**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 that impose a disproportional influence on the collective behaviors. 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., movements, foraging, and/or conflict resolution within or 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 matriarchs. Although our comparative perspective elucidates barriers to female leadership, it 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.

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**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 the 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 pervasive worldwide. As of June 1st 2018, women only occupied 19% of the total number of 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 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 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 (McClean, 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 hold more political positions in egalitarian societies than in more economically stratified societies (Dyble et al., 2015; Endicott & Endicott, 2008; Leacock, 1978). In these societies, female leaders tend to mediate conflict without imposing or promoting costly physical violence within the group; for example beneficial female leadership is well-documented for hunter-gathers of the Congo basin (J. 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 an 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 the understanding why sexual selection has shaped evolved sex differences in physical (e.g., body size, strength dimorphism (Buss, 1989, 2015) and behavioral (e.g., tendency form coalitions, engage in competition) (Benenson & Markovits, 2014; Campbell, 2013; Geary, 2013; Seabright, 2012) attributes. Together, these theories offer insights into the local ecological and social (cultural) conditions as well as the origins of sex differences over evolutionary time influence human behavioral decisions (Hedwig, DeBellis, & Wrege, 2018; Low, 2005). Both theories complement each other in their explanation of how evolved sex differences interact with local cultural norms in shaping behaviors and preferences. Importantly neither perspective aims to justify -- or otherwise defend -- these gender biases.

Evolutionary theory, for example, predicts that natural selection should favor individuals in battle with the largest body sizes, greatest physical strength or largest numbers of allies in conflicts. The tendency for men to lead during intergroup conflicts and to also be, on average, larger and physically stronger than women may be explained within an evolutionary context (Browne, 2001; van Vugt, Cremer, & Janssen, 2007). 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, for instance, 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 (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 mammals.

Here we define leaders as those individuals that 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 (R. J. 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, & Cowlishaw, 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). These definitions also align with findings from psychologists studying humans who conclude that leadership also cannot be defined in terms of personal dominance, the ability for one individuals 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 ways natural selection favors individuals to lead or follow when participating in collective behaviors, and the circumstances in which individuals choose to lead or follow. Understanding the costs and benefits of these behaviors may help to explain why observed social structures and traits of leaders persist within 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 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 studies of leadership focus in 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 these cases of strong 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 travelling together to a new location (Petit & Bon, 2010). Pioneering studies of non-human animals on collective behaviors 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. These seemingly complex patterns of swarming, shoaling (schooling), flocking and herding behaviors 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 consistently 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 individual group members (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), and particularly attributes that signal one’s competence to lead within a valued domain of 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 (Smith et al., 2016). Within the foraging domain, leaders emerge when cooperation is required to collectively locate, acquire and distribute food. For example, social carnivorans (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 (Kay E. Holekamp, Boydston, & Smale, 2000; Packer, Scheel, & Pusey, 1990). Within an evolutionary perspective, the lives of social carnivorans are of particular importance because convergent selective pressures likely shaped patterns of collective behavior in both mammalian carnivorans 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 and different individuals taking 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 strong 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 carnivorans), *Chiroptera* (1 bat species), *Perissodactyla* (3 species of odd-toed ungulates), *Primata* (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 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 was 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 construed 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](http://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. 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 other group members (followers), regardless of how this influence is achieved.

Here we focused on key cases for which female 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 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 leadership and identify those species for which adult females are regularly followed by other adults in multiple contexts within the natural world that permeate into domains 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 leadership (Fig. 2). That is, roughly 10% of the species are known to have predominantly female leaders across more than one domain. Although additional studies may reveal more cases of strong female leaders, all available evidence to date suggests that male-biased leadership 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-biases in leadership in each domain, and synthesize what we may learn from these data.

**Killer whales (Order *Artiodactyla*: Family *Delpinidae*)**

Female leadership, especially by elder females, is widespread in 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 matrilines, defined as groups comprised of the descendants of female group members. Killer whale matrilines in particular are usually composed of a female, her sons and daughters, and 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 carnivorans (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 or 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 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, Scheel, & Pusey, 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 of related females and their offspring, called prides (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 cooperation in non-human groups of mammals (Smith, 2014).

As occurs in killer whales (Baird, 2002) and in most social carnivorans (Smith, Swanson, Reed, & Holekamp, 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) also documented 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 social 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 and consistent across individuals (Heinsohn & Packer, 1995). That is, female lionesses fall into consistent roles — acting either as as highly cooperative leaders or as laggards that exploit the leadership roles 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); females also 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 those of other social carnivorans, such as those of lions, because hyena clans are made up of up to 130 individuals and are comprised of multiple matrilines and immigrant males (K. Holekamp, Smith, Strelioff, 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 carnivorans, 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 carnivorans — and most species of mammals other than lemurs and two species of mole rats (P. 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 the intensive feeding competition may have favored the evolution of female dominance in the spotted hyena (H. 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 whereas 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 (Kay E. 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 to resolve intragroup conflicts. 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 ascendency (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 the offspring remain in their home clan (Engh 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 social groups are unique among carnivorans in two ways. They cooperate between 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, cooperative hunting, and intervening 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 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, for example.

**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 (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). In contrast, chimpanzee leadership is 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; D. P. Watts, 2002), and intergroup warfare (Mitani, Watts, & Muller, 2002; Wilson, Hauser, & Wrangham, 2001). Adult chimpanzees of both sexes regularly lead in group travel (Goodall, 1986; Hockings, Anderson, & Matsuzawa, 2006).

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 (P. 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 also differ from most mammals in that females disperse whereas males remain in their home groups (Gerloff, Hartung, Fruth, Hohmann, & Tautz, 1999) such that 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-raking females climb 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 therefore 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 intervening on behalf of others 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 gender bias in resolving conflicts between groups of bonobos.

Overall, the 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 (P. M. 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 (P. M. Kappeler, 1990; Overdorff, Erhart, & Mutschler, 2005; Sauther, 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; Sauther, 1993; Sauther, 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; Sauther, 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.

Overall, lemur and spotted hyena societies 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 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 because the two traits. This finding has interesting implications for thinking of leadership in human societies given the large literature suggesting a bias by followers to favor taller, physically stronger leaders (Blaker et al., 2013; Murray & Schmitz, 2011; van Vugt et al., 2008). Our current findings therefore are consistent with the idea that an evolutionary bias among humans for physically formidable leaders may act as a barrier to women assuming leadership roles.

**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 the African savannah and grasslands (Moss, 1988). In contrast, the Asian elephant is generally smaller in body size and lives in smaller social groups persisting in the forests. Both species reside in complex, matrilineal societies with overlapping generations of adult females and their offspring and 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. On those occasion for which conflicts emerge between groups, matriarchs apparently lead these efforts in African bush elephants (Wittemyer & Getz, 2007) or 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 as a whole.

**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 female-biased leadership (as defined by domains in which females lead exclusively or more than males). 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 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 genetics relatives.

Second, for species with strong female leadership, several of them are female-dominated. Female dominance in which one female is able to, on her own, outrank one adult male is very limited among the roughly 5,416 species of mammals (Reeder & Wilson, 2005), occurring only in spotted hyenas (Frank, 1986) and most — but not all — species of lemurs (P. M. Kappeler, 1990; Pereira, Kaufman, Kappeler, & Overdorff, 1990; Raps & White, 1995). Some authors suggest that lemur dominance may be attributed to reproductive synchrony and their operational sex ratio (Sauther, 1993). However, this explanation alone appears insufficient to explain female dominance in mammals because spotted hyenas lack reproductive synchrony (K E Holekamp, Smale, & Szykman, 1996). Notably, these 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 dominant 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 (K. Holekamp et al., 2012) matrilines 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 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, & van 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 constraints and create the social and ecological conditions favoring the emergence of strong female leaders (Spisak, O’Brien, Nicholson, & van Vugt, 2015). There are numerous observations of note from our discussion of non-human mammals that may be relevant to aspiring female leaders in modern human societies.

First, as our review demonstrates, female leadership 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 during which 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 an ignored topic in leadership studies that tend to be biased towards understanding leadership in large formal 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 but, from an evolutionary perspective, are critically important (Brent et al., 2015; Croft et al., 2015; K. Holekamp et al., 2012; Moss, 1988). One implication is that if organizations are run more like families, then a female leader, or a leader with feminine characteristics, may be more acceptable. It would be interesting to conduct a systematic study of family-owned businesses (Nicholson, 2008) to see if women leadership is relatively more prevalent and successful.

Second, our synthesis suggests that strong female leaders are more likely to emerge when females form stable units. Stable female units may be the result of males migrating into the group, and thus females are more strongly genetically related to each other, or may result from females forming strong alliances with one another to keep dominant males in check. This pattern has obvious implications for women leaders as they are more likely to be successful when they can form strong coalitions with other women. For example, networking activities and other coalition-building activities (e.g., participating in team sports) 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.

A third observation concerns the role of female elders as repositories of knowledge. In various species in which we have observed female-biased leaders we see a combination of a long life span and groups consisting of multiple generations, including post-reproductive females with extensive knowledge. If this is correct, then it is unclear why women remain underrepresented in top leadership positions within humans societies given that humans are also long-lived and have a long evolutionary history of living in matrilineal societies comprised of multiple overlapping generations and large numbers of post-reproductive women (Behar et al., 2008). One hypothesis that has been suggested in humans is the grandmother hypothesis (Hawkes, O’Connell, Jones, Alvarez, & Charnov, 1998) which highlights the importance of older women as assisting their daughters with raising their children. Yet another hypothesis is that elder women have a functional role to play as informal leaders of their communities. Female mammals tend to live longer than males and thus they have more time to build their alliances and develop their knowledge as skills as leaders. One reason why these skilled elderly women may not emerge as leaders in modern 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. Nonetheless, it would be interesting to see how some of these barriers could be removed to exploit the superior knowledge and social networking 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 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 leader (Spisak et al., 2012). This case is interesting because nearly all recent secretaries of state in the United States were women and this was true regardless of whether there was a Democrat or Republican president in office. This suggests that in organizational environments in which people want to mediate in conflicts within and between groups there is a niche for women leaders to emerge.

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 taller than and stronger than women, the sexual dimorphism in humans is much smaller than that observed in other primates (Buss, 1989). Nonetheless, within a population, there are plenty of women who are physically taller and stronger than any randomly chosen men. 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 -- might help to even the playing field for women during campaign events.

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 within human groups, given the patterns of female-biased dispersal in both bonobos and chimpanzees, but only strong female leadership within bonobos.

Finally, we should note some practical implications of our findings for women leadership in modern business and politics. This analysis reveals a number of constraints on women to emerge as leaders in organizations. These constraints are 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 them 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 men leaders, which may go unrecognized in organizations. Finally, sexually selection forces 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 can 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 on 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 leader career trajectories for men and women are different. Due to the forces of sexual selection in combination with reproductive constraints, women 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 societies as these large-scale organizations 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 ago. 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 animal 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, but 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 & Hakonsson, 2015) which should favor a 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 women leadership that are deeply rooted in evolution. At the same time, some other obstacles are nothing more than skin-deep as they are products of recent cultural evolution. As a cultural species, we humans are able to evolve our own future (Wilson, Hayes, Biglan & Embry, 2014), get rid – if we want - of glass ceilings and pyramids, and create the kind of social structures that enables organizations to profit from the “female leadership advantage” (Eagly & Carli, 2013).

**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 to sexual-dimorphic differences in physical size and strength between men and women (von Rueden, Gurven, & Kaplan, 2011). 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, in coordinating community projects and resolution of conflicts; male-biased influence was attributed to mean having more cooperation partners, increased access to education, and greater body size and physical strength than women (von Rueden et al. 2018). Systematic study is required to understand the extent of gender bias across small-scale societies of humans.

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* — consistently 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 (de Waal, 1984). Moreover, gender-bias in 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 both occupy leadership positions to some extent and many cases 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 of the species reviewed here that extend beyond the cases highlighted by 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 power 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 shared use of resources (van Schaik & van Noordwijk, 1988)(Isbell, 1991)(Jennifer E. Smith, 2014). 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 (Seyfarth, 1980)(Barrett, Henzi, Weingrill, Lycett, & Hill, 1999)(Jennifer E. Smith et al., 2007). Female with the strongest social bonds have highest infant survival and female lifespan (Silk, Alberts, & Altmann, 2003, 2004)(Silk et al., 2010). Members of friendly matrilines are allies (K. Holekamp et al., 2012). Dominant females may suppress the reproduction of others within cooperative breeding groups, especially in mammalian carnivores (Young et al., 2006)(Montgomery, Pendleton, & Smith, 2018) . 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 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 others in 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 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 stimulate a new body of theory contributing to the study of leadership that fully encompasses the multiple ways in which individuals influence the outcomes of social lives of individuals 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 the many obstacles, including the ways that evolutionary history as well as current 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 help to inform our understanding of the origins and persistence of gender bias so that society may act to address these biases in effort to benefit from the leadership skills of women and to move towards a more equitable society.

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**Figure Legends**

**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*).

**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](https://commons.wikimedia.org/w/index.php?curid=7161455) via WikiMedia/[CC BY-SA 2.5](http://creativecommons.org/licenses/by-sa/3.0)), **C)** spotted hyenas (*Crocuta crocuta*; Photo by David S. Green), **D)** bonobos (*Pan paniscus;* Photo by [Pierre Fidenci](https://commons.wikimedia.org/wiki/File:Pan_paniscus11.jpg) via WikiMedia/[CC BY-SA 2.5](http://creativecommons.org/licenses/by-sa/3.0)), **E)** black-and-white ruffed lemurs (*Varecia variegata;* Photo by [Charles J. Sharp](https://en.wikipedia.org/wiki/Black-and-white_ruffed_lemur#/media/File:Black_and_white_ruffed_lemur.jpg) via WikiMedia/[CC BY-SA 3.0](http://creativecommons.org/licenses/by-sa/3.0)), **F)** ring-tailed lemurs (*Lemur catta;* Photo by [David Deniss](https://commons.wikimedia.org/wiki/File:Ringtailed_Lemurs_in_Berenty.jpg) via WikiMedia/[CC BY-SA 3.0](http://creativecommons.org/licenses/by-sa/3.0)), **G)** African bush elephants (*Loxodonta africana*; Photo by [Amoghavarsha](http://en.wikipedia.org/wiki/Elephant#mediaviewer/File:Elephants_at_Amboseli_national_park_against_Mount_Kilimanjaro.jpg) via WikiMedia/[CC BY-SA 3.0](http://creativecommons.org/licenses/by-sa/3.0)), **H)** Asian elephants (*Elephas maximus;* Photo by [Steve Evans](https://en.wikipedia.org/wiki/Asian_elephant#/media/File:Sri_Lanka_Elephants_03.jpg) via WikiMedia/[CC BY-SA 2.0](http://creativecommons.org/licenses/by-sa/3.0)). All photos are public domain under the Creative Commons License, except that used, with permission, from D.S.G.

Finally, it is worth comparing our findings with leadership in small-scale human societies that anthropologists have been studying (REFs). These societies, from the Kung-San in Southern Africa, the Tsimane in the Amazon rainforest, to the Inuit in Northern Canada, are a useful model of group living in early humans (von Rueden & van Vugt, 2015). Because these societies are small and relatively simple -- they lack institutions, formalized hierarchies, and material wealth acquisition is limited - these societies are more akin to the mammalian societies that we discussed in this review and thus are relevant to testing our evolutionary hypotheses about leadership. Many of our insights converge with reviews of female leadership in these small-scale societies, and they offer complementary knowledge about obstacles and opportunities for female leadership (von Rueden et al., 2018). A first insight is that male leadership is more prevalent than female leadership in these societies; men are more likely to be leading hunts, raids and wars, and emerge as political leaders of their community. Nevertheless, in various societies women leaders play an important role as conflict mediators in groups and societies benefit from women taking on these roles as they can prevent conflicts from escalating. Second, these anthropological studies converge with our findings by suggesting similar constraints on the emergence of female leadership as a result of differences in (a) physical size, (b) child care provision, (c) motivation to compete for high-status positions and (d) coalition-building activities. Among the Tsimane, for instance, political leaders are 3 times as likely to be men than women, and this difference is accounted for partly by men having more coalition partners outside their direct family – presumably as a way to accumulate status-enhancing resources -- and women being constrained by child care (von Rueden et al., 2018). Nevertheless, women still tend to wield more influence as community leaders in these small, traditional societies than in our large, complex modern societies (Dyble et al., 2015). These parallel insights from the animal and anthropological literature offer various implications for female leadership in business, politics and social movements.