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Obstacles and opportunities for female leadership in mammalian societies: A comparative perspective

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ABSTRACT

Women remain universally underrepresented in the top leadership positions. A comparative evolutionary framework may offer new insights into the value of and potential barriers to female leadership. Here we define leaders as individuals who impose a disproportional influence on the collective behaviors of group members. We reviewed data for 76 social species of non-human mammals to reveal the circumstances favoring female leadership and species exhibiting female-biased leadership in two or more contexts (e.g., collective movements, group foraging, conflict resolution within groups, or conflicts between groups). Although rare across the lineage, female-biased leadership is pervasive in killer whales, lions, spotted hyenas, bonobos, lemurs, and elephants; leaders emerge without coercion and followers benefit from the social support and/or ecological knowledge from elder females. Our synthesis elucidates barriers to female leadership, but also reveals that traditional operationalizations of leadership are themselves male-biased. We therefore propose a new agenda for assessing the overlooked ways that females exert influence in groups.

Introduction

In November 2016, many of us expected former Secretary of State Hillary Rodham Clinton to win the U.S. presidential election and become the first female president of the United States of America. Instead, as the results poured in, Hillary found herself saying, “This loss hurts, but please never stop believing that fighting for what’s right is worth it...And to all the women, and especially the young women, who put their faith in this campaign and in me: I want you to know that nothing has made me prouder than to be your champion. Now, I know we have still not shattered that highest and hardest glass ceiling, but someday someone will—and hopefully sooner than we might think right now. And to all of the little girls who are watching this, never doubt that you are valuable and powerful and deserving of every chance and opportunity in the world to pursue and achieve your own dreams (National Public Radio, 2016).” Why did Hillary need to remind us that women and girls are valuable and powerful? Answering this question is important because leadership permeates virtually every aspect of our lives—influencing day-to-day decisions in our families and work lives to decisions with far-reaching national and international policy implications.

Women remain underrepresented in top leadership positions in

virtually every discipline. This is true in science (Hill, Corbett, & St Rose, 2010), business (Cook & Glass, 2014; Kirsch, 2018) and education (Marshall, Johnson, & Edwards, 2017). Moreover, women hold fewer than 6% of CEO positions at the S&P 500 companies in the United States (Catalyst, 2018). Gender bias in governments is also pervasive worldwide. As of June 1st 2018, women only occupied 19% of the 279 posts of Presiding Officers of Parliament or its Houses in the world (Inter-Parliamentary Union, 2018). For example, in the U.S. House of Representatives and the Senate, respectively, women currently only hold 19% and 21% of the seats; disparities in representation for women of color are even higher (Rutgers, 2017). Meta-analyses offer some insights into these patterns, demonstrating that gender bias reinforces patriarchal structures and favors male leaders across modern institutions (Davidson & Burke, 2011; Eagly & Carli, 2003; Eagly & Johnson, 1990). In fact, attitudes about the effectiveness of female leaders often more strongly reflect local cultural beliefs about the roles of women within their societies than the performance of women in these roles per se (Jogulu & Wood, 2008).

Whereas female leaders tend to offer many advantages in terms of gender-specific leadership styles, women often suffer from prejudicial evaluations of their competence as leaders (Eagly & Carli, 2003). For example, women are less likely to emerge as leaders in more

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hierarchical organizational settings as women are often seen as less agentic – defined in terms of assertiveness, competitiveness, and independence – than men (Harrison & Klein, 2007). Moreover, potential followers favor the attributes of male voices over female voices even when individuals read from the exact same script, suggesting that some of these biases are implicit (McClellan, Martin, Emich, & Woodruff, 2017). Data also show that men in top executive functions are penalized for showing gender-incongruent behaviors (Heilman & Okimoto, 2007). The lack of value placed on female leadership constrains the social mobility of women, especially with respect to their ability to occupy positions of authority (Mezulis, Abramson, Hyde, & Hankin, 2004). This is unfortunate because female leaders are often more egalitarian and more democratic than are male leaders that occupy similar positions (Eagly & Johnson, 1990). Much of this evidence comes from egalitarian societies; women tend to have more political influence in egalitarian societies than in more economically-stratified societies (Endicott & Endicott, 2008; Leacock, 1978; von Rueden, Alami, Kaplan, & Gurven, 2018). In these egalitarian societies, women tend to mediate conflict without imposing or promoting costly physical violence; for example, beneficial female leadership is well-documented for hunter-gathers of the Congo Basin (Lewis, 2014). Women that do occupy leadership positions in male-dominated organizations, such as female executives in top-level positions, often – but not always (Derks, Van Laar, Ellemers, & de Groot, 2011) – create opportunities for other women and promote a positive environment for other women to contribute to the organization (Arvate, Galilea, & Todescat, 2018). Given these patterns, why do we (humans) so often select male leaders over female ones?

Novel theoretical and empirical approaches are required to understand why so few women occupy leadership roles in human societies. Integration of biological and social perspectives within a comparative evolutionary framework may therefore offer new insights into the origins and extent of these leadership biases; they may also inform policy decisions aimed at improving leadership practices (van Vugt, Hogan, & Kaiser, 2008; von Rueden & van Vugt, 2015). For example, social role theory posits that sexual division of labor gives rise to and reinforces the social expectation that women should assume less agentic roles than men (Eagly, 1987; Eagly & Karau, 2002; Eagly & Wood, 1999; Ridgeway, 2001). Evolutionary theory, in contrast, focuses upon understanding evolved sex differences in physical (e.g., strength and size dimorphisms; Buss, 1989, 2015) and behavioral (e.g., tendency to form coalitions, engage in competition) attributes over evolutionary time (Benenson & Markovits, 2014; Campbell, 2013; Geary, 2013; Seabright, 2012). Together, these complementary theories offer insights into how the local (current) ecological and social (cultural) conditions as well as evolutionary forces (over millions of years) contribute to observed sex differences in human behavior (Low, 2005). These theories are complementary with respect to gender-biased leadership by offering explanations at two distinct time scales. For example, social role theory offers insights into how leaders (and followers) emerge from the current, socially-defined categories via social norms encountered by individuals across developmental time. Evolutionary perspectives, instead, offer insights into how millions of years of natural (sexual) selection may have contributed to observed sex differences that persist in human societies today. Whereas both theories complement each other in their explanation of evolved and often dynamic behavioral phenomena, neither one aims to justify or otherwise defend these gender biases.

Evolutionary theory, for example, predicts that natural selection should favor individuals engaged in physical contests (i.e., within-group conflict, warfare) with the largest body sizes, greatest physical strength and/or largest numbers of allies in conflicts. In many species of animals, one form of natural selection—sexual selection—often favors the evolution of male traits that allow for individuals to outcompete male rivals for access to female mates. In most mammals, because female reproduction is constrained by the demands of lactation and gestation, sexual selection often favors choosy females, and this produces

intense male-male competition (Andersson, 1994). This biological perspective may offer some insights into the evolutionary history favoring men to, on average, be physically stronger than women and to lead during intergroup conflicts more often than women (Browne, 2001; Geary, 2013; van Vugt, De Cremer, & Janssen, 2007). For example, a public goods experiment supported this notion, showing that when agentic competition between groups is salient, groups prefer men over women as their leaders (van Vugt & Spisak, 2008). Yet it may well be that such leader preferences are exacerbated or inhibited by local cultural experiences, such as those shaped by recent episodes of intergroup conflict (van Vugt, 2009). Pioneering studies by anthropologists have done a remarkable job tackling the challenging topic of sex differences in leadership, demonstrating many exceptions to these rules, especially when it comes to humans (Hrdy, 2009; Smuts, 1992, 1995). In recent years, biologists have started to catch up with other fields and to gain an appreciation for the role of leaders. Nonetheless, a systematic study is required to understand the extent to which male-biased leadership occurs across social mammals, especially for non-primate species.

Here we define leaders as those individuals who have a disproportional influence on the collective decisions within a group, regardless of how influence is achieved (King, Johnson, & Van Vugt, 2009; Smith et al., 2016). Importantly, leadership is distinct from the concept of dominance—defined by biologists as a formalized relationship between a dominant and a subordinate individual in which the latter repeatedly signals to the former an understanding that the dominant is able to win fights and has priority of access to resources over the subordinate (deWaal, 1986; van Vugt, 2006). Whereas formalized submission and dominance are based upon the ability for a dominant individual to exert power using physical force or aggression (Lewis, 2002), there is remarkably little evidence of leadership based only upon physical force in non-human mammals (Smith et al., 2015). Biological studies of leadership instead typically focus on the asymmetric relationship in the relative influence of leaders versus followers in an effort to understand collective, coordinated action (Hollander, 1992). That said, in many cases, high-ranking individuals tend to also be leaders within the groups of non-human primates (Hemelrijk, Wantia, & Isler, 2008; King, Douglas, Huchard, Isaac, & Cowlshaw, 2008). Although distinct from dominance, the concept of leadership in biological studies aligns closely with the concept of power in sociology (Simon, 1953) as well the concepts of prestige and status in psychology (Cheng, Tracy, Foulsham, Kingstone, & Henrich, 2013). Our definition aligns with that of psychologists who posit that leadership is more than simply personal dominance, the ability for one individual to coerce the behavior of others (Bass & Bass, 2009; Hrdy, 2009).

Leadership studies of non-human animals are yielding exciting insights into the evolutionary forces favoring leadership in animal societies (Anderson & Franks, 2001; King et al., 2009; Smith et al., 2010, 2015). Studying the evolutionary forces shaping leadership is important because these studies offer insights into the circumstances during which natural selection favors individuals to lead (and follow) when participating in collective behaviors. We posit that understanding the costs and benefits of these behaviors may help to explain why observed social structures and traits of leaders persist in human societies today.

Humans are formally referred to as *Homo sapiens*, and members of the genus *Homo* first emerged in the fossil record roughly 2.5 million years ago (Cavalli-Sforza, Piazza, Menozzi, & Mountain, 1988; Potts, 2012). However, because patterns of behavior are often challenging to detect from fossil records, a comparative approach of studying patterns of leadership in living species of non-human mammals may shed light into the processes shaping behavioral patterns in our own evolutionary past. In some cases, shared traits—including patterns of behavior—may arise in related species via homology because of shared ancestry among mammalian species. Another process, convergent evolution, may also favor the evolution of similar traits in distantly related species of mammals coping with similar ecological and

social environments. Thus, shared ancestry and/or convergent selective pressures may have shaped similar patterns of leadership across the mammalian lineage, including those of gender bias in modern humans.

Despite leadership being ubiquitous within groups of non-human animals, most leadership studies of non-human animals focus on collective movements during group travel (Boinski & Garber, 2000; Reynolds, 1987; Smith et al., 2015). More recently, however, the concept of leadership has been extended to also explain coordination and collective action within the domains of foraging, within-group conflict resolution and between-group conflicts (Smith et al., 2016). Building upon this unifying framework for understanding the common properties of leadership across human and non-human mammalian societies (Smith et al., 2016), our major goal here is to identify the social and ecological contexts in which powerful female leaders emerge within non-human mammalian societies. Studies of human leadership indicate that gender bias is often situational, varying across society type and organizational context (Ayman & Korabik, 2010). For example, preferences for leaders with masculine traits are particularly strong during times of conflict whereas preferences for leaders with feminine traits appear during times of cooperation (Little, Burriss, Jones, & Roberts, 2007; Spisak, Homan, Grabo, & van Vugt, 2012). In this paper, we therefore provide an overview of four major biologically-relevant situations in which leaders and followers emerge within various mammalian societies. Then, we identify those species of mammals for which female-biased leadership is known to persist in at least two of these major situations. By describing the strongest cases of female leadership in non-human species, we aim to offer insights into the opportunities and potential challenges for female leadership in mammalian societies, most notably for the case of humans. We will return to this topic at the end of the paper.

Major situations of leadership in animals

Collective movement occurs when two or more individuals maintain spatial proximity while traveling together to a new location (Petit & Bon, 2010). Pioneering studies of collective animal behavior set out to understand the basic rules explaining coordinated, large-scale patterns of movements by aggregations comprised of hundreds of insects, fishes, starlings or hooved migratory animals traveling together in a coordinated manner (Boinski & Garber, 2000). These seemingly complex patterns of swarming, shoaling (schooling), flocking and herding may be explained by patterns of localized leadership and followership (Reynolds, 1987). That is, followers simply adjust their movements by maintaining spatial proximity to—and matching the speed of—nearby individuals (localized leaders) without bumping into them. Follow-up inquiries indicate that socially-complex mammals also tend to follow these simple rules when traveling in groups (Boinski & Garber, 2000). Natural selection often favors individuals to travel in groups—rather than alone—because individuals benefit from reduced predation risk; this is known as the selfish herd effect (Hamilton, 1971). Moreover, individuals living in groups often accrue benefits from the collective acquisition of shared resources, mating opportunities, and the increased ability to join forces in defense against neighboring social groups (Alexander, 1974; Boinski & Garber, 2000).

Leaders within mammalian groups also emerge to resolve conflicts of interest regarding the direction, timing and destination of travel (Conradt & Roper, 2005). Whereas foundational studies suggested that non-human groups typically were led by one or a few consistent dominant animals, emerging evidence indicates that multiple individuals often occupy leadership roles within groups of non-human animals (Smith et al., 2015), arguably a case of distributed leadership (Gronn, 2002). That is, leadership is often “attribute based”—defined as leadership that is dependent upon the specific traits of the non-human individuals (Smith et al., 2015). For example, the tendency for an individual to occupy a leadership role typically depends upon their motivational state, age, personality, social status, competence and, of

particular interest here, their sex (King et al., 2009). In general, adult female mammals, particularly those with specialized knowledge (e.g., about food sources or migratory routes) and/or with reproductive responsibilities (e.g., lactating females with dependent offspring) emerge as leaders most often within the context of groups travel; they do so in the absence of any forms of coercion (Smith et al., 2015). Intriguingly, human leaders also adhere most often to an attribute-based system of leadership (Bass & Bass, 2009); leaders often possess attributes that signal their competence to lead group activities.

Although most biological studies that discuss the concept of leadership do so within the context of group travel, a disparate literature shows that leaders also emerge within contexts of collective foraging and conflict resolution/escalation (Smith et al., 2016). Within the foraging domain, leaders emerge when cooperation is required to collectively locate, acquire and distribute food. For example, social carnivores (members of the mammalian Order *Carnivora*, such as African lions, *Panthera leo*, and spotted hyenas, *Crocuta crocuta*) often join forces to capture large prey that is too challenging to capture on one's own (Holekamp, Boydston, & Smale, 2000; Packer, Scheel, & Pusey, 1990). Within an evolutionary perspective, the lives of social carnivores are of particular importance because convergent selective pressures likely shaped patterns of collective behavior in both mammalian carnivores and early hominins (members of the genus *Homo*) (Schaller & Lowther, 1969; Smith, Swanson, Reed, & Holekamp, 2012). Interestingly, the roles of leaders may shift after food is cooperatively acquired. For example, the distribution of food in some taxa is egalitarian such that different individuals take on leadership roles, as occurs for example in lions (Packer, Pusey, & Elberly, 2001). In other societies, such as those of spotted hyenas, leadership in the distribution of resources is highly despotic such that social rank determines feeding order (Frank, 1986).

Finally, mammalian leaders often emerge to settle conflicts within and between groups. From an evolutionary perspective, effective conflict resolution is advantageous to both leaders and followers as it fosters group efficiency and social cohesion (deWaal, 1990). Conflict resolution reduces the dual costs of energy expenditure and the potential for injury or even death associated with escalated aggression (deWaal, 2000). The outcomes of conflicts between members of two different social groups can also have long-term reproductive consequences for individuals, such as in determining the size of territories and resource access within them (Boydston, Morelli, & Holekamp, 2001; Mitani, Watts, & Amsler, 2010). Moreover, leaders typically exert significantly more influence in contexts involving conflicts within groups (e.g., peacekeepers) or between groups (e.g., leaders in warfare) than in the previously mentioned situations of group travel or foraging (Smith et al., 2016).

Strong female leaders in mammalian societies

Building upon this foundational work, here we conduct an extensive literature review to identify those species of non-human mammals for which detailed data on the strongest cases of female leadership exist. We first compiled a list of species exhibiting leadership within at least one of the four domains – collective movement, foraging, and conflict management within and between groups – based on recent reviews of topic as well as on more recent publications citing those reviews. We started our inquiry by focusing on species known to engage in leadership to some extent, regardless of whether males, females or both sexes occupy leadership roles (Smith et al., 2010, 2015, 2016). This yielded 76 non-human species that spanned eight biological orders within the Class Mammalia: *Artiodactyla* (13 species of even-toed ungulates and whales), *Carnivora* (13 species of carnivores), *Chiroptera* (1 bat species), *Perissodactyla* (3 species of odd-toed ungulates), *Primate* (44 species of primates), and *Proboscidea* (2 species of elephants). The relationships among these species are shown in a phylogeny representing the shared evolutionary history among these social mammals for which

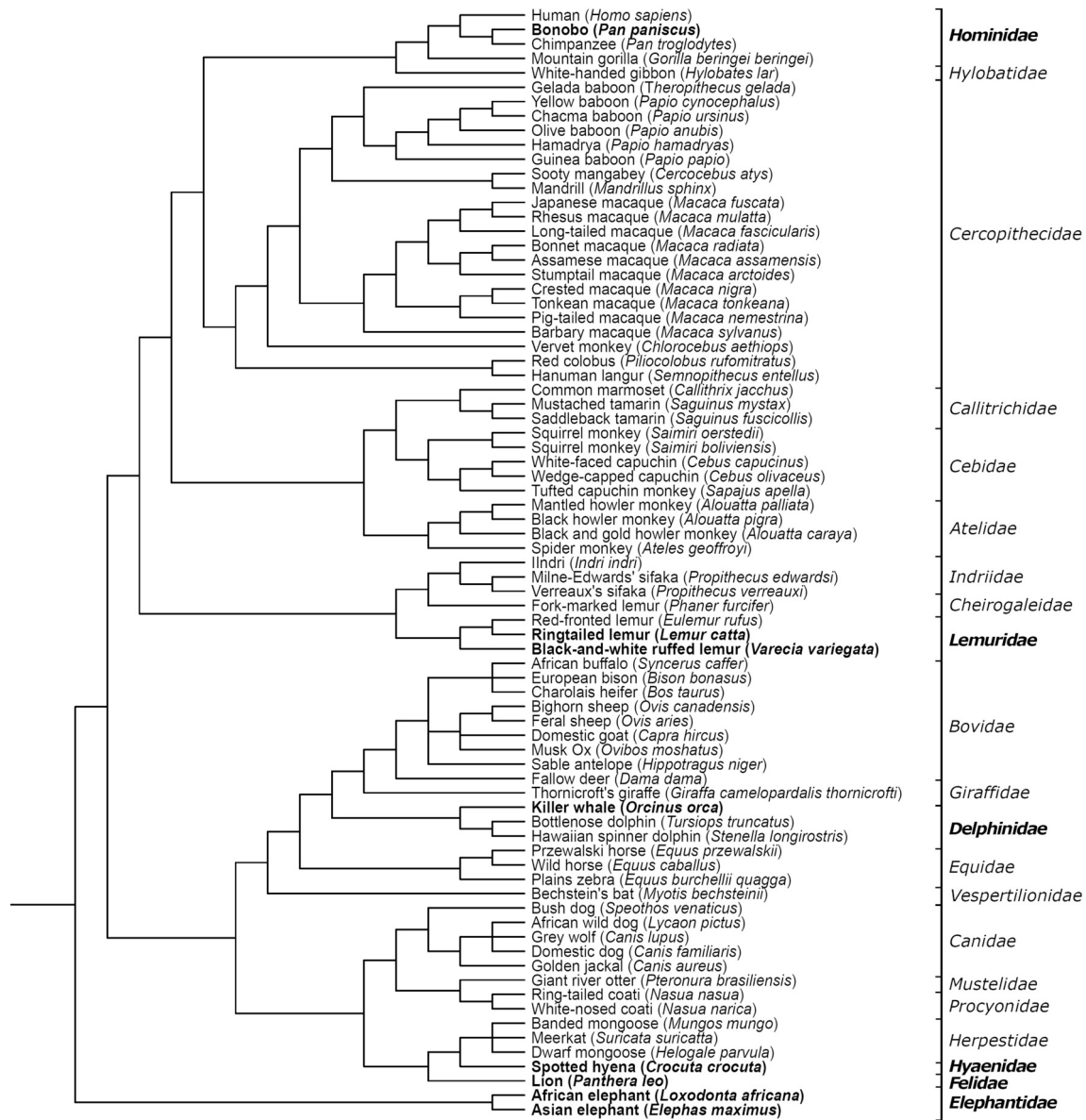


Fig. 1. Phylogeny of 77 species of social mammals, including humans (*Homo sapiens*) and 76 species of non-human mammals for which information was available on gender/sex roles of leaders emerging within the contexts of group movements, foraging, conflict resolution within groups, and/or conflict between groups. The diagram reflects the shared evolutionary history of mammals, with the left side depicting the origins (roots) of the lineage and the right side depicting extant (living) species at the tips of the tree. Bolded names represent the following species with strong female leadership: 1) bonobos (*Pan paniscus*), 2) ring-tailed lemurs (*Lemur catta*), 3) black-and-white ruffed lemurs (*Varecia variegata*), 4) killer whales (*Orcinus orca*), 5) spotted hyenas (*Crocuta crocuta*), 6) African lions (*Panthera leo*), 7) African bush elephants (*Loxodonta africana*), and 8) Asian elephants (*Elephas maximus*).

good data on patterns of leadership are currently available in the literature (Fig. 1). Notably, although females in two rodent species of naked mole rats are socially dominant to males, insufficient data on patterns of leadership during collective behavior with respect to group travel or conflicts within and between groups were available to be included in this synthesis (Sherman, Jarvis, & Alexander, 2017). To support our comparative framework, we also include humans in the phylogeny (Fig. 1). We constructed the phylogeny in the Phylotastic Project (<http://phylotastic.org>) and iTOL: Interactive Tree of Life (<https://itol.embl.de>) which pulls from NCBI IDs (www.ncbi.nlm.nih.gov/taxonomy).

We reviewed the available data for these 76 species of non-human mammals to identify those species for which female leadership is prominent across major situations. Although the social sciences often distinguish between biological sex and the cultural construct of gender—treating each separately (Patterson, Mavin, & Turner, 2012; Renn,

2007)—, biological research, and thus this review, is limited to information on biological sex—male versus female. We therefore defined female-biased leadership within each leadership context (movement, foraging, within-group conflict, between-group conflicts) as occurring in (a) species for which females exclusively lead collective behaviors or (b) species for which females, on average, occupy leadership roles more often than do males. As before, leaders within each context, were defined as leaders when their actions had a disproportional influence on the collective movements, foraging, or conflict (within or between groups) of group members (followers).

Here we focused on key cases for which female-biased leadership transcended into at least one additional domain beyond group travel. We adopted this approach because the role of female leaders within the domain of travel has been discussed extensively elsewhere and because we seek a more holistic view of the traits of female leaders who occupy leadership roles in domains for which male-biased leadership is most

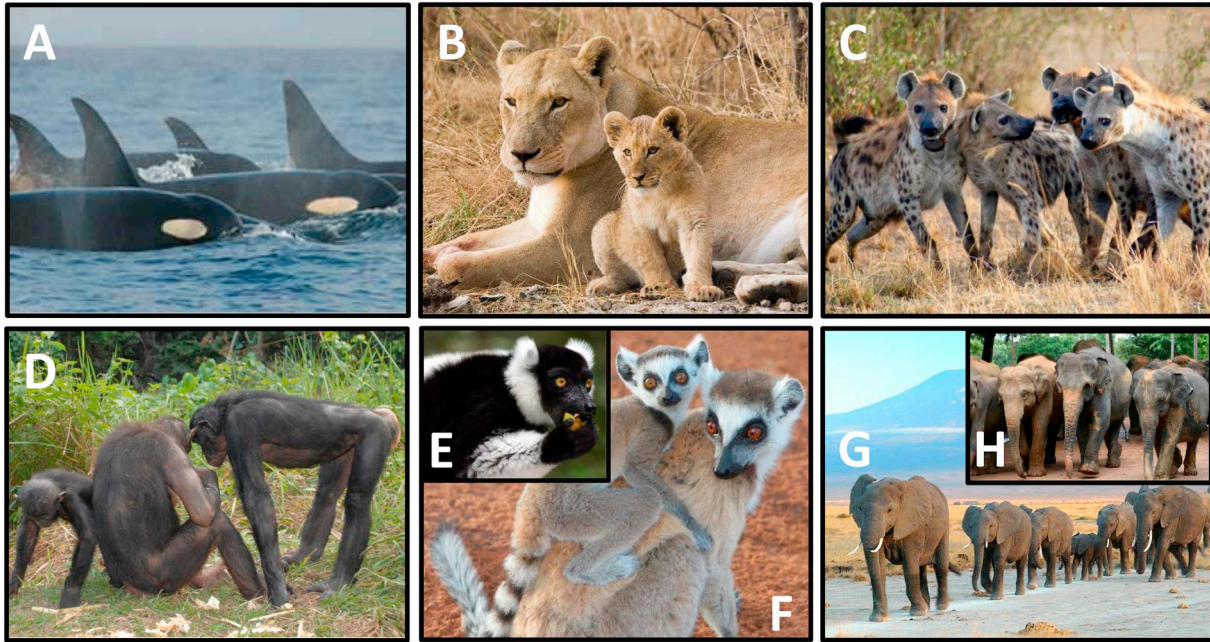


Fig. 2. Non-human mammalian societies for which females emerge as strong leaders during collective behaviors across multiple contexts include: A) killer whales (*Orcinus orca*), B) African lions (*Panthera leo*; Photo by Greg Willis via Wikimedia/CC BY-SA 2.5), C) spotted hyenas (*Crocuta crocuta*; Photo by David S. Green), D) bonobos (*Pan paniscus*; Photo by Pierre Fidenci via Wikimedia/CC BY-SA 2.5), E) black-and-white ruffed lemurs (*Varecia variegata*; Photo by Charles J. Sharp via Wikimedia/CC BY-SA 3.0), F) ring-tailed lemurs (*Lemur catta*; Photo by David Deniss via Wikimedia/CC BY-SA 3.0), G) African bush elephants (*Loxodonta africana*; Photo by Amoghavarsha via Wikimedia/CC BY-SA 3.0), H) Asian elephants (*Elephas maximus*; Photo by Steve Evans via Wikimedia/CC BY-SA 2.0). All photos are public domain under the Creative Commons License, except that used, with permission, from D.S.G.

evident in humans. Briefly, female leadership during travel is most often explained by dependent young [e.g., seeking nutrition from nursing, (Fischhoff et al., 2007)] and/or less informed individuals who follow elder females [e.g., who presumably possess enhanced local knowledge (Brent et al., 2015)]. Our current approach should therefore reveal the most salient cases of female-biased leadership and identify those species for which adult females are regularly followed by other adults in multiple contexts within the natural world and in domains involving followers beyond the immediate family.

Evidence for female-biased leadership in mammalian societies

In total, our analysis revealed that only eight of the 76 species exhibit strong, female-biased leadership (Fig. 2). That is, roughly 10% of the species are known to have predominantly female leaders across two or more domains. Although additional studies may reveal more cases of strong female leaders, all available evidence to date suggests that male-biased leadership, as defined here, indeed appears to be the norm across the mammalian lineage (Fig. 1). For each of these species, we provide a brief overview of its social structure, describe its patterns of sex-biased leadership in each domain, and synthesize what we may learn from these data.

Killer whales (order Artiodactyla: family Delphinidae)

Female-biased leadership, especially by elder females, is widespread across non-human mammalian societies within the domain of movement. A matriarch is defined as the oldest adult female within the family lineage of a mammalian society and matriarchal leadership offers evolutionary benefits to leaders and followers (Smith et al., 2015). Some of the most noteworthy work on female leadership within the movement domain and foraging domain is documented for one type of toothed whale, the killer whale (also called orcas, *Orcinus orca*, Fig. 2A). Killer whales live in social groups, called pods, and typically specialize on the hunting of marine mammals (transient killer whales) or fish

(resident killer whales). Social groups of killer whales are matrilineal, defined as groups comprised of the descendants of female group members. Killer whale matrilineal groups are usually composed of a female, her sons and daughters, and the offspring of her daughters (Baird, 2002). As occurs among some monkeys and most species of apes, including humans, as well as in most social species of carnivores (Aureli et al., 2008), killer whale societies are structured by fission-fusion dynamics in which individuals regularly break apart and come back together (Baird, 2002).

Killer whales are outliers among the mammals in several ways. First, females have the longest post-reproductive lifespan of any non-human animal, living into their 90s, despite the fact that females stop reproducing at around age 60 (Olesiuk, Ellis, & Ford, 2005). The long lives of these animals in combination with their matrilineal social structure gives rise to societies with as many as four overlapping generations of individuals who depend upon elder females for leadership (Baird, 2002). Second, neither males nor females remain in their home area for their entire lives (Baird, 2002). This is interesting because the typical condition across mammals is for females to remain in their natal (home) areas throughout their lives and for males to permanently disperse from their home areas upon reaching reproductive maturity (Greenwood, 1980). In addition to killer whales, a few other species of mammals also deviate from the typical mammalian pattern of female philopatry and male dispersal. Notably, humans, bonobos (*Pan paniscus*), and chimpanzees (*P. troglodytes*), all of which are closely related species of apes (Fig. 1), deviate from this pattern. For all three species, females disperse whereas males are philopatric (see the bonobo section below for further discussion).

Within groups of resident killer whales that focus on hunting salmon, post-reproductive (menopausal) females most often emerge as leaders (Brent et al., 2015). This is presumably due to their local knowledge and extensive experience as elders within these groups. Leadership by post-reproductive female killer whales is particularly important when salmon are scarce because females possess local knowledge about the locations of these limited food (salmon) sources

(Brent et al., 2015). When mothers act as leaders in this way, they promote the survival of their sons who often lack local ecological knowledge, providing strong evidence for the adaptive benefits of female leadership (Foster et al., 2012). Members within traveling groups use vocalizations to coordinate group movement (Miller, 2002). Although adult females often lead efforts in terms of cooperative searching and driving of prey into a centralized location, the final stage of collective foraging (food capture) is largely performed by individuals on their own such that leaders fail to emerge in the final stage of food capture (Hoelzel, 1991).

Together, these findings likely explain why menopausal female killer whales live so long and emerge as important leaders within their social groups. These data suggest that parallel adaptive explanations may favor prolonged life after reproduction by female leaders within human societies, especially within family units (Croft, Brent, Franks, & Cant, 2015). However, limited information is available on the extent to which killer whales lead within the contexts of conflicts within and between groups, so it is yet to be determined whether female leadership within killer whales is limited to the movement and foraging domains or is pervasive across the lives of these animals. Nonetheless, local knowledge by female elders clearly appears to be a major driver of female leadership within the societies of killer whales.

African lions (order Carnivora: family Felidae)

Of the wild cats (felids), African lions (Fig. 2B) are the only social species (Smith, Lehmann, Montgomery, Strauss, & Holekamp, 2017). Sociality in lions apparently evolved initially as a result of the benefits of cooperative territorial defense; later in the evolutionary history of lions, individuals gained direct benefits from cooperative hunting (Packer et al., 1990). Adult females (lionesses) are philopatric (remaining in their home/birth areas throughout their adult lives), forming a stable social unit and belonging to prides composed of related females and their offspring (Schaller, 1972). Prides are egalitarian, meaning that all group members have equal access to food and reproduction (Packer et al., 2001). Cooperation within prides is likely favored by kin selection through the indirect benefits gained by helping family members who share genes (Hamilton, 1964); this is the most common explanation for social tolerance and cooperation in non-human groups of mammals (Smith, 2014).

As occurs in killer whales (Baird, 2002) and in most social carnivores (Smith et al., 2012), lion societies are structured by fission-fusion dynamics in which individuals regularly break apart and come back together (Schaller, 1972). Within prides, lionesses virtually always lead group movements (Schaller, 1972). Lionesses engage in the majority of cooperative hunting and regularly share prey within prides (Packer et al., 2001, 1990; Packer & Scheel, 1991; Stander, 1992). Interventions in conflicts within social groups are rare and have yet to be the subject of systematic study. However, Schaller (1972) described a case in which three lionesses joined forces to intervene on behalf of their cubs to drive off what was presumably a resident adult male. Although females are more cooperative than males when it comes to group defense against intruders and in cooperative hunting, male lions may also group together to form coalitions to direct joint attacks towards intruding males (Schaller, 1972). Members of both sexes regularly lead efforts in defense against intruders. Females act as leaders, joining forces with each other to defend their territory against other prides as well as against infanticide by nonresident males (Grinnell, 2002; Grinnell & McComb, 1996; VanderWaal, Mosser, & Packer, 2009). Whereas males appear to cooperate unconditionally in group defense against intruders, leadership by females is more nuanced (Heinsohn & Packer, 1995). That is, female lionesses fall into consistent roles—acting either as highly cooperative leaders or as laggards that exploit the leadership of highly cooperative females (Heinsohn & Packer, 1995).

More research is needed to understand which attributes of females

contribute to their leadership styles in lion prides. Nonetheless, females benefit from defending themselves from intruders and from sharing food that they acquire cooperatively within these female-based and largely egalitarian societies. The lifestyles of lionesses may offer some insights into the circumstances favoring female leaders in human societies. Specifically, females join forces against outside threats who may harm their investments (offspring) and lack incentives to reduce their companions' access to resources.

Spotted hyenas (order Carnivora: family Hyaenidae)

Spotted hyenas (Fig. 2C) live in societies, called clans (Kruuk, 1972). Clans are far more complex than groups of other social carnivores, such as those of lions, because hyena clans contain up to 130 or more individuals and are comprised of multiple matriline and immigrant males (Holekamp, Smith, Strelieff, Van Horn, & Watts, 2012). Although adult females and their juvenile offspring within a single matriline are highly related, clans have low average relatedness overall (Van Horn, Engh, Scribner, Funk, & Holekamp, 2004). Thus, unlike in most social carnivores, spotted hyena clans regularly engage in collective behaviors with unrelated group mates and often follow leaders with whom they share very few genes (Smith, Lacey, & Hayes, 2017). Spotted hyena clans also differ from groups of other social carnivores—and most species of mammals other than lemurs and two species of mole rats (Kappeler, 1993)—in that they are female-dominated societies in which females have priority of access to resources (Frank, 1986). Constraints imposed by the development of a feeding apparatus specialized for bone cracking, in combination with intensive feeding competition, may have favored the evolution of female dominance in the spotted hyena (Watts, Tanner, & Holekamp, 2009). Moreover, social rank is inherited via the maternal line through the process of associative learning (Engh, Esch, Smale, & Holekamp, 2000). Although social rank is based on who an individual's mother is rather than based on an individual's strength per se, female spotted hyenas are physically larger and stronger than males (Swanson et al., 2013). As a result, adult female spotted hyenas wield the most power in these societies and low-ranking individuals of both sexes actively seek out associations with high-ranking adult females (Smith, Memenis, & Holekamp, 2007; Szykman et al., 2001). Although spotted hyenas are atypical in most aspects of their behavior compared to other mammals, they do adhere to the typical mammalian condition when it comes to dispersal. Female spotted hyenas are philopatric and males disperse (East & Hofer, 2001). Females remain in their home clan and retain their social ranks across their lifespan; in contrast, males disperse and start at the bottom of the dominance hierarchy when joining a new clan (Holekamp et al., 2012).

Within the context of group movements, spotted hyenas have a primarily attribute-based system of leadership (Smith et al., 2015). That is, adult females, especially high ranking and lactating females, lead group travel most often, but all group members, including low-ranking males may occupy leadership roles on some occasions (Holekamp et al., 2000; Smith et al., 2015). Spotted hyenas hunt up to 80% of their own prey (Kruuk, 1972). Although both sexes regularly join forces to lead efforts in the cooperative hunting of large ungulates, roughly 75% of prey are captured by lone hunters (Holekamp, Smale, Berg, & Cooper, 1997). Lone hunting is common in this species because dominants regularly usurp resources directly following cooperative hunting (Smith, Kolowski, Graham, Dawes, & Holekamp, 2008).

Leadership is strongly female-biased during both within-group and between-group conflicts in spotted hyenas. Female spotted hyenas lead in two major domains to intervene on behalf of group-mates. First, females regularly intervene on behalf of their juvenile offspring in fights to teach other members of their groups the social ranks of their offspring; offspring “inherit” the social rank directly below that of their mother with youngest ascendancy (Engh et al., 2000). This means that a cub born most recently to a mother is the one that slots in directly below his or her mother in the dominance hierarchy; this rank is

retained as long as an individual remains in his or her home clan (Engel et al., 2000). Second, adult females lead collective action during within-group conflicts involving other adult females; they typically intervene on behalf of their maternal and paternal relatives (Smith et al., 2010).

As is also the case for lions, sociality in spotted hyenas likely emerged due to the benefits of cooperative defense against intruders, while cooperative hunting emerged later (Smith et al., 2008). Although individual group members regularly split apart to reduce competition over limited resources, clan members regularly join forces to defend their shared territory against intruding conspecifics and lions (Smith et al., 2008). Within these dangerous, and potentially lethal contests, adult female spotted hyenas, especially high-ranking ones, are often in the front lines, leading charges to attack intruders (Boydston et al., 2001). Although males are often also involved in these joint attacks directed towards intruders, called clan wars, females consistently initiate and lead these collective acts of warfare directed towards intruders (Boydston et al., 2001; Kruuk, 1972). Interestingly, females often engage in elaborate greeting gestures involving the mutual investigation of their erectile pseudo-penises to reinforce social bonds and promote collective action among adult females prior to leading in clan wars (Smith et al., 2011).

Overall, spotted hyena groups are unique among social carnivores in two ways. They cooperate with kin and non-kin and they also live in female-dominated societies. Despite being female-dominated societies, female leaders emerge in the absence of coercion (Smith et al., 2011, 2015), suggesting that female leaders are followed because they represent powerful allies rather than because females impose threats upon their potential followers. Moreover, as occurs in the egalitarian prides of lionesses, female spotted hyenas are central within these fission-fusion societies, leading to at least some degree within the domains of group travel and cooperative hunting. Spotted hyena females also regularly intervene in conflicts occurring both within and between groups. Thus, although the female-dominated societies of spotted hyenas are also typified by strong patterns of female leadership, evidence from other species (e.g., killer whales, African lions) suggests that female dominance does not appear to be necessary for the emergence of strong female leaders within mammalian societies because similar patterns of female leadership emerge within some egalitarian societies, such as those of lions.

Bonobos (order Primata: family Hominidae)

The closest living relatives of modern humans—bonobos (Fig. 2D) and common chimpanzees—have strikingly different patterns of sex-biased leadership from each other (Fig. 1). Bonobos have female-biased leadership characterized by peaceful social interactions in which females use genital contact to reduce tensions with males and females alike (deWaal, 1995; Furuichi, 2011; Parish, 1994). Although adult chimpanzees of both sexes regularly lead in group travel (Goodall, 1986; Hockings, Anderson, & Matsuzawa, 2006), chimpanzee leadership is on the whole male-biased; dominant males occupy leadership roles most often, using aggression to reinforce their social status (Wroblewski et al., 2009). For example, males lead in group hunting (Gilby et al., 2015), within-group interventions (deWaal, 1984; Muller & Mitani, 2005; Watts, 2002), and intergroup warfare (Mitani, Watts, & Muller, 2002; Wilson, Hauser, & Wrangham, 2001). Interestingly, although males occupy leadership roles most often during intergroup warfare across study groups, female participation and leadership during intergroup conflict is also common in Tai chimpanzees (Boesch et al., 2008). Tai forest chimpanzees are more gregarious than those occurring elsewhere in Africa and offer increased support during intergroup encounters. These differences in patterns of leadership and participation, including that by females, appear to promote group-level benefits by reducing the rates of lethal attacks resulting from intergroup encounters compared to other populations (Boesch et al., 2008).

In contrast to most mammals, coalitions of female bonobos—but not

lone individual females, as occurs in spotted hyenas, two species of mole rats and lemurs (Kappeler, 1993)—are socially dominant to individual male bonobos (deWaal, 1995; Furuichi, 2011). Sex between female bonobos has been proposed as the mechanism that allowed female bonobos to overcome the phylogenetic legacy of male dominance in primates (Parish, 1994). Interestingly, bonobos—like chimpanzees—also differ from most mammals in that females disperse whereas males remain in their home groups (Gerloff, Hartung, Fruth, Hohmann, & Tautz, 1999). Strong affiliative relationships occur among unrelated female bonobos (Parish, 1994). However, female-biased dispersal appears insufficient to explain strong female leadership in bonobos. For example, females—not males—also disperse from chimpanzee communities and chimpanzee groups are characterized by male-biased leadership (Gerloff et al., 1999; Nishida et al., 2003). Female dispersal is also the norm for humans (Behar et al., 2008).

Within the context of group travel, adult female bonobos lead most often (Tokuyama & Furuichi, 2017). For instance, one study showed that the three oldest females were habitual initiators of group departures in their fission-fusion societies; in many cases, parties waited to move until high-ranking females climbed down from trees to initiate group departures (Furuichi, 2011; Tokuyama & Furuichi, 2017). Although females often lead groups to food, individuals mainly gather fruit and, occasionally, hunt on their own (Hohmann & Fruth, 2008). Once food is acquired, females have priority of access to food (Furuichi, 2011; Tokuyama & Furuichi, 2016) and will trade sex for food or to reduce tensions associated with feeding competition (Parish, 1994). Thus, females lead in determining how food is distributed within groups.

Perhaps the most unique aspect of their biology relative to other species of mammals is the tendency for bonobo females to resolve conflicts using sexual contact, “making love, not war” (deWaal, 1995; Furuichi, 2011). Bonobo groups are typified by low incidences of conflict within groups (deWaal, 1995; Furuichi, 2011). Although members of both sexes will intervene on behalf of others to resolve within-group conflicts, females lead most often in this domain, acting as peacekeepers more often than do males (deWaal, 1995; Furuichi, 2011). In fact, coalitions of females regularly intervene to settle conflicts among adult males (Legrain, Stevens, Alegria Iscoa, & Destrebecqz, 2012; Tokuyama & Furuichi, 2016). Mothers also regularly intervene on behalf of their sons and, as a result, maternal presence increases male reproductive success (Surbeck, Mundry, & Hohmann, 2011).

The peaceful nature of bonobos extends to between-group encounters (deWaal, 1995; Furuichi, 2011). Although bonobos show a high level of tolerance to members of neighboring groups, when conflicts do emerge, both sexes have been documented leading attacks (Furuichi, 2011; Sakamaki et al., 2015). Additional systematic study will be required to fully assess the extent of sex bias during these rare instances of intergroup conflicts in bonobos.

Overall, bonobos offer an interesting model of female leadership because of their peaceful style of leadership, acting to resolve conflicts in multiple domains and using female-based alliances to gain power within their groups. These patterns suggest that peaceful leadership styles of females may, on average, benefit group members—including males—by reducing the conflicts within groups and, instead, promoting cooperation. They also suggest that human organizations therefore may benefit from considering how leadership styles influence patterns of group stability, morale and efficiency.

Ring-tailed lemurs and black-and-white ruffed lemurs (order Primata: family Lemuridae)

In most mammals, males are substantially larger than and socially dominant to females, but female dominance and sexes of the same size (monomorphism) is typical for most species of lemurs, medium-sized monkeys found only on the island of Madagascar (Kappeler, 2010; Ralls, 1976). Among the five families of lemurs, at least two species of

lemurs, both of which belong to the family *Lemuridae*, have been studied extensively and shown to engage in female-biased leadership in multiple domains: the black-and-white ruffed lemurs (*Varecia variegata*, Fig. 2E) and the ring-tailed lemurs (*Lemur catta*, Fig. 2F). Both species are medium-sized, arboreal and live in cohesive matrilineal societies, called troops, in which all individual females are socially dominant to all individual males within the groups (Kappeler, 1990; Overdorff, Erhart, & Mutschler, 2005; Sautner, 1993).

As in many species of mammals, males lead on some occasions, but adult females lead most often. Interestingly, in both black-and-white ruffed lemurs (Overdorff et al., 2005; Pereira, Seeligson, & Macedonia, 1988) and ring-tailed lemurs (Jolly, 1966; Sautner, 1993; Sautner, Sussman, & Gould, 1999), the bias for adult female leadership is attributed to the influence of the highest-ranking adult female leading the group. Although females of both species are more likely than males to lead troops to foraging patches and females have priority of access to food over males, both species are primarily frugivorous such that food acquisition and consumption is simply done on an individual basis (Overdorff et al., 2005; Sautner, 1993).

Female lemurs regularly emerge as the strongest leaders in the two conflict domains. Although both male and female ring-tailed lemurs do intervene on behalf of each other, interventions within groups are generally rare and, when they do occur, females lead most often in settling these conflicts (Nakamichi & Koyama, 1997; Pereira & McGlynn, 1997). In contrast, there is no evidence of coalitionary interventions by male or female black-and-white ruffed lemurs (Morland, 1991; Pereira et al., 1988; Raps & White, 1995). Females emerge as the most prominent leaders during between-group conflicts for both species, with females leading the majority of collective attacks directed towards intruders by groups of ring-tailed (Nakamichi & Koyama, 1997) and black-and-white ruffed (Morland, 1991) lemurs. Although failing to meet our strict criteria of strong female leadership proposed here, two other lemur species are particularly noteworthy—red-ruffed lemurs (*V. rubra*) and Verreaux's sifakas (*Propithecus verreauxi*). For both species, females lead more often than males during collective movements (Pyritz, Kappeler, & Fichtel, 2011; Trillmich, Fichtel, & Kappeler, 2004). Moreover, female red-ruffed lemurs (pers. comm. Claudia Fichtel) and sifakas (Koch, Signer, Kappeler, & Fichtel, 2016b, 2016a) also participate to an equal extent as males during intergroup conflicts.

Overall, the societies of lemurs and spotted hyenas are similar in two ways, both of which deviate from the typical mammalian condition and may contribute to patterns of strong female leadership permeating all aspects of their social lives. First, females are larger than (i.e., spotted hyenas) or the same size as (i.e., lemurs) males in both groups. Thus, neither adheres to the typical mammalian pattern of males being larger than females within a species. Second, both live in female-dominated societies in which lone adult females consistently win conflicts involving lone adult males (dyadic fights). Taken together, these findings suggest that a reduction or reversal of sexual dimorphism via selection on large females may have co-evolved with female dominance and also promoted strong female leadership. Although female dominance does not appear to be a requirement for strong female leadership, strong female leaders consistently appear in those taxa with female dominance, suggesting a linkage between the two traits. This finding has interesting implications for understanding leadership in human societies given the large literature suggesting a bias by followers to favor taller, physically stronger leaders. Our current findings therefore are consistent with the idea that an evolutionary bias among humans for physically formidable leaders may act as a potential barrier to women assuming leadership roles in human societies.

African elephants (order Proboscidea: family Elephantidae)

Elephants are large herbivores that live in societies led by a matriarch, and groups are organized into multiple societal structures, all of which are based upon a lineage of philopatric females. In contrast,

males disperse and are relatively isolated from the social group. Of the three species of elephants, patterns of leadership have only been quantified for the African bush elephant (*Loxodonta africana*, Fig. 2G) and the Asian elephant (*Elephas maximus*, Fig. 2H). Both species have slow life histories, not reaching reproductive maturity until 18–20 years and living up to 60–80 years (Wilson, Mittermeier, & Cavallini, 2011). African elephants are particularly remarkable in that they are the largest mammals living on land today, have the longest gestation period of any mammal (22 months) and females typically only give birth to one calf every 4–5 years (Moss, 1988). Among the elephants, the African elephant lives in the largest social groups, residing in savannahs and grasslands (Moss, 1988). In contrast, the Asian elephant is generally smaller in body size and lives in smaller social groups in forests. Both species reside in complex, matrilineal societies with overlapping generations of adult females and their offspring; these groups are led by the oldest adult female, the matriarch, in multiple situations (Moss, 1988; Nandini, Keerthipriya, Vidya, & Barrett, 2018).

Groups of African and Asian elephants are structured by multiple levels of social organization (Nandini et al., 2018). Elephant societies are generally shaped by fission-fusion dynamics in which “core” family units (rather than individuals) regularly meet-up with and break apart from other family units (Archie, Moss, & Alberts, 2006). As family units move from place to place, the matriarch generally leads collective movements in African bush (Archie et al., 2006; McComb et al., 2011) and Asian elephants (Joshi, 2009; Mizuno, Sharma, Idani, & Sukumar, 2017). Because of their herbivorous diets, the African bush (Guy, 1976) and Asian elephants (Joshi, 2009; Santiapillai, Chambers, & Ishwaran, 1984) apparently lack leadership within the foraging domain, similar to the lemurs. Information on interventions within-groups is very limited, but female—not male—African bush elephants have been shown to intervene on behalf of others during within-group conflicts (Lee, 1987). We are unaware of any studies on within-group conflict resolution for Asian elephants. Moreover, between-group conflicts in which elephants join forces to attack intruders are rare. When conflicts emerge between groups, matriarchs lead these efforts in African bush elephants (Wittemyer & Getz, 2007) and direct Asian forest elephants to form a protective circle around calves (Joshi, 2009).

Matriarchs in African bush elephants serve as long-lived repositories of knowledge, sharing social and ecological information with less experienced group members and leading them away from potential threats (McComb, Moss, Durant, Baker, & Sayialel, 2001; Mizuno et al., 2017; Moss, 1988). In one study, human observers administered a personality test to African bush elephants in Amboseli National Park, Kenya; they assigned adjectives to rate the qualities of each adult female (Lee & Moss, 2012). The researchers found that effective and confident family leadership explained the greatest amount of variation in the personalities among adult females (Lee & Moss, 2012). Interestingly, the elder matriarch in the group scored the highest on elements associated with leadership (Lee & Moss, 2012). Thus, as in killer whales, the emergence of strong female leadership by elephant matriarchs appears to be linked to the tendency for long-lived females to persist for multiple, overlapping generations. Family structure is also a prominent feature of these groups, suggesting that female leaders may emerge first within their family units and secondary leadership roles may permeate across multiple levels of societal organization.

Understanding the origins of female leadership

Overall, our synthesis of the mammalian literature reveals several tentative conclusions about female leadership that may be relevant to humans. First, our analysis reveals the rarity of female leadership in the natural world with just 10% of mammalian species showing evidence of strong cases of female-biased leadership (as defined by our very strict criteria of females leading exclusively or more often than males in at least two domains of leadership). This aligns with the ubiquitous bias for male leaders across human societies, including both modern large-

scale societies (van Vugt et al., 2008) and traditional small-scale societies (von Rueden et al., 2018). The paucity of female-biased leadership across multiple domains is evident across the other primates, suggesting that male-biased leadership within the primate lineage has deep evolutionary roots and perhaps imposes a phylogenetic (historical) constraint on its evolution. The lemurs and bonobos are notable exceptions to this trend. The bonobo case is particularly relevant to this discussion, however, given that bonobos are one of our closest genetic relatives.

Second, for species with strong female leadership, several of them live in female-dominated societies. Female dominance in which one female is able to, on her own, outrank one adult male is very limited among the roughly 5416 species of mammals (Reeder & Wilson, 2005), occurring only in spotted hyenas (Frank, 1986) and most—but not all—species of lemurs (Kappeler, 1990; Pereira, Kaufman, Kappeler, & Overdorff, 1990; Raps & White, 1995) as well as two species of naked mole rats (Sherman et al., 2017). Some authors suggest that lemur dominance may be attributed to reproductive synchrony and their operational sex ratio (Sauter, 1993). However, this explanation alone appears insufficient to explain female dominance in mammals because spotted hyenas lack reproductive synchrony (Holekamp, Smale, & Szykman, 1996). Notably, species with strong female leadership and female dominance also deviate from the typical mammalian pattern in terms of sexual size dimorphism. That is, for lemurs and spotted hyenas, females are larger than or the same size as males of the species (Ralls, 1976; Swanson et al., 2013). These findings suggest that physical size may act as a potential barrier to female leadership within mammalian societies. Although coalitions of bonobo females are also socially-dominant to males, a single female on her own is not, yet female leadership is central to these socially tolerant and largely peaceful societies (deWaal, 1995; Furuichi, 2011). This finding for bonobos suggests that perhaps female bonobos have overcome the challenge of being physically smaller than male bonobos by joining forces with each other. Thus, for all species for which female-dominance occurs and for which leadership has been well-studied, strong female leaders are also a feature of the societal structures. Perhaps it is unsurprising that in the groups for which females have priority of access to resources they also invest most heavily in settling conflicts within and between groups because females have the most to gain from conflict management.

Third, a common feature of many of the species reviewed here is the importance of social alliances among genetic relatives, an inherent feature in egalitarian prides of lions (Packer et al., 2001) and in the matrilineal societies of elephants (Archie et al., 2006) and killer whales (Baird, 2002). However, one must be wary in reading too much into this given that the vast majority of mammalian societies are comprised of kin groups (Smith, 2014). Interestingly, although kinship is important in shaping leadership decisions within groups of spotted hyenas (Smith et al., 2010, 2015), individuals of low mean genetic relatedness to one another regularly join forces with unrelated group members when engaging in clan wars directed at intruders (Van Horn et al., 2004). Taken together, high degrees of kinship between females may promote the emergence of female-biased leadership within various mammalian societies, yet kin-based societal structure on its own is likely insufficient to explain the emergence of strong female leaders.

A fourth conclusion is the emergence of female elders as leaders. This is a major theme within the subgroup of species reviewed here. It also describes the common pattern among mammalian societies in which females tend to lead only within the domain of collective movements (Smith et al., 2015). This bias for matriarchs raises the possibility that the unique combination of extended (post-reproductive) lifespans, in combination with multiple overlapping generations persisting within the group at a time might be an important driver of female leadership. Elephant (Archie et al., 2006), killer whale (Baird, 2002) and spotted hyena (Holekamp et al., 2012) matrilineal societies all reside in complex societies consisting of up to three or four overlapping generations of females. These extended, multi-generation support

networks suggest that females may emerge as powerful leaders within societies through the inheritance of social structures and knowledge from one generation to the next within the maternal line.

Implications for women's leadership

Although it is exceedingly difficult – and perhaps contentious – to draw inferences from our analysis to the case of humans, it is something worth attempting. Humans are the ultimate niche-constructors and create social structures that are more flexible than those of other mammals (Spisak, O'Brien, Nicholson, & Vugt, 2015). With the help of their cultural capabilities, humans are able to create and thrive in structures ranging from egalitarian (democratic) to despotic (hierarchical) and from small-scale to large, complex societies. This has implications for leadership as humans may be able to rise above their biological history and create current social and ecological conditions favoring the emergence of strong female leaders (Hrdy, 2009; Spisak et al., 2015). There are numerous observations of note from our discussion of non-human mammals that may be relevant to human societies.

First, as our review demonstrates, female leadership in non-human groups occurs most often within families and within small egalitarian groups. The most ubiquitous case of female leadership in mammals occurs within the domain of collective movements; adult females with dependent offspring often take the lead (Smith et al., 2015). There are natural parallels to draw with humans, as mothers also play a crucial role in leading their children and helping to socialize them into becoming successful adults (Hrdy, 2011). Yet, leadership within families and communities is a relatively ignored topic in leadership studies. Instead, most studies focus on understanding leadership in large organizational structures such as businesses, governments and the military that tend to be complex and hierarchical [for notable exceptions see: (Buvinic & Gupta, 1997; Helgesen, 1995)]. A focus on smaller units, like households, and on more egalitarian organizations, like schools and nurseries, would reveal a preponderance of female leadership activities that have been much ignored. Our review reveals the many ways that female influence in these domains have been of critical importance across the mammalian lineage (Brent et al., 2015; Croft et al., 2015; Holekamp et al., 2012; Moss, 1988). This synthesis thus offers a possible explanation of—but certainly not justification for—the current distribution of women in professions such as education and healthcare. Additionally, it suggests that female mammals regularly influence societal outcomes in positive ways that are often overlooked or otherwise underappreciated when viewed within the traditional operationalizations of human leadership.

Second, our synthesis suggests that strong female leaders are more likely to emerge when females form cooperative units. This pattern has obvious implications because it suggests that women are more likely to be successful leaders when forming strong coalitions within their social networks. Interestingly, a study of small business owners in Northern Ireland showed that women are just as active in their networking as men, their personal contact networks are as diverse as those of men, and they are no more likely to consult family and friends than are men, but that both men and women rely most heavily upon a male colleague as their primary contact (Cromie & Birley, 1992). Although these results suggest that female entrepreneurs are already gaining access to the “old boys' network”, our comparative perspective indicates that women would additionally benefit from fostering female-female coalitions. With the advent of new technologies, women who have never met before are benefiting from virtual coalitions. For example, starting in October 2017, the hashtag “Me Too” went viral on twitter and permitted women to quickly join forces on social media to document the prevalence of sexual assault and harassment in the workplace (Lee, 2018). Networking activities (e.g., on social media) and other coalition-building activities (e.g., community-based mentoring, participating in team sports or other clubs) may be particularly helpful for women

because they permit women to form strong alliances with members of their own sex, resembling the infamous old boys' network in men. Indeed, gender-informed mentoring strategies can also increase the presence, retention and advancement of women as leaders in male-dominated fields, such as that of engineering (Chesler & Chesler, 2002). For example, peer-, multiple- and collective mentorships prove to be successful for most women (and many men) by contributing to a more egalitarian and cooperative atmosphere that supports the success of female leaders (Chesler & Chesler, 2002).

A third observation concerns the role of female elders as repositories of knowledge. In various species with female-biased leadership, we see a combination of a long lifespan and groups consisting of multiple generations of individuals belonging to the female lineage, including post-reproductive females with extensive knowledge. Although the long postmenopausal lifespans of humans distinguish them from all other primates (Hawkes, O'Connell, Jones, Alvarez, & Charnov, 1998), it is unlikely that a long post-reproductive lifespan alone may explain the emergence of female-biased leadership. In contrast to most mammals, most human societies lack matrilineal social structures that are so prominent in most mammalian groups with strong female leadership. That is, most human societies are patrilineal rather than matrilineal, such that status and intergenerational wealth are most often passed down the male family line (Mulder et al., 2009). Perhaps matrilineal societies in combination with postmenopausal lifespans are together important for the emergence of female-biased leadership. Nonetheless, there is evidence for the value of skilled, elder women that promote equity and knowledge within hunter-gatherer societies. For example, elder women are particularly skilled storytellers among the Agta of the Philippines, conveying messages relevant to coordinating collective action, such as cooperation, sex equality and egalitarianism (Smith, Schlaepfer, et al., 2017). Similarly, female elders in the Amazon become increasingly more skilled as post-reproductive adults (Schniter, Gurven, Kaplan, Wilcox, & Hooper, 2015). One reason why these skilled elderly women may not emerge as leaders in large-scale human organizations is because these organizations are not equipped enough to deal with the different career trajectories of women who in many cases may spend some of their adult time as primary caregivers. It would be interesting to see how some of these barriers could be removed to exploit the superior knowledge and social skills often possessed by experienced women.

Fourth, our findings suggest that in species for which conflict management within groups is vitally important, there is more room for strong female leaders to emerge. There are parallels in the human leadership literature. In traditional small-scale human societies, women take on leadership roles as conflict mediators, presumably because if men take on this role violence may escalate (von Rueden et al., 2018). Experimental studies also show that if voters are worried about exploitation by their leaders, then they choose a more feminine-looking leader (Laustsen & Petersen, 2015). Finally, when groups want to forge peaceful alliances with other groups, then they are more likely to select a woman as a leader (Spisak et al., 2012). This case is interesting because nearly all recent secretaries of state in the United States were women regardless of whether there was a Democrat or Republican president in office. This suggests that in organizational environments in which people mediate conflicts within and between groups, there is a niche for women to emerge as leaders.

A fifth observation from our study concerns the role of body size and physical strength. Some of the mammalian species with patterns of strong female leadership deviate from the typical mammalian pattern such that females are slightly bigger and stronger than males, either on their own or by joining forces with each other (Ralls, 1976; Swanson et al., 2013). Whereas men, on average, are typically taller and heavier than women, the sexual dimorphism in humans is much smaller than that observed in other primates (Buss, 1989). Notably, men are considerably stronger, on average, than are women (Wells, 2007), suggesting that this biological difference in fighting potential gives men an

advantage in direct combat. Nonetheless, within a population, there are plenty of women who are physically taller and heavier than a randomly chosen man. Research indeed finds that taller men and women are seen as more able leaders than their shorter counterparts (Blaker et al., 2013). These data suggest that physically formidable women may have an advantage in achieving senior leadership positions in business. Furthermore, clever ways to exaggerate the perceived height of women political leaders—such as permitting women to stand on platforms at debates or to engage in dialog using social media platforms—might help to even the playing field for women during campaign events. Moreover, the reliance upon the use of technologies in most large-scale modern societies levels the playing field between men and women involved in conflicts. Nonetheless, men may suppress female influence in groups by directing aggression towards them (Smuts, 1992). However, as mentioned above, female coalitions (virtual or otherwise) are mobilizing and empowering women to overcome these potential barriers to their success as leaders.

Sixth, our analysis suggests that some conditions may not be that important to explain the paucity of women in top leadership positions. For instance, a bias towards female dispersal within human groups – which seems to be the ancestral condition for the human species (Hill et al., 2011) – likely cannot explain the scarcity of female leaders in humans, given the patterns of female-biased dispersal in bonobos and chimpanzees, but only strong female leadership for bonobos.

Finally, we should note some practical implications of our findings for women's leadership in modern business and politics. This analysis reveals several constraints that evolutionary history and current social conditions may impose upon women seeking to become leaders in organizations. Some factors may be therefore partly the result of evolved sex differences in physique and behavior. For instance, the fact that women are, on average, shorter and physically less strong than men might give women a disadvantage in achieving their leadership potential because people tend to view physically strong leaders as being more dominant and more effective at recruiting and mobilizing followers. In addition, constraints due to childcare provisions might mean that the career trajectories of women leaders are slower and more gradual than that of male leaders, which may go unrecognized in organizations. Finally, sexual selection may have shaped the behaviors of men and women differently such that women are, on average, less motivated than men to engage in winner-take-all competitions for positions associated with high status and prestige. These evolutionary obstacles may, thus, partly explain the glass ceiling for women leaders in business and politics. Yet our review suggests that these obstacles are not insurmountable for three different reasons.

First, although men and women differ, on average, in these traits, there is much variability within the sexes. That means that in absolute terms there are plenty of women who will be taller, stronger, and more ambitious than the average man. Second, shifts in cultural and organizational practices might remove some of the evolutionary obstacles for women to achieve senior management positions. For instance, greater fatherly investment and good childcare provisions should make it easier for competent women to achieve their leadership potential. In addition, organizations should recognize that the career trajectories for men and women may differ. Due to the forces of sexual selection in combination with reproductive constraints, women often achieve positions of influence at a later age than men do. As our review shows, in some species postmenopausal females play a significant role as elders in their community. Organizations should be aware of and utilize the leadership contributions that older women could make to their organizations. Third, the structure of modern organizations in societies with multiple layers of hierarchy is an evolutionary novelty that disfavors female leadership. Large-scale complex societies only emerged after the agricultural revolution some 10,000 years ago, whereas humans have been around for at least 2.5 million years. The modern business environment only emerged after the industrial revolution some 250 years ago. Almost 99% of human evolutionary history took place in small-

scale societies with limited material wealth and no formal institutions, managers, or top-down hierarchical structures (von Rueden & van Vugt, 2015) – looking much more like the structure of the non-human societies that we reviewed here. This has important implications for female leadership opportunities. Anthropologists have found that women wield more political influence in these small-scale, relatively egalitarian societies than in the large-stratified societies of the modern, industrialized world (Dyble et al., 2015). Thus, these large, complex modern organizations present something of an evolutionary mismatch that may facilitate men but restrict women to fulfill their leadership potential (van Vugt & Ronay, 2014); we might refer to these hierarchical structures as “glass pyramids.” Yet these modern hierarchical structures are not set in stone. They are subject to cultural innovations as organizational environments change. As the costs of coordination have decreased recently (primarily due to advances in digital communication), many organizations are getting rid of management layers and focus their efforts instead on creating smaller, more egalitarian, self-organizing teams. In addition, there is a trend in industry towards “boss-less” organizations (Puranam & Håkonsson, 2015) which should favor more equal participation of women leaders. As the relative numbers of women in senior management positions increase – helped by quota systems – organizations may also evolve quite naturally to more egalitarian and participative structures, given that women tend to adopt a more democratic and less authoritarian style (Eagly & Johnson, 1990).

Taken together, our comparative analysis shows that there are several obstacles to leadership by women that are deeply rooted in the evolutionary history of mammals but that many possibilities for female leadership exist, including those that are often ignored within the operationalized definitions of leadership. At the same time, some other obstacles are nothing more than skin-deep, as they are products of recent cultural traditions. As a cultural species, we humans are able to select for our own future (Wilson, Hayes, Biglan & Embry, 2014), get rid of – if we want – glass ceilings and pyramids, and create the kinds of social structures that enable organizations to profit from the “female leadership advantage” (Eagly & Carli, 2003).

Future research and conclusions

Future studies are needed to place our findings into a quantitative framework that statistically controls for the evolutionary history across the mammalian lineage using phylogenetic independent contrasts to assess the ways that key variables emerge here. For example, it would be interesting to elucidate the extent to which factors (e.g., ecology, social structure, dispersal status, diet, and longevity) are unique to mammals with strong female leaders compared to those mammals for which leadership by females is absent or limited to the collective movement domain. Moreover, such an analysis would inform our understanding of the evolutionary origins and ecological factors promoting female leadership, offering insights into the ways that humans may help to cultivate contexts in which female leaders may thrive.

Second, we focused exclusively on non-human mammalian societies in our analysis. Future studies could therefore extend our approach to other societal types, such as those of small-scale human societies, defined as groups of humans lacking complex political institutions (e.g., more than two formal administrative levels) (Flannery & Marcus, 2012). Future studies into the role of gender-bias in these societies may prove fruitful because the most common societal structure of large-scale human societies today likely emerged from these small-scale societies of the past. Small-scale human societies are characterized by small kin-based communities, sharing resources within and across extended families, and the absence of formal institutions governing group life (von Rueden & van Vugt, 2015). Such societies, particularly those of hunter-gatherers, tend to be egalitarian overall, although women (and children) tend to have a lower status compared to adult men (Fried, 1967). This may be attributed only in part to sexual-dimorphic differences in

physical size and strength between men and women (von Rueden et al., 2018). Although systematic reviews of sex differences in leadership in these small-scale societies are currently lacking, we do know that women tend to wield some political influence within these small groups (e.g., women often have voice in community affairs). For example, in Amazonian horticulturalists, women show leadership by managing conflicts within their villages (Bowser & Patton, 2010). Nevertheless, men are more likely than women to exert political influence verbally at community meetings, to coordinate community projects and to resolve conflicts; male-biased influence is attributed to men having more co-operation partners, increased access to education, and greater body size and physical strength than women (von Rueden et al., 2018). These sex differences thus may be explained as a combination of evolved differences in strength and current cultural traditions (e.g., social roles). Systematic study is required to understand the extent of, and factors contributing to, gender bias across small-scale human societies.

Third, understanding whether the various dimensions of leadership systematically vary between societies identified here as having strong female-biased leadership – and those that do not – should also prove useful. Specifically, key dimensions of leadership for this comparison include: (1) *emergence*—the process by which one becomes a leader (ascribed vs. achieved), (2) *distribution*—the extent to which leadership roles are shared with the group, (3) *power*—amount of influence a leader exerts upon followers, (4) *relative benefit*—degree to which leaders benefit from actions relative to their followers, and (5) *generality*—consistency of leaders across multiple contexts (Smith et al., 2016). It may be, for example, that female-biased leadership is most common within societies for which leadership is ascribed (inherited at birth based on family status), the benefits of leadership are relatively shared between leaders and followers, and for which leaders wield the least power (influence) over group decisions. Of course, this is just one testable hypothesis emerging from our current synthesis and formal tests of hypotheses such as these using phylogenetically-controlled independent contrasts are required to tease apart the rules governing leadership across mammalian societies.

Fourth, regarding leadership domains, from an evolutionary perspective, female leaders might be expected to be more common when it comes to mediating conflicts within the groups given the evolutionary benefits for females of maintaining group cohesion and protecting their offspring. In contrast, because the evolutionary success of males is often limited by their ability to attract potential mates, natural selection might favor male leaders to exploit between-group conflicts (e.g., wars) when males benefit from occupying more resources that may attract more potential mates. This is evident in the human literature, as discussed above, and it may well be true for other primates. For instance, although there is clearly male-biased leadership in chimpanzees, females do play a role in peace-keeping activities within groups (deWaal, 1984). Moreover, sex-bias in chimpanzee leadership during food acquisition may depend upon the quality of resources at stake—with males leading hunting for nutrient rich meat, whereas females may lead efforts to gather distributed resources that are challenging to monopolize (Muller & Mitani, 2005). In addition, theory predicts that male leaders should be more likely to have inherited their leadership roles based on patriarchal systems of wealth distribution (Mulder et al., 2009) and to wield power when occupying leadership roles (van Vugt & Spisak, 2008) than do female leaders. Future tests of predictions such as these derived from the social science literature will prove important in understanding the evolutionary basis of male-biased leadership.

Finally, despite the rarity of our cases of species that adhere to our definition of female-biased leadership in two or more domains within their societies, we identified numerous species in which *both* females and males occupy leadership positions to some extent and many species for which males and females occupy leadership positions to equal extents within the four domains outlined in this paper. Thus, although cases of females having systematically *more* influence than males across multiple domains are rare across the mammalian lineage, females do

regularly contribute to societal structure in numerous species beyond those cases meeting our strict criteria.

Notably, females in non-human mammalian societies accomplish leadership that transcends beyond the four domains of leadership emphasized in our current analysis. Most species of social mammals are philopatric such that groups are comprised of matrilineal societies in which female social relationships are particularly important and resources are passed down the female lineage within these female-bonded groups (Sterck, Watts, & vanSchaik, 1997; Wrangham, 1980). To be clear, matrilineal refers to kinship based on the maternal line whereas matriarchal societies are those in which females wield *more* power than males. In matrilineal societies, females may not be socially (or physically) dominant to males, but females—especially older adult females—exert a great deal of influence within their social groups. In many, mothers fight to ensure their daughters assume their mothers' status (Cheney, 1977; Engh et al., 2000), and, in most cases, a female's closest allies are also her closest competitors because of the shared use of resources (Isbell, 1991; Smith, 2014; van Schaik & van Noordwijk, 1988). In non-human mammals, the high-ranking female(s) exert(s) disproportionate influence on the behavior of others, attracting commodities such as the most babysitters, grooming, and coalitionary partners (Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; Seyfarth, 1980; Smith et al., 2007). Females with the strongest social bonds have the highest infant survival and longest lifespans (Silk et al., 2010; Silk, Alberts, & Altmann, 2003, 2004). Members of friendly matrilineal are allies (Holekamp et al., 2012). Dominant females may suppress the reproduction of others within cooperative breeding groups, especially in mammalian carnivores (Montgomery, Pendleton, & Smith, 2018; Young et al., 2006). Even in male philopatric chimpanzees, females exclude immigrant females from settling in their communities (Kahlenberg, Thompson, Muller, & Wrangham, 2008) and, sometimes, even directly kill the infants born to other females (Townsend, Slocombe, Emery Thompson, & Zuberbühler, 2007).

For humans, female leaders also wield power and exert influence in numerous contexts beyond those four contexts examined here. For example, some studies suggest that senior women may act as “queen bees” in male-dominated organizations by dissociating themselves from other women (Derks, Ellemers, van Laar, & de Groot, 2011). This phenomenon of women suppressing other women occurs in male-dominated workplaces, such as in law enforcement (Derks, Van Laar, et al., 2011) and the sciences (Ellemers, Heuvel, Gilder, Maass, & Bonvini, 2004). Still other studies suggest that girls and women denigrate other females to enhance their own reproductive advantages (Etcoff, 2000). Human females influence their children, female kin, and husbands, and when they are older, their daughters-in-law (Smuts, 1992, 1995). Taken together, there are multiple ways in which females influence their (family groups) societies in addition to the domains of leadership considered here. Because female power is clearly situational, future studies should explicitly consider the degree to which females wield power over males in these domains within a phylogenetically-controlled comparative framework that explicitly models the effects of social and ecological constraints on female leadership outcomes. Moreover, future studies need to explicitly examine the aforementioned—and often overlooked—forms of female power within mammalian social groups. We suggest that further inquiry into these forms of female influence within a comparative perspective should prove fruitful. In other words, the lens used to view leadership itself appears to have a male-bias and, perhaps, with a close eye on the diversity of ways that individuals of both genders (sexes) derive power within their groups, we may start to understand that females indeed have evolved multiple forms of power across the mammalian phylogeny. Such an understanding would contribute to the study of leadership by stimulating a new body of theory that fully encompasses the multiple ways in which individuals influence collective behavior within their societies.

In closing, Hillary Rodham Clinton nearly became arguably one of the most powerful and influential leaders on the planet, winning the

popular vote in November 2016 and, nearly enough Electoral College votes to become the first female President of the United States of America. Our synthesis suggests perhaps it was her extensive knowledge and experience, strong family ties to the political system, and long-standing alliances with other women—and men—that prepared her to almost break through one of the tallest glass ceilings. Our synthesis of female leadership in a comparative framework also reveals how obstacles, including evolutionary history as well as current social (cultural) and ecological circumstances, can act to constrain women from occupying leadership positions. Nonetheless, shedding light on these and related issues within a comparative perspective should inform our understanding of the origins and persistence of gender bias so that society may address these biases in an effort to benefit from the leadership skills of women and to move towards a more equitable society.

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Declaration of interests

None.

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