pointing production and, more prolifically, comprehension. A review of this work is in order. In this paper we examine trends in the literature on pointing in nonhumans. Specifically, we examine publication frequencies of different study species from 1987 to 2016. We also review data on the form and function of pointing, and evidence either supporting or refuting the conclusion that various nonhuman species comprehend the meaning of pointing gestures.

Keywords: pointing, animal, nonhuman, object-choice task, referential communication

Animal Pointing: Changing Trends and Findings from 30 Years of Research

Manual pointing is a gesture that connects our physical and social worlds. Humans point in complex social contexts involving shared joint visual attention and perspective. Pointing is among the first communicative gestures to appear in human infancy, and allows child and adult to share needs, interests, and intentions (Butterworth, 1998). The early developmental origins of pointing evidence its functional utility, which remains throughout the lifespan as pointing becomes richly integrated with other aspects of symbolic gesture and speech. The need to orient the attention of conspecifics to outside entities or events is not unique to humans. Indeed, the diversity of ways in which nonhumans accomplish this is intriguing and complex. For the past three decades, comparative psychologists have pondered the evolutionary origins of the pointing gesture specifically, as well as the socio-cognitive processes that underlie it.

The vast majority of research on pointing in animals has been conducted on captive animals, and the initial studies focused on pointing in nonhuman primates (mostly apes and some monkeys). Menzel's (1974) naturalistic experiments on communication among a group of chimpanzees in a large open space demonstrated, among many things, that chimpanzees understood pointing gestures used by humans as a source of information about food locations. Pointing by apes taught to use American Sign Language or geometric lexigram symbols was described well before there was anything we could call a *pointing literature*. Many of the signs glossed as that/there/you/me, which involve index finger extension toward a specific referent, were acquired and used by signing chimpanzees (Gardner & Gardner, 1969; Gardner, Gardner, & Nichols, 1989), and pointing was a primary means by which chimpanzees and bonobos utilized the lexigram system developed at the Language Research Center (Rumbaugh, 1977; Savage-Rumbaugh, 1986; Savage-Rumbaugh et al., 1986). Woodruff and Premack (1979) were the first to systematically describe pointing by four chimpanzees, and work involving monkeys (*Macaca mulatta* and

Cebus apella) followed in the succeeding decades (Blaschke & Ettlinger, 1987; Hess, Novak, & Povinelli, 1993; Mitchell & Anderson, 1997).

Beginning in the mid-1990s, there was a surge in publications about pointing, mostly in great apes. For example, Call and Tomasello (1994) compared the pointing production and comprehension capacities of a language-trained orangutan and a nursery-reared orangutan. The language-trained subject, Chantek, demonstrated superior abilities in pointing production, comprehension of human pointing, and greater sensitivity to the attentional state of the human experimenter (e.g., eyes open versus closed) than did the nursery-reared animal. Leavens, Hopkins, and Bard (1996) reported pointing in three captive, non-language trained chimpanzees, and Krause and Fouts (1997) described the hand-shapes, accuracy, and audience effects (i.e., effects of audience visual orientation) in the pointing behavior of two language-trained chimpanzees. These early studies confirmed that the capacity for pointing is present in captive nonhuman primates and has important similarities observed in pointing by human infants and children. Namely, the pointing gestures were physically similar in form (outstretched arm with extended index finger), the meaning of the gesture was understood when others used it, and the animals showed evidence that joint visual attention was required to effectively communicate. Importantly, from early studies of pointing in nonhuman primates and onward, significant variation in each of these capacities has been observed in apes of differing rearing histories (Leavens, Bard, & Hopkins, 2010; Leavens, Hopkins, & Bard, 2005). Generally speaking, apes with more familiarity with humans point more like their human caregivers, in anatomical terms, and they display superior understanding of human nonverbal, directional cues (e.g., Lyn, Russell, & Hopkins, 2010).

Early Criticism and Debate

A peculiar aspect of the time period in which these early studies were published is that energetic debates about whether great apes actually point proceeded despite a dearth of published data that could inform either side (Povinelli & Davis, 1994; Povinelli, Bering, & Giambone, 2003). In fact, many of these debates used the absence of evidence as a basis for argument. Povinelli and Davis (1994) attempted to account for the supposed absence of pointing in chimpanzees by comparing the resting state of the

hand in humans and chimpanzees. When the forearm is held vertically and the hand at rest, the index finger of the human hand is typically slightly elevated relative to the second through fourth digits, whereas in chimpanzees, digits two through five align in parallel (Figure 1). They hypothesized that this difference reflected a morphological adaptive specialization that predisposed humans to point with the index finger extended. Butterworth (1998) offered another morphological account of the possible uniqueness of human pointing that was based on Charles Darwin's *principle of antithesis* as he had applied it to emotional expressions (Darwin, 1872). To paraphrase Darwin: For all habitual movements, there is an opposing movement that conveys the opposite state of mind (e.g., facial expressions for conveying positive versus negative affect). With regard to pointing, extension of the index finger away from the body serves to direct attention away from the individual, and the antithesis of indexical pointing is the index-thumb pincer grip that serves to bring something toward the individual. Butterworth used this concept to bolster his argument that pointing is a uniquely human adaptation. In contrast to humans, apes do not often use the tips of the index finger and thumb to form a pincer grip (but see Butterworth & Itakura, 1998; Christel, 1994, 1995; Jones-Engel & Bard, 1996). Rather, small objects are typically gathered by placing the side of the curled index finger against the object and drawing it toward the thumb until it is secured.

Insert Figure 1 here

The form of the pointing gesture was a focal point in debates about pointing in apes. Some investigators operationally defined pointing as index finger extension toward an object or event, while a similar appearing gesture that uses the whole hand constituted requesting (Blake, O'Rourke, & Borzellino, 1994; Franco & Butterworth, 1996). Wild and captive chimpanzees utilize a begging gesture consisting of a whole hand extended with upturned wrist, usually directed at a conspecific, but occasionally at the desired resource (see Hopkins & Wesley, 2002; Leavens, Hopkins, & Thomas, 2004a). Critics have suggested that the gesturing reported in studies of captive apes was akin to such food begging gestures, with mere superficial resemblance to human pointing (Povinelli, Bering, & Giambrone, 2003). The strength of this critique was reinforced by the fact that most studies of animal pointing used food as

an incentive. Thus, pointing in apes was viewed by many as a mindless, modified food begging gesture displayed by animals that presumably never point in their natural environments.

Recent research has, however, determined that pointing by captive apes meets all the criteria for intentional communication that define the human developmental transition to intentional communication. While it is true that apes (and humans) point using different hand shapes (see Figure 2), they do not point to food if nobody is there to see them gesture (Call & Tomasello, 1994; Leavens, Hopkins, & Bard, 1996; Leavens et al., 2004a; Poss, Kuhar, Stoinski, & Hopkins, 2006). Great apes adjust their signals to accommodate the visual orientation of an observer – gesturing less when an interlocutor is facing away from them, waiting for an interlocutor to turn and face them before pointing, and switching between auditory and visual channels depending on whether an interlocutor is looking at them (e.g., Bodamer & Gardner, 2002; Call & Tomasello, 1994; Hostetter, Cantero, & Hopkins, 2001; Krause & Fouts, 1997; Leavens, Hostetter, Wesley, & Hopkins, 2004; Leavens, Russell, & Hopkins, 2010; Poss et al., 2006). Great apes persist and elaborate on their communication depending on whether an interlocutor apparently understands the ape’s gestural requests (Cartmill & Byrne, 2007; Leavens, Russell, & Hopkins, 2005; Roberts, Vick, Roberts, & Menzel, 2014). Moreover, although rare, pointing – including declarative pointing – has been documented in wild populations of great apes (Hobaiter, Leavens, & Byrne, 2014; Veà & Sabater-Pi, 1998). Taken together, this body of research demonstrates that great apes use their signals tactically in much the same way that young humans demonstrate a developing awareness of the constraints on signaling efficacy. That wild apes do sometimes point, albeit rarely, suggests that exposure to human signaling conventions is not necessary for the emergence of pointing in great apes.

Insert Figure 2 here

Pointing and Context: Imperative and Declarative Communication

Pointing in humans typically originates around the time infants begin their second year, and the gesture serves multiple functions. Infants use imperative pointing to draw the attention of others toward distal entities that are needed or wanted (Bates, Camaioni, & Volterra, 1975). Thus, imperative pointing functions as a request. Declarative pointing is thought by many to differ in function from imperative

pointing. It is used for showing, for sharing information such as the location of an object (“there”), the referent of an interaction (e.g., “you”, “them”), and as a determiner (“that”). The experimental situations set up in most studies of animal pointing elicit imperative pointing (see Lyn, Greenfield, Savage-Rumbaugh, Gillespie-Lynch, & Hopkins, 2011). The alleged rarity of declarative pointing in animals, and the imperative nature of pointing or pointing-like food begging gestures, has been taken as evidence that declarative pointing is a psychological capacity unique to humans (Tomasello, Carpenter, & Liszkowski, 2007). According to “rich” interpretations of declarative pointing, it signifies human infants’ species-unique motivation to alter the contents of another’s mind, and is therefore viewed as an early precursor to theory of mind (e.g., Baron-Cohen, 1989). However, mentalistic interpretations rely on psychological processes that are quite different from those proposed by Bates and colleagues (1975), who viewed them as attempts to elicit infant-directed affective responses, such as laughter and smiling (e.g., Bates et al., 1975). Thus, much contemporary debate hinges around these competing theoretical perspectives on pointing: mentalistic vs. operant.

Moreover, declarative pointing and its apparent developmental precursors (exhibition of self, showing of objects) have been reported in great apes, including both captive and wild populations (see Leavens & Bard, 2011, for review). Virtually all language-trained apes will respond with deictic gestures when asked questions of the form, “Where is X?” (e.g., Witmer, 1909). Declarative pointing by great apes has also been described by Lyn, Greenfield, Savage-Rumbaugh, Gillespie-Lynch, and Hopkins (2011), Pedersen, Segerdahl, and Fields (2009), and in Van Cantfort, Gardner, and Gardner (1989); language-trained apes, for example, have been reported to draw attention to entities using both symbols and pointing gestures. Hence, the use of pointing to share information (i.e., declarative signaling) is well-established for great apes in the scientific literature, but there is little agreement about the psychological significance of this behavior. As discussed by Leavens (2012a,b) and also by Lyn et al. (2011), whether apes point declaratively seems to be largely a function of researchers’ pre-existing ideas about the cognitive requisites that declarative pointing entails. Leavens, Bard, and Hopkins (2017) have recently shown that the contemporary belief that declaratives must entail different cognitive processes in humans

and in nonhuman apes is not subject to empirical test; this is because pointing does not unambiguously identify its psychological bases. In brief, theoreticians who believe that pointing indexes human-specific cognitive adaptations tend to argue that examples of declarative communication by apes are over-interpreted, perhaps because their theory requires that apes lack this hypothetical underlying cognitive capacity to appreciate others as mental beings (e.g., Carpenter & Call, 2013; Tomasello et al., 2007). On the other hand, theoreticians who view pointing as a product of environmental influences on communication development tend to view declarative pointing as cognitively simple, explicable in operant terms, and therefore well within the capacities of nonhumans (e.g., Leavens, 2012a,b; Lyn et al., 2011; Moore & Corkum, 1994). Finally, hearkening back to the original definition of protodeclarative communication put forward by Bates and her colleagues (1975), pointing is just one of a suite of communicative behaviors displayed by human infants that also includes exhibition of self and the use of objects to attract attention—these kinds of communicative behaviors are widespread in the animal kingdom, in a wide variety of social contexts, including dominance displays and grooming solicitation (e.g., van Lawick-Goodall, 1968; Pika & Mitani, 2006).

Major debates about whether primates were pointing or food begging, and how scientists should interpret putative pointing gestures, ensued as publications on the topic flourished through the 1990s. A parallel interest to whether nonhuman primates could produce pointing gestures was whether they comprehended pointing by others. While some of the earlier work on pointing in primates tested for comprehension capacities (e.g., Call & Tomasello, 1994; Menzel, 1974), most of the early studies (e.g., prior to 2000) focused on production. Studies of comprehension became increasingly common as interest in pointing capacities expanded to include many non-primate species. Thus, while some of the early debates about animal pointing that originated with studies of primates continue, new and interesting questions have arisen concerning how widespread pointing capacities are among nonhumans, and the underlying developmental and evolutionary processes that support pointing.

Species Diversity of Pointing Behavior

Due to their close evolutionary relationships and behavioral and physical similarities with humans, nonhuman primates are a natural choice for comparative studies of pointing. However, as with other complex social and cognitive abilities such as mirror self-recognition (Plotnick, de Waal, & Reiss, 2006), language (Herman, Richards, & Wolz, 1984), and theory of mind (Udell, Dorey, & Wynne, 2011), comparative psychologists have expanded their scope by examining pointing in species with far greater evolutionary distances from humans.

A major shift in focus occurred with two publications on pointing comprehension in domestic dogs (Hare, Call, & Tomasello, 1998; Miklósi, Polgardi, Topál, & Csányi, 1998). The suggestion that pet dogs could perform as well as, or better than, non-human primates on human-guided tasks led to new questions about the possible origins of point-following behavior in non-primate species. Since this time the object-choice task, and its many variations, have become standard procedure for testing pointing and eye gaze comprehension in animals (Figure 3). Early hypotheses in this area focused on the role of domestication, including predictions that convergent evolution between dogs and humans may have produced a human-like social cognition in man's best friend (Hare, Brown, Williamson & Tomasello, 2002). Soon after, genetically tame and wild strains of foxes (Hare et al., 2005) and captive but genetically wild wolves (Hare et al., 2002; Miklósi et al., 2003; Kubinyi, Virányi & Miklósi, 2007; Virányi et al., 2008) were pulled into the debate. Early findings appeared to confirm dogs' superior point-following abilities compared to wild-type canids. However, later comparisons with an emphasis on equivalent rearing and testing conditions identified that human-reared wolves (Udell et al., 2008; Gácsi et al., 2009) and coyotes (Udell, Spencer, Dorey & Wynne, 2012) are capable of utilizing human points as effectively as pet dogs, given sufficient human exposure, demonstrating the importance of lifetime experience and context in the development of this behavior (Udell, Dorey & Wynne, 2010b). Since then, many studies have demonstrated that dogs living outside of human homes, including those in animal shelters (Udell, Dorey & Wynne, 2010b) and in kennels (D'Aniello et al., 2017; Lazarowski & Dorman, 2015), often fail to reliably follow human points, suggesting that while a species may have the capacity for this behavior, individual success can vary significantly due to lifetime variables and even the form of

the human pointing gesture used (Udell, Hall, Morrison, Dorey & Wynne, 2013). This debate spurred on the evaluation of a wide range of both domesticated species including goats (Kaminski, Reidel, Call, & Tomasello, 2005), horses (Maros, Gácsi & Miklósi, 2008; McKinley & Sambrook, 2000), ferrets (Hernádi, Kis, Turcsán, & Topál, 2012) and cats (Miklósi et al., 2005), and of captive wild-type species reared by humans including dolphins (Pack & Herman, 2004) and bats (Hall, Udell, Dorey, Walsh & Wynne, 2011), investigating the roles of both evolution and lifetime experience on the development of this behavior (Udell & Wynne, 2010). While these studies included many large-brained, highly social species such as cetaceans (Xitco, Gory, & Kuczaj, 2001), the inclusion of a diverse range of species of all sizes, shapes, and clades in the testing of this behavioral phenomenon is especially noteworthy and has led to a truly comparative literature on this subject matter.

Insert figure 3 here

Over the past few decades, the animal pointing literature has seen lively debate, and has brought varying scientific perspectives and species-diverse data to light. While the animal pointing literature has been previously reviewed in specific groups, such as apes (Krause, 1997; Leavens, 2004) and canids (Udell, Dorey & Wynne, 2010a), Miklósi and Soproni (2006) provided the most extensive comparison of various aspects of pointing across numerous species to date. However, much has happened in the past decade, and until now an overview of the historical trends dating to the inception of work on pointing in nonhumans has been lacking.

There were two primary objectives in producing this review. ~~Our first objective is~~First, to describe trends in the animal pointing literature over a roughly 30-year period. ~~Second, Our second objective is~~to provide a general overview of how different species have performed on different aspects of pointing. For example, research on pointing in animals has focused on whether some species are capable of producing pointing (or “pointing-like”) gestures, while another approach has been to test whether animals understand what it means when humans point. Related to production and comprehension of pointing is the attentional focus of the individual interacting with the animal. In studies of production, some researchers have tested whether animals are more likely to point when they have secured the visual

attention of a human, and in studies of comprehension, how animals respond to eye gaze cues in conjunction with pointing is often assessed. Our review examines trends in research on these aspects of pointing (production, comprehension, attentional sensitivity) and analyzes the performances of different species.

Method

We searched out and reviewed the primary literature on pointing in all nonhuman species studied. The pointing literature on humans is vast and beyond the scope of this review, and we take it as given that typically developing adult humans point and follow points, although there is both cross- and within-cultural variation in the forms of pointing (e.g., Wilkins, 2003). Indeed, the questions asked about animal pointing are largely based on studies of pointing in human infancy and early childhood. We attempted to include all peer-reviewed studies examining production or comprehension of pointing, or their combination, in nonhumans that could be identified. Much of the work in this area is labor intensive and involves species that are rare or unique in some way (e.g., language-trained animals). Thus, even those studies with very small sample sizes, in some cases just one or two individuals, were included. In addition, the roles of joint visual attention and eye gaze direction are essential to social interactions that involve pointing, and are incorporated into many study designs. If visual attentional status was manipulated or measured in the context of pointing we also recorded whether subjects were sensitive to this type of cue. There is a large collection of literature exclusively examining gaze sensitivity (audience effects) in nonhumans, and this literature was not included if pointing was not also examined in the study (see Davidson & Clayton, 2016, for a recent review on gaze sensitivity). We did not distinguish different levels of sensitivity to attentional state, such as whether gesturing occurred in eyes open versus closed conditions, or whether a human was present or absent during experimental trials.

We searched the PsycINFO and PubMed databases by separately combining “pointing (and) ...” with the following as the second search terms: monkeys, apes, chimpanzees, orangutans, gorillas, bonobos, dogs, canines. We also included papers found in a search using “pointing (and) animal (and) communication” as search terms because it is well known that pointing has been studied in many other

species. The term “referential gesture” is sometimes used as a preferred term for pointing, particularly when it comes to animal communication. Thus, we replaced “pointing” with “referential gestures” and conducted the search again using the same secondary terms through 2016. The object-choice task has become a standard, common procedure for examining comprehension of pointing. We therefore searched using “object-choice task” in conjunction with the common animal names listed above, as well as “object-choice task (and) animals”.

Because our scope was the pointing literature, and pointing is one type of the very general phenomenon of *referential communication*, we needed to impose a more refined set of criteria to address our main aims. While one could argue that waggle dances of honeybees or alarm calls in monkeys are other potential forms of referential communication, here we were specifically interested in pointing and related deictic behaviors. While we believe pointing behavior between conspecifics is fascinating in its own right, we further narrowed the focus of the current analysis to include only research involving pointing interactions between animal subjects and human experimenters, specifically to increase the level of methodological consistency across studies. For pointing production, extension of a limb and/or digit(s) to communicate about a distal entity has become a standard operational definition, but one that is only applicable to primates. We hoped to accommodate greater morphological diversity, but at the same time avoid including nearly any instance of referential communication. Thus, we included studies reporting animals using a quantifiable, ~~communicative~~ behavioral response to communicate the location of an object to a human experimenter. For example, this could include (e.g., “showing” behavior in dogs (Heberlein, Turner, Range, & Virányi, 2016)s or head and neck extension toward an out of reach object in horses (Malavasi & Huber, 2016)). While arguments could be made for additional or alternative categorizations or areas of focus, these criteria served the purpose of providing a clear focus and manageable scope for the current review. No doubt many additional areas of inquiry remain within this broad literature for future investigations.

There are also numerous peer-reviewed papers that refer to pointing gestures in animals, but do not focus on pointing specifically, and were therefore outside the purview of our work. For example,

literature dating back to the 1970s described pointing behavior in monkeys that had undergone corpus callosotomy (Beaubaton & Chapuis, 1974) or deafferentation surgery (Taub, Goldberg, & Taub, 1975). Similarly, current literature describes pointing responses by animals engaged in various cognitive tasks. For example, Bohn, Call, and Tomasello (2016) present data on whether chimpanzees communicate about absent entities. A primary dependent measure used in the study involved chimpanzees pointing to various locations within the study apparatus. However, the focus of the study was on whether chimpanzees communicate to humans about objects that are no longer present. Thus, the topic is not pointing per se, though use of the gesture was described (but was not directly quantified). It could be argued that we miss important data or misrepresent pointing behavior in animals by excluding studies such as these. However, in much of this work the pointing behavior is not described in detail or may be presented along with other communicative gestures. Also, these types of studies would not likely be suitable for describing literature trends that keeps with the intent of the researchers conducting work on pointing over this time period. Thus, during our literature search process we excluded some studies that may have included the key terms “pointing” (and) “animals”, “monkeys”, etc.

We recorded the following information from each article: Year published (in print format, or when first publicly available for online-only journals), species studied, and sample size (including all animals that at least began the study). We recorded whether production, comprehension, audience effects/gaze sensitivity or a combination of any of these three, were measured. We also recorded whether the subjects demonstrated evidence for whichever of these three behavioral measures were studied.

The last item, whether subjects showed evidence for pointing behaviors, was the most challenging to extract from the literature. Many studies involve multiple experiments, often progressing from simple to more complex tasks, or with a new variable integrated (e.g., teasing apart the effects of different gaze-related cues). Also, although the object-choice procedure is a widely used task for studying pointing comprehension and audience effects, there is a wide diversity of procedures used in the literature we reviewed (see Lyn, 2010; Mulcahy & Hedge, 2012). Finally, results are reported differently across studies. For example, some studies report group level data, typically because there is a large sample size,

whereas others report individual data for each subject (e.g., comparing each subject's performance to chance levels, and no analyses of group level results). These inconsistencies preclude making quantitative comparisons across the many studies, species, and paradigms we were interested in exploring. Therefore, we evaluated evidence for pointing based on 1) whether study authors reported statistical group-level significance on any one measure of pointing production, comprehension, or audience effects in their study, 2) whether 50% or more individual subjects showed this evidence and 3) whether any individual animal was reported as performing significantly above chance at the individual level (e.g. $p \leq 0.05$ on a one-tailed binomial test) assuming adequate individual data were presented, which is often used as a measure of behavioral capacity, even if less than 50% of the animals tested were successful. This method of scoring study results would not likely skew interspecific comparisons we can make, or general conclusions we can draw from the literature. However, this method does not offer a uniform statistical procedure or criteria for comparing studies, species, and behaviors.

Results & Discussion

Based on our search criteria, the time frame for our review begins with Blaschke and Ettlinger's (1987) experiment with rhesus monkeys (*Macaca mulatta*). Papers published between 1987 and 2016 are thus included in our review. These papers are denoted with an asterisk in the reference section. First, we provide some general descriptions of the literature, including the species for which there are reports, and changes in the types of questions asked and research emphases over the nearly 30-year period. We then describe the varying capacities for pointing in nonhumans, and, when possible, draw some comparisons on the pointing abilities among different study species.

Literature Trends

Between 1987 and 2016, a total of 136 papers, as defined by our study criteria, were published on pointing in nonhuman species. Figure 4 shows the number of papers published on pointing in five-year blocks. The past 10 years have witnessed a substantial increase in studies of pointing in animals, with 90 of the total 136 papers (66.2%) published during this time. Figure 4 also reveals the increased species diversity in the pointing literature over the study time period. Based on our search criteria, production,

comprehension, or their combination have~~s~~ been reported in over 4,000 individual animals comprising 38 different species. Among these include all four species of great apes, one gibbon, and ten species of monkey (including both New World and Old World species; see Table 1). Five species/sub-species of canid were studied within this time period. Compared to primates and canids, a smaller body of literature was found for a diverse array of species. Four papers examined pointing in three species of Pinniped, and five papers examined pointing in bottlenose dolphins. There were six papers for five species of bird (three corvids, Australian magpies, and African gray parrots). Three studies were conducted on elephants (two on African elephants, and one on Asian elephants). Also found were studies of pointing in domesticated animals including cats, pigs, goats, horses, and ferrets. A single study examined responses to pointing in bats. Increased species diversity in the pointing literature is particularly evident when comparing the study period by halves. Between 1987 and 2001, roughly the first half of the time frame for this review, publications about pointing encompassed nine species. Between 2002 and 2016, 29 additional species were studied.

Insert Table 1 and Figure 4

Overall, primates and canids are by far the most frequently represented taxonomic groups in the pointing literature (Table 1). Plotting frequencies of papers for both groups separately over the course of the review period shows a dramatic increase in studies involving canids compared with primates (Figure 5). Over the past 10 years, papers on pointing in canids have outnumbered th~~ose~~~~at~~ of primates by a nearly two-to-one ratio.

Insert Figure 5

The first papers on pointing comprehension in dogs (*Canis familiaris*) that we identified were published in 1998 (Hare, Call, & Tomasello, 1998; Miklósi, Polgardi, Topál, & Csányi, 1998). These and other early studies on dogs suggested that they were uniquely and inherently prepared to succeed on human-guided tasks, unlike their wild counterparts, as a product of domestication. Questions on the role of domestication in dogs' point comprehension abilities led to numerous studies examining responses to human pointing by genetically wild-type canids including wolves (*Canis lupus*, e.g., Hare et al., 2002,

Miklósi et al., 2003; Kubinyi, Virányi & Miklósi, 2007; Virányi et al., 2008, Udell et al., 2008, Gácsi et al., 2009), foxes (*Vulpes vulpes*, Hare et al., 2005), coyotes (*Canis latrans*, Udell, Spencer, Dorey, & Wynne, 2012) and dingoes (Smith & Litchfield, 2010). While early results were mixed, it is now well established that many wild canids have the capacity to respond to human pointing gestures given adequate socialization and experience with humans (see Udell et al., 2010, for a review), even though some individuals and populations fail to follow points. Such findings have served as an important indicator that absence of evidence for gesture responsiveness in early studies, especially where only a few individuals of a species from a single environment have been tested, should be considered with care. Demonstrations of individual capacity, where one or several individuals perform above chance, should indicate the need for further testing, even if the group average of a particular population does not appear to be statistically above chance. Importantly, a series of additional studies addressing the role of life experience and environment on the domestic dog's ability to respond to human gestures has demonstrated something quite similar. Not all domestic dogs follow human points; socialization and lifetime experience appear to be important for the development of gesture responsiveness in many species including dogs and even humans (Gácsi et al., 2009, Lazarowski & Dorman, 2015, Udell et al., 2010ab, Udell et al., 2011). Overrepresentation of pet dogs living in homes in this early research, and underrepresentation of dogs living in shelters, kennels, or in free-roaming populations, along with insufficient attention to individual level data has been increasingly addressed. ~~As a result there is, resulting in a larger~~ greater body of information about the contexts in which ~~canine point~~ comprehension of pointing by canines is most likely to develop, as well as conditions under which dogs fail to comprehend ~~human pointing points~~. However, the rich and growing literature on ~~domestic dogs' domestic dog point~~ comprehension of pointing has contributed much to our understanding of both evolutionary and lifetime sources of this behavior (Udell et al., 2010). Because large populations of domestic dogs are readily accessible to researchers around the world, and because many captive wild relatives can be accessed for comparison, this trend will likely continue.

The literature trends, both in terms of publication frequency and species diversity, also reveal changing perspectives in terms of emphasis on different aspects of pointing: namely production of pointing, comprehension of pointing by others, and sensitivity to the attentional status of communication partners (e.g., audience effects, gaze/head orientation). Studies of production are primarily restricted to species that extend forelimb and finger(s) toward distal entities (e.g., primates, but see below), ~~comprehension~~ studies of comprehension have mostly used different variations of the object-choice procedure, and attentional status has been tested using a variety of different conditions in which the salience of any social cues provided by the experimenter is manipulated. Of the 136 studies, 54 were focused on comprehension alone, 46 on both comprehension and attentional status, 16 on production alone and 14 on production and attentional status, two studies examined both production and comprehension, and four studies examined all three aspects of pointing. The object-choice procedure has become a standard method for testing animals that will, at minimum, watch what humans in their vicinity are doing. The procedure also does not require that the animal be able to point as conventionally defined (e.g., manually) or evince a distinctive, salient referential act as is the case in pointing production. These factors likely account for why 100 of the 136 (73.5%) studies have examined comprehension alone or in combination with attentional sensitivity. They also present the opportunity to describe how pointing capacities are expressed across different species.

Species Variation in Expression of Pointing Capacities

Table 2 summarizes the results of studies of pointing production, comprehension, and attentional sensitivity in the 38 species that were studied between 1987 and 2016. Overall performance on each of the three aspects of pointing for all species is summarized based on a 50% and above criteria. For example, in 11 of 12 published studies of production of pointing in chimpanzees, as least 50% of the animals ~~(n = 558)~~ tested produced pointing gestures during experimental tasks. In 10 out of 14 studies of comprehension of pointing in chimpanzees, at least 50% of ~~the chimpanzee~~ subjects ~~(n = 286)~~ reliably used human points to locate food or objects ~~in 10 out of 14 studies~~. In 10 of the 12 studies for which audience effects were manipulated at least 50% of the chimpanzees ~~tested (n = 440)~~ demonstrated

sensitivity to the attentional status of the experimenter. Some studies summarized in Table 2 examined more than one aspect of pointing (e.g., both production and attentional sensitivity) and the same animals were likely tested in separate publications. It is not feasible to control or account for this repetition, as identifying animals on an individual basis is in many cases not possible. Thus, the results in Table 2 should be interpreted with this limitation in mind.

In addition, while it might be tempting to reach broad stroke conclusions about species differences based on the results summarized in Table 2, caution is needed. For example, one might conclude that chimpanzees are not as adept at comprehending pointing as are dogs. After all, 53/53 studies of comprehension showed evidence of comprehension in dogs in comparison to the 10/14 studies with chimpanzees. Such a comparison is confounded by several factors. For instance, Hare et al. (2010) argued that no-choice data – where a dog fails to follow a point to either container during a response trial – should not be counted; only approaches to the correct or incorrect container should be scored and included in the statistical analysis. However, the majority of studies count no-choice responses as ~~and~~ incorrect or minimally account for these responses statistically in some way. Consequently, such methodological differences, especially across studies where different species are tested, could influence interpretation of results. Also, the context and format of the object-choice task may not always elicit the same kind of engagement or interest in different species. Some animals may maintain high levels of motivation even when tested on the same task repeatedly over many discrete trials (e.g., scavengers or grazing animals might be biologically prepared to engage in repetitive food getting behaviors for long periods). ~~do very well with repeated measure testing over many discrete trials,~~ whereas other species may require are more prepared to excel on shorter single trial tests or free response tests to prevent loss of interest or motivation during testing. For example, there is some research suggesting to suggest that while dogs often excel on the traditional object-choice task, ~~that~~ under more naturalistic conditions in which dogs and humans freely interact, dogs may be less likely to respond to pointing, or ~~to~~ do so with less accuracy than they do in the object-choice task (Mitchell, Reed, & Alexander, in press). Furthermore, when the task is set up as a ‘food-finding’ task (e.g. the point is used to locate food hidden in one of two

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containers), the natural foraging behavior or predatory behavior of the species may influence motivation or performance independent of socio-cognitive ability (Udell et al., 2014). Therefore, when investigating apparent species differences, many factors, including motivation level, testing methods and context, need to be addressed ~~when considering how data are scored and interpreted~~ before ~~strong hard~~ conclusions about capacity can be drawn.

Furthermore, there are many different variations on the object-choice task that manipulate the distance between objects, objects and experimenters, and objects and subjects. In some cases direct comparisons between species are possible (Miklósi & Soproni, 2006), but task variation may confound or limit species comparisons than can or have already been made. For example, when chimpanzees are tested using the distal variant of the object-choice task (containers far apart) instead of the proximal one (containers close together) they perform much better (Mulcahy & Call, 2009; Mulcahy & Hedge, 2011). However, much of the previous work done with chimpanzees that is included in this review used only the proximal method.

Insert Table 2 species performance on pointing tasks

Direct comparisons of pointing between different species, or within species of different rearing histories, have been made in 25 publications. For example, Udell, Spencer, Dorey, and Wynne (2012) compared human-socialized wolves (*Canis lupus*), pet dogs (*Canis familiaris*), and hand-raised coyotes (*Canis latrans*) using the object-choice task. At the group level, the wolves and dogs performed remarkably similarly across a variety of cue conditions (although dogs outperformed wolves in response to distal pointing from an experimenter facing away from the subject). A smaller, preliminary experiment examined how coyotes respond to momentary distal pointing by a human. One of the two animals tested selected the baited container at above chance levels (90% accuracy, reaching statistical significance). The other coyote chose correctly 70% of the time, but this outcome was not statistically significant. Hare et al. (2005) compared dogs and wild and experimentally domesticated foxes (*Vulpes vulpes*) on different versions of an object-choice task. Puppies and domesticated kits, but not wild kits, were able to use a pointing and eye gaze cue to locate hidden food (Experiment 1). Adult domesticated foxes are similarly

better able than wild foxes to use human pointing and gaze cues to locate food. However, the difference is one of magnitude, as adult wild foxes performed at above chance levels in an object-choice task (Experiment 4).

Capacity for Pointing and Interpretation of Negative Results

Eight species identified in Table 2 did not show 50% or greater performance levels on production, comprehension, attentional sensitivity or some combination of these. The species include cotton-top tamarins (Neiworth et al., 2002), ravens (Schloegl et al., 2008), Asian elephants (Plotnick et al., 2013), *Mustela* hybrids—consisting of crosses between domestic ferrets and one of several wild *Mustela* species (Hernádi et al., 2012), squirrel monkeys (Anderson et al., 2007), dingoes (Smith & Litchfield, 2010), grey seals (Shapiro et al., 2003), and African grey parrots (Giret et al., 2009). However, lessons learned from both the nonhuman primate and canid literature suggest that average and group performance may not always accurately predict species capacity. This is especially true for species where only a small number of individuals or individuals from a specific population type have been tested. For example, if the first studies of point following in dogs had exclusively been conducted in kennels (Lazarowski & Dorman, 2015) or animal shelters (Udell, Dorey & Wynne, 2010b), instead of with pet dogs, it could have easily been concluded that domestic dogs do not follow points. This would have no doubt changed the trajectory of the comparative research described in this review. Therefore, it is important to consider both examples of success and failure within a species as data requiring replication and exploration of contributing variables including degree of prior exposure to humans and environment.

Furthermore, object-choice tasks require animals to attend to the communicative behaviors of a human experimenter, which may impose an unusual and ecologically unsound situation. Miklósi and Soproni (2006) show that procedural differences in the object-choice task, such as whether a point is proximal or distal in relation to the object, can result in major differences both within and between species tested. Furthermore, what may appear to be an inability to respond or comprehend may be explained by species-typical dispositions or anatomical variations, rather than cognitive differences. Different individuals may also display different levels of motivation, especially with regard to a specific hidden

item in an object-choice task (see Vitale Shreve, Mehrkam, & Udell, 2017 for an example of how stimulus preference can affect individual motivation levels). Such factors could reduce the chances of success on such a task, especially at the group level.

Consequently, many studies now evaluate both group and individual performance on point following tasks, as successful performance by even one individual may indicate a capacity for point following or production behavior under the right environmental, experiential or developmental conditions. For example, in the current data set, we have included Neiworth, Burman, Basile, and Lickteig's (2003) study of attentional sensitivity and object-choice task performance in cotton-top tamarins (*Saguinus oedipus*). They found that, on average, the subjects did not reliably visually co-orient toward distal objects using human gaze or pointing cues alone. However, one subject did learn to use human cues in the object-choice task, and thus demonstrated the capacity for comprehension of pointing in this species. Interestingly, while visual co-orientation to a human experimenter was relatively rare, the tamarin pairs themselves frequently co-oriented toward visual stimuli. Thus, this species (and surely others) demonstrate a capacity that could remain obscured or unobserved because the object-choice task typically presents an unusual or ecologically invalid context. Whether animals show evidence for passing the object-choice task may also depend on the response measure used. Ravens show relatively weak evidence for comprehending human pointing cues, as measured by whether they will touch a baited location with their beak. However, ravens are more likely to approach (but not touch) locations that an experimenter has pointed toward (Schloegl, Kotrschal, & Bugnyar, 2008).

Different species, as well as individual animals within a species, vary in how they respond to pointing, as well as the attentional sensitivity of the humans they interact with (e.g., whether they are looking toward or away from the subject). For example, Anderson, Kuwahata and Fujita (2007) found that squirrel monkeys (*Saimiri sciureus*) can learn to produce point-like gestures, but are indifferent to whether humans are looking toward them when the monkeys point to a food-baited object. Dingoes (*Canis dingo*) comprehend a variety of types of point (e.g., momentary distal and proximal pointing, pointing with gaze cue, etc.), but are less apt at using gaze cues alone in an object-choice task (Smith &

Litchfield, 2010). The single gray seal (*Halichoerus grypus*) tested by Shapiro, Janik and Slater (2003) showed some evidence that it could learn to respond correctly to certain types of pointing gesture, but it was not sensitive to the attentional status of the experimenter. African gray parrots (*Psittacus erithacus*) reliably followed human pointing, but only one of three birds tested used proximal gaze cues alone when selecting a baited location (Giret, Miklósi, Kreutzer, & Bovet, 2009). Plotnick et al. (2013) found that one of seven Asian elephants was able to reliably follow human pointing in an object-choice task. It should be noted that while individual ability may indicate species capacity, these results should still be interpreted with care. For such examples, scientific replication remains critical to broader claims, but could provide important guidance for future research.

Hernádi, Kis, Turcsán, and Topál's (2012) study of pointing comprehension in dogs and domestic and hand-reared ferret hybrids reveals an interesting pattern of results that pertain to ongoing debates about the role of genetic selection on social and cognitive capacities. While both dogs and pet ferrets accurately followed momentary pointing in an object-choice task, many of the ferret hybrids (wild-domestic crosses) did not even complete testing, and those that did had relatively high domestic ferret blood ratios (due to fewer cross-breeds between wild and domestic lines). Still, the hybrid animals that completed testing did not succeed at the object-choice task. Thus, the authors suggested that domestication affected the socio-cognitive abilities of ferrets (Hernádi et al., 2012). However, as with the canine literature, replications exploring additional lifetime and genetic factors that could contribute to these differences would be useful. Just as care should be taken when interpreting positive results with limited subject numbers, the past literature has demonstrated the need for equal caution in ruling out the capacity for pointing comprehension in species where only a small number of animals from a specific population have failed to follow human points.

Species Comparisons: What, if Anything, Do They Tell Us?

An enduring goal of comparative psychology is to use comparisons among species to better understand the evolution of nonhuman and human behavior and cognition. However, making comparisons in meaningful and scientifically valid ways has been easier said than done. Hodos and

Campbell's (1969) suggestion that our field would do well to abandon the notion of a *scala naturae* is still worth repeating. Relatedly, Shettleworth (1993) reminded us that meaningful species comparisons are not based on mere assortments of interesting animals to study, but rather should be assembled by evolutionary and ecological logic. Also, signs of pointing or understanding of pointing by nonhumans ought to be interpreted within the ecological and developmental context of natural occurring behavior. Menzel's (1974) impressive, detailed observations of communication about object locations among a group of young chimpanzees serve as a reminder of this point. Body orientation, movement direction, and similar nonverbal cues among conspecifics may be the most salient and critical cues for deciding where to travel. For chimpanzees, as with many other species (e.g., Vail, Manica, & Bshary 2013), this may be the basis for which pointing capacities are expressed in studies of captive and wild animals.

The contents of Table 2 resemble that of many large-scale comparative reviews of a specific cognitive ability. Could we use this information to map the phylogenetic distribution of pointing in nonhumans? Might the object-choice task be a common measure by which species can be compared? Indeed, it is *plausible* that phylogenetic comparative methods could be used to study the evolution of pointing comprehension as measured by the object-choice task. Maclean et al. (2014) attempted to examine the evolution of inhibitory control in nonhumans by comparing the performance of 36 species on two standard measures (the cylinder and A-not-B tasks). Their phylogenetic analysis incorporated a massive quantity of data collected on animals from different laboratories. However, a similar approach to examining the evolution of the capacity for pointing in nonhumans is currently not possible to do in any meaningful way. While we will avoid commenting on sources of variation in performance on inhibitory control tasks, we can offer that cross-species comparisons of pointing in nonhumans will be of little value until we better understand, at very least, the developmental processes that account for pointing in both humans and nonhumans.

Skills such as pointing production and pointing comprehension have developmental foundations in great apes. For example, Leavens, Bard, and Hopkins (2010) reported that the production and comprehension of pointing by chimpanzees varies systematically with the level of exposure they have to

human (particularly western European) communicative conventions (i.e., their level of enculturation). Russell, Lyn, Schaefer, and Hopkins (2011) reported that enculturated chimpanzees significantly outperformed non-enculturated (institutionalized) chimpanzees in their comprehension of human-provided communicative cues. To date, no direct ape-human comparison on production or comprehension of pointing has matched across species for a number of factors that systematically co-vary with species classification, including testing environments, task-relevant pre-experimental experience, population sampling protocols, and testing procedures; moreover, almost all of these comparative studies compare very young human children with much older apes (Leavens, Bard, & Hopkins, 2017). To take one example, Povinelli, Bierschwale, and Čech (1999) reported that three-year-old human children performed poorly when tasked with using an experimenter's gaze to locate a baited container, when that gaze was directed to the correct hemispace, but significantly above the baited container. In contrast, adolescent chimpanzees performed well above chance in this condition. They interpreted this "species difference" to suggest that the human children had a sophisticated grasp of visual attention that prevented them from linking the averted gaze with the intended referent (the baited container); in contrast, according to Povinelli et al., the older chimpanzees lacked this sophisticated grasp of the referential nature of gaze, and so were unimpeded in using the head orientation to the correct hemispace as a cue to the location of hidden food. This interpretation was later significantly challenged by the finding that human adults responded like the adolescent chimpanzees in a partial replication of this same experimental situation (Thomas, Murphy, Pitt, Rivers, & Leavens, 2008). This suggests either (a) that the human adults had lost their sophisticated grasp of visual attention sometime after childhood, if Povinelli et al.'s interpretation is correct, or—and we think more plausibly—(b) the adolescent chimpanzees in their study had displayed the mature pattern of response to this experimental challenge, as validated by comparison with human adults (Thomas et al., 2008). Not infrequently, human infants are compared with adult apes in their production and comprehension of pointing (e.g., Liszkowski, Schäfer, Carpenter, & Tomasello, 2009; van der Goot, Tomasello, & Liszkowski, 2014), and differences in response pattern interpreted to the detriment of the apes. In fact, it is ambiguous whether the group differences reported in these studies are

attributable to differences between species in their evolutionary histories or simply differences in the life history stages at which the subjects are tested, because species classifications and life history stages are systematically confounded in these studies (see Leavens et al., 2017, Table 2). Thus, there are substantial methodological limitations in the existing literature that obviate species comparisons, especially between humans and nonhumans.

Conclusions

The literature on the capacity to produce and comprehend manual pointing among nonhuman species has undergone significant expansion and progress over the past 30 years. The diversity of species studied has grown considerably, with initial studies focusing on nonhuman primates and expanding to include many non-primate species of both wild and domesticated stock. Increased use of the object-choice task, providing a standardized measure to assess pointing comprehension, has opened up possibilities for studying pointing across many species, most of which do not communicate by extending a limb or digit and thus would not be captured by the literature examining the capacity to produce pointing gestures.

In the early phases of the 30-year period we have reviewed, investigators and critics alike focused on the basic question of whether animals, specifically nonhuman primates, are capable of pointing (Blaschke & Ettlinger, 1987; Call & Tomasello, 1994; Leavens et al., 1996; Povinelli & Davis, 1994). During the 1980s and most of the 1990s, there was no published evidence that monkeys or apes in the wild produce anything resembling a pointing gesture (but see Veà & Sebater-Pi, 1998). Thus, it seemed plausible that the pointing observed in captive primates could be a modified form of food begging seen among wild animals, or was referred to as “pointing-like” or “indicative gesturing,” with no significance or relationship to pointing by humans (Butterworth, 1998). Hand configuration was of particular interest during of the early phases of comparative research on pointing, with index finger extension exemplifying true “pointing” behavior. The variable hand shapes used by primates when pointing (or “indicative gesturing”) became a focal point of debate over whether human pointing and animal pointing were in any way similar. Indeed, index finger extension was described in some of the earlier studies of pointing in apes (Krause & Fouts, 1997; Leavens et al., 1996; Miles, 1990). The nature of captive environments,

which often include cage mesh surfaces, may have inflated the number of single-digit (e.g., index extended) points in existing reports. To this end, Leavens, Ely, Hopkins, and Bard (2012) found that pointing with index finger extension was more frequent when the apertures of the cage mesh were smaller (although some whole-hand points were extended through the smaller cage mesh apertures). A similar analysis is not available for language-trained chimpanzees (e.g., Krause & Fouts, 1997), but there are numerous descriptions and observations of language-trained chimpanzees using an extended index finger while pointing, as well as forming the hand configurations required to create many other types of gesture and sign (Gardner, Gardner, & Nichols, 1989); importantly, these index-finger points were usually not subject to external physical constraints on the shapes of the pointing hands.

One of the most challenging observations to account for is why pointing has appeared among so many captive monkeys and apes. With regard to the former, it is often the case that monkeys have been explicitly shaped through reinforcement procedures to point (e.g., Anderson, et al., 2007; Blaschke & Ettlinger, 1987). Of course, training combined with social learning could similarly account for the pointing behavior observed among captive apes, and, for that matter, humans. Referring to pointing as “spontaneous” has been taken by some to imply the operation of underlying cognitive mechanisms that cannot be fully accounted for by reinforcement history or simple associative processes—or, alternatively, an innate predisposition to use gestures to redirect the attention of others (e.g., Bohn et al., 2016; Carpenter & Call, 2013). As Leavens et al. (2017) noted:

when a behavioral scientist claims that a capability is displayed “spontaneously,” this is tantamount to a confession that the ontogenetic pathway to that capability is not known—it cannot be taken as evidence that the behavior of interest has no developmental history, nor can “spontaneous” exhibition of a behavior constitute evidence that this behavior has no learned basis. (p. 13)

As of yet we are unaware of any convincing evidence that “spontaneous” pointing could be described as either innate or insightful in any species. A more accurate account for why pointing appears in captive animals, namely apes, is that regardless of whether they are in captivity or the wild, their capacity to acquire communicative signals is wide and variable, and sensitive to social context (Leavens, Hopkins, & Bard, 2005). Thus, pointing is expressed in idiosyncratic but referentially accurate ways in both humans and nonhumans, when learning environments support the use of pointing.

Studies of pointing comprehension, which have become far more prevalent than studies of production, greatly changed the face of the nonhuman pointing literature. This trend allowed for a greater number and diversity of study species and opened up new theoretical debates. The majority of studies of pointing in nonhumans utilize the object-choice procedure to assess comprehension. Prior to the current paper, Miklósi and Soproni’s (2006) review offered the most species-diverse, direct examination of how animals perform on object-choice tasks, including along specific dimensions of pointing (e.g., proximal, distal, dynamic, momentary). At the time their review was published, pointing comprehension using the object-choice task had been tested on twelve different species (rhesus macaque and capuchin monkeys, chimpanzees, gorillas, orangutans, dogs, wolves, cats, dolphins, horses, seals and goats). As shown in our review, much has been done in the area of animal pointing in the 10 years that has passed since Miklósi and Soproni (2006). In addition to the increased diversity of species studied, theories of how pointing comprehension relates to the evolution of social cognition have also advanced. For example, initial reports suggesting that domesticated dogs are superior performers among canids in object-choice tasks now stand in contrast to results showing that wolves (and other non-domesticated canids) succeed as well (Gácsi et al., 2009; Udell, Spencer, Dorey, & Wynne, 2012; Udell, Dorey, & Wynne, 2008). Our analysis of the literature (e.g., Table 2) shows that domestication in general cannot account for species-level differences in performance on the object-choice task, although interesting cases can be found in the data on foxes (Hare et al., 2005) and ferrets (Hernádi et al., 2012).

The literature on pointing in general shares the same limitations and caveats as with other areas of study. For example, statistically non-significant results are less likely to be published than are ones

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showing significance (file drawer effect), which may lead to a generous account of how animals perform on pointing tasks. We remind ourselves that this applies to the current review. One hundred percent (53/53; see Table 2) of studies of pointing comprehension in dogs (*Canis familiaris*) reported statistically significant evidence that they understand at least some form of pointing at either the group or individual level (though, of course, not all experiments and manipulations within studies show this, and rearing history certainly plays a significant role here, D’Aniello et al., 2017). The degree to which the 53/53 figure, and all other data reported here, are inflated remains to be seen. Also, negative evidence is quite valuable in comparative studies, as the (possible) absence of a character is as useful as its presence when it comes to phylogenetic analyses.

Relatedly, the issue of replication as it pertains to studies of pointing in nonhumans requires attention. Major efforts are being made to organize and share procedures for replicating psychological research conducted on humans (Open Science Collaboration, 2015), and comparative psychology would do well to follow suit (Stevens, 2017). Research on canids and many primate species demonstrates robust evidence for pointing production or comprehension, as evidenced by the quantity of studies conducted across multiple labs showing convergent evidence. However, claims of successful replication cannot necessarily be extended across all individuals of a given species. Dogs or chimpanzees with different rearing histories, for example, do not necessarily point or respond to pointing in the same ways (Ittyerah & Gaunet, 2009; Leavens et al., 2005; Udell, Dorey, & Wynne, 2010). Also, of the 38 species in the pointing literature summarized here, 22 were represented by only a single paper each. Testing whether study results replicate among these and other species with a relatively small representation in the pointing literature is needed.

Replication, file drawer effects, and important statistical issues could be addressed by study pre-registration, data archiving, and publishing both individual and group level data. Our criteria for evaluating species capacity included whether an overall main effect was found in an omnibus test such as ANOVA, or if 50% or more of the individual animals performed above chance. To ensure we did not overlook capacity, we checked papers reporting negative results to see if at least one subject performed

above chance levels (e.g., on the object-choice task). These different ways of looking at overall results provides valuable insight into the state of the pointing literature to date, but comparative approaches to these questions would be greatly enhanced with more complete access to raw data or results of individual animals. Study pre-registration and testing for replication, however, should not replace or come at great cost to work focusing on developmental and environmental contexts that elicit pointing, or testing of yet more species that may have the capacity to understand pointing.

In summary, this analysis reveals an opposite trend in the literature from that reported by Beach (1950)—who noted the significant reduction in numbers of different taxa represented in the learning literature of the early 20th cCentury. In contrast, we find a dramatic increase in the numbers of different taxa represented in research on the production and comprehension of pointing, although many groups are still represented by only a single species. With the diversity in taxonomic representation, however, there has not been a commensurate standardization of protocols, and there are systematic confounds of method with taxon (e.g., Lyn, 2010; Mulcahy & Hedge, 2012). Early conceptions of pointing with the index finger as a human species-specific gesture derived from our unique adaptations for language have been revealed by subsequent research to be both cross-culturally and evolutionarily inadequate to account for the full range of nonverbal referential capacities manifested by a large range of vertebrate species.

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1282

Table 1

Animals Tested for Production or Comprehension of Pointing, Number of Subjects Tested, and Number of Publications Appearing between 1987 and 2016.

Group	Species	Number tested	Number of publications
Hominoidea	chimpanzees (<i>Pan troglodytes</i>)	832	28
	bonobos (<i>Pan paniscus</i>)	56	11
	gorillas (<i>Gorilla gorilla</i>)	5	3
	orangutans (<i>Pongo pygmaeus</i>)	56	10
	-gibbon (<i>Hlylobates lar</i>)	1	1
Cercopithecoidea	rhesus macaques (<i>Macaca mulatta</i>)	12	4
	long-tailed macaques (<i>Macaca fascicularis</i>)	10	1
	Tonkean macaques (<i>Macaca tonkeana</i>)	6	1
	Japanese monkey (<i>Macaca fuscata</i>)	1	1
	guenons (<i>Cercopithecus campbelli</i>)	12	1
	red-capped mangabeys (<i>Cercocebus torquatus</i>)	16	1
	olive baboons (<i>Papio anubis</i>)	21	2
Platyrrhini	capuchins (<i>Cebus apella</i>)	25	6
	squirrel monkeys (<i>Saimiri sciureus</i>)	3	1
	cotton-top tamarins (<i>Saguinus oedipus</i>)	10	1
Canidae	dogs (<i>Canis familiaris</i>) ^a	2510	57
	wolves (<i>Canis lupus</i>)	90	6
	foxes (<i>Vulpes vulpes</i>) ^a	17	1
	dingoes (<i>Canis dingo</i>)	7	1
	coyotes (<i>Canis latrans</i>)	2	1
Pinnipedia	gray seal (<i>Halichoerus grypus</i>)	1	1
	South African fur seals (<i>Arctocephalus pusillus</i>)	4	1
	sea lions (<i>Zalophus californianus</i>)	8	2

Corvidae	ravens (<i>Corvus corax</i>)	11	1
	jackdaws (<i>Corvus monedula</i>)	10	1
	Clark's nutcrackers (<i>Nucifraga columbiana</i>)	10	2
Elephantidae	African elephants (<i>Loxodonta africana</i>)	16	2
	Asian elephants (<i>Elephas maximus</i>)	7	1
<i>Miscellaneous^b</i>			
Pteropodidae	bats (<i>Pteropus</i> spp.)	4	1
Equidae	horses (<i>Equus caballus</i>) ^a	113	6
Mustelidae	ferret (<i>Mustela</i> spp.) ^a	23	1
Bovidae	goats (<i>Capra hircus</i>) ^a	34	2
Suidae	pigs (<i>Sus scrofa domestica</i>) ^a	42	2
Felidae	cats (<i>Felis catus</i>) ^a	14	1
Delphinidae	dolphins (<i>Tursiops truncatus</i>)	16	5
Artamidae	Australian magpies (<i>Gymnorhina tibicen</i>)	20	1
Psittacoidea	African gray parrots (<i>Psittacus erithacus</i>)	3	1
Totals		4027	168^c

Note. The total number of animals that completed testing and the number of papers found in PsycInfo and pubmed.gov databases for each species are given (see Method section for database search procedures). These numbers are representative of the pooled subject numbers reported across studies, thus the same animal participating in multiple studies may be counted more than once. The table is organized for convenience by parvorder, superfamily, or family.

^a Indicates domesticated animals. The fox study (Hare et al., 2005) compared groups of domesticated (n=11) and feral (n=6) subjects. The ferret study (Hernádi, Kis, Tucsán, & Topál, 2012) compared domesticated ferrets (n=13) with wild hybrid mustelids (n=10).

^b Taxa for which only a single species has been studied

^c Twenty-five studies included more than one species so the total number of papers reported here exceeds 136.

Table 2.

Summary Results from 136 Studies of Pointing Production, Comprehension and Attentional Sensitivity in 38 Species.

Group	Species	Production		Comprehension		Attentional sensitivity	
		# of papers ≥50%	# of subjects	# of papers ≥50%	# of subjects	# of papers ≥50%	# of subjects
Hominoidea	chimpanzees (<i>Pan troglodytes</i>)	11/12	558	10/14	286	10/12	440
	bonobos (<i>Pan paniscus</i>)	3/4	33	4/5	27	1/1	4
	gorillas (<i>Gorilla gorilla</i>)	1/1	1	1/2	4	1/2	4
	orangutans (<i>Pongo pygmaeus</i>)	3/4	14	6/7	49	3/3	6
	-gibbon (<i>Hylobates lar</i>)	-	-	1/1	1	1/1	1
Cercopithecoidea	rhesus macaques (<i>Macaca mulatta</i>)	2/2	9	2/3	12	1/2	11
	long-tailed macaques (<i>M. fascicularis</i>)	-	-	1/1	10	-	-
	T h onkean macaques (<i>M. tonkeana</i>)	1/1	6	-	-	-	-
	Japanese monkey (<i>M. fuscata</i>)	1/1	1	1/1	10	1/1	1
	guenons (<i>Cercopithecus campbelli</i>)	1/1	12	-	-	-	-
	red-capped mangabeys (<i>Cercocebus torquatus</i>)	1/1	16	-	-	-	-
	olive baboons (<i>Papio anubis</i>)	2/2	21	-	-	1/1	9
Platyrrhini	capuchins (<i>Cebus apella</i>)	4/4	19	2/2	6	4/4	16

	squirrel monkeys (<i>Saimiri sciureus</i>)	1/1	3	-	-	0/1	3
	cotton-top tamarins (<i>Saguinus oedipus</i>)	-	-	0/1	6	0/1	6
Canidae	dogs (<i>Canis familiaris</i>) ^a	4/4	120	53/53	2351	20/24	865
	wolves (<i>Canis lupus</i>)	1/1	8	5/5	82	-	-
	foxes (<i>Vulpes vulpes</i>) ^a	-	-	1/1	11	-	-
	foxes (<i>Vulpes vulpes</i>) [feral]			1/1	6	-	-
	dingoes (<i>Canis dingo</i>)	-	-	1/1	7	1/1	7
	coyotes (<i>Canis latrans</i>)	-	-	1/1	2	-	-
Pinnepedia	gray seal (<i>Halichoerus grypus</i>)	-	-	1/1	1	0/1	1
	South African fur seals (<i>Arctocephalus pusillus</i>)	-	-	1/1	4	1/1	4
	sea lions (<i>Zalophus californianus</i>)	-	-	2/2	8	1/2	8
Corvidae	ravens (<i>Corvus corax</i>)	-	-	0/1	11	0/1	11
	jackdaws (<i>Corvus monedula</i>)	-	-	1/1	10	1/1	10
	Clark's nutcracker (<i>Nucifraga columbiana</i>)	-	-	2/2	10	1/1	6
Elephantidae	African elephants (<i>Loxodonta africana</i>)	-	-	2/2	16	-	-
	Asian elephants (<i>Elephas maximus</i>)	-	-	0/1	7	-	-

Miscellaneous^b

Pteropodidae	bats (<i>Pteropus</i> spp.)	-	-	1/1	4	-	-
Equidae	horses (<i>Equus caballus</i>) ^a	1/1	14	4/5	97	2/2	36
Mustelidae	ferret (<i>Mustela</i> spp.) ^a	-	-	1/1	13	-	-
	ferret (<i>Mustela</i> spp.) [feral]	-	-	0/1	10	-	-
Bovidae	goats (<i>Capra hircus</i>) ^a	-	-	1/2	34	0/1	23
	pigs (<i>Sus scrofa domestica</i>) ^a	-	-	1/2	42	1/1	14
Felidae	cats (<i>Felis catus</i>) ^a	-	-	1/1	14		
Delphinidae	dolphins (<i>Tursiops truncatus</i>)	2/4	8	4/4	12	4/4	12
	Australian magpies (<i>Gymnorhina tibicen</i>)	1/1	20	-	-	1/1	20
Psittacoidea	African gray parrots (<i>Psittacus erithacus</i>)	-	-	1/1	3	0/1	3
Totals		40/45	863	112/127	3,166	56/71	1521
		(88.9%)		(88.2%)		(78.9%)	

Note. Taxonomic organization is the same as Table 1. Shown are the ratios of the number of papers in which 50% or more subjects were reported to have demonstrated each of the three capacities, and the total number of subjects that completed testing in all of the studies combined. Dashes indicate that the species has not yet been tested for production, comprehension, or attentional sensitivity during pointing interactions. Total number of papers and subjects may exceed those reported in Table 1 because some studies examined a combination of pointing production, comprehension, and attentional sensitivity, and also because the same subjects may have been tested multiple times within and across studies.

^a Indicates domesticated animals.

^b Taxa for which only a single species has been studied

Figure captions

Figure 1. Differences in resting state of chimpanzee and human hand (from Povinelli & Davis, 1994).

Figure 2. Examples of whole hand and indexical pointing in chimpanzees. A. Chester, at left, points with his whole hand towards a pile of food (photograph by Lisa A. Reamer, from Leavens et al., 2015, supporting information). B. Merv points with his index finger to a bottle of juice (photograph by David A. Leavens, from Leavens & Hopkins, 1998). C. Panzee points with her index finger to distant, hidden food (photograph by Charles R. Menzel; see Roberts et al., 2014, for full description). D. Panzee adjusts her point upwards to indicated increased distance (photograph by Charles R. Menzel; see Roberts et al., 2014, for full description). Common methods employed for testing pointing production in captive primates involves placing food that is visible but out of reach to the subjects within an occluded container. An experimenter that is blind to the location of the food then becomes available to retrieve the food in response to the subject's behavior, such as pointing.

Figure 3. A wolf participating in the object-choice task. The task is designed to test whether animals can use social cues emitted by human experimenters, such as pointing, as a source of information about the location of an object (typically food). In this task the experimenter provides a cue toward one of (usually) two containers that includes a food reward. The animal is temporarily restrained until the cue is given, and is then allowed to approach either container. The basic design varies greatly according to study species. For example, primates living in fully enclosed quarters may make their choice by gesture (Photograph by Monty Sloan).

Figure 4. Total number of papers (n=136) on nonhuman pointing behavior within time blocks (black bars) and cumulative increase in species (gray bars) represented between 1987 and 2016 in the pointing literature.

Figure 5. Publication frequencies for pointing papers in primates (monkeys and apes) and canids (dogs, wolves, foxes, dingoes, coyotes) from 1987 to 2016.

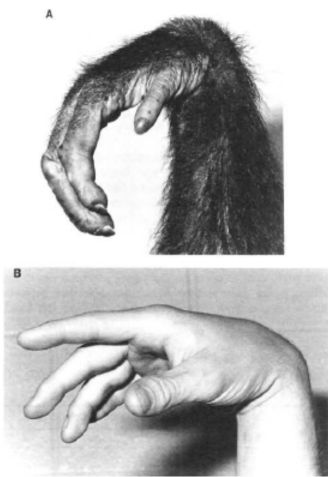


Figure 1

A.



B.



C.



D.



Figure 2



Figure 3

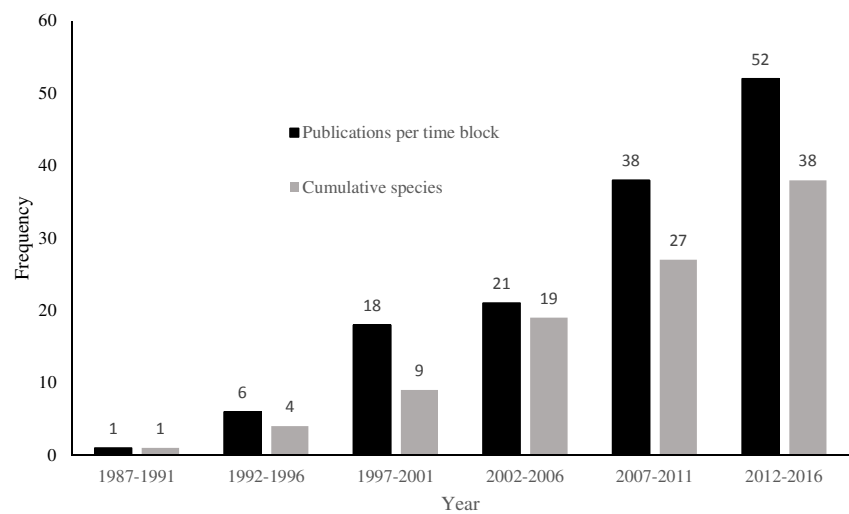
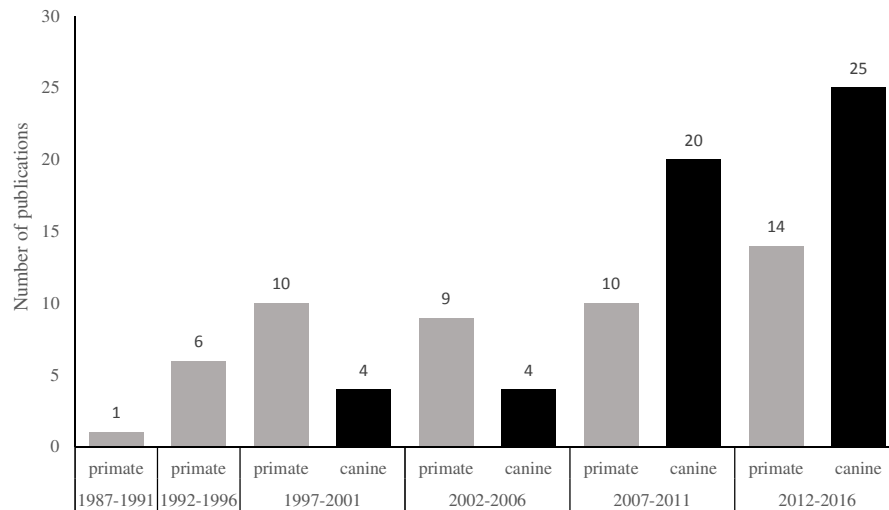


Figure 4



Note: Total publications for primates = 50, canines = 53. These numbers differ from the totals in Table 1 (72 papers on primates, 66 on canines) because several studies involving primates and canines compared multiple species within the same publication. Two studies (Bräuer et al., 2006; Kirchhofer et al., 2012) compared primates and canines in the same paper and are not included in this figure.

Figure 5.