Abstract

Owl monkeys have the potential to be a great model to accomplish a thorough integration of zoo and field research. The most salient features of owl monkeys are their nocturnal habits, monogamous social organization and intensive paternal care; features that should make them of interest to the public. Following a brief historical perspective on our knowledge of owl monkey biology, I describe in detail, drawing from research with both captive and wild animals, those aspects that make owl monkeys unusual among primates and mammals. First, owl monkeys are the only anthropoids with nocturnal habits and the study of their remarkable activity patterns has benefited enormously from an integrated approach that combined field research with research in semi-natural conditions and the laboratory. Secondly, up until recently, our understanding of social monogamy and the intensive involvement of the male in infant care, two defining features of the genus have been primarily informed by studies of captive individuals. In the future, a truly integrated lab-field approach that focuses on certain areas that cannot be examined in only one or the other setting (e.g. reproductive biology, communication, energetics) will offer unique opportunities for synergistic interactions between zoo and field research that will have both intellectual and practical benefits.
Keywords: monogamy, paternal care, cathemerality, nocturnality, pairbonds (not mentioned in text), reproduction,

The most salient features of owl monkeys are their nocturnal habits, monogamous social organization and intensive paternal care. Some of these features should make them of interest to the public, still owl monkeys are rarely displayed in zoos. In the following discussion I will argue that owl monkeys, probably more than most primates, can become a great model to accomplish a thorough integration of zoo and field research with both intellectual and practical benefits. I will first provide a brief historical perspective on our knowledge of owl monkey biology drawing attention to the fact that for a several decades most of our understanding came from captive populations and field demographic work. I then describe in some detail, drawing from research with both captive and wild animals, the aspects that make owl monkeys unusual among primates and mammals. In the last section I focus on a few areas of research that offer unique opportunities for synergistic interactions between zoo and field research.

**Historical Perspective on the Study of Owl Monkey Biology**

Even by the late 1990s, most field data on neotropical primates were coming from relatively few genera (*Alouatta, Ateles, Cebus, Leontopithecus, Saimiri*) at long-term research sites or from studies of one or two groups in a single location (e.g., Brachyteles hypoxanthus (italicize), *Cebus apella* (italicize) Fernandez-Duque et al. in press; Garber et al. 2009; Strier 1994). Except for a few isolated cases (Cabrera 1939; Crile and Quiring 1940; Hanson and Montagna 1962; Mann 1956; Morrison and Simoes 1962; Moynihan 1964; Park 1940), it is only in the 70’s that we find in the western (?) necessary?) scientific literature the first reports of studies specifically conducted with owl monkeys as research subjects (Dixson et al. 1979; Erkert 1976; Heltne 1977; Hunter et al. 1979; Thorington et al. 1976; Wright 1978).

Initially, most field studies were primarily focused on estimates of density, population structure, distribution and taxonomy, with little attempt at examining aspects of their behavioral ecology. Some 30 years of field research have provided us with some solid understanding of their distribution. Owl monkeys range from Panamá to northern Argentina and from the foothills of the Andes to the Atlantic Ocean (Aquino and Encarnación 1988; Aquino and Encarnación 1994; Aquino et al. 1992; Barnett et al. 2002; Bennett et al. 2001; Castaño and Cardona 2005; Cornejo et al. 2008; de Sousa e Silva Jr. and Nunes 1995; Defler 2003; Defler 2004; Fernandes 1993; Fernandez-Duque et al. 2008a; Ford 1994; García and Tarifa 1988; Hernández-Camacho and Cooper 1976; Hernández-Camacho and Defler 1985; Hershkovitz 1983; Kinzey 1997; Maldonado et al. 2010; Peres 1993; Pyritz et al.; Ruiz-Garcia et al.; Svensson et al.; Villavicencio Galindo 2003; Wright 1981; Zunino et al. 1985). At the southern end of their range, in the South American Gran Chaco, they can be found in dry forests that receive only 500 mm of annual rainfall (Brooks 1996; Campos et al. 2004; Lowen et al. 1996; Stallings et al. 1989).

Owl monkeys, also known as night monkeys in the English literature, belong in the genus *Aotus*. (I would mention this earlier) Several taxonomic issues remain largely unsettled, including the classification of the genus at the family and subfamily levels and the number of recognized species and subspecies within it (Defler and Bueno 2007). Regarding its suprageneric classification, the genus was for many years placed alternatively in the Atelidae or in the Cebidae families. Based on morphological data, owl monkeys were considered to be closely related to the pithecines within the atelids (Rosenberger 1981; Schneider and Rosenberger 1996). A close
affinity between owl monkeys and the atelines has also been suggested based on dental morphology (??) (Tejedor 2001; Tejedor 1998). On the other hand, the analysis of molecular genetic data led researchers to place the genus within the cebids (Porter et al. 1997; Schneider and Rosenberger 1996; Schneider et al. 1996). More recently, *Aotus* was placed in its own separate family Aotidae (Rylands and Mittermeier 2009; Rylands et al. 2000).

The genus only included a single species *Aotus trivirgatus* when first described. Following the discovery of various karyotypes by Brumback (1973; 1974; 1971; 1973) and Ma et al. (1976; 1978), Hershkovitz divided the genus into nine species organized in two groups based on their karyotypes, coloration of the neck and susceptibility to *Plasmodium falciparum*, one of the pathogens of human malaria (Hershkovitz 1983): the gray-necked group occurs to the north and the red-necked group to the south of the Amazon River. More recently, extensive and systematic research using both phenotype, karyotype and molecular data led researchers to recognize up to 11 species (Babb et al. in press; Defler and Bueno 2003; Defler et al. 2001; Galbreath 1983; Menezes et al. 2010; Mudry de Pargament et al. 1984; Mudry et al. 1990; Pieczarka et al. 1993; Plautz et al. 2009; Rylands et al. 2000; Torres et al. 1998). Although classification by lumping all owl monkey diversity as *A. trivirgatus* is not longer tenable and should be carefully considered when evaluating the published literature, there is no justification nor urgency to recognize new species until all adequate biogeographic, genetic, morphological and behavioral information are considered.

Regarding knowledge of their behavioral ecology, although there were a few short-term attempts in the late 70’s and 80’s, to this date most species in the genus *Aotus* have not been thoroughly studied in the wild. There has been very adequate population biology and demographic data on *A. nancymaeae* and *A. vociferans* (Aquino and Encarnación 1986b; Aquino and Encarnación 1988; Aquino and Encarnación 1989; Aquino and Encarnación 1994; Aquino et al. 1990; Aquino et al. 1992; Aquino et al. 1993; Moya et al. 1990) convincingly showing that owl monkeys in those species were found in small groups with only one reproducing pair of adults. A set of relatively brief studies on *A. nigriceps* and some behavioral ecology data has been generated during …? (Aquino and Encarnación 1986a; Bicca-Marques and Garber 2004; Carretero-Pinzón et al. 2008; Fernandez-Duque et al. 2008a; García and Braza 1987; García and Braza 1993; Marin-Gómez 2008; Puertas et al. 1995; Puertas et al. 1992; Wright 1978; Wright 1984; Wright 1985; Wright 1986; Wright 1994). Without any doubt, much of the sparse knowledge has been due to the difficulties of studying strictly nocturnal species (Wright 1989).

**Activity Patterns: Nocturnality and Cathemerality**

Owl monkeys are the only anthropoids that show nocturnal activity. They concentrate their activities during the dark portion of the 24 hr cycle, with peaks of activity at dawn and dusk. The study of activity patterns is one particular aspect of owl monkey biology that has benefited enormously from an integrated approach that combined field research with research in semi-natural conditions and the laboratory.

Across species and populations, it has been conclusively shown that most species are primarily nocturnal as indicated by observational studies of free-ranging *A. nigriceps* (Wright 1984; Wright 1986; Wright 1994), *A. a. boliviensis* (Garcia and Braza 1987; García and Braza 1993; Garcia Yuste 1989), *A. a. azarai* (Fernandez-Duque et al. 2010), *A. vociferans* (Fernandez-Duque et al. 2008a) and *A. miconax* (Cornejo et al. 2008). The nocturnal activity of all these species is strongly, and positively, influenced by available moonlight. Despite a preference for being active during the night, at least one owl monkey species is also active during daylight. *A.
azarai of the Argentinean and Paraguayan Chaco shows peaks of activity during the day as well as during the night (Arditi 1992; Fernandez-Duque 2011; Fernandez-Duque et al. 2010; Rotundo et al. 2000; Wright 1989).

Thanks to the integration of studies from the wild, from captivity and from the wild using lab technology, an understanding of the mechanisms regulating cathemerality and nocturnality in the genus is emerging. The strictly nocturnal owl monkeys of Colombia (A. griseimembra) were the focus of a series of laboratory experiments analyzing circadian rhythms of locomotor activity, as well as their entrainment and masking (explain these terms for zoo readers – influenced??) by light (Erkert 2008; Erkert 1976; Erkert 1991; Erkert and Grober 1986; Erkert and Thiemann-Jager 1983; Rappold and Erkert 1994; Rauth-Widmann et al. 1991). When new-moon conditions were simulated by means of continuous low light intensity, there was suppression of locomotor activity, indicating that low light intensity or brightness changes during the dark phase causes particularly strong masking of the light/dark-entrained circadian activity rhythm. Under nonmasking lighting conditions, A. lemurinus females showed an increase in locomotor activity every 2 weeks, which corresponds approximately to the ovarian cycle length (Rauth-Widmann et al. 1996).

The cathemeral owl monkeys have also been recently examined with an approach that improves on the purely observational nature of field studies. First, the results from observational studies were confirmed by fitting owl monkeys with accelerometer collars that allow uninterrupted activity recordings over a span of 6 months (Fernandez-Duque 2003; Fernandez-Duque et al. 2010). At full moon, they were active throughout the night and showed reduced activity during the day. With a new moon, activity decreased during the dark portion of the night, peaked during dawn and dusk, and extended over the bright morning hours. There is also good evidence showing that owl monkeys adjust their periods of activity to changes in ambient temperature, although the effects of temperature are contingent on ambient luminance. In captivity, A. lemurinus was most active when ambient temperature was 20°C and least active when it was 30°C (Erkert 1991). The activity of free-ranging A. azarai, even under optimal luminance conditions, tended to be maximum between 15-25 °C, reduced when temperatures were slightly lower or higher and almost non-existent when 5°C or lower (Fernandez-Duque et al. 2010). At El Beni in Bolivia, where harpy eagles are present, owl monkeys (A. a. boliviensis) showed diurnal activity when the climate was unusually cold (Mann 1956). All these results strongly suggest that the stimulatory and/or inhibitory effects of ambient luminance and temperature factors on locomotor activity (i.e. masking) are key determinants of the unusual activity pattern of Azara’s owl monkeys. Unique and conclusive evidence for the direct masking effect of light was provided by data showing that locomotor activity was almost completely inhibited when moonlight was shadowed during three lunar eclipses (Fernandez-Duque et al. 2010).

Behavioral Ecology

Social Organization

Owl monkeys are one of the few socially monogamous primates. They live in small groups that include only one pair of reproducing adults, one infant, one or two juveniles, and sometimes a subadult. From Panamá to Argentina, from evergreen rain forests to semi-deciduous dry forests, whether nocturnal or cathemeral, owl monkeys were found in small groups generally composed of an adult heterosexual pair, one infant, and one or two individuals of smaller size (Aquino and Encarnación 1986a; Aquino and Encarnación 1994; Brooks 1996; Castaño 2006;
Cornejo et al. 2008; Fernandes 1993; Fernandez-Duque 2011; Kinzey 1997; Moynihan 1964; Rathbun and Gache 1980; Robinson et al. 1987; Stallings et al. 1989; Wright 1981; Wright 1994). In an A. a. azarai population in Formosa, Argentina, groups regularly include 3- and 4-year-old subadults of adult size (Huck et al. in press), something that could mistakenly lead field researchers to conclude that groups include more than one reproducing male or female.

The social system of owl monkeys has facilitated their keeping and breeding in captivity (Cicmanec and Campbell 1977; Erkert 1999; Gozalo and Montoya 1990; Málaga et al. 1997) since there are solid ecological justifications for housing individuals in small social groups that only include one pair of reproducing adults. Still, in captivity, high levels of aggression have been reported (Hunter and Dixson 1983) which may have been initially difficult to reconcile with a picture of “low intensity, low frequency competition” traditionally described in the literature (Plavcan and van Schaik 1992). Aggression was intense during experimental testing, but also in well established family groups. New information from Aotus azarai in northern Argentina sheds some light on what could be a serious management issue for individuals in captivity.

In the Formosa population of Azara’s owl monkeys, both sexes disperse (Fernandez-Duque 2009), hardly a surprise given the monogamous social system of the species. Still, it was somewhat unexpected to discover that a significant number of dispersing adults travel widely and live as solitary “floater” animals from a few weeks to several months before disappearing or successfully assuming a position as part of an adult pair in an established group. Interactions between members of social groups and floaters can be aggressive, sometimes leading to the death of individuals. A survey of Aotus spp. in northern Colombia also found a significant number of solitary individuals (Villavicencio Galindo 2003) and fights have also been reported in free-ranging A. nigriceps (Wright 1985) and A. nancymaae (Aquino and Encarnación 1989). It seems likely that the less conspicuous solitary individuals will be detected in other populations and species as more long-term studies of identified individuals are conducted. An adequate management of captive individuals and groups will benefit from considering the period of life when sub-adults or young adults disperse and spend time alone, as well as the information suggesting that the social system of owl monkeys may be better described as serial monogamy (Fernandez-Duque and Huck in preparation) resulting in social groups that consistently include step-parents and step-siblings (Huck and Fernandez-Duque submitted).

**Biparental Care**

The intensive involvement of the male in infant care is one of the most fascinating and unique (is it truly unique? – see following for Callicebus) aspects of the social organization of the genus (Fernandez-Duque et al. 2009). Comparable only to the pattern described in titi monkeys (Callicebus spp.) where there is intensive paternal care, and very rarely is there any involvement of the siblings in the care of infants (Hoffman et al. 1995; Mendoza and Mason 1986; Wright 1984).

Among owl monkeys, paternal investment is intensive and apparently obligate. Females give birth to a single infant each year and the male is the primary carrier for the infant from soon after birth. There have been several detailed studies of parental behavior and infant development in captive groups (Dixson and Fleming 1981; Erkert 1999; Jantschke et al. 1996; Málaga et al. 1997; Meritt 1980; Wright 1984). Dependent infants may be carried as much as 90% of the time by their putative fathers and transfer to the mother only for brief periods usually surrounding active nursing bouts (Dixson and Fleming 1981; Rotundo et al. 2005; Wright 1984). In captivity, the mother is the main carrier of the single offspring only during the first week in A. lemurinus.
(Dixson and Fleming 1981) and during the first 2 weeks of life in *A. a. boliviensis* (Jantschke et al. 1996); thereafter, the male takes over the role. Rather than providing comfort and extended periods of physical contact with their infants, it appears that female owl monkeys have evolved mechanisms to reject the developing offspring once suckling is complete and to encourage it to transfer to the adult male. For example, 40 of 146 suckling bouts were followed by maternal rejection in captive *A. lemurinus* (Dixson 1994). Sibling care has been recorded infrequently in captive groups of *A. lemurinus* and *A. a. boliviensis* (Dixson and Fleming 1981; Jantschke et al. 1996; Wright 1984), and once in free-ranging *A. a. azarai* following the eviction of the putative father of the infant (Fernandez-Duque et al. 2008b).

Studies of free-ranging *A. a. azarai* have confirmed these findings from captivity. After the first week of life, males carry the infant 84% of the time (Rotundo et al. 2005). The male not only carries the infant most of the time but also plays, grooms, and shares food with the infant (reference?? And surely these observations were made in captivity). Food sharing, prevalent among captive *A. nancymaeae* and *A. lemurinus*, was also observed in free-ranging *A. azarai* (Wolovich et al. 2006; Wolovich et al. 2008b). The closer relationship of the male with the infant continues as the infant approaches maturity and becomes a juvenile (Dixson 1983; Huck and Fernandez-Duque submitted).

**Territoriality, Ranging and Diet**

Owl monkeys are territorial, each group occupying a range that overlaps only slightly with the area used by neighboring groups (ref?). Groups regularly encounter other groups at range boundaries (García and Braza 1987; García Yuste 1989; Wright 1978; Wright 1994), vocalizing and chasing each other. Confrontations last from a few minutes to almost half an hour and may include resonant whooping by both groups (Moynihan 1964; Wright 1981). In the *A. a. azarai* population of Argentina, some of the most aggressive interactions involve the resident group and a dispersing animal (is this a floater or a marginalized maturing offspring?) not neighboring groups. Ranging over the territory is strongly influenced by available moonlight. The distance traveled was significantly longer during full-moon nights than during new-moon nights in *A. a. boliviensis* in Bolivia, *A. a. azarai* in Argentina and Paraguay, *A. nigriceps* in Perú, and *A. vociferans* in Ecuador (Fernandez-Duque 2011).

Regarding their diet, there are still no satisfactory quantitative estimates of diet composition and foraging for any of the strictly nocturnal species. Wright’s work (1986, 1994a) on *A. nigriceps* in Manú National Park, Perú, is the only thorough attempt at quantifying diet in one of the nocturnal species, but the problems of obtaining quantitative estimates in a nocturnal primate were numerous. Cathemeral owl monkeys have provided opportunities to examine the diet in some detail during daylight hours (Arditi 1992; Fernandez-Duque and Van der Heide in preparation; Giménez 2004; Van der Heide et al. accepted with revisions; Wright 1985), but determining their foraging habits during the night remains a challenge.

Owl monkeys are primarily frugivorous (Fernandez-Duque 2011). Fruits are the most consumed item in *A. nigriceps*, *A. a. azarai*, and *A. vociferans*. Leaf and insect eating has virtually impossible to quantify during the night, but leaf consumption has been regularly observed in the cathemeral *A. a. azarai*. Most authors have observed owl monkeys eating insects with some detailed observations on insect foraging among captive individuals living in outdoor enclosures (Wolovich et al. 2010b). Flowers may be an important food item for *A. a. azarai* and *A. lemurinus* during certain times of the year.
The Future: An Integrated Lab-Field Approach to the Study of Owl Monkey Biology

In the following paragraphs I will argue that owl monkeys are, like few other primates, an excellent model to promote a lab-field research approach; an approach that would only be the natural consequence of a rich history of research in both settings as clearly shown in the sections above. The full integration must be accomplished through collaborative research that includes researchers with experience in both settings (e.g. Wolovich et al. 2008a; Wolovich et al. 2008b). Naturally, there are certain areas of research that are more amenable to field or to lab research; but then there are those that can only be fully investigated through a combination.

Reproductive Biology

Although a full understanding of the reproductive biology of owl monkeys will require continued studies in a controlled laboratory setting, only studies of free-ranging animals can elucidate the functional significance of certain reproductive characteristics. This is particularly true when examining reproductive development and maturation. In captivity, *A. lemurinus* males enter puberty at a surprisingly early age (Dixson 1994; Dixson et al. 1980), with testosterone first increasing when individuals were between 7 and 11 months of age (n = 6 males), and full sexual maturation taking place at approximately 2 years of age, as indicated by measures of body mass, growth of the subcaudal scent gland, and circulating reproductive hormones (Dixson 1982; Dixson 1983; Dixson 1994; Dixson and Gardner 1981; Dixson et al. 1980; Hunter et al. 1979). The timing of first reproduction in captive *A. vociferans* and *A. nancymaee* females occurred between 3 and 4 years of age. An examination of growth and development in Azara’s owl monkeys showed that they did not reach adult body mass or exhibit a fully developed subcaudal gland until they were approximately 4 years of age and age at first birth was at least 5 years (Huck et al. in press). Why do Azara’s owl monkeys not reproduce earlier when they have apparently reached the necessary developmental milestones? Are there social factors preventing them from doing so in the wild that are not manifested in captivity? Probably nutritional – large body of literature on this subject for other non-human and human primates

Mating seems to be relatively infrequent in owl monkeys, whether in captivity or free-ranging. For example, Dixson (1994) recorded it on only 19 occasions during 278 hr of observation. Mating in captive *A. nancymaee* was more frequent among newly formed pairs than established ones (Wolovich and Evans 2007). Mating has been observed during pregnancy in free-ranging *A. a. azarai* and in captive *A. lemurinus* and *A. nancymaee* (Dixson 1994, Hunter, 1979; Wolovich and Evans 2007) and at least some pairs of captive *A. nancymaee* mated when confronted with a male stimulus animal (Wolovich et al. 2010a). If mating serves a guarding function it is possible that it will be more frequently observed in wild populations where the threats from potential competitors will be more ubiquitous than in captivity.

Owl monkey females’ reproductive cycle lasts between 13–25 days and gestation length between 117-159 days depending on the species (Dixson et al. 1980; Fernandez-Duque et al. in preparation; Wolovich et al. 2008a), and females produce one infant per year. In captivity, twinning occurred in one of 169 births (Gozalo and Montoya 1990) and in one of 287 births (Málaga et al. 1997) in *A. nancymaee* and in three of 365 births in a colony of unknown karyotypes (Gibson et al. 2008). In the wild, it has been reported only once in *A. vociferans* (Aquino et al. 1990). There is some indirect evidence suggesting that females may be cycling and receptive at similar times during the year, given the apparent birth seasonality that has been reported. All nine births recorded in four groups of *A. nigriceps* in Perú occurred between August and February (Wright 1985). Births were estimated to occur between December and
March in *A. nancymaee* based on the presence of dependent and independent offspring in 75 captured groups in northeastern Perú (Aquino et al. 1990). In the Argentinean Chaco, most births (81%, n=106) took place during an 8-week period between late September and late November (unpublished data). On the other hand, in captivity, the tropical species *A. lemurinus* and *A. nancymaee* bred throughout the year when photoperiod was kept constant (Dixson 1994; Málaga et al. 1997), but *A. nancymaee* and *A. vociferans* adjusted their reproduction accordingly when housed under conditions of natural photo-period (Gozalo and Montoya 1990; Montoya et al. 1995). What does this mean?

Our understanding of the hormonal correlates of biparental care and monogamy has been restricted to information gathered from captive animals. In the future, it will be important to develop studies that integrate the intensive and regular monitoring of reproductive cycles that is possible in captivity using both non-invasively and invasively collected samples (Wolovich et al. 2007) with field studies that generate richer information on how the social and ecological context may influence those cycles. A better understanding of reproductive biology will contribute to illuminating the process by which male and female owl monkeys choose their socially monogamous pairmates. (is mate sufficient?)

**Mate Choice and Pair Formation**

How do socially monogamous groups form in owl monkeys? How do adults choose their pairmates? What are ecological and social factors that influence the success or failure of a pair? Unfortunately we have no solid answers for those questions, nor will we obtain them without a thorough understanding of reproductive biology informing the behavioral and demographic aspects of mate choice, pair formation and group dynamics.

In the field, *A. a. azarai* individuals appear to disperse from their natal groups to find reproductive opportunities (Fernandez-Duque 2009). There is no indication that young adults find reproductive opportunities within their natal territory, as has been described for gibbons (Brockelman et al. 1998; Palombit 1994). Both male and female floaters (is floater defined somewhere?) replace resident adults through a process that may take several days and involves aggressive interactions (Fernandez-Duque and Huck in preparation). Frequently, mating takes place as soon as the new adult is accepted into the group. The observation of mating following pair formation agrees well with results from pair-testing experiments in captivity. *A. lemurinus* and *A. nancymaee* individuals mated more frequently in the presence of a new partner than when paired with their regular mate (Dixson 1994; Wolovich and Evans 2007).

New pairs of free-ranging *A. a. azarai* take at least 1 year until the female produces offspring, even if the pair is formed during the mating season. In captivity, the latency to reproduce could be taken as an indirect indicator of successful pairbonding. Montoya et al. (1995) found that, on average, a captive reproducing *A. vociferans* female took 26 months to reproduce after pairing. Another indirect indication of an improved pairbond with time could be the shortening of interbirth intervals in multiparous pairs. *A. nancymaee* captive females took, on average, 11 months between the first and second births but only 8.8 months following the third one (Málaga et al. 1997).

**Communication**

Vocal, olfactory, and visual communication are undoubtedly important for owl monkeys (Herrera et al. 2011; Macdonald et al. 2008; Wolovich and Evans 2007; Wright 1989; Zito et al. 2003). Still, the challenges of studying certain aspects of communication (e.g. olfactory) in the
field, make this aspect of owl monkey biology fertile groups for a lab-field approach. In fact, most detailed descriptions of communication have been generated in the lab, but it has been the field work that is helping us understand its functional value.

The two most salient calls are resonant whoops and hoots (Moynihan 1964). Resonant whoops are usually produced by both sexes during intergroup encounters and occur together with visual displays like swaying or arching. Hoots are low-frequency calls given by one individual in the social group or by a solitary individual that convey information over long distances. Playback of these calls to free-ranging *A. azarai* elicits responses from animals in the area, both groups and solitaries (Depeine et al. 2008) suggesting that the function of the hoot may not necessarily be to identify (and locate?) a mate, but it may be a more generalized contact call.

Owl monkeys rely heavily on olfactory cues for communication, using both urine and cutaneous secretions in their scent-marking behaviors to relay information between mates and other conspecifics. Among the peculiar behaviors that are most likely associated to olfactory communication, captive male owl monkeys were observed rubbing their glands (specify subcaudal here because it was mentioned earlier) against their mate’s fur, as well as drinking their urine and self-annointing with plants and millipedes (Wolovich and Evans 2007; Zito et al. 2003). The secretions from their sternal and subcaudal glands most likely play a role in mediating social interactions as suggested by differences between sex, age, and family in the chemical constitution of the secretions (Macdonald et al. 2008). Olfaction also plays a prominent role in sexual recognition and aggression (Hunter and Dixson 1983; Hunter et al. 1984). During the confrontations of *A. lemurinus*, contact aggression between same-sex individuals was always preceded by some form of olfactory communication. Blocking olfactory input led to a reduction in intermale aggression (Hunter and Dixson 1983).

**Energetic Costs and Benefits of Social Monogamy and Biparental Care**

As explained before, it has been hypothesized that the intense contribution that the male owl monkey makes to infant care has evolved, and is now maintained, because it lessens the costs of female reproduction. Thus, the proper evaluation of the hypothesis requires measuring energetic costs of males and females. Measuring energetics in the field remains an unresolved challenge. The use of observational data for estimating food intake and energy expenditure provides, at best, a very crude measure of the actual energy incorporated and used. This is particularly true for species like owl monkey that may be difficult to follow due to their activity patterns (e.g. nocturnal) or relatively small size. In captivity we can more precisely measure food availability and food intake, we can control some of the factors that influence metabolic demands in the field (e.g. temperature, humidity, predator risk, competition, within and between year fluctuations in food availability) and we can more intensively monitor the physiological status of individuals. Thus, it cannot be disputed that the combined study of captive and free-ranging owl monkeys will be more powerful than either approach individually when trying to understand the energetic benefits and costs of social monogamy and its associated biparental care system (Löttker et al. 2009).

We recently conducted a preliminary study to evaluate a field-lab approach to measuring energetics using dependent variables that can only be measured in the lab (C-peptide), or in both the lab and the field (activity, body mass). In captivity we fitted one adult male and one adult female with accelerometer collars that record activity uninterruptedly (Fernandez-Duque et al. 2010) while housed in enclosures of two different sizes during two weeks. The study showed that the reduced activity in the smaller enclosure, while keeping food intake constant, resulted in a
positive energy balance reflected in higher C-peptide values and weight gain. In the future, the set of dependent variables that can be measured in both settings will be used as proxies for those that can only be evaluated in the field or lab. The simultaneous assessment of behavior, activity, and C-peptide in the lab will be used to better interpret possible changes in body weight in the field. The use of activity collars both in the field and captivity will allow us to determine specific threshold values for the different behavioral categories and to validate those thresholds through behavioral observations (Löttker et al. 2009). The research in captivity will help us identify possible mechanisms of energy management that, even if operating in the field, may not be easily identified.

Conclusions

Our understanding of owl monkeys’ behavior, ecology, and evolution remains severely limited. A comprehensive picture is emerging about the social organization, behavior, and ecology of the southernmost taxon (*A. a. azarai*), still several intriguing aspects of this subspecies will need to be examined in comparison to other species before any broad generalizations can be made for the genus. For example, although owl monkeys are undoubtedly socially monogamous, the unexpected fast rate of adult replacement in the *A. a. azarai* population suggests that serial monogamy may be the norm. Thus, the long-held assumption of stable, lasting pair bonds in monogamous primates will need to be once more revised, both for managing captive populations and for advancing our understanding of the evolution of monogamy. For example, if it is confirmed that putative and nonputative father provide similar care to infants, the function of the intensive care provided by owl monkey males will have to be reevaluated.

The function of territoriality in owl monkeys will also need careful examination. To successfully identify some of the relevant factors driving and maintaining territoriality, it will be necessary to develop a semi-experimental approach to examine some of the unresolved issues. For example, playback experiments to simulate intruders or food-provisioning experiments to manipulate available food resources will need to be considered and implemented following similar experimental studies with captive animals (Wolovich et al. 2010a).

Finally, advancing our understanding of the evolutionary forces favoring monogamy, biparental and nocturnality in owl monkeys will benefit from a comparative approach that considers some of the other more tropical, strictly nocturnal owl monkey or prosimian species, as well as some of the other socially monogamous primates. Such comparative approach should include research in both the lab and the field.

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