



Infant Handling Among Primates

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Primates, particularly females, tend to be attracted to infants that are not their own, and are often motivated to touch and handle them. However, species vary markedly in forms of handling and extents to which handling constitutes direct care, other affiliative behaviors, or aggression/abuse. Here, we review infant handling among primates from ultimate and proximate perspectives, focusing on a promising, but understudied hypothesized benefit—that handling enhances social bonds. We pay special attention to macaques and baboons, because handling in most of these species poses a special challenge in that it involves little actual care, and hence may be shaped by different and as yet unclear selective pressures from typical alloparental care. Costs, benefits, and hypothesized functions appear to vary across species based on multiple factors: a) individuals' roles and characteristics, b) relationships between handlers and mothers, and c) the social context within the group. As a result, observed patterns of handling appear to be complex outcomes of the interaction between different, sometimes conflicting interests. Consequently, single unitary explanations for handling are as yet elusive. The most promising hypotheses based on short/medium term benefits appear to vary with species, breeding system, reproductive biology, socioecological factors, and life history characteristics. Explanations based on life history variables or long-term evolutionary processes related to cooperation appear to have broader applications, but nevertheless fail to explain infant handling in all its manifestations. We end by calling for more quantitative comparative and longitudinal research to further elucidate our understanding of this puzzling behavior.

Keywords: infant handling, allocare, social bonds, macaques, baboons

Among many mammalian species, including primates, individuals other than the mother show strong attractions towards infants, and frequently touch/handle them (e.g., elephants [*Loxodonta africana*], Lee, 1987; lions [*Panthera leo*], Packer & Pusey, 1984; bottlenose dolphins [*Tursiops truncatus*], Mann & Smuts, 1998; bats [*Nycticeius humeralis*], Wilkinson, 1992; and mongooses [*Suricata suricatta*], Clutton-Brock et al., 2001, reviewed in Reidman, 1982). The goal of this paper is to review the literature surrounding infant handling by nonmothers, specifically among non-human primates. We use the terms “infant handling” or “non-maternal touch” which have replaced “aunting,” a term used in some early literature that is potentially misleading about the sex and kinship of handlers. We do not discuss male infanticide, which is functionally distinct and recently reviewed (e.g., Palombit, 2012). We focus on handling of infants during their first few months, omitting discussions of adult male associations with older infants and immatures, as these associations are not typically delineated as infant handling *per se*, and may be more characterized by proximity relationships rather than touch (for recent investigations, see Moscovice, Heesen, Di Fiore, Seyfarth, & Cheney, 2009; Minge, Berghänel, Schülke, & Ostner, 2016). First, we describe the varied forms of handling observed among species. We also discuss several proximate characteristics that appear to influence not only the infant's attractiveness to non-maternal group members, but also its propensity to be handled by them. We then discuss several proposed functional explanations for infant handling among primates based on immediate benefits and costs as well as longer term effects on life history variables and fitness, making special distinctions for macaques and baboons because their limited forms of handling pose special challenges to our understanding of its function. Finally, we pay special attention to the potential role infant handling may have in shaping social

bonds between mothers, infants, and handlers, outlining the need for future comparative and longitudinal studies. We aim to emphasize three related points: 1) handling exchanges are influenced by a variety of factors (e.g., the individual's role in the interaction, dominance relationships of the species, socioecological factors, breeding system, etc.), 2) as yet, no unitary explanation accounts for all aspects and observed variations of handling within and across species, and 3) valid explanations for handling may differ depending on the species.

Infant Handling: Forms and Species Differences

Infant handling among primates takes a variety of forms (Table 1). Some forms, such as prolonged or protective carrying, provisioning, and allolactation, provide direct benefits to infants and mothers (Bales, Dietz, Baker, Miller, & Tardif, 2000; Stanford, 1992), and are considered to represent types of alloparental care. Extensive or protective carrying is common across a range of Old and New World species (see Table 1, Ross & MacLarnon, 2000), whereas direct provisioning of solid food is primarily confined to Callitrichids, a few New World species, and chimpanzees (*Pan troglodytes*) (Whitten, 1987). While allolactation, also commonly referred to as allonursing or non-maternal nursing, has been observed in some primate species (wedge-capped capuchins [*Cebus olivaceus*], O'Brien & Robinson, 1991; ring-tailed lemurs [*Lemur catta*], Gould, 1992; Bolivian squirrel monkeys [*Saimiri boliviensis*], Williams et al., 1994; patas monkeys [*Erythrocebus patas*] and some guenons [*Cercopithecus spp.*], Chism, 2000; snub-nosed monkeys [*Rhinopithecus spp.*], Clutton-Brock, 2016; Ren, Li, Garber, & Li, 2012; Packer, Lewis, & Pusey, 1992; reviewed in Reidman, 1982), it is characteristically rare compared to other mammals.

Other forms of handling, including passive touching, nuzzling, grooming, and nonprotective or brief forms of embracing or carrying (Dunayer & Berman, 2017; Silk, Rendall, Cheney, & Seyfarth, 2003) are affiliative, but provide no direct care or discernible benefits to either the infant or mother. Often, would-be affiliative handlers approach infants while they are on their mothers and spend some time grooming the mother before attempting to touch her infant (e.g., Muroyama, 1994). The use of grooming along with specialized affiliative vocalizations (e.g., girneys and soft grunts) preceding and during the handling interactions (macaques [*Macaca spp.*], Bauers, 1993; Silk, Kaldor, & Boyd, 2000; baboons [*Papio spp.*], Silk, Rendall, et al., 2003) may function to signal benign intent to the mother (but see Whitham, Gerald, & Maestriperi, 2007).

In addition to these widespread forms of affiliative handling, some macaque species (Barbary macaque [*M. sylvanus*], Tibetan macaque [*M. thibetana*], Assamese macaque [*M. assamensis*], and stump-tail macaque [*M. arctoides*]) engage in a unique form of handling known as bridging (Ogawa, 1995a; personal communication, H. Ogawa), also referred to as male-infant-male interactions. Although the details of the behavior vary between species, a typical bridging interaction involves one individual briefly carrying and presenting the infant to another individual, both individuals simultaneously lifting the infant, and creating what resembles a "bridge" between them (Figure 1). Bridging is often accompanied by teeth-chattering by both adults, along with genital inspection/manipulation of the infant. Bridging is most commonly observed between adult males, though adult female (H. Ogawa, personal communication) and heterosexual bridging pairs also occur (Ogawa, 1995b). It is hypothesized that bridging between males may function as a social tool to buffer aggression (Barbary macaque, Paul, Kuester, & Arneemann, 1996; Whiten & Rumsey, 1973; Tibetan macaque, Ogawa, 1995a), to facilitate interaction (Tibetan macaque, Ogawa, 1995a; Barbary macaque, Henkel, Heistermann, & Fischer, 2010), and/or to forge, maintain, or manipulate bonds between bridging partners (Assamese macaque, Kalbitz, Schülke, & Ostner, 2017). Savanna and gelada baboon males also carry infants to other males without performing other ritualized behaviors associated with bridging, a behavior that also appears to serve a similar function of agonistic buffering and appeasement (baboons, Packer, 1980; Smith &

Whitten, 1988; gelada [*Theropithecus gelada*], Dunbar, 1984). These interactions are normally gentle in nature; infants rarely show signs of distress (Ogawa 1995a, 2018) and sometimes appear to solicit the behavior by approaching adult males while teeth-chattering (Observation, 2011). Nevertheless, as these behaviors provide no immediate/discernible benefits to either the infant or mother, they are not considered to constitute forms of alloparental care.

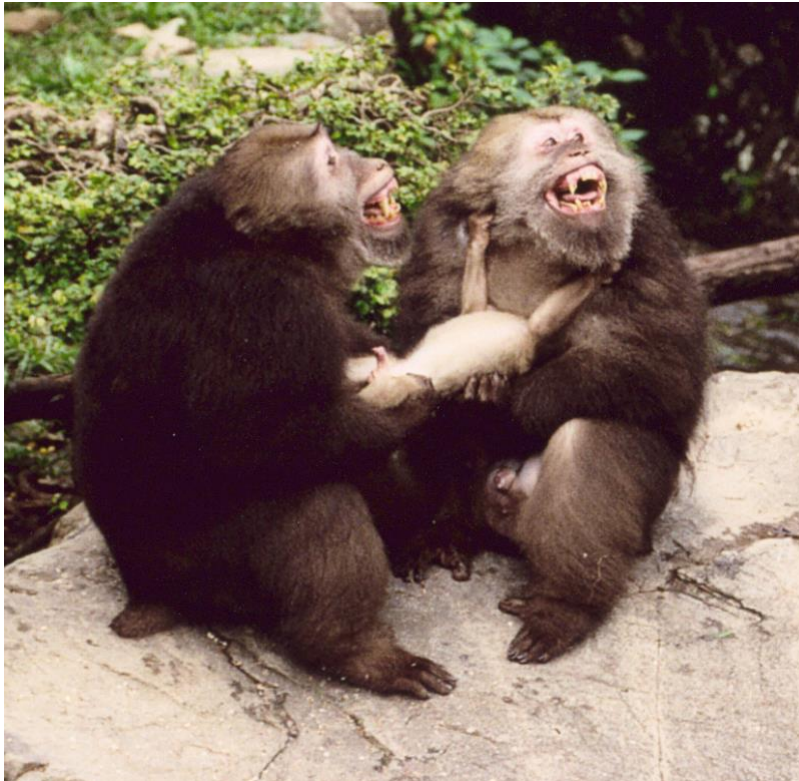


Figure 1. Bridging behavior between two male Tibetan macaques. Photo credit: Carol Berman and Consuel Ionica.

Play with infants also typically involves various forms of touch. However, many primate researchers, unlike researchers of other mammals, exclude play from their definitions of infant handling, considering it to be distinct not only in form, but also in function (Dunayer & Berman, 2017).

Finally, some primates engage in apparently abusive handling, which can include biting, forceful removal from the mother, and sitting on, stepping on, or even dragging the infant over rough terrain (Nicolson, 1987). The variety of handling forms (e.g., alloparental, affiliative, and/or abusive) most likely serve different functions, and may be under different selective pressures.

Table 1
Handling Forms and Amounts of Allocare among Primates

Genus	Common Name	% Allocare^a	Allocare Group^b	Handling Forms	Handling Forms References
Callimico	Goeldi's monkey	70.5	4	Carry	Schradin & Anzenberger, 2001
Callithrix, Cebuella, Leontopithecus, & Saguinus	Callitrichids	46.7-86.7; <i>M</i> = 63.2	2-4; 4	Carry, Provision, Allonurse	Goldizen, 1987; Tardif et al., 1992; Digby, 1995
Alouatta	Howler Monkey	8.4-11; <i>M</i> = 9.7	2	Cuddle, Carry, 'Interest'	Clarke et al., 1998
Ateles & Lagothrix	Spider & Woolly Monkey	NA	1	Greet, Sniff, Nuzzle, Inspect	Slater et al., 2007
Cebus & Sapajus	Capuchin	NA	2	Allonurse, Inspect, Nuzzle Groom, Touch, Carry	O'Brien & Robinson, 1991; Manson, 1999; Baldovino & Di Bitetti, 2008; Sargeant et al., 2015
Samiri	Squirrel Monkey	30	3	Allonurse, Dorsal Cling, Carry	Williams et al., 1994
Aotus	Owl Monkey	91-92.1; <i>M</i> = 91.5	4	Carry	Dixson & Fleming, 1981
Callicebus	Titi Monkey	86-96; <i>M</i> = 91	4	Carry, Groom, Nuzzle	Fragaszy et al., 1982
Cercopithecus	Guenons	19.6	1-2; 2	Touch; Investigate; Carry; Hold; Groom; Cuddle	Lancaster, 1971; Fairbanks, 1990; Meaney et al., 1990
Erythrocebus	Patas Monkey	10.3	2	Carry, Contact, Nuzzle, Groom, Close Visual Inspection, Allonurse	Zucker & Kaplan, 1981, Chism, 2000
Colobus	Colobines	52	3	Carry	Horwich & Manski, 1975
Semnopithecus	---	33.2	3	Ventral Contact, Hug, Carried	Scollay & DeBold, 1980
Trachypithecus	---	33.1	3	Carry, Hold, Groom, Nuzzle, Inspect	Kumar et al., 2005; Jin et al., 2015
Rhinopithecus	Snub-nosed Monkeys	NA	NA	Allonurse	Ren et al., 2012
Macaca	Macaques	0-13; <i>M</i> = 3.9	1-2; 1	Touch, Nuzzle, Smell, Inspect, Groom, Distinct Vocalizations, Limited Holding/ Carrying, Bridging (in select species)	Small, 1990; Silk, 1999, Dunayer & Berman, 2017
Papio	Baboons	1.3	1	Touch, Nuzzle, Smell, Inspect, Groom, Distinct Vocalizations, Limited Holding/ Carrying	Silk, Rendall, et al., 2003
Hylobates	Gibbons	0	1	NA	NA
Symphalangus	Siamangs	50	3	Carry, Groom	Lappan, 2008
Gorilla	Gorillas	NA	1	NA	NA

Table 1 Continues

Table 1 Continued

Pongo	Orangutan	0	1	NA	NA
Pan paniscus	Bonobo	NA	1	Grooming, Carrying, Cradling	Boose et al., 2018
Pan troglodytes	Chimpanzee	3.8	1	Touch, Groom, Hold, Carry	Bădescu, Watts, et al., 2016

Note. NA indicates not available. ^aValues based on Ross and MacLarnon (2000): amount of time an infant is held or carried by non-mothers as the percentage of total time the infant is held or carried. ^bValues based on Ross and MacLarnon (2000): 1 = no or very low allocare, 0-5%; 2 = low allocare, >5-30%; 3 = medium allocare, >30-55%; 4 = high allocare, >55%.

Attractiveness, Access, and Handling

The attractiveness of infants to members of their group is virtually universal within the primate order, and attraction to infants is hypothesized to form the motivational basis that leads to most forms of handling by individuals in addition to the mother. Conceptually, attraction to infants is related to but distinct from handling. Attraction does not necessarily involve touch, and does not inevitably lead to touch (see below) due to interaction with other factors. Moreover, attraction can be measured separately, for example, through proximity seeking, specialized vocalizations, and gestures (e.g., Dunayer & Berman, 2017). However, given the conceptual closeness between attraction and handling, we discuss infant attractiveness, also called natal attraction, as it may relate to the proximate and functional factors that appear to shape infant handling.

Physical characteristics of infants, such as their small size, clumsy gait, relative hairlessness, and disproportionately large and rounded facial features and ears all seem to contribute to strong levels of attraction (Alley, 1980; Hrdy, 1976), and typically disappear by about three months of age in most Cercopithecines. Some primate infants (e.g., Colobines, stumptail macaques, vervets [*Chlorocebus pygerythrus*], baboons) also have flamboyant or conspicuous natal coats that begin to give way to more adult forms after six weeks of age, and, in many species, are completely gone by around 18 weeks after birth (Treves, 1997; but see Li, 1999, for Tibetan macaques whose fur continuously darkens from infancy throughout life). Cross-species analysis ties conspicuous natal coat color to high levels of allocare (Ross & Regan, 2000). As these infantile features disappear, so does the infant's attractiveness to handlers (Bădescu, Sicotte, Ting, & Wikberg, 2015; Hrdy, 1976). Consequently, infant age is an important proximate characteristic that influences the handling interactions (colobus [*Colobus spp.*], Horwich & Manski, 1975; Bădescu et al., 2015; Hanuman langur [*Semnopithecus entellus*], Scollay & DeBold, 1980; bonnet macaque [*M. radiata*], Silk, 1999; and chacma baboon [*P. ursinus*], reviewed in, Hrdy, 1976; MacKinnon, 2011; Maestripieri, 1994a; Silk, Rendall, et al., 2003). Data from bonnet macaques (Silk, 1999) illustrate the relationship of handling to infant age well; mean rates of handling were more than eight times higher for one-month-old infants (5 events/hr), and over three times higher for three-month-old infants (2 events/hr) than for six-month-old infants (0.6 events/hr).

Additional proximate factors also contribute to an infant's attractiveness, evidenced by the observation that some similarly aged infants appear to be more attractive than others. Variations in attractiveness, as well as whether attractiveness translates into actual handling, is influenced by both the potential handler's and the mother's characteristics (Table 2), particularly as they interact with the mother's degree of protectiveness/permisiveness. High levels of protectiveness among mothers appear to be particularly common in more despotic species (e.g., most macaques and baboons), compared to more tolerant species (e.g., Colobines). For example, Colobine mothers allow others to carry their infants within the first few hours of birth (Jin, Wang, Pan, & Yao, 2015; Kumar, Solanki, & Sharma, 2005; McKenna, 1979). In contrast, despotic mothers typically restrain their infants from being handled, by holding onto them tightly, or by behaving

aggressively towards non-mothers attempting to interact with their young infants (Schino, Speranza, Ventura, & Troisi, 2003). However, protective despotic mothers tend to be more tolerant of attempts to handle their infants by their close associates than by others. As such, many of the proximate social characteristics mediating handling interactions tend to mirror those that shape mothers' social relationships in the group (Berman, 1982a; Silk, Rendall, et al., 2003). One especially salient characteristic is maternal kinship, particularly in species in which females remain in their natal groups for life (i.e., species with female philopatry). In these species, which include macaques and most baboons, female social relationships are typically structured along lines of maternal kinship such that females form strong and enduring social bonds preferentially with close maternal kin. Given mothers' increased tolerance for her close associates, infant handling is more commonly observed between close maternal kin than distant kin or unrelated individuals in species and groups with strong degrees of affiliative kin bias among females (macaques, Berman, 1982a; Dunayer & Berman, 2017; Schino et al., 2003; Silk, 1999; vervets, Fairbanks, 1990; wedged-capped capuchins, O'Brien & Robinson, 1991; chacma baboons, Silk, Rendall, et al., 2003; and black and white colobus [*C. vellerosus*], Bădescu et al., 2015). For example, in a recent study of rhesus macaques (*M. mulatta*) (Dunayer & Berman, 2017), close kin (siblings and grandmothers) were found to handle infants more than five times as much as unrelated individuals did (3.44% vs. 0.66% of time they spent in proximity to the infant). In other species or groups, maternal kinship does not appear to influence the handling interaction (capped langurs [*Trachypitecus pileatus*], Stanford, 1992; patas monkeys, Muroyama, 1994; Bolivian squirrel monkeys, Williams et al., 1994; blue monkeys [*C. mitis*], Förster & Cords, 2005; black capuchins [*Sapajus nigritus*], Baldovino & Di Bitetti, 2008; and Formosan macaques [*M. cyclopis*], Hsu, Lin, Lin, Lin, & Agoramoorthy, 2015), mirroring tendencies for kin preferences among females to be less pronounced (e.g., in langurs, patas monkeys, blue monkeys, mangabeys [*Cercocebus atys*]), or for levels of aggression among females to be low (see below; Chism, 2000; Maestriperieri, 1994a).

Rank also appears to play an important role in shaping handling, though the direction of its effects is not entirely consistent. While some studies report that infants of high-ranking mothers are more attractive and are handled more frequently (chacma baboons, Cheney, 1978; macaques, Berman, 1982b; Dunayer & Berman, 2017; Paul & Kuester, 1996; and black capuchins, Baldovino & Di Bitetti, 2008), others describe an interaction between rank and mothers' tendencies and abilities to prevent handling. In highly protective species, high-ranking mothers are better able to prevent handling. In these species, would-be handlers tend to have greater access to infants whose mothers are subordinate to them, resulting in handling being directed down the hierarchy (wedge-capped capuchins, O'Brien & Robinson, 1991; bonnet macaques, Silk, 1999; and some chacma baboons, Silk, Rendall, et al., 2003). Still other studies have found minimal to no rank effects (moor macaques [*M. maurus*], Matsumara, 1997; yellow baboons [*P. cynocephalus*], Bentley-Condit, Moore, & Smith, 2001; black and white colobus, Bădescu et al., 2015; and white-faced capuchins [*C. capucinus*], Sargeant, Wikberg, Kawamura, & Fedigan, 2015). Taken together, the evidence suggests that the mother's rank may influence the infant's attractiveness, but the rank relationship between mother and handler, the amount of competition to handle particular infants (Cheney, 1978), and importantly, the mother's propensity to limit handling (cf. Silk, Rendall, et al., 2003) may all interact to ultimately dictate accessibility of the infant to the handler.

Handler age and parity, factors that are often tightly correlated and consequently not always distinguishable, also appear to greatly influence handling interactions; however, again the effects of these factors are not consistent across species. In several species, immature nulliparous females are most attracted to infants (Hanuman langurs, Hrdy, 1977; Scollay & DeBold, 1980; vervets, Fairbanks, 1990; Meaney, Lozos, & Stewart, 1990; macaques, Schino et al., 2003; Dunayer & Berman, 2017; blue monkeys, Förster & Cords, 2005; and black and white colobus, Bădescu et al., 2015; Brent, Teichroeb, & Sicotte, 2008; reviewed in Hrdy 1976; MacKinnon, 2011). However, as with rank, age-related attraction does not always translate into

handling, as mothers sometimes prevent handling by young inexperienced nulliparous females (capped langurs, Stanford, 1992; Kumar et al., 2005). In other species, either multiparous adult females show the highest rates of attraction and handling, or age/parity is not associated with measures of attraction or handling (colobus, Horwich & Manski, 1975; patas monkeys, Muroyama, 1994; Zucker & Kaplan, 1981; ring-tailed lemurs, Gould, 1992; some macaques, Hsu et al., 2015; Matsumara, 1997; mantled howler monkeys [*Alouatta palliata*], Clarke, Glander, & Zucker, 1998; white-faced capuchins, Manson, 1999; and mangabeys, Fruteau, van de Waal, van Damme, & Noë, 2011). In some studies, multiparous females were most attracted to infants and handled infants most when the handlers were lactating and had infants of their own (macaques, de Waal, 1990; Hsu et al., 2015; Maestripieri & Wallen, 1995; Paul & Kuester, 1996; and chacma baboons, Silk, Rendall, et al., 2003). This suggests that natal attraction and infant handling may be partly mediated by the same hormonal processes that influence maternal responsiveness (Maestripieri & Wallen, 1995; Silk, Rendall, et al., 2003). Finally, infant sex is an important factor for a few forms of handling. For example, Tibetan macaque males show strong preferences to use male infants for bridging (Ogawa, 1995a), though infant sex seems to be less important for other forms of handling (e.g., grooming) (capped langurs, Stanford, 1992; macaques, Dunayer & Berman, 2017; Schino et al., 2003; Silk, 1999; blue monkeys, Förster & Cords, 2005; and white-faced capuchins, Sargeant et al., 2015).

Handling and Breeding Systems

While the manifestations and quantity of behavior related to natal attraction and infant handling vary considerably across the primate order, they have been documented in virtually all taxa (prosimians: ring-tailed lemurs, Gould, 1992; spectral tarsiers [*Tarsius spectrum*], Gursky, 2000; New World monkeys: gracile capuchins [*Cebus spp.*], Manson, 1999; O'Brien & Robinson, 1991; Tiddi, Aureli, & Schino, 2010; Bolivia squirrel monkeys, Williams et al., 1994; mantled howler monkeys, Clarke et al., 1998; tamarins [*Saguinus spp.*], Goldizen, 1987; Tardif, Carson, & Gangaware, 1992; black-handed spider monkeys [*Ateles geoffroyi*], Slater, Schaffner, & Aureli, 2007; Old World monkeys: langurs [*Trachypithecus spp.*], Jin et al., 2015; Kumar et al., 2005; Stanford, 1992; Hanuman langurs, Hrdy, 1977; Jay, 1963; Scollay & DeBold, 1980; snub-nosed monkeys, Ren et al., 2012; Xi, Li, Zhao, Ji, & Zhang, 2008; doucs [*Pygathrix spp.*], Hill, 1972; colobus, Bădescu et al., 2015; Brent et al., 2008; Horwich & Manski, 1975; patas monkeys, Muroyama, 1994; Zucker & Kaplan, 1981; vervets, Fairbanks, 1990; Fruteau et al., 2011; Lancaster, 1971; Meaney et al., 1990; mangabeys, Fruteau et al., 2011; baboons, Bentley-Condit et al., 2001; Cheney, 1978; Frank & Silk, 2009; Henzi & Barrett, 2002; Silk, Rendall, et al., 2003; macaques, de Waal, 1990; Dunayer & Berman, 2017; Gumert, 2007; Hiraiwa, 1981; Hsu et al., 2015; Maestripieri, 1994b; Paul & Kuester, 1996; Schino et al., 2003; Small, 1990; Silk, 1980; Silk, 1999; Thierry, 1985; apes: siamangs [*Symphalangus syndactylus*], Lappan, 2008; chimpanzees, Bădescu, Watts, Katzenberg, & Sellen, 2016; Nishida, 1983; bonobos [*Pan paniscus*], Boose, White, Brand, Meinelt, & Snodgrass, 2018; Chism, 2000; reviewed in, Hrdy, 1976; Maestripieri, 1994a; MacKinnon, 2011; McKenna, 1979; Nicolson, 1987; Quiatt, 1979; Ross & MacLarnon, 2000).

Table 2
Individual Characteristics Mediating Infant Handling among Primates^a

Genus	Common Name	Kinship	Rank Effects	Handler Characteristics ^b	References
Lemur	Ring-tailed lemur	NA	0	Adult female	Gould, 1992
Saguinus	Cotton-top Tamarin	0	NA	Adult & subadult	Savage, 1990 ^c
Leontopithecus	Golden-lion Tamarin	+	NA	Male helpers	Baker, 1991
		0	NA	Female helpers	
Cebus	Wedge-capped capuchin	+	-	Old juvenile female; young adult female	O'Brien & Robinson, 1991
	White-faced capuchin	+	0	Parous female - allonursing Female, all ages - other forms	Sargeant et al., 2015; Manson, 1999
Sapajus	Black capuchin	0	+	Female — allonursing	Baldovino & Di Bitetti, 2008
Samiri	Bolivian squirrel monkey	0	NA	Young adult female	Williams et al., 1994
Colobus	Black and white colobus	+	0	Immature nulliparous female	Brent et al., 2008; Bădescu et al., 2015
Cercopithecus	Vervet monkey	+	+	Immature nulliparous female	Lancaster, 1971; Fairbanks, 1990; Meaney et al., 1990
	Blue monkey	0	NA	Immature nulliparous female	Förster & Cords, 2005
Trachypithecus	Capped langur ^d	0	NA	Parous adult female	Stanford, 1992; Kumar et al., 2005
Erythrocebus Macaca	Patas monkey	0	+	Parous adult female	Zucker & Kaplan, 1981; Muroyama, 1994
	Rhesus macaque	+	+	Immature nulliparous female	Berman, 1982a,b; Dunayer & Berman, 2017
	Bonnet macaque	+	-	Female, all ages	Silk, 1999
	Japanese macaque	+	+	Immature nulliparous female	Schino et al., 2003
	Barbary macaque	+	+	Nulliparous female	Paul & Kuester, 1996
				All age/sex classes	Small, 1990
	Moor macaque	NA	0	Female, all ages	Matsumara, 1997
Papio	Chacma baboon ^d		+		Cheney, 1978
		+	-	Adult female with young infants of their own	Silk, Rendall, et al., 2003
	Yellow baboon	NA	0	NA	Bentley-Condit et al., 2001
Pan	Bonobo	+	0	Immature nulliparous female	Boose et al., 2018

Note. += Handling is biased towards closely related individuals (Kinship column) and/or high-ranking infants (Rank Effects column). - = Handling is biased towards high-ranking handlers (Rank effects column). 0 = Handling is not biased towards closely related individuals (Kinship column) and/or no rank effects are observed (Rank effect column). NA = The data are not presented in the subsequent study. J = juvenile, A = Adult, F = Female, N = nulliparous, P = parous. ^aThe chosen taxa represent those with enough available data. ^bThe most common age and sex classes are listed; however, in several of these studies, handling is also observed, though less frequently, from individuals comprising other age/sex classes. ^cThe potential influence of kinship on carrying was only investigated for juvenile handlers, which as an age class handled less than adults. ^dThe effects of kinship, rank, and handler age/sex class may interact with mother's protectiveness/ permissiveness of handling. For example, Silk, Rendall, et al. (2003) found that females were attracted to infants of all ranks, but only had access to infants whose mothers they outranked or were related to.

The most extensive handling is observed in the cooperatively breeding *Callitrichidae*, and most forms of Callitrichid handling constitute allocare. In cooperative breeding systems, it is typical for only one dominant pair to breed in a group, but they are usually accompanied by a number of (usually related) subordinate helpers. These helpers assist with the rearing of the dominant pair's young and either completely forgo their own breeding or breed infrequently. Twinning is the norm in many Callitrichid species and subordinate helpers, along with fathers, all cooperate with infant care, sharing food with and provisioning infants, and carrying them extensively (Goldizen, 1987). While allolactation occasionally occurs among the cooperatively breeding Callitrichids (see below; Digby, 1995), infants are normally returned to their mothers for nursing. Communal breeding societies, like those of gray mouse lemurs (*Microcebus murinus*), are comprised of several breeding females that may share parental responsibilities for all infants born in their group. Specifically, gray mouse lemurs form day nests with two to five females that are closely related through maternal lines. Although they favor their own offspring, they groom and nurse (but do not carry) all infants in the nest (e.g., Eberle & Kappeler, 2006; Radespiel, 2006). Plurally breeding Colobines also engage in high amounts of handling and intermediate amounts of actual care, with mothers relinquishing their infants to other females within the first few hours of the infant's birth (Jin et al., 2015; Kumar et al., 2005; McKenna, 1979). On the other end of the infant handling spectrum are most plurally breeding macaques and baboons. Unlike many other plurally breeding Old World monkeys that display intermediate amounts of alloparental handling (see below; Chism, 2000), handling among most macaques and baboons is limited to the non-allocare forms, with mothers often restricting access to their infants. In some relatively solitary, dispersed species, such as orangutans (*Pongo spp.*), and some nocturnal prosimians, allocare is virtually absent because handlers are rarely available.

Socioecological Contexts

McKenna (1979) first suggested that the differences in socioecology, stemming from dietary adaptations between Colobines and Cercopithecines, played a profound role in the evolution of infant handling, leading to observed differences in forms and frequencies of handling. Among the leaf-eating Colobines, dietary adaptations affecting both dental morphology and the digestive system are hypothesized to have facilitated the evolution of concomitant social features, including a reduction in within-group competition, a higher incidence of co-feeding, and more generally speaking, a more relaxed and egalitarian dominance relationship among Colobine females compared to Cercopithecine females. These social changes in turn fostered a social environment in which handling could evolve in part because low rank would not necessarily prevent mothers from retrieving their infants from higher-ranking handlers. However, dietary adaptations alone do not appear to explain all observed variations; more recent data indicate that differences in amounts of handling between Colobines and Cercopithecines are no longer seen as clear-cut as was once believed. Extensive handling (including both affiliative forms and actual allocare) has since been reported in several Cercopithecine species (e.g., vervets, Fairbanks, 1990; Fruteau et al., 2011; Lancaster, 1971; Meaney et al., 1990; patas monkeys, Muroyama, 1994; Zucker & Kaplan, 1981; and mangabeys, Fruteau et al., 2011). Ross and MacLarnon (2000) also did not find that diet was significantly related to levels of allocare in a large cross-species analysis.

Chism (2000) focused on variation in allocare within Cercopithecines, noting it was variable among guenons and generally rare among macaques and baboons. In a qualitative analysis of social, ecological, and life history variables, she hypothesized that several factors may predispose Cercopithecines toward allocare, provided that certain aspects of social structure do not produce risks that outweigh the benefits of allocare. This hypothesis was based on her finding that the most (but not entirely) consistent feature of species with allocare was related to female dominance relationships; when the influence of dominance is moderate to weak,

Chism's qualitative analysis found that mothers are more relaxed about allowing allocare (also see Maestriperi, 1994a). She speculated that this was because their infants are less likely to encounter aggression and/or because mothers are less likely to have difficulty retrieving them from higher-ranking handlers (Figure 2). In these more relaxed species, Chism's qualitative analysis also led to the hypothesis that seasonal reproduction further encourages allocare handling, because any energetic benefits for mothers (e.g., due to increased foraging time) could allow them to return to a reproductive condition earlier, reducing their chances of missing an entire mating season. In this regard, species with shorter interbirth intervals and rapid infant development should also be associated with higher rates of allocare handling (see below; also see Fairbanks, 1990; Mitani & Watts, 1997; Ross & MacLarnon, 2000). Finally, Chism's qualitative analysis led to the hypothesis that the presence of experienced and related handlers should encourage allocare handling, as it reduces the risk of injury to infants. Factors that Chism (2000) hypothesized to discourage allocare include synchronized foraging and seasonal food availability because handling could detrimentally affect the allocarer's ability to forage efficiently, particularly when the food supply is low. Some aspects of this model have also been tested quantitatively (see the foraging and reproductive rates hypotheses below), but most have not.



Figure 2. A female rhesus macaque attempts to retrieve her infant from a higher-ranking handler. Photo credit: Erica Dunayer.

Costs of Handling

Although allocare by definition is thought to benefit mothers and infants, there may be associated costs in some cases. For example, infants may be affected by extensive handling from non-mothers if it interrupts suckling bouts, interferes with the mother's ability to continue to produce sufficient amounts of milk, or if the mother is unable to retrieve her infant (MacKinnon, 2011). Inexperienced nullipares may also clumsily

carry/handle infants, potentially injuring them in the process. Consequently, mothers may resist handling from inexperienced juveniles (e.g., capped langurs, Kumar et al., 2005; Stanford, 1992) and/or be reluctant to allow handling from high-ranking individuals, even though these females are often the most persistent.

Lactation is generally considered the costliest form of parental behavior among mammals (Altmann & Samuels, 1992; Clutton-Brock, Albon, & Guinness, 1989), imposing significant physiological stress and body weight reduction in mothers. Studies among mammals have found that lactation poses greater fitness costs to mothers than gestation alone; indeed, lactation, but not gestation, is associated with longer interbirth intervals and higher mortality rates (Clutton-Brock et al., 1989). Given the significant energetic costs associated with lactation (Clutton-Brock et al., 1989; Oftedal, 1984; Speakman, 2008), and the fact that allolactation does not contribute to a female's direct fitness, allolactation would not necessarily be expected to evolve.

For the most part, primate allonursing is rare compared to other mammals (MacLeod & Lukas, 2014; Packer et al., 1992; reviewed in Reidman, 1982; Roulin, 2002), and is typically restricted to some lemurs (black and white ruffed lemurs [*Varecia variegata*], Pereira, Klepper, & Simons, 1987; ring-tailed lemurs, Gould, 1992; gray mouse lemurs, Eberle & Kappeler, 2006; Radespiel, 2006), and New World monkeys (gracile capuchins, O'Brien, 1988; O'Brien & Robinson, 1991; Perry, 1996; Sargeant et al., 2015; black capuchins, Baldovino & Di Bitetti, 2008; Bolivian squirrel monkeys, Milligan, Gibson, Williams, & Power, 2008; Williams et al., 1994; and common marmosets [*Callithrix jacchus*], Digby, 1995). Among cooperatively breeding Callitrichids, allonursing is rare given that mating is confined to the dominant pair, and subordinate helpers are unable to lactate without becoming pregnant. This is in contrast to some other cooperatively breeding mammals (e.g., dwarf mongoose [*Helogale parvula*], Creel, Monfort, Wildt, & Waser, 1991), that are able to lactate without first becoming pregnant, and that allonurse regularly. Nevertheless, allonursing has been observed in Callitrichids during rare instances when subordinate females give birth, but their infants fail to survive, usually because they receive no help from others (Roda & Pontes, 1998), or the infants are attacked by the dominant female (Digby, 1995). In the few cases where allonursing does occur among Callitrichids, it may provide immediate direct benefits to allonursers by allowing for the evacuation of excess milk and/or the reduction of painful pressure in the breast (cf. Roulin, 2002) as well as indirect benefits when the dominant female is related. This may also be the case for Bolivian squirrel monkeys, as the majority of observed allonursing is by females that have lost their own infants (Milligan et al., 2008; Williams et al., 1994). Among communally breeding gray mouse lemurs, costs of allonursing are likely to be minimized because females that share a nest nurse all infants in the nest, particularly when their mothers are away foraging (Eberle & Kappeler, 2006; Radespiel, 2006). Thus, each mother is likely to have her own infants nursed when she is absent. Among most plurally breeding species, allonursing is hypothesized to be a consequence of milk theft by parasitic infants and/or accidental nursing (O'Brien, 1988; Packer et al., 1992).

Although lactation is energetically expensive, some evidence suggests that lactating females may not be any more physiologically stressed compared to cycling females, and are actually less stressed than pregnant females. For the most part, field studies among a variety of primates have found no differences in glucocorticoid concentrations between lactating and cycling females (chacma baboon, Weingrill, Gray, Barrett, & Henzi, 2004), and higher levels in pregnant than lactating females (brown spider [*A. hybridus*] and Venezuelan red howler monkeys [*A. seniculus*], Rimbach, Heymann, Link, & Heistermann, 2013; baboons, Crockford, Witig, Whitten, Seyfarth, & Cheney, 2008; Engh et al., 2006; and mandrills [*Mandrillus sphinx*], Setchell, Smith, Wickings, & Knapp, 2008). It may be that lactation costs are mitigated, at least in part, via slight modifications to foraging behavior. For example, lactating white-faced capuchin females ingest more food and increase their energy intake compared to cycling and gestating females (McCabe & Fedigan, 2007). Costs of allonursing, compared to nursing one's own infant, may be further reduced, because plurally breeding

females nurse their own infants much more than they nurse other infants, (e.g., black capuchins, Baldovino & Di Bitetti, 2008; white-faced capuchins, Sargeant et al., 2015). Nevertheless, the relative paucity of allonursing among the primate order, especially when compared to other mammals, suggests that for the most part, the costs of allolactation outweigh its benefits, and it may only evolve under certain limited conditions. For example, Perry (1996) suggests that allonursing in white-faced capuchins is associated with the fact that mothers often become separated from their infants during foraging. Infants may have a difficult time relocating their mothers when they need to nurse; in these scenarios, the benefits of allonursing to infants and their mothers could offset the costs to the allonurse (Perry, 1996), especially if allonursing is reciprocally distributed or performed by close kin.

After lactation, infant carrying is the second most energetically costly form of parental care among primates (Altmann & Samuels, 1992). As such, extensive alloparental infant carrying should pose major costs to handlers. Several studies have found that alloparents spend less time foraging and more time resting when carrying infants (Hanuman langur, Vogel, 1984; capped langur, Stanford, 1992; and tamarins, Goldizen, 1987; Sánchez, Peláez, Gil-Bürmann, & Kaumanns, 1999). As the infant grows, the energetic costs of carrying them also increase, and carrying costs are expected to be greater in species that travel farther to forage (Altmann & Samuels, 1992). In addition to energetic costs, handlers may also suffer from increased maternal aggression from protective mothers, and may spend less time engaging in other social activities (Fairbanks, 1990). The dynamics of alloparental carrying may also involve a conflict of interest between mothers and alloparents. Because of the increased costs associated with carrying heavier individuals, mothers have the potential to maximize gains and reduce risk of injury by allowing alloparents to carry only after their infants reach a few months of age. However, handlers can mitigate carrying costs by preferentially carrying younger infants. As described above, in most species that have been studied, attraction and handling is most common in younger infants (colobus, Bădescu et al., 2015; Hanuman langur, Scollay & DeBold, 1980; Horwich & Manski, 1975; bonnet macaque, Silk, 1999; and chacma baboon, Silk, Rendall, et al., 2003; reviewed in, Hrdy, 1976; MacKinnon, 2011; Maestripieri, 1994a). It is particularly common in Colobines; mothers allow their infants to be carried extensively from a young age, perhaps because in these species, the risk of aggression to infants (and hence cost) is low at a time when interest by potential handlers is high. In contrast, prolonged carrying by others is relatively rare in most macaques and baboons that live in groups with more intense aggression, perhaps because mothers tend to resist carrying attempts by others when their infants are young and particularly vulnerable to aggression, or because potential handlers are less interested in their infants when they are older.

Grooming is another common form of handling, though it is not considered a type of allocare handling. Providing grooming is theoretically costly for the handler; however, debate exists over its precise costs, a topic that few studies have explicitly tested. While proposed costs to the groomer include decreased vigilance (Cords, 1995; Maestripieri, 1993) and resting time (Dunbar, 1992), they seem to be minor (Russell & Phelps, 2013), and also exist for the recipient. Furthermore, groomers may receive some short-term benefits, such as reductions in stress (Aureli & Yates, 2010; Shutt, MacLarnon, Heistermann, & Semple, 2007). Importantly, there are multiple short-term benefits (e.g., hygienic, pleasurable) for grooming recipients (Aureli, Preston, & de Waal, 1999; Boccia, Reite, & Laudenslanger, 1989; Keverne, Martensz, & Tuite, 1989; Takahashi & Furuichi, 1998; Reichard & Sommer, 1994). Because alloparental grooming most often occurs when the infant is on the mother, it poses fewer risks to the infant compared to other forms of handling. Consequently, grooming as a form of infant handling appears to pose minimal costs to all parties involved.

Finally, bridging and other forms of infant handling that males use to regulate bonds with other males may involve physiological costs. Henkel et al. (2010) found that glucocorticoid levels in Barbary macaques were higher in males that carried infants than in other males, and were higher in the spring when carrying was

most frequent. This suggests that carrying males incur measurable increases in stress as they use infants as social tools.

Benefits and Hypothesized Functions

The discussion so far suggests that infant handling appears to be a complex heterogeneous phenomenon influenced on a proximate level by the interaction of several social factors (Maestriperieri, 1994a), including attributes of each interactor (infant, mother, and potential handler), characteristics of social relationships among interactors, and social contexts within groups. Given the complex nature of handling, involving three distinct roles and sets of interests, it has been difficult to construct unitary or integrated functional explanations that apply to all participants and its various forms and manifestations. Rather, most hypotheses focus on benefits accrued to individuals in only one role. Below, we describe in detail several of these functional hypotheses, emphasizing how each individual in the interaction is purported to benefit or not (summarized in Table 3). The proposed hypotheses are not mutually exclusive. Different hypotheses may apply to different classes of handlers, and several selective forces may interact to influence the way handling is ultimately displayed. Moreover, different sets of hypotheses may apply to different species. We make special distinctions for macaques and baboons in our discussion of each hypothesis, as many of the hypotheses may be less relevant to forms of handling that are not considered allocare.

We begin with the byproduct hypothesis as a sort of null hypothesis with regard to benefits and functions. The byproduct hypothesis, sometimes referred to as the natal attraction hypothesis (Silk, Rendall, et al., 2003), posits that attraction and handling of infants other than one's own has no adaptive function, and is the byproduct of selection acting on maternal responsiveness (Paul, 1999; Paul & Kuester, 1996; Quiatt, 1979; Scollay & DeBold, 1980; Silk, 1999; Silk, Rendall, et al., 2003). Proponents of this view reason that responsiveness towards one's own infants benefits mothers, with maternal behavior "spilling over" to other infants; however, it results in no short-term benefits for the mother, handler, or infant. Accordingly, the byproduct hypothesis predicts that females will show higher rates of attraction and handling compared to males, with handling performed at high rates by both adult multiparous and juvenile nulliparous females. Most investigations of the byproduct hypothesis have focused on macaques and baboons, finding strong support (Paul & Kuester, 1996; Silk, 1999; Silk, Rendall, et al., 2003) for these predictions. However, the byproduct hypothesis cannot explain why males in some species also show high rates of attraction and handling (e.g., chacma baboons, Busse & Hamilton, 1981; Busse, 1984; mangabeys, Busse & Gordon 1984; siamangs, Lappan, 2008), in some cases even when the probability is low that the infant is their own (e.g., Barbary macaques, Ménard et al., 2001; Paul et al., 1996; Taub, 1984). It also does not address why immatures often handle infants more than adults (macaques, Dunayer & Berman, 2017; Schino et al., 2003), and why high-ranking infants are often the most attractive (chacma baboons, Cheney, 1978; macaques, Berman, 1982b; Dunayer & Berman, 2017; Paul & Kuester, 1996). Finally, the byproduct hypothesis alone cannot explain why macaque and baboon mothers are reluctant to allow their infants to be handled.

Table 3

Functional Hypotheses for Infant Handling: Proposed Costs and Benefits by Role and Level of Empirical Support

Hypothesis	Mother	Handler	Infant	Macaque & Baboon Support	Strong Support Among Other Primates	Sources
Byproduct	None	None	None	Strong	Langurs	Quiatt, 1979; Scollay & DeBold, 1980; Paul & Kuester, 1996; Paul, 1999; Silk, 1999; Silk, Rendall, et al., 2003
Learning to Mother	NA/-	+	NA/-	Weak	Guenons, Callitrichids,	Lancaster, 1971; Nicolson, 1987; Tardif et al., 1984; Fairbanks, 1990; Meaney et al., 1990
Abuse: Dominance Reinforcement & Reproductive Competition	-	+	-	Moderate	Langurs, Howler Monkeys	Hrdy, 1977; Silk, 1980; Wasser & Barash, 1981; Maestriperi, 1994a, 1999; Clarke et al., 1998; Kleindorfer & Wasser, 2004
Adoption	NA	NA/-	+	Untested but unlikely	NA	Jay, 1963; Hrdy, 1976; Thierry & Anderson, 1986; Nicolson, 1987
Forage	+	NA/-	NA/-/ Indirect +	Untested but unlikely	Langurs, Vervets, Snubnose Monkeys	Hrdy, 1976; Vogel, 1984; Nicolson, 1987; Stanford, 1992
Social Bond	+	+	+	Relatively untested but plausible	Capuchins	Hrdy, 1976; Cheney, 1978; Small 1990; de Waal, 1990; Manson 1999; Dunayer & Berman, 2017
Reproductive Rate	+	NA/-	NA/-/ Unclear +	Untested but unlikely	Colobus Monkeys, Siamangs, Chimpanzees	Mitani & Watts, 1997; Ross & MacLarnon, 2000; Lappan, 2008; Bădescu, Watts, et al., 2016
Cooperation: Kin Selection, Reciprocal Altruism, Mutualism, & Biological Markets	Assumed +	Immediate -/ Indirect +/ Delayed +	NA/ + depend on the form	Unlikely	Langurs	Hrdy, 1976; Reidman, 1982; Nicolson, 1987; Stanford, 1992; Henzi & Barrett, 2002; Hsu et al., 2015

Note. + = The effect of handling for that individual is beneficial. - = The effect of handling for that individual is harmful. NA = The effect of handling for that individual is not expressly described by the hypothesis.

The hypothesis that has received the most attention by far is the learning-to-mother hypothesis. Several researchers are quick to point out that among primates, there is disparity in maternal competence between primiparous and multiparous females (Hrdy, 1976), with primiparous females often displaying poorer mothering skills, longer interbirth intervals, and increased infant mortality (reviewed in Pusey, 2012). Young females reared without access to infants often display particularly poor mothering skills when they have their first infants (Altmann, 1980). Supporters of the learning-to-mother hypothesis suggest that immature females learn mothering skills through prior handling (Hrdy, 1976; Lancaster, 1971; Nicolson, 1987). It predicts that immature nulliparous females should handle at higher rates than adult multiparous females and that handling experience should translate into successful rearing of their firstborn infants. However, it makes no predictions about the ways other social characteristics (e.g., kinship, rank) should impact handling interactions. While this hypothesis posits that handlers should benefit from these interactions, it does not consider possible benefits or costs accruing to mothers or infants; however, if immatures are clumsy and inexperienced in their handling, as assumed by the hypothesis, then infants may potentially be injured in the process. Thus, it is reasonable to

predict that mothers and infants should attempt to prevent or resist handling from immatures, albeit to a lesser extent if the immature is related. As already discussed, several studies support the first prediction—that attraction is highest among immature females (Hanuman langurs, Hrdy, 1977; Scollay & DeBold, 1980; vervets, Fairbanks, 1990; Meaney et al., 1990; macaques, Schino et al., 2003; Dunayer & Berman, 2017; blue monkeys, Förster & Cords, 2005; black and white colobus, Bădescu et al., 2015; Brent et al., 2008; and bonobos, Boose et al., 2018; reviewed in Hrdy 1976; MacKinnon, 2011). Boose and colleagues (2018) in particular note that handling increases oxytocin levels in adolescent and juvenile handlers, but not in others. Studies asking whether handling experience improves maternal competence are sparse; few have enough longitudinal data to investigate later rearing success of immature handlers. Among Colobines, this prediction is particularly difficult to investigate, as most/all immature females have experienced handling by the time they have their own offspring. In Callitrichids, offspring of primiparous mothers with extensive handling experience often have higher survival rates compared to inexperienced primiparous mothers (Tardif, Richter, & Carson, 1984), although this is not always the case (Tardif et al., 1992). To date, the strongest support for the learning-to-mother hypothesis has been demonstrated in vervet monkeys. Meaney et al. (1990) found that nulliparous females show improvements in their carrying skills, measured by an increase in infant clinging and a decrease in infant support, after just one season with infant carrying experience. Furthermore, Fairbanks (1990) found that immature females that spent more time carrying were more likely to produce surviving offspring, compared to immature females that spent less time carrying (also see Lancaster, 1971). Nevertheless, experience does not always translate into more skilled handling. Among Hanuman langurs, even though juvenile females performed the majority of handling, handling skills appeared to deteriorate with age and experience; older juvenile and adult females handled infants more aggressively and carried them less adeptly (Scollay & DeBold, 1980).

On the other hand, the learning-to-mother hypothesis may have less applicability to most macaques and baboons. While it is true that their attraction to infants tends to be higher among juvenile females than older females (Berman, 1982a; Dunayer & Berman, 2017; Hiraiwa, 1981; Schino et al., 2003), this is not always the case (de Waal, 1990; Hsu et al., 2015; Silk, Rendall, et al., 2003). Indeed, some older females are highly attracted to infants and frequently handle them (Dunayer & Berman, 2017; Hsu et al., 2015; Silk, 1999; Small, 1990). Moreover, prior experience with infants does not necessarily translate into later reproductive success. For example, Silk (1999) found no relationship between prior handling experience and successful rearing in bonnet macaques. In fact, the few juvenile macaques whose first infants survived had been less frequent handlers. While this finding may appear counterintuitive at first, it is important to consider that most macaques and baboons primarily engage in forms of handling that are not considered *allocare*. Thus, handling may not provide immatures with much appropriate practice.

Some researchers have focused on apparently deliberate forms of kidnapping and rough handling directed towards infants. Kidnapping has been observed in a variety of primate species (Silk, 1980), and can result in injury or even death of the infant (Kleindorfer & Wasser, 2004; Silk, 1980), thus posing significant costs to mothers and infants. Abusive handling, particularly when it is performed by females that handle their own infants skillfully, appears deliberate and suggests that infantile physical characteristics that typically elicit affiliative behavior or care are not foolproof releasers of benign behavior. Nicolson (1987) suggested that such apparently deliberate abuse may serve to reinforce positions in the dominance hierarchy, as it is often directed towards infants of lower-ranking females (Kleindorfer & Wasser, 2004; Silk, 1980). Given that kidnapping and abusive handling can result in the infant's injury or death, it has also been suggested that these behaviors may function as a form of reproductive competition (bonnet macaques, Silk, 1980; mantled howler monkeys, Clarke et al., 1998; rhesus macaques, Maestriperi, 1999; reviewed in Wasser & Barash, 1981; Maestriperi, 1994a), where handlers benefit by reducing potential future competitors to themselves and their own infants.

In this regard, kidnapping and infant abuse may be cost effective ways of reducing future competition, as aggression directed towards infants is likely to be less costly than aggression directed towards adult females (Silk, 1980). Although the functions of the dominance reinforcement and reproductive competition hypotheses may be different, both hypotheses predict that handling should be most common among females, with abusive handling directed towards unrelated lower-ranking females, although it makes no clear predictions about handlers' parity. Additionally, abusive handling should be more common in species with strict dominance hierarchies and high levels of within-group competition (Maestriperi, 1994a), in which retrieval of kidnapped infants from lower-ranking mothers may be more difficult. As such, mothers should show high degrees of reluctance and resistance to attempts of others to handle their infants, and this should especially be true for despotic species. Among macaques and baboons, abuse hypotheses have received moderate support (Hiraiwa, 1981; Kleindorfer & Wasser, 2004; Maestriperi, 1994a), as the patterns of abusive handling mostly support the above predictions (but see Silk, 1980, that found evidence of kidnapping/abuse in bonnet macaques, a species with moderately relaxed dominance hierarchies). Moreover, these hypotheses cannot explain the overwhelming prevalence of affiliative handling over more abusive handling, even among despotic macaques and baboons (e.g., see Schino et al., 2003, in which rates of affiliative and abusive handling among Japanese macaques were 17.8 and 1.0 per hour, respectively). On the other hand, one might speculate that abusive handling would not be expected to be stable in a population unless benign or affiliative handling was the rule, because maternal resistance would be expected to rise to extreme levels, and any signals of benign intent would be ignored.

Some researchers suggest that another function of infant handling may be to facilitate adoption in cases where the infant's own mother dies (Hrdy, 1976; Jay, 1963; Nicolson, 1987). Adoptions among primates occur, though they are rare, with adoption of young infants more common by lactating or pregnant females than by cycling or anestrus females. Adoption is also more common by these females than by juveniles or adult males; however, juveniles and/or adult males may sometimes adopt older infants (reviewed in Thierry & Anderson, 1986). While the adoption hypothesis makes no explicit predictions regarding the form of handling, it predicts that frequent handlers should disproportionately adopt the orphans they handled. Should adoption result in infant survival, which is often not the case, the infant gains obvious benefits. While the adoption hypothesis makes no predictions regarding costs to the handler, adoption is likely to involve substantial energetic costs as well as costs associated with protection. Cases of adoption have been reported in macaques in which the adopters were close associates of the mother and highly familiar to infants (e.g., rhesus macaques, Berman, 1982c); however, it is unclear whether adoption is linked to previous handling *per se*. Indeed, experimental data from captive Hanuman langur infants argues against a link with handling. When mothers were removed from their group, their infants were readily adopted by other females. However, these associations were initiated by the infants, and they did not seek out the females who had frequently approached them prior to the loss of their mother (Dolhinow & Taff, 1993). Although the adoption hypothesis is largely untested in other species, it is unlikely that the evolution of infant handling was driven primarily by its effects on adoption, given that adoption is rare and costly, and seldom results in the survival of orphans in the wild. This is particularly the case for unweaned orphans (Hasegawa & Hiraiwa, 1980; Thierry & Anderson, 1986, but see Eberle & Kappeler, 2006; Perry, 2008), in spite of the fact that young, unweaned infants are more attractive and handled more than older, more independent orphans (see *Attractiveness, Access, and Handling*).

Other researchers have suggested that infant handling functions to free up foraging time for the mother (Hrdy, 1976; Vogel, 1984; Nicolson, 1987; Stanford, 1992). Mothers typically lose weight during lactation, so gaining extra time to forage, and particularly when unencumbered by an infant, should have important benefits. Although this hypothesis does not make specific predictions about effects on handlers and infants, handlers are likely to experience energetic costs associated with extensive carrying while the mother forages. If handling

keeps the infant from the mother for extended time periods, it may reduce its access to milk; however, it is also possible that the infant may gain net benefits indirectly if the mother's ability to care for the infant or its future siblings is sufficiently enhanced. Accordingly, the foraging hypothesis predicts that mothers should show higher rates of foraging while their infants are being handled compared to when their infants are in their own care. Several studies across primates support this prediction (capped langurs, Stanford, 1992; Hanuman langurs, Vogel, 1994; golden snub-nosed monkeys [*R. roxellana*], Xi et al., 2008; cf. vervets, Whitten, 1982). Like the byproduct hypothesis, the foraging hypothesis does not incorporate any social characteristics into its predictions. To our knowledge, the foraging hypothesis remains largely untested in macaques and baboons; however, we speculate that foraging benefits to mothers are unlikely to exert strong selective pressures in these species. Mothers of these species rarely allow handlers to carry infants for prolonged periods of time, and most handling occurs when infants are on their mothers. Because of their restrictiveness, handling is unlikely to free up substantial amounts of foraging time for them.

Infant Handling and Social Bonds

A final benefit-oriented hypothesis views handling as a form of social bond investment, and has a number of parallels to hypotheses about the role of grooming in social bond formation and maintenance. Unlike other hypothetical benefits, handling as social investment has the potential to benefit interactors in all three roles: handler, mother, and infant as well as handlers in a variety of age/sex classes (Dunayer & Berman, 2017). It is also potentially applicable to both forms of handling that are considered allocare and merely affiliative. The hypothesis posits that through handling, handlers may be able to form or enhance bonds with infants. Bonds between mothers and handlers may also be enhanced (or tested; cf. Manson, 1999), especially when handling is preceded by a cooperative exchange in which the handler grooms the mother and receives a demonstration of trust (and possibly willingness to cooperate in the future) from the mother when she gives 'permission' to handle her infant (see below). Although the enhancement of social bonds is not a new hypothesis (e.g., Cheney, 1978; de Waal, 1990; Dunayer & Berman, 2017; Hrdy, 1976; Mumme, 1997; Small, 1990), it is receiving renewed attention due to recent evidence about the adaptive value of strong and enduring social relationships among primates (Brent, Ruiz-Lambides, & Platt, 2017; Silk, Alberts, & Altmann, 2003; Silk et al., 2009, 2010; Schülke, Bhagavatula, Vigilant, & Ostner, 2010). For example, Silk and her colleagues (2009, 2010) found that chacma baboon females with strong and enduring affiliative relationships with other females enjoyed longer lives, and their infants were more likely to survive than those without such relationships. Similarly, Archie, Tung, Clark, Altmann, and Alberts (2014) found that female yellow baboons with strong grooming relationships with either same or opposite sex partners (and particularly both) had higher survival rates. As such, if handling functions to form, maintain, and/or enhance bonds between the handler, mother, and infant, then handling may be adaptive in much the same way as other bond promoting behaviors (e.g., grooming).

The social bond hypothesis predicts that infants that are handled relatively more will go on to develop stronger and/or more enduring affiliative social bonds with their handlers than would be expected based on other social characteristics (e.g., kinship, sex, rank, etc.). Furthermore, if handling functions like other bond-promoting behaviors, early handling might be expected to have rank-related benefits. For example, early handling might facilitate coalitionary support of the infant and/or the mother from higher-ranking handlers (cf. de Waal, 1990; Hrdy, 1976). Similarly handling of a high-born infant by a low-ranking individual might be expected to increase the probability of receiving agonistic support, access to monopolizable resources, or reduced levels of aggression (Cheney, 1978; Nicolson, 1987). Specific tests of these predictions are rare. Nevertheless, Dunayer and Berman (2017) recently found that free-ranging rhesus macaque infants formed

stronger bonds than expected (based on kinship, age, sex, and rank) with their most frequent previous handlers by the time they reached 25-30 weeks of age, an age when infants have substantial control over their own interactions with others, and when their relationships are considered to be substantially differentiated and distinct from those of their mothers (Berman, 1982b). Handling was measured per unit of time the handler was in proximity to the infant in order to isolate its effects from other interactions that did not involve touch. In addition, Manson (1999) found that white-faced capuchin females preferentially handled infants of mothers that they frequently groomed and formed coalitions with, suggesting that handling may help maintain bonds and alliances (Manson, 1999; also see Lazaro-Perea, De Fátima Arruda, & Snowden, 2004). However, allonurses were not close associates of mothers (Perry, 1996). Similarly, Stanford (1992) found that allomothering relationships failed to enhance proximity relationships between capped langur mothers and allomothers. In this case, capped langur females typically spend little time near one another. Hence, Stanford's findings may simply reflect the fact that female-female relationships are much weaker in this species compared to female bonded species (e.g., macaques and baboons).

Additionally, if handling functions to form, maintain, and/or enhance social bonds, then handling should be more common among females than males in female bonded species, as it is in most macaques (Berman, 1982a; Dunayer & Berman, 2017; Silk, 1999; Schino et al., 2003; also see Nguyen, Van Horn, Alberts, & Altmann, 2009). In species in which males receive benefits from close relationships with females, such as increased mating access (Smuts, 1985; Smuts & Gubernick, 1992), male handling may be expected to be more common than in species that do not. There is evidence of links between strong heterosexual affiliative relationships (i.e., friendships) in which males frequently handle the female's infant (regardless of paternity), and go on to receive increased mating access to the female when she resumes reproductive cycling (olive baboons [*P. anubis*], Smuts, 1985; Barbary macaques, Ménard et al., 2001; but see Paul et al., 1996). In others, friendships during the mating season include increased mating access, and are followed by close associations between the male and both the mother and the infant that last two to three years (e.g., Assamese macaques, Ostner, Vigilant, Bhagavatula, Franz, & Schülke, 2013). In species in which infants are highly vulnerable to rough handling or infanticide, friendships may provide likely fathers with protective access to their infants (Nguyen et al., 2009; Palombit, 2012), although these relationships rarely extend beyond weaning. On the other hand, links between affiliative heterosexual relationships and increased mating access in chimpanzees (Langergraber, Mitani, Watts, & Vigilant, 2013) and rhesus macaques (Massen et al., 2012; also see Kulik, Muniz, Mundry, & Widdig, 2011) are not typically associated with infant handling. In addition, increased mating access does not always translate into increased paternity (Ménard et al., 2001; Paul et al., 1996). Hopefully, future studies will help resolve these inconsistencies, as disparities may be influenced both by ecological and demographic factors.

Finally, males in species that use infants to form, enhance, or maintain relationships with other males (e.g., as in bridging interactions, Henkel et al., 2010; Kalbitz et al., 2017; Ogawa, 1995a), should handle infants more than those that do not. Among Tibetan macaques, bridging serves these functions and is done more frequently by male pairs than by female pairs or heterosexual pairs (personal communication, H. Ogawa). Similarly, infant handling among Barbary macaque (Henkel et al., 2010) and Assamese macaque (Kalbitz et al., 2017) males appears to function as bond maintenance, as bridging males have stronger affiliative ties to one another than others. In contrast, bridging is not seen in rhesus (Observation, 2017) or crested macaques (personal communication, M. Tyrrell, 2017), species that have weaker relationships among males.

In a related hypothesis, Manson (1999) proposed that handling might function to test bonds between mother and handler. Manson's study found tentative support among white-faced capuchin females; females more often handled the infants of their frequent grooming and coalition partners, and mothers tolerated longer

handling episodes from females that they had groomed at higher rates before the birth of their infant. Countering arguments that the initial grooming of mothers by handlers is sufficient to maintain bonds with mothers, and hence that subsequent handling is irrelevant (Nishida, 1983), Manson emphasized the presumed effects of mothers subsequently allowing handlers access to their infants. He argued that allowing handling signaled trust and willingness to cooperate in the future. As such, handling (both giving and allowing), like reciprocal grooming, could be viewed as a low cost investment in long-term social bonds, even for despotic species, as long as the risks of injury to their infants are minimized (e.g., by allowing handling only by closely related individuals and/or when the infant is on the mother).

Further Implications of Handling as Social Investment

If handling plays a special role in enhancing social bonds for infants, as indicated by our study of rhesus infants (see above; Dunayer & Berman, 2017), it may play a larger role than previously appreciated in the social integration of infants into the social structure of their groups (cf. Small, 1990). As discussed above, the fact that mothers are able to control access of handlers to their infants, the extent to which they do so is a major determinant of who handles infants. Given that mothers in despotic species tend to be highly restrictive, favoring their own close associates, the social characteristics of handlers tend to mirror those of the mother's social network and the social structure of the group (e.g., siblings, close maternal kin of similar ranks, and their offspring; Dunayer & Berman, 2017). Moreover, through handling, infants are introduced not only to their handlers, but also to handlers' immature offspring, including other infants (de Waal, 1990), who may be too young to handle themselves, thus further perpetuating the kin/rank-based social structure of the group. Conversely, given that mothers in more tolerant species exert less control over who is allowed to handle their infants, handlers tend to be a larger and more diverse set, including more unrelated individuals of diverse ranks (Cheney, 1978; Nicolson, 1987; Small, 1990). Nevertheless, in this sense they also mirror their mother's larger and more diverse social network and the social structure of their group (Berman, 2004; Caine & Mitchell, 1980; Chauvin & Berman, 2004; Maestriperieri, 1994a,b, 2004; Rosenblum, Coe, & Bromley, 1975). In this way, handling for these species may play a large role in shaping infant social networks that reflect typically more tolerant social structures.

Although the effects of handling on later social bond strength have yet to be explicitly investigated in tolerant species, certain findings from our study of despotic rhesus macaques raise intriguing questions about the role of handling in tolerant species. For example, we found that the effects of handling in rhesus infants were confined to maternally related handlers; the few frequent handlers that were unrelated did not go on to form enhanced bonds with infants (Dunayer & Berman, 2017). In this sense, kinship functioned as a sort of prerequisite for handling to translate into enhanced bonds. This is consistent with findings in other despotic species that found that the fitness benefits of strong social relationships depend more on the strength of bonds rather than their quantity (Silk, Alberts, & Altmann, 2003; Silk et al., 2009, 2010). Given that infants of tolerant species tend to be handled by a more diverse set of handlers and go on to form relationships with a more diverse set of group members (Berman, 2004; Caine & Mitchell, 1980; Chauvin & Berman, 2004; Maestriperieri, 1994a,b, 2004; Rosenblum et al., 1975), it is reasonable to hypothesize that if handling also enhances social bonds in tolerant species, then the development of enhanced social bonds with handlers would not be limited to kin.

Our findings also raise questions about the effects of group size on handling, another issue that remains largely untested (but see Hsu et al., 2015). In general, larger groups display more within-group competition for resources than smaller groups of the same species (Balasubramaniam, Dunayer, Gilhooly, Rosenfield, &

Berman, 2014; Sterck, Watts, & van Schaik, 1997). Hence, one might hypothesize that handlers experience more competition for access to infants, particularly infants of high-ranking mothers, in large groups than small groups. In addition, natural field experiments with rhesus macaques found that as group size increases, the proportion of close kin within the group decreases (Berman, Rasmussen, & Suomi, 1997). These changes result in a suite of outcomes that influence the infant's relationship not only with its mother, but also with other group members. As group size increases, infants are surrounded by a larger proportion of unrelated and less familiar individuals. Mothers respond protectively by keeping their infants near them more often, during which time they are better able to monitor their interactions with group members and where close kin predominate (Berman et al., 1997). As a result, infants in larger groups develop social networks that are more intensely kin-biased compared to smaller groups (Berman et al., 1997; also see Berman & Thierry, 2010, for similar group size effects on kin bias in grooming networks among adult females in three macaque species). Although Berman et al. (1997) focused on older infants, we hypothesize that among despotic species, group size differences should affect early infancy handling in similar ways. Specifically, we predict that among larger groups, infant handling should be more restricted to closely related individuals than in smaller groups of the same species. Conversely, the proportion of unrelated handlers should be higher in smaller groups than larger groups. Whether group size would also impact the "kinship prerequisite" for handling to translate into strong bonds is unclear. Also unclear is the extent to which these group size effects operate in more tolerant species.

Finally, our findings raise questions about possible fitness effects of forming enhanced social bonds through handling. Although several studies describe the fitness benefits of strong and enduring social bonds for adults (see above; Brent et al., 2017; Schülke et al., 2010; Silk, Alberts, & Altmann, 2003; Silk et al., 2009, 2010), to our knowledge there are currently no primate studies that explicitly investigate whether infants that form enhanced bonds with handlers increase their chances of survival either during infancy or beyond (also see Keller & Bard, 2017, who hypothesized that human mothers in small scale societies encourage their infants to form relationships with many non-mothers to achieve similar goals). Additionally, it is not clear whether enhanced bonds endure past infancy, and, if so, how long. Recent research by Thompson and Cords (2018) on blue monkeys indicates that strong social bonds alone are not always adaptive; among adult females, strong social bonds that were short lived across years were actually associated with increased mortality (Thompson & Cords, 2018). Whether this is also the case for more despotic species is not clear; however, it may be that in order for handling bonds to be adaptive, enhanced bonds formed between handlers and infants may need to endure over multiple years, possibly into adulthood. Although more research is needed to ascertain whether enhanced bonds from handling persist beyond infancy, we speculate that they do, particularly among despotic macaques; in rhesus macaques, for example, immature females maintain social networks based on the same organizing principles (e.g., kinship, rank, etc.) as they mature into adults (de Waal, 1996; Kapsalis & Berman, 1996). Thus, it is likely that their social networks also include many of the same individuals as they did when they were infants (also see Minge et al., 2016, for evidence that male-infant bonds among more relaxed Assamese macaques, although not necessarily established through handling, endure into the second year of life). Finally, future research needs to address possible fitness effects for handlers and mothers. Do they also enjoy enhanced social bonds due to handling? If so, are these enhancements enduring and/or associated with increased survival or reproductive success in the same way that strong and enduring grooming relationships are adaptive for adults?

Life History Variables and Evolutionary Processes

Another set of hypotheses focus less on immediate benefits and costs (none of which may be adequate to drive the evolution of handling), and more on its effects on life history variables and fitness. For example,

the reproductive rate hypothesis focuses on the effects of allocare on life history variables (Mitani & Watts, 1997; Ross & MacLarnon, 2000). In a large cross-species analysis of the relationships between allocare levels, diet, and life history variables of mothers and infants that controlled for both phylogenetic relationships and body size, Ross and MacLarnon (2000) found that species with high levels of allocare (measured as the proportion of carrying and holding that is done by the alloparent vs. the mother) had higher birth rates and younger weaning ages (also see Fairbanks, 1990; Mitani & Watts, 1997). They suggested that allocare handling allows mothers to wean their infants earlier, thus reducing their interbirth intervals and increasing their reproductive rates (Ross & MacLarnon, 2000). While mothers gain substantial fitness benefits under this hypothesis, the consequences for infants are unclear. Earlier weaning was neither associated with earlier maturation for infants, something that would allow them to begin reproducing earlier, nor with less vulnerability to infanticide, as might be expected when weaning is early (Ross & MacLarnon, 2000). Infant survival was not analyzed *per se*, and some results for infants appeared contradictory. For example, high levels of allocare were not associated with increased infant growth rates (but see Mitani & Watts, 1997), yet infants reached comparable weaning weights while also being weaned earlier.

Nevertheless, some recent studies on single species have found additional support for the reproductive rate hypothesis. In a study investigating male handling among monogamous and polyandrous siamangs, Lappan (2008) suggested that the durations of interbirth intervals may be linked with aspects of male care, evidenced by the multiple findings: a) Females adjusted their levels of care depending on amounts of care provided by males, b) the onset of male care was precipitated by a reduction in female care, and c) mothers that provided more care had longer interbirth intervals. Similarly, Fairbanks (1988a, 1988b) found that when vervet infants had grandmothers, a) mothers were less protective and restrictive of their infants, b) infants spent less time in contact with their mothers, and importantly, c) infants became independent at an earlier age. Moreover, Bădescu et al. (2015) and Bădescu, Wikberg, et al. (2016) suggested indirect links between handling, faster infant development, and reduced infanticide risk in black and white colobus monkeys. Handling in this species is more common during earlier natal coat stages (Bădescu et al., 2015), and transitions through natal coat stages are quickened when risks of infanticide are higher (Bădescu, Wikberg, et al., 2016). Similarly, male colobus infants, who are more vulnerable to infanticide, experience more handling and mature more quickly than female colobus. Although not explicitly tested, Bădescu and colleagues suggest that handling, and more general increased maternal investment, may speed up infant development, as evidenced by more rapid changes in infant coat coloration, when infants are at more vulnerable stages and at higher risk of infanticide. Another recent study of chimpanzee mothers found that alloparenting did not benefit mothers energetically by freeing up foraging time (Bădescu, Watts, et al., 2016). However, they found that mothers whose infants were handled at higher rates had lower nursing rates, transferred less milk to their infants, and weaned their offspring earlier, as predicted by the reproductive rate hypothesis. They suggested that reduced maternal lactation effort and earlier weaning may not necessarily be achieved through increases in energetic gains vis-à-vis increases in foraging, but rather by increasing time intervals between nursing bouts when their infants are being handled. Given that observed reductions in maternal nursing effort were associated with allocare handling but not affiliative handling (Bădescu, Watts, et al., 2016), and that macaques and baboons show little to no allocare handling, variation in handling levels among baboons and macaques are unlikely to be related to reproductive rates vis-à-vis weaning ages.

Finally, researchers that focus on long term evolutionary processes view handling as a generalized form of altruism on the part of the handler (Reidman, 1982; Nicolson, 1987), and hence focus on theories that deal explicitly with altruism and cooperation. These theories focus more on the long-term effects of allocare rather than on the particular immediate benefits or costs. In this regard, costs and benefits to handlers and mothers and/or infants are assumed and may represent any of the proposed costs and benefits already described.

One such theory is kin selection. Under this explanation, handlers can compensate for the costs and gain indirect fitness, if the benefits of handling to mothers and/or infants outweigh its costs to the handler, discounted by the handler's degree of relatedness to the mother and infant (Hamilton, 1964). Kin selection theory predicts that attraction and handling are most common among kin, and, all things being equal, more common among close kin than distant kin. There is overwhelming support for this prediction across primates (vervets, Fairbanks, 1990; wedge-capped capuchins, O'Brien & Robinson, 1991; black and white colobus, Bădescu et al., 2015), especially in macaques (Berman, 1982a; Dunayer & Berman, 2017; Schino et al., 2003; Silk, 1999) and baboons (Silk, Rendall, et al., 2003). However, kin selection does not account for the occurrence of non-kin handling (capped langurs, Stanford, 1992; patas monkeys, Muroyama, 1994; Bolivian squirrel monkeys, Williams et al., 1994; blue monkeys, Förster & Cords, 2005; black capuchins, Baldovino & Di Bitetti, 2008; and Formosan macaques, Hsu et al., 2015).

Handling among nonkin could be the outcome of reciprocal altruism, whereby individuals take turns acting as altruist and beneficiary (Trivers, 1971). In this regard, kinship is no longer a prerequisite, although reciprocal exchanges among kin would be expected to yield more benefit than similar exchanges among nonkin. In any case, handlers should be parous females, reciprocally trading handling over time (cf. Stanford, 1992). Few studies have explicitly investigated the reciprocal exchange of handling between parous females; however, those that have found little support for reciprocal altruism driving the handling interaction (Perry, 1996; Manson, 1999). Nevertheless, gray mouse lemurs that routinely groom and allonurse related infants in their nests (Eberle & Kappeler, 2006; Radespiel, 2006) may be the most promising candidates for an investigation of kin-based reciprocity. Furthermore, reciprocal altruism cannot explain why nullipares often show high levels of attraction (Hanuman langurs, Hrdy, 1977; Scollay & DeBold, 1980; vervets, Fairbanks, 1990; Meaney et al., 1990; macaques, Dunayer & Berman, 2017; Schino et al., 2003; blue monkeys, Förster & Cords, 2005; and black and white colobus, Bădescu et al., 2015; Brent et al., 2008; reviewed in, Hrdy 1976; MacKinnon, 2011), unless one also hypothesizes that reciprocity for an altruistic act could occur over long temporal intervals, something that some researchers see as beyond the cognitive abilities of most nonhuman primates (see Barrett & Henzi, 2002). Empirical tests of this type of reciprocity are lacking for macaques and baboons (but see Hsu et al., 2015). Handlers could conceivably exchange allocare for other benefits (e.g., later agonistic support, tolerance, mating access) for handling in accord with reciprocal altruism. It is also plausible that mutualism could operate when the costs are low/minimal and both parties simultaneously benefit (e.g., if Colobine females trade learning opportunities in exchange for providing foraging opportunities to mothers). To our knowledge, these sorts of exchanges have not been explicitly tested; nevertheless, it remains an important area of research for future studies.

Biological markets theory (BMT) provides a final cooperative framework that has been applied to the exchange of grooming and/or other affiliative behaviors (e.g., embracing) for opportunities to handle infants. BMT is an extension of reciprocal altruism, but unlike reciprocal altruism, BMT, in which group members act like "traders" in a market place, views cooperation as an interaction based on partner choice rather than partner control (Noë, van Schaik, & van Hooff, 1991; Noë & Hammerstein, 1994). Supply and demand relationships are purported to operate in these biological markets, with individuals "paying" more for access to rare commodities. Several studies among primates (vervets, Fruteau et al., 2011), including macaques and baboons (Gumert, 2007; Henzi & Barrett, 2002), have found support for biological market based exchanges, specifically with handlers trading grooming of mothers for access to their infants, and with grooming time increasing as the availability of infants within the group decreased (and vice versa). However, other studies have not found these predicted market effects (Frank & Silk, 2009; Tiddi et al., 2010; reviewed in Dunayer & Berman, 2016). Problematically, BMT does not address why infants are intrinsically attractive in the first place, and it rests on the assumption that handling infants could be a desirable commodity in and of itself. On the other hand, BMT

does incorporate social characteristics (e.g., kinship, rank) into its predictions, as kinship and rank may influence the “price” to handle, with close kin and high-ranking handlers grooming mothers less and with mothers of high-born infants groomed more by handlers. Therefore, while market effects are likely to play a role in mediating the handling interaction, they are not likely to constitute a selective force driving it.

Summary and Conclusions

Among primates, infant handling encompasses a variety of forms, some of which constitute allocare, while other affiliative forms of handling provide no extensive parental assistance. Still other forms of handling appear to be deliberately abusive on the part of the handler. The observed variations may reflect the propensities and interests of each interactor (handler, mother, and infant) to behave in a particular manner during handling interactions. Consequently, selective forces driving the behaviors of each interactor may not necessarily align; as such, most functional explanations focus on the benefits accrued to only one individual. Similarly, the most promising hypotheses related to short- or medium-term benefits for particular species appear to vary with breeding system, reproductive biology, socioecological factors, and life history characteristics. For example, the extensive allocare handling seen in Callitrichids appears to be a specialized adaptation for cooperative breeding, which permits rapid reproduction in the dominant female and has likely evolved in response to offspring having limited opportunities for independent breeding in saturated habitats (Goldizen, Mendelson, van Vlaardingen, & Terborgh, 1996; Rylands, 1996). On the other hand, in species in which plural breeding is possible, allocare is less extensive and appears to be the outcome of a variety of other selective forces. For example, the learning-to-mother hypothesis may be the most likely explanation for vervet monkeys (Fairbanks, 1990; Lancaster, 1971; Meaney et al., 1990), whereas the foraging hypothesis may be a better fit for leaf-eating Colobines (capped langurs, Stanford, 1992; Hanuman langurs, Vogel, 1994; golden snub-nosed monkeys, Xi et al., 2008). Explanations based on life history variables (e.g., reproductive rates) or long term evolutionary processes related to cooperation (e.g., kin selection) appear to have broader applications, but nevertheless fail to explain infant handling in all its manifestations.

Dominance relationships between females appear to be one of the strongest factors influencing the appearance of handling, in both form and frequency (Chism, 2000). This may be particularly the case for differences between guenons versus many macaques and baboons (Chism, 2000). In macaques and baboons, particularly those with despotic rather than relaxed social styles (Thierry, 2000), the strong influence of female dominance relationships, intense inter-group aggression, and high levels of within-group competition appear to preclude the display of allocare handling, despite high levels of attraction to infants (Chism, 2000). Consequently, handling hypotheses relying on most direct and immediate benefits related to allocare do not receive strong support for these species. In this regard, the social bond hypothesis, in which handling is viewed as an investment in long-term social bonds, appears especially promising. Under this hypothesis, all parties (e.g., handler, mother, and infant) potentially benefit much in the same way that individuals gain social benefits (e.g., coalitionary support, access to resources) from other bond-promoting behaviors. The social bond hypothesis could also play a contributory role in handling for other primate species, including those that display more allocare handling, though its influence is likely to be most important in species that display strong bonds between specific kinds of individuals—female-female, male-female, or male-male. Thus, the social bond hypothesis may not play as large a role among species where females are not philopatric (e.g., chimpanzees) or have weak bonds between females for other reasons (e.g. Colobines).

Of course, the social bond hypothesis has not yet been tested extensively. Hence, problems with it may appear as research progresses. Thus, it behooves us to also consider the byproduct hypothesis, which has

received strong support, particularly for macaques and baboons (e.g., Silk, 1999; Silk, Rendall, et al., 2003). It is reasonable to hypothesize that handling initially evolved as a byproduct of maternal responsiveness, ensuring that mothers provide appropriate care. The infantile physical characteristics that evoke maternal responsiveness could consequently elicit attention from other females and to a lesser extent from males, with maternal care “spilling over” onto other females’ infants. However, once handling became widespread in a species, it is likely to have brought opportunities for new adaptive functions to evolve. In this regard, handling may have since been co-opted, for example, in macaques and baboons, by functioning to promote social bonds between handler, mother, and infant. It is also plausible that in species in which handling posed few risks for mothers and infants, a variety of other functions (e.g., learning to mother, freeing up foraging time) may have similarly emerged, with the result that handling became a heterogeneous phenomenon, serving multiple functions. If so, a single, integrated hypothesis may remain elusive for the foreseeable future. Nevertheless, progress even with regard to single, limited models of handling will be greatly enhanced by future studies that incorporate both more quantitative single species designs and cross-species comparative analyses. Finally, there is an especial need for longitudinal studies on the effects of infant handling on reproductive success and other measures of fitness, as they pertain to both the social bond and other hypotheses (e.g., learning to mother, reproductive rate).

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