Title
Fish out of water: Insights from a case study of a highly social animal that failed the mirror self-recognition test

Journal
International Journal of Comparative Psychology, 33(0)

ISSN
0889-3675

Authors
Barber-Meyer, Shannon
Schmidt, Lori

Publication Date
2020

DOI
10.46867/C4KG6W

INTERNATIONAL JOURNAL OF COMPARATIVE PSYCHOLOGY

2020, 33
Heather M. Hill
Editor
Peer-reviewed

Fish Out of Water: Insights from a Case Study of a Highly Social Animal that Failed the Mirror Self-Recognition Test

Shannon Michelle Barber-Meyer[1] and Lori Jean Schmidt[2,3]

[1]U.S. Geological Survey, Northern Prairie Wildlife Research Center, U.S.A.
[2]International Wolf Center, U.S.A.
[3] Natural Resources Program Coordinator, Vermilion Community College, U.S.A.

Mirror self-recognition (MSR) tests have been conducted in a variety of species to assess whether these animals exhibit self-awareness. To date, the majority of animals that have convincingly passed are highly social mammals whose wild counterparts live in complex societies, though there is much debate concerning what constitutes "passing" and what passing means in terms of self-awareness. Amid recent reports that a fish (cleaner wrasse, *Labroides dimidiatus*) passed, it is intriguing that a mammal as highly social, tolerant, attentive, and cooperative as the gray wolf (*Canis lupus*) has reportedly failed the test. Given the many possible reasons for failure, we were interested in reexamining wolves as a case study of MSR in socially complex mammals as part of a broader overview of the MSR test. We aimed to elucidate the wolves' responses at various stages of the MSR test to pinpoint potential problem areas where species-specific modifications to the test may be needed. We evaluated 6 socialized, captive gray wolves during July 2017. At a minimum, wolves did not respond to their reflection as an unfamiliar conspecific. Unfortunately, the wolves rapidly lost interest in the mirror and were uninterested in the applied marks. We note limitations of the MSR test for this species, recommend changes for future MSR tests of wolves, discuss other emerging self-cognizance methods for socially complex canids, and highlight the need for a suite of ecologically relevant, potentially scalable self-cognizance methods. Our findings and recommendations may aid in understanding self-cognizance in other MSR-untested, highly social, cooperatively-hunting, coursing, terrestrial carnivores such as African wild dogs (*Lycaon pictus*), spotted hyenas (*Crocuta crocuta*), and African lions (*Panthera leo*).

Keywords: awareness, cognizance, cooperative hunting, empathy, mark, reflection, social response, theory of mind

Brief History of the Mirror Self-Recognition Test

In 1970, Gordon Gallup, Jr., published a series of experiments that revealed chimpanzees (*Pan troglodytes*) apparently recognized themselves (i.e., possessed self-recognition) in a mirror as demonstrated through an ingenious mark self-recognition test (Gallup, 1970). The experiment consisted of Gallup, Jr., marking the chimpanzees on their heads where they could not directly see the mark themselves without the use of a mirror. After prolonged exposure to a mirror, the chimpanzees touched where the mark was on their heads, implying that they understood they were looking at a reflection of themselves (or, in terms of bodily self-awareness, "perceiving one's own image as an image of one's own body", DeGrazia, 2009, p. 211; but see also Breed & Moore, 2012). Prior to this experiment, self-recognition was thought to be restricted to humans (Gallup, 1970).

Since Gallup, Jr.'s, (1970) original mirror self-recognition (MSR) tests in chimpanzees, many other animals have been tested with ambiguous or failing results (e.g., squid [*Sepioteuthis lessoniana*], Ikeda & Matsumoto, 2007; manta rays [likely *Manta birostris*], Ari & D'Agostino, 2016; pigeon [*Columba liva domestica*], Epstein et al., 1981; magpie [*Pica pica*], Prior et al., 2008; Rhesus monkeys [*Macaca mulatta*], Rajala et al., 2010; ants [*Myrmica sabuleti, M. rubra, M. ruginodis*], Cammaerts Tricot & Cammaerts, 2015; horses [*Equus caballus*], Baragli et al., 2017; cotton-top tamarins [*Saguinus oedipus*], Hauser et al., 1995; Hauser et al., 2001). According to some researchers, extremely convincing evidence of self-recognition is rare

Please send correspondence to Shannon Michelle Barber-Meyer, 1393 Hwy 169, Ely, MN 55731. Electronic mail may be sent to sbarber-meyer@usgs.gov

(Anderson & Gallup, 2011; Chang et al., 2017; Gallup et al., 2002; Gallup & Anderson, 2017). With respect to mammals, apart from chimpanzees, MSR appears to have only been demonstrated in other highly social animals including just two common bottlenose dolphins (*Tursiops truncatus*; Reiss & Marino, 2001), one Asian elephant (*Elephas maximus*; Plotnik et al., 2006), and only in trained (they did not spontaneously show MSR) Rhesus monkeys (*Macaca mulatta*; Chang et al., 2017).

Passing the MSR Test: The Self-Awareness Debate

What does it mean to pass the MSR test? The "strong interpretation" of passing is that it demonstrates self-recognition and self-awareness that is associated with theory of mind (De Veer & Van Den Bos, 1999). A more moderate interpretation is that the animal has demonstrated it differentiates itself from other environmental objects, can recognize its reflection (i.e., differentiate its reflection from conspecific reflections), and can use the mirror as a grooming tool (De Veer & Van Den Bos, 1999). This may be considered a simpler form of self-awareness that does not rise to theory of mind. An even more conservative interpretation suggests that passing the MSR test may not even confirm self-recognition in that, for example, an animal seeing a mark on an animal in the mirror may merely think that it too may have a mark on its face, as some human children attempt to wipe a nonexistent mark off of their face if they see another child with a facial mark (see De Veer & Van Den Bos, 1999, for review). Some even contend MSR tests merely measure problem-solving ability (Breed & Moore, 2012).

Many have maintained that passing or failing the MSR test should not be all-or-nothing, following the idea that self-awareness potentially exists along a spectrum (Bekoff & Sherman, 2004; De Veer & Van Den Bos, 1999; de Waal, 2019; Kohda et al., 2019; McCallum, 2019; Vonk, 2019; but see also Gallup & Anderson, 2020, for an alternate view). Although it is beyond the scope of this paper to review self-awareness in detail, we note that others have reasoned that most animals behave as if they have at least some level of self-awareness (though it may not include recognizing themselves in a mirror), such as judging whether to engage in a high-risk conflict for a mate (de Waal, 2019) or traveling in a coordinated hunting group (Bekoff & Sherman, 2004). Moreover, three degrees of self-cognizance were outlined by Bekoff and Sherman (2004) from lower complexity to higher, including self-referencing, self-awareness, and self-consciousness, whereas Brandl (2016) highlighted partial accomplishments related to self-awareness. Expanding the pass/no-pass paradigm, Plotnik et al. (2006) delineated four progressive stages in the MSR test including social response to the mirror, physical mirror inspection, repetitive mirror-testing, and self-directed behaviors in front of the mirror.

A Highly Social Animal Fails

Depending on the complexity, behaviors associated with self-cognizance may be closely associated with theory of mind and empathy (i.e., being able to mentally put oneself in another's position and act accordingly; Bekoff & Sherman, 2004; De Veer & Van Den Bos, 1999; Reiss, 2011). Because the capacity for theory of mind is associated with animals that live in socially complex societies (Dunbar, 1998), animals that demonstrate socially complex behaviors related to self-cognizance should be more likely to pass the MSR test than those that do not (Kohda et al., 2019). Gray wolves (*Canis lupus*) are known for highly social, tolerant, attentive, and cooperative behavior (Lampe et al., 2017; Range & Virányi, 2015). They have been observed to cooperatively hunt with apparent strategy (e.g., wolves waiting in ambush while others "push" prey toward those waiting, Mech et al., 2015), suggesting wolves use foresight and planning and may be able to consider the perspective of other wolves with whom they are cooperatively hunting. Others have provided similar empirical evidence that wolves possess higher-order mental abilities based, in part, on their adaptive learning and flexible and complex hunting strategies (Gable et al., 2018). Some have suggested that such complex hunting behaviors are the result of simple rules (Escobedo et al., 2014; Muro et al., 2011), whereas others have challenged that view as "probably an oversimplification in many instances" (Bailey et al., 2013, p. 7). Captive research has shown that wolves are successful in following causal cues, human gazes, and conspecific's behavior to solve tasks (Range & Virányi, 2014) and can "adapt their social cognitive abilities to their social environment" (Lampe et al., 2017, p. 4). Thus, based on such social complexity, we hypothesized that wolves possess a higher form of self-cognizance (Bekoff & Sherman, 2004; DeGrazia, 2009), including possible self-

awareness sufficient to pass the MSR test.

Given our hypothesis, we were intrigued by a sentence in a book chapter indicating this highly social species reportedly did not pass the MSR test (Bekoff, 2014). The brief mention of wolves and MSR tests stated both they and dogs (*C. familiarus*) failed at least one version of the test, "…dogs and wolves do not pass the mirror test. Michael Fox and I tried to use this method in the early 1970s and tried to publish the negative results, but the paper was repeatedly rejected because of the results were negative" (Bekoff, 2014, p 70). Because the detailed methods and specific results from that study were not published, it is not possible to determine precisely why this highly social animal that demonstrates advanced cognitive abilities might have failed the test. The varying potential reasons for the failure (e.g., differences in study design, rearing conditions, intraspecific variation, sensory issues, environmental conditions, other method particulars, age of wolves, etc.; see below) that may or may not have had to do with the canid's actual level of self-cognizance or ability to understand mirrors, remained unknown. Beyond this reference, we were unaware of other published records that include detailed methods, specific results, etc., of MSR tests in wolves or domestic dogs.

Do Fish Demonstrate Greater Self-Cognizance Than Wolves?

In addition to the mystery of why wolves did not pass the MSR test, a surprising report was recently published indicating that a fish (cleaner wrasse, *Labroides dimidiatus*) apparently passed the MSR test (Kohda et al., 2019). To their credit, the authors of the fish study did not then claim that the fish possessed self-awareness based on the ostensible passing of the MSR test (Kohda et al, 2019). Rather, they presented three options for interpreting their findings and welcomed discussion and scientific debate: (1) the documented behaviors were not self-directed and so the cleaner wrasse did not pass the mark test; (2) the cleaner wrasse fish passed the mark test and are therefore self-aware; and (3) the cleaner wrasse passed the mark test, "but this does not mean they are self-aware" (Kohda et al., 2019, p. 10) (indicating the test does not accurately assess self-awareness in this species). The authors further pose that even if the fish are determined to have fulfilled the criteria for passing the MSR test, the most parsimonious explanation is that the fish are self-referencing (i.e., the fish perceive a part of their body as their own), which does not involve theory of mind or self-awareness necessarily (Bekoff & Sherman, 2004; Dunbar, 1998).

Because of the nature of the injected mark used in the fish study, it may be that the cleaner wrasse did not actually pass the MSR but rather passed the Felt-Mark Test (de Waal, 2019) or the modified tactile-visual mark test (Kohda et al., 2019), similar to Rhesus monkeys after visual-somatosensory training with laser beams (Anderson & Gallup, 2015; Chang et al., 2015). Moreover, although four fish showed an increase in face scraping in the presence of a mirror after being marked on their heads, three of these fish also showed face scraping prior to being marked, so the authors concluded that face scraping "cannot be taken as unequivocal evidence of mirror-induced self-directed behavior" (Kohda et al., 2019, p. 12). It has also been suggested the increased time that aquatic animals spend watching themselves in a mirror when marked is not necessarily because they recognize it is their body in the mirror or that they are causing the image in the mirror to change, but because it is a more interesting visual experience for them to expose the marked area to the mirror (Vonk, 2019).

Why Do Animals Fail the MSR Test?

How can fish apparently pass the MSR but highly social animals that demonstrate advanced cognition such as wolves do not? Potential reasons why animals fail the MSR test are many. A species may fail if the taxonomic distance between the study species and the original species that the test was designed for is too great, if the test is inappropriate for that species' behavior (e.g., some animals avoid eye contact), and/or if there are sensory system disparities (human visual detection of the mark does not guarantee the same for the trial species; Bekoff & Sherman, 2004; De Veer & Van Den Bos, 1999; de Waal, 2019; Gallup & Anderson, 2020; Kohda et al., 2019). Individuals may fail (even if conspecifics have passed) due to intraspecific genetic variation, lack of motivation (i.e., have no interest in the mark), and/or differences in rearing conditions during development (Bekoff & Sherman, 2004; De Veer & Van Den Bos, 1999; de Waal, 2019; Gallup & Anderson,

2020; Kohda et al., 2019). Differences in the methods of a particular MSR test may also influence success, including differences in response training / reward trials, mirror exposure variability, and/or in the subjective interpretation of behavioral responses including assessing the intention of nonhuman behavior (Bekoff & Sherman, 2004; De Veer & Van Den Bos, 1999; de Waal, 2019; Gallup & Anderson, 2020; Kohda et al., 2019). Of course, animals may also fail if they lack the degree of self-awareness required to pass the MSR test (Bekoff & Sherman, 2004; De Veer & Van Den Bos, 1999; de Waal, 2019; Gallup & Anderson, 2020; Kohda et al., 2019).

Furthermore, animals may actually pass the MSR cognitive test but not other tests designed to assess similar abilities (Vonk, 2019). Also, intraspecific success and the stability of individual success over time in the MSR test among nonhumans vary significantly (e.g., passing the MSR test ranges from 10-100% in chimpanzees and 50% of individual chimpanzees that showed spontaneous mirror self-exploration later failed a mark test; see De Veer & Van Den Bos, 1999, for review). Thus, researchers have asserted one type of test alone is not sufficient to measure self-awareness and that collective evidence from a body of cognitive tests (including nonvisual) should be used assess levels of self-cognizance in both intraspecific and interspecific comparisons (Bekoff & Sherman, 2004; De Veer & Van Den Bos, 1999; de Waal 2019; Vonk, 2019).

A Need to Reexamine Wolves with the MSR Test

Given the paucity of information on wolves and MSR, we aimed to rectify the absence in the scientific record of specific details regarding gray wolf performance at various stages of the MSR test. In revisiting the wolf MSR test, we also anticipated identifying features of the test that may need to be modified to better assess this in wolves and other similar, highly socially complex predators (Hill et al., 2018; Vonk, 2019). Understanding the specific stage(s) of the MSR test (as delineated by Plotnik et al., 2006) that wolves failed (if, indeed, they failed, because differences in intraspecific variation, rearing conditions, etc., in our study relative to Bekoff's study [Bekoff 2014] could contribute to them passing) is important for focusing future research. Moreover, any partial accomplishments of wolves in MSR (Brandl, 2016) could help determine where along the potential spectrum of self-cognizance wolves may lie (Bekoff & Sherman, 2004, de Waal, 2019). We were also interested in providing information useful to captive management, such as insight into wolf perceptions of their reflections that may affect their psychological state and, therefore, pack dynamics.

MSR Case Study of a Highly Social Animal

Thus, we attempted the MSR test with socialized, captive wolves of differing age, gender, and pack status. We investigated behavioral responses to mirrors and MSR in wolves housed at the International Wolf Center (IWC) in Ely, Minnesota, USA (Table 1). Besides being of interest to research, the IWC's management plan (that includes introducing pups to nonrelated adult wolves) would benefit from an increased understanding of the wolves' cognitive abilities and perceptions of their reflections that may affect their psychological state at varying ages, especially as it relates to pups versus adults.

Table 1

Details of the Socialized, Captive Wolves at the International Wolf Center, Minnesota, USA

Wolf	Sex	Age	Main Coat Colors	Pack Status	Enclosure	Comments
Aidan	M	9	Gray/white/brown	Dominant male	Exhibit	Denali's brother
Denali	M	9	Gray/white	Nondominant adult	Exhibit	Aidan's brother
Boltz	M	5	Brown/white/gray	Nondominant adult	Exhibit	Luna's unrelated pupmate, unable to mark
Grayson	M	1	White	Yearling	Exhibit	Axel's brother
Axel	M	1	White	Yearling	Exhibit	Grayson's brother
Luna	F	5	Black/speckled gray	Dominant female	Off-exhibit[a]	Boltz's unrelated pupmate
Grizzer	M	13	Gray/white	Nondominant adult	Off-exhibit[a]	Old injury above right eye, some possible visual impairment

[a]Luna and Grizzer were housed on-exhibit until they were ~4 and ~7 years old, respectively, and moved off-exhibit to an enclosure they share.

Because dog puppies (< 4 months) initially reacted to a mirror as if it was a conspecific (Zazzo, 1979), we hypothesized that juvenile wolves would be more likely to persist in a social response to the mirror (as if they were viewing a conspecific) compared to older wolves. Also, because of varying roles in aggressive conflict among wild wolves based on pack status, age, and gender (Cassidy et al., 2017), we hypothesized that dominant adult males, followed by dominant adult females and then nondominant adults, would be more likely to aggressively engage with the mirror if they perceived the reflection as a conspecific.

We evaluated seven captive IWC wolves (Table 1) with the MSR test. Five wolves (Table 1) were housed in the main, outdoor exhibit enclosure, flanked by public viewing windows (semi-reflective surfaces) on the building side (Figure 1). Two other wolves (Table 1) were maintained in an off-exhibit, outdoor habitat enclosure. There were no windows off-exhibit, but off-exhibit wolves had previously lived in the main exhibit (and thus, were exposed to potential semi-reflections). We examined behavioral responses to mirrors and conducted the MSR test using a mirror sized to allow wolves to view their entire body (see Figures 2 and 3 for examples of mirror positioning). Typical MSR tests include exposure of the subject to the mirror while the subject has no visible mark (i.e., sham mark) and also when the subject had a visible mark applied in a place where the subject was unable to see it unless using the mirror (Gallup, 1970). Comparisons between self-directed behaviors among the mirror exposures (sham mark vs. visible mark) are used to conclude whether the animal exhibited self-recognition. We recorded behavioral responses of wolves to the mirror when sham marked and when marked with a highly visible mark on their foreheads (Figures 4 and 5).

Figure 1

Exhibit Wolves are Housed in an Enclosure with Semi-Reflective Windows along the Main Building Side. Here, Axel Gazes through the Window

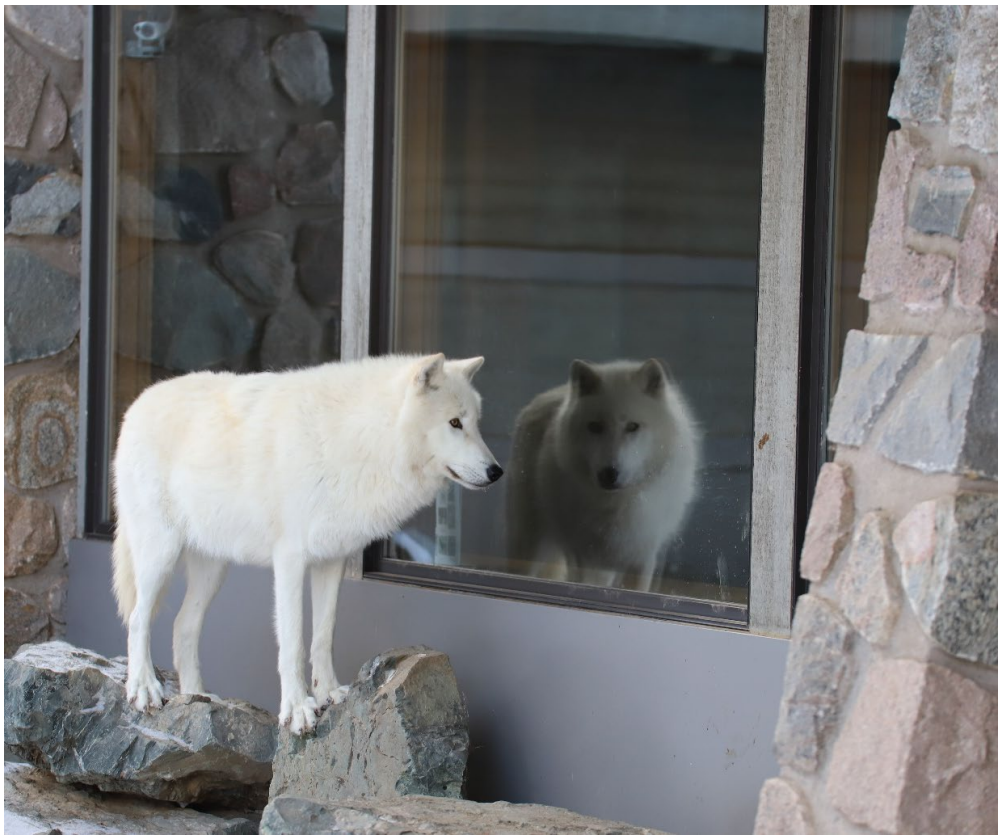


Figure 2

Axel Visually Engages with the Reflection in the Mirror through the Fence during the Sham Mark Test, while Boltz Rests in the Background

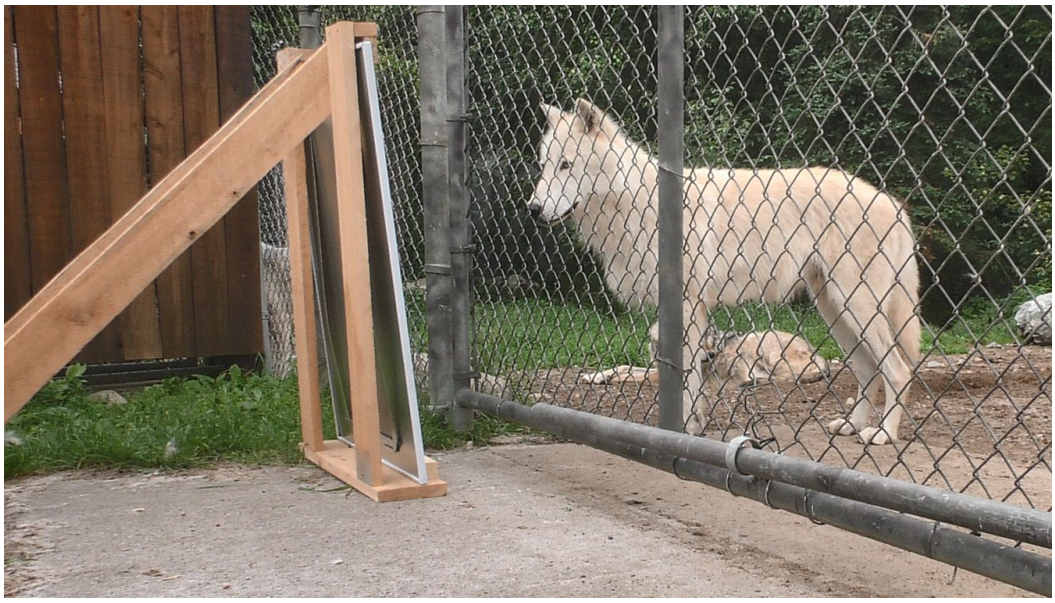


Figure 3

Aidan Sniffs the Mirror during the Sham Mark Test

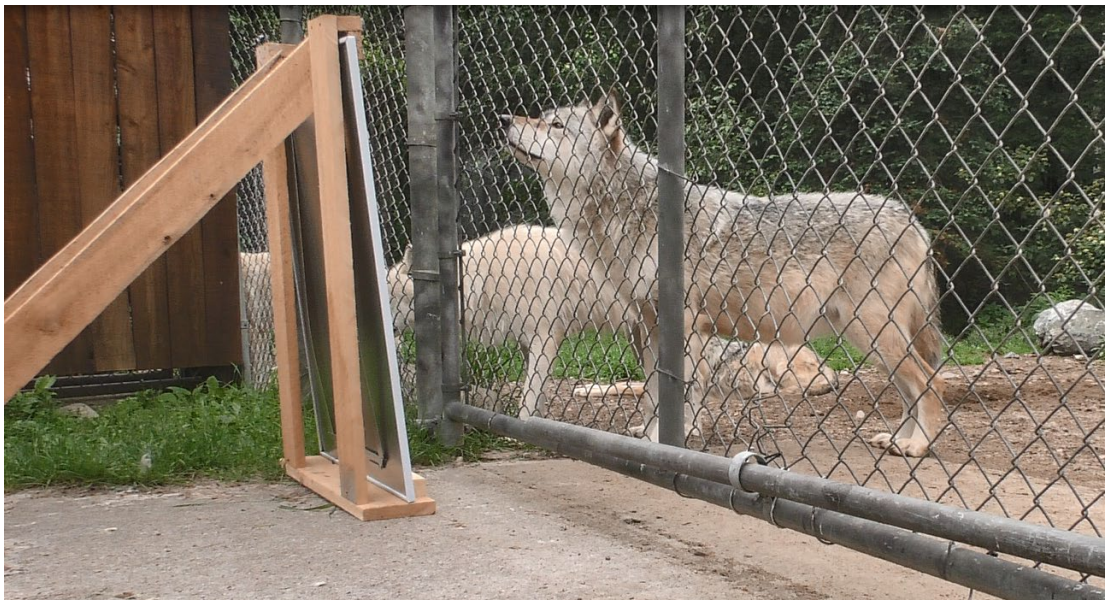


Figure 4

Axel Relaxes during the Highly Visible Mark Test, Showing No Attention to the Blue Mark on his Foot or his Forehead

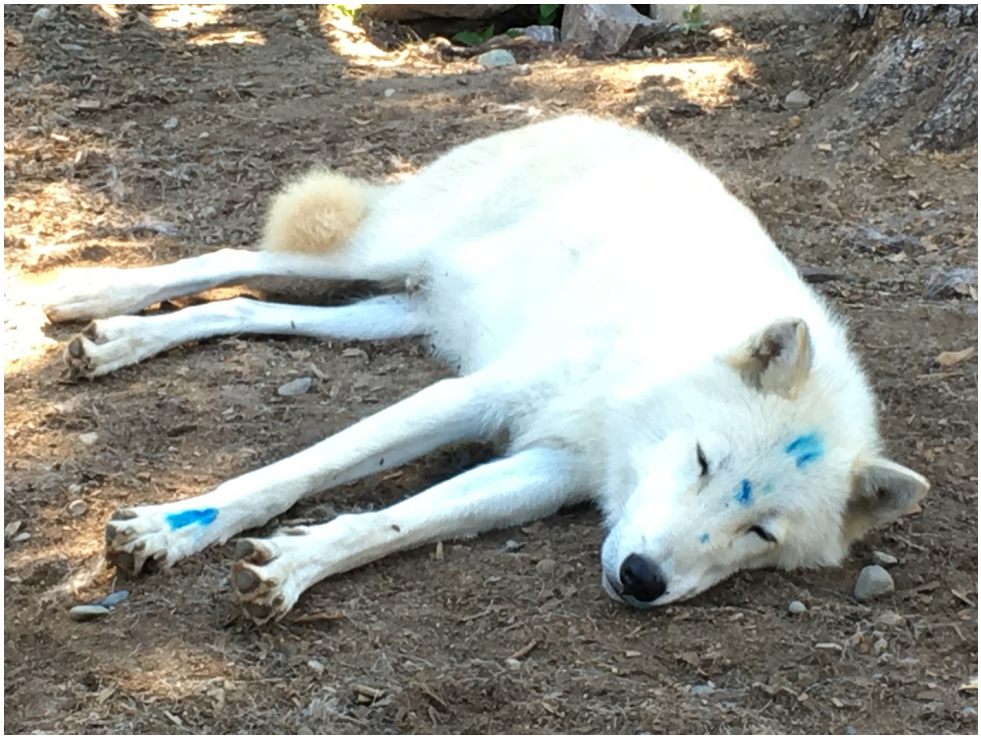


Figure 5

Grayson Rests Sternally, Showing No Attention to the Blue Mark on his Foot or his Forehead. Boltz (unmarked) Stands Nearby, also Showing No Interest in Grayson's Marks

Immediately after mirror positioning, we videotaped the wolves and analyzed the first 10 min of all recordings. We characterized contextual wolf behaviors (Goodman et al., 2002) as corresponding to four behavioral categories detailed in Plotnik et al. (2006): 1) social response, 2) physical mirror inspection, 3) repetitive mirror-testing behavior, and 4) self-directed behavior (Table 2). We calculated the total time that each wolf engaged with the mirror per test and tallied the number of mirror engagement bouts (e.g., Figures 2 and 3). Behavioral occurrences were summed for each category for each test for each wolf and were maximally equal to the number of mirror engagements attributed to that animal. Stages 1-3 can be demonstrated in either the sham mark or highly visible mark tests. Progression through Stage 4 is demonstrated by comparison between the sham mark and highly visible mark test results. Because we were interested in how wolves performed in all stages of the MSR in order to elucidate test features that may need modification for this and other similar species, we continued the test even if the wolves did not display behaviors consistent with progressing through a particular stage. Please see Appendix for expanded methods.

Table 2

Description and Example Wolf Behaviors (Goodman et al., 2002) Relating to 4 Stages or Behavioral Categories in the Mirror Self-recognition (MSR) Test (as in Plotnik et al., 2006)

Stage or Behavioral Category	Description and Example Behaviors
Social response	Responding as if the reflection in the mirror were an unfamiliar or strange, threatening conspecific with behaviors such as lip curl, ears flat and out to the side, raised hackles, etc. (aggressive and defensive behaviors as per the Wolf Park ethogram, Goodman et al. [2002]), other social responses like neutral or friendly were not considered because as territorial animals pack wolves (in contrast perhaps to lone wolves) do not tend to initially respond to unfamiliar wolves with neutral or friendly responses.
Physical mirror inspection	Pawing at the mirror, sniffing at the frame of the mirror, approaching for visual inspection of the mirror and support structure, and visually examining the area behind the mirror.
Repetitive mirror-testing	Repeated non-aggressive mirror approaching (as determined by ear, tail, and other body posture per Goodman et al. [2002]), parallel walking in front of the mirror, or other repeated movements such as head bob, allowing wolves to observe a "one-to-one correspondence" (Morrison & Reiss, 2018) between their actions and the image in the reflection.
Self-directed behaviors	Behaviors directed toward self when viewing the mirror, also including physically and visually examining the mark (i.e., paw to the head, paw to the mark, positioning the wolf's body for increased visual inspection of the mark) and/or viewing and examining body parts in the mirror not normally visible (e.g., mouth open widely for examination in the reflection).

None of the wolves showed apparent social responses to their reflection (Stage 1 of MSR), all of the wolves physically inspected the mirror at least once (Stage 2), all but one (Boltz) engaged in apparent mirror-testing behavior (Stage 3), and none of the wolves demonstrated self-directed behaviors at the mirror (Stage 4) (Table 3). Prior to mirror positioning, one wolf (Grizzer) responded to being marked on his forehead by scent-rubbing his flank on a nearby tree. During the mark test (when the mirror was available to the wolves), no wolves demonstrated interest in their own or each other's forehead marks (Figures 2 & 3). Unfortunately, all wolves lost interest in the mirror during each test (well before 10 min elapsed). Thus, prolonged mirror exposure to potentially, eventually elicit self-directed behaviors (Gallup, 1970) was not feasible. Various metrics declined from the sham mark test to the highly visible mark test including time at the mirror, number of mirror engagements, physical mirror inspections, and mirror-testing behaviors (Table 3). Following the highly visible mark test with the mark on the forehead, we immediately tested if the wolves would remain uninterested in their own marks even if they could see them directly without the use of the mirror (Gallup & Anderson, 2020) by marking them with the same highly visible mark on their front feet. Except for one wolf (Denali) that licked his foot immediately post-marking and then gave it no more attention, no wolves directed any obvious attention to their own or their pack mates' marked feet (Figures 4 and 5). Please see Appendix for expanded results.

Table 3

Summary of Occurrence of Behaviors (Goodman et al., 2002) Observed During Mirror Exposure, Classed According to the 4 Stages or Behavioral Categories of the Mirror Self-recognition (MSR) Test (as defined in Plotnik et al., 2006) for the Sham Mark and Highly Visible Mark Tests by Wolf

	Luna[a]	Grizzer[a]	Aidan	Denali	Boltz	Axel	Grayson
Sham mark test - July 5, 2017							
Mirror engagements	9	10	11	9	2	17	11
Total time at mirror (min:s)	2:17	2:16	5:00[b]	1:29	0:43	2:11	2:39
Social response	0	0	0	0	0	0	0
Physical mirror inspection	7	6	7	5	1	8	5
Repetitive mirror-testing behavior	1	2	4	1	0	6	4
Self-directed behavior	0	0	0	0	0	0	0
Highly visible mark test - July 26, 2017							
Mirror engagements	3	3	4	3	0	4	4
Total time at mirror (min:s)	0:22	0:23	0:19	0:08	0:00	0:22	0:14
Social response	0	0	0	0	0	0	0
Physical mirror inspection	3	1	3	0	0	1	2
Repetitive mirror-testing behavior	0	0	0	0	0	0	0
Self-directed behavior	0	0[c]	0	0	N/A[d]	0	0

[a]Luna and Grizzer were housed on-exhibit until they were ~4 and ~7 years old, respectively, and moved off-exhibit to an adjacent enclosure that they share.
[b]Aidan was distracted from the mirror by the videographer for 1 min and 10 s.
[c]Grizzer rubbed his flank against a tree immediately after being marked on the forehead but showed no self-directed behaviors while in front of the mirror. No other wolves showed responses to being marked on their forehead.
[d]Boltz was in the exhibit enclosure during the mark test but was not marked because we were unable to approach him close enough to mark him. Although he was in the enclosure, he never engaged with the mirror during the mark test.

General Findings as Related to Proposed Stages of MSR

Overall, our findings confirm Bekoff's (2014) report (i.e., that this highly social animal does not pass the MSR test) and highlight potential problem areas with the MSR test for wolves based on stage-specific responses. None of the wolves responded socially as if an unfamiliar wolf were in the mirror (Stage 1 of MSR). We suspect that the wolves may have initially exhibited social responses to their semi-reflections in the public viewing windows and became desensitized to these semi-reflections well before this experiment began. In not responding socially, we conclude that wolves having this level of semi-reflection exposure also do not demonstrate behaviors consistent with the "Puzzling Other" hypothesis related to self-other distinction (de Waal et al., 2005, p. 11,145). Because none of the wolves exhibited behavior consistent with perceiving their mirror reflection as an unfamiliar conspecific, we were unable to investigate (even in a very limited scope) potential effects of age, dominance, or gender on aggressive behavior toward the mirror reflection. However, it is interesting to note that the exhibit pack's dominant male, Aidan, spent the most time engaged with the mirror (5 min during the sham mark test; Table 3).

The benchmark information that wolves by at least 14 months of age do not respond to their reflections as unfamiliar conspecifics (Stage 1 of MSR) will help facilitate improved captive management of wolves by confirming that wolf reflections in exhibits with semi-reflective surfaces (windows) or where mirrors are used for enrichment stimuli are not a source of stress to wolves $\geq$ 14 months of age. This lack of stress response was also supported by the wolves' greatly diminished interest in the mirror as the experiment progressed and even their resting nearby the mirror. Additional future research is needed to examine when pups begin to respond as if the wolf in the mirror is not a conspecific. Ideally, pups would be tested earlier (at least <4 months), before they gain exposure to semi-reflective windows to better assess differences among age classes (pup, yearling,

adult).

In addition to not responding to the mirror aggressively, the wolves appeared to visually inspect the area behind the mirror and the frame itself (Stage 2 of MSR). Because of the mirror setup, this "looking behind" behavior was restricted to visually examining the area behind the mirror from a distance while still within the enclosure. Also, all wolves but one engaged in at least one instance of apparent mirror-testing behavior (Stage 3 of MSR; Table 3). The apparent mirror-testing behavior we observed was largely restricted to brief, parallel walking (and at least once instance of head-bobbing), so additional documentation of potential mirror-testing behavior is warranted (this was not possible for our study because wolves rapidly lost interest in the mirror).

While none of the wolves showed any self-directed behaviors (Stage 4 of MSR), this behavior may have eventually surfaced over time with prolonged mirror exposure (Gallup, 1970). Unfortunately, we were unable to examine whether those behaviors would develop over time, because these wolves rapidly lost interest in the mirror. Even apart from their marks, none of the wolves exhibited other self-directed behaviors such as opening one's mouth and examining the buccal cavity via the reflection. Because no self-directed behaviors occurred and the wolves were uninterested in their marks even when they could see them directly (e.g., on their own feet and on packmates' foreheads and feet), we were unable to appropriately assess wolf self-recognition in the mirror (Stage 4 of MSR).

Wolves did not pass the 4th stage of the MSR test – and there are a number of potential reasons. They may not possess self-awareness, though high social attentiveness, tolerance, and cooperation in captive wolves (Lampe et al., 2017; Range & Virányi, 2015) seem to cast doubt on this, as do behavioral observations of wild wolves (Gable et al., 2018; Mech et al., 2015). It could be due to intraspecific variation (perhaps other wolves would pass; De Veer & Van Den Bos, 1999). It could be that features of the captive rearing of these specific wolves did not allow for their full self-recognition capabilities to develop, given that their socially complex lives in the wild may not necessarily parallel their captive experience (De Veer & Van Den Bos, 1999). Alternatively, they may have failed because they required additional exposure to the mirror for MSR to develop (Gallup, 1970), although we are skeptical of this because most of the wolves we tested were exposed to semi-reflective surfaces for years. We note that besides this article, we are not aware of any other published information on wolf understanding of and/or ability to use mirrors. Thus, additional wolf-mirror research is warranted such as whether wolves can use mirrors to find hidden objects as has been tested with dogs (Howell & Bennett, 2011; Howell et al., 2013).

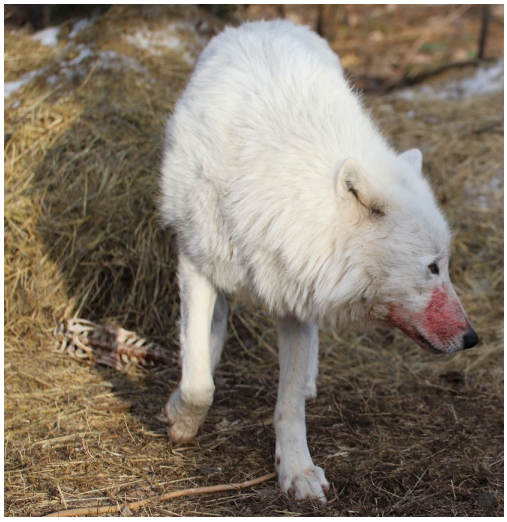
Unremarkable Marks

While the above are all valid potential reasons for why the wolves failed the MSR test, our stage-specific results also highlight that there were conclusive, fundamental issues with the mark. When wolves were able to observe their marks in the mirror, 1) they did not realize it was themselves, 2) they were not interested in their reflection or mark, and/or 3) they could not detect the mark. Similarly, none of the wolves (except Denali licking his foot immediately after it was marked) exhibited interest in the other wolf's marks or in the marks applied to their own feet (situations where marks could be viewed without mirror use). Given canid dichromatic visual sensitivity (Jacobs et al., 1993; Neitz et al., 1989) and because Denali licked the mark on his foot, we doubt that they could not detect the mark. While dogs have been shown to have inferior task performance through a fence compared to without a fence (Udell et al., 2008), this was not the reason for the wolves' lack of attention to their marks in the mirror, as they were similarly uninterested in the marks even when they could see them on their own feet and other wolves' foreheads and feet. Plus, we documented wolves exhibiting behaviors consistent with two and possibly three MSR behavioral categories through the fence. We suspect the lack of wolf response to the mark was because the mark itself was simply "unremarkable". Wolves have variable coat colors (individual and species-wide) and frequently have splatter or streaks (e.g., blood, dirt, etc.) on their faces and elsewhere from eating and scent-rolling on the ground, etc. (Figures 6A and 6B). As Brandl (2016, p. 5) commented, "It could well be that animals recognize changes in their appearance yet feel no compulsion to respond to them; they might simply lack any such motivation".

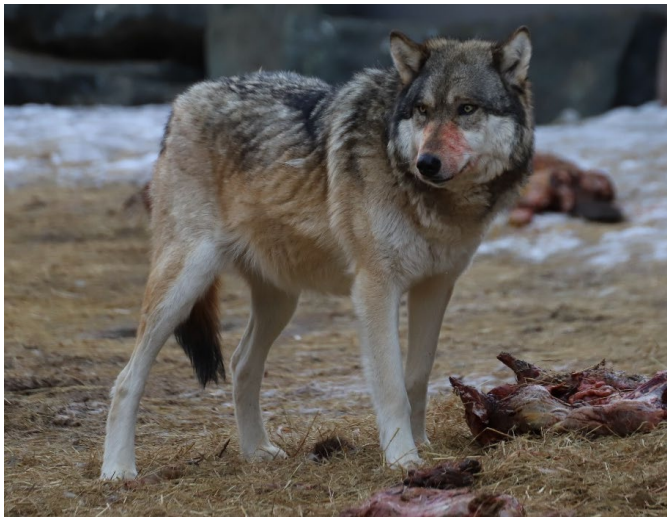
Figure 6A and 6B

Axel's (White Wolf; Figure 6A) and Boltz's (Brown/White/Gray Wolf; Figure 6B) Muzzles are Naturally "Marked" with Blood After Feeding

A



B



Is the MSR Test Appropriate?

Some scientists have suggested that because the MSR test relies on vision, rather than scent, it is therefore an inappropriate test for dogs or wolves (Bekoff, 2014; Cazzolla Gatti, 2016; Horowitz, 2017; but also see Gallup & Anderson, 2017). However, we suggest that the well-developed sense of smell in wolves does not preclude them from passing the visual-based MSR test. As coursing hunters, vision is a critical sense for wolves (Gable & Gable, 2019) in precisely positioning their bite on kicking, fleeing predators that could injure them (Mech et al., 2015), and significant visual communication occurs between wolves through different ear and tail positions which are detected by vision (Goodman et al., 2002). Furthermore, because an important step in the MSR test is cessation of prior social response to the animal's own reflection, it follows then that it is not a barrier that the reflection lacks some properties of a conspecific (e.g., scent in the case of wolves) and perhaps even helps the animal to advance more quickly through that stage in MSR precisely because some conspecific cues are lacking. Thus, we do not concur that a vision-based self-cognizance test is preemptively inappropriate for canids, but we conclude rather that a test that relies on responding to a visually detected, ecologically irrelevant mark is likely inappropriate (Hill et al., 2018; Vonk, 2019) for this and similar species.

Future Research Directions and Recommendations

Because the wolves quickly lost interest in the mirror (as apparent from the decline in time at the mirror and number of mirror engagements during the highly visible mark test), we are unable to proceed with additional MSR experiments with these wolves. Future research including tests of younger wolves (not yet exposed to any reflective or semi-reflective surfaces) to determine if they initially exhibit a social response to their reflection in the mirror (and if so, when that response disappears) should be conducted. Here, we suggest additional areas for research to better elucidate other possible explanations for the failure of wolves to pass the MSR test and to explore other self-cognizance tests.

Foremost, additional research is needed to determine what may constitute an ecologically relevant "mark" for wolves in MSR (e.g., see Hauser et al., 1995). We do not recommend using tape to mark the wolves (as has been done with elephants; Plotnik et al., 2006) because it would tug on the wolf's fur (i.e., feel different) making them aware of the mark on their head even without viewing their reflection in a mirror. Similarly,

marks should also ideally be scentless. Others have anesthetized study animals and shaved or dyed a portion of their forehead hair/fur. In our case, we were unable to do this because of pack dynamics and differing recovery times from drugs that are not completely antagonizable/reversible (e.g., some wolves would still be recovering while others would be walking around and we did not consider this an appropriate risk given the particulars of this captive wolf pack and ramifications to social rank). This approach might be appropriate for wolves that are housed by themselves. However, if the fur were shaved or dyed, it would be even more critical to compare self-directed behaviors (e.g., pawing at their mark) when not looking in a mirror with self-directed behaviors while looking in the mirror because the area may simply feel different (e.g., cooler, itchy, etc.). Apart from the features of the mark and its application, the question remains, what constitutes an ecologically relevant or interesting visual mark for a wolf? Perhaps a pattern that is not observed by wolves in nature (such as uniformly spaced, filled triangles) may constitute a more "remarkable" mark from a wolf's perspective, though this still would not seem to be ecologically relevant.

Recent research also emphasizes the importance of "rearing conditions and environmental factors in the development of higher-level cognitive abilities" in canids (Udell et al., 2008, p. 1,767). In earlier cognitive tests, dogs appeared to outperform wolves in following human cues to locate hidden food (Miklósi et al., 2003), but in more recent tests, when dogs were tested in similar environments to wolves (e.g., both outdoors), wolves performed better (Udell et al., 2008). Thus, both rearing and environmental conditions must be considered in cognitive tests (Lampe et al., 2017). Depending on particular captive management protocols, we recommend rearing wolves in a social context but testing them in isolation, when possible, to minimize behavioral interactions among wolves during the test that may distract them from the mirror or otherwise alter their behavior. We note though that when testing wolves in isolation, caretakers must be aware of potential anxiety caused by the isolation if wolves are not normally separated as part of pack management (e.g., some captive programs routinely separate wolves at night and anxiety would not likely be as much of an issue in that case) and be prepared for ramifications to social rank when isolated wolves are returned to the pack. We note that testing wolves at different times of the year may result in varying responses to the mirror given the effect of seasonally fluctuating hormones on social aggression in captive packs (e.g., late spring or early summer is a calmer time of the year compared to fall and the winter breeding season) (Asa et al., 1990; Asa & Valdespino, 1998; Packard, 2003).

A suite of ecologically relevant self-cognizance tests that consider life history and sensory characteristics and that can also be scaled along a potential self-recognition spectrum are needed (Hill et al., 2018). Tests regarding olfactory and auditory self-recognition have been proposed as potential MSR analogs (Bekoff, 2001, 2014; Cazolla Gatti, 2016; De Veer & Van Den Bos, 1999; Horowitz, 2017). Recent domestic dog self-cognizance research has focused on scent-based tests conducted with the subject's own urine representing "self" (Bekoff, 2001, 2014; Cazolla Gatti, 2016; Horowitz, 2017). However, some assert that additional olfactory tests are needed that include a control for comparable changes in other familiar odors beyond just the dog's own urine (Gallup & Anderson, 2017). It has also been argued that because the dogs in the Horowitz (2017) study did not attempt to smell themselves after smelling the self-altered odor, they did not demonstrate self-recognition per the criteria of the MSR test (Gallup & Anderson, 2017, 2020). While there is certainly debate regarding whether olfactory self-recognition tests are true correlates of the MSR (Gallup & Anderson, 2017), they, nevertheless, represent a promising line of investigation into canid self-other distinction (de Waal et al., 2005) and, potentially, wolf self-awareness.

In addition to olfaction-based tests, research highlighting individual recognition of wolves (*Canis* spp.) by their unique howls (Palacios et al., 2007; Palacios et al., 2015; Root-Gutteridge et al., 2014; Tooze et al., 1990) suggests auditory self-recognition tests may also be a fruitful line of inquiry. However, there are also potential issues with auditory-self recognition tests. For example, one's own vocalizations already sound altered when heard from a playback versus heard directly because of sound transmission differences. Also, it has been noted that auditory self-recognition is, at least in some species, a simpler cognitive process than MSR (e.g., auditory recognition "in some birds is mediated by a single neuron", Parker et al., 1994, p. 16). Additionally, noninvasive neurobiology techniques have been proposed as a method for self-cognizance research (Bekoff & Sherman, 2004).

Another interesting avenue for future self-cognizance research in wolves would be to test for differences in responses among wolf-coat colors, genders, and pack status (e.g., dominant, nondominant). Differences in mirror responses among these categories might be expected based on what is known from wild wolf behavior. For example, research in Yellowstone National Park indicated that gray-colored wolves were more aggressive in social conflict than black wolves and that males were more aggressive than females (Cassidy et al., 2017). We were unable to explore mirror responses among these categories, but we note that in our study the dominant male (gray/white/brown coat) spent the most time engaged with the mirror.

Because ours is the first report detailing specific results and the problems encountered at each stage of the MSR test in a highly social, cooperatively hunting, coursing, terrestrial carnivore, our findings and recommendations may aid in understanding self-awareness in MSR-untested species, such as African wild dogs (*Lycaon pictus*), spotted hyenas (*Crocuta crocuta*), and African lions (*Panthera leo*). Our recommendations should enable future researchers to build on this baseline information of wolf responses in the MSR test to gain greater insights into the possibility of empathy in wolves and potentially other similar species through ecologically relevant, scalable self-cognizance tests.

Acknowledgments

SB-M's time and some research equipment was funded by the U.S. Geological Survey. LJS's time, some research equipment, and everything required to care for the captive wolves and maintain their enclosures was funded through the International Wolf Center (IWC). We thank IWC wolf care members, staff, and interns for study assistance. We thank Marc Bekoff, Roberto Cazzolla Gatti, Gordon Gallup, Jr., and Kristina Spaulding for helpful discussions and information. We thank Ellen Heilhecker (Washington Department of Fish and Wildlife) and anonymous reviewers for suggestions that improved earlier drafts. Any mention of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

Anderson, J. R. & Gallup, G. G., Jr. (2011). Do rhesus monkeys recognize themselves in mirrors? *American Journal of Primatology*, *73*(7), 603–606.

Anderson, J. R. & Gallup, G. G., Jr. (2015). Mirror self-recognition: A review and critique of attempts to promote and engineer self-recognition in primates. *Primates, 56*(4), 317–326.

Ari, C., & D'Agostino, D. P. (2016). Contingency checking and self-directed behaviors in giant manta rays: Do elasmobranchs have self-awareness? *Journal of Ethology, 34,* 167–174.

Asa, C. S., Mech, L. D., Seal, U. S., & Plotka, E. D. (1990). The influence of social and endocrine factors on urine-marking by captive wolves (*Canis lupus*). *Hormones and Behavior*, *24*(4), 497–509.

Asa, C. S., & Valdespino, C. (1998). Canid reproductive biology: An integration of proximate mechanisms and ultimate causes. *American Zoologist*, *38*(1), 251–259.

Bailey, I., Myatt, J. P., & Wilson, A. M. (2013). Group hunting within the Carnivora: Physiological, cognitive and environmental influences on strategy and cooperation. *Behavioral Ecology and Sociobiology*, *67*(1), 1–17.

Baragli, P., Demeru, E., Scopa, C., & Palagi, E. (2017). Are horses capable of self-recognition? A pilot study. *PLoS ONE, 12*(5), e0176717.

Bekoff, M. (2001). Observations of scent-marking and discriminating self from others by a domestic dog (*Canis familiaris*): Tales of displaced yellow snow. *Behavioural Processes*, *55*(2), 75–79.

Bekoff, M. (2014). The significance of ethological studies: Playing and peeing. In A. Horowitz (Ed.), *Domestic dog cognition and behavior: The scientific study of Canis familiaris* (pp. 59–75). Springer-Verlag Publishing. https://doi.org/10.1007/978-3-642-53994-7_3

Bekoff, M., & Sherman, P.W. (2004). Reflections on animal selves. *Trends in Ecology & Evolution*, *19*(4), 176–180.

Brandl, J. L. (2016). The puzzle of mirror self-recognition. *Phenomenology and the Cognitive Sciences*, 1–26.

Breed, M. D., & Moore, J. (2012). *Animal behavior.* Academic Press.

Cammaerts Tricot, M. C., & Caemmaerts, R. (2015). Are ants (Hymenoptera, Formicidae) capable of self-recognition? *Journal of Science, 5*(7), 521–532.

Cassidy, K. A., Mech, L. D., MacNulty, D. R., Stahler, D. R., & Smith, D. W. (2017). Sexually dimorphic aggression indicates male gray wolves specialize in pack defense against conspecific groups. *Behavioural Processes*, *136*, 64–72.

Cazzolla Gatti, R. (2016). Self-consciousness: Beyond the looking-glass and what dogs found there. *Ethology, Ecology & Evolution*, *28*(2), 232–240.

Chang, L., Fang, Q., Zhang, S., Poo, M. M., & Gong, N. (2015). Mirror-induced self-directed behaviors in rhesus monkeys after visual-somatosensory training. *Current Biology*, *25*(2), 212–217.

Chang, L., Zhang, S., Poo, M. M., & Gong, N. (2017). Spontaneous expression of mirror self-recognition in monkeys after learning precise visual-proprioceptive association for mirror images. *Proceedings of the National Academy of Sciences*, *114*(12), 3258–3263.

DeGrazia, D. (2009). Self-awareness in animals. In R. W. Lurz (Ed.), *The philosophy of animal minds* (pp. 201–217). Cambridge University Press.

De Veer, M. W. & Van den Bos, R. (1999). A critical review of methodology and interpretation of mirror self-recognition research in nonhuman primates. *Animal Behaviour*, *58*(3), 459–468.

de Waal, F. B. M. (2019). Fish, mirrors, and a gradualist perspective on self-awareness. *PLoS Biology, 17*(2), e3000112.

de Waal, F. B., Dindo, M., Freeman, C. A., & Hall, M. J. (2005). The monkey in the mirror: Hardly a stranger. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(32), 11140–11147.

Dunbar, R. I. (1998). The social brain hypothesis. *Evolutionary Anthropology: Issues, News, and Reviews*, *6*(5), 178–190.

Epstein, R., Lanza, R. P., & Skinner, B. F. (1981). "Self-awareness" in the pigeon. *Science*, *212*(4495), 695–696.

Escobedo, R., Muro, C., Spector, L., & Coppinger, R. P. (2014). Group size, individual role differentiation and effectiveness of cooperation in a homogeneous group of hunters. *Journal of the Royal Society Interface*, *11*(95), p.20140204.

Gable, T. D. & Gable, D. P. (2019). Wolf (*Canis* sp.) attacks life-like deer decoy: Insight into how wolves hunt deer? *The Canadian Field Naturalist, 133*(1), 16–19.

Gable, T. D., Stanger, T., Windels, S. K., & Bump, J. K. (2018). Do wolves ambush beavers? Video evidence for higher-order hunting strategies. *Ecosphere*, *9*(3), p.e02159.

Gallup, G. G., Jr. (1970). Chimpanzees: Self-recognition. *Science*, *167*(3914), 86–87.

Gallup, G. G., Jr. & Anderson, J. R. (2017). The "olfactory mirror" and other recent attempts to demonstrate self-recognition in non-primate species. *Behavioural Processes*, *148*, 16–19.

Gallup. G. G., Jr. & Anderson, J. R. (2020). Self-recognition in animals: Where do we stand 50 years later? Lessons from cleaner wrasse and other species. *Psychology of Consciousness: Theory, Research, and Practice, 7*(1), 46–58.

Gallup, G. G., Jr., Anderson, J. R., & Shillito, D. J. (2002). The mirror test. In M. Bekoff, C. Allen, & G. M. Burghardt (Eds.), *The cognitive animal: Empirical and theoretical perspectives on animal cognition*, (pp. 325-333). MIT Press.

Goodman, P. A., Klinghammer E., Willard J., & Sloan, M. (2002). *Wolf ethogram.* Ethology Series No. 3. Eckhard H. Hess Institute of Ethology.

Hauser, M. D., Kralick, J., Botto-Mahan, C., Garrett, M., & Oser, J. (1995). Self-recognition in primates: Phylogeny and the salience of species-typical features. *Proceedings of the National Academy of Sciences of the United States of America*, *92*, 10811–10814.

Hauser, M. D., Miller, C. T., Liu, K., & Gupta, R. (2001). Cotton-top tamarins (*Saguinus oedipus*) fail to show mirror-guided self-exploration. *American Journal of Primatology, 53,* 131–137.

Hill, H. M., Dietrich, S., Cadena, A., Raymond, J., & Cheves, K. (2018). More than a fluke: Lessons learned from a failure to replicate the false belief task in dolphins. *International Journal of Comparative Psychology*, *31*.

Horowitz, A. (2017). Smelling themselves: Dogs investigate their own odours longer when modified in an "olfactory mirror" test. *Behavioural Processes*, *143*, 17–24. http://doi.org/10.1016/j.beproc.2017.08.001

Howell, T. J. & Bennett, P. C. (2011). Can dogs (*Canis familiaris*) use a mirror to solve a problem? *Journal of Veterinary Behavior: Clinical Applications and Research*, *6*(6), 306–312.

Howell, T. J., Toukhsati, S., Conduit, R., & Bennett, P. (2013). Do dogs use a mirror to find hidden food? *Journal of Veterinary Behavior: Clinical Applications and Research*, *8*(6), 425–430. http://doi.org/10.1016/j.jveb.2013.07.02

Ikeda, Y. & Matsumoto, G. (2007). Mirror image reactions in the oval squid *Sepioteuthis lessoniana*. *Fisheries Science, 73*(6), 1401–1403.

Jacobs, G. H., Deegan, J. F., Crognale, M. A., & Fenwick, J. A. (1993). Photopigments of dogs and foxes and their implications for canid vision. *Visual Neuroscience*, *10*(1), 173–180.

Kohda, M., Hotta, T., Takeyama, T., Awata, S., Tanaka, H., Asai, J. Y., & Jordan, A. L. (2019). If a fish can pass the mark test, what are the implications for consciousness and self-awareness testing in animals?. *PLoS Biology*, *17*(2), e3000021.

Lampe, M., Bräuer, J., Kaminski, J., & Virányi, Z. (2017). The effects of domestication and ontogeny on cognition in dogs and wolves. *Scientific Reports*, *7*(1), 1–8.

Mech, L. D., Smith, D. W., & MacNulty, D. R. (2015). *Wolves on the hunt: The behavior of wolves hunting wild prey*. University of Chicago Press.
Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., & Csányi, V. (2003). A simple reason for a big difference: Wolves do not look back at humans, but dogs do. *Current Biology*, *13*(9), 763–766.
McCallum, E. (2019). Are fish self-aware? *Journal of Experimental Biology, 222*(9), jeb192781.
Morrison, R. & Reiss, D. (2018). Precocious development of self-awareness in dolphins. *PloS One*, *13*(1), e0189813, 1–12.
Muro, C., Escobedo, R., Spector, L., & Coppinger, R. P. (2011). Wolf-pack (*Canis lupus*) hunting strategies emerge from simple rules in computational simulations. *Behavioural Processes*, *88*(3), 192–197.
Neitz, J., Geist, T., & Jacobs, G. H. (1989). Color vision in the dog. *Visual Neuroscience*, *3*(2), 119–125.
Packard, J. M. (2003). Wolf behaviour: reproductive, social and intelligent. In L. D. Mech & L. Boitani (Eds.), *Wolves: Behavior, ecology, and conservation* (pp. 35–65). The University of Chicago Press.
Palacios, V., Font, E., & Márquez, R. (2007). Iberian wolf howls: Acoustic structure, individual variation, and a comparison with North American populations. *Journal of Mammalogy, 88*, 606–613.
Palacios, V., Font, E., Márquez, R., & Carazo, P. (2015). Recognition of familiarity on the basis of howls: A playback experiment in a captive group of wolves. *Behaviour, 152*, 593–614.
Parker, S. T., Mitchell, R. W., & Boccia, M. L. (1994). Expanding dimensions of the self: through the looking glass and beyond. In S. T. Parker, R. W. Mitchell, & M. L. Boccia (Eds.), *Self-awareness in animals and humans* (pp. 166–186). Cambridge University Press.
Plotnik, J. M., de Waal, F. B., & Reiss, D. (2006). Self-recognition in an Asian elephant. *Proceedings of the National Academy of Sciences*, *103*(45), 17053–17057.
Prior, H., Schwarz, A., & Güntürkün, O. (2008). Mirror-induced behavior in the magpie (*Pica pica*): Evidence of self-recognition. *PLoS Biology*, *6*(8), e202. http://doi.org/10.1371/journal.pbio.0060202
Rajala, A. Z., Reininger, K. R., Lancaster, K. M., & Populin, L. C. (2010). Rhesus monkeys (*Macaca mulatta*) do recognize themselves in the mirror: Implications for the evolution of self-recognition. *PLoS One*, *5*(9), e12865.
Range, F., & Virányi, Z. (2014). Wolves are better imitators of conspecifics than dogs. *PLoS One*, *9*(1), e86559, 1–9.
Range, F. & Virányi, Z. (2015). Tracking the evolutionary origins of dog-human cooperation: The "Canine Cooperation Hypothesis". *Frontiers in Psychology*, *5*, 1582, 1–10.
Reiss, D. (2011). *The dolphin in the mirror: Exploring dolphin minds and saving dolphin lives*. Houghton Mifflin Harcourt.

Reiss, D., & Marino, L. (2001). Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence. *Proceedings of the National Academy of Sciences*, *98*(10), 5937-5942.
Root-Gutteridge, H., Bencsik, M., Chebli, M., Gentle, L. K., Terrell-Nield, C., Bourit, A., & Yarnell, R. W. (2014). Identifying individual wild Eastern grey wolves (*Canis lupus lycaon*) using fundamental frequency and amplitude of howls. *Bioacoustics, 23*(1), 55–66.
Tooze, Z. J., Harrington, F. H., & Fentress, J. C. (1990). Individually distinct vocalizations in timber wolves, *Canis lupus*. *Animal Behaviour*, *40*, 723–730.
Udell, M. A., Dorey, N. R., & Wynne, C. D. (2008). Wolves outperform dogs in following human social cues. *Animal Behaviour*, *76*(6), 1767–1773.
Vonk, J. (2019). A fish eye view of the mirror test. *Learning & Behavior, June 17*, 1–2.
Zazzo, R. (1979). Des enfants, des singes et des chiens devant le miroir. *Revue de Psychologie Appliquée*, *29*, 235–246.

Financial conflict of interest: No stated conflicts.
Conflict of interest: No stated conflicts.

Submitted: *May 18th, 2020*
Resubmitted: *August 7th, 2020*
Accepted: *September 28th, 2020*