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The evolution of food sharing in primates

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Abstract The aim of this study is to explain the occurrence of food sharing across primates. Defined as the unresisted transfer of food, evolutionary hypotheses have to explain why possessors should relinquish food rather than keep it. While sharing with offspring can be explained by kin selection, explanations for sharing among unrelated adults are more controversial. Here we test the hypothesis that sharing occurs with social partners that have leverage over food possessors due to the opportunity for partner choice in other contexts. Thus, we predict that possessors should relinquish food to potential mates or allies, who could provide or withhold matings or coalitionary support in the future. We used phylogenetic analyses based on both maximum likelihood and Bayesian approaches in a sample of 68 primate species to test these predictions. The analyses strongly indicate that (1) sharing with offspring is predicted by the relative processing difficulty of the diet, as measured by the degree of extractive foraging, but not overall diet quality, (2) food sharing among adults only evolved in species already sharing with offspring, regardless of diet, and (3) male–female sharing co-evolved with the opportunity for female mate choice and sharing within the sexes with coalition formation. These results provide comparative support for the hypothesis that sharing is "traded" for matings and coalitionary support in the sense that these services are statistically associated and can thus be selected for. Based on this, we predict that sharing should occur in any species with opportunities for partner choice.

Keywords Coalitions · Cooperation · Food sharing · Mate choice · Reciprocal altruism · Social bonds · Provisioning

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Introduction

Food sharing (henceforth sharing) is defined as the unresisted transfer of food from one food-motivated individual, the "possessor", to another, the "recipient" (Feistner and McGrew 1989). We define possession as being in physical contact with the food and this definition excludes transfers in which there was no clear possession, such as collecting scraps from the vicinity of a feeding individual. Thus, it should be clear that our trait of interest is that possessors voluntarily (as far as we can infer) relinquish food to the benefit of the recipient, which requires an evolutionary explanation. Sharing with related offspring is relatively common in various animal taxa (Clutton-Brock 1991; Ydenberg 1994; Brown et al. 2004; Mas and Kölliker 2008; Rapaport and Brown 2008) and its evolution can be explained by kin selection (Hamilton 1964). In contrast, sharing among unrelated adults is far less common and the benefits of sharing to possessors may

vary in different taxa (Stevens and Gilby 2004). It is therefore surprising that, among non-human primates, non-kin sharing is relatively common (Feistner and McGrew 1989; Brown et al. 2004).

There are two major hypotheses to explain non-kin sharing in primates: harassment and reciprocal exchange (Feistner and McGrew 1989; Brown et al. 2004).[1] While the two hypotheses are not mutually exclusive (Stevens and Gilby 2004; Gilby 2006), harassment is often assumed to be the more parsimonious explanation because it does not evoke delayed benefits but describes sharing as a mutualistic interaction (Stevens and Stephens 2002; Clutton-Brock 2009). Furthermore, the fact that the vast majority of transfers in primates are passive (>95% in most species, reviewed by Jaeggi et al. 2010a) also supports the notion that it is induced by harassment. According to Stevens and Stephens' (2002) harassment model, possessors share to avoid the costs (in terms of decreased consumption rate) inflicted by beggars. Similarly, tolerated theft models explain sharing by the differential marginal value of food to increasingly sated possessors vs. continually hungry beggars in light of the constant costs of defending food (Blurton Jones 1984; Blurton Jones 1987). In both models, the possessors' cost/benefit ratio is manipulated by beggars in such a way that sharing is the most beneficial option.

Although the harassment model provides a strong and simple explanation for why sharing occurs at all, an additional explanation may sometimes be warranted to explain the specific possessor–recipient combinations seen to share food and the distribution of sharing across species. For instance, some troops of olive baboons (*Papio anubis*) hunt and eat meat; possession is biased towards dominant males and sharing is rare, suggesting that the costs of defending food are small for dominant possessors (Strum 1975, 1981). Surprisingly, the few instances of sharing do not occur with other males but rather with females, who are much smaller than males and should be less costly to rebuff. Rather than the harassment costs inflicted on males, what seems to be the decisive factor are the *social costs* of rebuffing females: sharing almost exclusively occurs with consort partners or, if outside of consorts, among males and females "with previously established affiliative bond" (Strum 1981, p. 278). Hence, by not sharing, the male might risk to upset and possibly lose his consort or long-term social partner, both of which could decrease his mating chances and thus ultimately his reproductive success. These social costs have actually been shown in orangutans, where males share easily defendable food with females because females may end the association by

seeking out other males if the male does not comply, thus eliminating his mating opportunities (van Noordwijk and van Schaik 2009).

The idea of social costs has long been acknowledged in human food sharing, where stingy individuals may be excluded from future shares (Hill and Kaplan 1993; Gurven 2004), and "when weighing the costs of defending a resource against tolerated theft, therefore, an owner can be expected to include in the costs the likelihood of any forgone future favors" (Cashdan 1997, p. 69). Hence, harassment-induced sharing is inextricably linked to the social relationships of the individuals involved. Even if primates cannot consciously represent future costs, natural selection should thus favor the respective emotional proxies (Schino and Aureli 2009) to make possessors respond more to the harassment of an important social partner.

This indicates that harassment-induced sharing does not preclude reciprocal exchange as long as it can be selective. Indeed there is some good evidence among chimpanzees that sharing is usually directed towards important social partners. For instance, dominant males at Mahale will try to gain possession of carcasses after a successful hunt and only their long-term allies are allowed in the begging cluster, where they can get a share of the meat (Kawanaka 1982; Nishida et al. 1992). Long-term allies are more likely than others to provide the dominant male with grooming or coalitionary support in the future, having already done so in the past. This selective sharing with important social partners thus leads to a statistical association with other social services and can explain why almost every statistical test for reciprocal exchange among chimpanzees found some evidence for it (e.g., de Waal 1989, 1997; Gilby 2006; Mitani 2006; Gomes and Boesch 2009; Jaeggi et al. 2010c).

Although many are reluctant to embrace the idea of reciprocal exchange among animals (e.g., Clutton-Brock 2009) because of the supposed cognitive constraints (Stevens and Hauser 2004), there is a lot of good evidence for a statistical contingency between favors given and received over long time periods (see, e.g., Watts 2002; Schino 2007; Gomes et al. 2009; and food sharing references mentioned above). Such exchanges do not have to be regulated by sophisticated cognitive mechanisms but could reflect social bonds with loose emotional (rather than strict mental) score-keeping, just like friendships in humans (Trivers 1971; Silk 2002; Schino and Aureli 2009). Such bonds are formed in many primate species (Cords 1997; Tomasello and Call 1997; Silk 2002; Massen et al. 2010) and are sufficient to account for the loose exchange of low-cost altruistic acts common in primate groups (Schino and Aureli 2009).

In sum, the aim of this paper is to trace the evolution of food sharing in primates and explain its occurrence across

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[1] Other hypotheses explaining sharing in humans or other animals such as costly signaling are not discussed here because there is no convincing evidence supporting them in primates.

species. We will first test the hypotheses that explain the evolution of sharing with offspring and then sharing among (unrelated) adults. In particular, we test the hypothesis that sharing among adults coevolved with opportunities for partner choice, giving recipients leverage over possessors because they can withhold future services such as mating or coalitionary support, thus inflicting *social costs* on stingy possessors. By selectively tolerating harassment from recipients who have such leverage, possessors avoid these social costs, which leads to a statistical association of favors given and received over longer time periods, and this selective tolerance can thus be favored by natural selection. While many studies have tested for reciprocal exchange within a species, we take a comparative approach and test for the correlated evolution of sharing with conditions that favor reciprocal exchange in a large sample of primates. In particular, we suggest that the opportunity for female mate choice can account for male–female sharing and coalition formation for sharing within the sexes. This is the first study to conduct a phylogenetically controlled analysis on the conditions associated with food sharing in primates and thus extends intraspecific analyses in important ways that allow predictions about species not included in this sample.

Methods

Comparative sample

We compiled an exhaustive list of 173 references related to sharing in primates (Table 1). Species were included in the analyses if either sharing had been reported or if no sharing had been reported despite considerable study effort (at least ten behavioral studies on the species listed in ISI Web of Science by end of 2010). Sharing with offspring and among adults was quantified as absent (0), present (1, mentioned occasionally) or common (2, more than one study explicitly addressing sharing) or present (1) or absent (0), depending on the statistical method (see "Comparative Analyses"). Furthermore, sharing between particular sex combinations of adults, namely, from males to females, among males, and among females, was scored as present or absent. Sharing from females to males was too rare to test and there is no clear hypothesis associated with it. If the only reported sharing occurred in artificial experimental settings but never in naturalistic conditions and it was not clear whether the reported sharing was tolerated or resisted, it was not counted as present (since the trait of interest is *tolerated* sharing). In particular, this concerns sharing in *Saimiri sciureus* (Fragaszy and Mason 1983; Stevens 2004) and adult *Hylobates lar* (Schessler and Nash 1977; Nettelbeck 1998). Thus, a total of 68 primate species could be included in the comparative sample (Table 1; Fig. 1).

Predictor variables

In the following section, we elaborate the hypotheses explaining the evolution of sharing with offspring as well as sharing among adults in general and within specific sex combinations and provide predictor variables to test them in a comparative analysis. It should be noted that variables in a comparative study, where the units of analysis are *species*, are necessarily much cruder than in within-species analysis where we can correlate one detailed behavioral measure with another on the level of *individuals* (e.g., A sharing food with B, with B providing coalitionary support to A). Thus, rather than describing a precise behavioral mechanism, we can identify the conditions under which natural selection could install such mechanisms. While the variables may not be ideal, comparative analyses are unlikely to produce false positives and have the additional benefit that they allow us to infer the presence of certain traits in other species, given the conditions found to be predictive in this sample, which can subsequently be confirmed with a more detailed study.

Sharing with offspring

Sharing with offspring will be favored by kin selection when the costs of relinquishing food are relatively low for parents or helpers and the benefits of receiving food are high for offspring. This should be the case when there is high variation and differential skill in food acquisition or, in other words, when adults regularly acquire food which the offspring cannot yet acquire themselves. As transfers of such food items do not only provide the offspring with additional nutrients but also with information about the affordances of otherwise unreachable items, this has also been named the *informational hypothesis* (Brown et al. 2004). Here we operationalize the required skill in food acquisition by the degree of *extractive foraging*, as defined by Gibson (1986). Species were thus classified as non-extractive foragers (0), un-skilled/specialized extractive foragers (1), and skilled extractive foragers (2). In contrast to Gibson (1986), we classified *Pongo* as skilled extractive foragers since there is now good evidence for complex extractive foraging skills such as tool use (van Schaik et al. 1996) and that skills are acquired through prolonged periods of social and individual learning in both orangutan species (Forss et al. 2009; Jaeggi et al. 2010b).

Furthermore, it has been proposed that adults may use food provisioning to increase growth rates and facilitate weaning and that sharing with offspring should thus specifically target high-quality food items. This is known as the *nutritional hypothesis* (Brown et al. 2004). Thus, we predicted that sharing with offspring should be more common in species with high-quality diets, possibly in

Table 1 List of all the species included in the comparative analyses and the variables of interest

Species[a]	FS off.	FS ad.	FS ♂-♀	FS ♂-♂	FS ♀-♀	Extr. For.	DQI	Multi-male	Monog.	♂-♂ coal.	♀-♀ coal.	Ref.[b]
Alouatta palliata	1	0	0	0	0	0	0.43	1	0	0	0	1–4
Aotus azarae	2	2	1	0	0	0	0.65	0	1	0	0	5–7
Ateles geoffroyi	1	0	0	0	0	0	0.61	1	0	1	0	8–10
Callicebus discolor	1	1	1	0	0	0	0.59	0	1	0	0	11, 12
Callicebus lugens	1	0	0	0	0	0	0.65	0	1	0	0	13
Callimico goeldii	2	0	0	0	0	0	0.67	0	1	0	0	14–17
Callithrix argentata	2	0	0	0	0	1	0.67	1	1	0	0	18–20
Callithrix jacchus	2	1	1	0	0	1	0.67	1	1	0	0	21–32
Callithrix pygmaea	2	0	0	0	0	0	0.67	0	1	0	0	33, 34
Cebus albifrons	1	1	1	1	0	1	0.67	1	0	1	0	35
Cebus apella	1	1	1	1	1	2	0.87	1	0	1	1	36–43
Cebus capucinus	1	1	1	1	0	2	0.65	1	0	1	0	44–46
Cebus olivaceus	0	0	0	0	0	2	0.87	1	0	0	0	
Cercocebus atys	0	0	0	0	0	0	0.67	1	0	0	0	
Cercocebus torquatus	0	0	0	0	0	0	0.67	1	0	0	1	
Cercopithecus campbelli	0	0	0	0	0	0	0.70	0	0	0	0	
Cercopithecus diana	0	0	0	0	0	0	0.69	0	0	0	0	
Cercopithecus mitis	0	0	0	0	0	0	0.68	0	0	0	0	
Chiropotes satanas	0	0	0	0	0	0	0.67	1	0	0	0	
Chlorocebus aethiops	0	0	0	0	0	0	0.69	1	0	0	1	
Colobus guereza	0	0	0	0	0	0	0.40	1	0	0	0	
Daubentonia madagascarensis	1	0	0	0	0	2	0.84	0	0	0	0	47–49
Erythrocebus patas	0	0	0	0	0	0	0.69	0	0	0	0	
Eulemur fulvus	0	0	0	0	0	0	0.59	1	0	0	0	
Eulemur rufus	0	0	0	0	0	0	0.59	1	0	0	0	
Galago senegalensis	1	0	0	0	0	0	0.63	0	0	0	0	50, 51
Gorilla beringei	1	0	0	0	0	1	0.34	0	0	0	0	52
Gorilla gorilla	1	0	0	0	0	1	0.38	0	0	0	0	53
Hylobates lar	1	0	0	0	0	0	0.71	0	1	0	0	54–59
Indri indri	0	0	0	0	0	0	0.55	0	1	0	0	
Lemur catta	0	0	0	0	0	0	0.59	1	0	0	0	
Leontopithecus rosalia	2	1	1	0	0	1	0.67	1	1	0	0	60–70
Lophocebus albigena	0	0	0	0	0	0	0.69	1	0	0	1	
Macaca arctoides	1	0	0	0	0	1	0.68	1	0	0	0	71
Macaca fascicularis	1	0	0	0	0	1	0.74	1	0	1	1	72, 73
Macaca fuscata	1	0	0	0	0	1	0.68	1	0	0	1	74, 75
Macaca mulatta	0	0	0	0	0	1	0.68	1	0	0	1	
Macaca nemestrina	0	0	0	0	0	1	0.62	1	0	0	1	
Macaca radiata	0	0	0	0	0	1	0.68	1	0	1	0	
Macaca silenus	0	0	0	0	0	1	0.68	1	0	0	0	
Macaca sylvanus	0	0	0	0	0	1	0.68	1	0	1	0	
Mandrillus sphinx	0	0	0	0	0	0	0.67	1	0	0	0	
Microcebus murinus	0	0	0	0	0	0	0.76	0	0	0	0	
Nasalis larvatus	0	0	0	0	0	0	0.53	1	0	0	0	
Nomascus concolor	1	1	0	0	1[c]	0	0.43	0	1	0	0	76
Nycticebus coucang	1	0	0	0	0	0	0.79	0	1	0	0	77
Pan paniscus	2	2	1	1	1	2	0.61	1	0	0	1	78–87
Pan troglodytes	2	2	1	1	1	2	0.61	1	0	1	1	88–136

Table 1 (continued)

| Species[a]	FS off.	FS ad.	FS ♂-♀	FS ♂-♂	FS ♀-♀	Extr. For.	DQI	Multi-male	Monog.	♂-♂ coal.	♀-♀ coal.	Ref.[b]
Papio anubis	1	1	1	0	0	1	0.66	1	0	1	0	137–139
Papio cynocephalus	0	0	0	0	0	1	0.65	1	0	0	0	
Papio hamadryas	0	0	0	0	0	1	0.66	1	0	0	0	
Papio ursinus	0	0	0	0	0	1	0.63	1	0	0	0	
Piliocolobus badius	1	0	0	0	0	0	0.40	1	0	1	0	140
Pithecia pithecia	1	1	0	1[c]	0	0	0.67	0	0	0	0	141
Pongo abelii	2	1	1	0	1[c]	2	0.59	1	0	0	0	142–144
Pongo pygmaeus	2	1	1	0	1[c]	2	0.59	1	0	0	0	145–149
Presbytis thomasi	0	0	0	0	0	0	0.55	0	0	0	0	
Propithecus verreauxi	0	0	0	0	0	0	0.56	1	0	0	0	
Pygathrix nemaeus	1	1	1	0	1[d]	0	0.54	1	0	0	0	150
Saguinus fuscicollis	2	1	0	1[c]	0	0	0.67	1	1	0	0	151–153
Saguinus mystax	2	1	1	0	0	0	0.67	1	1	0	0	154, 155
Saguinus nigricollis	1	0	0	0	0	0	0.67	1	1	0	0	156
Saguinus oedipus	2	0	0	0	0	0	0.67	1	1	0	0	157–168
Saimiri sciureus	0	0	0	0	0	1	0.94	1	0	0	1	169, 170
Semnopithecus entellus	1	0	0	0	0	0	0.42	1	0	0	0	171
Symphalangus syndactylus	1	0	0	0	0	0	0.49	0	1	0	0	172
Tarsius spectrum	1	0	0	0	0	0	1.00	0	1	0	0	173
Theropithecus gelada	0	0	0	0	0	0	0.40	1	0	0	1	

[a] Species names follow Groves (2001) and Brandon-Jones et al. (2004)

[b] References for food sharing information. The full citation information for this list can be obtained from the first author

[c] Food sharing only reported among (confirmed or suspected) relatives, as indicated by the respective authors. The species were consequently given 0 in the non-kin only analyses

[d] No information on relatedness could be obtained for the subjects of this study and the occurrence of non-kin food sharing was thus treated as unknown in the respective analyses

FS food sharing, with offspring (off.), among adults (ad.), from males to females (♂–♀), among males (♂–♂), and among females (♀–♀), respectively, *Extr. For.* the degree of extractive foraging, *DQI* diet quality index, *Multi-male* multi-male groups, *Monog.* monogamy, ♂–♂/♀–♀ *coal.* male–male and female–female coalitions, respectively; *1–4* Carpenter (1934, 1965), Baldwin and Baldwin (1973), Whitehead (1986), *5–7* Wolovich et al. (2006, 2008a, b), *8–10* Dare (1974), Watt (1994), Pastor-Nieto (2001), *11, 12* Fragaszy and Mason (1983), Wright (1984), *13* Starin (1978), *14–17* Lorenz (1969, 1972), Feistner and Price (1991), Jurke and Price (1994), *18–20* Carroll (1978), Omedes (1981), Feistner and Price (1991), *21–32* Epple (1967), Hearn and Lunn (1975), Chalmers and Lockehaydon (1984), Feistner and Price (1991), Vitale and Queyras (1997), Yamamoto and Box (1997), Westlund et al. (2000), Caldwell and Whiten (2003), Brown et al. (2005), de Lyra-Neves et al. (2007), Kasper et al. (2008), Saito et al. (2008), *33, 34* Christen (1968), Feistner and Price (1991), *35* M. van Noordwijk and C. van Schaik (unpubl. data), *36–43* Thierry et al. (1989), de Waal et al. (1993), Fragaszy et al. (1997, 2004), Westergaard and Suomi (1997), Westergaard et al. (1998, 1999), de Waal (2000), *44–46* Perry and Rose (1994), Rose (1997, 2001), *47–49* Feistner and Ashbourne (1994), Winn (1994), Krakauer and van Schaik (2005), *50, 51* Nash (1991, 1993), *52* Watts (1985), *53* Nowell and Fletcher (2006), *54–59* Carpenter (1940), Berkson and Schusterman (1964), Ellefson (1968), Fox (1972), Schessler and Nash (1977), Nettelbeck (1998), *60–70* Wilson (1976), Brown and Mack (1978), Hoage (1982), Price and Feistner (1993), Rapaport (1999, 2001, 2006), Ruiz-Miranda et al. (1999), Rapaport and Ruiz-Miranda (2002, 2006), Tardif et al. (2002), *71* Bertrand (1969), *72, 73* Kummer and Cords (1991), M. van Noordwijk (pers.comm.), *74, 75* Hikami et al. (1990), Matusbara and Funakoshi (2001), *76* Fan and Jiang (2009), *77* Zimmermann (1989), *78–87* Kano (1980), Badrian and Badrian (1984), Badrian and Malenky (1984), Kuroda (1984), de Waal (1992), Hohmann and Fruth (1993, 2008), White (1997), Fruth and Hohmann (2002), Surbeck and Hohmann (2008), Jaeggi et al. (2010), *88–136* Nissen and Crawford (1936), van Lawick-Goodall (1968), Nishida (1970, 1983), Suzuki (1971), Teleki (1973), McGrew (1975), Wrangham (1975), Silk (1978, 1979), Nishida et al. (1979, 1992), Tutin (1979), Kawanaka (1982), Takahata et al. (1984), Goodall (1986), Boesch and Boesch-Achermann (1989, 2000), de Waal (1989, 1992, 1997), Hiraiwa-Hasegawa (1990a, b), Boesch (1994), Kuroda et al. (1996), Nishida and Turner (1996), Hemelrijk et al. (1999), Mitani and Watts (1999, 2001), Newton-Fisher (1999), Stanford (1999), Bethell et al. (2000), Nakamura and Itoh (2001), Hunt and McGrew (2002), Matsumoto-Oda (2002), Watts and Mitani (2002), Hirata and Celli (2003), Ueno and Matsuzawa (2004), Stevens (2004), Reynolds (2005), Slocombe and Newton-Fisher (2005), Gilby (2006), Lonsdorf (2006), Mitani (2006), Hockings et al. (2007), Pruetz and Bertolani (2007), Gomes and Boesch (2009), Gilby et al. (2010), Jaeggi et al. (2010), *137–139* Harding (1973), Strum (1975, 1981), *140* Starin (2006), *141* Homburg (1997), *142–144* Utami and van Hooff (1997), van Noordwijk and van Schaik (2009), Forss et al. (2009), *145–149* Horr (1977), Bard (1987, 1992), Jaeggi et al. (2008), van Noordwijk and van Schaik (2009), *150* Kavanagh (1972), *151–153* Cebul and Epple (1984), Yoneda (1984), Goldizen (1989), *154,155* Heymann (1996), Huck et al. (2004), *156* Izawa (1978), *157–168* Wolters (1978), Neyman (1989), Cleveland and Snowdon (1984), Feistner and Chamove (1986), Feistner and Price (1990, 1991, 1999), Savage et al. (1996), Roush and Snowdon (2000, 2001), Joyce and Snowdon (2007), Humle and Snowdon (2008), *169, 170* Fragaszy and Mason (1983), Stevens (2004), *171* Jay (1965), *172* Fox (1972), *173* Gursky (2000)
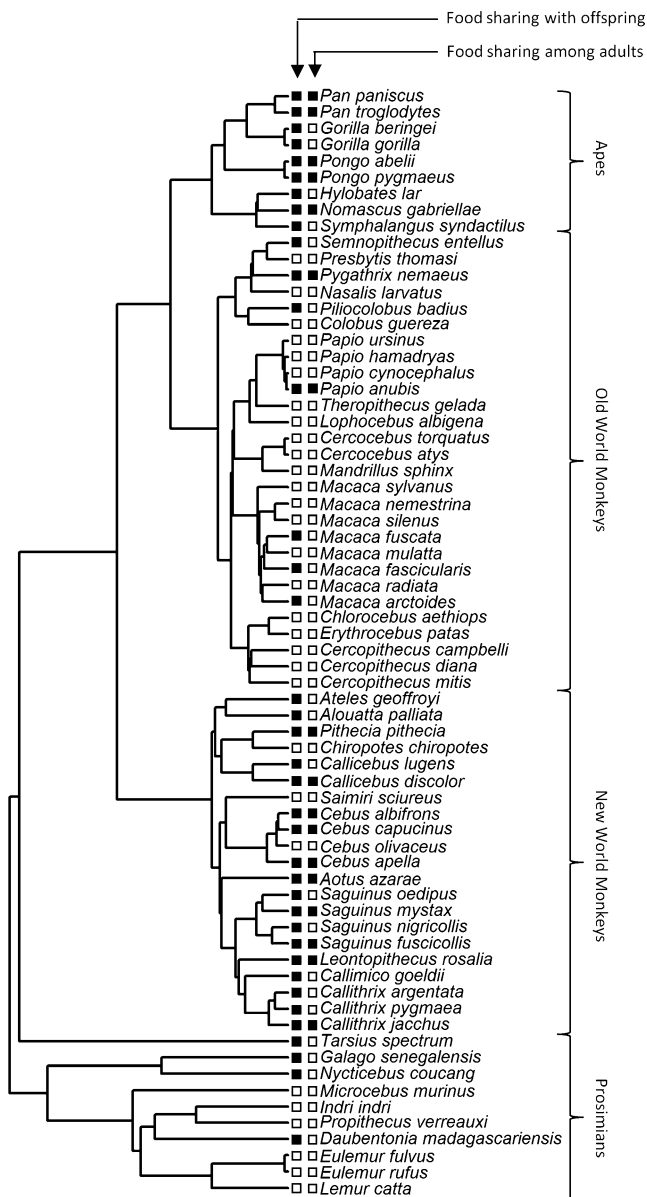
Fig. 1 The phylogenetic tree, based on Bininda-Emonds et al. (2007), of the 68 species in our sample representing all major taxonomic groups of primates (see Table 1). The traits "food sharing with offspring" and "food sharing among adults" are marked as present (*black*) or absent (*white*)

interaction with extractive foraging. We operationalized this by using a *diet quality index* (DQI) as defined by Fish and Lockwood (2003):

$$DQI = 0.33L + 0.67F + M$$

where L, F, and M are the percentages of time spent foraging for leaves and other vegetative plant parts, fruit (including gum and flowers), and meat (indeed any animal matter), respectively. The possible range of DQI values is 0.33–1. The values were obtained directly from Fish and Lockwood (2003) or calculated from Rowe (1996). If

numbers were unavailable for a species, the value of the sister species was used.

Sharing among adults (general)

Our first prediction, inspired by classic ethology, is that sharing among adults is derived from sharing with offspring, the same way courtship feeding in birds is derived from chick provisioning (Tinbergen 1952; Lorenz 1965). Indeed most affiliative behaviors and their proximate regulations are derived from the mother–offspring context (Hrdy 1999, 2009) and the presence of *sharing with offspring* may thus be a *precondition or a constraint* on the evolution of sharing among adults.

Furthermore, as in sharing with offspring, one would predict sharing among adults to occur whenever the cost/benefit ratio of transferring the food item at stake is favorable, in particular when food items are large and/or highly valuable and when possession is biased and/or unpredictable (Kaplan and Hill 1985). Indeed most sharing occurs with items that fulfill these criteria, such as meat (e.g., Strum 1975; Perry and Rose 1994; Utami and van Hooff 1997; Stanford 1999; Mitani and Watts 2001; Hohmann and Fruth 2008; Gomes and Boesch 2009) or large fruits (e.g., White 1994; Hockings et al. 2007; D. Watts, personal communication). However, sharing also occasionally occurs with easily defendable or accessible food items such as small fruits (Slocombe and Newton-Fisher 2005; van Noordwijk and van Schaik 2009) or plentiful browse (Kavanagh 1972), suggesting that the social relationships of the involved individuals were more important than the food items at stake. Nonetheless, it is possible that diet acts as a constraint on the evolution of adult sharing and we thus included the same diet variables used to explain sharing with offspring, i.e., *extractive foraging* and *diet quality index* in the analyses.

Sharing from males to females—female mate choice and pair bonds ("food for sex")

Popularly known as the meat-for-sex hypothesis, it is sometimes assumed that males "buy" immediate mating benefits with high-quality food. However, in chimpanzees, contingent exchanges of food and matings (in the short term) are rare and males also commonly share with lactating females (reviewed by Gilby et al. 2010). Sharing is therefore better seen as an expression of long-term investment in social relationships that might eventually relate to higher mating success, possibly because *not* sharing might lead to *lower* mating success. Thus, the hypothesis can be formulated more generally: Whenever females can exert mate choice, males should allow females to take food in order to maintain their chances of mating with the female in the future (Strum 1981; Gomes and

Boesch 2009; van Noordwijk and van Schaik 2009). In more proximate terms, it could be said that, in the presence of female choice, males and females may form affiliative social bonds, one expression of which is the sharing of food. Hence, we predict that *female mate choice* favors sharing from males to females.

How do we operationalize female choice? First of all, we have to make clear that we are interested in behavioral female choice (and not cryptic female choice), wherein females initiate or terminate association, consortship, or mating (Clutton-Brock and McAuliffe 2009) because the consequences of these behaviors are actually experienced by males and can thus shape their own behavior. Ideally, we would use a direct measure of expressed female choice such as the percentage of female-initiated matings or refused matings. However, such detailed behavioral data are not available for a large sample of species. More generally, female preferences for certain males occur in virtually every species in which researchers have looked for it (Keddy-Hector 1992; Clutton-Brock and McAuliffe 2009). It is difficult to compare the relative influence of female preferences on the distribution of matings across species because this distribution may also be influenced by other factors. For instance, mating skew can be a consequence of both female preference as well as male coercion and male–male competition which can both constrain female choice (Clutton-Brock and McAuliffe 2009). Furthermore, female preferences can vary between species such that mating skew may be high in one species because all females prefer the alpha male but low in other species because females prefer to mate with many males. Other measures such as paternity concentration introduce yet more confounding effects like cryptic female choice or sperm competition. Hence, no clear behavioral measure that captures the actually expressed degree of female choice is available across species.

One thing however is certain: where there is only one male, there is little or no opportunity for female choice. As obvious as it may sound, this can have serious consequences for male–female relationships: For instance, in species where both one-male and multi-male groups occur, female choice is expressed only in multi-male groups (Launhardt et al. 2001), and only males in multi-male groups engage in consorts (Hamilton and Bulger 1992). In species that live in one-male units but form modular societies, which are effectively like multi-male groups because other males are constantly present and threaten to lure away or take over females, male–female grooming rates within units are significantly higher than in non-modular species (Grueter 2009). In fact, affiliative male–female relationships have never been reported in single-male, multi-female groups but are common in multi-male, multi-female groups (Tomasello and Call 1997; Silk 2002). Hence, we use the occurrence of

multi-male groups in a species (yes/no) as a proxy for the opportunity for female choice (source: Rowe 1996) because the only clear "0's" for female choice are one-male groups. If different types of social organization occur in a species, the multi-male score was given. It is important to point out that the presence of multiple males does not simply lead to more opportunities for sharing because male–female proximity is generally *lower* in multi-male groups (e.g., baboons vs. langurs); otherwise, females would be monopolizable by a single male and it would not be a multi-male group (van Schaik and van Hooff 1983). Hence, a positive result is not a by-product of male–female proximity.

In addition, we used a bibliographic frequency measure to validate our use of this binary variable and to predict the actually expressed frequency of male–female sharing and female mate choice within multi-male species. To this end, we searched the ISI Web of Science (all years) for the name of species X (e.g., "*Pan troglodytes*") and also for the name of species X and the term "female mate choice" (e.g., "*Pan troglodytes* female mate choice"). We then divided the number of male–female food sharing studies on species X from Table 1 by the number of hits for the search on that species (we will call this variable *bibliographic frequency of male–female food sharing*) and the number of hits on species X and "female mate choice" by the total number of hits on species X (*bibliographic frequency of female mate choice*).

Another hypothesis is that male–female sharing is a form of provisioning or mating effort in pair-bonded species (e.g., Fragaszy and Mason 1983; Wolovich et al. 2006, 2008a, b). Because pair bonds mainly occur in single-male species, we tested this hypothesis by comparing male–female sharing in *socially monogamous* vs. harem (single-male, multi-female) species (source: Rowe 1996). If other types of social organization (e.g., polyandry) also occur in a species, the monogamy score was given.

Sharing among males/among females—coalitions ("food for support")

In species in which individuals may form coalitions during agonistic interactions, potential recipients have leverage over possessors because they may provide or withhold coalitionary support in the future. As with female mate choice, it is the possibility of partner choice in coalition formation, and hence the risk of losing a valuable partner, that should make possessors comply with recipients' request. Thus, we predict that the occurrence of sharing is associated with the occurrence of *coalitions* (yes/no) across species. In particular, sharing among males should be associated with male–male coalitions and sharing among females with female–female coalitions (source: Plavcan et al. 1995). In order to control for the possibility

that both sharing and coalition formation independently evolved by kin selection alone, we also restricted the dataset to non-kin, i.e., we scored all species as "0" in which the only reported instances of sharing occurred among relatives, as indicated by the authors of the respective studies (Table 1).

Future analyses could also incorporate more detailed variables such as the relative frequency of coalitions and their contribution to an individual's reproductive success as well as same-sex grooming rates. We propose that the presence or absence of coalitions is an appropriate predictor for the presence or absence of social bonds which are translated into the presence or absence of sharing per se, whereas the more detailed measures above could be used to quantify the relative strength of these bonds and thus predict the frequency of sharing.

Comparative analyses

We used both maximum likelihood and Bayesian approaches to test for correlated evolution of the traits of interest while controlling for phylogenetic non-independence. The phylogeny of primates including branch lengths was based on Bininda-Emonds et al. (2007) (see Fig. 1). First, we fitted phylogenetic regression models using generalized estimating equations (GEEs) for discrete traits and phylogenetic generalized least squares (PGLS) for continuous variables (Paradis 2006). All models were fitted with the ape package (Paradis et al. 2009) in R 2.12.1 (R Development Core Team 2010), with binomial (for binary traits) or poisson (for 0/1/2) error distributions for GEE and Brownian correlation structure for PGLS.

Second, for binary traits, we also used a Bayesian method called reversible-jump Markov chain Monte Carlo (RJ MCMC; Pagel and Meade 2006). RJ MCMCs are used to model the evolution of two binary traits assuming either dependent or independent evolution (the latter being the null hypothesis). Similar to a likelihood ratio test, the dependent and independent models are compared by their harmonic means, the Bayesian equivalent of the log likelihood, by calculating the log Bayes factor (BF). Rather than testing the BF against a distribution such as chi square, by convention, a BF >2 is taken as positive evidence for dependent evolution, BF >5 as strong positive evidence, and BF >10 as very strong positive evidence (Pagel and Meade 2006). Furthermore, even in the dependent models, the chain can visit models with independent evolution. Thus, if the proportion of independent models visited, $P_{independent}$, is small, the null hypothesis of independent evolution of the two traits can also be rejected.

In addition, RJ MCMC can be used to indicate the likelihood of trait changes, so-called rate parameters, q (Pagel and Meade 2006). If two traits can have the states 0,

0 (both absent), 0, 1 (first trait absent, second trait present), 1, 0 (first trait present, second trait absent), or 1, 1 (both traits present), the rate parameters q indicate the likelihood of transition between these states (cf. Fig. 3). Hence, one can test whether the evolution of one trait, e.g., "sharing among adults", is more likely in the presence or the absence of the other trait, e.g., "sharing with offspring", by comparing the q for the transition from 0, 1 to 1, 1 with the q for the transition from 0, 0 to 1, 0. For a first examination of this, one can plot the posterior distribution of rate parameters simulated by the RJ MCMC (cf. Online resource 1). Furthermore, one can graphically indicate the likely evolutionary routes of state transitions by modifying the thickness of the arrows according to the mean rate parameters (cf. Fig. 3). In all models, the ancestral state for every trait was estimated to be 0 or 1 with almost equal probability (range of probability for 0=0.49–0.53). However, given that relinquishing food to another individual's benefit as well as providing coalitionary support is costly and thus more unexpected than not doing so, and given that ancestral primates were most probably solitary and nocturnal and all other social systems derived (van Schaik and van Hooff 1983), we propose that ancestral states were probably 0, 0.

RJ MCMC models were run in BayesTraits 1.0 (Pagel and Meade 2011) with a burn-in of 50,000 and 5,050,000 iterations in total, except for male–female sharing, for which 10,050,000 iterations were run because the Markov chains tended to converge later. The first 1,000,000 iterations (2,000,000 for male–female) were discarded. We used an exponential hyperprior (Pagel et al. 2004) because of the relatively weak signal in the data (compared to, e.g., genetic data) and because small values of parameters were more likely than larger ones (i.e., the traits of interest evolved only relatively rarely) and made sure that the posterior distribution of parameters was not truncated by the range of the parameter (see Online resource 1). We used three different rate deviation settings and each model was run six times for each setting to verify that the results were stable (see Online resource 2). The reported BF and $P_{independent}$ are based on means of the six runs for the rate deviation setting that produced the best converging chains and recommended acceptance (see Online resource 2). Furthermore, for each analysis, we plotted the Markov chains and histograms of harmonic means for the reported dependent and independent models to show that the chains did indeed converge to a stable level and the difference between dependent and independent models was constant (Online resource 3). Finally, we ran each analysis once using a much higher number of iterations (20,050,000) to ensure that the chains did not deviate again from the converged level (figure available on request).

Results

General patterns

Of the 68 species in the sample, 38 (55.9%) were reported to share food with offspring. In no species was food shared among adults but not with offspring. Of those 38 species in which food was shared with offspring, in 17 (44.7%) food was also shared among adults. In particular, in 14 species males shared with females, and in seven species each males and females shared among themselves. This distribution of sharing among adults in relation to the presence of sharing with offspring and other predictor variables is summarized in Table 2. Fisher's exact probabilities indicate that these variables are significantly associated. Restricting sharing to non-kin improved the association with coalition formation for males and females. This overview lends preliminary support to the hypothesis that sharing among adults is related to opportunities for partner choice.

Sharing with offspring

Sharing with offspring was significantly positively predicted by the degree of extractive foraging (GEE: $F_{1,65}=7.23$, $P<0.05$) but not by diet quality index ($F_{1,65}=0.25$, $P=0.62$) and the interaction term was a significant negative predictor ($F_{1,65}=6.12$, $P<0.05$; see Table 3 for parameter estimates). This indicates that the difficulty of acquisition, rather than the nutritional quality of food, predicts sharing with offspring and that difficult high-quality diets do not lead to more sharing than difficult low-quality items.

Sharing among adults (general)

Species sharing among adults represented a strict subset of those species sharing with offspring (Fig. 1; Table 2). Thus, sharing with offspring strongly predicted sharing among adults (GEE: $F_{1,65}=21.75$, $P<0.001$) whereas the two diet variables did not (extractive foraging: $F_{1,65}=2.42$, $P=0.15$; DQI: $F_{1,65}=0.95$, $P=0.35$; see Table 3 for parameter estimates). The RJ MCMC provided very strong support for the dependent evolution of these two traits: the log Bayes factor, comparing the harmonic means of the dependent and the independent model, was very high and the chain never (!) visited independent evolution (see Table 3). The posterior distribution of rate parameters (given in Online resource 1 and summarized in Fig. 3a) also strongly indicated dependent evolution (compare, e.g., $q=0.0$ vs. $q=13.0$ for probability of evolutionary gain of the trait "sharing among adults" in the absence or presence of the trait "sharing with offspring").

Because sharing with offspring can thus be seen as a necessary precondition for or a constraint on the evolution of sharing among adults, we reduced our sample to species already sharing with offspring ($N=38$) in order to further test what factors explain sharing among specific sex combinations of adults. The two diet variables did not predict sharing among adults in general and were also never significant if included in the subsequent models; thus, the details of these analyses are not reported.

Sharing among adults (specific sex combinations)

From males to females

The presence of multi-male groups significantly predicted sharing from males to females ($F_{1,37}=6.53$, $P<0.05$; see Table 3) and the RJ MCMC also provided positive evidence for the dependent evolution of these two traits (Table 3; Online resource 1). Within single-male species ($N=15$), male–female sharing only occurs in socially monogamous and never in single-male multi-female species (means, 0.20 vs. 0; because of the strong association, GEE could not be computed). Hence, the female mate choice hypothesis for the evolution of sharing from males to females was supported (Fig. 2a), whereas the pair–bonds hypothesis may be supported within single-male species.

Table 2 Contingency table showing the distribution of species in Table 1 across food sharing contexts and our predictor variables, as well as Fisher's exact tests for the association of these variables

		Sharing with offspring[a]		Multiple males[b]		Male–male coalitions[c]		Female–female coalitions[c]	
		1	0	1	0	1	0	1	0
Sharing among adults	1	17	0	12	2	4	3 (1)	3	4 (1/0)
	0	21	30	11	13	4	27 (29)	2	29 (32/33)
Fisher's exact		$P<0.001$		$P<0.05$		$P<0.05$ ($P<0.01$)		$P<0.05$ ($P<0.01$)	

[a] This refers to the whole sample ($N=68$) and any dyad of adults

[b] Multi-male species vs. single-male species; this refers to male–female sharing in species already sharing with offspring ($N=38$)

[c] This refers to male–male and female–female sharing, respectively, in species already sharing with offspring ($N=38$). The numbers in parentheses refer to sharing only among non-kin (for females, P. nemaeus was assumed to be non-kin/kin)

Table 3 Overview of the comparative analyses testing for the correlated evolution of food sharing and other traits, and the support for the related hypotheses. Significant factors are in bold

Food sharing	N	Factors	GEE[a]	RJ MCMC[b]	Related hypotheses	Supported?
With offspring	68	Intercept	−1.03			
		Extractive foraging	1.86*		Informational hypothesis	+
		DQI	0.86		Nutritional hypothesis	−
		Extractive foraging* DQI	−2.32*			−
Among adults (general)	68	Intercept	−2.84			
		Sharing with offspring	1.35***	P_{ind}=0, BF=30.94	Constraint/precondition	+++
		Extractive foraging	0.38			−
		DQI	−0.49			−
From males to females[c]	38	Intercept	−1.87			
		Multi-male groups	1.96*	P_{ind}=0.004, BF=3.9	Female mate choice ("food for sex")	+
Among males[c]	38	Intercept	−2.20			
		Male–male coalitions	2.20*	P_{ind}=0.001, BF=8.58 (P_{ind}=0.0003, BF=9.94)[d]	Coalition partner choice ("food for support")	++
Among females[c]	38	Intercept	−1.98			
		Female–female coalitions	2.39*	P_{ind}=0.001, BF=6.6 (P_{ind}=0, BF=11.92)[d]	Coalition partner choice ("food for support")	++

[a] Generalized Estimating Equations, a version of phylogenetic generalized least squares analyses used for discrete response variables (Paradis 2006). Reported are the parameter estimates (SE not available for GEE) with significance level (see text for F-values)

[b] Reversible-jump Markov chain Monte Carlo, a Bayesian method for testing the dependent evolution of two discrete traits (Pagel and Meade 2006). Reported are the proportion of dependent models that jumped to independent evolution of the traits, indicated by the probability for independent evolution (P_{ind}), as well as the log Bayes factor, which measures the fit of the dependent model relative to the independent model (see also Supplementary Table 1 for the stability of Bayes factors across different parameter settings of the models). By convention, a BF >2 is taken as a positive evidence for dependent evolution, >5 indicates strong positive evidence, and >10 indicates very strong positive evidence

[c] Only species in which there is food sharing with offspring

[d] The values in parentheses refer to the analyses restricted to sharing among non-kin

*P<0.05; ***P<0.001

Furthermore, the bibliographic frequency of female mate choice was significantly higher in multi-male species than in single-male species (Wilcoxon: W=432, P<0.01; Online resource 4), indicating that females in multi-male groups do indeed have more opportunities for mate choice, which validates our use of this binary variable to measure female choice. Finally, within multi-male species (N=23), the bibliographic frequency of female mate choice significantly predicts the bibliographic frequency of male–female food sharing (PGLS: *Intercept* (±SE)=0.001 (±0.003), t=0.37, P= 0.72; *female mate choice*=0.22 (±0.09), t=2.35, P<0.05; Online resource 4), suggesting that male–female sharing is more frequent in multi-male species with more female choice.

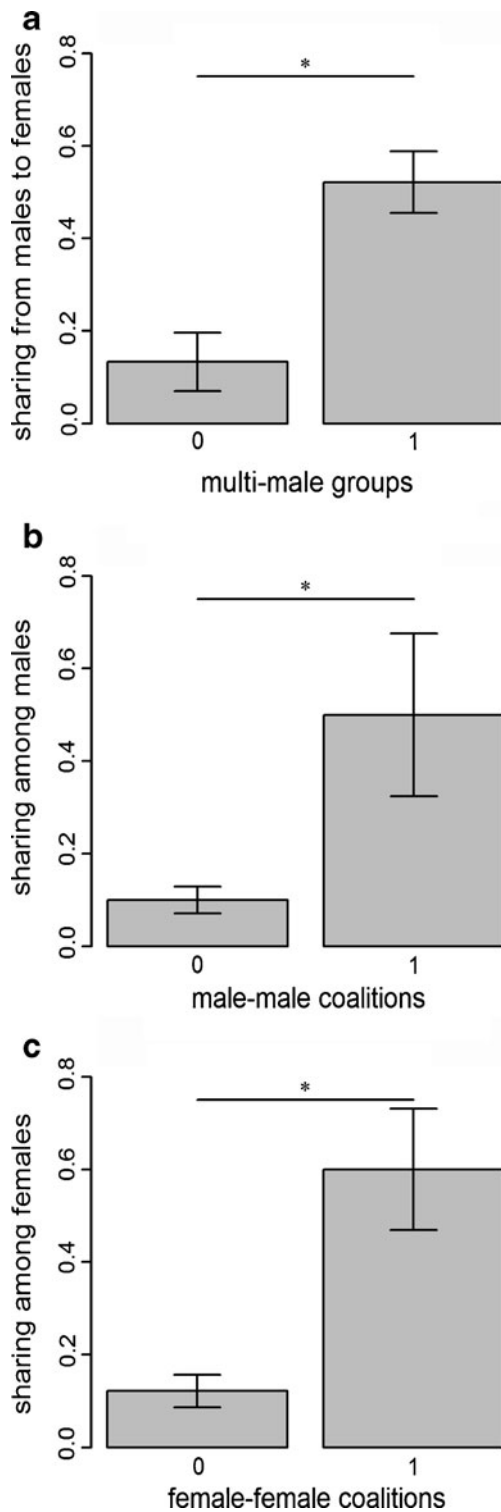### Among males

The presence of male–male coalitions significantly predicted male–male sharing (GEE: $F_{1,37}$=6.15, P<0.05; Table 3; Fig. 2b) and the RJ MCMC also provided strong support for dependent evolution (Table 3; Fig. 3b; Online resource 1). Hence, the hypothesis that male–male sharing co-evolved with male–male coalitions was supported.

To further exclude the influence of kinship, species for which sharing has only been reported among (confirmed or suspected) relatives were given a "0". Specifically, this concerned *Saguinus fuscicollis* and *Pithecia pithecia*, both of which do not form male–male coalitions (Table 1). Because there was an even stronger association between sharing (1) and coalition formation (1) and not sharing (0) and no coalition formation (0), respectively, in the resulting sample (cf. Table 2), GEEs could not be computed. However, as expected from this stronger association, the RJ MCMC provided an even stronger support for the correlated evolution of sharing among unrelated males and male–male coalitions (Table 3; Fig. 3b; Online resource 1). Thus, the hypothesis that male–male sharing co-evolved with male–male coalitions was supported even better when only sharing among unrelated males was considered.

Among females

The presence of female–female coalitions significantly predicted sharing (GEE: $F_{1,37}$=7.91, P<0.05; Table 3; Fig. 2c) and the RJ MCMC also provided a strong evidence

Fig. 2 Mean (± SEM) occurrence of food sharing **a** from males to females, **b** among males, and **c** among females in species in which **a** multi-male groups, **b** male–male coalitions, and **c** female–female coalitions are absent (*0*) or present (*1*). In all cases, the occurrence of food sharing is significantly higher in species in which the traits are present. The significance values (**P*<0.05) refer to the respective GEE models (Table 2)

for dependent evolution (Table 3; Fig. 3b; Online resource 1). Hence, the hypothesis that female–female sharing co-evolved with female–female coalitions was supported.

To further exclude the influence of kin selection, species for which sharing has only been reported among (confirmed or suspected) relatives were given a "0". Specifically, this concerned *Nomascus concolor*, *Pongo abelii*, and *Pongo pygmaeus*. No relatedness information could be obtained for the group of *Pygathrix nemaeus* studied by Kavanagh (1972); hence, non-kin food sharing was treated as unknown. None of these species form female–female
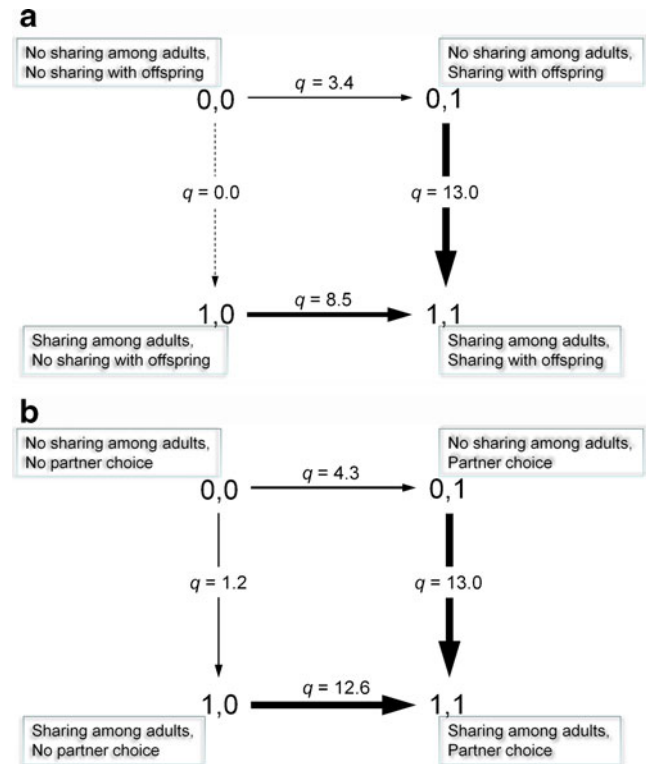
Fig. 3 Flow charts for the evolution of food sharing among adults (first trait) in the presence or absence of **a** food sharing with offspring and **b** opportunities for partner choice (second traits) as analyzed with the RJ MCMC method. The thickness of the arrows is proportional to the mean value of the rate parameters *q* in the posterior sample and thus indicates the likelihood of the transition from one state to another. By comparing *opposite* arrows, it can clearly be seen that the evolution of sharing among adults is much more likely if **a** sharing with offspring or **b** opportunities for partner choice is already present as a trait (and vice versa, although sharing among adults is unlikely to evolve first). The values of *q* in **b** are the means of the sex combination-specific analyses, i.e., male–female, male–male, and female–female sharing and multi-male groups, male–male coalitions, and female–female coalitions, respectively (see Online resources 1 for full details). Note that **a** is based on 68 species while **b** is based on only 38 species, namely, those in which sharing with offspring was already present, and only refers to sharing among unrelated adults. Furthermore, note that only the arrows for evolutionary gains of traits are represented; the ones for losses were omitted in this figure (but not in the analyses, see Online resources 1) because we assume the ancestral state here to be 0, 0

coalitions (Table 1). Again, because there was an even stronger association between sharing (1) and coalition formation (1) and not sharing (0) and no coalition formation (0), respectively, in the resulting dataset (cf. Table 2), GEEs could not be computed. However, as expected from this stronger association, the RJ MCMC provided an even stronger support for correlated evolution of sharing among unrelated females and female–female coalitions (Table 3; Fig. 3b; Online resource 1). Thus, the hypothesis that female–female sharing co-evolved with female–female coalitions was supported even better when only sharing among unrelated females was considered.

Discussion

In this study, we tested several hypotheses about the evolution of food sharing in primates. Firstly, sharing with offspring was predicted by the degree of extractive foraging, which should indicate the relative processing difficulty of food items and thus the relative benefits to offspring gained from food transfers. Secondly, sharing with offspring in return strongly predicted sharing among adults to the extent that the latter could only evolve in presence of the former (see Fig. 3a). Diet variables, on the other hand, did not predict sharing among adults. Thirdly, food sharing among (unrelated) adults coevolved with conditions for partner choice and thus the opportunity for reciprocal exchange (see Fig. 3b). In particular, our analyses suggest that males share with females whenever these can bias matings to other males, i.e., when there is opportunity for female mate choice ("food for sex"), and males and females share in species that form coalitions ("food for support"). By excluding sharing among relatives, we could rule out kin selection as a primary evolutionary mechanism. Thus, reciprocal exchange seems to be a main explanation accounting for the presence of sharing among unrelated adults across a large sample of primates. These overall findings are summarized in Fig. 4. In addition, there was some indication that within single-male species, male–female sharing was more common in socially monogamous species. The current analyses could, in the future, be extended with more detailed behavioral variables such as sex combination-specific grooming rates, the frequency of coalitions and their influence on reproductive success, the actual amount of exerted female mate choice (e.g., the percentage of female-initiated matings), etc. and predict frequencies rather than just the presence of sex combination-specific sharing.

The result that sharing coevolved with opportunities for partner choice across a broad range of species is in line with more detailed, within-species analyses testing for the exchange of food with itself and various other services
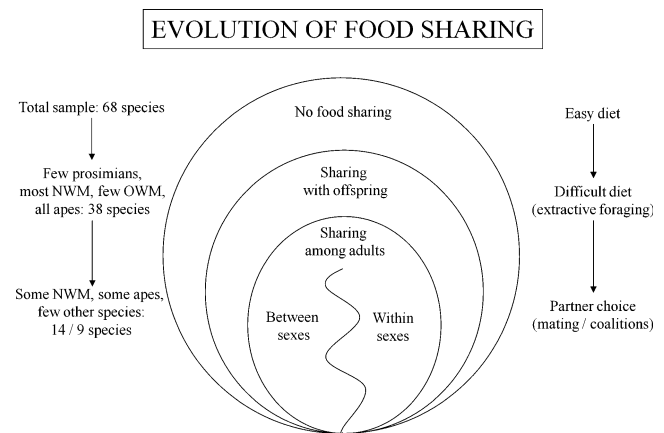
Fig. 4 This figure summarizes our findings on the evolution of food sharing in primates: Of the 68 species in the total sample, sharing with offspring evolved in the subset of those with relatively difficult diets, as measured by the degree of extractive foraging, indicating differential acquisition of food by adults and offspring and thus high benefits to sharing. Within those 38 species sharing food with offspring, sharing among adults was more likely to evolve in the subset of species with opportunities for partner choice, indicating that food is shared in order to increase (or not decrease) the chance of future matings (between sexes) or coalitionary support (within sexes). NWM New World monkeys, OWM Old World monkeys

between individuals of the same population (e.g., de Waal 1989, 1997, 2000; Gilby 2006; Mitani 2006; Gomes and Boesch 2009; Jaeggi et al. 2010c). As laid out in the introduction, the fact that sharing is most often elicited by harassment does not speak against the occurrence of reciprocal exchange in a statistically measurable way that can be under selection. This study thus lends further support to the growing body of evidence for the reciprocal exchange of low-cost altruistic acts among primates (Silk 2002; Schino 2007; Schino and Aureli 2009).

Sharing among adults only evolved in a subset of species, namely, those in which sharing with offspring had already been established, indicating that the preexistence of sharing with offspring may constrain the evolution of sharing among adults (Fig. 3a). The latter can therefore be seen as derived behavior (Tinbergen 1952), which could be pressed into service in another context. An analogous example would be courtship feeding in birds (Amat 2000), which is clearly derived from offspring provisioning, employing the same behavioral patterns (Lorenz 1965). Interestingly, courtship feeding is also used among juvenile birds to strengthen social bonds (von Bayern et al. 2007) or establish dominance relationships (Scheid et al. 2008). However, the bird studies also show a clear functional difference between *possessor-initiated* sharing, which is derived from provisioning and actively used as a costly signal, and *recipient-initiated* sharing, which is a passive response to a request by an important social partner and may thus lead to reciprocal exchange (Scheid et al. 2008).

Only the latter form is common among adult primates (Jaeggi et al. 2010a).

Diet did not seem to predict or constrain sharing among adults as the diet variables included in the analysis never improved the models or reached significance. It may well be that the diet variables were too broad to capture any variation in the occurrence of feeding situations with cost/benefit ratios conducive to food transfers that may exist between species (Kaplan and Hill 1985). On the other hand, while certain food types such as meat and large fruit in the diet will surely lead to *more frequent* sharing, the fact that sharing also occurs with trivial food items (Kavanagh 1972; Slocombe and Newton-Fisher 2005; van Noordwijk and van Schaik 2009) indicates that diet alone cannot explain the presence of sharing *per se*.

Although the associations we found between food sharing and the predictor variables were significant, they were not absolute. Thus, some species in which sharing could potentially have been used to maintain coalitionary relationships or facilitate mate choice did not do so (cf. Table 2). For instance, no sharing occurs among olive baboon males despite the presence of male–male coalitions (Table 1). This can be explained by the steep dominance hierarchy in this species, allowing dominant males to acquire food by force and not having to depend on (and thus share with) other males for coalitionary support. Coalitions are only formed by post-prime males who do not get a chance to become food possessors and thus cannot trade food for support (Strum 1975; Strum 1981; Noë and Sluijter 1995). Similar arguments can be made for dominance constraints on food for support among females or female mate choice. Hence, strong dominance hierarchies can obviate opportunities for reciprocal exchange (Trivers 1971; Noë and Hammerstein 1995; Jaeggi et al. 2010c).

Given shareable items and the conditions shown here to be associated with sharing, our results allow predictions that can be tested with more detailed analyses. For instance, the causal link between multi-male groups and male–female sharing could be investigated by comparing single-male vs. multi-male groups of the same species (Hamilton and Bulger 1992; Launhardt et al. 2001) or by comparing closely related modular and non-modular species (Yeager and Kirkpatrick 1998; Grueter and van Schaik 2009). In particular, among Asian colobines, tolerance within one-male units is higher in modular species (Grueter 2009) and some sharing has been reported in captivity (Kavanagh 1972; Zhang et al. 2008). Furthermore, species with high levels of cooperation among males, such as *Ateles geoffroyi* (Aureli et al. 2006) or *Cacajao calvus* (Bowler and Bodmer 2009), should have evolved strong bonds potentially expressed in sharing. If sharing is rare or absent in the wild, simple experiments using monopolizable food in captivity (e.g., de Waal 1989; de Waal 1997; Zhang et al.

2008; Jaeggi et al. 2010c) could be used to test these predictions.

Furthermore, any other animal species in which opportunities for partner choice and thus social bonds occur should potentially share food. However, diet type may turn out to be a stronger constraint on sharing than in primates where virtually every species consumes some items prone to be shared (Harding 1981). For instance, dolphins and other toothed whales form alliances and have long-lasting social relationships (Connor et al. 1998; Connor 2007), but there are only a few reports of food sharing (Johnson 1982; Hoelzel 1991; Guinet et al. 2000), probably because the majority of consumed items (fish) are too small to be shared and because of observation difficulties. Similarly, elephants (Poole and Moss 2008) and many birds (Emery et al. 2007) have complex social relationships but may not encounter food items likely to be shared. Nonetheless, these species could easily be tested in captivity. On the other hand, very large food items such as animal carcasses containing many times the quantity an individual could consume alone make sharing almost inevitable because the benefits of defending are minimal to the point of monopolization becoming impractical. Thus, carcass sharing occurs in ravens (Heinrich 1988a; Heinrich 1988b) and many social carnivores (e.g., East and Hofer 1991) but may not represent sharing as defined here and is thus not necessarily linked to exchange of other favors. Furthermore, some instances of non-kin sharing among animals clearly serve other functions such as mate provisioning (Vahed 1998) or costly signaling (Zahavi 1990; Scheid et al. 2008).

Lastly, food sharing is also a universal feature of human forager societies where most of the functional hypotheses discussed here probably apply to some extent (Kaplan and Hill 1985; Hawkes 1993; Gurven 2004; Marlowe 2004; Gurven and Hill 2009). However, it should be noted that, rather than being a relatively infrequent event as in primates, human food sharing takes the form of daily provisioning both within and between families and is an indispensable component of the human foraging niche and cooperative breeding system (Kaplan and Gurven 2005; Hrdy 2009; Kaplan et al. 2009). Thus, sharing has a higher adaptive value than in other species which has probably led to a more active and prosocial sharing psychology in humans (Jaeggi et al. 2010a).

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