

# SOCIAL PARASITISM IN MAMMALS WITH PARTICULAR REFERENCE TO NEOTROPICAL PRIMATES

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**ABSTRACT:** Organisms often respond in ways that appear to benefit others rather than themselves. This phenomenon is consistent with the views of Darwin (1859) and Dawkins (1999) that individuals may exploit the responses of others. This phenomenon, "social parasitism", has been extensively investigated in social insects, particularly, ants. Other empirical studies have demonstrated social parasitism in fish, birds, and mammals. This paper reviews several possible examples of mammalian social parasitism, with an emphasis upon intraspecific social parasitism (ISP) in Neotropical primates. Social parasitism is discussed as a life history feature of long-lived, social organisms such as many primates, including humans. A simple mathematical model, applied to social parasitism, is presented linking parasite transmission to a parasite's influence on its host. Phenotypic manipulation is assessed as a mechanism of social parasitism, and possible examples from the literature on Neotropical primates are provided. Social parasitism is discussed in relation to the evolution of higher grades of sociality (eusociality, cooperative breeding), manipulation success (infectivity), and the evolution of virulence (e.g., aggression, punishment). It is proposed that an understanding of variations in virulence and infectivity by social parasites is likely to reveal important evolutionary dynamics for an integrated view of social evolution.

**Key words.** Social parasitism. Phenotypic manipulation. Neotropical primates. Life history. Social evolution.

## INTRODUCTION

Dawkins (1999: 69) proposed that, "Any nervous system can be subverted if treated in the right way." Consistent with this view, group-living individuals often act in ways that appear to benefit others (altruism) instead of themselves (selfishness or cooperation). Several hypotheses have been advanced to explain ostensibly altruistic behavior in which the donor bears a (genotypic or phenotypic) cost and the recipient experiences a genotypic or phenotypic advantage over the donor or a third party. These hypotheses, kin selection (Hamilton, 1964; Bertram, 1983; West et al.,

2002), reciprocal altruism (Trivers, 1971), manipulation (West-Eberhard, 1975; Ridley and Dawkins, 1981; Stuart, 2002), and/or "trait group" selection (DS Wilson, 1975), are fundamental schemas in most attempts to explain the evolution of social behavior in invertebrate and vertebrate societies. Students of social behavior have been particularly concerned with those interindividual interactions in which one individual's responses benefit the genotypic and/or phenotypic interests of another (West, 1967; EO Wilson, 1975; West-Eberhard, 1979) since these responses are not explained in a straightforward manner by classical evolutionary theory. Darwin (1859: 208) argued, for

example, “[N]o instinct can be shown to have been produced for the good of other animals, though animals take advantage of the instincts of others.”

For mammals, the highest social grades are achieved among cooperatively breeding species such as the Latin American marmosets and tamarins (Tardif, 1997; Abbott et al., 1998; Saltzman, 2003; also see Andersson, 1984; Emlen, 1991, 1995; Solomon and French, 1997) and the eusocial naked mole rats of Africa (Sherman et al., 1991, 1995; Lacey and Sherman, 1997; Burland et al., 2004). In these groups, some individuals, generally females, more or less temporarily (marmosets and tamarins: Cebidae, Primates) or more or less permanently (naked mole rats: Bathyergidae, Rodentia) delay individual (selfish) reproduction to assist dominant group members rear one or more offspring who are usually the helper’s kin. Altruistic behavior in these cases, then, is thought to arise via kin selection in combination with other factors (e.g., ecological effects such as habitat saturation: Andersson, 1984; Emlen, 1991, 1995; Faulkes, et al. 1997) and to be beneficial to the helper (host, victim). Helping behavior and consequent reproductive suppression may represent a “decision” by the helper or may be imposed by a dominant (reproductive parasite), often through mechanisms of behavioral “policing” or chemical communication.

It is relatively straightforward to formulate sound Darwinian hypotheses explaining altruism when the actor’s selfish interests appear to be served. It has proven difficult, however, to proffer credible evolutionary scenarios for numerous actions that appear counterintuitive within a Darwinian paradigm (e.g., same sex partner preference, homicide, suicide, delaying or foregoing reproduction, spite, dependency complexes, alloparenting: see, for example, Dawkins, 1999; Berdoy et al., 2000). This challenge has led some researchers to propose group-level (Wilson, 1980) or other controversial constructs (Fehr and Henrich, 2003) to explain altruism (Kerr et al., 2004). The **evolutionary trap of altruism** will exist when assisting another’s reproductive (genotypic or phenotypic) interests is detrimental to

one’s own interests, a dilemma that is expected to arise wherever interindividual (genotypic and/or phenotypic) conflicts of interest exist (Reeve and Keller, 1996).

While the ecology of social parasitism has not been studied thoroughly, Jamieson et al. (2000), studying parasitic birds, suggested that social parasitism is most likely to be expressed in temporally and spatially heterogeneous regimes. Furthermore, Savolainen and Vepsäläinen (2003) argued that polygyny is a prerequisite for intraspecific social parasitism and that social parasites are often related (“Emery’s rule”). Neotropical primates are an excellent test for these propositions because of the extensive variability of their behavior and social organization (Fleagle, 1999). These studies have been initiated by O’Brien’s (1988) investigations of parasitic nursing by infant *Cebus olivaceus*, Jones’ (1997a) research on reproductive parasitism by female *Alouatta palliata*, and Treves’ (2001) review of the role of conspecific threat and constraints on individual fitness imposed by conspecifics in *Alouatta* spp. The present paper explores the topic of intraspecific social parasitism (ISP) in mammals relying, in particular, upon examples from the literature on Neotropical primates (Platyrrhini: Groves, 2001).

### **Defining criteria for the classification of social parasitism**

Mammalogists have probably not emphasized the role of social parasitism in the evolution of behavior and social organization among social mammals because the pertinent models have been associated with the insect literature, invertebrate constructs that are rarely employed for the investigation of mammals. **Parasitism** generally implies a non-fatal interspecific relationship whereby one actor benefits at the expense of another. The familiar parasite is a fungus, virus, bacteria, protozoan, arthropod or other small organism exploiting the tissues, blood, or other products of a host (the victim). This classical body of work on non-social parasitism is used in the present paper as a conceptual framework for the analysis of social parasitism, in particular, intraspecific social parasitism (ISP). **Social parasitism**, some-

times termed “involuntary altruism,” implies associations characterized by an exploitative relationship (interspecific or intraspecific) whereby the parasite is wholly or partially dependent upon the social behavior and/or social organization of the host. As Poulin (2002) points out, all forms of parasitism reflect Dawkins’ (1982) concept of the “extended phenotype” whereby exploitation by parasites of their hosts can be viewed as the former expressing his/her genes in the latter.

Several patterns of social parasitism have been described. “Brood parasitism” is a type of social parasitism common among birds and entails one individual laying its egg(s) in the nest of the bird of another species who raises the parasitic egg(s) at the expense of its own young (Lack, 1968; Rothstein, 1990; Cichon, 1996). Some types of adoption in mammals may be similar to brood parasitism in birds (see, for example, Nicolson, 1987; Hrdy, 1979). “Kleptoparasitism,” reported for mammals and common among birds (Bautista et al., 1998), is another type of social parasitism in which one species steals the prey of another species. Kleptoparasitism of the food supply of the African wild dog (*Lycaon pictus*) by the spotted hyaena (*Crocuta crocuta*), for example, was documented by Gorman et al. (1998). Each of these types of exploitative interspecific associations has analogies at the intraspecific level, such as reports of “manipulation by harassment” in primates [Stevens and Stephens, 2002; Stevens, 2004 (see below)]. Bronstein (2001, 2003) has pointed out that, like herbivory and predation, parasitism is defined primarily by its costs. Thus, students of social mammals need to develop confident measures or estimates of cost (to phenotypic and/or genotypic success) in order to distinguish social parasitism from other types of associations (e.g., spite, cooperation, mutualism, symbiosis, parasitoidism, inquilism).

Ecologists define **exploitation** as a form of competition in which the interaction of two or more species or individuals indirectly reduces a limiting resource, yielding differential fitness benefits to the interactants (Begon and Mortimer, 1986). A necessary, but not sufficient, feature of a parasite is that it exist in

close association, often, but not necessarily, obligate, with a host for some part, if not most, of its life (Begon and Mortimer, 1986). By definition, parasites obtain resources from and harm their hosts, and only experimental studies can determine whether or not these costs harm the inclusive fitness of hosts beyond critical threshold values (spite). Parasitism, then, implies **dependency**, a characteristic that may predispose its expression where individuals characterized by asymmetries live in groups and/or exhibit long lifespans, virtually ubiquitous conditions for primates.

### **Analogies between social parasitism in insects and in Neotropical primates**

Social parasitism is particularly common among ants (Hölldobler and Wilson, 1990; Bourke and Franks, 1995) and has been extensively studied in these and other social insects (Stuart, 2002). Several patterns of (interspecific) social parasitism have been described for social insects, classified from least (e.g., temporary kleptoparasitism) to most “intimate” associations whereby the whole life cycle of the social parasite is completed within that of the host (see Stuart, 2002: 318-324). Stuart points out that these associations may be temporary and facultative or obligate and relatively permanent, and the insect classification system has utility as a representative schema for social mammals. Strier (2000: 307), for example, described two examples of temporary polyspecific associations among Neotropical primates in the Atlantic forest of Brazil that may involve interspecific social parasitism because the associations appear to be costly for one of the species. In these cases, one species may initially assist another in predator or food detection (see, for example, Eckardt and Zuberbühler, 2004), providing an opportunity for subsequent exploitation.

Stuart’s (2002: 318-324) discussion highlights patterns of “intimacy,” dependence, and exploitation, and it is likely that initial stages of research on social parasitism in social mammals will rely heavily upon the rich literature existing on this topic for social insects. Caveats are required for these comparisons, however, since social mammals and insects may

differ significantly in their genetics, anatomy and morphology, behavior, social organization, and in other traits. Studies of social parasitism in insects (Hölldobler and Wilson, 1990; Bourke and Franks, 1995) and other taxa are fundamental because within-species local competition for limiting resources is believed to drive social evolution (Perez-Tomé and Toro, 1982; West et al., 2002; Dybdahl and Storfer, 2003). Only additional theoretical and empirical, including experimental, research can determine which features of invertebrate social parasitism will apply to vertebrates. For example, several researchers have found that social insect parasites lose many traits characteristic of higher grades of sociality (e.g., worker castes: Parker and Rissing, 2002; multiple mating by females: Sumner et al., 2004). By analogy, research on primates and other social mammals may find that social parasites are more likely to demonstrate infantilized behavior such as the paedomorphic vocalizations exhibited by a subordinate male mantled howler competing with a dominant for a female in estrus (Jones, 1985, 1995a).

Several conditions can be proposed for the delimitation of social parasitism in social mammals and, perhaps, other social vertebrates, based upon the discussion of Lewis et al. (2002): (1) social parasitism is a one- or two-trophic level interaction in which the social parasite receives a (genotypic and/or phenotypic) benefit at the expense of the host (victim, involuntary altruist); (2) the social parasite must exhibit some degree of dependence upon or "intimacy" with the host; and, (3) social parasites demonstrate tactics and strategies for the expression and proliferation (transmission) of their phenotypes. Condition (2) implies that organisms may benefit from dependency and/or host status under some conditions (e.g., immatures or nursing female mammals). Condition (3) suggests that social parasitism is beneficial to the actor, setting the (evolutionary) stage for parasite virulence (e.g., aggression and/or punishment). Stuart (2002) has argued that a social parasite's host might be one or more than one organism.

Poulin (2002) has pointed out that the methods of behavioral ecology are powerful tools

for the analysis of "parasites of all kinds." This author discusses the application of optimality models, game theory, and inclusive fitness theory to a study of parasitism in order to demonstrate the ways in which Tinbergen's (1951) program for answering questions in behavioral ecology might be realized. Tinbergen's emphasis upon function, proximate and ultimate causation, and development remains the conceptual framework for work in animal behavior and behavioral ecology (Alcock, 1993; Strier, 2000; Jones, 2003a), providing the context for studies of social parasitism, most of which have investigated only the proximate level of analysis (Poulin, 2002; but see Taborsky, 2001).

An integrated approach to social parasitism requires a careful assessment of differential costs and benefits of social parasitism to both parasite and host for an understanding of its adaptive significance, although Poulin (2002) has pointed out that, in some conditions, parasitism may not be costly to the parasite (see above). Moore (2002) argued that parasitism might benefit the parasite, benefit the host, benefit both parasite and host, or benefit neither, a range of possibilities revising original definition(s) of parasitism given above whereby parasitism is necessarily deleterious to the host. A resolution of this potential inconsistency may lie with an understanding that the value of cost is relative to costs of alternative responses and with an investigation of thresholds of costs and benefits. Research on the evolutionary history of dependent and exploitative associations, including experimental manipulations, are required in order to understand not only the initial conditions favoring social parasitism but also the counteradaptations that may be adopted by hosts in some conditions which may decrease the costs of parasitism to them, all other things being equal.

### **The costs and benefits of intraspecific social parasitism (ISP)**

In general, it is expected that ISP will be favored where the fitness benefits to parasites and hosts outweigh the costs. Benefits to the host will parallel those addressed in the literature for the advantages of all social responses,

such as improved predator or competitor detection, improved foraging efficiency, increased access to mates, access to information centers, increased defense of limiting resources, and increased survivorship of the host and/or her/his offspring. Costs to the host may entail increased competition for limiting resources, increased risk of phenotypic manipulation (see below), increased risk of exploitation of offspring, increased interference with parenting, vulnerability to spite, or increased mortality (e.g., by predation). Moore (2002) has discussed many of these effects in detail.

Following May and Anderson (1990, cited in Moore, 2002), Moore points out that the fitness of the parasite can be measured as reproductive rate ( $R_0$ ), a density-dependent value. May and Anderson's equation linking parasite transmission to a parasite's influence on its host (Moore, 2002: 6) is related to virulence by way of a measure of cost to host fitness [e.g., increased inter-birth intervals (IBI) among social mammals or decreased litter size]. May and Anderson's equation can be modified for social parasitism such that

$$R_0 = y(N)/(a+b+v)$$

where  $y$  is **transmission** (infectivity, manipulation success),  $N$  is host population density,  $a$  is rate of host cost (e.g., rate of decrease in IBI) from **virulence** (aggression),  $b$  is rate of host cost from all but virulence, and  $v$  is **recovery rate** (the host's ability to completely or partially escape the deleterious effects of social parasitism). For example, in the case described by Jones (1997a), *Alouatta palliata* females may parasitize males (hosts) reproductively by leading males to a feeding source which males defend. Females feed before "deciding" to copulate or not to copulate. Reproductive parasitism by these females may increase a female parasite's reproductive rate by decreasing her interbirth interval (IBI). Following May and Anderson's equation, decreased IBI (increased  $R_0$ ) is a function of manipulation success which might be measured as energy obtained by females for conversion into offspring. Virulence (host cost) might be measured as decreased male IBI resulting from "punishment" by females (e.g., time expended to guard a female who does not copulate after

feeding: see Jones, 2002d). Rate of host cost ( $b$ ) might be measured as time expended by males in following and guarding females who deceive them or who extract more time for feeding than they, in fact, require to produce a viable offspring. Finally,  $v$ , the host's ability to escape or avoid parasitic females ("negative reinforcement") might be measured as the standard deviation of a male's "persistence" in guarding parasitic females. As Moore (2002) points out,  $R_0$  increases as  $a$  decreases when virulence, transmission, and recovery rate are independent. Under these conditions, the parasite should evolve towards a harmless state since the costs of social parasitism would not outweigh its benefits. In such conditions, the potential for female manipulation of males should be minimized (*Brachyteles*?). Where virulence, transmission, and/or recovery rate are related, however, social parasitism should be favored, and the degree of virulence should be determined by the relative degree of benefit to the social parasite, all other things being equal (*Alouatta*).

### Intraspecific social parasitism (ISP) and life history theory

May and Anderson's (1990, cited in Moore, 2002) treatment links the topic of parasitism, and, by extension, social parasitism, to life history theory since  $R_0$  is a life history expression (Stearns, 1992; Jones, 1997b; Alberts and Altmann, 2003). Discussing social parasitism in ants, Stuart (2002) provides a robust schema for the preliminary analysis of social parasitism in social mammals and other social vertebrates. This author classifies systems of social parasitism in a binary manner, with one class representing breeding systems that raise young more or less selfishly (without helpers) and the other class representing breeding systems raising young more or less cooperatively or communally. Both of these systems are represented in Neotropical primates.

Female social spiders, *Stegodyphus dumicola*, rear their own cocoons in an attempt to avoid ISP (Kürpick, 2000). Similarly, female mantled howlers (*A. palliata*) rear their single offspring with little or no assistance from relatives, unrelated females, or males (Jones, 1978, 2005;

Clarke and Glander, 1984; Clarke, 1990; Calegario-Marques and Bicca-Marques, 1993; Clarke et al., 1998), a reproductive tactic that may have evolved in response to the costs of ISP. Alloparenting and other behaviors characteristic of more gregarious systems (e.g., grooming) are rare in this and other species of *Alouatta* (Jones, 1979; Brockett et al., 2000). Altmann (1959) noted that weaning in mantled howlers is harsh, suggesting that these mothers' tolerance for infant dependence is limited. Since Galef, (1981; also see O'Brien, 1988) has suggested that immature mammals are "ultimate subordinates" because of their tendency to employ deceptive tactics and strategies to achieve their selfish ends (Trivers, 1974, 1985; Crespi and Semeniuk, 2004), mantled howlers may be an excellent model for the investiga-

tion of the genetic, ecological, and other factors limiting social parasitism by this age group. If developmental costs are sufficiently high for young mantled howlers and if the potential for offspring parasitism of mothers is restricted by maternal behaviors, selection may favor infants who parasitize the responses of group members other than their mother (**Fig. 1**).

At the other extreme, some callitrichids are cooperative breeders, and mothers receive assistance from putative fathers and other group members who are often infants' older siblings (Mitani and Watts, 1997; Porter, 2001; Saltzman, 2003). Porter (2001) reports that the reproductive output of female Goeldi's marmosets (*Callimico goeldii*; **Fig. 2**) is increased by assistance from other group members as well as the presence of biannual birth seasons.



**Fig. 1.** Juvenile mantled howler monkey (*Alouatta palliata*) carrying unrelated conspecific infant across a space between trees impassable to the infant. Distress vocalizations emitted by the infant may have functioned to induce the juvenile's helping behavior. Photo by © Clara B. Jones.



**Fig. 2.** Adult male Goeldi's marmoset (*Callimico goeldii*) helper. Photo taken at San Sebastian, Bolivia by © Edilio Nascimento B.

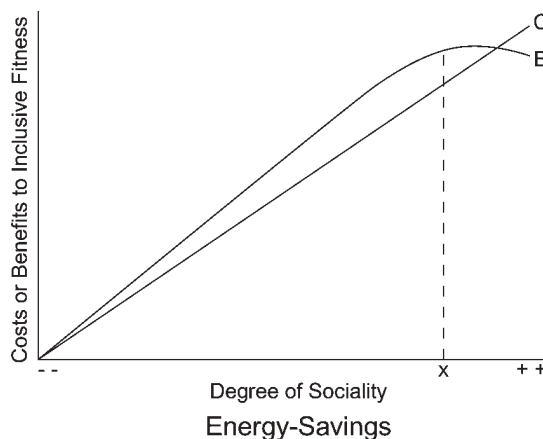
In addition to some callitrichids, the socially monogamous *Aotus* and *Callicebus* as well as polygynous *Saimiri* and *Cebus* are the only Neotropical taxa exhibiting extensive allocare (Hrdy, 1976; Nicolson, 1987; Tardif, 1997). These taxa belong to the Neotropical primate family Cebidae. Charnov's (1978; Mousseau and Fox, 1998) mathematical result that maternal parasitism is more likely to be found in species with low levels of multiple mating by females can be tested for this rearing guild, as well as Savolainen and Vepsäläinen's (2003) argument that polygyny is a prerequisite for ISP. The pattern of rearing identified for Neotropical primates whereby members of the family Atelidae, folivorous primates, exhibit little maternal parasitism or allocare may indicate that the potential costs (to fitness) from ISP are prohibitively high in some ecological regimes, a possibility deserving investigation.

Stuart's (2002; van Schaik and Kappeler, 1997) binary system based upon female rearing strategies is consistent with a life history approach whereby female "decisions" ultimately determine a population's profile. Emlen and Oring (1977) and others (Trivers, 1972; Wittenberger, 1980; Wrangham, 1980, 1987; Shuster and Wade, 2003; Lindenfors et al., 2004) have shown that the abundance of

fertilizable females limits male fitness and that male reproductive strategies depend upon females' choices. It is important to recall, however, that, since the interests of the sexes will often differ, males and females may be engaged in a coevolutionary race to minimize the deleterious effects of one sex upon the other (Rice, 2000). Nonetheless, because higher grades of sociality are expected to evolve in response to energetic savings, as suggested by Heinze and Keller (2000), and because females are expected to be more sensitive than are males to energetic costs (Schoener, 1971), females are expected to be more social than males where sociality delivers an energetic gain benefiting inclusive fitness, all other things being equal (Queller, 1997). These hypothesized relationships are depicted in a graphical manner in Fig. 3.

### Phenotypic manipulation in primates

In 1997, Byrne and Whiten stated: "For each individual primate, [group living] sets up an environment favouring the use of **social manipulation** to achieve individual benefits at the expense of other group members...." (p. 2, emphasis in original). This statement reflects not only the neo-Darwinian view that an individual's actions are expected to be selfish rather than altruistic but also the view that some



**Fig. 3.** A graphical model describing the costs (C) or benefits (B) to female inclusive fitness (lifetime reproductive success) of relative degree of sociality as a function of differential energy-savings, from low (—) to high (++) (see Heinze and Keller 2000; Jones and Agoramorthy, 2003: 124-124). Benefits will increase and then level off as the costs increase linearly (because resources are limiting), and the maximum net benefit (benefit minus cost) to females should occur at "x". The location of "x" will depend upon the position and shape of the benefit and cost curves, a function of environmental unpredictability over the short and long terms.

individuals may manipulate others against the latter's interests. As pointed out above, numerous hypotheses have been proposed to explain this apparent inconsistency. The type of animal discussed by Byrne and Whiten (1997; also see Frith and Frith, 1999) is one with a plastic or flexible phenotype vulnerable to a range of manipulations.

The view that primate, including human, phenotypes are modifiable to a greater degree than those of other organisms has a long history, extending at least to the early psychologists such as Baldwin (1902; West-Eberhard, 2003, Chapter 1; Jones, 2005; see Smuts et al., 1987; Dunbar, 1997). These views no doubt account for the radical behaviorism representative of the early stages of American Psychology and its emphasis upon exogenous stimulation and the mechanisms of learning. Currently, however, psychologists are more likely to advance cognitive rather than behavioral explanations for the responses observed in primates and other animals showing "complex adaptations" (Byrne and Whiten, 1988; Whiten and Byrne, 1997; Dunbar, 2003).

The chapters in Byrne and Whiten's volumes cited previously pertain specifically to the ways that organisms use intellectual processes (e.g., "theory of mind") to deceive others ("social intelligence"). The topic of intraspecific deceit has a long history in evolutionary biology, including primatology (Otte, 1975; Byrne and Whiten, 1985); however, scientists have recognized that a variety of mechanisms may explain the various forms of signaling and communication. Indeed, any sensory modality may be employed by the sender of a deceptive signal to manipulate the phenotype of a receiver (Eberhard, 2000; Lenoir et al., 2001; Double and Cockburn, 2002; Heiling et al., 2003; Mizutani et al., 2003; Pennisi, 2003). Costa Rican mantled howler monkeys, for example, demonstrate a broad array of behaviors suggesting that olfactory (Jones, 2002a, 2003b) and visual (Jones, 2002b, c), in addition to vocal (Jones, 1985, 2000) communication are important in intraspecific communication and in the coordination and control of conspecifics, patterns of response that may involve **phenotypic manipulation**, defined as a social

parasite's ability to alter the phenotype of a host in a manner beneficial to the manipulator but costly to the host (Lobue and Bell, 1993; Poulin, 2003). Some mammalian studies have documented intraspecific phenotypic manipulation (e.g., maternal behavior: Meaney, 2001; Crabbe and Phillips, 2003; group foraging: Held et al., 2002; mate choice: Jones, 1997a; alloparental behavior: Hrdy, 1976; Jones, 1986). However, none of these studies unequivocally measures costs to the putative host.

Deception may be employed by parasites as a social tool to effect phenotypic manipulation. Although students of animal, including human, communication continue to debate the extent to which signals are reliable ("honest"), there seems to be general agreement that deception may occur where its benefits (to inclusive fitness) outweigh its costs (Otte, 1975; Bradbury and Vehrencamp, 1998; Royle et al., 2002). Importantly, recent theoretical and empirical treatments (Reeve 2000; Stevens and Stephens, 2002; Stevens, 2004) stress "the selfish nature of generosity" (Stevens and Stephens, 2002), providing an alternative interpretation of sharing and cooperation based upon self-interest (also see Johnstone and Bshary, 2002). Like foraging common cranes, *Grus grus*, the primates studied by Stevens and his colleagues may be sharing to prevent "intraspecific kleptoparasitism" (Bautista et al., 1998). Variations of these interpretations might be applied to numerous observations of osten-



**Fig. 4.** Anesthetized adult female mantled howling monkey (*Alouatta palliata mexicana*) showing genital hypertrophy (arrow). Photo by © Juan Carlos Serio Silva.



**Table 1**

Documented examples of parasitic phenotypic manipulation (virus, insects, fish, birds, mammals) including empirical evidence and possible analogies in Neotropical primates. See text for further explanation.

<b>Example of parasitic phenotypic manipulation</b>	<b>Empirical evidence</b>	<b>Possible analogy in Neotropical primates</b>
Virus: Varaldi et al., 2003	Virus causes wasp to modify its reproductive behavior	Mantled howler females appear to cause males to alter reproductive strategy (Jones, 1997a; see Dixon, 1998; Jones and Agoramoorthy, 2003)
Chemical strategies employed by ants and other insects to parasitize communication systems (Mercier et al., 1985 cited in Bourke and Franks, 1995; Lenoir et al., 2001)	Chemical suppression of conspecifics' reproduction inducing subordination	Chemical suppression of reproduction by cooperatively breeding marmosets and tamarins (Saltzman, 2003; see Dixon, 1998) inducing helping behavior
Evolution of organs that induce behavioral change in the host (Poulin, 2002)	Sexual mechanisms and structures may evolve to manipulate behavior of the same or opposite sex (Eberhard 1985, 1996; Dixon 1998)	Female mantled howlers have variable and often extravagant vulvas employed during pre-copulatory interactions with males and possibly enhancing copulation (Jones, 1997c; <b>Fig. 4</b> ); female structures may also function in female-female competition for resources and/or mates to manipulate the responses of other females; mantled howler males exhibit showy scrotal areas presumably attractive to females and, possibly, a sign of quality to other males and to females (Jones, 1999, 2002b)
Sex-ratio dependent intraspecific aggression (Brown et al., 2003)	Sex-ratio dependent execution of queens in polygynous ants	Sex-ratio dependent infanticide in red howler monkeys ( <i>Alouatta seniculus</i> : Crockett and Janson, 2000; see Dixon, 1998)
Slavery (dulosis) in ants (Hare and Alloway, 2001; Stuart, 2002)	Slaves ("functional workers" or hosts) generally obtained by aggressive raids to perform labor in parasites' nests	Kidnapping (Scollay, 1978) and "enforced adoption" in squirrel monkeys (Taub et al., 1977) may be preadaptations for slavery in Neotropical primates
Cape honeybee workers ( <i>Apis mellifera capensis</i> Escholtz) disperse to locate hosts (Neumann et al., 2001, 2003)	Social parasitism by some Cape honeybee workers induces other workers of the same species and colony to disperse, thereby increasing likelihood of successful reproduction	Male red howler monkeys ( <i>A. seniculus</i> ) may disperse to parasitize females and other males (hosts, victims) by infanticide (Crockett and Janson, 2000)
Crab-spiders ( <i>Thomisus spectabilis</i> ) manipulate flower signals (Heiling et al., 2003)	Spiders manipulate flowers, making them more attractive to their prey	Monkeys, in particular, females, may induce changes in plant morphology or other features (e.g., taste, color) making them less attractive to competitors or more attractive to themselves (see Jones, 1983 as a possible case)
Dispersal by helpers dependent upon expulsion risk (Skubic et al., 2004)	Parasitism by subordinates induced by expulsion risk	Dominant female mantled howlers may expel subordinates to decrease likelihoods of social parasitism (Jones, 2004; see Johnstone and Bshary, 2002; Hager, 2003b)

(Table 1 cont.)

Example of parasitic phenotypic manipulation	Empirical evidence	Possible analogy in Neotropical primates
Dominants parasitize labor of subordinates (Khromova, 1995)	Individuals or groups with greater resource holding potential (RHP) induce individuals with lesser RHP to invest time and energy costly to the latter individuals or groups	Old non-reproductive female mantled howler monkeys most likely to exhibit social foraging, possibly to avoid expulsion from group and to obtain benefits from manipulating phenotypes of progeny (e.g., "grandmothering": Jones, 1996; see Bicca-Marques, 2003; Hawkes, 2004)
Adoption, a form of parasitism, reduces exposure to parasites (Bize et al., 2003)	Adoption induced by parasitism	Adoption induced by maternal loss and, possibly, harassment by group members and/or exposure to non-social parasites ( <i>A. palliata</i> : Clarke and Glander, 1981; Estrada, 1982; <i>A. seniculus</i> : Agoramoorthy and Rudran, 1992; <i>Ateles geoffroyi</i> : Estrada and Paterson, 1980; also see Hrdy, 1976; Nicolson, 1987; Lewis and Pusey, 1997)
Dominant individuals reduce subordinates' access to more or higher quality mates (Linklater and Cameron, 2000)	Individuals or groups with greater RHP apparently induce individuals or groups with lesser RHP to defend groups, thereby reducing time for reproductive activities	Dominant male mantled howler monkeys and their allies may ostracize other males who refuse to join in group defense, thereby limiting access to mates (Jones, 2000; Jones unpublished data; also see Nunn, 2000)
Female parasitism of male parental care in marmosets and tamarins (Porter, 2001; Saltzman, 2003; see Alexander et al., 1997; Taborsky, 1998)	Females induce males to invest more time and energy than offspring need for survival or females need in assistance	Male solicitation and/or care of young is emergent or expressed in many species of primates (e.g., <i>A. fusca clamitans</i> : Biedzicki de Marques and Ades, 2000; also see Taub and Mehlman, 1991; Lewis and Pusey, 1997; van Schaik and Kappeler, 1997)

sibly altruistic or cooperative behavior such as grooming, the most common social behavior among primates, especially females (Silk et al., 2003). In order to understand phenotypic manipulation and its relationship to ISP in mammals, it will be necessary to explore the costs as well as the benefits of associations and to measure the differential effect of costs in determining patterns of interindividual response. **Table 1** presents possible examples of parasitic phenotypic manipulation in Neotropical primates based upon documented cases from the literature on other taxa. Empirical research, including laboratory and field experiments, are required to determine the utility of the social

parasitism paradigm for primates and other social mammals.

**Avoidance of intraspecific social parasitism (ISP) within and between the sexes**

Several apparent cases of escape from or avoidance of social parasitism have been documented for mammals and other taxa, and the growing theoretical literature treating parasitism as a form of punishment is an important development (e.g., Gardner and West, 2004; Skubic et al., 2004; also see Jones, 2002d). Studying foraging pigs (*Sus scrofa*), Held et al. (2002) showed that exploited individuals altered their food-finding behavior in order to

increase their time spent foraging. These authors argued that such a counterstrategy is most likely to occur where parasitized individuals are not able to disperse or to become producers or scroungers themselves. This study is particularly pertinent to species in which some individuals locate food that is, over time, parasitized by conspecifics, especially other group members (e.g., Jones, 1996) and may, as well, assist in the interpretation of some mixed-species feeding groups (Terborgh, 1983; Jones, 1995b). Held and her colleagues also suggested that the counterstrategy they describe for foraging pigs represents learned behavior and that exploited individuals exhibited greater behavioral flexibility than less exploited or unexploited pigs. Several papers have discussed the relationship between parasitic exploitation and the evolution of diversity, including components of phenotypic plasticity (Poulin and Thomas, 1999; Summers et al., 2003). Although the primary emphasis of these papers is non-social parasitism, this topic is in need of investigation for ISP in primates and other social mammals.

Mimicry may represent another category of responses to escape or avoid social parasitism and/or phenotypic manipulation (Holen et al., 2001; Neumann, 2002). Possible examples in Neotropical primates may include pseudopregnancy by females of some taxa, pseudofemale morphology by sub-adult male mantled howlers, and paedomorphic vocalizations (Jones, 1995c). Multiple mating by females, a pattern of response that is probably ubiquitous among mammals (e.g., Jones and Cortés-Ortiz, 1998), including primates, may also represent a countertactic to avoid parasitic males. This view supports Wolff and Macdonald's (2004: 127) conclusion that multi-male mating by female mammals "functions to confuse paternity, which, in turn, deters infanticide," a hypothesis originally proposed by Hrdy (1979). Multi-male mating by females may represent female parasitism of males, an interpretation supported by some avian studies (Richardson and Burke, 1999; Hughes et al., 2003) and may indicate antagonistic coevolution between the sexes (Rice, 2000; Nunn, 2003; also see Rice and Holland, 1997; Holland and Rice, 1999).

## DISCUSSION AND CONCLUSIONS

The main conclusion of the present paper holds that individuals may exhibit responses serving a social parasite's self-interests rather than those of the host or victim and that the study of intraspecific social parasitism has the potential to explain many responses that appear inconsistent with Darwinian principles. Analogies from non-social parasitism suggest that intraspecific social parasitism may result in the manipulation of hosts' phenotypes, possibly because it is in the interests of the host to be parasitized (Dawkins, 1999), particularly over the short-term. Possible examples might be parental manipulation of offspring or some forms of manipulation by individuals of their mates. Theoretical and empirical, including experimental, research must be conducted to determine the extent to which it may benefit individuals to become hosts. For example, individuals with little or no opportunity for future reproduction (e.g., individuals whose reproductive costs are very high or whose benefits are very low) may gain from settling for host status (e.g., helpers) imposed by a dominant. In addition, in some environmental regimes, it may benefit parents (or dominants) to resist offspring's (or other subordinates') independence and/or autonomy through phenotypic manipulation.

Intraspecific social parasitism, in particular, phenotypic manipulation, will bias an association for high levels of **reproductive skew** (apportionment of reproduction within groups) because some individuals (parasites) are expected to reproduce much more than others (hosts). Intraspecific social parasitism is related to reproductive skew because the social parasite (subordinate: see Taborsky, 2001) harnesses the labor and/or resources of his/her host to the detriment of the latter's inclusive fitness, possibly marking a major evolutionary transition (see Wahl, 2002; Crespi et al., 2004). These harmful responses may increase reproductive skew, creating a division of labor within groups. Intraspecific social parasitism, then, is related to the evolution of complex social behavior, a topic of interest to all students of social vertebrates. Andersson (1984) reviewed

the literature for the evolution of eusociality in insects and vertebrates, noting that several traits, including parental manipulation, appear to be preconditions for advanced sociality in both of these groups. The treatment by Andersson and others (e.g., Emlen, 1995; Dawkins, 1999) supports the view that general principles of social evolution may be identified, and papers by Reeve and others (2001; Reeve and Emlen, 2000; Shellman-Reeve and Reeve, 2000; also see Hager, 2003a, b; Jones and Agoramoorthy, 2003) link reproductive skew models with the identification of these general causes and effects.

Finally, the study of intraspecific social parasitism is also likely to reveal important information about the evolution of virulence (e.g., aggression, punishment) since the costs and benefits of direct or indirect damage to the host are expected to vary as a function of their differential costs and benefits to the parasite's inclusive fitness, environmental heterogeneity, and the potential for antagonistic coevolution. Discussing Grafen's (1979) game theoretical analysis of evolutionary stable queen and worker strategies, Dawkins (1999: 77) emphasized the importance of division of power within groups (see Jones, 2000; Hager, 2003b). It will be instructive for students of social mammals and other social vertebrates to identify the abiotic and biotic, including social, conditions favoring low, moderate, or high levels of virulence by social parasites. In addition to studies of infectivity or manipulation success by social parasites, then, research on virulence by social parasites can be employed as a measure of parasite fitness, as suggested by Dybdahl and Storfer (2003). An understanding of variations in virulence and infectivity by social parasites, as defined above, is likely to reveal important evolutionary dynamics for an integrated view of social evolution.

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