Female Power: A New Framework for Understanding “Female Dominance” in Lemurs

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Keywords

Strepsirrhine · Intersexual relationships · Leverage · Biological markets

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Abstract

Female dominance is often associated with lemurs. However, consensus does not exist among primatologists on how to define, measure, or explain female dominance. This review explores the utility of applying a broader concept of power to understanding lemur intersexual relationships. In this framework, power is defined as arising from an asymmetry in a dyadic relationship and can be divided into 2 types: dominance and leverage. Intersexual asymmetries based upon females having superior fighting ability are considered female dominance. However, economic power also exists, and females with resource-based power exhibit female leverage. Additionally, power has 4 characteristics (base, means, amount, and scope) that describe the precise nature of observed phenomena. This article utilizes the 4 characteristics outlined in the power framework to review the existing “female dominance” literature for lemurs and highlights the value of adopting both an expanded concept of power and a more precise language. By placing the multiple phenomena currently labeled under the single term “female dominance” within the power framework, much of the confusion disappears. Thus, not only is the debate reframed, facilitating endeavors to find evolutionary explanations, but the uniqueness of female power in lemurs can be determined empirically rather than by definition.

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Introduction

Lemurs are unusual in that females often dominate males [Hrdy, 1981; Jolly, 1984; Kappeler, 1993a]. In most other primates and nonprimate mammals, males are dominant over females [Ralls, 1976; Holenkamp and Engh, 2009; French et al., 2013;

but see Lewis, 2018]. Because of its prevalence among lemurs, female dominance has been suggested to be a synapomorphy of the lemuriform clade [Jolly, 1984; Radespiel and Zimmermann, 2001; Schülke and Kappeler, 2003] and many researchers have sought unique evolutionary explanations [for review, see Lewis, 2018]. Nevertheless, no consensus has emerged on why female dominance arises because primatologists dispute the nature of the phenomenon as well as how to study it. Until primatologists can agree on how to define, measure, and analyze female dominance, adaptive explanations will continue to be elusive.

One key factor complicating the search for evolutionary explanations of female dominance is a lack of consensus regarding how to define the phenomenon. While primatologists agree that female dominance exists, researchers have argued for decades about the definition. Some authors have asserted that female dominance is fundamentally different from male dominance, asserting that female dominance is "... not "dominance" in the male baboon-based sense of a threat hierarchy which confers privilege" [p. 197 in Jolly, 1984]. Others have suggested that it is the same as male dominance but with females in control [Wright, 1993]. Some examples of how female dominance has been defined include: (1) priority of access to resources [Hrdy, 1981; Jolly, 1984], (2) consistent directionality of agonism in more than just the feeding context [Roeder and Fornasieri, 1995], (3) decided aggressive interactions [Pochron et al., 2003], and (4) the ability to consistently evoke submissive behaviors from all males in dyadic interactions [Kappeler, 1993a]. Recognizing the variation subsumed under a single term, Radespiel and Zimmermann [2001] suggested dividing female dominance into different types, i.e., unambiguous, moderate, and feeding priority. These exist along a continuum from "clear agonistic superiority... [to] ... conflicts less often decided and males more often aggressive" independently of the context, to only winning in the feeding context [p. 181–182 in Radespiel and Zimmermann, 2001]. This classification system has not been adopted widely, however [but see Eichmueller et al., 2013].

Indeed, the dispute over female dominance derives in part from the fact that the term "female dominance" is used to refer to all types of female intersexual power [Lewis, 2002]. Female feeding priority refers to a female's ability to win contests in the feeding context. This type of power is very different from the power of a female to evoke a spontaneous submissive signal from a male in any context. Females may have both of these types of power or just one. Labeling any type of female power as "female dominance" obscures the underlying phenomenon that is being described. Consequently, researchers disagreeing about female dominance are not necessarily referring to the same phenomenon. Thus, in order to best understand female dominance, researchers must adopt a more inclusive concept of power and a more precise terminology.

Explanations of female dominance are also hindered by researchers measuring it in different ways. While this problem of operationalizing dominance troubles all students of animal behavior [e.g., Bernstein, 1981; Drews, 1993; Lewis, 2002], measuring dominance has been particularly contentious in the study of intersexual relationships in lemurs. Moreover, different methods of determining dominance can lead to different results [Lewis, 2002]. Assigning dominance status by recording who wins a conflict can produce rankings that differ from the rankings produced by assigning status according to the direction of aggression or submission. Indeed, because hierarchies function to clarify the allocation of resources and reduce disputes,

Fig. 1. Schematic of the power framework.

conflicts are expected to be rare when status is well resolved. Methods that rely on assigning status based upon conflicts may, therefore, focus on a narrow range of social dynamics.

Finally, the study of female dominance in lemurs has become intellectually isolated [Lewis, 2018]. Current understandings of female dominance are rooted in the explosion of research on the topic in the 1980s and 1990s. During this time period, primatological theory was heavily influenced by a historical focus on catarrhines and cultural stereotypes about gender [Strier, 1994; Lewis, 2018]. Over the intervening decades, a substantial amount of new data on a wider variety of species has become available, more sophisticated statistical analysis has become the norm, a greater appreciation of intraspecific behavioral variation has developed [Strier, 2017], and ethological theory has changed considerably [e.g., Clutton-Brock and Janson, 2012; Clutton-Brock and Huchard, 2013]. Primatologists now tend to focus on spheres of power and rarely investigate male dominance [Lewis, 2018]. By contrast, social interactions in lemurs continue to be filtered through the lens of female dominance. Consequently, female dominance continues to be compartmentalized and dismissed as a clade-specific peculiarity [Lewis, 2018] even though it is found in other primates, other

Table 1. Terminology used in the power framework that can standardize and reconceptualize power in nonhuman societies

Term	Definition
Power	A phenomenon that arises due to an asymmetry in a dyadic relationship that allows A to induce behaviors in B; general term described by 4 characteristics (base, means, amount, and scope)
Base	The source of power; the asymmetry that gives rise to the power
Dominance	Term used for power based upon the ability to use physical force or the threat of that force (can be intrinsic or derived)
Leverage	Term used for power based upon a resource that cannot be taken by force
Means	How power is accomplished; the mechanism used by the powerful individual
Amount	The probability of achieving an outcome in a particular context
Scope	The outcome of power; what the powerful individual can evoke

mammals, and other vertebrates [Ralls, 1976; Smith, 1982; Jolly, 1984; Wright, 1993; Dunham, 2008; Holenkamp and Engh, 2009; French et al., 2013; Lewis, 2018].

The Power Framework

Lewis [2002] introduced a broader framework of power that combines concepts from the social sciences with concepts from ethology (Fig. 1). It is not an evolutionary framework per se. Instead, it helps resolve many of the problems that plague the study of female dominance by incorporating the various definitions into a single framework and facilitates interspecific comparisons by providing a precise terminology. This clarification is a necessary step in the endeavor to find evolutionary explanations. Importantly, the framework leads to novel predictions and reintegrates the study of female dominance in lemurs within the broader ethological literature [Lewis, 2018].

In this framework, the general term “power” is a phenomenon that arises from an asymmetry in a dyadic relationship (i.e., it is an intervening variable [Hinde and Datta, 1981]). Power is defined by 4 characteristics, i.e., base, means, amount, and scope (Table 1), which are discussed in turn below. The base of power explains the source of power – in other words, the specific asymmetry that causes one individual to have the ability to influence another. Two different bases of power exist, i.e., dominance and leverage. Dominance is power based upon fighting ability and can further be subdivided into 2 types because the asymmetry in the ability to use force may be intrinsic or derived. For example, when an individual increases its fighting ability by enlisting the help of a coalition partner, this base of power is labeled as derived dominance (Fig. 2). Note that dominance refers to the ability to influence another due to an asymmetry in the underlying physical abilities to coerce and not the actual use of force itself. Leverage, on the other hand, is economic power, i.e., power based upon resources (or services) that cannot be taken by force [Hand, 1986; see also “cost asymmetry hypothesis” in Dunham, 2008]. Leverage builds upon the concept that power is affected by “market effects,” i.e., the influence of supply and demand for a commodity or service [Noë et al., 1991; Noë and Hammerstein, 1994, 1995]. Thus, an

Fig. 2. Coalitions have the potential to produce both dominance and leverage. **a** Individual A has derived dominance in its relationship with B because of its coalition with C, the A + C coalition results in a superior fighting ability over B. At the same time, C has leverage in its relationship with A because A depends on it for a coalition (A + C) against B. The extent of C's leverage over A can vary due to market effects. If A needs a coalition partner to achieve derived dominance over B but only C is available as a potential collaborator, then C has substantial leverage in its relationship with A. C can exercise this leverage over A by refusing to collaborate. A is likely to incentivize C's collaboration by providing benefits to C, such as grooming. **b** However, if multiple potential coalition partners are available, then A is not as dependent on C to form a coalition against B (coalitions A + D and A + E are also possibilities). C does not have as much leverage over A because A is less dependent on C, and A is unlikely to provide the same level of incentives for C's "collaboration service."

asymmetry within the dyad in the need for an inalienable resource or a service can be a base of power.

In addition to differentiating between the bases of power, the power framework emphasizes the importance of distinguishing among the various means of power. "Means" refers to how the power is executed. Aggression (i.e., the use of force) is often employed as a means of power regardless of whether the base of the power is dominance or leverage. A female might exercise leverage (base) by using aggression (means) to get priority of access to resources (scope). However, aggression is only one of many ways for an individual to achieve its goal. Powerful individuals can also influence the behavior of another with a reward or by simply refusing to act (Fig. 2). For example, a female can exercise leverage by means of refusing to mate with a male [Lewis, 2002]. Similarly, an alliance partner can exercise leverage by opting not to offer coalitionary support (Fig. 2a). These more subtle means of power are not always taken into account in the traditional, narrower dominance framework, which emphasizes agonistic interactions. For decades, primatologists have expressed concern about conflating dominance and aggression [Rowell, 1974; Bernstein, 1981]. By broadening the "dominance" paradigm to include other instruments of power beyond aggression, the Lewis [2002] framework provides an alternative approach to studying power in animal behavior.

While base is the initial asymmetry that results in power and means is the instrument of power, the amount of power refers to the probability of winning conflicts in various contexts. Note that the term “winning” is used here to refer generally to any outcome of power and not to whether an interaction is “decided” [when one individual in an agonistic interaction is submissive: Pereira and Kappeler, 1997]. An individual may have a greater magnitude of power in one context than in another. For example, a female might supplant male A 100% of the time in the feeding context and only 60% of the time in the resting context. By contrast, she might be able to supplant male B 90% of the time across all contexts. In this example, the female has a greater amount of power in the feeding context than in the resting context in her relationship with male A. In the feeding context, she has a greater amount of power in her relationship with male A versus male B. In the resting context, however, she has a greater amount of power in her relationship with male B versus male A. Thus, according to the power framework, measuring the amount of power is critical for understanding a dyadic relationship because it addresses the fact that power can sometimes be situational. Power across all contexts is different from power only in limited contexts. Moreover, having complete (100% of the time) power is different from being more likely (>50% of the time) to win.

The final characteristic of power, i.e., scope, characterizes the result of the asymmetry in the dyad. It describes the specific consequence that the more powerful individual is able to evoke in the less powerful individual, such as tolerance, a copulation, and a submissive signal. In fact, the “formal dominance” of de Waal [1986] refers to the *scope* of power [Lewis, 2002]. Some individuals are able to evoke asymmetrical grooming as a result of their power. For instance, new infants give baboon [Henzi and Barrett, 2002] and sifaka [Lewis, 2010] mothers the leverage to obtain more grooming than females without new infants. Other individuals exhibit power by being able to evoke peaceful contact after conflicts [e.g., ring-tailed lemurs: Palagi and Norscia, 2015; Verreaux’s sifaka: Palagi et al., 2008]. Researchers often combine scope and amount of power into one category and just record whether an interaction resulted in a win or loss. This method, however, merges distinct characteristics of power and clouds the phenomenon. Wittig and Boesch [2003], for example, analyzed amount and scope separately and found that the ability to evoke reconciliation varied by context in chimpanzees. Similarly, means and scope are combined when researchers analyze aggression and submission as agonistic encounters, even though aggression and submission matrices can differ [e.g., Norscia and Palagi, 2015].

Female Power in Lemurs

By placing “female dominance” in the broader context of power, much of the disagreement over the nature of the phenomenon disappears. The term should be replaced with “female power” unless the base of power is understood. A species should only be called female dominant if females have a greater ability to use force than males. If, on the other hand, the base of female power is an inalienable resource, then the phenomenon of “female dominance” is better termed “female leverage” [Lewis, 2002]. Many lemur species are monomorphic [Kappeler, 1990b], for instance, and thus more likely exhibit female leverage than female dominance. In other species, such as indri (*Indri indri*), females are larger than males [Smith and Jungers, 1997; Powzyk, 1998], and the term female dominance may indeed accurately describe the underlying phenomenon. Furthermore, the terms “female power,” “female domi-

nance,” and “female leverage” should only be used when all adult females have power over all adult males. Power is dyadic and these terms must be understood as shorthand for the intersexual dyadic relationships in a species [Lewis, 2002]. The term “female-biased power structures” can be used when power is not completely sex dependent [Lewis, 2018].

Other aspects of female power are elucidated with this framework. For example, female feeding priority refers to the female’s amount of power (because it is restricted to only a single context: feeding), while unidirectional submissive signals by males towards females fall under the scope of female power (because it refers to the outcome irrespective of context). While both female priority of access to resources in the context of feeding and the ability to evoke submissive signals from males may occur together (receiving submissive signals in the feeding context), these characteristics of power may also occur independently. They may be based upon an asymmetry in intersexual fighting abilities, or they may be based upon leverage derived from limited mating opportunities. Some species may even have both female dominance and female leverage. Two species, 2 populations, or indeed 2 females may share the same base of power but the other characteristics of power may vary. Similarly, species, populations, or dyads may exhibit the same means, amount, and scope of power but differ on which asymmetry serves as the base of power.

For example, Verreaux’s sifaka (*Propithecus verreauxi*) have been reported to be “female dominant” [Richard, 1987; Brockman, 1994, 1999; Kubzdela, 1997]. At the Beza Mahafaly Special Reserve, the sifaka are monomorphic [Richard et al., 2000], while at Kirindy Forest females are significantly larger than males [Lewis and Kappeler, 2005]. Body size can be one important factor for determining an individual’s ability to physically coerce another. Even though some females at Beza Mahafaly may have dominance over males, presumably due to monomorphism, not every female has a greater ability to use force than males. As a result, sifaka at Beza Mahafaly may exhibit female leverage rather than female dominance per se (although the term “power” is preferred until the base of power can be identified). By contrast, at Kirindy Forest, most females are larger than males, and hence “dominance” may be a correct depiction of female power in this population. However, the term female dominance may still be problematic because some exceptions to the female-biased sexual dimorphism occur at Kirindy Forest [Lewis and Kappeler, 2005] and because fighting ability is probably influenced by more than just body size (e.g., canine size, agility, strength, and androgens).

Application of the Power Framework

A theoretical framework is especially useful when it can be applied precisely to empirical data. In order to illustrate the utility of the power framework for understanding the phenomenon known as “female dominance,” this section explores some examples of how the framework can be applied to lemur social dynamics. These examples demonstrate how the framework goes beyond changing nomenclature to provide an alternative concept of intersexual power relationships. Additionally, the following section illustrates the explanatory power of the framework, how the 4 characteristics of power can be operationalized, and some of the novel predictions that arise. Note that this review does not evaluate the validity of particular proximate or ultimate

causes of female intersexual power. By defining power as dyadic, the framework lends itself well to proximate explanations but it does not have an evolutionary focus. Instead, the aim of this review is to show how application of the power framework to lemurs (1) results in a reconceptualization of the phenomenon of female dominance and (2) facilitates the endeavor of finding evolutionary explanations.

Base

In order to determine the base of female intersexual power, researchers must establish the source of the asymmetry in the dyad. Dominance can be measured by recording variables that influence whether males and females differ in their abilities to use force. Fighting abilities probably result from the sum of various traits, such as body mass, canine size, and agility. In many lemur species, these traits may be relatively easily measured by capturing animals. Methods for measuring leverage depend on the resource upon which the power is based. For example, the population sex ratio, the degree of estrous synchrony, and the length of estrus can all indicate whether females are likely to have leverage based upon their abilities to offer mating opportunities [Lewis, 2018]. Measuring leverage thus also requires measuring the supply and demand of the inalienable resource. For instance, knowledge confers leverage only when it is both valuable and asymmetrical. Additionally, while leverage is resource-based power, it is different from the socioecological concept of resource competition. Because food resources generally can be taken by force, they are not a source of leverage-based power. If, however, food can only be accessed by using a skill that is uncommon in the population, then the food-processing skill can be a source of leverage but the food itself is not.

Fighting Ability

Body mass can be a good proxy for fighting ability [Clutton-Brock, 1985] and changes in body mass can lead to changes in intersexual power. For instance, Marolf et al. [2007] reported that one male crowned lemur (*Eulemur coronatus*), who was overweight and larger than the female groupmate, was dominant over her while other males in the study were subordinate to females. When that male lost weight, the female became more aggressive towards him. As discussed above, female Verreaux's sifaka at Kirindy Forest have a significantly greater body mass than males for most of the year [Lewis and Kappeler, 2005]. Thus, female dominance is a good possibility in the Kirindy Forest population. If the female-biased sexual dimorphism is the basis of female dominance, the power relationship is likely dynamic due to drastic weight loss during the dry season. During the dry season, the sifaka are monomorphic [Lewis and Kappeler, 2005] and dominance as a base of power is less likely. Despite this fluctuation in body mass, female power continues throughout the year [Lewis, 2004]. Canine length is monomorphic in this population [Lewis, unpubl. data]. Thus, the Kirindy Forest sifaka may exhibit female leverage in addition to seasonal female dominance.

New predictions about female power can therefore be developed based upon the power framework. For instance, by suggesting that female dominance may not occur year-round due to the seasonal monomorphism, one resulting hypothesis is that female Verreaux's sifaka exhibit intersexual power based on leverage. Thus, a consequence of the power framework is that researchers are directed towards looking for the source of leverage, such as a fertilizable egg [Hand, 1986; Lewis, 2002], sex ratio [Noë et al., 1991], or dependency on a coalition [Lewis, 2002] (Fig. 2a). Moreover,

because the base of power may change by season, one might predict that other characteristics of power change at the same time. For example, the scope of power may be reduced as female dominance decreases, or the amount of power may become more context specific, or the means of power may shift.

Fertilizable Egg

The reproductive cycle and internal gestation of female mammals result in asymmetries specific to intersexual dyads. The number of female eggs that are available for fertilization at any given time is quite limited in most lemurs, and thus having a fertilizable egg can be a source of leverage [Hand, 1986; Lewis, 2002]. Multiple researchers report that female power in lemurs only begins at puberty [e.g., ring-tailed lemurs: Pereira, 1993; Sauther, 1993; mouse lemurs: Hohenbrink et al., 2015]. The timing of this change in power suggests that a female's ability to increase male reproductive success via fertilization of an egg is the base of power. For instance, female Verreaux's sifaka can become sexually active as early as 3 years of age [Richard et al., 2000] but they do not become reproductively mature until age 5 [Lawler, 2003] because the offspring of younger females generally do not survive [Richard et al., 2000]. Hence, a good test of female leverage based upon a fertilizable egg [Hand, 1986] is to compare females aged 3–4 years and females aged >5 years to determine whether their relationships with males differ. For example, if males are submissive towards females prior to reproductive maturity, a fertilizable egg is probably not the source of female power that causes the male submission. Because body size changes with age, controlling for body size dimorphism within the dyad is important when determining whether a female has leverage based on a fertilizable egg: males are expected to be submissive only towards females aged 5 years or older, regardless of size differences. Indeed, Voyt et al. [in press] found that female reproductive maturity (base = fertilizable egg) determines the direction of submission (scope) in intersexual sifaka dyads and that dyadic dimorphism (base = fighting ability) influences submission (scope) only for immature females.

Importantly, not all mating opportunities are equal. Infants born to first-time mothers have a lower probability of survival [e.g., Jarcho et al., 2012]. Consequently, siring offspring with older, more experienced females may be preferred in nonhuman primates. The power framework predicts that female leverage varies with the value of the resource [Lewis, 2002]. Indeed, female mouse lemurs (*Microcebus murinus* and *M. lehilahytsara*) with no breeding experience win fewer intersexual conflicts than experienced females [Hohenbrink et al., 2015]. Similarly, in Verreaux's sifaka, female leverage is more consistently expressed after a female has an infant survive past weaning [Voyt et al., in press].

Researchers have previously studied the development of dominance relationships in lemurs. Consistent with the power framework, juvenile dominance is determined by weight rather than sex in ring-tailed lemurs (*Lemur catta*) [Pereira, 1993; see also Meredith, 2018]. New predictions, however, can be derived based upon the power framework. For example, in species exhibiting female dominance, a female is expected to become more powerful than males when she achieves a greater ability to use force, such as when she grows larger than males. Because male size is variable, females are expected to dominate the smaller males first and the larger males last. By contrast, if female intersexual power is not female dominance but rather female leverage based on her reproductive maturity, a female is expected to become more powerful than all males at roughly the same time.

Sex Ratio

Brown, red-fronted, and red lemurs (*Eulemur* spp.) have puzzled primatologists because of their lack of sex-dependent power [Sussman, 1975; Pereira et al., 1990; Kappeler, 1993a; Pereira and McGlynn, 1997; Gerson, 2000]. However, some data suggest that the sex ratio may influence power dynamics in these species. For example, Pereira and Kappeler [1997] examined both decided and undecided conflicts in red-fronted lemur (*E. rufifrons*) dyads. Group composition changed during their study, and as a result the adult sex ratio shifted from 3:3 to 5:3. With the increase in the number of males in the group, the percent of decided conflicts won by males decreased, while female wins simultaneously increased. Roeder and Fornasieri [1995] also observed a similar change in the directionality of agonism with a change in group composition in brown lemurs (*E. fulvus mayottensis*). Thus, the sex ratio may be a base of power in these species, especially if changes in the sex ratio lead to changes in the supply and demand of services that can be provided best by a particular sex [Lewis, 2004].

Sex ratios also seem to play an important role in bamboo lemur power dynamics. Waeber and Hemelrijk [2003] found that Lac Aloatra bamboo lemurs (*Hap Alemur aloatrensis*) are essentially monomorphic and have social groups with variable sex ratios. Nevertheless, females won most feeding conflicts, received spontaneous submission in 83% of the interactions, and were groomed by the opposite sex more. If the sex ratio is a base of intersexual power for female bamboo lemurs, then one might predict that these results were strongest in the groups with the male-biased sex ratios.

By expanding the concept of power to include “market effects,” a new set of predictions can be derived. For instance, individuals are expected to attempt to manipulate sex ratios in their favor by encouraging or discouraging group membership [e.g., Verreaux’s sifaka: Lewis, 2008], altering birth sex ratios [e.g., mouse lemurs: Perret, 1996], or even infanticide [Hrdy, 1979]. Similarly, females can influence the supply and demand of mating opportunities in the mating market by adjusting estrous synchrony [Pereira, 1991]. Supply has been shown to influence intersexual social dynamics in lemurs; dominant male Verreaux’s sifaka living in multi-male groups, for example, experience different relationships with females than males in single-male groups [Lewis, 2004]. Additionally, groups or populations with male-biased sex ratios are predicted to exhibit greater female leverage. Notably, many lemurs exhibit male-biased sex ratios [Jolly, 1984; Richard, 1987; van Schaik and Kappeler, 1993, 1996; Kappeler, 2000; Norscia and Palagi, 2008]. While most Verreaux’s sifaka populations exhibit male-biased sex ratios, the Ankoatsifaka population in Kirindy Mitea National Park is female biased [Leimberger and Lewis, 2017], and female leverage based on the sex ratio is expected to differ at this site.

Coalition Partners

Another interesting aspect of some *Eulemur* societies is that adults intervene in conflicts [Pereira and Kappeler, 1997; Pereira and McGlynn, 1997; Roeder et al., 2002]. Approximately half of all red-fronted lemur polyadic conflicts involve male intervention to the benefit of females [Pereira and Kappeler, 1997]. When males intervene on behalf of females, females have a derived dominance [sensu Lewis, 2002] (Fig. 2a). *Eulemur* does not exhibit sexual dimorphism in body size [Kappeler, 1990b]. Thus, intersexual power may be influenced more by coalitions in these species than by individual fighting abilities. Valuable coalition partners have leverage because they are an

important resource [Lewis, 2002] (Fig. 2a). Male intersexual power in this species may arise from being key coalition partners for females. Variability in the value of coalition partners may help to explain why power is so variable in red-fronted and brown lemurs. Owing to sexual monomorphism, sometimes a male may be a better coalition partner than a female, but sometimes a female may be a better coalition partner. Moreover, the supply and demand of potential coalition partners can influence power [Noë, 1990; Noë et al., 1991] (Fig. 2b). Hence, the finding that intersexual power changes with the sex ratio [Roeder and Fornasieri, 1995; Pereira and Kappeler, 1997] supports the hypothesis that market forces influence male-female relationships in *Eulemur*.

The broader concept of power leads to a new set of predictions about the lack of sex-dependent power in red-fronted and brown lemurs. For instance, valuable coalition partners are expected to receive peaceful contact after conflicts more than when relationships are less valuable [e.g., Verreaux's sifaka: Palagi et al., 2008; ring-tailed lemurs: Palagi and Norscia, 2015]. Indeed, brown lemur reconciliation does not vary by sex class [Norscia and Palagi, 2011]. This power to induce reconciliatory behaviors is further enhanced when combined with other bases of power, such as when the demand for coalition partners is high.

Knowledge and Social Position

Experimental ring-tailed lemur research using social network analysis demonstrates that an individual's power changes when it acquires novel information and frequently displays this knowledge [Kulachi et al., 2018]. Social network analysis also has demonstrated that some primate societies exhibit an emergent property whereby key individuals experience powerful positions independently of rank [Flack and Krakauer, 2006; Beisner et al., 2016]. In this case, social position is a base of power that derives from an asymmetry in prestige (sometimes referred to as conferred power, consensus power, or authority). While the above studies did not examine female intersexual power, they exemplify how leverage can arise from a variety of sources. The power framework allows for the incorporation of new understandings of power into studies of "female dominance" in lemurs.

Means

In order to measure the means of female intersexual power, researchers need to record any behavior that allows a female to exercise her power. Aggression is the most obvious instrument of power. However, the most powerful individuals may not be the most aggressive individuals in the group [Rowell, 1974; Bernstein, 1981; Lewis, 2002]. Individuals can also use other means, such as tantrums, to achieve outcomes [e.g., bonobos: Vervaeke et al., 2000]. The absence of certain behaviors may also indicate the means of female power because individuals can assert power by refusing to act. Additionally, outcomes can be achieved via rewards or incentives (Fig. 2; c.f. biological markets: Noë and Hammerstein, 1994, 1995). Hence, subtle behaviors that may be species specific, the behaviors of other individuals that indicate a refusal to act, and rewards are important but often neglected indicators of power.

Roeder and Fornasieri [1995] examined the means of power in captive experiments with brown lemurs. They found that not all females have priority of access to resources over all males. When females did have priority over males, they did not use the means of aggression (although the authors did not address the means used by females). By contrast, the males frequently used aggression in order to gain priority to

the prized resource. Thus, one sex difference in power in this case is a sex difference in means. A similar example of a sex difference in the means of power is the finding that juvenile female ring-tailed lemurs use the means of aggression more than juvenile males [Pereira, 1993].

Aggression is only one instrument of power, however (Fig. 1). Other behavioral means are often not reported in studies of intersexual power. The power framework highlights how other ways of executing power are overlooked in the traditional dominance paradigm. Pheromones may be another means of power in lemurs. Génin et al. [1996] found that sensory cues of females inhibit seasonal fattening in male gray mouse lemurs. They suggested that this social inhibition of weight gain results from “female dominance.” Socioendocrinology, therefore, may prove to be an important method for measuring means of power in lemurs [c.f. Petty and Drea, 2015].

Amount

In order to assess amount of power, researchers need to determine the probability of accomplishing desired outcomes in particular contexts. Many researchers currently measure the amount of power in lemurs by recording wins and losses. For example, Kappeler [1990a] studied the context of intersexual agonistic interactions in ring-tailed lemurs. He found that the percent of female wins over males varied from 60 to 100% depending on the context. His data show that female ring-tailed lemurs have the greatest amount of power in sexual, olfactory, and grooming contexts and the lowest amount of power in the context of agonism. By contrast, Hohenbrink et al. [2016] found that female mouse lemurs (*M. murinus* and *M. lehilahytsara*) win the majority of intersexual conflicts regardless of the context but that conflict rates are influenced by reproductive season. This type of seasonal change may reflect a change in the amount (mating context) or base (mating opportunities) of power or both. This distinction can be investigated by determining whether non-reproductive individuals experience the seasonal change.

Pochron et al. [2003] examined the extent to which “female dominance” is context dependent in Milne-Edward’s sifaka (*P. edwardsi*). They demonstrated that female Milne-Edward’s sifaka have a greater amount of power than males by showing that the percentage of wins by females was greater than males regardless of the context. However, the amount did vary by context. Females won 100% of aggressive interactions during allogrooming but only 80% during mutual grooming. Thus, female Milne-Edward’s sifaka have a lower amount of power when they are mutually grooming than during unidirectional grooming. The authors did not differentiate between when an individual gives and receives grooming in their analysis. One prediction based upon the power framework is that females have a lower amount of power when giving grooming than when receiving grooming. Females are predicted to have a greater amount of power when they receive grooming because receiving grooming indicates that they are able to evoke this grooming behavior in the first place. The authors also found that the amount of power varied by the means of power used. For instance, nondisplacement aggression was more successful than displacement aggression (85 vs. 93% wins).

Scope

Researchers often demonstrate the scope of power when they examine submissive signals. In fact, the common method of recording conflicts as decided or unde-

cided based upon whether one individual exhibits submissive behaviors [Pereira et al., 1990; Pereira and Kappeler, 1997; Pereira, 2006] is a useful approach to explore scope of power. However, when just submissive behaviors are used to define whether a conflict is decided, then only a subset of power interactions will be recorded because power differentials can lead to more than just submission. Additional behaviors that traditionally have not been examined under the umbrella of power are also important for understanding lemur power dynamics. Services such as grooming, vigilance, infant care, and territorial defense can be measured to determine whether females can provoke these behaviors in males as a result of a power asymmetry [Lewis, 2004]. The ability to lead group movement and have others follow [Erhart and Overdorff, 1999; Jacobs et al., 2011] is also a scope of power.

Lemur studies are consistent with the idea that an individual's scope of power is not limited to submission. A power asymmetry may cause asymmetries in affiliative behaviors [Lewis, 2002]. Verreaux's sifaka groom up the hierarchy [Lewis, 2010], consequently males groom females more. In ring-tailed lemurs, subordinate individuals greet and groom higher ranking individuals more frequently than they receive these behaviors [Nakamichi and Koyama, 1997] and knowledgeable lemurs receive more grooming [Kulachi et al., 2018]. A power asymmetry can also result in some lemurs leading group movement more often because group members follow them more [Erhart and Overdorff, 1999; Jacobs et al., 2011]. In other words, lemurs are able to evoke a number of different behaviors (submission, greet, groom, and follow) as a consequence of power.

In addition to examining *scope* within a species, differences in behaviors can be compared across species to determine interspecific variation in the scope of power [e.g., Norscia and Palagi, 2015]. For instance, Verreaux's sifaka and silky sifaka (*P. candidus*) differ in their scope of power. Both species of sifaka exhibit female feeding priority (i.e., a large amount of power in the feeding context), and both species communicate submission with a similar vocalization. The chatter vocalization in Verreaux's sifaka is unidirectional [Richard and Heimbuch, 1975] and often spontaneous [Kraus et al., 1999], indicating that it is a formal signal of status [sensu de Waal, 1986; Lewis and van Schaik, 2007; Lewis, 2019]. By contrast, the chatter-squeal vocalization in silky sifaka is not emitted spontaneously but only in response to aggression [Erik R. Patel, pers. commun.]. Hence, Verreaux's sifaka have a greater scope of power than the silky sifaka because Verreaux's sifaka are able to evoke spontaneous submission [see also subordination signaling: Flack and de Waal, 2007; Lewis, 2019]. Ring-tailed lemurs, like Verreaux's sifaka, have a very ritualized submissive signal (the spat call) which is sometimes emitted without provocation [Jolly, 1966; Pereira and Kappeler, 1997] and is thus considered a formal signal of status. By contrast, black-and-white ruffed lemurs (*Varecia variegata*) do not even exhibit submissive signals [Overdorff et al., 2005]. Thus, the scope of female power in ruffed lemurs is considerably different from the scope of power in silky sifaka, Verreaux's sifaka, and ring-tailed lemurs.

It is important to clarify how means, amount, and scope in the power framework relate to the decided/undecided methodology recommended by Pereira and colleagues [Pereira et al., 1990; Pereira and Kappeler, 1997; Pereira, 2006]. Using their method, researchers score whether a particular dyadic interaction involves aggressive, submissive, and/or neutral behaviors. Conflicts including a submissive behavior by only one individual (e.g., one individual is aggressive and the other is submissive or one individual is neutral while the other is submissive) are termed "decided,"

whereas conflicts not meeting this criterion are termed “undecided” (e.g., aggressive-aggressive, aggressive-neutral, and submissive-submissive). Thus, a conflict is decided when an individual has the scope of evoking submission (except in submissive-submissive encounters). Researchers using this method typically combine aggressive-submissive and neutral-submissive interactions into the single category of decided, which commingles how the power is accomplished (means) with the outcome of power (scope). Thus, while this method provides an important description of the conflict, it obscures both the behaviors of the two actors (Fig. 1) and potentially meaningful variation.

As is apparent from this limited review, lemur researchers have already been measuring many aspects of power. However, this research has been incomplete. For example, the study of Digby and Kahlenberg [2002] on “female dominance” in blue-eyed black lemurs (*E. macaco flavifrons*) is typical, demonstrating the amount of female power by examining the percent of decided interactions in the feeding and non-feeding contexts. Kappeler [1996] examined the base of female power in his study of strepsirrhine canine dimorphism and suggested that “female dominance” in lemurs is not based upon fighting ability. These studies provide excellent insight into intersexual power but they are limited because they do not examine other characteristics of power. Finding an evolutionary explanation for female intersexual power in lemurs is therefore difficult until the full nature of power is understood. Indeed, female power is highly variable across lemurs [Radespiel and Zimmermann, 2001; Eichenmueller et al., 2013; Hohenbrink et al., 2016] and may have arisen for different reasons in different species.

Variation in populations and among closely related species may explain the heated debate over how to define “female dominance.” The disparity may actually be a result of fundamentally different underlying phenomena. For instance, Sauther [1993; Sauther et al., 1999] states that “female dominance” in ring-tailed lemurs refers to the combination of female aggression towards males, priority of access to resources, and leadership of group movement, and Overdorff et al. [2005] suggest that this type of female power may only occur in ring-tailed lemurs. This assertion of species differences is well illustrated by the comparison of Kappeler [1993a, b] of 3 lemur species, i.e., ring-tailed lemurs, crowned lemurs, and red-fronted lemurs. Ultimately, he showed that, of the 3 species, female ring-tailed lemurs have the greatest amount of power over males because female ring-tailed lemurs won 100% of conflicts with males, as determined by submission. Female crowned lemurs have a greater amount of power than female red-fronted lemurs because (1) crowned lemurs regularly exhibited male submissive behavior, which was rare in red-fronted lemurs, and (2) only half of the conflicts were undecided as opposed to two thirds in red-fronted lemurs. Here submissive behavior is the scope and regular, rare, half, and two thirds are the amount of power. Females of the two *Eulemur* species were more likely to win by means of aggression than female ring-tailed lemurs. With so many differences in means and the amount of power in these species, one might predict that the base and scope of power differ among them as well. Indeed, the findings of Norscia and Palagi [2015, 2016] suggest differences in the amount and scope of power in ringtails and *Eulemur*, as well as sifaka. Hence the power framework can not only help elucidate what researchers have already been claiming by providing a useful set of terms, but the framework also leads to new testable predictions.

Measuring every parameter associated with all 4 of the characteristics of power can be quite daunting. While completely understanding power asymmetries and dynamics should be the goal to which primatologists strive, achieving this ideal will be difficult in many study populations. Researchers can focus, nonetheless, on particular aspects of power. For instance, Voyt et al. [in press] examined 2 potential bases of intersexual power (fighting ability and mating opportunities) in Verreaux's sifaka and found that the base of female power to evoke male submission (scope) changes with age. As researchers endeavor to record the variables pertinent to determining power and to use a common terminology, a more detailed picture will emerge. For example, Hohenbrink et al. [2016] examined some aspects of all 4 characteristics of power in 2 species of *Microcebus* and found that they vary in subtle but important ways. Moreover, simply recording the direction of submission, the number of decided aggressive conflicts won, or priority of access to resources will continue to provide critical information about power relationships. When only some aspects of power are studied, however, it is important to acknowledge that the results paint only a partial picture of power.

The Next Steps in Studying Female Power in Lemurs

The definition of "female dominance" has been disputed for decades as researchers have attempted to constrain which behaviors are considered most relevant. Rather than debating narrow definitions of dominance that explain only some phenomena, a more fruitful strategy moving forward is to embrace a broader concept of power, expand the discussion of "female dominance in lemurs" to include all types of female intersexual power, and then define the specific characteristics of female power in each species. For instance, the definition of Kappeler [1993a] of "female dominance" excludes all types of power that (1) are based upon coalitions of females against males (female derived dominance) and (2) do not involve the scope of submission. Using this narrow definition, he concluded that the phenomenon only occurs in lemurs and no other mammals. By expanding the concept of female intersexual power rather than constraining it, primatologists can better understand how and why it arises because the uniqueness of female intersexual power in lemurs can be determined empirically rather than by definition.

Despite the extensive data on a growing number of taxa, however, our understanding of "female dominance" in lemurs is still quite limited. The power framework is a useful next step because it expands and organizes our understanding of the existing data, creates a new set of expectations that can be tested, and encourages new kinds of data and new analyses. For instance, recent innovative research associates female dominance with androgens [Charpentier and Drea, 2013; French et al., 2013; Petty and Drea, 2015]. The connection between androgens and the means of aggression is clear but it is less straightforward when examining androgens and other characteristics of power, or even other means (e.g., refusal to act). In other words, a more inclusive concept of power can lead to new questions in lemur socioendocrinology and new evolutionary hypotheses. The power framework is also useful for comparing the "female dominance" phenomenon to "male dominance" and to "codominance" [Lewis, 2018]. By breaking power down into its 4 characteristics, researchers can more accurately determine the similarities and differences of intersexual power across taxa, which in itself will likely lead to new adaptive explanations.

The framework is particularly useful for understanding the effects of seasonality on lemur social relationships because the framework embraces the dynamic aspect of power; power relationships are rarely static [Bernstein, 1981]. Future research should examine which characteristics of power change seasonally, whether they change as a unit or independently, and whether a time lag exists. With such extreme mating seasonality (often just 1 or 2 days of estrus in many species), lemurs are a great group to test the effect of mating opportunities (fertilizable egg) as a base of power and whether that power wanes outside of the mating season. Some species exhibit influxes of males when a female is in estrus [e.g., Verreaux's sifaka: Lewis, 2004]. Researchers can explore whether an increase in female power due to changes in sex ratio is associated with changes in intersexual aggression (means) or any change in the amount of power. With its molecular approach to a broader concept of power, the framework encourages investigation into whether and how power fluctuates across time and contexts.

The relationship between dominance and leverage is currently unresolved, and thus an important future direction is to explore the interaction between dominance and leverage. This review has focused on the extreme forms of power but dominance and leverage actually exist at 2 ends of a continuum [Lewis, 2002]. For example, leverage can be derived from a resource that can be taken by force but using force would decrease the aggressor's fitness (c.f. "winning inappropriately": Hand, 1986). Intersexual relationships in lemurs are ideal for testing how various bases of power interact to produce an overall power relationship. Some bases of power may have more of an impact on overall power. Alternatively, some bases of power may only be associated with particular contexts (amount) or particular means or have a limited scope. Because (1) the existing lemur intersexual power literature is so rich, (2) lemurs exhibit a highly seasonal reproduction [e.g., Wright, 1999; Lewis and Kappeler, 2005], (3) morphological proxies of fighting ability can be readily measured, and (4) some species exhibit groups with highly variable sex ratios, lemur research is well positioned to move the field of power studies forward.

In addition to providing a theoretical structure for understanding intersexual interactions, the power framework provides a much-needed common language for interspecific comparisons that is not clade specific. It also has the potential to be combined with existing classifications. For example, Radespiel and Zimmermann [2001] suggest a possible classification system for understanding "female dominance," where power structures are unambiguously sex dependent, moderately sex dependent, context limited, or unrelated to sex. While it was originally put forth for lemurs, this system can be applied more generally and is not incompatible with the power framework. A lemur species may exhibit seasonal, context-dependent male leverage within a female-biased power structure. For instance, the threat of infanticide is a source (base) of leverage that can be used by males to induce (scope) females to mate with them. As primatologists look for, and document, sex-dependent power and all of its characteristics, we may find that unambiguous sex-dependent power is rare, even in lemurs.

Conclusion

The phenomenon known as "female dominance" is better understood within the broader umbrella of female power. Female intersexual power is more than female dominance and occurs in more than just lemurs [Ralls, 1976; Smith, 1982; Jolly, 1984;

Fig. 3. Power includes both dominance and leverage but exactly how they interact is currently unknown. However, as the ability for physical coercion decreases, market forces likely exert an increasing influence on power dynamics. The monomorphism seen in many lemurs thus may at least partially explain the common occurrence of female-biased power structures in this clade.

Wright, 1993; Dunham, 2008; Holenkamp and Engh, 2009; French et al., 2013; Lewis, 2018]. It may be based on one or more asymmetries in an intersexual dyad, and this asymmetry can influence relationships in various ways. In lemurs, female intersexual power is often associated with monomorphism or female-biased sexual dimorphism [Richard, 1987; Kappeler, 1993a; Dunham, 2008; Lewis, 2018], whereas in most primates males are able to dominate females because of male-biased sexual dimorphism [Richard, 1987]. Hence, an important question to address for understanding female power in lemurs is the presence of monomorphism [see also Dunham, 2008]. Many lemur societies also exhibit a male-biased sex ratio [Jolly, 1984; Richard, 1987; van Schaik and Kappeler, 1993, 1996; Kappeler, 2000]. This sex bias differs from many anthropoids, which exhibit a female-biased sex ratio [Mitani et al., 1996; van Schaik and Kappeler, 1996; Kappeler, 2000], and creates a situation where market effects are likely to play an important role in intersexual social relationships [Noë et al., 1991; Noë and Hammerstein, 1994, 1995]. As the ability for physical coercion decreases, market forces increasingly influence power dynamics (Fig. 3). The power framework directs research on lemur social relationships towards exploring multiple possible bases of power.

“Female dominance” is greatly clarified with the new terminology and by placing it within the broader concept of power. Some species have female dominance, some female leverage, and some have both. Until the base of power is known, the term “female dominance” should be avoided and the term “female power” should be used. As researchers explicitly study the 4 characteristics of power as they relate to lemurs, female power in all of its forms can be better understood in and of itself in species with both female-biased and male-biased power structures. Importantly, the goal of this review is not to promote any one adaptive explanation, proximate or ultimate, although the framework is particularly useful for identifying potential proximate causes. The framework embraces a broad concept of power while simultaneously utilizing a very molecular approach. Each characteristic can be examined at the proximate and ultimate level, and even variation within each characteristic can be examined. This review instead attempts to show how use of the power framework facilitates the endeavor of solving the evolutionary puzzle.

The framework applied here uses a human model of power to expand the concept of power in nonhuman societies. This expansion of the concept not only provides the much needed terminology to study female intersexual power more precisely, but it also leads to new predictions about when, how, and why female intersexual

power arises in lemurs and other animals. Extensive existing lemur research conducted by numerous primatologists over the decades maintains its high level of value as it fits easily within the power framework. This review has attempted to show how this vast body of literature can be reconceptualized to more clearly show where species, populations, and even dyads differ. Importantly, application of the power framework reframes the debate about “female dominance” in lemur societies but it does not advocate for any particular proximate or ultimate explanation for why the phenomenon occurs. By placing the phenomenon of “female dominance” in lemurs within the broader concept of power, the study of lemur social behavior can become less intellectually isolated and more fully integrated into the existing ethological literature [Lewis, 2018].

Acknowledgement

The ideas in this paper were greatly improved by discussions with C. van Schaik, D. Brockman, K. Glander, C. Kirk, K. Smith, M. Munger, and D. Overdorff. C. Kirk and R. Lawler and 6 anonymous reviewers provided helpful comments on this paper.

Statement of Ethics

The author has no ethical conflicts to declare.

Disclosure Statement

The authors have no financial interests or nonfinancial relationships that may be interpreted as having influenced the writing of this paper to disclose.

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