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A Tool for Every Job: Assessing the Need for a Universal Definition of Tool Use

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Once considered only a human behavior, reports of tool use by a variety of animals have accumulated. Likewise, various definitions of tool use have also amassed. Although some researchers argue that understanding the evolutionary drivers of tool use is more important than identifying and describing these behaviors, the central issue of defining what constitutes tool use has not been fully addressed. Here we analyze prominent definitions of tool use and review the application of these definitions in scientific and educational literature. We demonstrate that many behaviors recently described as tool use do not meet criteria for prevalent definitions, while other neglected behaviors may constitute a form of tool use. These examples show how the use of inconsistent definitions of tool use in research can result in different conclusions from the same observations. Our aim is to demonstrate that a universally acceptable definition of tool use based on traditional, evolutionary, and operational understanding of behavior is needed. The rationale is that this review will stimulate the consistent and explicit use of specific terminology in tool use research. This would help define specific examples of each natural observation from a common measuring stick, allowing better comparative studies and classification of these unique behaviors.

When Plato defined man as "a two-footed featherless animal," and was applauded, Diogenes plucked a fowl and brought it in, saying, "Here is Plato's man." Afterward, Plato added, "having broad flat nails" to the definition.

-From Diogenes Laertius

Historically, prominent researchers considered tool use to be a critical behavior that separated humans from other animals (e.g., Bartholomew & Birdsell, 1953; Darwin, 1871). As time passed, however, researchers began to question that claim in light of newer evidence relating to the evolution of humans (e.g., Alcock, 1972; Lovejoy, 1981) and because of the relatively consistent discovery of apparent tool use in other species (see Bentley-Condit & Smith, 2010 and references therein). Consequently, these discoveries have generated tremendous fascination with potential tool use behavior by non-human members of the animal kingdom.

Recently, Finn, Tregenza, and Norman (2009) documented an intriguing behavior of the veined octopus (*Amphioctopus marginatus*), emphasizing that this behavior constitutes a new example of tool use. They report that these octopodes collect, carry, and then assemble shelters with discarded coconut husks. More recently, (Bernardi, 2012) documented a behavior of the orange-dotted tuskfish (*Choerodon anchorago*), where the fish uses a rock anvil, as a form of tool use. These discoveries are undoubtedly as significant as they are fascinating, but are they really

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tool use? These examples and similar behavioral studies (e.g., Caffrey, 2000; Levey, Duncan, & Levins, 2004) motivated us to question what specifically defines a behavior as tool use.

Here we examine the concept of *tool use*, review how the term is defined and applied in animal behavior studies, and discuss the common issues associated with the use of prominent definitions (Bentley-Condit & Smith, 2010; Hansell & Ruxton, 2007; Preston, 1998; St. Amant & Horton, 2008). To expand upon previous analyses of tool use concepts, we provide a concise breakdown of the prominent definitions and assess how they are applied historically and contemporarily by reviewing their application in books, primary literature, and in the classroom. Our aim is not only to offer a comprehensive discussion of tool use concepts, but to present a suitable reference for students, researchers, and educators who focus on these behaviors. This review will provide a thorough analysis of the issues surrounding tool use definitions and perhaps serve as a model that leads to further discussions of this important area of science in both classrooms and laboratories.

Background

The specific concepts used to describe and interpret animal behaviors stimulate comparative or cross-species investigations, aid classifications, and determine types of questions asked by biologists. While many research groups (e.g., Finn et al., 2009; Fragaszy, Izar, Visalberghi, Ottoni, & De Oliveira, 2004) have documented interesting behaviors that they consider forms of tool use, they often neglect to reference a precise definition of the term, making it difficult to draw explicit conclusions or critiques. This is especially problematic for scientists, teachers, and students alike, since precise definitions of phenomena are a fundamental requirement for repeatability and reproducibility in science (e.g., Jasny, Chin, Chong, & Vignieri, 2011). Perhaps such difficulties are a consequence of the variety of definitions that have been published in recent times (see Table 1). This tendency exposes an imperative and recurring issue in ethology and indeed all sciences, namely, the need for overt and universal definitions that allow for comparative analysis and repeatable scientific testing (see Abramson, 1997; 2010; Abramson & Place, 2005; Parker & Gibson, 1977; Preston, 1998; Réale, Reader, Sol, McDougall, & Dingemanse, 2007).

The use of variable definitions in biology has led to apparent contention among researchers in several instances (e.g., Hansell & Ruxton 2007). A few terms that are used regularly in biological research can serve to highlight some of the issues that can arise from ambiguity in terminology. For example, the debate over how to define a "species" is multi-sided and often heated (e.g., Coyne & Orr, 2004; Harrison, 1998; Hey, 2001, 2006; Templeton 1992). Such irresolution can generate significant problems, for instance, when the conservation status of an organism is dependent on its status as a "true species." Thus, a universal definition is warranted in this case to prevent delays in regulatory procedures.

Likewise, differential interpretations of the term "sexual selection" have resulted in an impassioned dispute regarding applications and revisions of the term. In this instance, some argue that the term sexual selection needs to be updated or redefined to align with current evidence while others vehemently disagree with the idea and make the claim that doing so would undermine the basic canons of science (Carranza, 2010; Clutton-Brock, 2010; Roughgarden & Akçay, 2010a, 2010b; Shuker, 2010). In the end, it appears that no agreement has been reached because the arguments and evidence presented are grounded in various interpretations of the definition. Consequently, comparative analyses on the topic of sexual selection will be inherently subjective.

Table 1

Categorical breakdown of the various components of published definitions of tool use. Note that for many of the definitions, at least two listed criteria must operate simultaneously to define tool use behavior (e.g. use of an external object to extend range).

Category	Paraphrased Criteria	References
Objects	Use of another living organism	Hall, 1963
	Use of an external object	Beck, 1980; Bentley-Condit & Smith, 2010; Hall, 1963; Pierce Jr., 1986; Shumaker et al. 2011; St. Amant & Horton, 2008; van Lawick-Goodall 1970
	Use of inanimate object	Alcock, 1972; Pierce Jr., 1986
	Use of object not internally manufactured	Alcock, 1972; Pierce Jr., 1986
	Use of a manipulated object	Alcock, 1972; Bentley-Condit & Smith, 2010; Pierce Jr., 1986; Shumaker et al. 2011; St. Amant & Horton, 2008
	Use of unattached object	Beck, 1980; Shumaker et al., 2011
Actions	Use of object that alters form or position	Alcock, 1972; Beck, 1980; Pierce Jr., 1986; Shumaker et al., 2011
	Use of object that alters condition	Beck, 1980; Pierce Jr., 1986; Shumaker et al., 2011
	Use of object that alters the user	Beck, 1980; Bentley-Condit & Smith, 2010; Pierce Jr., 1986; Shumaker et al., 2011; St. Amant & Horton, 2008;
	Use of object that is held	Beck, 1980; Shumaker et al., 2011
	Use of object that is carried	Beck, 1980
	Use of object that is oriented by the user	Beck, 1980; Pierce Jr., 1986; Shumaker et al., 2011;
	Adaptively relating one object to another	Matsuzawa, 2001
	Use of an object involving a dynamic interaction	Bentley-Condit & Smith, 2010; St. Amant & Horton, 2008
	Use of object as a functional extension of mouth, beak, hand, or claw	van Lawick-Goodall, 1970
	Use of an object that alters physical properties of a target	Bentley-Condit & Smith, 2010; St. Amant & Horton, 2008
Purposes	Use of object to attain an immediate goal	van Lawick-Goodall, 1970; Westergaard, 1993
	Use of object or organism to extend range of movement, increase efficiency, or gain advantage	Hall, 1963; Pierce Jr., 1986
	Use of an object to mediate the flow of information	Bentley-Condit & Smith, 2010; St. Amant & Horton, 2008

Similarly, there have been lengthy debates over the appropriate definition of "eusociality" (Batra, 1966; Costa & Fitzgerald, 1996, 2005; Crespi & Yanega, 1995; Gadagkar, 1994; Lacey & Sherman, 2005; Reeve, Sherman, & Keller, 1996; Sherman, Lacey, Reeve, & Keller, 1995; Wcislo, 1997a, 1997b; Wilson, 1971). Although these debates demonstrate that defining a term to describe observations in nature before all the "data" are in, say on the 10+ million known species, may arbitrarily limit questions and potential observations, a shared definition may work as a collective point of departure. A common, operational, and traditional definition (such as for eusociality) then could serve as a useful measuring stick.

The debate surrounding the definition of tool use is perhaps even more convoluted and certainly a common measuring stick is needed (Preston, 1998; Shumaker, Walkup, & Beck, 2011). Over time, numerous researchers have attempted to develop a universally applicable definition, an undertaking that has been easier to attempt than to accomplish (Bentley-Condit & Smith, 2010; Lestel & Grundmann, 1999; Pierce, 1986; Preston, 1998; Shumaker et al., 2011). Variation in the morphology, perceived intelligence levels, and intentions of various animals

make it an inherently difficult task (Paśko, 2010). Within primary literature, claims are often made that Beck's (1980) concept of tool use:

> the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool (page 10)

is the most influential and the validity of it has been repeatedly examined on several grounds. Morphological, behavioral, cognitive, and evolutionary differences between species have led to numerous criticisms (e.g., Lestel & Grundmann, 1999; Preston, 1998; St. Amant & Horton, 2008). Thus it is not surprising that revised versions, e.g., Shumaker et al., 2011:

> the external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool (page 5)

or entirely new definitions, e.g., St. Amant & Horton, 2008:

> the exertion of control over a freely manipulable external object (the tool) with the goal of (1) altering the physical properties of another object, substance, surface or medium (the target, which may be the tool user or another organism) via a dynamic mechanical interaction, or (2) mediating the flow of information between the tool user and the environment or other organisms in the environment (page 1203)

have been put forth recently. Nevertheless, for the purposes of behavioral description, experimentation, and analysis, a precise and universally accepted definition of the concept is still required as behavioral research on tool use continues to advance in multiple directions from an inconsistent foundation. The lack of a common or clearly identified definition makes reproducibility (see Jasny et al., 2011 and references therein) more difficult in this dynamic field of science.

A Review of Tool Use Definitions

Although Beck's (1980) definition is often considered the current standard in the field, a review of scientific literature quickly reveals an assortment of widely cited definitions of tool use (e.g., Alcock, 1972; Bentley-Condit & Smith, 2010; Hall, 1963; Matsuzawa, 2001; Pierce, 1986; Shumaker et al., 2011; St. Amant & Horton, 2008; van Lawick-Goodall, 1970; Westergaard, 1993), each of which contains a unique, although sometimes overlapping, set of criteria (Table 1). For the sake of comparison, these criteria may be summarized and divided into three broad categories: 1) types of objects used, 2) types of actions performed, and 3) purposes of the actions. When summarized, there is no criterion shared by all of these definitions and none of the definitions includes each of the criteria on the list. The only frequently shared criterion (included in seven of ten definitions) is the "use of an external object." Four of the 19 listed criteria are only included in a single author's definition. Specific details about the types of objects that may be

used (e.g., inanimate, unattached, or external), how the object is employed (e.g., by hand, foot, mouth, claw, or beak), and the types of tasks the tool must be used for (e.g., alteration of form, position, or condition of an object, organism, or self) are distinctive within each definition. Nevertheless, each of the definitions in the aforementioned publications is frequently cited in behavioral research and each of them is unique (Table 1; Appendix 1).

The problem with defining tool use in the scientific literature is also evident in the materials used to train our students. Textbooks and encyclopedias are the primary source of information for students and professionals within a given area of study (Coleman, Fanelli, & Gedeon, 2000) and are often an undergraduate's only exposure to a particular research area. As such, inconsistent definitions can be especially problematic in these settings. For example, a survey regarding the term "behavior" in textbooks produced intriguing results that demonstrated a lack of consistency among definitions and their usage (Abramson & Place, 2005). Given the many definitions associated with tool use in the scientific literature, we thought it would be informative to survey animal behavior textbooks and encyclopedias on their coverage of tool use and for discussions of definitional issues.

We selected a wide variety of books associated with the field of animal behavior to review for definitions and discussions of tool use behaviors (Table 2). The selection included a series of texts and encyclopedias in the fields of comparative psychology, learning, and zoology. These disciplines were selected because the dominant focus is the study of animal behavior. In total, we sampled 24 textbooks, seven encyclopedias, and a dictionary with publication dates ranging from 1908–2009 for the texts and from 1998–2004 for the encyclopedias; the dictionary was published in 1962. Overall the selected publications offered a highly diverse and representative sample of books dealing with the subject of animal behavior over time.

Of the 24 textbooks reviewed (Table 2) only eight discuss tool use (33%). Of these eight texts only two, Papini (2002) and Tolman (1932), made substantive comments regarding definitional issues and what constitutes a tool. The Tolman text is especially interesting because he considers language as a tool and reviews some of the pre-1932 literature on tool use in animals. The remaining six texts did not discuss definitional issues and provided only examples of animals using what the author(s) considered a tool. The series of Alcock texts (Alcock, 1989, 1998, 2001, 2005, 2009) was intriguing because the fourth edition (Alcock, 1989) includes a discussion of tool use that reviews several examples of the behavior but no definition. After 1989, however, this discussion is excluded from the series, although some of the examples are included in other sections on topics such as prey capture (Alcock, 1998, 2001, 2005, 2009). The Danchin, Giraldeau, and Cézilly (2008) text does not discuss definitions of tool use but does suggest experimental designs in which tool use can be examined. Of the seven encyclopedias reviewed (Table 2) only two discuss tool use. Both the encyclopedias edited by Bekoff (2004) and by Greenberg and Haraway (1998) provide some substantive comments on issues related to tool use. The dictionary (Hanson, 1962) provides no definition of tool or tool use behaviors. Overall, it appears that the topic of tool use is often overlooked in books and presented in an inconsistent manner.

Such discrepancies between definitions of tool use make it extremely difficult to characterize tool use behavior systematically (Bentley-Condit & Smith, 2010). This is particularly true when attempting to analyze the behaviors of different organismal groups that may have radically variable morphologies, niches, behaviors, and adaptations. Furthermore, the diversity of functional definitions provides too much potential for subjective interpretation and introduction of experimental bias as researchers may be tempted to cite the definition most suitable to their subject or the behavior they are describing, while ignoring others that may be more problematic

(Hansell & Ruxton, 2007). As long as observations and experiments are conducted within an inconsistent methodological framework, comparative analysis of tool use research is implausible. This fact directly hinders the potential for researchers to address some of the most important evolutionary issues relating to tool use behaviors, i.e. identifying instances where tool use arises for addressing problems not solved by morphological or behavioral adaptations or instances where learning or reasoning may be involved (Seed & Byrne, 2010).

Table 2
Textbooks, encyclopedias, and dictionaries on animal behavior and comparative psychology searched for the term "tool use."

	Text	**Book category**	**Information on tool use**
1	Alcock, 1989	Textbook	Discussion of examples, no definition
2	Alcock, 1998	Textbook	None
3	Alcock, 2001	Textbook	None
4	Alcock, 2005	Textbook	None
5	Alcock, 2009	Textbook	None
6	Anderson, 1995	Textbook	Briefly mention, no definition, no discussion of issues
7	Bekoff, 2004	Encyclopedia	Discussed, uses definition of Beck (1980), no discussion of issues
8	Bekoff, 2007	Encyclopedia	None
9	Byrne, 2003	Encyclopedia	None
10	Cloudsley-Thompson, 1961	Textbook	None
11	Danchin et al., 2008	Textbook	Briefly mentioned, no definition, suggests experiments
12	Denny & Ratner, 1970.	Textbook	None
13	Dugatkin, 2004	Textbook	None
14	Freeman & Herron, 2004	Textbook	Briefly mentioned, no definition, no discussion of issues
15	Goodenough et al., 2001	Textbook	None
16	Greenberg & Haraway, 1998	Encyclopedia	Detailed discussion, definition, discussion of issues
17	Hanson, 1962	Dictionary	None
18	Hutchins et al., 2004a	Encyclopedia	None
19	Hutchins et al., 2004b	Encyclopedia	None
20	Hutchins et al., 2004c	Encyclopedia	None
21	Lester, 1973	Textbook	None
22	Maier & Schneirla, 1964	Textbook	None
23	Mazur, 1990	Textbook	None
24	Papini, 2002	Textbook	Detailed discussion, definition, discussion of issues
25	Pierce & Cheney, 2008.	Textbook	None
26	Pitt, 1926	Popular text	Briefly mention, no definition, no discussion of issues
27	Stone, 1951	Textbook	None
28	Tolman, 1932	Popular text	Detailed discussion, definition, discussion of issues
29	Warden et al., 1935	Textbook	None
30	Warden et al., 1936	Textbook	Briefly mention, no definition, no discussion of issues
31	Warden et al., 1940	Textbook	None
32	Washburn, 1908	Textbook	None

Other complications arise in ethological studies (particularly for their reproducibility) because it is often unclear exactly which definitions of tool use are being used during analyses;

the diversity of seemingly acceptable definitions only exacerbates this problem (see Appendix 1). We reviewed 100 publications issued from 1887 to 2009 that describe tool use behaviors and found that less than half of them unambiguously cite the specific definition used for describing their findings (Appendix 1). For instance, Finn et al. (2009) allude to Beck's (1980) definition of tool use and briefly discuss a single feature of it: the significance of tools versus shelters, but then fail to test the behavior of the veined octopus against this definition. Bernardi (2012) makes no reference to any definition of tool use and yet makes a comparison to other tool use studies that cite different definitions from one another (Coyer, 1995; Jones, Brown, & Gardner, 2011; Paśko, 2010). Alternatively, some publications cited multiple definitions, while others defined tools but not tool use (e.g., Brockman, 1985; Clayton & Jolliffe, 1996; Fitch-Snyder & Carter, 1993; Wittiger & Sunderland-Groves, 2007). In total, 18 unique definitions of tool use were applied in the publications we reviewed (see Appendix 1).

An argument can be made that the definition of tool use is so obvious that it does not need to be included in most publications. This argument would be substantiated, for example, if students were asked to provide a definition of tool use and the definitions were similar. To provide some anecdotal information on this issue we asked students taking an upper level class on comparative psychology at a large university in the United States to provide a definition of tool use. The majority of students were in their third or fourth year of studies and they majored in a variety of subjects including zoology, psychology, and education. Prior to the exercise, the class discussed the use of tools by animals, the definition offered by Beck (1980), and examples of tool use in a variety of invertebrates and vertebrates. The discussion of tool use was part of a larger lecture on the importance of operational definitions in the analysis of behavior and the dangers associated with imprecise and conflicting definitions. Thirty definitions were collected from the students. Although the most common component included among the various definitions was the use of an external object to reach some desired goal, there was substantial variation among the definitions provided by the students (Appendix 2). For instance, based on the students' definitions, for some of them, pressing a lever in a "Skinner box" would be an example of tool use, for others it would not. This example highlights the fact that the definition of tool use is not intuitive, a claim that many researchers agree with (e.g., Seed & Byrne, 2010).

Additionally, we further questioned the argument that the definition of tool use is obvious by asking students whether invertebrates can use tools. This topic is widely cited and discussed in scientific literature (e.g., Seed & Byrne, 2010) as a borderline or paradoxical example of tool use because it is often assumed that invertebrates (e.g., insects) lack the cognitive abilities to understand causality or to demonstrate intent when using tools. The concept of causality is often included in some form as an important component of describing a behavior as tool use (Beck, 1980; St. Amant & Horton, 2008). Strikingly, twelve students believed that invertebrates can use tools while the remainder specifically excluded the use of tools by invertebrates. This near equal split of responses highlights how scholarly concepts can be interpreted differently unless they are explicitly defined. Thus, in classroom settings an exercise in which students search for definitions of tool use may be useful to stimulate further discussion on the importance of operational definitions while providing additional data on their application in contemporary sources of information.

Overall, the publication review data suggests that authors should include discussions of tool use and how it is defined. The majority of the articles and books we surveyed did not discuss tool use, and if they did, provided only cursory information. The anecdotal information gleaned from the student surveys reflects the lack of sufficient coverage. In short, the inconsistencies

within publications dealing with tool use highlight the need for an explicit and universal definition of the concept.

Tool Use Definitions in Practice

Each of the definitions that are regularly employed in scientific research has been criticized for a number of reasons (e.g., Bentley-Condit & Smith, 2010; Hansell & Ruxton, 2007; Preston, 1998; Shumaker et al., 2011; St. Amant & Horton, 2008). Since each definition includes unique components, the concept of what constitutes tool use varies greatly between them. Preston (1998), Lestel and Grundmann (1999), Hansell and Ruxton (2007), St. Amant and Horton (2008), and Shumaker et al. (2011) outline several significant cases in which tool use definitions encounter problems and lead to different conclusions. For example, tool use paradoxes can occur in such instances when an organism uses an attached object (Shumaker et al., 2011; St. Amant & Horton, 2008), when animate objects or body parts are used (Alcock, 1972; Shumaker et al., 2011), or when specific goals are considered.

Recently, St. Amant and Horton (2008) have attempted to modify and expand upon Beck's (1980) definition to alleviate many of the problems associated with it. Likewise, Shumaker et al. (2011) have updated Beck's original definition with similar intentions. Nevertheless, analytical thought experiments demonstrate that many of the existing problems with older definitions are unresolved by the new ones that have been put forth until now. As an exercise, we attempted to develop our own concise definition of tool use that is grounded in the earlier definitions of Beck (1980), St. Amant and Horton (2008), and Shumaker et al. (2011). Our aim was to address the issues associated with many of the paradoxical examples discussed in the literature. Therefore, we define tool use here as: "the deliberate and directed use of a selected object exclusive of oneself to perform an intermediate task related to the advancement of the users goal."

The way that Beck's (1980) definition treats attached objects is a primary concern among critics (Bentley-Condit & Smith, 2010; Shumaker et al., 2011; St. Amant & Horton, 2008). According to his definition, tool use behaviors require the external employment of an unattached object (Beck 1980). Beck presents the example of a rat pressing a lever on a Skinner box to receive a reward as a behavior not to be considered tool use based on the attachment clause. St. Amant and Horton (2008) argue that Beck's definition raises questions concerning unattached objects. They contend that Beck's unattached clause is actually referring to manipulability of an object and present the scenario where an inaccessible reward in a container is retrieved with a hook and string that is tied to the container as an example of tool use with an attached object. Similar examples of apparent tool use with attached objects are relatively abundant (e.g., Bernardi, 2012; Jones et al., 2011) and are troublesome for Beck's definition.

St. Amant and Horton (2008) presented a new definition to address the issue of attachment that includes a clause stating that tool use is the exertion of control over a freely manipulable external object. Shumaker et al. (2011) also expressed concern over the issue of attachment and revised Beck's original definition to state that tool use is the external employment of an unattached or manipulable attached object. Causes of concern regarding this issue seem to remain unaddressed by each of these updates, however. For example, according to each definition, an otter is using a tool when it holds a rock to pound open a shell (Hall & Schaller, 1964) whereas a wrasse is not using a tool when it pounds a shell (or other food source) on a specific rock to open it (Bernardi, 2012; Coyer, 1995; Jones et al., 2011; Paśko, 2010). Clearly, the behaviors are very similar, yet they are treated as very different by Beck (1980), St. Amant

and Horton (2008), and Shumaker et al. (2011) because the rock used by the wrasse is attached or un-manipulated. It could be argued that this distinction is simply a consequence of morphological limitations of the wrasse, however (see Paśko, 2010). It is because of examples like these that we refrained from differentiating attached objects in our own definition.

Furthermore, the rocks used by wrasses can be seen as analogous to an anvil, i.e., a common tool used by humans that is attached and does not require manipulation. In some instances, the anvil is considered a proto-tool because it is manipulated prior to use and not during (Bentley-Condit & Smith, 2010; Parker & Gibson, 1977; Shumaker et al., 2011). Returning to the otter example, however, in many instances the otter lets the stone anvil rest on its body and manipulates the shell by pounding it on the anvil. Is this behavior still to be considered true tool use? It is according to the new definitions of St. Amant and Horton (2008) and Shumaker et al. (2011) despite the fact that the behavior becomes virtually identical to that of the wrasse, which would still be excluded. Consequently, this example demonstrates that the issue of attached/unmanipulated objects in tool definitions has yet to be fully resolved and how variable conclusions can result from the chosen definition.

A second concern among critics of the early definitions of tool use is in regard to appendages, internally made objects, or "animate" objects (Shumaker et al., 2011). While many researchers would agree that identifying such objects as tools would be far too inclusive (e.g., Alcock, 1972; Shumaker et al., 2011), their exclusion is not explicit in many definitions (e.g., Beck, 1980; Shumaker et al., 2011; St. Amant & Horton, 2008). In fact, Shumaker et al. (2011) acknowledged this fact after presenting their definition by simply stating later in their work that a tool cannot be an attached part of the user's body. In light of this, the employment of the tool user's body parts is specifically excluded as a form of tool use in our definition. Still, several paradoxical instances of behaviors that make use of animate objects exist in the literature.

As an example, consider the "bait fishing" behavior of an angler fish, whereby its elongated dorsal spine with a prominent skin tag resembling a small fish is used to lure in prey (Alcock, 1998; Wilson, 1939). This behavior is in many ways comparable to the behaviors of crocodiles that use fish to lure in bird prey (Shumaker et al., 2011) and to the behavior of green herons that toss bread into a pond to attract fish which can then be captured (Lovell, 1958; Robinson, 1994). Despite the similarities of these behaviors, whether or not they are considered a form of tool use depends on the definition. It could be argued that each of these behaviors could be considered tool use according to St. Amant and Horton (2008) since each behavior involves the control of a manipulable external object. Likewise, there is nothing inherent to Beck's (1980) or Shumaker et al.'s, (2011) definitions that would exclude these behaviors although they stipulate otherwise later in their work. Conversely, according to Alcock (1972) only the heron is exhibiting tool use behavior as the others are using appendages and animate objects. Accordingly, if we accept Beck's (1980), St. Amant and Horton's (2008), or Shumaker et al.'s (2011) definitions we can consider external appendages and animate objects as tools. Alcock's definition forces us to exclude each of the behaviors while our own definition would only exclude the behavior of the angler fish.

Another example highlights the shortcomings of many tool use definitions with regard to internally produced objects. According to Alcock (1972), the use of a spider web is not a form of tool use since the web is internally produced and could perhaps be considered part of an animate object. Robinson and Robinson (1971) documented a unique behavior involving spider webs, however, whereby the ogre-faced spider (*Dinopis longipes*) makes and holds a small web which it uses to actively net prey items. This behavior seemingly fits the definitions of St. Amant and Horton (2008) and Shumaker et al. (2011), yet it could also be argued that the behavior does not

fit these definitions if the web is considered an internal object as each of these definitions excludes such objects. According to our own definition, how this behavior is perceived depends on whether the web is exclusive of the user. Thus, the example underscores how ambiguity within and among tool use definitions can lead to conflicting interpretations of the same observation.

A third concern among critics of the foundational definitions of tool use is in regard to goals (Shumaker et al., 2011; St. Amant & Horton, 2008). While it seems that most researchers would agree that tool use behaviors are aimed at some sort of goal (Alcock, 1972; Beck, 1980; Shumaker et al., 2011; St. Amant & Horton, 2008; van Lawick-Goodall, 1970), the range and scope of these goals is the subject of debate. For example, Alcock (1972), Beck (1980), and Shumaker et al. (2011) emphasize "physical" goals, i.e., altering form, position, or condition in their definitions. These criteria certainly limit the types of goals that can be attained and seem to be overly restrictive. For example, consider the use of a ruler, which could be considered comparable to the western lowland gorilla (*Gorilla gorilla*) using a stick to measure water depth (see Breuer, Ndoundou-Hockemba, & Fishlock, 2005). According to Alcock (1972), Beck (1980), and Shumaker et al. (2011) this behavior cannot be considered tool use because the goal is not to alter form, position, or condition. Thus, acceptable goals in tool use behaviors appear to have been overlooked in these definitions. For this reason, we do not stipulate specific types of goals in our own definition that are applicable to tool use behaviors.

St. Amant and Horton (2008) include goals in their definition that are similar to those that the others included but also include the goal of mediating the flow of information. Thus, according to their definition, the gorilla is using a tool when it uses a measuring stick as it is obtaining information on water depth. Likewise, a bower bird's (*Ptilonorhynchus violaceus*) use of an array of materials to construct a display for attracting a mate (Coleman, Patricelli, & Borgia, 2004) should be considered a form of tool use as it is conveying information about its suitability as a mate.

This new goal of mediating information is more problematic, however, when considering the scenario presented by St. Amant and Horton involving an orangutan (*Pongo borneo*) hiding behind a detached branch (see van Schaik et al., 2003). The authors argued that this was a form of tool use as the orangutan was mediating information via deception. By this logic, use of a wide variety of shelters to conceal an organism, e.g., hermit crab (Paguroidea) shells (Shumaker et al., 2011) or rocks barricading an octopus lair (Mather, 1994), should be considered forms of tool use. Many researchers contend that these examples do not constitute tool use, however, because the shells and rocks are effectively in use all the time (Beck, 1980; Finn et al., 2009). Conversely, Shumaker et al. (2011) accept the behavior of the hermit crab and the veined octopus (Finn et al., 2009) as tool use. Thus, the inclusion of certain specific goals in tool use definitions while omitting others has led to conflicting conclusions among tool use researchers.

A final concern about tool use definitions relates to the paradox between tool use and construction behaviors as presented by Beck (1980) and Hansell and Ruxton (2008). According to Hansell and Ruxton (2008), vertebrate nest building is considered construction behavior and indistinguishable from tool use behavior. Conversely, Beck (1980) specifically excludes the use of materials for nest construction from tool use behavior because nests are attached. St. Amant & Horton (2008) appear to reject these behaviors as well because they believe that placing any object would then be considered tool use.

It seems, however, that construction can be reasonably differentiated from tool use according to our definition based on the criteria that states a tool must be used to perform an intermediate task. This criterion separates the goal from the task and tool that is used to obtain it. Some examples are useful for highlighting this distinction and how these construction behaviors

are problematic for many definitions. First, consider a beaver's (*Castor canadensis*) use of logs to construct a dam (Naiman, Johnson, & Kelley, 1988) or a bower bird's use of an array of materials to construct a display (Coleman et al., 2004). Both of these behaviors are excluded as tool use according to Beck (1980); St. Amant and Horton (2008); and Shumaker et al. (2011) despite involving the controlled use of an object to alter the target. According to our definition, however, these construction behaviors are acceptable forms of tool use since the construction (i.e., the dam or nest) is the object used to perform the task (increase flooded area or enhance display) that advances the attainment of a goal (predator defense or mate attraction). Conversely, the use of materials in the construction of a basic shelter (e.g., as with the veined octopus or the hermit crab) can be excluded because the coconuts or shells are not used to construct the shelter; in essence, they are the shelter. Thus, paradoxes will remain for definitions without a criterion that successfully distinguishes tool use from construction behaviors.

Discussion

The various definitions of tool use put forth over the past 50 years have provided an important foundation for behavior studies. In the end, however, it seems that attempts to develop precise criteria for categorizing tool use have generated definitions of tool use that are perhaps overly restrictive or exceedingly broad. The examples presented here clearly highlight the need for a consistent basis for studying tool use behaviors and certainly additional examples of problematic behaviors for the currently accepted definitions exist (see Table 3). The examples presented here clearly highlight the need for transparency in tool use research which surely includes citing the definition that a behavior will be tested against.

Table 3
Examples of behaviors not consistently defined as tool use but which meet several criteria outlined in published definitions. Behavior categories follow Bentley-Condit & Smith (2010).

	Publication	Behavior category	Specific behavior
1	Clark & Mason, 1985; 1988	Nest construction, Other (parasite defense)	European Starlings using specific plants for nest construction whose volatiles act as pesticides and anti-pathogens
2	Hemmes et al., 2002	Nest construction, Other (parasite defense)	Wood Rats using Bay leaves with volatiles toxic to ectoparasites near sleeping nests as a fumigant
3	Lafuma et al., 2001	Nest construction, Other (parasite defense)	Corsican Blue Tits using specific mixtures of plants to repel mosquitoes and to mask chemical cues used by parasites
4	Prozesky-Shulze et al., 1975	Mate attraction	Tree crickets using modified leaves to create a sound baffle to intensify their calls
5	Thomas, 1983	Predator defense	Plain-fronted Thornbirds using thorny twigs in nest construction to deter predators

Presumably, new definitions of tool use behavior are forthcoming based on the conflicting opinions presented on the topic. New definitions should aim to include behaviors that are widely considered tool use but also to resolve the paradoxical examples that exist (e.g., Hansell & Ruxton, 2007; Preston, 1998; St. Amant & Horton, 2008). This process could certainly reform the scope of behaviors that may be considered tool use. Beck (1980) argued, however, that we must accept several important restrictions to what we consider tool use or we will render the behaviors insignificant. Thus, a universally accepted definition should be structured to maintain the claim that tool use is a unique and distinct behavioral category (Beck, 1980; Preston, 1998).

An ideal definition should address several important considerations. First, a universally acceptable definition should be evolutionarily and comparatively neutral. For example, a suitable definition should permit innate behaviors as well as intelligent behaviors to be classified or excluded as tool use under the same criteria. This will allow all forms of tool use to be encompassed under a single definition and to be delineated as unique from non-tool use behaviors prior to the assessment of other pertinent factors. An ideal definition should also deviate from the hominid-centric trends in previous definitions, such as the need to hold tools in one's hand or the need to understand how or why a tool works (Hansell & Ruxton, 2007; Shettleworth, 2009; van Lawick-Goodall, 1970). Since a significant number of insects, fish, birds, and marine mammals have been observed using tools (Brockman, 1985; Krützen, Mann, Heithaus, Connor, Bejder, & Sherwin, 2005; Paśko, 2010; Tebbich & Bshary, 2004), a neutral definition is essential for catalyzing objective analyses. This distinction should greatly enhance our abilities to systematically analyze tool use behaviors, and to generate comparative studies and meta-analyses.

Additionally, an ideal definition should eliminate the need to make judgments about the cognitive requirements of tool use. The diverse examples of tool use behaviors we reviewed represent a level of plasticity that could be due to experiential, cultural, and/or evolutionary responses to the environment. Examples of these classes of tool use include, the ability of woodpecker finches and macaques to learn the use of stick tools through experience (Anderson, 1985; Tebbich & Bshary, 2004), the cultural transmission of tool use by dolphins or captive chimpanzees (Krützen et al., 2005; Whiten, Horner, & de Waal, 2005), the apparent instinctive use of stone hammers by digger wasps (Brockman, 1985), and the various stick tool use behaviors of New Caledonian crows which may involve multiple driving forces (Kenward, Rutz, Weir, & Kacelnik, 2006). A suitable definition should allow such variable levels of sophistication to be considered under the same system so that tool use behaviors could be described systematically and then more specifically within the context of cognitive demand or level of plasticity. With a neutral definition in place, behaviors could then be further "qualified" as experiential or learning-based plasticity, indicating a certain level of cognitive involvement, as cultural, indicating a different level of cognitive involvement, as inherited behavioral differences, indicating an evolutionary process likely not directly linked to cognition, or some combination of the above.

Lastly, a universally acceptable definition should be scientifically testable. Definitions that are based on inferences or unobservable criteria raise difficulties (St. Amant & Horton, 2008). For example, if inferred components such as goals are included, they must be presented with a means to systematically test if a tool is used to obtain them.

In sum, we believe there is a high demand for an updated and universally applicable definition of tool use (Hansell & Ruxton, 2007; Lestel & Grundmann, 1999), especially because accounts of tool use behavior based on variable or unstated definitions continue to be documented and published (Bentley-Condit & Smith, 2010). In our opinion, development of a common tool use definition, perhaps along with a classification system for differentiating various categories of tool use behaviors, and an understanding of the limitations of inferences based solely on observing tool use, is critical for studying animal behavior. This review demonstrates this point and we hope it catalyzes future research and continuing discussions towards this end.

References

Abramson, C. I. (1997). Where have I heard it all before: Some neglected issues of invertebrate learning. In G. Greenberg & E. Tobach (Eds.), *Comparative psychology of invertebrates: The field and laboratory study of insect behavior* (pp. 55-78). New York, NY: Garland Publishing.

Abramson, C. I. (September, 2010). Some issues in the cognitive interpretation of invertebrate behavior. *Proceedings of the 4th European Conference of Apidology, Ankara, Turkey, 4*, 88.

Abramson, C. I., & Place, A. (2005). Note regarding the word 'behavior' in glossaries of introductory textbooks, dictionaries, and encyclopedias devoted to psychology. *Perceptual and Motor Skills, 101*, 568-574.

Alcock, J. (1972). The evolution of the use of tools by feeding animals. *Evolution, 26*, 464-473.

Alcock, J. (1989). *Animal behavior: An evolutionary approach*, 4th ed. Sunderland, MA: Sinauer Associates.

Alcock, J. (1998). *Animal behavior: An evolutionary approach*, 6th ed. Sunderland, MA: Sinauer Associates.

Alcock, J. (2001). *Animal behavior: An evolutionary approach*, 7th ed. Sunderland, MA: Sinauer Associates.

Alcock, J. (2005). *Animal behavior: An evolutionary approach*, 8th ed. Sunderland, MA: Sinauer Associates.

Alcock, J. (2009). *Animal behavior: An evolutionary approach*, 9th ed. Sunderland, MA: Sinauer Associates.

Anderson, J. (1985). Development of tool-use to obtain food in a captive group of *Macaca tonkeana*. *Journal of Human Evolution*, *14*, 637-645.

Anderson, J. (1995). *Learning and memory: An integrated approach*. New York, NY: Wiley.

Bartholomew, G., Jr., & Birdsell, J. (1953). Ecology and the protohominids. *American Anthropologist, 55*, 481-498.

Batra, S. (1966). Nests and social behavior of halictine bees of India (Hymoneptera: Halictidae). *Indian Journal of Entomology*, *28*, 375-393.

Beck, B. (1980). *Animal tool behavior: The use and manufacture of tools*. New York, NY: Garland Publishing.

Bekoff, M. (2004). *Encyclopedia of animal behavior*, Vol 3. Westport, CT: Greenwood Press.

Bekoff, M. (2007). *Encyclopedia of human-animal relationships*, Vol 4. Westport, CT: Greenwood Press.

Bentley-Condit, V., & Smith, E. (2010). Animal tool use: Current definitions and an updated comprehensive catalogue. *Behaviour*, *147*, 185-221.

Bernardi, G. (2012). The use of tools by wrasses (Labridae). *Coral Reefs*, *31*, 39.

Breuer, T., Ndoundou-Hockemba, M., & Fishlock, V. (2005). First observation of tool use in wild gorillas. *PLoS Biology*, *3*, 2041-2043.

Brockmann, H. (1985). Tool use in digger wasps (Hymenoptera: Sphecinae). *Psyche*, *92*(2/3), 309-330.

Byrne, J. (2003). *Learning and memory*. New York, NY: Macmillian Reference USA.

Caffrey, C. (2000). Tool modification and use by an American crow. *Wilson Bulletin*, *11*, 283-284.

Carranza, J. (2010). Sexual selection and the evolution of evolutionary theories. *Animal Behavior*, *79*, 5-6.

Clark, L., & Mason, J. (1985). Use of nest material as insecticidal and anti-pathogenic agents by the European starling. *Oecologia*, *67*, 169-176.

Clark, L., & Mason, J. (1988). Effect of biologically active plants used as nest material and the derived benefit to starling nestlings. *Oecologia*, *77*, 174-180.

Clayton, N., & Jolliffe, A. (1996). Marsh tits *Parus palustris* use tools to store food. *Ibis*, *138*, 554-554.

Cloudsley-Thompson, J. (1961). *Animal behavior*. New York, NY: Macmillan.

Clutton-Brock, T. (2010). We do not need a sexual selection 2.0 - nor a theory of genial selection. *Animal Behavior*, *79*, 7-10.

Coleman, S., Fanelli, A., & Gedeon, S. (2000). Psychology of the scientist: LXXII. Coverage of classical conditioning in textbooks in the psychology of learning, 1952-1995. *Psychological Reports*, *86*, 1011-1027.

Coleman, S., Patricelli, G., & Borgia, G. (2004). Variable female preferences drive complex male displays. *Nature*, *428*, 742-745.

Costa, J., & Fitzgerald, T. (1996). Developments in social terminology: Semantic battles in a conceptual war. *Trends in Ecology & Evolution*, *11*, 285-289.

Costa, J., & Fitzgerald, T. (2005). Social terminology revisited: Where are we 10 years later? *Annales Zoological Fennici*, *42*, 559-564.

Coyer, J. (1995). Use of a rock as an anvil for breaking scallops by the yellowhead wrasse *Halichoeres garnoti* (Labridae). *Bulletin of Marine Science*, *57*, 548–549.

Coyne, J., & Orr H. (2004). *Speciation*. Sunderland, MA: Sinauer Associates.

Crespi, B., & Yanega, D. (1995.) The definition of eusociality. *Behavioral Ecology*, *6*, 109-115.

Danchin, E., Giraldeau, L., & Cézilly F. (2008). *Behavioural ecology*. New York, NY: Oxford University Press.

Darwin, C. (1871). *The descent of man*. London, England: John Murray Press.

Denny, M., & Ratner, S. (1970). *Comparative psychology: Research in animal behavior*, Revised ed. Homewood, IL: Dorsey Press.

Dugatkin, L. (2004). *Principles of animal behavior*. New York, NY: W. W. Norton & Company.

Finn, J., Tregenza, T., & Norman, M. (2009). Defensive tool use in a coconut-carrying octopus. *Current Biology*, *19*, 1069-1070.

Fitch-Snyder, H., & Carter, J. (1993). Tool use to acquire drinking water by free-ranging long-tailed macaques. *Lab Primate Newsletter*, *32*, 1-4.

Fox, E., & bin'Muhammad, I. (2002). Brief communication: New tool use by wild Sumatran orangutans (*Pongo pygmaeus abelii*). *American Journal of Physical Anthropology*, *119*, 186-188.

Fragaszy, D., Izar, P., Visalberghi, E., Ottoni, E., & De Oliveira, M. (2004). Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology*, *64*, 359-366.

Freeman, S., & Herron, J. (2004). *Evolutionary analysis*, 3rd ed. Upper Saddle River, NJ: Pearson Prentice Hall.

Gadagkar, R. (1994). Why the definition of eusociality is not helpful to understand its evolution and what we should do about it. *Oikos*, *70*, 485-488.

Goodenough, J., McGuire, B., & Wallace, R. (2001). *Perspectives on animal behavior*, 2nd ed. New York, NY: Wiley.

Greenberg, G., & Haraway, M. (1998). *Comparative psychology: A handbook*. New York, NY: Garland Publishing.

Hall, K. (1963). Tool-using performances as indicators of behavioral adaptability. *Current Anthropology*, *4*, 479-494.

Hansell, M., & Ruxton, G. (2007). Setting tool use within the context of construction behaviour, *Trends in Ecology & Evolution*, *23*, 73-78.

Hanson, H. (1962). *Dictionary of ecology*. New York, NY: Philosophical Library Inc.

Harrison, R. (1998). Linking evolutionary pattern and process: The relevance of species concepts for the study of speciation. In D. Howard & S. Berlocher (Eds.), *Endless forms: Species and speciation* (pp. 19-31). New York, NY: Oxford University Press.

Hemmes, R., Alvarado, A., & Hart, B. (2002). Use of California bay foliage by wood-rats for possible fumigation of nest-borne ectoparasites. *Behavioral Ecology*, *13*, 381-385.

Hey, J. (2001). The mind of the species problem. *Trends in Ecology & Evolution*, *16*, 326-329.

Hey, J. (2006). On the failure of modern species concepts. *Trends in Ecology & Evolution*, *21*, 447-450.

Hutchins, M., Evans, A., Garrison, R., & Schlager, N. (2004a). *Grzimek's animal life encyclopedia,* Vol 1, *lower Metazoans and lesser Deuterostomes*, 2nd ed. Farmington Hills, MI: Gale Group.

Hutchins, M., Evans, A., Garrison, R., & Schlager, N. (2004b). *Grzimek's animal life encyclopedia,* Vol 2, *Protostomes*, 2nd ed. Farmington Hills, MI: Gale Group.

Hutchins, M., Evans, A., Garrison, R., & Schlager, N. (2004c). *Grzimek's animal life encyclopedia,* Vol 3, *Insects*, 2nd ed. Farmington Hills, MI: Gale Group.
Jasny, B., Chin, G., Chong, L., & Vignieri, S. (2011). Again, and again, and again… *Science*, *334*, 1225.
Jones, A., Brown, C., & Gardner, S. (2011). Tool use in the tuskfish *Choerodon schoenleinii*? *Coral Reefs*, *30*, 865.
Kenward, B., Rutz, C., Weir, A., & Kacelnik, A. (2006). Development of tool use in New Caledonian crows: Inherited action patterns and social influences. *Animal Behavior*, *72*, 1329-1343.
Krützen, M., Mann, J., Heithaus, M., Connor, R., Bejder, L., & Sherwin, W. (2005). Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 8939-8943.
Lacey, E., & Sherman, P. (2005). Redefining eusociality: Concepts, goals, and level of analysis. *Annales Zoologici Fennic*, *42*, 573-577.
Lafuma, L., Lambrechts, M., & Raymond, M. (2001). Aromatic plants in bird nests as protection against blood-sucking flying insects. *Behavioral Processes*, *56*, 113-120.
Lestel, D., & Grundmann, E. (1999). Tools, techniques and animals: The role of mediations of actions in the dynamics of social behaviours. *Social Science Information*, *38*, 367-407.
Lester, D. (1973.) *Comparative psychology: Phyletic differences in behavior*. Van Nuys, CA: Alfred Publishing Company.
Levey, D., Duncan, R., & Levins, C. (2004). Use of dung as a tool by burrowing owls. *Nature*, *431*, 39.
Lovejoy, C. (1981). *The origin of man*. *Science*, *211*,341-350.
Lovell, H. (1958). Baiting of fish by a green heron. *Wilson Bulletin*, *70*, 280-281.
Maier, N., & Schneirla, T. (1964). *Principles of animal psychology*. Mineola, NY: Dover Publications.
Mather, J. (1994). 'Home' choice and modification by juvenile *Octopus vulgaris* (Mollusca: Cephalopoda): Specialized intelligence and tool use? *Journal of Zoology*, *233*, 359–368.
Matsuzawa, T. (2001). Primate foundations of human intelligence: A view of tool use in nonhuman primates and fossil hominids. In T. Matsuzawa (Ed.), *Primate origins of human cognition and behavior* (pp. 1-25). New York, NY: Springer-Verlag Press.
Mazur, J. (1990). *Learning and behavior*, 2nd ed. Upper Saddle River, NJ: Pearson Prentice Hall.
Naiman, R., Johnson, C., & Kelley, J. (1988). Alteration of North American streams by beaver. *BioScience*, *38*, 753-762.
Papini, M. (2002). *Comparative psychology: Evolution and development*. Upper Saddle River, NJ: Pearson Prentice Hall.
Parker, S., & Gibson, K. (1977). Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. *Journal of Human Evolution*, *6*, 623-641.
Paśko, Ł. (2010). Tool-like behavior in the sixbar wrasse, *Thalassoma hardwicke* (Bennett, 1830). *Zoo Biology*, *29*, 767–773.
Pierce, J., Jr. (1986). A review of tool use in insects. *Florida Entomologist*, *69*, 95-104.
Pierce, W. & Cheney, C. (2008). *Behavior analysis and learning*, *4th ed*. New York, NY: Psychology Press.
Pitt, F. (1926). *Animal mind*. New York, NY: F. A. Stokes.
Preston, B. (1998). Cognition and tool use. *Mind & Language*, *13*, 513-547.
Prozesky-Shulze, L., Prozesky, O., Anderson, F., & Van Der Merwe, G. (1975). Use of a self-made sound baffle by a tree cricket. *Nature*, *255*, 142-143.
Réale, D., Reader, S., Sol, D., McDougall, P., & Dingemanse N (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, *82*, 291-318.
Reeve, H., Sherman, P., & Keller, L. (1996). The eusociality continuum revisited. *Trends in Ecology & Evolution*, *11*, 472.
Robinson, S. (1994). Use of bait and lures by green-backed herons in Amazonian Peru. *Wilson Bulletin*, *106*, 567-569.
Robinson, M., & Robinson, B. (1971). The predatory behavior of the ogre-faced spider *Dinopis longipes* F. Cambridge (Araneae: Dinopidae). *American Midland Naturalist*, *85*, 85-96.
Roughgarden, J., & Akçay, E. (2010a). Do we need a sexual selection 2.0? *Animal Behavior*, *79*, 1-4.

Roughgarden, J., & Akçay, E. (2010b). Final response: Sexual selection needs an alternative. *Animal Behavior*, *79*, 18-23.
Seed, A., & Byrne, R. (2010). Animal tool-use. *Current Biology, 20*, R1032-R1039.
Sherman, P., Lacey, E., Reeve, H., & Keller, L. (1995). Eusociality continuum. *Behavioral Ecology, 6*, 102-108.
Shettleworth, S. (2009). *Cognition, evolution, and behavior* (pp. 399-408). New York, NY: Oxford University Press.
Shumaker, R., Walkup, K., & Beck, B. (2011). *Animal tool behavior: The use and manufacture of tools by animals*. Baltimore, MD: Johns Hopkins University Press.
Shuker, D. (2010). Sexual selection: Endless forms or tangled bank? *Animal Behavior, 79*, 11-17.
St. Amant, R., & Horton, T. (2008). Revisiting the definition of animal tool use. Animal *Behavior*, *75*, 1199-1208.
Stone, C. (1951). *Comparative psychology*. Westport, CT: Greenwood Press.
Tebbich, S., & Bshary, R. (2005). Cognitive abilities related to tool use in the woodpecker finch, *Cactospiza pallida*. *Animal Behavior*, *67*, 689-697.
Templeton, A. (1992). The meaning of species and speciation: A genetic perspective. In M. Ereshefsky (Ed.), *The units of evolution: Essays on the nature of species* (pp. 159-184). Cambridge, MA: Massachusetts Institute of Technology Press.
Thomas, B. (1983).The plain-fronted thornbird: Nest construction, material choice, and nest defense behavior. *Wilson Bulletin*, *95*, 106-117.
Tolman, E. (1932). *Purposive behavior in animals and men*. Berkeley, CA: University of California Press.
van Lawick-Goodall, J. (1970). Tool-using in primates and other vertebrates. In D. Lehrman, R. Hinde, & E. Shaw (Eds.), *Advances in the study of behavior,* Vol 3. (pp.195-249). New York, NY: New York Academic Press.
van Schaik, C., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C., Singleton, I., … Merrill, M. (2003). Orangutan cultures and the evolution of material culture. *Science, 299*, 102-105.
Warden, C., Jenkins, T., & Warner, L. (1935). *Comparative psychology: Vol 1, principles and methods*. New York, NY: Ronald Press.
Warden, C., Jenkins, T., & Warner, L. (1936). *Comparative psychology: Vol 2, vertebrates*. New York, NY: Ronald Press.
Warden, C., Jenkins, T., & Warner, L. (1940). *Comparative psychology: Vol 3, plants and invertebrates*. New York, NY: Ronald Press.
Washburn, M. (1908). *The animal mind: A text-book of comparative psychology*. New York, NY: Macmillan.
Wcislo, W. (1997a). Social terminology: What are words worth? *Trends in Ecology & Evolution*, *12*, 161.
Wcislo, W. (1997b). Are behavioral classifications blinders to studying natural variation? In J. Choe, B. Crespi (Eds.), *The evolution of social behavior in insects and arachnids* (pp. 8-13). Cambridge, MA: Cambridge University Press.
Whiten, A., Horner, V., & de Waal, F. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature, 437*, 737-740.
Wilson, E. (1971). *The insect societies*. Cambridge, MA: Harvard University Press.
Wilson, D. (1939). The habits of the angler-fish, *Lophius piscatorius* L., in the Plymouth aquarium. *Journal of the Marine Biology Association of the United Kingdom*, *1*, 477-496.
Westergaard, G. (1993). Development of combinatorial manipulation in infant baboons (*Papio cynocephalus anubis*). *Journal of Comparative Psychology*, *107*, 34-38.
Wittiger, L., & Sunderland-Groves, J. (2007). Tool use during display behavior in wild Cross River gorillas. *American Journal of Primatology, 69*, 1307-1311.

Appendix A

Summary of publications describing specific behaviors as tool use and the definitions cited therein. Behavioral categories (n = 10) are based on those defined in Bentley-Condit & Smith (2010).

	Publication	Behavior category	Definition cited?
1	Alp, 1997	Other (protection)	None
2	Anderson et al., 1983	Food extraction	None
3	Anderson, 1985	Food capture	None
4	Anderson, 2002	Food transport, Physical maintenance, Predator defense, Food extraction	Beck, 1980
5	Andersson, 1989	Food extraction	McFarland, 1987
6	Antinuecci & Visalbergh, 1986	Food extraction	Parker & Gibson, 1977
7	Babitz, 2000	Food extraction	None
8	Banschbach et al., 2006	Food transport	Alcock, 1972
9	Barber et al., 1989	Food transport	Pierce, 1985
10	Barnes, 2005	Other (extension)	Alcock, 1972
11	Bauer, 2001	Physical maintenance	None
12	Beck, 1976	Food capture	Beck, 1976
13	Benhar & Samuel, 1978	Food capture	van Lawick-Goodall, 1970
14	Bermejo et al., 1989	Food extraction	None
15	Boesch & Boesch, 1990	Food extraction	Goodall, 1980
16	Boesch-Achermann & Boesch, 1993	Food extraction	None
17	Borsari & Ottoni, 2005	Food extraction	Beck, 1980
18	Breuer et al., 2005	Other (measurement)	Beck, 1980
19	Brockman, 1985	Nest construction	Alcock, 1972; Wilson, 1975
20	Caffrey, 2000	Food extraction	None
21	Carpenter, 1887	Food extraction	None
22	Chevalier-Skolnikoff, 1990	Agonism, Predator defense, Food extraction	None
23	Chevalier-Skolnikoff & Liska, 1993	Physical maintenance, Other (measure), Food capture, Agonism, Other (obstruct)	Beck, 1980
24	Chiang, 1967	Other (cleaning)	None
25	Chisholm, 1954	Nest construction, Mate attraction, Food extraction	None
26	Clayton & Jolliffe, 1996	Food transport	None
27	Ellis & Brunson, 1993	Food preparation	None
28	Fay & Carroll, 1994	Food extraction	None
29	Fellers & Fellers, 1976	Food transport	Alcock, 1972

Appendix A (cont.)

	Publication	Behavior category	Definition cited?
30	Fernandes, 1991	Food extraction	None
31	Finn et al., 2009	Predator defense	None
32	Fitch-Snyder & Carter, 1993	Food capture, food transport	None
33	Fox & bin'Muhammad, 2001	Other (protection, resource capture)	None
34	Fragaszy et al., 2004	Food extraction	None
35	Galdikas, 1989	Physical maintenance, Predator defense	None
36	Gayou, 1982	Food extraction	Morse, 1980
37	Goodall, 1964	Food extraction, Food capture, Physical maintenance, Agonism	None
38	Green, 1972	Food extraction	None
39	Hall & Schaller, 1964	Food extraction	None
40	Hamilton III et al., 1975	Predator defense	None
41	Hannah & McGrew, 1987	Food extraction	None
42	Hart & Hart, 1994	Physical maintenance	Beck, 1980
43	Heinrich, 1988	Agonism	None
44	Henry & Aznar, 2006	Food capture	None
45	Hernandez-Aguilar et al., 2007	Food extraction	None
46	Hicks et al., 2005	Food extraction	None
47	Hirata et al., 1998	Nest construction	None
48	Hobbs, 1971	Food extraction	None
49	Hohmann, 1988	Food preparation	None
50	Huffman & Kalunde, 1993	Food capture	None
51	Hundley, 1963	Food extraction	None
52	Hunt, 1996	Food extraction	None
53	Hunt & Grey, 2004	Food extraction	None
54	Janzen et al., 1976	Personal maintenance	None
55	Jones & Kamil, 1973	Food capture	Hall, 1963
56	Jones & Pi, 1969	Food extraction	Hall, 1963
57	Karrer, 1970	Food capture, Other (communication)	None
58	Katz, 1980	Nest construction	None
59	Kumar et al., 2008	Food transportation	Beck, 1980
60	Lethmate, 1982	Food capture, Food transport, Agonism	Parker & Gibson, 1977
61	Levey et al., 2004	Other (luring prey)	None
62	Lindshield & Rodrigues, 2009	Physical maintenance	Beck, 1980
63	Malaivijitnond et al., 2007	Food extraction	None
64	Marks & Hall, 1992	Food extraction	van Lawick-Goodall, 1970
65	Matsusaka et al., 2006	Food transport	Matsusaka et al., 2006
66	McGrew & Tutin, 1973	Personal maintenance	None

Appendix A (cont.)

	Publication	Behavior category	Definition cited?
67	Mendes et al., 2007	Food capture	None
68	Meyerriecks, 1972	Physical maintenance	van Lawick-Goodall, 1970
69	Michener, 2004	Food capture	Beck, 1980
70	Mitchell, 1993	Food extraction	None
71	Montevecchi, 1978	Agonism	McGrew et al., 1975
72	Morse, 1968	Food extraction	Thorpe, 1963
73	de Moura & Lee, 2004	Food extraction	None
74	Nakamichi, 1999	Food capture	None
75	Oyen, 1979	Food extraction	None
76	Phillips, 1998	Food transport	None
77	Pollack, 1998	Food capture	None
78	Pruetz & Bertolani, 2007	Food capture	Beck, 1980
79	Richard-Hansen et al., 1998	Agonism	Beck, 1980
80	Sabater-Pí, 1974	Food extraction	None
81	Sherrow, 2005	Food extraction	None
82	Shuster & Sherman, 1998	Other (protection)	Alcock, 1972
83	Smolker et al., 1997	Other (protection)	Beck, 1980
84	Stanford et al., 2000	Food transport	None
85	Starin, 1990	Agonism	None
86	Stoinski & Beck, 2001	Physical maintenance, Food extraction	None
87	Sugiyama, 1995	Food extraction	None
88	Thomsen et al., 2007	Agonism	Beck, 1980
89	Tutin et al., 1995	Food extraction, Food transport	None
90	van Lawick-Goodall, 1973	Physical maintenance	van Lawick-Goodall, 1973
91	van Lawick-Goodall & van Lawick-Goodall, 1966	Food extraction	None
92	Watanabe et al., 2007	Personal maintenance	None
93	Weldon & Hoffman, 1975	Other (weights)	Weldon & Hoffman, 1975
94	Westergaard, 1993	Food transport	Westergaard, 1993
95	Westergaard & Suomi, 1993	Food extraction	Westergaard, 1993
96	Wheeler & Wheeler, 1924	Nest construction	None
97	Wittiger & Sunderland-Groves, 2007	Agonism	Beck, 1980
98	Yamagiwa et al., 1988	Food extraction	None
99	Yamakoshi & Sugiyama, 1995	Food extraction	None
100	Yamamoto et al., 2008	Food extraction	None

Appendix B

Representative samples of definitions of the term "tool use" provided during a survey of university students in an upper level comparative psychology class.

	Definition
1	"Tool use includes taking something in one's environment that is not part of that individual or any other individual, performing a task with that object in order to fulfill a desire"
2	"An organism using an internal or external object for their advantage"
3	"The use of an object by an animal in conjunction to reach a desired goal"
4	"Tool use is taking anything from the environment (not a part of the animal itself) and utilizing it to achieve a particular goal"
5	"The use of an object to help facilitate a goal"
6	"The use of an object for the purpose of completing a task"
7	"Anything used to help perform a task"
8	"The use of another object to help getting the selected reward that the organism would otherwise have a difficult time in obtaining"
9	"A tool is something that an animal uses to help it perform a task"
10	"A tool is an object of benefit to the organism"
11	"The use of an object to solve a problem."

Additional Literature Cited in Appendices

Alp, R. (1997). "Stepping-sticks" and "seat-sticks:" New types of tools used by wild chimpanzees (*Pan troglodytes*) in Sierra Leone. *American Journal of Primatology*, *41*, 45-52.

Anderson, J. (2002). Gone fishing: Tool use in animals. *Biologist*, *49*, 15-18.

Anderson, J., Williamson, E., & Carter, J. (1983). Chimpanzees of Sapo Forest, Liberia: Density, nests, tools and meat-eating. *Primates*, *24*, 594-601.

Andersson, S. (1989). Tool use by the fan-tailed raven (*Corvus rhipidurus*). *Condor*, *91*, 999.

Antinucci, F., & Visalberghi E (1986). Tool use in *Cebus paella*: A case study. *International Journal of Primatology*, *7*, 351-363.

Babitz, M. (2000). Object manipulation and tool use in Sulawesi crested black macaques. *American Journal of Primatology*, *51*, 38.

Banschbach, V., Brunelle, A., Bartlett, K., Grivetti, L., & Yeamans, R. (2006). Tool use by the forest ant *Aphaenogaster rudis*: ecology and task allocation. *Insectes Sociaux*, *53*, 463-471.

Barber, J., Ellgaard, E., Thien, L., & Stack A (1989). The use of tools for food transportation by the imported fire ant, *Solenopsis invicta*. *Animal Behavior*, *38*, 550-552.

Barnes, D. (2005). Possible tool use by beavers, *Castor canadensis*, in a northern Ontario watershed. *The Canadian Field-Naturalist*, *119*, 441-443.

Bauer, H. (2001). Use of tools by lions in Waza National Park, Cameroon. *African Journal of Ecology*, *39*, 317.

Beck, B. (1976). Tool use by captive pigtailed macaques. *Primates*, *17*, 301-310.

Benhar, E., & Samuel, D. (1978). A case of tool use in captive olive baboons (*Papio anubis*). *Primates*, *19*, 385-389.

Bermejo, M., Illera, G., & Pi, J. (1989). New observations on the tool-behavior of chimpanzees from Mt. Assirik (Senegal, West Africa). *Primates*, *30*, 65-73.

Boesch, C., & Boesch, H. (1990). Tool use and tool making in wild chimpanzees. *Folia Primatology*, *54*, 86-99.

Boesch-Acherman, H., & Boesch, C. (1993). Tool use in wild chimpanzees: New light from dark forests. *Current Directions in Psychological Science*, *2*, 18-21.

Borsari, A., & Ottoni, E. (2005). Preliminary observations of tool use in captive hyacinth macaws (*Anodorhynchus hyacinthinus*). *Animal Cognition*, *8*, 48-52.

Carpenter, A. (1887). Monkeys opening oysters. *Nature*, *36*, 53.

Chevalier-Skolnikoff, S. (1990). Tool use by wild cebus monkeys at Santa Rosa National Park, Costa Rica. *Animal Behavior*, *46*, 209-219.

Chevalier-Skolnikoff, S., & Liska, J. (1993). Tool use by wild and captive elephants. *Animal Behavior*, *31*, 375-383.

Chiang, M. (1967). Use of tools by wild macaque monkeys in Singapore. *Nature* , *214*, 1258-1259.

Chisholm, A. (1954).The use by birds of "tools" or "instruments." *Ibis*, *96*, 380-383.

Ellis, D., & Brunson, S. (1993). Tool use by the red-tailed hawk (*Buteo jamaicensis*). *The Journal of Raptor Research*, *27*, 128.

Fay, J., & Carroll R (1994). Chimpanzee tool use for honey and termite extraction in Central Africa. *American Journal of Primatology*, *34*, 309-317.

Fellers, J., & Fellers, G. (1976). Tool use in a social insect and its implications for competitive interactions. *Science*, *192*, 70-72.

Fernandes, M. (1991) .Tool use and predation of oysters (*Crassostrea rhizophorae*) by the tufted capuchin, *Cebus apella apella*, in brackish water mangrove swamps. *Primates*, *32*, 529-531.

Galdikas, B. (1989). Orangutan tool use. *Science*, *243*, 152.

Gayou, D. (1982). Tool use by green jays. *Wilson Bulletin*, *94*, 593-594.

Goodall, J. (1964). Tool-using and aimed throwing in a community of free-living chimpanzees. *Nature*, *201*, 1264-1266.

Green, C. (1972) .Use of tool by orange-winged sittella. *Emu*, *72*, 185-186.

Hall, K., & Schaller, G. (1964). Tool-using behavior of the California sea otter. *Journal of Mammalogy*, *45*, 287-299.

Hamilton, W., III, Buskirk, R., & Buskirk, W. (1975). Defensive stoning by baboons. *Nature, 256*, 488-489.
Hannah, A., & McGrew, W. (1987). Chimpanzees using stones to crack open oil palm nuts in Liberia. *Primates, 28*, 31-46.
Hart, B., & Hart, L. (1994). Fly switching by Asian elephants: Tool use to control parasites. *Animal Behavior, 48*, 35-46.
Heinrich, B. (1988). Raven tool use? *The Condor, 90*, 270-271.
Henry, P., & Aznar, J. (2006). Tool-use in Charadrii: Active bait fishing by a herring gull. *Waterbirds, 29*, 233-234.
Hernandez-Aguilar, R., Moore, J., & Pickering, T. (2007). Savanna chimpanzees use tools to harvest the underground storage organs of plants. *Proceedings of the National Academy of Sciences USA, 104*, 19210-19213.
Hicks, T., Fouts, R., & Fouts, D. (2005). Chimpanzee (*Pan troglodytes troglodytes*) tool use in the Ngotto Forest, Central African Republic. *American Journal of Primatology, 65*, 221-237.
Hirata, S., Myowa, M., & Matsuzawa, T. (1998). Use of leaves as cushions to sit on wet ground by wild chimpanzees *American Journal of Primatology, 44*, 215-220.
Hobbs, J. (1971) .Use of tools by the while-winged chough. *Emu, 71*, 84-85.
Hohmann, G. (1988). A case of simple tool use in wild liontailed macaques (*Macaca silenus*). *Primates, 29*, 565-567.
Huffman, M., & Kalunde, M. (1993). Tool-assisted predation on a squirrel by a female chimpanzee in the Mahale Mountains, Tanzania. *Primates, 34*, 93-98.
Hundley, M. (1963). Notes on the methods of feeding and the use of tools in the Geospinzinae. *Auk, 80*, 372-373.
Hunt, G. (1996). Manufacture and use of hook-tools by New Caledonian crows. *Nature, 379*, 249-251.
Hunt, G., & Gray, R. (2004). Direct observations of pandanus-tool manufacture and use by a New Caledonian crow (*Corvus moneduloides*). *Animal Cognition, 7*, 114-120.
Janzen, M., Janzen, D., & Pond, C. (1976.) Tool-using by the African grey parrot. *Biotropica , 8*, 70.
Jones, T., & Kamil, A. (1973). Tool-making and tool-using in the northern blue jay. *Science, 180*, 1076-1078.
Jones, C., & Pi, J. (1969). Sticks used by chimpanzees in Rio Muni, West Africa. *Nature, 223*, 100-101.
Karrer, R. (1970). The use of the tail by an old world monkey. *Primates, 11*, 171-175.
Katz, S. (1980). Tool-using behavior of the pocket gopher, *Thomomys bottae* (Geomyidae). *Southwestern Naturalist, 25*, 270-271.
Kumar, S., Kumara, H., & Singh, M. (2008). Observations on tool use in captive lion-tailed macaque (*Macaca silenus*). *Current Science India, 94*, 925-928.
Lethmate, J. (1982). Tool-using skills of orang-utans. *Journal of Human Evolution, 10*, 49-64.
Lindshield, S., & Rodrigues, M. (2009). Tool use in wild spider monkeys (*Ateles geoffroyi*). *Primates, 50*, 269-272.
Malaivijitnond, S., Lekprayoon, C., Tandavanittj, N., Panha, S., Cheewatham, C., & Hamada, Y. (2007). Stone-tool usage by Thai long-tailed macaques (*Macaca fascicularis*). *American Journal of Primatology, 69*, 227-233.
Marks, J., & Hall, C. (1992). Tool use by bristle-thighed curlews feeding on albatross eggs. *The Condor, 94*, 1032-1034.
Matsusaka, T., Nishie, H., Shimada, M., Kutsukake, N., Zamma, K., Nakamura, M., & Nishida, T. (2006). Tool-use for drinking water by immature chimpanzees of Mahale: Prevalence of an unessential behavior. *Primates, 47*, 113-122.
McGrew, W., & Tutin, C. (1973). Chimpanzee tool use in dental grooming. *Nature , 241*, 477-478.
McGrew, W., Tutin, G., & Midgett, P., Jr. (1975). Tool use in a group of captive chimpanzees. I. Escape. *Zeitschrift für Tierpsychologie, 37*, 142-165.
Mendes, N., Hanus, D., & Call, J. (2007). Raising the level: Orangutans use water as a tool. *Biology Letters, 3*, 453-455.
Meyerriecks, A. (1972). Tool-using by a double-crested cormorant. *Wilson Bulletin, 84*, 482-483.
Michener, G. (2004). Hunting techniques and tool use by North American badgers preying on Richardson's ground squirrels. *Journal of Mammalogy, 85*, 1019-1027.
Mitchell, T. (1993). Tool use by a white-breasted nuthatch. *Bulletin of the Oklahoma Ornithological Society, 26*, 6-7.

Montevecchi, W. (1978). Corvids using objects to displace gulls from nests. *The Condor, 80,* 349.
Morse, D. (1968). The use of tools by brown-headed nuthatches. *Wilson Bulletin, 80,* 220-224.
Morse, D. (1980). *Behavioral mechanisms in ecology,* Cambridge, MA: Harvard University Press.
de Moura, A., & Lee, P. (2004). Capuchin stone tool use in caatinga dry forest. *Science, 306,* 1909.
Nakamichi, M. (1999). Spontaneous use of sticks as tools by captive gorillas (*Gorilla gorilla gorilla*). *Primates, 40,*487-498.
Oyen, O. (1979). Tool-use in free-ranging baboons of Nairobi National Park. *Primates, 20,* 595-597.
Phillips, K. (1998). Tool use in wild capuchin monkeys (*Cebus albifrons trinitatis*). *American Journal of Primatology, 46,* 259-261.
Pollack, D. (1998). Spontaneous tool use in a vervet monkey (*Cercopithecus aethiops sabaeus*). *American Journal of Primatology, 45,* 201.
Pruetz, J., & Bertolani, P. (2007). Savanna chimpanzees, *Pan troglodytes verus,* hunt with tools. *Current Biology, 17,* 412-417.
Richard-Hansen, C., Bello, N., & Vie, J. (1998). Tool use by a red howler monkey (*Alouatta seniculus*) towards a two-toed sloth (*Choloepus didactylus*). *Primates, 39,* 545-548.
Sabater- Pí, J. (1974). An elementary industry of the chimpanzees in the Okorobikó Mountains, Rio Muni (Republic of Equatorial Guinea), *West Africa Primates, 15,* 351-364.
Sherrow, H. (2005). Tool use in insect foraging by the chimpanzees of Ngogo, Kibale National Park, Uganda. *American Journal of Primatology, 65,* 377-383.
Shuster, G., & Sherman, P. (1998). Tool use by naked mole-rats. *Animal Cognition, 1,* 71-74.
Smolker, H., Richards, A., Conner, R., Mann, J., & Berggren, P. (1997). Sponge carrying by dolphins (Delphinideae, *Tursiops* spp.): Foraging specialization involving tool use? *Ethology, 103,* 454-465.
Stanford, C., Gambaneza, C., Nkurunungi, J., & Goldsmith M (2000). Chimpanzees in Bwindi-Impenetrable National Park, Uganda use different tools to obtain different types of honey. *Primates, 41,* 337-341.
Starin, E. (1990). Object manipulation by wild red colobus monkeys living in the Abuko Nature Reserve, The Gambia. *Primates, 31,* 385-391.
Stoinski, T., & Beck, B. (2001). Spontaneous tool use in captive, free-ranging golden lion tamarins (*Leontopithecus rosalia rosalia*). *Primates, 42,* 319-326.
Sugiyama, Y. (1995). Tool-use for catching ants by chimpanzees at Bossou and Monts Nimba, West Africa. *Primates, 36,* 193-205.
Thomsen, L., Campbell, R., & Rosell, F. (2007). Tool-use in a display behaviour by Eurasian beavers (*Castor fiber*). *Animal Cognition, 10,* 477-482.
Thorpe, W. (1963). *Learning and instinct in animals,* 2nd ed. London, England: Methuen and Co.
Tutin, C., Ham, R., & Wrogemann, D. (1995). Tool-use by chimpanzees (*Pan troglodytes troglodytes*) in the Lopé Reserve, Gabon. *Primates, 36,* 181-192.
van Lawick-Goodall, J., van Lawick, H., & Packer, C. (1973). Tool-use in free-living baboons in the Gombe National Park, Tanzania. *Nature, 241,* 212-213.
van Lawick-Goodall, J., & van Lawick, H. (1966). Use of tools by the Egyptian vulture, *Neophron percnopterus*. *Nature, 212,* 1468-1469.
Watanabe, K., Urasopon, N., & Malaivijitnond, S. (2007). Long-tailed macaques use human hair as dental floss. *American Journal of Primatology, 69,* 940-944.
Weldon, P., & Hoffman, D. (1975). Unique form of tool-using in two gastropod mollusks (Trochidae). *Nature, 256,*720-721.
Westergaard, G., & Suomi, S. (1993). Use of tool-set by capuchin monkeys (*Cebus apella*). *Primates, 34,* 459-462.
Wheeler, G., & Wheeler, E. (1924). The use of a tool by a sphecid wasp. *Science, 59,* 486.
Yamagiwa, J., Yumoto, T., Ndunda, M., & Maruhashi, T. (1988). Evidence of tool-use by chimpanzees (*Pan troglodytes schweinfurthii*) for digging out a bee-nest in the Kahuzi-Biega National Park, Zaire. *Primates, 29,* 405-411.
Yamakoshi, G., & Sugiyam, Y. (1995). Pestle-pounding behavior of wild chimpanzees at Bossou, Guinea: A newly observed tool-using behavior. *Primates, 36,* 489-500.
Yamamoto, S., Yamakoshi, G., Humle, T., & Matsuzawa, T. (2008). Invention and modification of a new tool use behavior: ant-fishing in trees by a wild chimpanzee (*Pan troglodytes verus*) at Bossou, Guniea. *American Journal of Primatology, 70,* 699-702.