Evolution of Cooperation among Mammalian Carnivores and Its Relevance to Hominin Evolution

by Jennifer E. Smith, Eli M. Swanson, Daphna Reed, and Kay E. Holekamp

Anthropological theory suggests direct links between the origins of cooperation in hominins and a shift toward an energy-rich diet. Although the degree to which early hominins ate meat remains controversial, here we reevaluate the notion, originally suggested by Schaller and Lowther in 1969, that mammalian carnivores can shed light on human origins. Precisely when cooperation evolved in hominins or carnivores is unknown, but species from both groups cooperatively hunt large game, defend resources, guard against predators, and rear young. We present a large-scale comparative analysis of extant carnivore species, quantifying anatomical, ecological, and behavioral correlates of cooperation to determine whether metabolic rate, body and relative brain size, life history traits, and social cohesion coevolved with cooperation. We focus heavily on spotted hyenas, which live in more complex societies than other carnivores. Hyenas regularly join forces with kin and nonkin to hunt large antelope and to defend resources during intergroup conflicts and disputes with lions. Our synthesis highlights reduced sexual dimorphism, increased reproductive investment, high population density, fission-fusion dynamics, endurance hunting of big game in open habitats, and large brains as important correlates of cooperation among carnivores. We discuss the relevance of our findings to understanding the origins of cooperation in hominins.

The evolutionary trajectory from hominin to humanity, from small-brained australopithecine to encephalised Homo erectus, began 2.6 Ma with an interest in meat. (Bunn 2006:205)

The evolutionary origins and maintenance of cooperation pose an evolutionary puzzle for anthropologists and biologists (reviewed by Clutton-Brock 2009*a*; Dugatkin 2002; Melis and

Semmann 2010; Noë 2006; Nowak 2006; Queller 1985; West, El Mouden, and Gardner 2011; West, Griffin, and Gardner 2007). Nevertheless, solving this mystery remains central to understanding the unprecedented capacity for human range expansion into an extraordinary diversity of habitats across the globe (Bingham 1999).

Although there is much ongoing debate about the precise composition of the diet of early hominins (e.g., degree to which it included nuts, tubers, and protein and fat from animals), most current anthropological scenarios suggest a direct link between a transition toward eating a high-quality diet and the evolution of cooperation in hominins (e.g., Aiello and Wheeler 1995; Bramble and Lieberman 2004; O'Connell, Hawkes, and Blurton Jones 1999; O'Connell et al. 2002; Pontzer 2012; Wrangham et al. 1999). Although the precise timing of events remains elusive, the suite of cooperative behaviors that have been suggested to coevolve with a rich hominin diet includes group hunting, defense of food and space, protection from predators, and care of young (e.g., Bunn 2006; Bunn and Kroll 1986; Byrne 1995; Grove 2010; Hart and Sussman 2009; Milton 1999; Ungar 2012; Wrangham et al. 1999).

Three major ecological models proposed to explain hom-

Jennifer E. Smith is an Assistant Professor of Biology at Mills College (5000 MacArthur Boulevard, Oakland, California 94613, U.S.A. [jesmith@mills.edu]). **Eli M. Swanson** is a PhD candidate in the Zoology Department and Ecology, Evolutionary Biology, and Behavior (EEBB) Program (203 Natural Science Building, Michigan State University, East Lansing, Michigan 48824, U.S.A.). **Daphna Reed** is an undergraduate in the Institute for Society and Genetics, University of California, Los Angeles (Box 957221, 1323 Rolfe Hall, Los Angeles, California 90095-7221, U.S.A.). **Kay E. Holekamp** is a Distinguished University Professor of Zoology and Director of the EEBB Program (203 Natural Science Building, Michigan State University, East Lansing, Michigan 48824, U.S.A.). This paper was submitted 12 XII 11, accepted 6 VII 12, and electronically published 13 XI 12.

inin evolution are currently prevalent in the literature. The first two models focus on the importance of eating a calorie-rich diet but differ in their emphasis on the nature of the calorie-rich diet and how foraging shaped the origins of cooperation (reviewed by Pontzer 2012). The "hunting-scavenging" model emphasizes the importance of energy-rich meat and bone marrow in the hominin diet. Some variants of this model propose that natural selection favored cooperation among individuals that hunted large game using persistence running (also called "cursorial hunting"), while others emphasize cooperation and food sharing with younger, less able or less successful kin (Aiello and Wheeler 1995; Bramble and Lieberman 2004; Kaplan et al. 2000). The second model is the "underground storage organ" (USO) model that emphasizes gathering USOs (such as tubers), food sharing, and sometimes cooking (O'Connell, Hawkes, and Blurton Jones 1999; Wrangham et al. 1999). It suggests that a shift toward an arid climate favored exploitation of these calorie-rich foods and emphasizes the role of elders in provisioning younger kin. Where these models posit increased energetic benefits from intergenerational cooperation, arguments can be made for the coevolution of increases in the length of lactation, gestation, and longevity as well as increases in neonate and adult body mass and daily energy expenditure but a decrease in sexual dimorphism. In contrast to these two diet-related hypotheses, the "predator protection" hypothesis suggests that cooperation evolved because of intense predation by large-bodied carnivores and that selection favored an increase in relative brain size to permit complex forms of cooperative defense required to outwit predators (Hart and Sussman 2009).

Relevance of Extant Mammalian Carnivores to Testing of Ecological Models

Foundational inquiries about the social lives of early hominins focused primarily on nonhuman primates (e.g., Reynolds 1966; Washburn and Devore 1961), and primate research continues to be an import source of inference today (e.g., Fuentes, Wyczalkowski, and MacKinnon 2010). Nonetheless, Schaller and Lowther (1969) provided the transformative insight that the ecologies of modern hunter-gathers—and by inference those of early hominins—might closely resemble those of extant carnivores. Schaller and Lowther (1969:308) proposed that "it might be more productive to compare hominids [now hominins] with animals which are ecologically but not necessarily phylogenetically similar, such as the social carnivores." This landmark paper was followed by several pioneering studies on wild carnivores (e.g., Kruuk 1972; Mech 1970; Schaller 1972). Ongoing research continues to reveal new complexities about the social lives of carnivores. Because the behavioral traits proposed to be important for hominin evolution are also salient features in the lives of social carnivores, study of this taxonomic group might indeed offer important insights.

Here we use the term "carnivore" to refer to those extant species of mammals belonging to the order Carnivora regardless of their dietary niche. The order Carnivora arose during the late Paleocene from a radiation of mammals whose diet was comprised primarily of meat (Wilson and Mittermeier 2009). Importantly, however, extant carnivores occupy a vast range of habitats and many ecological niches; species in this order belong to dietary classes that include herbivores, insectivores, omnivores, piscivores, and carnivores (Wilson and Mittermeier 2009). Although the extent to which early hominins ate meat is the subject of ongoing debate, there is growing evidence that additional aspects of hominin sociality might resemble extant mammalian carnivores. For instance, as is the case for many mammalian carnivores (reviewed by Palomares and Caro 1999), early hominins also were likely hunted or otherwise killed by carnivores (Hart and Sussman 2009). The evolution of cooperative defense of food and space, breeding, and protection from predators as well as fission-fusion dynamics (see below) in the order Carnivora suggests that this taxonomic group continues to offer underexploited opportunities for testing hypotheses relevant to the evolution of hominins regardless of the precise diets of early hominins.

Evidence that early hominins included some meat in their diet from the Pleistocene onward and perhaps earlier becomes increasingly common as we move forward in the archaeological record. Although stone tools may have been used primarily for processing vegetative foods (Grine and Fleagle 2009), discoveries of fossilized bones with butchery marks suggest early hominins might have used stones to remove energy-rich flesh from the carcasses of large mammals by 2.5–3.4 Ma (McPherron et al. 2010; but see Domínguez-Rodrigo, Pickering, and Bunn 2010, 2011). Moreover, sharp-edged cutting tools and cut-marked animal bones at Gona, Ethiopia (Semaw et al. 1997), and stone caches at Olduvai, Tanzania (Bunn and Kroll 1986; Potts and Shipman 1981), suggest hominin butchery and consumption of skeletal muscle and tissues by 2.6 Ma (Potts 2012). By 2.5–2.0 Ma, stone tool transport (e.g., carrying stones hundreds of meters) for extractive foraging permitted access to new resources (Potts 2012). Molar morphology and microwear data indicate dietary expansion to include items with mechanical properties consistent with those of animal fat and protein around 2.0–1.8 Ma (Ungar 2012). Fauna in archeological contexts suggest persistent foraging on game by 2.0–1.5 Ma (Potts 2012).

Nonetheless, the debate continues regarding how early hominins acquired prey animals (Bunn and Kroll 1986; Potts and Shipman 1981). Were prey run to exhaustion, ambushed at short range, or passively scavenged from carcasses abandoned by mammalian carnivores (Bramble and Lieberman 2004; Bunn and Pickering 2010; Domínguez-Rodrigo and Pickering 2003; Shipman 1986)? Which physical, ecological, and social factors facilitated the evolutionary leap from *Australopithecus* to early *Homo*? To answer these questions, we search here for convergences between early hominin foragers

and extant carnivores (e.g., Finarelli 2010; Finarelli and Flynn 2009).

Our overarching goal is to provide an updated assessment regarding whether the behavior of extant mammalian carnivores is indeed relevant to understanding early hominins irrespective of the degree to which the hominins may have been carnivorous. We draw on a unique combination of new knowledge and new computational tools unavailable to Schaler and Lowther in the 1960s to reevaluate this notion. We first review the current literature on cooperation in mammalian carnivores, focusing primarily on new data on one highly cooperative species, the spotted hyena *Crocuta crocuta*, to update the original framework presented by Schaller and Lowther (1969). Then we perform a large-scale comparative analysis on extant species from Carnivora to identify variables permitting and constraining cooperation. Finally, we consider these findings in light of current ecological models proposed to explain the evolutionary origins for cooperation in the genus *Homo*.

Feeding Competition and Fission-Fusion Dynamics in Extant Social Carnivores

Most (85%–90%) terrestrial mammalian carnivores are solitary, interacting exclusively with their mates and offspring or alien conspecifics at territorial boundaries (reviewed by Holekamp, Boydston, and Smale 2000). Sociality appears to have arisen as a derived trait because the ancestral condition within most carnivore families is to live solitarily (Dalerum 2007). Group life permits individuals to detect or evade predators or to improve their ability to acquire or defend resources (Johnson et al. 2002). In some species of carnivores, gregariousness itself may have been favored by improved energy intake (Creel and Macdonald 1995; Dalerum 2007). Some of the best-studied cooperative hunters include spotted hyenas (Holekamp et al. 1997; Kruuk 1972; Smith et al. 2008), lions (*Panthera leo*; Packer and Ruttan 1988; Packer, Scheel, and Pusey 1990; Scheel and Packer 1991), African wild dogs (*Lycaon pictus*; Creel 1997; Creel and Creel 1995), and wolves (*Canis* spp.; Mech 1970). For these species, prey animals represent large, ephemeral packets of energy-rich food that occur unpredictably in space and time. Often several hunters may be required to secure a single prey animal, each of which may weigh hundreds of kilograms. Although lions assume specific roles when hunting in groups (Heinsohn and Packer 1995; Stander 1992), there is no evidence that lions or other carnivores rely on advanced planning to capture prey (Holekamp, Boydston, and Smale 2000). For example, even though spotted hyenas are efficient hunters and directly kill 60%–95% of the food they eat, these carnivores appear to follow simple rules when hunting together, such as "move wherever you need to in order to keep the selected prey animal between you and another hunter."

Given the nature and distribution of their food resources, contest competition at ungulate carcasses is often intense among carnivores, and access to food is critical to individual fitness (e.g., Carbone et al. 2005; Courchamp, Rasmussen, and Macdonald 2002; Holekamp, Smale, and Szykman 1996). Even within the most stable groups of carnivores, intense competition disrupts grouping behavior (reviewed by Aureli et al. 2008; Holekamp, Boydston, and Smale 2000; Smith et al. 2008). Whereas individual African wild dogs living in cohesive groups maximize per capita energy gain when hunting in large packs (Creel and Creel 1995), individual spotted hyenas, especially low-ranking ones, accrue the greatest energetic benefits when they hunt alone (fig. 1; Smith et al. 2008). Hunting in groups larger than an optimal size is also costly to lions (Packer, Scheel, and Pusey 1990).

Intense competition leads most social carnivores to live in groups structured by fission-fusion dynamics in which individuals regularly break up into small foraging parties when food is scarce and gather again when food is abundant (reviewed by Smith et al. 2008). For example, dholes (*Cuon alpinus*; Venkataraman, Arumugam, and Sukumar 1995), white-nosed coatis (*Nasua narica*; Gompper 1996), European badgers (*Meles meles*; Kruuk and Parish 1982), and kinkajous (*Potos flavus*; Kays and Gittleman 2001), as well as spotted, brown (*Hyaena brunnea*), and striped (*Hyaena hyaena*; Kruuk 1976; Mills 1990; Smith et al. 2008; Wagner 2006) hyenas temporarily leave (fission from) their companions to avoid competitors when feeding. Members of each of these species also regularly meet up again and spend time with (fusion with) conspecifics when the benefits of group living are high (reviewed by Aureli et al. 2008; Creel and Macdonald 1995).

Maternal Capital, Tolerance, and Coalitions in Hyenas and Other Carnivores

Social Complexity of Spotted Hyenas

Spotted hyenas represent a well-studied species; these hyenas live in societies that are considerably more complex than those of other gregarious carnivores (Drea and Frank 2003; Holekamp, Sakai, and Lundrigan 2007). In fact, their social lives are strikingly similar to those of many species of Old World monkeys. Spotted hyenas are an interesting species in which to investigate the evolution and mechanisms promoting cooperation in carnivores. Most social carnivores—including wolves, social mongooses such as meerkats (*Suricata suricatta*), lions, and wild dogs—live in small groups in which adult members of each sex are closely related to one another (Clutton-Brock 2002; Creel and Creel 1991). In contrast, spotted hyenas reside in large permanent social groups called "clans" (Kruuk 1972), consisting of up to 90 or more individuals with low mean relatedness (Holekamp et al. 2012).

Hyena clans are strikingly similar in their size, composition, and hierarchical organization to troops of Old World monkeys. Like troops of macaques, baboons, and vervet monkeys, hyena clans contain multiple adult males and multiple matrilines of adult female kin and their offspring (Frank 1986).
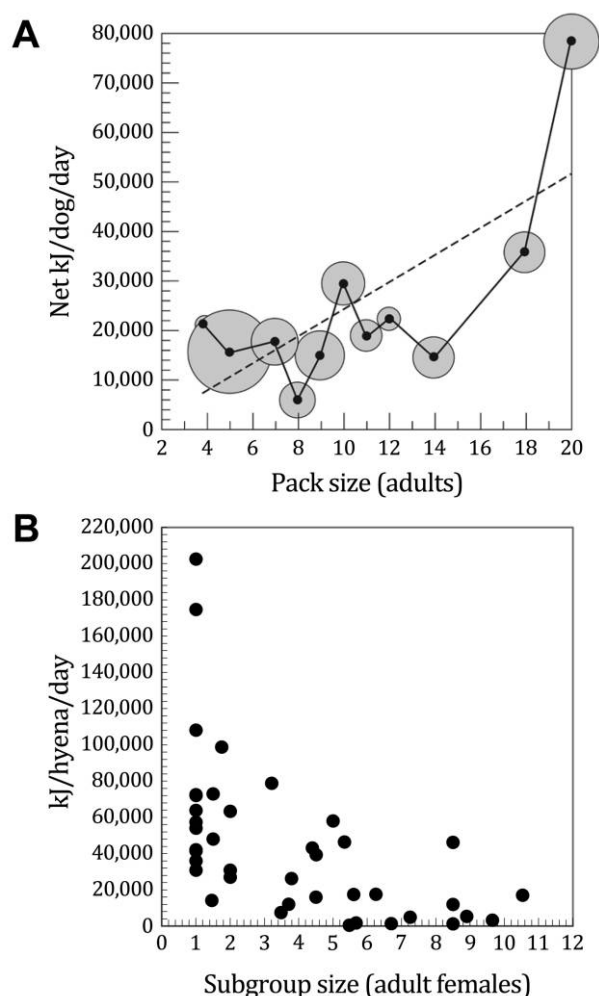
Figure 1. Per capita energy gain as a function of foraging group size among adult (*A*) African wild dogs *Lycaon pictus* (reprinted from Creel 1997 with permission from Elsevier) and (*B*) spotted hyenas *Crocuta crocuta* (reprinted from Smith 2008 with permission from Elsevier). Points in *A* represent mean numbers of wild dogs, with point size proportional to the number of observations, and the dashed line represents the linear regression; points in *B* represent individual hyenas found in subgroups of various sizes.

As in these species of monkeys, individual hyenas within each clan can be ranked in a linear dominance hierarchy based on outcomes of agonistic interactions (Frank 1986; Kruuk 1972; Smith et al. 2008; Tilson and Hamilton 1984). Dominance relationships are extremely stable across years and ecological contexts (Frank 1986; Smith et al. 2011), but rank itself is not correlated with size or fighting ability (Engh et al. 2000). Instead, as in many monkeys (e.g., Chapais 1992; Cheney 1977; Horrocks and Hunte 1983; Walters 1980), coalition formation plays an important role in acquisition and maintenance of social rank among spotted hyenas (Engh et al. 2000; Holekamp and Smale 1993; Smale, Frank, and Holekamp 1993; Smith et al. 2010; Zabel et al. 1992).

During an early stage of ontogeny, each hyena comes to understand its own position in its clan's dominance hierarchy (Holekamp and Smale 1993; Smale, Frank, and Holekamp 1993). This process requires a type of associative learning called "maternal rank inheritance" in which the mediating mechanisms are virtually identical to those operating in cercopithecine primates (Engh et al. 2000; Holekamp and Smale 1991). In fact, because of their aptitude for social learning, spotted hyenas are capable of solving cooperation problems in captivity (Drea and Carter 2009).

Maternal Capital Influences Reproductive Success of Spotted Hyenas

Recent data suggest that maternal capital, in terms of both social allies and energy reserves, has important life history consequences for mammals (Bribiescas, Ellison, and Gray 2012; Isler and van Schaik 2012; Wells 2012). Social capital of mothers clearly is important for nonhuman primates such as in baboons *Papio* spp. (Silk, Alberts, and Altmann 2003; Silk et al. 2009). Similarly, data from spotted hyenas living in "baboon-like" societies suggest that maternal phenotype and maternal rank in particular have profound effects on female reproductive success (Holekamp et al. 2012). Support networks, especially among maternal kin, endure across the life span despite ecological constraints imposed on them by fluctuating availability of resources (Holekamp et al. 2012). Because social status determines priority of access to kills, high rank has enormous effects on hyenas' net energy gain (Hofer and East 2003; Smith et al. 2008). Birthrates and survivorship are so much greater for high- than for low-ranking hyenas (Watts et al. 2009) that dominants tend to have many more surviving kin in the population than do subordinates (Holekamp et al. 2012). As a result of these large networks of allies, high-ranking hyenas have the most social capital (e.g., Smith et al. 2010; Van Horn et al. 2004).

Compared with most other carnivores, spotted hyenas have a prolonged period of fetal development, are of unusually large mass at birth, and are remarkably precocial; they are born with open eyes and fully erupted canine and incisor teeth (Drea and Frank 2003). Nevertheless, cubs undergo an exceptionally long period of nutritional dependence after birth, and dependence on the mother continues long after cubs are weaned because their feeding apparatus develops very slowly, and this handicaps their feeding (Watts et al. 2009). Maternal capital is extremely influential in determining the pace of development and reproduction (Holekamp et al. 2012). Cubs usually nurse for over a year and may nurse for up to 2 years. Because it takes juveniles years of practice to become proficient at hunting and at cracking through bone to access marrow (Holekamp et al. 1997; Mills 1990; Tanner et al. 2010), mothers use coalitionary aggression to help their offspring gain access to ungulate kills long after weaning.

Among nonkin, adult female hyenas preferentially tolerate feeding at shared kills by those nonkin with which they as-

sociate most often (Smith, Memenis, and Holekamp 2007). Dominants engage in reciprocal trading for services provided by subordinates, such as help hunting and defense of territory boundaries. In exchange, dominants withhold aggression from those unrelated hyenas with which they maintain the strongest relationships. In this respect, spotted hyenas differ from most carnivores, because most species of mammalian carnivores allow only their kin to feed at kills. For example, lions and African wild dogs (Creel and Creel 1995; Packer, Pusey, and Eberly 2001) only hunt cooperatively and share meat with relatives or mates (reviewed by Clutton-Brock 2009*b*). Individual differences in the extent to which spotted hyenas tolerate one another in feeding contexts suggest some degree of meat sharing among unrelated individuals (Smith, Memenis, and Holekamp 2007).

Although all adult female hyenas breed, rates of reproduction vary based on social rank and prey density (Frank, Holekamp, and Smale 1995; Hofer and East 2003; Holekamp, Smale, and Szykman 1996). Rank-related variation in females' ability to access food (e.g., Frank 1986; Smith et al. 2008) has striking effects on the growth rates of their cubs; high-ranking cubs grow faster than their low-ranking peers (Hofer and East 1996, 2003). Dominant females start breeding at younger ages than do subordinates (Frank, Holekamp, and Smale 1995; Holekamp, Smale, and Szykman 1996; Watts et al. 2009). Interestingly, above and beyond the effects of rank, larger female hyenas produce more offspring over their lifetimes than do smaller females, suggesting that large body size confers an evolutionary advantage (Swanson, Dworkin, and Holekamp 2011).

Evolutionary Forces and Mechanisms Promoting Intragroup and Intergroup Coalitions

As in most monkeys and great apes, spotted hyenas bias their social support toward kin during intragroup disputes (reviewed by Smith et al. 2010). We recently elucidated the evolutionary forces favoring intragroup coalitions among adult female spotted hyenas (Smith et al. 2010). First, we tested the prediction from kin selection theory (Hamilton 1964*a*, 1964*b*) that individuals should bias helpful behavior toward relatives and harmful behavior away from relatives if doing so provides inclusive fitness benefits. Second, we examined the hypothesis that natural selection might favor interventions on behalf of nonkin via reciprocal altruism if the projected future benefits to the donor outweigh the immediate costs (Trivers 1971). Finally, we asked whether females gain direct benefits from cooperative acts through better access to food or by reinforcing the status quo (Brown 1983; Connor 1995; West-Eberhard 1975). As predicted by kin selection theory, female spotted hyenas support close maternal and paternal kin most often, and the density of cooperation networks increases with genetic relatedness. As is the case in most animal societies (reviewed by Clutton-Brock 2009*a*), we found no evidence of reciprocal altruism (e.g., enduring alliances based on re-

ciprocal support among nonkin). Instead, hyenas gained direct benefits from joining forces to attack subordinates and monitored the number of dominant bystanders in the "audience" at fights to minimize costs to themselves. Taken together, the combined evolutionary forces of kin selection and direct benefits appear to favor flexible decisions regarding whether or not adult female hyenas intervene in fights (Smith et al. 2010).

Local ecology determines whether hyena clans maintain well-defined and vigorously defended territories (e.g., Masai Mara, Kenya; Boydston, Morelli, and Holekamp 2001) or more permeable territorial boundaries with considerable range overlap and tolerance of outsiders (e.g., the Kalahari Desert; Mills 1990). Populations that engage in territory defense form large intergroup coalitions against members of other social groups. These intergroup disputes over territory boundaries or kills may involve up to 56 group mates joining forces against a common enemy (fig. 2; Smith et al. 2008). Individuals within hyena clans are on average more closely related to one another than to individuals belonging to neighboring clans, but relatedness among hyena clan members is low (Van Horn et al. 2004). Thus, as in chimpanzees (e.g., *Pan troglodytes*; Goldberg and Wrangham 1997), spotted hyenas on average derive large net direct fitness benefits from joining forces with large numbers of nonrelatives during intergroup conflicts despite the risk of serious injury or death (Boydston, Morelli, and Holekamp 2001; Henschel and Skinner 1991; Hofer and East 1993; Kruuk 1972; Mills 1990). Several other social carnivores, including white-nosed coatis (*Nasua narica*; Gompper, Gittleman, and Wayne 1998) and gray wolves (*Canis lupus*; Lehman et al. 1992), also engage in lethal intergroup conflicts at territorial borders. However, in contrast to most social carnivores who only join forces with genetic relatives during intergroup conflicts (reviewed by Clutton-Brock 2009*b*), spotted hyenas do so with large numbers of unrelated group mates.

Whereas both cognitive and noncognitive (emotional and temperamental) factors promote cooperation and tolerance in living chimpanzees and humans (Hrdy 2009; Melis and Semmann 2010; Tomasello et al. 2005), all available evidence to date suggests that cooperation among extant carnivores is facilitated by noncognitive mechanisms. For example, greeting ceremonies facilitate intra- and intergroup cooperation among hyenas, helping potential allies to reach the same motivational state before cooperating (Smith et al. 2011). Greetings occur when two hyenas stand parallel to one another and sniff each others' anogenital regions (East, Hofer, and Wickler 1993; Kruuk 1972). These signals allow hyenas to quickly confirm relationship status in a society in which group members spend much of their time apart (Smith et al. 2011). Similarly, in African wild dogs (Creel 1997; Creel and Creel 2002) and gray wolves in North America (Mech 1970), greetings function to promote group hunting.

Because cooperation is vulnerable to cheaters, theory predicts that punishment and threats should evolve, but there is
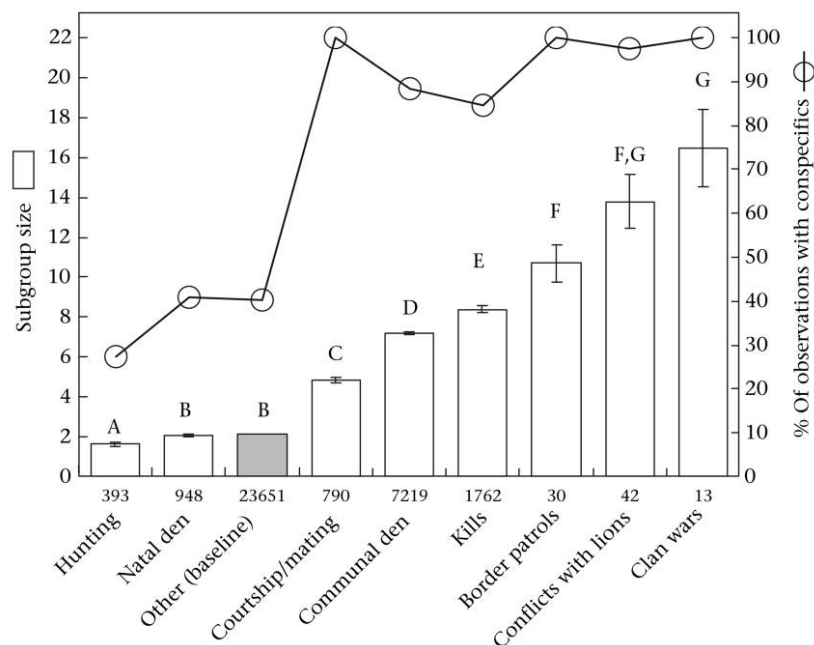
Figure 2. Mean ± SE subgroup size (left vertical axis, histogram bars) and proportion of observations in which spotted hyenas were found in subgroups containing more than one individual (right vertical axis, circles) in each of the following contexts: (1) hunting: one or more resident hyenas chased a prey animal for at least 50 m, regardless of the outcome; (2) natal den: one or more resident hyenas observed at an isolated den used by only one mother for shelter of a single litter until her cubs are 2–5 weeks old; (3) kills: one or more resident hyenas observed feeding on at least one fresh ungulate carcass; (4) courtship/mating: immigrant male(s) direct mating tactics toward a sexually mature female; (5) communal den: one or more resident hyenas observed at a den used concurrently by several litters; (6) border patrols: residents engaged in high rates of scent marking and defecation along territory boundaries; (7) clan wars (intergroup conflicts, called "clan wars" by Kruuk 1972): agonistic interactions between resident and alien hyenas at territory boundaries; (8) conflict with lions: agonistic interactions observed between resident hyenas and at least one lion; (9) other: none of the contexts above applied. Sample sizes, shown below each bar, represent numbers of observation sessions assigned to each context. Different letters indicate statistically significant differences between contexts after correcting for multiple testing. The shaded bar represents the baseline value of subgroup sizes occurring in "other" sessions against which other groups were compared. Figure adopted with permission from Smith et al. (2008).

limited evidence of effective threats against "free riders" among carnivores (reviewed by Cant 2011). Spotted hyenas use unprovoked aggression to reinforce dominance status, yet there is no evidence that these attacks promote coalition formation (Engh et al. 2005; Smith et al. 2010). Lions similarly fail to punish cheaters in the context of group hunting (Packer, Pusey, and Eberly 2001) despite their ability to recognize laggards (Heinsohn and Packer 1995). Finally, although banded mongooses *Mungos mungo* and meerkats do enforce cooperative breeding, the threat of eviction is ineffective at preventing cheating in the first place (Cant et al. 2010; Clutton-Brock, Hodge, and Flower 2008).

Testing Ecological Models Using Data from Extant Mammalian Carnivores

We next used phylogenetic comparative methods to evaluate the extent to which each of the competing ecological models of human evolution explains cooperation among extant mam-

malian carnivores. To test competing hypotheses, we assessed the extent to which anatomical, life history, ecological, or behavioral variables coevolved with cooperation among all species ($N = 87$) of carnivores for which all of the salient predictor variables of interest were currently available. This data set (see CA+ online supplement A) captures the diverse suite of social and ecological traits exhibited by members of the order Carnivora. Whenever possible, we extracted all data for a single variable (e.g., diet or forms of cooperation exhibited) from the same source.

Forms of Cooperation Exhibited by Carnivores

We based the current analysis on reports from the literature to calculate a composite score of cooperation by counting and summing the number of different forms of cooperation exhibited by each species from among the following possibilities: (1) alloparental care, (2) group hunting, (3) intragroup coalition formation, (4) coalition formation during intergroup

contests or warfare among conspecifics, and (5) cooperative protection from predators. Most cooperation data were extracted from Creel and Macdonald (1995). Intragroup coalition data were from Smith et al. (2010).

Each of our five cooperation types was assigned a value of 0 if it did not occur and 1 if it did occur in a particular species. The only exception to this rule was alloparenting; following Creel and Creel (1991), intermediate species were assigned a score of 0.5 for alloparenting if they shared a communal den (e.g., home base at which young born to more than one mother are raised) but did not engage in true alloparental care such as allonursing or provisioning of the offspring of others. Although this composite "cooperation score" assumes values ranging from 0 to 5, in some analyses, we simply asked whether or not a species engaged in any of these five forms of cooperation.

Alloparental care is defined here as all aspects of care in which individuals guard, groom, carry, play with, feed, or nurse the offspring of others (Creel and Creel 1991). We define group hunting as concurrent attack by more than one conspecific directed toward a selected prey item regardless of its outcome or fitness consequences (Holekamp et al. 1997). Coalition formation occurs when two or more individuals join forces to direct aggression toward the same target(s). Intragroup coalitions are directed toward group mates, whereas intergroup coalitions are directed toward conspecifics belonging to a different social group. Cooperative defense against predators includes mobbing of predators (e.g., group members collectively fend off potential predators by attacking them) or cooperative vigilance, defined here as any behavioral adjustments that reduce the risk of predation for members of the group.

Ecological Predictors of Cooperation

We defined two binary variables based on diet. First, we categorized species as "meat eaters" using an absolute definition based on whether their diet was comprised mainly of any form of meat, including small prey (e.g., rodents, birds). "Meat eaters" excluded primarily insectivorous, omnivorous, piscivorous, or herbivorous species. Second, we inquired whether species with diets comprised mainly of large vertebrate prey (>10 kg; Gittleman 1989) had the highest cooperation scores. Habitat types increased in vegetative cover from open (e.g., savannah) to mixed (e.g., woodland savannah) to closed (e.g., forest) habitats. Population density was the number of individuals per square kilometer.

Behavioral Predictors of Cooperation

Home range sizes were average values for adults of both sexes. We also assigned a binary variable based on whether or not a species hunted cursorially regardless of hunting group size. Cursorial hunters were defined as carnivores that primarily used endurance to exhaust targets by chasing them for long distances before capturing them. Noncursors were those species that relied on stealth while stalking and capturing prey at short distances or that displayed no hunting whatsoever. Finally, we assigned a cohesion index to reflect the increasing degree of sociality for each focal species ranging from (1) solitary (only with conspecifics for mating), (2) pair living (stable bond between adult male and female of the same species), (3) fission-fusion dynamics, and (4) obligately gregarious (always found in close proximity to conspecifics).

Anatomical and Physiological Predictors of Cooperation

Sexual dimorphism was measured as the body mass ratio of adult males to adult females. We corrected brain volume (mm^3) for body size by taking the residuals from phylogenetically corrected regressions of log-transformed brain volume on log-transformed mass. We used basal metabolic rates corrected for body mass as a measure of energy expenditure because existing field metabolic data are rarely available for carnivores.

Life History Predictors of Cooperation

Longevity was the maximum life span (in years) in the wild for each species. Gestation length was the number of days between conception and birth. Litter size, a measure of reproductive investment, was the mean number of offspring born in a single litter. Neonate mass was offspring weight at birth (kg) corrected for adult mass. Lactation duration was the mean number of days between birth and cessation of lactation in nursing females, and did not include subsequent periods of offspring dependence.

Comparative Methods and Phylogenetic Generalized Least Squares Regression

Phylogenetic comparative methods represent powerful tools to study adaptation because they account for potential autocorrelation due to shared evolutionary history (e.g., Clutton-Brock and Harvey 1977; Felsenstein 1985; Gittleman and Luh 1992; Swanson et al. 2006). We considered shared ancestry of these 87 species by building a phylogeny primarily based on Bininda-Emonds et al. (2007) and adjusting some relationships based on updated phylogenies or phylogenies focused on smaller taxonomic subgroups (Finarelli 2008; Flynn et al. 2005; Gottelli et al. 1994; Johnson et al. 2006; Koepfli et al. 2006, 2007, 2008; Patoua et al. 2009; Perini, Russo, and Schrago 2009; Sato et al. 2009; Yoder et al. 2003). We resolved polytomies wherever possible, assigning branch lengths of 1×10^{-6} million years ago when branch lengths were not estimated in the source. The only unknown relationships for our phylogeny were those of gray wolves, Ethiopian wolves *Canis simensis*, and coyotes *Canis latrans*; this polytomy was retained for regressions and randomly resolved. The resulting branch lengths were set to 0 for estimation of phylogenetic signal and ancestor reconstruction. Unless stated

otherwise, all analyses were carried out in *R* version 2.12.1 (R Foundation for Statistical Computing 2010).

We estimated the strength of the phylogenetic signal using Blomberg's *K* and tested whether it differed from that predicted by a null model specifying no effect of phylogeny. Specifically, we asked whether *K* estimated for the actual tip arrangement differed from that generated based on 100,000 randomized tip arrangements (Blomberg, Garland, and Ives 2003) using the "picante" package in *R* (Kembel et al. 2010). Our estimate of *K* revealed a moderate phylogenetic autocorrelation that was significantly different from 0 ($K = 0.195$, $Z = -1.58$, $P = .032$).

Phylogenetic generalized least squares regression (PGLS) allows for simultaneous consideration and estimation of the degree of phylogenetic nonindependence using Pagel's lambda (λ). Allowing character evolution through modes other than Brownian motion is one of the main advantages of PGLS over phylogenetically independent contrasts (PIC), another common approach (Felsenstein 1985). Lambda represents a continuous variable for which 0 describes a trait that displays no phylogenetic signal and 1 describes a trait that has evolved under Brownian motion. PGLS is equivalent to PIC for characters evolving under Brownian motion with completely resolved phylogenies (Rohlf 2001).

We built general linear models in a PGLS framework using the "nlme" package in *R* with the composite cooperation score as the response variable and behavioral, ecological, morphological, and life history variables as predictors. We allowed λ to take its Maximum Likelihood Estimate (MLE) in each model. We sequentially entered and dropped all potential explanatory terms, including two-way interactions predicted by our hypotheses. We deemed the candidate model with the smallest Akaike Information Criterion corrected (AICc) for small sample size to be the best while retaining any models with dAICc (difference between the AICc of the best model and the model being considered) values of less than 2 as essentially equivalent (Burnham and Anderson 2002). We obtained statistics for terms removed from our best model by individually adding each term to the minimal model. We only report interaction terms that improved the fit of our best model.

We also used phylogenetic generalized estimating equations (Paradis, Claude, and Strimmer 2004) with a binary response variable to estimate the effect of each predictor on the five binary cooperation variables, including the alloparenting variable for which animals were cooperative if they either alloparented or shared a communal den. Because some MLE estimates of models failed to converge, we estimated univariate models for each predictor variable.

Factors Predicting Composite Cooperation Scores in Carnivora

The MLE for the strength of phylogenetic signal for the final model (λ) was 0.060, suggesting that more closely related species display weakly similar residual errors. Our data set was limited to $N = 57$ and $N = 46$ species, respectively, for which data on longevity in the wild and mass-corrected basal metabolic rates were available. We first inquired whether each of these variables predicted our cooperation score. After correcting for phylogeny, neither longevity ($\beta \pm SE = .139 \pm .564$, $t = .246$, $P = .806$) nor mass-corrected basal metabolic rate ($\beta \pm SE = .098 \pm .521$, $t = .187$, $P = .852$) significantly predicted cooperation across Carnivora. Therefore, we removed these predictors from our final analysis because doing so permitted us to test the remaining variables using the statistical power of our full data set ($N = 87$ species).

We used AICc to recover our best model explaining variation in the cooperation scores among carnivores (table 1). After correcting for the effects of phylogeny, the results from our best model suggest that the greatest number of cooperative behaviors occurs among cursorial hunters in species lacking strong male-biased size dimorphism that have large litters and engage to some extent in hunting big game (table 1). In addition, we have some evidence that species that are tall for their size (e.g., have large relative shoulder heights compared with their mass) display a greater number of cooperative behaviors but only in species that exhibit cursorial hunting (table 1). The only additional model that is statistically indistinguishable from our best model (within 2 dAICc; Burnham and Anderson 2002) further suggests that species living in open habitats engage in a greater number of cooperative behaviors than do those in dense habitats.

In general, the degree of social cohesion was an important determinant of the cooperation score assigned to each species (table 2). We excluded solitary species from this analysis because these animals had no group members with which to cooperate. Even after correcting for multiple testing (Storey and Tibshirani 2003), fission-fusion and obligately gregarious species had significantly greater cooperation scores than did species living in pairs (table 2). Interestingly, our finding that species with fission-fusion lifestyles were just as cooperative as those species always found in cohesive social groups suggests that fission-fusion dynamics permit species to avoid costly competition without sacrificing benefits accruing from cooperation with group mates.

The overall tendency for carnivore species to cooperate was generally low (cooperation score: mean $\pm$ SE = 0.76 ± 0.14, range 0–5, $N = 87$ species), but our results indicate strong variation both within and among families regarding cooperative tendencies (fig. 3). The proportion of species that engaged in each form of cooperation contributing to the cooperation score was also variable. A higher proportion of species participated in alloparental care (0.20 ± 0.04), intergroup contests (0.18 ± 0.04), and group hunting (0.18 ± 0.04) than in cooperative protection from predators (0.13 ± 0.04) or intragroup coalitions (0.07 ± 0.03; CA+ supplement A).

We found no evidence of cooperation among Ailuridae, Ursidae, or Viverridae (fig. 3). In contrast, most members of

Table 1. Best candidate model and the only model <2 dAICc of the best model explaining the composite cooperation score across Carnivora

	β	SE	t	P	AICc	dAICc
Best candidate model:						
Intercept	1.719	.790	2.176	.032	247.2	
Relative shoulder height	−.736	.515	−1.429	.157		0
Cursorial hunting	**1.691**	**.484**	**3.492**	**.001****		
Litter size (log)	**.488**	**.233**	**2.092**	**.040****		
Sexual dimorphism (log)	**−2.162**	**.935**	**−2.312**	**.023****		
Hunting of big game	.462	.297	1.557	.123		
Relative shoulder height: cursorial hunting	4.340	2.414	1.798	.076**		
Only model <2 dAICc of the best model:						
Intercept	1.441	.766	1.881	.064	249.1	
Relative shoulder height	−.718	.478	−1.502	.137		1.9
Cursorial hunting	**1.701**	**.481**	**3.535**	**.001****		
Litter size (log)	.419	.220	1.910	.060**		
Open vs. mixed habitat	.265	.238	1.115	.268		
Open vs. closed habitat	**.763**	**.334**	**2.282**	**.025****		
Mixed vs. closed habitat	.498	.303	1.641	.105		
Sexual dimorphism (log)	**−2.061**	**.916**	**−2.249**	**.027****		
Hunting of big game	.420	.284	1.475	.144		
Relative shoulder height: cursorial hunting	4.237	2.425	1.747	.085**		

Note. dAICc = difference between the AICc of the best model and the model being considered. Addition of these variables failed to improve the fit of our best candidate model: log neonate mass corrected for log adult mass; log brain size corrected for log adult mass, log mass, log duration of lactation, log home range size, log gestation length, and diet. In addition, none of these variables were significant at $\alpha < .10$ when added to the best model. The addition of log population density to the best model did not significantly improve the model, resulting in a model with a dAICc > 2, but the variable was statistically significant when added ($\beta = .125 \pm .061$, $t = 2.07$, $P = .042$). Results of ANOVA for overall habitat for model B are $F = 3.05_{2,80}$, $P = .0846$.
* $\alpha < .10$.
** $\alpha < .05$ (in bold).

Canidae and Herpestidae investigated here were highly cooperative, engaging on average in at least one form of cooperation (fig. 3). In particular, African wild dogs engaged in all five types of cooperation. Lions, cheetahs, and snow leopards (*Panthera uncia*) represent interesting outliers because they are the only cooperative species in the family Felidae. Interestingly, although Hyaenidae had a low mean cooperation score (1.25 ± 1.09, $N = 4$ species), spotted hyenas were far more cooperative than any other members of their family (score = 4.5). Members of Eupleridae, Mephitidae, and Procyonidae had low mean cooperation scores and high variation in the degree of cooperation among family members.

Factors Predicting Each Form of Cooperation in Carnivora

Next, we used univariate tests to consider the effects of each of the predictor variables on each unique form of cooperation. Perhaps because cooperation among carnivores is generally rare, some models failed to converge. Thus, those variables not explicitly stated here as either having a significant or nonsignificant effect on each form of cooperation failed to successfully converge (table 3). Overall, the results of these tests resembled the general patterns found for our composite cooperation scores; the tendency to cooperate generally increased with cursorial hunting of big game (table 3).

This analysis also revealed coevolution of particular traits with each specific form of cooperation. For example, coop-

erative hunters produced larger litters and were less sexually dimorphic than noncooperatively hunting species (table 3). Additional meat gained from cooperative hunting, therefore, appears to permit mothers to increase their investment in current reproductive effort by increasing offspring number and also increasing their own body size relative to that of males. Similarly, mothers of species that cooperatively defended themselves from predators also invested more in current reproduction, weaning offspring at later ages than did mothers of noncooperative species. Species living in dense populations were also the most likely to cooperatively defend themselves from predators, presumably because cooperative defense is mainly a numbers game, requiring a large number of individuals to detect and cooperatively mob predators.

Table 2. Effects of sociality on composite cooperation scores across nonsocial species of Carnivora

Effect	β	SE	t	P
Intercept	.759	.518	1.466	.154
Pair bonding vs. fission-fusion	**1.788**	**.597**	**2.995**	**.015****
Pair bonding vs. obligately social	**1.869**	**.679**	**2.754**	**.015****
Fission-fusion vs. obligately social	.082	.717	.114	.910

Note. Solitary species were excluded from this analysis because these species had no group members with which to cooperate. P values are presented in their corrected form to account for multiple comparisons.
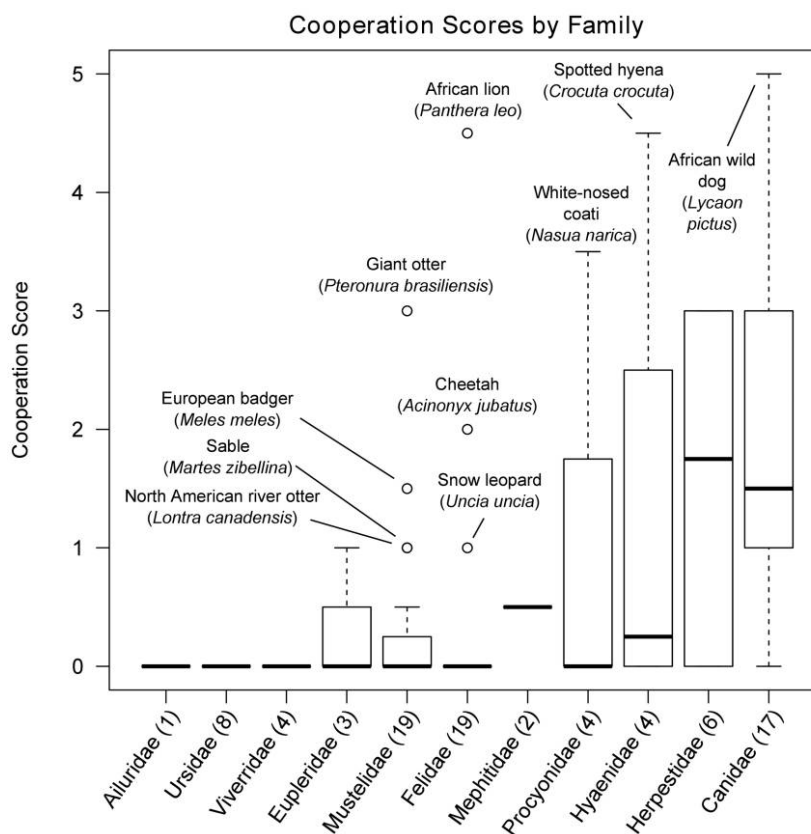** $\alpha < .05$ (in bold).

Figure 3. Cooperation scores among and within families in the order Carnivora. Dark horizontal lines in box plots represent medians, with boxes spanning the middle 50% of the data for each family group. Whiskers stretch to any values that are outside boxes but within 2.5 quartiles from the median. Families are ranked by mean cooperation scores from least cooperative to most cooperative (left to right). Outliers within each family are those values greater than 2.5 quartiles away from the median and are indicated by circles.

Moreover, because predators often aggregate in areas of high prey density (known as the "pantry effect"; Ford and Pitelka 1984), prey in dense populations are under strong selection to evolve effective antipredator behavior. Interestingly, our data suggest that increased brain size might have coevolved with alloparenting, an important finding consistent with comparative data on primates suggesting that alloparenting enhances energy required to sustain expensive neural tissue (Isler and van Schaik 2012).

Evolutionary Losses and Gains of Cooperation in Carnivora

We next used each binary cooperation variable in an ancestor reconstruction using MLE to ask whether the data support a greater likelihood of cooperation arising or being lost across evolutionary transitions within Carnivora. Using the "ape" package in *R*, we estimated ancestral values for the common ancestors of the species present in our phylogeny. For every ancestral node, each signifying the ancestor of a pair of taxa, we estimated the probability that the last common ancestor at that node was cooperative.

Our ancestor reconstruction suggests that extant species of carnivores probably evolved from noncooperative ancestors (fig. 4). Furthermore, the same is generally true at the family level, with the most recent common ancestors of most families displaying very low probabilities for any cooperation with the exceptions of Canidae, Herpestidae, Hyaenidae, and Mephitidae. In particular, Felidae, Ursidae, Eupleridae, and Viverridae exhibit almost no suggestion of cooperative behavior in the family's ancestral state. Interestingly, cooperative species appear in every extant family except for Ailuridae, Ursidae, and Viverridae.

Insights into the Evolutionary Origins of Cooperation in *Homo*

Multiple Factors Coevolve with the Emergence of Cooperation

Overall, the results of comparative analysis revealed that multiple factors are important correlates of cooperation in mammalian carnivores. These data therefore suggest that meaningful links exist between cooperation and changes in

Table 3. Factors influencing the tendency to engage in each of the five forms of cooperation across Carnivora

Factor	β	SE	t	P
Cooperative hunting:[a]				
Hunting of big game	**1.74**	**.63**	**2.75**	**.013****
Litter size (log)	**1.34**	**.59**	**2.26**	**.037****
Sexual dimorphism	−5.02	2.74	−1.83	.084*
Intragroup coalitions:[b]				
Cursorial hunting	**4.23**	**.99**	**4.26**	**.001****
Hunting of big game	**2.77**	**1.14**	**2.43**	**.026****
Litter size (log)	1.82	.91	2.00	.060*
Flesh diet	2.02	1.13	1.78	.092*
Territory defense:[c]				
Cursorial hunting	1.57	.79	1.98	.064*
Predator protection:[d]				
Hunting of big game	**1.87**	**.67**	**2.80**	**.012****
Cursorial hunting	**1.89**	**.80**	**2.40**	**.027****
Population density (log)	**.33**	**.15**	**2.13**	**.047****
Weaning age (log)	.96	.55	1.74	.099*
Alloparenting (none vs. any form):[e]				
Flesh diet	**1.34**	**.50**	**2.68**	**.015****
Hunting of big game	**1.20**	**.53**	**2.27**	**.036****
Relative brain size	1.55	.89	1.74	.099*

Note. Results from generalized estimating equations with each cooperation variable as a binary response for significant variables that converged. Each test given is from a univariate model.

[a] $P > .10$ for relative brain volume, flesh diet.

[b] $P > .10$ for sexual dimorphism, log gestation length, log weaning age, neonate mass corrected for adult mass, relative brain volume.

[c] $P > .10$ for log home range, sexual dimorphism, log litter size, log population density, log gestation length, relative shoulder height, neonate mass corrected for adult mass, relative brain volume, big game.

[d] $P > .10$ for log home range, sexual dimorphism, log litter size, log gestation length, relative shoulder height, neonate mass corrected for adult mass, relative brain volume, flesh diet.

[e] $P > .10$ for log-log home range, sexual dimorphism, log population density, log gestation length, log weaning age, neonate mass corrected for adult mass, cursorial hunting.

* $\alpha < .10$.

** $\alpha \leq .05$ (in bold).

morphology (e.g., relative height at shoulder for body mass, reduced sexual dimorphism, increase in relative brain size), foraging and ranging behaviors (e.g., endurance hunting of big game in open landscapes, fission-fusion sociality), and life history traits (e.g., increased age of weaning, increased reproductive output), all of which are relevant to early hominins. These findings extend earlier studies suggesting a positive relationship between hunting large game in open habitats and the emergence of sociality in carnivores (Gittleman and Harvey 1982; Packer, Scheel, and Pusey 1990). Early *Homo* apparently exhibited larger body and brain sizes and perhaps slower growth rates than did *Australopithecus* (Antón 2012). Our data suggest that meaningful inferences about social evolution are possible based on these morphological shifts.

Whereas each of the factors elucidated here for extant carnivores likely played some role in hominin evolution, only some of them depend on meat eating, and none of them are fully predicted by a singular referential model evaluated here. Our analysis underscores the need for paleoanthropologists to consider a multitude of factors (rather than a single or relatively small number of factors) simultaneously when attempting to explain the evolution of cooperation in hominins. This notion of a multifaceted approach to hominin evolution has been suggested previously (e.g., Potts 1994), but here we provide new lines of evidence to support it. Briefly, as predicted by the hunting-scavenging model involving persistence running, we found that carnivores engaging in cursorial hunting of large-bodied prey are most likely to cooperate. Moreover, morphological traits important for hunting, such as large relative shoulder height, and those theorized to result from reduced male-male competition (e.g., Plavcan 2012), such as a reduction in sexual dimorphism, were most common in highly cooperative species. These morphological changes are of particular relevance because such factors may be evaluated in the fossil remains of early *Homo*. Nevertheless, those species of carnivores that were most cooperative in breeding generally had larger relative brain sizes and greater reproductive investment than did noncooperative carnivores. Relative brain size failed to predict cooperative defense against predators, which does not support the prediction of the predator protection model. Species that weaned offspring at the oldest ages (enhanced reproductive investment) and lived at the highest population densities (presumably in areas with clumped resources) were most likely to cooperate in defense against predators.

Relevance of Extant Carnivores for Understanding Behavioral Shifts in Hominins

Large mammalian carnivores might have coexisted with *Homo* by as early as 2.6 Ma. However, tooth marks on bones suggest that carnivores only started to regularly visit butchery sites by roughly around 2.0 Ma (Domínguez-Rodrigo and Martinez-Navarro 2012). Despite the surprisingly high number of tooth marks on animal bones around this time, extrinsic mortality of early *Homo* apparently declined, a pattern that has been attributed to either increased cooperative defense against predators (Hart and Sussman 2009) or cooperative breeding (Hrdy 2009). Both forms of cooperation occur in extant carnivores reviewed here. Evidence from carnivores more broadly indicates that both the emergence of cooperative defense against predators and the pace of reproduction can respond in a flexible fashion to variation in the availability and acquisition of energy-rich foods. Thus, it is possible that similar flexibility influenced shifts in reproductive investment and rates of reproduction among early hominins. Interestingly, just as flexibility in female reproduction among spotted hyenas exceeds that of most extant carnivores, the plastic reproductive responses typical of early *Homo* appear to surpass those of chimpanzees or gorillas (Bribiescas, Ellison, and Gray 2012; Isler and van Schaik 2012; Wells 2012). Thus, maternal capital might have played a central role in hominin
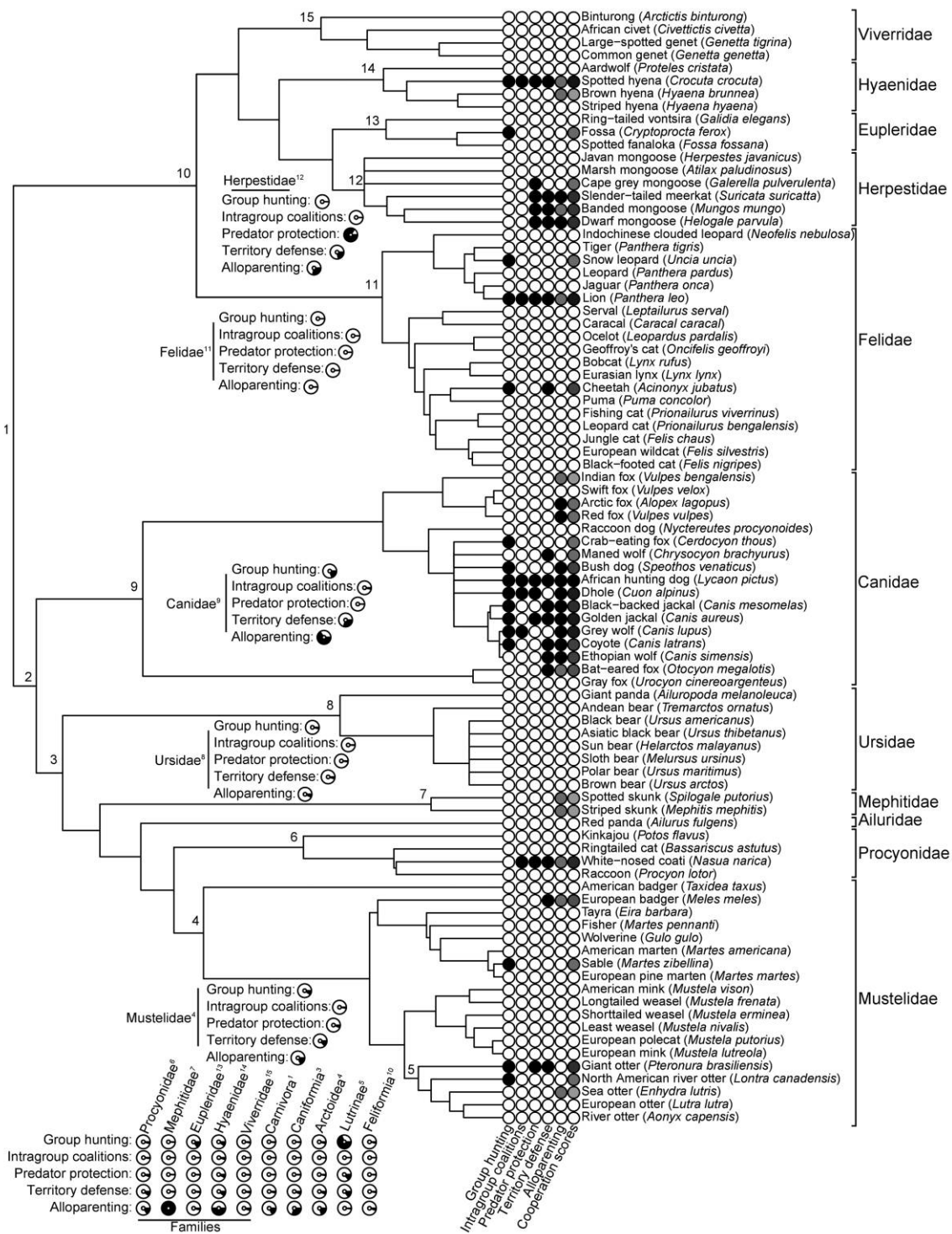
Figure 4. Phylogeny of the carnivore species used in our study. Tip labels display species names. At tips of the phylogeny are circles shaded to varying degrees indicating for each cooperation variable whether or not the species exhibits the trait. Black indicates trait presence, whereas white indicates that the species does not exhibit that trait. For alloparenting, gray indicates communal denning. Circles representing composite cooperation scores (a continuous measure of cooperation) are shaded, with dark shading representing the highest cooperation score. Pie charts are given for each binary variable for select taxonomic groups indicating the probabilities that common ancestors were uncooperative (white) or cooperative (black). Superscripts for each taxonomic grouping refer to labeled nodes on the phylogeny.

evolution of large brains and slow life histories, although the precise timing of each remains enigmatic.

Around 2.3–1.7 Ma, a major shift in a suite of behaviors became persistent in the fossil record of early *Homo* (Potts 1998*a*, 2012); these included stone transport, tool making, and access to large animals. In the Turkana and Olduvai basins, stone transport distances increased, artifacts were distributed more widely, and processing of animal tissues intensified, including the extraction of meat and marrow from large animals (e.g., Blumenschine 1995; Bunn and Kroll 1986; Potts 1988). Although no evidence currently exists of tool use among extant carnivores, most carnivores are well endowed with massive jaws that permit them to capture prey and gain access to animal tissues without tool use. Nonetheless, most mammalian carnivores are unable to capture prey exceeding 10 kg (Gittleman 1989). Those that capture large prey hunt cooperatively when doing so, but there is no evidence of advanced planning before hunts by carnivores. In contrast, modern hunts by the Ache of Paraguay (Kaplan and Hill 1985) and subsistence whale hunters of Lamalera, Indonesia (Alvard and Nolin 2002; O'Connell, Hawkes, and Blurton Jones 1988), regularly capture prey of much larger than 10 kg in hunts requiring advanced planning. Recent comparative data suggest that cumulative culture, the summation of innovations over time, may indeed be unique to modern humans (Dean et al. 2012). Altogether, these data suggest that cooperative capture of some prey items might have been possible before the evolution of large brains, but complex forms of cooperative hunting requiring advanced planning probably emerged later in hominin evolution.

Around 1.9–1.5 Ma, landscape instability likely promoted carrying of stones and meat over greater distances (e.g., 2–13 km; Potts 1998*a*). Selection favoring other behavioral traits, including sociality, of early hominins was also likely driven by intense variation in ecological and climatic conditions (Potts 1998*b*, 2012). Similarly, spotted hyenas, the most abundant large carnivore in sub-Saharan Africa, may have also been subject to strong selection for their behavioral flexibility to cope with demands of life in a socially and ecologically dynamic landscape (Holekamp and Dloniak 2010; Holekamp et al. 2012). The ecological dominance of spotted hyenas over other carnivores in Africa may in large part be attributed to the behavioral flexibility that their impressive morphology affords them (Holekamp and Dloniak 2010). Adult spotted hyenas are efficient hunters (Holekamp et al. 1997) and extractive foragers (Tanner et al. 2010) capable of fully exploiting a wide array of foods ranging from termites to large ungulate prey. These hyenas effectively crack through bones as large as giraffe leg bones to access marrow, allowing them to efficiently consume entire carcasses. In the face of burgeoning human populations across Africa, their behavioral flexibility has permitted these animals to persist at high densities despite the energetic demands of being a top predator (Boydston et al. 2003). It might be this behavioral flexibility with respect to foraging that permits spotted hyenas to cope with ecological

insults more effectively than can most other large carnivores with more restricted dispersal abilities or less versatile morphological adaptations (Holekamp et al. 2012). In this respect, data on spotted hyenas are consistent with the notion that natural selection favors species living in variable habitats that are best able to cope with and respond to changing environmental conditions.

Fission-fusion sociality may have played an underappreciated role in reducing the costs confronted by early hominins in changing environments. That is, hominin communities might have retained their ability to cooperate with group mates despite their splitting into more and more complex levels of temporary subgroups as the total area required per group increased (e.g., from those occupied by *Australopithecus* and *Homo habilis* to that occupied by *Homo erectus*; reviewed by Grove, Pearce, and Dunbar 2012). Our comparative data are consistent with the notion that fission-fusion sociality permits the maintenance of cooperation; extant carnivores living in societies structured by fission-fusion dynamics engaged in just as many forms of cooperation as species in highly cohesive groups and were more cooperative than those restricted to living in pairs. Despite spending much of their time apart from group members, most gregarious carnivores regularly meet up with conspecifics for protection from predators, reinforcement of social bonds, and sharing of spoils from hunts. Evolution of an increasingly complex multilevel fission-fusion society beyond that observed in any extant mammalian carnivore may have similarly helped early hominins cope with increased foraging demands attributed to ranging over large areas as they migrated toward high latitudes (Grove, Pearce, and Dunbar 2012). Taken together, evidence from extant mammalian carnivores reviewed here as well as that from nonhuman primates (e.g., Wrangham, Gittleman, and Chapman 1993) and modern small-scale hunter-gathers (e.g., Marlowe 2005) suggests the most parsimonious interpretation of the fossil record is that development toward an increasingly complex multilevel fission-fusion society allowed for both cooperation and range expansion at key transitional stages of hominin evolution.

In conclusion, it has long been recognized that understanding the evolution and mechanisms of cooperation among mammalian carnivores might shed light on the factors shaping hominin evolution (Hill 1982; Kaplan and Hill 1985; Schaller and Lowther 1969). Our study confirms that meaningful links are possible between measurable morphological traits and seemingly elusive behavioral traits. New analyses on cooperative breeding and predator protection for these species, some but not all of which also happen to eat meat, make this taxonomic group relevant today even if *Homo* was not substantially carnivorous. Our results also move the field forward by emphasizing the need for the consideration of multiple factors rather than predictions from a single existing model when explaining social evolution of early hominins. New insights suggesting convergent evolution between extant mammalian carnivores and early hominins will undoubtedly

emerge as we continue to learn more about the biology of extant mammalian carnivores.

Acknowledgments

References Cited

Aiello, Leslie C., and Peter Wheeler. 1995. The expensive tissue hypothesis: the brain and the digestive system in human and primate evolution. *Current Anthropology* 36:199–221.

Alvard, Michael S., and David A. Nolin. 2002. Rousseau's whale hunt? coordination among big-game hunters. *Current Anthropology* 43:533–559.

Antón, Susan C. 2012. Early *Homo*: who, when, and where. *Current Anthropology* 53(suppl. 6):S278–S298.

Aureli, Filippo, Colleen M. Schaffner, Christophe Boesch, Simon K. Bearder, Josep Call, Colin A. Chapman, Richard Connor, et al. 2008. Fission-fusion dynamics: new research frameworks. *Current Anthropology* 49:627–654.

Bingham, Paul M. 1999. Human uniqueness: a general theory. *Quarterly Review of Biology* 74:133–169.

Bininda-Emonds, Olaf R. P., Marcel Cardillo, Kate E. Jones, Ross D. E. MacPhee, Robin M. D. Beck, Richard Grenyer, Samantha A. Price, Rutger A. Vos, John L. Gittleman, and Andy Purvis. 2007. The delayed rise of present-day mammals. *Nature* 446:507–512.

Blomberg, Simon P., Theodore Garland Jr., and Anthony R. Ives. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57:717–745.

Blumenschine, Robert J. 1995. Percussion marks, tooth marks, and experimental determinations of the timing of hominid and carnivore access to long bones at FLK Zinjanthropus, Olduvai Gorge, Tanzania. *Journal of Human Evolution* 29:21–51.

Boydston, Erin E., Karen M. Kapheim, Heather E. Watts, Micaela Szykman, and Kay E. Holekamp. 2003. Altered behaviour in spotted hyenas associated with increased human activity. *Animal Conservation* 6:207–219.

Boydston, Erin E., Toni Lyn Morelli, and Kay E. Holekamp. 2001. Sex differences in territorial behavior exhibited by the spotted hyena (Hyaenidae, *Crocuta crocuta*). *Ethology* 107:369–385.

Bramble, Dennis M., and Daniel E. Lieberman. 2004. Endurance running and the evolution of *Homo*. *Nature* 432:345–352.

Bribiescas, Richard G., Peter T. Ellison, and Peter B. Gray. 2012. Male life history, reproductive effort, and the evolution of the genus *Homo*. *Current Anthropology* 53(suppl. 6):S424–S435.

Brown, Jerram L. 1983. Cooperation: a biologist's dilemma. *Advances in the Study of Behavior* 13:1–37.

Bunn, Henry T. 2006. Meat made us human. In *Evolution of the human diet: the known, the unknown, and the unknowable*. Peter Ungar, ed. Pp. 191–211. Oxford: Oxford University Press.

Bunn, Henry T., and Ellen M. Kroll. 1986. Systematic butchery by Plio-Pleistocene hominids at Olduvai Gorge, Tanzania. *Current Anthropology* 27:431–452.

Bunn, Henry T., and Travis R. Pickering. 2010. Bovid mortality profiles in paleoecological context falsify hypotheses of endurance running-hunting and passive scavenging by early Pleistocene hominins. *Quaternary Research* 74:395–404.

Burnham, Kenneth P., and David R. Anderson. 2002. *Model selection and inference: a practical information-theoretic approach*. 2nd edition. New York: Springer.

Byrne, Richard R. 1995. *The thinking ape: evolutionary origins of intelligence*. Oxford: Oxford University Press.

Cant, Michael A. 2011. The role of threats in animal cooperation. *Proceedings of the Royal Society B: Biological Sciences* 278:170–178.

Cant, Michael A., Sarah J. Hodge, Matthew B. V. Bell, Jason S. Gilchrist, and Hazel J. Nichols. 2010. Reproductive control via eviction (but not the threat of eviction) in banded mongooses. *Proceedings of the Royal Society B: Biological Sciences* 277:2219–2226.

Carbone, Chris, Lory Frame, George Frame, James R. Malcolm, John H. Fanshawe, Clare D. FitzGibbon, George B. Schaller, Iain J. Gordon, J. Marcus Rowcliffe, and Johan T. du Toit. 2005. Feeding success of African wild dogs (*Lycaon pictus*) in the Serengeti: the effects of group size and kleptoparasitism. *Journal of Zoology* 266:153–161.

Chapais, Bernard. 1992. The role of alliances in the social inheritance of rank among female primates. In *Coalitions and alliances in humans and other animals*. Alexander H. Harcourt and Frans B. M. de Waal, eds. Pp. 29–60. Oxford: Oxford Science.

Cheney, Dorothy L. 1977. The acquisition of rank and the development of reciprocal alliances among free-ranging immature baboons. *Behavioral Ecology and Sociobiology* 2:303–318.

Clutton-Brock, Timothy H. 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* 296:69–72.

———. 2009a. Cooperation between non-kin in animal societies. *Nature* 462:51–57.

———. 2009b. Structure and function in mammalian societies. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364:3229–3242.

Clutton-Brock, Timothy H., and Paul H. Harvey. 1977. Primate ecology and social organization. *Journal of Zoology* 183:1–39.

Clutton-Brock, Timothy H., Sarah J. Hodge, and T. P. Flower. 2008. Group size and the suppression of subordinate reproduction in Kalahari meerkats. *Animal Behaviour* 76:689–700.

Connor, Richard C. 1995. The benefits of mutualism: a conceptual framework. *Biological Reviews of the Cambridge Philosophical Society* 70:427–457.

Courchamp, Franck, Gregory S. A. Rasmussen, and David W. Macdonald. 2002. Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*. *Behavioral Ecology* 13:20–27.

Creel, Scott. 1997. Cooperative hunting and group size: assumptions and currencies. *Animal Behaviour* 54:1319–1324.

Creel, Scott, and Nancy M. Creel. 1991. Energetics, reproductive suppression and obligate communal breeding in carnivores. *Behavioral Ecology and Sociobiology* 28:263–270.

———. 1995. Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Animal Behaviour* 50:1325–1339.

———. 2002. *The African wild dog: behavior, ecology, and conservation*. Monographs in Behavior and Ecology. Princeton, NJ: Princeton University Press.

Creel, Scott, and David Macdonald. 1995. Sociality, group size, and reproductive suppression among carnivores. *Advances in the Study of Behavior* 24:203–257.

Dalerum, Fredrik. 2007. Phylogenetic reconstruction of carnivore social organizations. *Journal of Zoology* 273:90–97.

Dean, Lewis G., Rachel L. Kendal, Steven J. Schapiro, Bernard Thierry, and Kevin N. Laland. 2012. Identification of the social and cognitive processes underlying human cumulative culture. *Science* 335:1114–1118.

Domínguez-Rodrigo, Manuel, and Bienvenido Martinez-Navarro. 2012. Taphonomic analysis of the early Pleistocene (2.4 Ma) faunal assemblage from A.L. 894 (Hadar, Ethiopia). *Journal of Human Evolution* 62:315–327.

Domínguez-Rodrigo, Manuel, and Travis R. Pickering. 2003. Early hominid hunting and scavenging: a zooarcheological review. *Evolutionary Anthropology* 12:275–282.

Domínguez-Rodrigo, Manuel, Travis R. Pickering, and Henry T. Bunn. 2010. Configurational approach to identifying the earliest hominin butchers. *Proceedings of the National Academy of Sciences of the USA* 107:20929–20934.

———. 2011. Reply to McPherron et al.: doubting Dikika is about data, not paradigms. *Proceedings of the National Academy of Sciences of the USA* 108: E117.

Drea, Christine M., and Allisa N. Carter. 2009. Cooperative problem solving in a social carnivore. *Animal Behaviour* 78:967–977.

Drea, Christine M., and Laurence G. Frank. 2003. The social complexity of spotted hyenas. In *Animal social complexity: intelligence, culture, and individualized societies*. Frans B. M. de Waal and Peter L. Tyack, eds. Pp. 121–148. Cambridge, MA: Harvard University Press.

Dugatkin, Lee A. 2002. Animal cooperation among unrelated individuals. *Naturwissenschaften* 89:533–541.

East, Marion L., Heribert Hofer, and Wolfgang Wickler. 1993. The erect "penis" as a flag of submission in a female-dominated society: greetings in Serengeti spotted hyenas. *Behavioral Ecology and Sociobiology* 33:355–370.

Engh, Anne L., Katrina Esch, Laura Smale, and Kay E. Holekamp. 2000. Mechanisms of maternal rank "inheritance" in the spotted hyaena, *Crocuta crocuta*. *Animal Behaviour* 60:323–332.

Engh, Anne L., Erin R. Siebert, David A. Greenberg, and Kay E. Holekamp. 2005. Patterns of alliance formation and postconflict aggression indicate spotted hyaenas recognize third-party relationships. *Animal Behaviour* 69: 209–217.

Felsenstein, Joseph. 1985. Phylogenies and the comparative method. *American Naturalist* 125:1–15.

Finarelli, John A. 2008. A total evidence phylogeny of the Arctoidea (Carnivora: Mammalia): relationships among basal taxa. *Journal of Mammalian Evolution* 15:231–259.

———. 2010. Does encephalization correlate with life history or metabolic rate in Carnivora? *Biology Letters* 6:350–353.

Finarelli, John A., and John J. Flynn. 2009. Brain-size evolution and sociality in Carnivora. *Proceedings of the National Academy of Sciences of the USA* 106:9345–9349.

Flynn, John J., John A. Finarelli, Sarah Zehr, Johnny Hsu, and Michael A. Nedbal. 2005. Molecular phylogeny of the Carnivora (Mammalia): assessing the impact of increased sampling on resolving enigmatic relationships. *Systematic Biology* 54:317–337.

Ford, R. Glenn, and Frank A. Pitelka. 1984. Resource limitation in populations of the California vole. *Ecology* 65:122–136.

Frank, Laurence G. 1986. Social organization of the spotted hyaena (*Crocuta crocuta*). 2. Dominance and reproduction. *Animal Behaviour* 34:1510–1527.

Frank, Laurence G., Kay E. Holekamp, and Laura Smale. 1995. Dominance, demography, and reproductive success of female spotted hyenas. In *Serengeti II: dynamics, management, and conservation of an ecosystem*. Anthony R. E. Sinclair and Peter Arcese, eds. Pp. 364–384. Chicago: University of Chicago Press.

Fuentes, Agustín, Matthew A. Wyczalkowski, and Katherine C. MacKinnon. 2010. Niche construction through cooperation: a nonlinear dynamics contribution to modeling resilience and evolutionary history in the genus *Homo*. *Current Anthropology* 51(3):435–444.

Gittleman, John L. 1989. *Carnivore behavior, ecology and evolution*. Ithaca, NY: Cornell University Press.

Gittleman, John L., and Paul H. Harvey. 1982. Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology* 10:57–63.

Gittleman, John L., and Hang-Kwang Luh. 1992. On comparing comparative methods. *Annual Review of Ecology and Systematics* 23:383–404.

Goldberg, Tony L., and Richard W. Wrangham. 1997. Genetic correlates of social behaviour in wild chimpanzees: evidence from mitochondrial DNA. *Animal Behaviour* 54:559–570.

Gompper, Matthew E. 1996. Sociality and asociality in white-nosed coatis (*Nasua narica*): foraging costs and benefits. *Behavioral Ecology* 7:254–263.

Gompper, Matthew E., John L. Gittleman, and Robert K. Wayne. 1998. Dispersal, philopatry, and genetic relatedness in a social carnivore: comparing males and females. *Molecular Ecology* 7:157–163.

Gottelli, Dada, Claudia Sillero-Zubiri, Geoffrey D. Applebaum, Michael S. Roy, Derek J. Girman, Jesus Garcia-Moreno, Elaine A. Ostrander, and Robert K. Wayne. 1994. Molecular genetics of the most endangered canid: the Ethiopian wolf *Canis simensis*. *Molecular Ecology* 3:301–312.

Grine, Frederick, and John G. Fleagle. 2009. The first humans: a summary perspective on the origin and early evolution of the genus *Homo*. In *The first humans: origin and early evolution of the genus* Homo. Fred E. Grine, John G. Fleagle, and Richard E. Leakey, eds. Pp. 197–207. New York: Springer.

Grove, Matt. 2010. Logistical mobility reduces subsistence risk in hunting economies. *Journal of Archaeological Science* 37:1913–1921.

Grove, Matt, Eiluned Pearce, and Robin I. M. Dunbar. 2012. Fission-fusion and the evolution of hominin social systems. *Journal of Human Evolution* 62:191–200.

Hamilton, William D. 1964*a*. The genetical evolution of social behavior. 1. *Journal of Theoretical Biology* 7:1–16.

———. 1964*b*. The genetical evolution of social behavior. 2. *Journal of Theoretical Biology* 7:17–52.

Hart, Donna, and Robert W. Sussman. 2009. *Man the hunted: primates, predators, and human evolution*. Expanded edition. Boulder, CO: Westview.

Heinsohn, Robert, and Craig Packer. 1995. Complex cooperative strategies in group-territorial African lions. *Science* 269:1260–1262.

Henschel, Johannes R., and John D. Skinner. 1991. Territorial behaviour by a clan of spotted hyaenas *Crocuta crocuta*. *Ethology* 88:223–235.

Hill, Kim. 1982. Hunting and human evolution. *Journal of Human Evolution* 11:521–544.

Hofer, Heribert, and Marion L. East. 1993. The commuting system of Serengeti spotted hyaenas: how a predator copes with migratory prey. 2. Intrusion pressure and commuter's space use. *Animal Behaviour* 46:559–574.

———. 1996. The components of parental care and their fitness consequences: a life history perspective. *Verhandlungen der Deutschen Zoologischen Gesellscaft* 89:149–164.

———. 2003. Behavioral processes and costs of co-existence in female spotted hyenas: a life history perspective. *Evolutionary Ecology* 17:315–331.

Holekamp, Kay E., Erin E. Boydston, and Laura Smale. 2000. Group travel in social carnivores. In *On the move: how and why animals travel in groups*. Sue Boinski and Paul A. Garber, eds. Pp. 587–627. Chicago: University of Chicago Press.

Holekamp, Kay E., and Stephanie M. Dloniak. 2010. Intraspecific variation in the behavioral ecology of a tropical carnivore, the spotted hyena. *Advances in the Study of Behavior* 42:189–229.

Holekamp, Kay E., Sharleen T. Sakai, and Barbara L. Lundrigan. 2007. Social intelligence in the spotted hyena (*Crocuta crocuta*). *Philosophical Transactions of the Royal Society B: Biological Sciences* 362:523–538.

Holekamp, Kay E., and Laura Smale. 1991. Dominance acquisition during mammalian social development: the "inheritance" of maternal rank. *American Zoologist* 31:306–317.

———. 1993. Ontogeny of dominance in free-living spotted hyaenas: juvenile rank relations with other immature individuals. *Animal Behaviour* 46:451–466.

Holekamp, Kay E., Laura Smale, Richard J. Berg, and Susan M. Cooper. 1997. Hunting rates and hunting success in the spotted hyena (*Crocuta crocuta*). *Journal of Zoology* (London) 242:1–15.

Holekamp, Kay E., Laura Smale, and Micaela Szykman. 1996. Rank and reproduction in the female spotted hyaena. *Journal of Reproduction and Fertility* 108:229–237.

Holekamp, Kay E., Jennifer E. Smith, Christopher C. Strelioff, Russell C. Van Horn, and Heather E. Watts. 2012. Society, demography and genetic structure in the spotted hyena. *Molecular Ecology* 21:613–632.

Horrocks, Julia, and Wayne Hunte. 1983. Maternal rank and offspring rank in vervet monkeys: an appraisal of the mechanisms of rank acquisition. *Animal Behaviour* 31:772–782.

Hrdy, Sarah B. 2009. *Mothers and others: the evolutionary origins of mutual understanding*. Cambridge, MA: Harvard University Press.

Isler, Karin, and Carel P. van Schaik. 2012. How our ancestors broke through the gray ceiling: comparative evidence for cooperative breeding in early *Homo*. *Current Anthropology* 53(suppl. 6):S453–S465.

Johnson, Dominic D. P., Roland Kays, Paul G. Blackwell, and David W. Macdonald. 2002. Does the resource dispersion hypothesis explain group living? *Trends in Ecology and Evolution* 17:563–570.

Johnson, Warren E., Eduardo Eizirik, Jill Pecon-Slattery, William J. Murphy, Agostinho Antunes, Emma Teeling, and Stephen J. O'Brien. 2006. The Late Miocene radiation of modern Felidae: a genetic assessment. *Science* 311: 73–77.

Kaplan, Hillard, and Kim Hill. 1985. Food sharing among Ache foragers: tests of explanatory hypotheses. *Current Anthropology* 26:223–246.

Kaplan, Hillard, Kim Hill, Jane Lancaster, and A. Magdalena Hurtado. 2000. A theory of human life history evolution: diet, intelligence, and longevity. *Evolutionary Anthropology* 9:156–185.

Kays, Roland W., and John L. Gittleman. 2001. The social organization of the kinkajou *Potos flavus* (Procyonidae). *Journal of Zoology* (London) 253:491–504.

Kembel, Steven W., Peter D. Cowan, Matthew R. Helmus, William K. Cornwell, Helene Morlon, David D. Ackerly, Simon P. Blomberg, and Campbell O. Webb. 2010. Picante: *R* tools for integrating phylogenies and ecology. *Bioinformatics* 26:1463–1464.

Koepfli, Klaus-Peter, Kerry A. Deere, Graham J. Slater, Colleen Begg, Keith Begg, Lon Grassman, Mauro Lucherini, Geraldine Veron, and Robert K. Wayne. 2008. Multigene phylogeny of the Mustelidae: resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. *BMC Biology* 6:10.

Koepfli, Klaus-Peter, Matthew E. Gompper, Eduardo Eizirik, Cheuk-Chung Ho, Leif Linden, Jesus E. Maldonado, and Robert K. Wayne. 2007. Phylogeny of the Procyonidae (Mammalia: Carnivora): molecules, morphology and the Great American Interchange. *Molecular Phylogenetics and Evolution* 43:1076–1095.

Koepfli, Klaus-Peter, Susan M. Jenks, Eduardo Eizirik, Tannaz Zahirpour, Blaire Van Valkenburgh, and Robert K. Wayne. 2006. Molecular systematics of the Hyaenidae: relationships of a relictual lineage resolved by a molecular supermatrix. *Molecular Phylogenetics and Evolution* 38:603–620.

Kruuk, Hans. 1972. *The spotted hyena: a study of predation and social behavior.* Chicago: University of Chicago Press.

———. 1976. Feeding and social behaviour of the striped hyaena (*Hyaena vulgaris* Desmarest). *East African Wildlife Journal* 14:91–111.

Kruuk, Hans, and Tim Parish. 1982. Factors affecting population density, group size and territory size of the European badger, *Meles meles. Journal of Zoology* 196:31–39.

Lehman, Niles, Peter Clarkson, L. David Mech, Thomas J. Meier, and Robert K. Wayne. 1992. A study of the genetic relationships within and among wolf packs using DNA fingerprinting and mitochondrial DNA. *Behavioral Ecology and Sociobiology* 30:83–94.

Marlowe, Frank W. 2005. Hunter-gatherers and human evolution. *Evolutionary Anthropology* 14:54–67.

McPherron, Shannon P., Zeresenay Alemseged, Curtis W. Marean, Jonathan G. Wynn, Denné Reed, Denis Geraads, René Bobe, and Hamdallah A. Béarat. 2010. Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature* 466:857–860.

Mech, L. David. 1970. *The wolf: ecology and behavior of an endangered species.* Minneapolis: University of Minnesota Press.

Melis, Alicia P., and Dirk Semmann. 2010. How is human cooperation different? *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2663–2674.

Mills, Gus L. 1990. *Kalahari hyaenas: comparative behavioral ecology of two species.* London: Unwin Hyman.

Milton, Katharine. 1999. A hypothesis to explain the role of meat-eating in human evolution. *Evolutionary Anthropology* 8:11–21.

Noë, Roland. 2006. Cooperation experiments: coordination through communication versus acting apart together. *Animal Behaviour* 71:1–18.

Nowak, Martin A. 2006. Five rules for the evolution of cooperation. *Science* 314:1560–1563.

O'Connell, James F., Kristen Hawkes, and Nicholas Blurton Jones. 1988. Hadza scavenging: implications for Plio/Pleistocene hominid subsistence. *Current Anthropology* 29:356–363.

———. 1999. Grandmothering and the evolution of *Homo erectus. Journal of Human Evolution* 36:461–485.

O'Connell, James F., Kristen Hawkes, Karen D. Lupo, and Nicholas Blurton Jones. 2002. Male strategies and Plio-Pleistocene archaeology. *Journal of Human Evolution* 43:831–872.

Packer, Craig, Anne E. Pusey, and Lynn E. Eberly. 2001. Egalitarianism in female African lions. *Science* 293:690–693.

Packer, Craig, and Lore Ruttan. 1988. The evolution of cooperative hunting. *American Naturalist* 132:159–198.

Packer, Craig, David Scheel, and Anne E. Pusey. 1990. Why lions form groups: food is not enough. *American Naturalist* 136:1–19.

Palomares, Francisco, and Tim M. Caro. 1999. Interspecific killing among mammalian carnivores. *American Naturalist* 153:492–507.

Paradis, Emmanuel, Julien Claude, and Krbinian Strimmer. 2004. APE: analyses of phylogenetics and evolution in *R* language. *Bioinformatics* 20:289–290.

Patoua, Marie-Lilith, Patricia A. Mclenachan, Craig G. Morley, Arnaud Couloux, Andrew P. Jennings, and Géraldine Verona. 2009. Molecular phylogeny of the Herpestidae (Mammalia, Carnivora) with a special emphasis on the Asian Herpestes. *Molecular Phylogenetics and Evolution* 53:69–80.

Perini, Fernando A., Claudia M. Russo, and Carlos G. Schrago. 2009. The evolution of South American endemic canids: a history of rapid diversification and morphological parallelism. *Journal of Evolutionary Biology* 23:311–322.

Plavcan, J. Michael. 2012. Body size, size variation, and sexual size dimorphism in early *Homo. Current Anthropology* 53(suppl. 6):S409–S423.

Pontzer, Herman. 2012. Ecological energetics in early *Homo. Current Anthropology* 53(suppl. 6):S346–S358.

Potts, Richard. 1988. *Early hominid activities at Olduvai.* New York: Aldine.

———. 1994. Variables versus models of early Pleistocene hominid land-use. *Journal of Human Evolution* 27:7–24.

———. 1998*a*. Environmental hypotheses of hominin evolution. *Yearbook of Physical Anthropology* 41:93–136.

———. 1998*b*. Variability selection in hominid evolution. *Evolutionary Anthropology* 7:81–96.

———. 2012. Environmental and behavioral evidence pertaining to the evolution of early *Homo. Current Anthropology* 53(suppl. 6):S299–S317.

Potts, Richard, and Pat Shipman. 1981. Cutmarks made by stone tools on bones from Olduvai Gorge, Tanzania. *Nature* 291:577–580.

Queller, David C. 1985. Kinship, reciprocity and synergism in the evolution of social behaviour. *Nature* 318:366–367.

R Development Core Team. 2010. *R: a language and environment for statistical computing.* Vienna: R Foundation for Statistical Computing.

Reynolds, Vernon. 1966. Open groups in hominid evolution. *Man*, n.s., 1:441–452.

Rohlf, F. James. 2001. Comparative methods for the analysis of continuous variables: geometric interpretations. *Evolution* 55:2143–2160.

Sato, Jun J., Mieczyslaw Wolsan, Shinji Minami, Tetsuji Hosoda, Martua H. Sinaga, Kozue Hiyama, Yasunori Yamaguchi, and Hitoshi Suzuki. 2009. Deciphering and dating the red panda's ancestry and early adaptive radiation of Musteloidea. *Molecular Phylogenetics and Evolution* 53:907–922.

Schaller, George B. 1972. *The Serengeti lion.* Chicago: University of Chicago Press.

Schaller, George B., and Gordon R. Lowther. 1969. Relevance of carnivore behavior to study of early hominids. *Southwestern Journal of Anthropology* 25:307–341.

Scheel, David, and Craig Packer. 1991. Group hunting behaviour of lions: a search for cooperation. *Animal Behaviour* 41:697–709.

Semaw, Sileshi, Paul Renne, John W. K. Harris, Craig S. Feibel, Raymond L. Bernor, N. Fessesha, and Kenneth Mowbray. 1997. 2.5-million-year-old stone tools from Gona, Ethiopia. *Nature* 385:333–336.

Shipman, Pat. 1986. Scavenging or hunting in early hominids: theoretical framework and tests. *American Anthropologist* 88:27–43.

Silk, Joan B., Susan C. Alberts, and Jeanne Altmann. 2003. Social bonds of female baboons enhance infant survival. *Science* 302:1231–1234.

Silk, Joan B., Jacinta C. Beehner, Thore J. Bergman, Catherine Crockford, Anne L. Engh, Liza R. Moscovice, Roman M. Wittig, Robert M. Seyfarth, and Dorothy L. Cheney. 2009. The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B: Biological Sciences* 276:3099–3104.

Smale, Laura, Laurence G. Frank, and Kay E. Holekamp. 1993. Ontogeny of dominance in free-living spotted hyaenas: juvenile rank relations with adult females and immigrant males. *Animal Behaviour* 46:467–477.

Smith, Jennifer E., Joseph M. Kolowski, Katharine E. Graham, Stephanie E. Dawes, and Kay E. Holekamp. 2008. Social and ecological determinants of fission-fusion dynamics in the spotted hyaena. *Animal Behaviour* 76:619–636.

Smith, Jennifer E., Sandra K. Memenis, and Kay E. Holekamp. 2007. Rank-related partner choice in the fission-fusion society of spotted hyenas (*Crocuta crocuta*). *Behavioral Ecology and Sociobiology* 61:753–765.

Smith, Jennifer E., Katherine S. Powning, Stephanie E. Dawes, Jillian R. Estrada, Adrienne L. Hopper, Stacey L. Piotrowski, and Kay Holekamp. 2011. Greetings promote cooperation and reinforce social bonds among spotted hyaenas. *Animal Behaviour* 81:401–415.

Smith, Jennifer E., Russell C. Van Horn, Katherine S. Powning, Alison R. Cole, Katharine E. Graham, Sandra K. Memenis, and Kay E. Holekamp.

2010. Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. *Behavioral Ecology* 21:284–303.

Stander, Philip E. 1992. Cooperative hunting in lions: the role of the individual. *Behavioral Ecology and Sociobiology* 29:445–454.

Storey, John D., and Robert Tibshirani. 2003. Statistical significance for genomewide studies. *Proceedings of the National Academy of Sciences of the USA* 100:9440–9445.

Swanson, Brook O., Todd A. Blackledge, Adam P. Summers, and Cheryl Y. Hayashi. 2006. Spider dragline silk: correlated and mosaic evolution in high-performance biological materials. *Evolution* 60:2539–2551.

Swanson, Eli M., Ian Dworkin, and Kay E. Holekamp. 2011. Lifetime selection on a hypoallometric size trait in the spotted hyena. *Proceedings of the Royal Society B: Biological Sciences* 278:3277–3285.

Tanner, Jaime B., Miriam L. Zelditch, Barbara L. Lundrigan, and Kay E. Holekamp. 2010. Ontogenetic change in skull morphology and mechanical advantage in the spotted hyena (*Crocuta crocuta*). *Journal of Morphology* 271:353–365.

Tilson, Ronald T., and William J. I. Hamilton. 1984. Social dominance and feeding patterns of spotted hyaenas. *Animal Behaviour* 32:715–724.

Tomasello, Michael, Malinda Carpenter, Josep Call, Tanya Behne, and Henrike Moll. 2005. Understanding and sharing intentions: the origins of cultural cognition. *Behavioral and Brain Sciences* 28:675–735.

Trivers, Robert L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology* 46:35–57.

Ungar, Peter S. 2012. Dental evidence for the reconstruction of diet in African early *Homo*. *Current Anthropology* 53(suppl. 6):S318–S329.

Van Horn, Russell C., Anne L. Engh, Kim T. Scribner, Stephan M. Funk, and Kay E. Holekamp. 2004. Behavioural structuring of relatedness in the spotted hyena (*Crocuta crocuta*) suggests direct fitness benefits of clan-level cooperation. *Molecular Ecology* 13:449–458.

Venkataraman, Arun B., R. Arumugam, and R. Sukumar. 1995. The foraging ecology of dhole (*Cuon alpinus*) in Mudumalai Sanctuary, southern India. *Journal of Zoology* (London) 237:543–561.

Wagner, Aaron P. 2006. Behavioral ecology of the striped hyaena (*Hyaena hyaena*). PhD dissertation, Montana State University.

Walters, Jeffrey. 1980. Interventions and the development of dominance relationships in female baboons. *Folia Primatologica* 34:61–89.

Washburn, Sherwood L., and Irven Devore. 1961. Social behavior of baboons and early man. In *Social life of early man*. Sherwood Washburn, ed. Pp. 91–105. Viking Fund Publications in Anthropology, no. 31. London: Methuen.

Watts, Heather E., Jaime B. Tanner, Barbara L. Lundrigan, and Kay E. Holekamp. 2009. Post-weaning maternal effects and the evolution of female dominance in the spotted hyena. *Proceedings of the Royal Society B: Biological Sciences* 276:2291–2298.

Wells, Jonathan C. K. 2012. The capital economy in hominin evolution: how adipose tissue and social relationships confer phenotypic flexibility and resilience in stochastic environments. *Current Anthropology* 53(suppl. 6): S466–S478.

West, Stuart A., Claire El Mouden, and Andy Gardner. 2011. Sixteen common misconceptions about the evolution of cooperation in humans. *Evolution and Human Behavior* 32:231–262.

West, Stuart A., Ashleigh S. Griffin, and Andy Gardner. 2007. Evolutionary explanations for cooperation. *Current Biology* 17:R661–R672.

West-Eberhard, Mary Jane. 1975. The evolution of social behavior by kin selection. *Quarterly Review of Biology* 50:1–33.

Wilson, Don E., and Russell A. Mittermeier. 2009. *Handbook of mammals of the world*. Madrid: Lynx.

Wrangham, Richard W., John L. Gittleman, and Colin A. Chapman. 1993. Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. *Behavioral Ecology and Sociobiology* 32:199–209.

Wrangham, Richard W., James H. Jones, Greg Laden, David Pilbeam, and NancyLou Conklin-Brittain. 1999. The raw and the stolen: cooking and the ecology of human origins. *Current Anthropology* 40:567–594.

Yoder, Anne D., Melissa M. Burns, Sarah Zehr, Thomas Delefosse, Geraldine Veron, Steven M. Goodman, and John J. Flynn. 2003. Single origin of Malagasy Carnivora from an African ancestor. *Nature* 421:734–737.

Zabel, Cynthia, J., Stephen E. Glickman, Laurence G. Frank, Katya B. Woodmansee, and Geoffrey Keppel. 1992. Coalition formation in a colony of prepubertal spotted hyenas. In *Coalitions and alliances in humans and other animals*. Alexander H. Harcourt and Frans B. M. de Waal, eds. Pp. 112–135. Oxford: Oxford University Press.