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Owl monkeys *Aotus* spp in the wild and in captivity

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Owl monkeys *Aotus* spp have the potential to be a great model to accomplish a thorough integration of zoo and field research. Their most salient features are their nocturnal habits, monogamous social organization and 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. Second, up until recently, our understanding of social monogamy and the involvement of the ♂♂ in infant care, two defining characteristics of the genus, have been primarily informed by studies of captive individuals. In the future, a truly integrated laboratory–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.

Key-words: alloparental care; cathemerality; monogamy; nocturnality; pair bonds; paternal care; reproduction; territoriality.

INTRODUCTION

The most salient features of owl monkeys are their nocturnal habits, monogamous social organization and intensive paternal care. Some of these characteristics should make them of interest to the public, yet owl monkeys are rarely displayed in zoos. Owl monkeys can become a great model to accomplish a thorough integration of zoo and field research with both intellectual and practical benefits. In fact, given their nocturnality, small size and arboreality, we will never fully understand owl monkey biology unless we complement field research with detailed observations and measurements from captive individuals.

A brief historical perspective on our knowledge about owl monkey biology is presented, drawing attention to the fact that for several decades, most of our understanding came from captive populations and field demographic studies. Drawing from research with both captive and wild animals, the aspects that make owl monkeys unusual among primates and mammals are described in some detail. Then, a few areas of research that offer unique opportunities for synergistic interactions between zoo and field research are focused upon in the final section.

HISTORICAL PERSPECTIVE ON THE STUDY OF OWL MONKEY BIOLOGY

Even in 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. Northern muriqui *Brachyteles hypoxanthus* or Tufted capuchin *Cebus apella*: Strier, 1994; Garber *et al.*, 2009; Fernandez-Duque *et al.*, in press). Except for a few isolated cases (Cabrera, 1939; Crile & Quiring, 1940; Park, 1940; Mann, 1956; Hanson & Montagna, 1962; Morrison & Simoes, 1962; Moynihan, 1964), it is only in the 1970s that the first reports of studies specifically conducted with owl monkeys appeared in the scientific literature (Erkert, 1976; Thorington *et al*., 1976; Heltne, 1977; Wright, 1978; Dixson *et al*., 1979; Hunter *et al*., 1979). Initially, most field studies were primarily focused on estimates of density, population structure, distribution and taxonomy, with little attempt at examining aspects of behavioural ecology. However, 30 years of field research have provided a solid understanding of species distribution. Owl monkeys range from Panamá to northern Argentina and from the foothills of the Andes to the Atlantic Ocean (Hernández-Camacho & Cooper, 1976; Wright, 1981; Hershkovitz, 1983; Hernández-Camacho & Defler, 1985; Zunino *et al*., 1985; Aquino & Encarnación, 1988, 1994; García & Tarifa, 1988; Aquino *et al*., 1992; Fernandes, 1993; Peres, 1993; Ford, 1994; de Sousa e Silva & Nunes, 1995; Kinzey, 1997; Bennett *et al*., 2001; Barnett *et al*., 2002; Defler, 2003, 2004; Villavicencio Galindo, 2003; Castaño & Cardona, 2005; Cornejo *et al*., 2008; Fernandez-Duque, Di Fiore *et al*., 2008; Maldonado *et al*., 2010; Pyritz *et al*., 2010; Ruiz-Garcia *et al*., 2010; Svensson *et al*., 2010).

Owl monkeys, also known as night monkeys, belong in the genus *Aotus*. Several taxonomic issues remain largely unsettled, including the classification at the family and subfamily levels, and the number of recognized species and subspecies (Defler & 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 & Rosenberger, 1996). A close affinity between owl monkeys and the atelines has also been suggested based on dentition (Tejedor, 1998, 2001). However, analysis of molecular genetic data led researchers to place the genus within the cebids (Schneider & Rosenberger, 1996; Schneider *et al*., 1996; Porter *et al*., 1997). More recently, *Aotus* was placed in its own separate family Aotidae (Rylands *et al*., 2000; Rylands & Mittermeier, 2009).

When first described, the genus only included a single species *Aotus trivirgatus*. Following the discovery of various karyotypes (Brumback *et al*., 1971; Brumback, 1973, 1974; Brumback & Willenborg, 1973; Ma *et al*., 1976, 1978), Hershkovitz (1983) 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. The grey-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 phenotype, karyotype and molecular data led researchers to recognize up to 11 species (Galbreath, 1983; Mudry de Pargament *et al*., 1984; Mudry *et al*., 1990; Pieczarka *et al*., 1993; Torres *et al*., 1998; Rylands *et al*., 2000; Defler *et al*., 2001; Defler & Bueno, 2003; Plautz *et al*., 2009; Menezes *et al*., 2010; Babb *et al*., 2011). Although it is no longer tenable to classify all owl monkey diversity as *A. trivirgatus* (even if this form of classification should be remembered when evaluating the published literature), it is imperative that adequate biogeographic, genetic, morphological and behavioural information is obtained and considered before any taxon is given species status.

Although there were a few short-term studies in the late 1970s and 1980s, to date, the behavioural ecology of most species in the genus *Aotus* has not been thoroughly studied in the wild. There has been reasonable population biology and demographic data about Nancy Ma's night monkey *Aotus nancymaae* and Spix's night monkey *Aotus vociferans* (Aquino & Encarnación, 1986b, 1988, 1989, 1994; Aquino *et al*., 1990, 1992, 1993; Moya *et al*., 1990) convincingly showing that these species are found in small groups with only one breeding pair of adults. A set of relatively brief studies on Black-headed night monkey *Aotus nigriceps*, *A. vociferans*, *A. nancymaae* and Bolivian night monkey

Aotus azarai boliviensis provided the first valuable behavioural-ecology data in the 1970s and 1980s (Wright, 1978, 1984, 1985, 1986, 1994; Aquino & Encarnación, 1986a; García & Braza, 1987, 1993; Puertas *et al*., 1992, 1995; Bicca-Marques & Garber, 2004; Carretero-Pinzón *et al*., 2008; Fernandez-Duque, Di Fiore *et al*., 2008; Marín-Gómez, 2008). Those studies contributed the first quantitative information to confirm the general nocturnal habits of most species, the relatively small groups including only one reproducing ♀ and the territorial use of space. Without doubt, the relatively slow pace for learning about the genus, when compared with the impressive progress made in many other Neotropical taxa, is because of the severe limitations associated with studying strictly nocturnal species (Wright, 1989).

ACTIVITY PATTERNS: NOCTURNALITY AND CATHEMERALITY

Owl monkeys are the only anthropoids that show nocturnal activity, concentrating their activities during the dark portion of the 24 hour cycle, with peaks of activity at dawn and dusk. The study of this aspect of owl monkey biology has benefited from an integrated approach that combined field research with research in semi-natural conditions and captivity.

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

The integration of studies from the wild and captivity, and from the wild using laboratory technology, has provided an understanding of the mechanisms regulating cathemerality and nocturnality. The strictly nocturnal Grey-handed night monkey *Aotus griseimembra* of Colombia was the focus of a series of laboratory experiments analysing circadian rhythms of locomotor activity, as well as the regulation of those rhythms by light (Erkert, 1976, 1991, 2008; Erkert & Thiemann-Jager, 1983; Erkert & Grober, 1986; Rauth-Widmann *et al*., 1991; Rappold & Erkert, 1994). 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 cause particularly strong masking of the light/dark-entrained circadian activity rhythm. Under non-masking lighting conditions, Colombian night monkey *Aotus lemurinus* ♀♀ 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 free-ranging 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, the owl monkeys 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). Even under optimal luminance conditions the activity of free-ranging *A. a. azarai*, which tended to be maximum at around 15–25°C, was reduced when temperatures were slightly lower or higher, and almost non-existent when temperatures were 5°C or lower (Fernandez-Duque *et al*., 2010). At El Beni in Bolivia, *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 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).

BEHAVIOURAL 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 Panama 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 non-infant individuals that are smaller than the adults (Moynihan, 1964; Rathbun & Gache, 1980; Wright, 1981, 1994; Aquino & Encarnación, 1986a, 1994; Robinson *et al*., 1987; Stallings *et al*., 1989; Fernandes, 1993; Brooks, 1996; Kinzey, 1997; Cornejo *et al*., 2008; Fernandez-Duque, 2011). In an *A. a. azarai* population in Formosa, Argentina, groups regularly include subadults (3–4 years old) of adult size (Huck *et al*., 2011), something that could mistakenly lead field researchers to conclude that groups include more than one reproducing ♂ or ♀ when they do not.

The social system of owl monkeys has facilitated their keeping and breeding in captivity (Cicmanec & Campbell, 1977; Gozalo & Montoya, 1990; Málaga *et al*., 1997; Erkert, 1999), 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 & Dixson, 1983; Evans *et al*., 2009) that may have been initially difficult to reconcile with a picture of 'low intensity, low frequency competition' traditionally described in the literature (Plavcan & van Schaik, 1992). Aggression has been intense during experimental testing, but also in well-established family groups. New information from *A. a. 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 & 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. Management of captive individuals and groups will benefit from considering the period of life when subadults 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 resulting in social groups that consistently include step-parents and step-siblings (pers. obs).

Biparental care

The intensive involvement of the ♂ in infant care is one of the most fascinating 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, there is rarely any involvement of the siblings in the care of infants (Wright, 1984; Mendoza & Mason, 1986; Hoffman *et al*., 1995).

Among owl monkeys, paternal investment is intensive and apparently obligate. Females give birth to a single infant each year, and the ♂ is the primary carrier for the infant soon after birth. There have been several detailed studies of parental behaviour and infant development in captive groups (Meritt, 1980; Dixson & Fleming, 1981; Wright, 1984; Jantschke *et al*., 1996; Málaga *et al*., 1997; Erkert, 1999). 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 & Fleming, 1981; Wright, 1984; Rotundo *et al*., 2005). In captivity, the mother is the main carrier of the single offspring only during the first week in *A. lemurinus* (Dixson & Fleming, 1981) and during the first 2 weeks of life in *A. a. boliviensis* (Jantschke *et al*., 1996); thereafter, the ♂ takes over the role. Rather than providing comfort and extended periods of physical contact with their infants, it appears that ♀ owl monkeys have evolved mechanisms to reject the developing offspring once suckling is complete and to encourage it to transfer to the adult ♂. 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 & Fleming, 1981; Wright, 1984; Jantschke *et al*., 1996), and once in free-ranging *A. a. azarai* following the eviction from the group of the putative father of the infant (Fernandez-Duque, Juárez *et al*., 2008).

Studies of free-ranging *A. a. azarai* have confirmed these findings from captivity. After the first week of life, ♂♂ carry the infant 84% of the time (Rotundo *et al*., 2005). The ♂ not only carries the infant most of the time but also plays, grooms and shares food with the infant. Food sharing, prevalent among captive *A. nancymaae* and *A. lemurinus*, was also observed in free-ranging *A. a. azarai* (Wolovich *et al*., 2006; Wolovich, Perea-Rodriguez *et al*., 2008). The closer relationship of the ♂ with the infant continues as the infant approaches maturity and becomes a juvenile (Dixson, 1983; Huck & Fernandez-Duque, in press; pers. obs).

Territoriality, ranging and diet

Owl monkeys are territorial, each group occupying a range that overlaps only slightly with the area used by neighbouring groups (Fernandez-Duque, 2011). Groups regularly encounter other groups at range boundaries (Wright, 1978, 1994; García & Braza, 1987; Garcia Yuste, 1989), 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 from a different group, not neighbouring groups. Ranging over the territory is strongly influenced by available moonlight. The distance travelled 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 Peru and *A. vociferans* in Ecuador (Fernandez-Duque, 2011).

There are still no satisfactory quantitative estimates of diet composition and foraging for any of the strictly nocturnal species. Wright's work (Wright, 1986, 1994) on *A. nigriceps* in Manu National Park, Peru, 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 (Wright, 1985; Arditi, 1992; Giménez, 2004; Van der Heide *et al*., in press), 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 been 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, Rivera *et al*., 2010).

Flowers may be an important food item for *A. a. azarai* and *A. lemurinus* during certain times of the year. Azara's owl monkeys of Argentina and Paraguay regularly feed on *Tabebuia heptaphylla* flowers during the winter season when food is less readily available (Wright, 1989; Van der Heide *et al*., in press), and the *Tabebuia* flowers are known to contain six amino essential to humans (Milton, 1999).

THE FUTURE: AN INTEGRATED CAPTIVE–FIELD APPROACH TO THE STUDY OF OWL MONKEY BIOLOGY

Owl monkeys are, like few other primates, an excellent model to promote a captive–field research approach; an approach that would only be the natural consequence of a rich history of research in both settings. The full integration must be accomplished through collaborative research that includes researchers with experience in both settings (e.g. Wolovich, Evans *et al*., 2008; Wolovich, Perea-Rodriguez *et al*., 2008). Naturally, there are certain areas of research that are more amenable to field or to captive research; but then there are those that can only be fully investigated through a combination. An integration of laboratory and field research should not be an option for the study of *Aotus*, it needs to become a goal if we are ever to understand fully owl monkey biology.

Reproductive biology

Although a full understanding of the reproductive biology of owl monkeys will require continued studies in a controlled captive 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* ♂♂ enter puberty at a surprisingly early age (Dixson *et al*., 1980; Dixson, 1994), with testosterone first increasing when individuals were 7–11 months of age ($n = 6$ ♂♂), and full sexual maturation taking place at *c*. 2 years of age, as indicated by measures of body mass, growth of the subcaudal scent gland and circulating reproductive hormones (Hunter *et al*., 1979; Dixson *et al*., 1980; Dixson & Gardner, 1981; Dixson, 1982, 1983, 1994). The timing of first reproduction in captive *A. vociferans* and *A. nancymaae* ♀♀ occurred at 3–4 years of age (Gozalo & Montoya, 1990; Montoya *et al*., 1995). 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 *c*. 4 years of age, and age at first birth was at least 5 years (Huck *et al*., 2011). 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? Is the *ad libitum* access to food in captivity favouring earlier reproduction?

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 hours of observation. Mating in captive *A. nancymaae* was more frequent among newly formed pairs than established pairs (Wolovich & Evans, 2007). Mating has been observed during pregnancy in free-ranging *A. a. azarai* (Fernandez-Duque *et al.*, 2002), and in captive *A. lemurinus* and *A. nancymaae* (Hunter *et al.*, 1979; Dixson, 1994; Wolovich & Evans, 2007), and at least some pairs of captive *A. nancymaae* mated when confronted with a ♂ stimulus animal (Wolovich, Evans *et al.*, 2010). 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.

The reproductive cycle in ♀ owl monkeys lasts 13–25 days and gestation is 117–159 days, depending on the species (Dixson *et al.*, 1980; Wolovich, Evans *et al.*, 2008; Fernandez-Duque *et al.*, 2011), and ♀♀ produce one infant per year. In captivity, twinning occurred in one of 169 births (Gozalo & Montoya, 1990) and in one of 287 births (Málaga *et al.*, 1997) in *A. nancymaae*, and in three of 365 births in a colony of unknown karyotypes (Gibson *et al.*, 2008). In the wild, twinning has been reported only once in *A. vociferans* (Aquino *et al.*, 1990). There is some indirect evidence suggesting that ♀♀ 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 Peru occurred between August and February (Wright, 1985). Births were estimated to occur between December and March in *A. nancymaae* based on the presence of dependent and independent offspring in 75 captured groups in north-eastern Peru (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 (E. Fernandez-Duque, unpubl. data). On the other hand, in captivity, the tropical species *A. lemurinus* and *A. nancymaae* bred throughout the year when photoperiod was kept constant (Dixson, 1994; Málaga *et al.*, 1997), but *A. nancymaae* and *A. vociferans* adjusted their reproduction accordingly when housing included natural photoperiod conditions (Gozalo & Montoya, 1990; Montoya *et al.*, 1995).

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.

Mate choice and pair formation

A better understanding of reproductive biology will contribute to illuminating the process by which ♂ and ♀ owl monkeys choose their socially monogamous pair mates. What are the ecological and social factors that influence the success or failure of a pair? Unfortunately, we have no solid answers, nor will we obtain them without a thorough understanding of reproductive biology informing the behavioural and demographic aspects of mate choice, pair formation and group dynamics.

In the field, *A. a. azarai* individuals 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 (Palombit, 1994; Brockelman *et al.*, 1998). Both ♂ and ♀ dispersing individuals replace resident adults through a process that may take several days and involves aggressive interactions. 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. *Aotus lemurinus* and *A. nancymaae* individuals mated more frequently in the presence of a new partner than when paired with their regular mate (Dixson, 1994; Wolovich & Evans, 2007).

New pairs of free-ranging *A. a. azarai* take at least 1 year until the ♀ 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 pair-bonding. Montoya *et al.* (1995) found that, on average, a captive reproducing *A. vociferans* ♀ took 26 months to reproduce after pairing. Another indirect indication of an improved pair bond with time could be the shortening of interbirth intervals in multiparous pairs. *Aotus nancymaae* ♀♀ in captivity 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 (Wright, 1989; Zito *et al.*, 2003; Wolovich & Evans, 2007; Macdonald *et al.*, 2008; Herrera *et al.*, 2011). Still, the challenges of studying certain aspects of communication (e.g. olfactory) in the field make this aspect of owl monkey biology fertile for a captivity–field approach. In fact, most detailed descriptions of communication have been generated with captive animals, but it has been the field work that has helped us to 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 such as 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 (Wright, 1989). Playback of these calls to free-ranging *A. 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 behaviours to relay information between mates and other conspecifics. Among the peculiar behaviours that are most likely associated to olfactory communication, captive ♂ owl monkeys were observed rubbing their subcaudal glands against their mate's fur, as well as drinking their urine and self-anointing with plants and millipedes (Zito *et al.*, 2003; Wolovich & Evans, 2007). 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 & 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 inter-male aggression (Hunter & Dixson, 1983).

Energetic costs and benefits of social monogamy and biparental care

It has been hypothesized that the intense contribution that the ♂ owl monkey makes to infant care has evolved, and is now maintained, because it lessens the costs of ♀ reproduction. Thus, the proper evaluation of the hypothesis requires measuring energetic costs of ♂♂ and ♀♀. 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 such as Owl monkeys that may be difficult to follow owing to their activity patterns (e.g. nocturnal) or relatively small size. In captivity, we can measure food availability and intake more precisely, and we can control some of the factors influencing metabolic demands (e.g. temperature, humidity, predator risk, competition, within and between year fluctuations in food availability); therefore, the physiological status of individuals can be monitored more intensively. 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).

A recently conducted preliminary study to evaluate a field–laboratory approach to measuring energetics used dependent variables that can only be measured in the laboratory (C-peptide) or in both the laboratory and the field (activity, body mass). In a study in captivity, one adult ♂ and one adult ♀ were fitted with accelerometer collars that record activity uninterruptedly (Fernandez-Duque *et al*., 2010) while housed in enclosures of two different sizes during 2 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 in a captive setting. The simultaneous assessment of behaviour, activity and C-peptide in captivity will be used to enable better interpretation of possible changes in body mass 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 behavioural categories and to validate those thresholds through behavioural observations (Löttker *et al*., 2009). The research in captivity will help to identify possible mechanisms of energy management that even if operating in the field may not be easily identified there.

CONCLUSIONS

Our understanding of owl monkey behaviour, ecology and evolution remains severely limited. A comprehensive picture is emerging about the social organization, behaviour and ecology of the southern-most taxon (*A. a. azarai*); even so, several intriguing aspects of this subspecies will need to be examined in comparison with 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 revised, both for managing captive populations and for advancing our understanding of the evolution and maintenance of social monogamy. For example, if it is confirmed that putative and non-putative fathers provide similar care to infants, the function of the intensive care provided by owl monkey ♂♂ will have to be re-evaluated.

The function of territoriality in owl monkeys will also need careful examination. To 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, Evans *et al*., 2010).

Finally, advancing our understanding of the evolutionary forces favouring monogamy, biparental behaviour 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 a captive setting and the field.

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REFERENCES
Aquino, R. & Encarnación, F. (1986a): Characteristics and use of sleeping sites in *Aotus* (Cebidae: Primates) in the Amazon lowlands of Perú. *American Journal of Primatology* **11:** 319–331.

Aquino, R. & Encarnación, F. (1986b): Population structure of *Aotus nancymai* (Cebidae: Primates) in Peruvian Amazon lowland forest. *American Journal of Primatology* **11:** 1–7.

Aquino, R. & Encarnación, F. (1988): Population densities and geographic distribution of night monkeys (*Aotus nancymai* and *Aotus vociferans*) (Cebidae: Primates) in northeastern Perú. *American Journal of Primatology* **14:** 375–381.

Aquino, R. & Encarnación, F. (Eds) (1989): *Aspectos de la dinámica poblacional de* Aotus nancymai *(Cebidae: Primates)*. Washington, DC: UICN/CSE-WWF.

Aquino, R. & Encarnación, F. (1994): Owl monkey populations in Latin America: field work and conservation. In Aotus: *the owl monkey*: 59–95. Baer, J. F., Weller, R. E. & Kakoma, I. (Eds). San Diego, CA: Academic Press.

Aquino, R., Puertas, P. E. & Encarnación, F. (1990): Supplemental notes on population parameters of northeastern Peruvian night monkeys, Genus *Aotus* (Cebidae). *American Journal of Primatology* **21:** 215–221.

Aquino, R., Puertas, P. E. & Encarnación, F. (1992): Las poblaciones de *Aotus vociferans* y *Aotus nancymae* en la amazonía peruana. *Alma Máter* **3:** 77–82.

Aquino, R., Puertas, P. E. & Encarnación, F. (1993): Effects of cropping on the *Aotus nancymae* population in a forest of Peruvian Amazonia. *Primate Report* **37:** 31–40.

Arditi, S. I. (1992): Variaciones estacionales en la ctividad y dieta de *Aotus azarae* y *Alouatta caraya* en Formosa, Argentina. *Boletín Primatológico Latinoamericano* **3:** 11–30.

Babb, P. L., Fernandez-Duque, E., Baiduc, C., Gagneux, P., Evans, S. & Schurr, T. G. (2011): mtDNA diversity in Azara's owl monkeys (*Aotus azarai azarai*) of the Argentinean Chaco. *American Journal of Physical Anthropology* **146:** 209–224.

Barnett, A. A., Borges, S. H., de Castilho, C. V., Neri, F. M. & Shapley, R. L. (2002): Primates of the Jaú National Park, Amazonas, Brazil. *Neotropical Primates* **10:** 65–70.

Bennett, C. L., Leonard, S. & Carter, S. (2001): Abundance, diversity, and patterns of distribution of primates on the Tapiche River in the Amazonian Perú. *American Journal of Primatology* **54:** 119–126.

Bicca-Marques, J. C. & Garber, P. (2004): Use of spatial, visual and olfactory information during foraging in wild nocturnal and diurnal anthropoids: a field experiment comparing *Aotus*, *Callicebus* and *Saguinus*. *American Journal of Primatology* **62:** 171–187.

Brockelman, W. Y., Reichard, U., Treesucon, U. & Raemaekers, J. J. (1998): Dispersal, pair formation and social structure in gibbons (*Hylobates lar*). *Behavioral Ecology and Sociobiology* **42:** 329–339.

Brooks, D. M. (1996): Some observations of primates in Paraguay. *Neotropical Primates* **4**(1): 15–19.

Brumback, R. A. (1973): Two distinctive types of owl monkeys (*Aotus*). *Journal of Medical Primatology* **2:** 284–289.

Brumback, R. A. (1974): A third species of the owl monkey (*Aotus*). *Journal of Heredity* **65:** 321–323.

Brumback, R. A. & Willenborg, D. O. (1973): Serotaxonomy of *Aotus*. A preliminary study. *Folia Primatologica* **20:** 106–111.

Brumback, R. A., Staton, R. D., Benjamin, S. A. & Lang, C. M. (1971): The chromosomes of *Aotus trivirgatus* Humboldt 1812. *Folia Primatologica* **15:** 264–273.

Cabrera, A. (1939): Los monos de la Argentina. *Physis* **16:** 3–29.

Carretero-Pinzón, X., Defler, T. R. & Ferrari, S. F. (2008): Observation of black-capped capuchins (*Cebus apella*) feeding on an owl monkey (*Aotus brumbacki*) in the Colombian Llanos. *Neotropical Primates* **15:** 62–63.

Castaño, J. H. & Cardona, D. M. (2005): Presencia del mono nocturno andino (*Aotus lemurinus* I. Geoffroy-St. Hilaire, 1843) en fragmentos de bosque de la cuenca media del Río Cauca. *Museo de Historia Natural* **9:** 111–117.

Cicmanec, J. C. & Campbell, A. K. (1977): Breeding the owl monkey (*Aotus trivirgatus*) in a laboratory environment. *Laboratory Animal Science* **27:** 512–517.

Cornejo, F. M., Aquino, R. & Jiménez, C. (2008): Notes on the natural history, distribution and conservation status of the Andean night monkey, *Aotus miconax* Thomas, 1927. *Primate Conservation* **23:** 1–4.

Crile, G. & Quiring, D. P. (1940): A record of the body weight and certain organ and gland weights of 3690 animals. *The Ohio Journal of Science* **40:** 219–259.

Defler, T. R. (2003): *Primates de Colombia*. Bogota: Conservation International.

Defler, T. R. (2004): *Primates of Colombia*. Washington, DC: Conservation International.

Defler, T. R. & Bueno, M. L. (2003): Karyological guidelines for *Aotus* taxonomy. *American Journal of Primatology* **60:** 134–135.

Defler, T. R. & Bueno, M. L. (2007): *Aotus* diversity and the species problem. *Primate Conservation* **22:** 55–70.

Defler, T. R., Bueno, M. L. & Hernández-Camacho, J. I. (2001): Taxonomic status of *Aotus hershkovitzi*: its relationship to *Aotus lemurinus lemurinus*. *Neotropical Primates* **9:** 37–52.

Depeine, C. C., Rotundo, M., Juárez, C. P. & Fernandez-Duque, E. (2008): Hoot calling in owl monkeys (*Aotus azarai*) of Argentina: sex differences and function. *American Journal of Primatology* **70:** 69 (abstract).

Dixson, A. F. (1982): Some observations on the reproductive physiology and behaviour of the owl monkey. *International Zoo Yearbook* **22:** 115–119.

Dixson, A. F. (1983): The owl monkey (*Aotus trivirgatus)*. In *Reproduction in New World primates. New models in medical sciences*: 69–113. Hearn, J. P. (Ed.). Lancaster: International Medical Publishers.

Dixson, A. F. (1994): Reproductive biology of the owl monkey. In Aotus: *the owl monkey*: 113–132. Baer, J. F., Weller, R. E. & Kakoma, I. (Eds). San Diego, CA: Academic Press.

Dixson, A. F. & Fleming, D. (1981): Parental behaviour and infant development in owl monkeys (*Aotus trivirgatus griseimembra*). *Journal of Zoology, London* **194:** 25–39.

Dixson, A. F. & Gardner, J. S. (1981): Diurnal variations in plasma testosterone in a male nocturnal primate, the owl monkey (*Aotus trivirgatus*). *Journal of Reproduction and Fertility* **62:** 83–86.

Dixson, A. F., Martin, R. D., Bonney, R. C. & Fleming, D. (1979): Reproductive biology of the owl monkey, *Aotus trivirgatus griseimembra*. In *7th Congress International Primatological Society, Bangalore, India*: 61–68. Anand Kumar, T. C. (Ed.). Basel: Karger.

Dixson, A. F., Gardner, J. S. & Bonney, R. C. (1980): Puberty in the male owl monkeys (*Aotus trivirgatus griseimembra*): a study of physical and hormonal development. *International Journal of Primatology* **1:** 129–139.

Erkert, H. G. (1976): Beleuchtungsabhangiges Aktivitatsoptimum bei Nachtaffen (*Aotus trivirgatus*). *Folia Primatologica* **25:** 186–192.

Erkert, H. G. (1991): Influence of ambient temperature on circadian rhythms in Colombian owl monkeys, *Aotus lemurinus griseimembra*. In *Primatology today*: 435–438. Ehara, A., Kimura, T., Takenaka, O. & Iwamoto, M. (Eds). Amsterdam: Elsevier Science Publishers B.V. (Biomedical Division).

Erkert, H. G. (1999): Owl monkeys. In *The UFAW handbook on the care and management of laboratory animals*: 574–591. Poole, T. (Ed.). London: Blackwell Science Ltd.

Erkert, H. G. (2008): Diurnality and nocturnality in nonhuman primates: comparative chronobiological studies in laboratory and nature. *Biological Rhythm Research* **39:** 229–267.

Erkert, H. G. & Grober, J. (1986): Direct modulation of activity and body temperature of owl monkeys (*Aotus lemurinus griseimembra*) by low light intensities. *Folia Primatologica* **47:** 171–188.

Erkert, H. G. & Thiemann-Jager, A. (1983): Dark switch in the entrainment of circadian activity rhythms in night monkeys, *Aotus trivirgatus* Humboldt. *Comparative Biochemistry and Physiology Part A: Physiology* **74:** 307–310.

Evans, S., Wolovich, C. K. & Herrera, J. P. (2009): Aggression in captive owl monkeys (genus *Aotus*). *American Journal of Primatology* **S71:** 97 (abstract).

Fernandes, M. E. B. (1993): New field records of night monkeys, genus *Aotus*, in northern Brazil. *Neotropical Primates* **1**(4): 6–8.

Fernandez-Duque, E. (2003): Influences of moonlight, ambient temperature and food availability on the diurnal and nocturnal activity of owl monkeys (*Aotus azarai*). *Behavioral Ecology and Sociobiology* **54:** 431–440.

Fernandez-Duque, E. (2009): Natal dispersal in monogamous owl monkeys (*Aotus azarai*) of the Argentinean Chaco. *Behaviour* **146:** 583–606.

Fernandez-Duque, E. (2011): The Aotinae: social monogamy in the only nocturnal anthropoid. In *Primates in perspective*: 140–154. Campbell, C. J., Fuentes, A., MacKinnon, K. C., Bearder, S. K. & Stumpf, R. M. (Eds). Oxford: Oxford University Press.

Fernandez-Duque, E., Rotundo, M. & Ramírez-Llorens, P. (2002): Environmental determinants of birth seasonality in night monkeys (*Aotus azarai*) of the Argentinean Chaco. *International Journal of Primatology* **23:** 639–656.

Fernandez-Duque, E., Di Fiore, A. & Carrillo-Bilbao, G. (2008): Behavior, ecology and demography of *Aotus vociferans* in Yasuní National Park, Ecuador. *International Journal of Primatology* **29:** 421–431.

Fernandez-Duque, E., Juárez, C. & Di Fiore, A. (2008): Adult male replacement and subsequent infant care by male and siblings in socially monogamous owl monkeys (*Aotus azarai*). *Primates* **49:** 81–84.

Fernandez-Duque, E., Valeggia, C. R. & Mendoza, S. P. (2009): The biology of paternal care in human and nonhuman primates. *The Annual Review of Anthropology* **38:** 115–130.

Fernandez-Duque, E., de la Iglesia, H. & Erkert, H. G. (2010): Moonstruck primates: owl monkeys (*Aotus*) need moonlight for nocturnal activity in their natural environment. *PLoS ONE* **5**(9): e12572.

Fernandez-Duque, E., Burke, K., Schoenrock, K., Wolovich, C. & Valeggia, C. (2011): Hormonal monitoring of reproductive status in wild monogamous female owl monkeys (*Aotus azarai*) of the Argentine Chaco. *Folia Primatologica* **82:** 143–153.

Fernandez-Duque, E., Di Fiore, A. & Huck, M. (In press): The behavior, ecology, and social evolution of New World monkeys. In *Primate societies*. Call, J.,

Kappeler, P., Palombit, R., Silk, J. & Mitani, J. (Eds). Chicago, IL: Chicago University Press.
FORD, S. M. (1994): Taxonomy and distribution of the owl monkey. In Aotus: *the owl monkey*: 1–57. Baer, J. F., Weller, R. E. & Kakoma, I. (Eds). San Diego, CA: Academic Press.
GALBREATH, G. J. (1983): Karyotypic evolution in *Aotus*. *American Journal of Primatology* **4:** 245–251.
GARBER, P. A., ESTRADA, A., BICCA-MARQUES, J. C., HEYMANN, E. W. & STRIER, K. B. (Eds) (2009): *South American primates. Comparative perspectives in the study of behavior, ecology, and conservation*. New York, NY: Springer.
GARCÍA, J. E. & BRAZA, F. (1987): Activity rhythms and use of space of a group of *Aotus azarae* in Bolivia during the rainy season. *Primates* **28:** 337–342.
GARCÍA, J. E. & BRAZA, F. (1993): Sleeping sites and lodge trees of the night monkey (*Aotus azarae*) in Bolivia. *International Journal of Primatology* **14:** 467–477.
GARCÍA, J. E. & TARIFA, T. (1988): Primate survey of the Estación Biológica Beni, Bolivia. *Primate Conservation* **9:** 97–100.
GARCIA YUSTE, J. E. (1989): Patrones etológicos y ecológicos del mono nocturno, *Aotus azarae boliviensis*. *Dissertation Abstracts International* **50:** 473.
GIBSON, S. V., TUSTIN, G. W., WILLIAMS, L. E., SCHULER, A. M., BRADY, A. G. & ABEE, C. R. (2008): Reproduction in an owl monkey breeding colony (*Aotus spp.)*. *American Journal of Primatology* **70:** 29 (abstract).
GIMÉNEZ, M. C. (2004): *Dieta y comportamiento de forrajeo en verano e invierno del mono mirikiná* (Aotus azarai azarai) *en bosques secos y húmedos del Chaco Argentino*. Argentina: Licenciate, University of Buenos Aires.
GOZALO, A. & MONTOYA, E. (1990): Reproduction in the owl monkey (*Aotus nancymai*) (Primates: Cebidae) in captivity. *American Journal of Primatology* **21:** 61–68.
HANSON, G. & MONTAGNA, W. (1962): The skin of primates. XII. The skin of the owl monkeys (*Aötus trivirgatus*). *American Journal of Physical Anthropology* **20:** 421–429.
HELTNE, P. G. (1977): *Census of* Aotus *in northern Colombia*. Washington, DC: Pan American Health Organization.
HERNÁNDEZ-CAMACHO, J. & COOPER, R. W. (1976): The nonhuman primates of Colombia. In *Neotropical primates: field studies and conservation*: 35–69. Thorington, R. W. & Heltne, J. P. G. (Eds). Washington, DC: National Academy of Sciences.
HERNÁNDEZ-CAMACHO, J. & DEFLER, T. R. (1985): Some aspects of the conservation of non-human primates in Colombia. *Primate Conservation* **6:** 42–50.
HERRERA, J. P., TAYLOR, L. L. & EVANS, S. (2011): Use of auditory and olfactory signals in the night monkeys (*Aotus nancymaae*). *American Journal of Physical Anthropology* **144**(Suppl. 52): 161 (abstract).
HERSHKOVITZ, P. (1983): Two new species of night monkeys, genus *Aotus* (Cebidae: Platyrrhini): a preliminary report on *Aotus* taxonomy. *American Journal of Primatology* **4:** 209–243.
HOFFMAN, K. A., MENDOZA, S. P., HENNESSY, M. B. & MASON, W. A. (1995): Responses of infant titi monkeys, *Callicebus moloch*, to removal of one or both parents: evidence for paternal attachment. *Developmental Psychobiology* **28:** 399–407.
HUCK, M. G. & FERNANDEZ-DUQUE, E. (In press): Building babies when dads help: infant development of owl monkeys and other primates with allo-maternal care. In *Building babies: proximate and ultimate perspectives of primate developmental trajectories*. Clancy, K., Hinde, K. & Rutherford, J. (Eds). Heidelberg: Springer.
HUCK, M. G., ROTUNDO, M. & FERNANDEZ-DUQUE, E. (2011): Growth and development in wild owl monkeys (*Aotus azarai*) of Argentina. *International Journal of Primatology* **32:** 1133–1152.
HUNTER, A. J. & DIXSON, A. F. (1983): Anosmia and aggression in male owl monkeys (*Aotus trivirgatus*). *Physiology & Behavior* **30:** 875–879.
HUNTER, A. J., FLEMING, D. & DIXSON, A. F. (1984): The structure of the vomeronasal organ and nasopalatine ducts in *Aotus trivirgatus* and some other primate species. *Journal of Anatomy* **138:** 217–225.
HUNTER, J., MARTIN, R. D., DIXSON, A. F. & RUDDER, B. C. C. (1979): Gestation and interbirth intervals in the owl monkey (*Aotus trivirgatus griseimembra*). *Folia Primatologica* **31:** 165–175.
JANTSCHKE, B., WELKER, C. & KLAIBER-SCHUH, A. (1996): Rearing without paternal help in the Bolivian owl monkey *Aotus azarae boliviensis*: a case study. *Folia Primatologica* **69:** 115–120.
KINZEY, W. G. (1997): *Aotus*. In *New World primates: ecology, evolution and behavior*: 186–191. Kinzey, W. G. (Ed.). New York, NY: Aldine de Gruyter.
LÖTTKER, P., RUMMEL, A., TRAUBE, M., STACHE, A., SUSTR, P., MULLER, J. & HEURICH, M. (2009): New possibilities of observing animal behaviour from a distance using activity sensors in GPS-collars: an attempt to calibrate remotely collected activity data with direct behavioural observations in red deer *Cervus elaphus*. *Wildlife Biology* **15:** 425–434.
MA, N. S., JONES, T. C., MILLER, A. C., MORGAN, L. M. & ADAMS, E. A. (1976): Chromosome polymorphism and banding patterns in the owl monkey (*Aotus*). *Laboratory Animal Science* **26:** 1022–1036.
MA, N. S., ROSSAN, R. N., KELLEY, S. T., HARPER, J. S., BEDARD, M. T. & JONES, T. C. (1978): Banding patterns of the chromosomes of two new karyotypes of the owl monkey, *Aotus*, captured in Panama. *Journal of Medical Primatology* **7:** 146–155.
MACDONALD, E., FERNANDEZ-DUQUE, E., EVANS, S. & HAGEY, L. (2008): Sex, age and family differences in the chemical composition of owl monkey (*Aotus nancymaae*) subcaudal scent secretions. *American Journal of Primatology* **70:** 12–18.
MÁLAGA, C. A., WELLER, R. E., BUSCHBOM, R. L., BAER, J. F. & KIMSEY, B. B. (1997): Reproduction of the owl monkey (*Aotus* spp.) in captivity. *Journal of Medical Primatology* **26:** 147–152.
MALDONADO, A., NIJMAN, V. & BEARDER, S. K. (2010): Trade in night monkeys *Aotus* spp. In the Brazil-Colombia-Peru tri-border area: international wildlife

trade regulations are ineffectively enforced. *Endangered Species Research* **9:** 143–149.
Mann, G. F. (1956): Efecto del frío en mamíferos amazónicos. *Investigaciones Zoológicas Chilenas* **III:** 155.
Marín-Gómez, O. H. (2008): Consumo de néctar por *Aotus lemurinus* y su rol como posible polinizador de las flores de *Inga edulis* (Fabales: Mimosoideae). *Neotropical Primates* **15:** 30–32.
Mendoza, S. P. & Mason, W. A. (1986): Parental division of labour and differentiation of attachments in a monogamous primate (*Callicebus moloch*). *Animal Behaviour* **34:** 1336–1347.
Menezes, A. N., Bonvicino, C. R. & Seuanez, H. N. (2010): Identification, classification and evolution of owl monkeys (*Aotus*, Illiger 1811). *BMC Evolutionary Biology* **10:** 248.
Meritt, D. A. J. (1980): Captive reproduction and husbandry of the Douroucouli and the titi monkey *Callicebus* spp. *International Zoo Yearbook* **20:** 52–59.
Milton, K. (1999): Nutritional characteristics of wild primate foods: do the diets of our closest living relatives have lessons for us? *Nutrition* **15:** 488–498.
Montoya, E. G., Moro, J., Gozalo, A. & Samame, H. (1995): Reproducción de *Aotus vociferans* (Primates: Cebidae) en cautiverio. *Revista de Investigaciones Pecuarias IVITA* **7:** 122.
Morrison, P. & Simoes, J. (1962): Body temperatures in two Brazilian primate. *Zoologia* **24:** 167–178.
Moya, L., Encarnación, F., Aquino, R., Tapia, J., Ique, C. & Puertas, P. (1990): El Estado de las poblaciones naturales de primates y los beneficios de las cosechas sostenidas. In *Primates de las Américas*: 173–192. Arámbulo III, P., Encarnación, F., Estupinan, J., Samame, H., Watson, C. R. & Weller, R. E. (Eds). Columbus, OH: Battelle Press.
Moynihan, M. (1964): Some behavior patterns of playtyrrhine monkeys. **I.** The night monkey (*Aotus trivirgatus*). *Smithsonian Miscellaneous Collections* **146:** 1–84.
Mudry, M. D., Slavutsky, I. & Labal de Vinuesa, M. (1990): Chromosome comparison among five species of platyrrhini (*Alouatta caraya, Aotus azarae, Callithrix jacchus, Cebus apella, Saimiri sciureus*). *Primates* **31:** 415–420.
Mudry de Pargament, M., Colillas, O. J. & de Salum, S. B. (1984): The *Aotus* from northern Argentina. *Primates* **25:** 530–537.
Palombit, R. (1994): Dynamic pair bonds in hylobatids: implications regarding monogamous social systems. *Behaviour* **128:** 65–101.
Park, O. (1940): Nocturnalism – the development of a problem. *Ecological Monographs* **10:** 485–536.
Peres, C. (1993): Notes on the primates of the Juruá River, western Brazilian Amazonian. *Folia Primatologica* **61:** 97–103.
Pieczarka, J. C., de Souza Barros, R. M., de Faria, F. M. & Nagamachi, C. Y. (1993): *Aotus* from the southwestern Amazon region is geographically and chromosomally intermediate between *A. azarae boliviensis* and *A. infulatus*. *Primates* **34:** 197–204.
Plautz, H. L., Goncalves, E. C., Ferrari, S. F., Schneider, M. P. & Silva, A. (2009): Evolutionary inferences on the diversity of the genus *Aotus* (Platyrrhini, Cebidae) from mitochondrial cytochrome c oxidase subunit II gene sequences. *Molecular Phylogenetics and Evolution* **51:** 382–387.
Plavcan, J. M. & van Schaik, C. P. (1992): Intrasexual competition and canine dimorphism in anthropoid primates. *American Journal of Physical Anthropology* **87:** 461–477.
Porter, C. A., Page, S. L., Czelusniak, J., Schneider, H., Schneider, M. P. C., Sampaio, I. & Goodman, M. (1997): Phylogeny and evolution of selected primates as determined by sequences of the e-globin locus and 5' flanking regions. *International Journal of Primatology* **18:** 261–295.
Puertas, P. E., Aquino, R. & Encarnación, F. (1992): Uso de alimentos y competición entre el mono nocturno *Aotus vociferans* y otros mamíferos, Loreto, Perú. *Folia Amazónica* **4:** 135–144.
Puertas, P. E., Aquino, R. & Encarnación, F. (1995): Sharing of sleeping sites between *Aotus vociferans* with other mammals in the Peruvian Amazon. *Primates* **36:** 281–287.
Pyritz, L. W., Buntge, A. B., Herzog, S. K. & Kessler, M. (2010): Effects of habitat structure and fragmentation on diversity and abundance of primates in tropical deciduous forests in Bolivia. *International Journal of Primatology* **31:** 796–812.
Rappold, I. & Erkert, H. G. (1994): Re-entrainment, phase-response and range of entrainment of circadian rhythms in owl monkeys (*Aotus lemurinus g.*) of different age. *Biological Rhythm Research* **25:** 133–152.
Rathbun, G. B. & Gache, M. (1980): Ecological survey of the night monkey, *Aotus trivirgatus*, in Formosa Province, Argentina. *Primates* **21:** 211–219.
Rauth-Widmann, B., Thiemann-Jager, A. & Erkert, H. G. (1991): Significance of nonparametric light effects in entrainment of circadian rhythms in owl monkeys (*Aotus lemurinus griseimembra*) by light–dark cycles. *Chronobiology International* **8:** 251–266.
Rauth-Widmann, B., Fuchs, E. & Erkert, H. G. (1996): Infradian alteration of circadian rhythms in owl monkeys (*Aotus lemurinus griseimembra*): an effect of estrus? *Physiology & Behavior* **59:** 11–18.
Robinson, J. G., Wright, P. C. & Kinzey, W. G. (1987): Monogamous cebids and their relatives: intergroup calls and spacing. In *Primate societies*: 44–53. Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. & Struhsaker, T. T. (Eds). Chicago, IL: The University of Chicago Press.
Rosenberger, A. L. (1981): Systematics: the higher taxa. In *Ecology and behavior of Neotropical primates*: 9–27. Coimbra-Filho, A. F. & Mittermeier, R. A. (Eds). Rio de Janeiro: Academia Brasileira de Ciencias.
Rotundo, M., Sloan, C. & Fernandez-Duque, E. (2000): Cambios estacionales en el ritmo de actividad del mono mirikiná (*Aotus azarai*) en Formosa Argentina. In *Manejo de Fauna Silvestre en Amazonía y*

Latinoamérica: 413–417. Cabrera, E., Mércolli, C. & Resquin, R. (Eds). Asunción, Paraguay: Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

ROTUNDO, M., FERNANDEZ-DUQUE, E. & DIXSON, A. F. (2005): Infant development and parental care in free-ranging *Aotus azarai azarai* in Argentina. *International Journal of Primatology* **26:** 1459–1473.

RUIZ-GARCIA, M., LEGUIZAMON, N., VASQUEZ, C., RODRIGUEZ, K. & CASTILLO, M. I. (2010): Genetic methods for the reintroduction of primates *Saguinus*, *Aotus* and *Cebus* (Primates: Cebidae) seized in Bogota, Colombia. *Revista de Biologia Tropical* **58:** 1049–1067.

RYLANDS, A. B. & MITTERMEIER, R. A. (2009): The diversity of the New World primates (Platyrrhini): an annotated taxonomy. In *South American primates. Comparative perspectives in the study of behavior, ecology, and conservation*: 23–54. Garber, P. A., Estrada, A., Bicca-Marques, J. C., Heymann, E. W. & Strier, K. B. (Eds). New York, NY: Springer.

RYLANDS, A. B., SCHNEIDER, H., LANGGUTH, A., MITTERMEIER, R. A., GROVES, C. P. & RODRIGUEZ-LUNA, E. (2000): An assessment of the diversity of New World Primates. *Neotropical Primates* **8:** 61–93.

SCHNEIDER, H. & ROSENBERGER, A. L. (1996): Molecules, morphology and platyrrhine systematics. In *Adaptive radiations of neotropical primates*: 3–19. Norconk, M. A., Rosenberger, A. L. & Garber, P. A. (Eds). New York, NY: Plenum Press.

SCHNEIDER, H., SAMPAIO, I., HARADA, M. L., BARROSO, C. M. L., SCHNEIDER, M. P. C., CZELUSNIAK, J. & GOODMAN, M. (1996): Molecular phylogeny of the New World monkeys (Platyrrhini, Primates) based on two unlinked nuclear genes: IRBP intron 1 and epsilon-globin sequences. *American Journal of Physical Anthropology* **100:** 153–179.

DE SOUSA E SILVA JR, J. & NUNES, A. (1995): Geographic distribution of night monkeys, *Aotus*, in Northern Brazil: new data and a correction. *Neotropical Primates* **3:** 72–74.

STALLINGS, J. R., WEST, L., HAHN, W. & GAMARRA, I. (1989): Primates and their relation to habitat in the Paraguayan Chaco. In *Advances in Neotropical mammalogy*: 425–442. Redford, K. H. & Eisenberg, J. F. (Eds). Gainesville, FL: The Sandhill Crane Press, Inc.

STRIER, K. B. (1994): Myth of the typical primate. *Yearbook of Physical Anthropology* **37:** 233–271.

SVENSSON, M. S., SAMUDIO, R., BEARDER, S. K. & NEKARIS, K. A. (2010): Density estimates of Panamanian owl monkeys (*Aotus zonalis*) in three habitat types. *American Journal of Primatology* **72:** 187–192.

TEJEDOR, M. F. (1998): La Posicion de *Aotus* y *Callicebus* en la Filogenia de los Primates Platirrinos. *Boletin Primatologico Latinoamerica* **7:** 13–29.

TEJEDOR, M. F. (2001): *Aotus* y los atelinae: nuevas evidencias en la sistemática de los primates platirrinos. *Mastozoologia Neotropical* **8:** 41–57.

THORINGTON, R. W., MUCKENHIRN, N. A. & MONTGOMERY, G. G. (1976): Movements of a wild night monkey (*Aotus trivirgatus)*. In *Neotropical primates. Field studies and conservation*: 32–34. Thorington, R. W. J. & Heltne, P. G. (Eds). Washington, DC: National Academy of Sciences.

TORRES, O. M., ENCISO, S., RUIZ, F., SILVA, E. & YUNIS, I. (1998): Chromosome diversity of the genus *Aotus* from Colombia. *American Journal of Primatology* **44:** 255–275.

VAN DER HEIDE, G. W. E., IRIART, D. & FERNANDEZ-DUQUE, E. (In press): Do forest composition and fruit availability predict demographic differences among territorial owl monkey (*Aotus azarai*) groups? *International Journal of Primatology*. DOI: 10.1007/s10764-011-9560-5.

VILLAVICENCIO GALINDO, J. M. (2003): Distribución geográfica de los primates del género *Aotus* en el Departamento Norte de Santander, Colombia. In *Primatología del Nuevo Mundo*: 264–271. Pereira-Bengoa, V., Nassar-Montoya, F. & Savage, A. (Eds). Bogotá: Centro de Primatología Araguatos Ltda.

WOLOVICH, C. K. & EVANS, S. (2007): Sociosexual behavior and chemical communication of *Aotus nancymaae*. *International Journal of Primatology* **28:** 1299–1313.

WOLOVICH, C. K., FEGED, A., EVANS, S. & GREEN, S. M. (2006): Social patterns of food sharing in monogamous owl monkeys. *American Journal of Primatology* **68:** 663–674.

WOLOVICH, C. K., EVANS, S. & FRENCH, J. A. (2007): Dads don't pay for sex but do buy the milk: food sharing and reproduction in owl monkeys (*Aotus nancymaae*). *American Journal of Primatology* **69**(Suppl.): 34 (abstract).

WOLOVICH, C. K., EVANS, S. & FRENCH, J. A. (2008): Dads do not pay for sex but do buy the milk: food sharing and reproduction in owl monkeys (*Aotus* spp.). *Animal Behaviour* **75:** 1155–1163.

WOLOVICH, C. K., PEREA-RODRIGUEZ, J. P. & FERNANDEZ-DUQUE, E. (2008): Food transfers to young and mates in wild owl monkeys (*Aotus azarai*). *American Journal of Primatology* **70:** 211–221.

WOLOVICH, C. K., EVANS, S. & GREEN, S. M. (2010): Mated pairs of owl monkeys (*Aotus nancymaae*) exhibit sex differences in response to unfamiliar male and female conspecifics. *American Journal of Primatology* **72:** 942–950.

WOLOVICH, C. K., RIVERA, J. & EVANS, S. (2010): Insect-foraging in captive owl monkeys (*Aotus nancymaae*). *Folia Primatologica* **81:** 63–72.

WRIGHT, P. C. (1978): Home range, activity patterns, and agonistic encounters of a group of night monkeys (*Aotus trivirgatus*) in Perú. *Folia Primatologica* **29:** 43–55.

WRIGHT, P. C. (1981): The night monkeys, genus *Aotus*. In *Ecology and behavior of Neotropical primates*: 211–240. Coimbra-Filho, A. & Mittermeier, R. A. (Eds). Rio de Janeiro: Academia Brasileira de Ciencias.

WRIGHT, P. C. (1984): Biparental care in *Aotus trivirgatus* and *Callicebus moloch*. In *Female primates: studies by women primatologists*: 59–75. Small, M. (Ed.). New York, NY: Alan R. Liss Inc.

WRIGHT, P. C. (1985): *The costs and benefits of nocturnality for* Aotus trivirgatus *(the night monkey)*. PhD thesis, City University of New York, USA.

WRIGHT, P. C. (1986): Ecological correlates of monogamy in *Aotus* and *Callicebus*. In *Primate ecology and conservation*: 159–167. Else, J. G. & Lee, P. C. (Eds). New York, NY: Cambridge University Press.
WRIGHT, P. C. (1989): The nocturnal primate niche in the New World. *Journal of Human Evolution* **18:** 635–658.
WRIGHT, P. C. (1994): The behavior and ecology of the owl monkey. In Aotus: *the owl monkey*: 97–112. Baer, J. F., Weller, R. E. & Kakoma, I. (Eds). San Diego, CA: Academic Press.
ZITO, M., EVANS, S. & WELDON, P. (2003): Owl monkeys (*Aotus* spp.) self-anoint with plants and millipedes. *Folia Primatologica* **74:** 159–161.
ZUNINO, G. E., GALLIARI, C. A. & COLILLAS, O. J. (1985): Distribución y Conservación del Mirikiná (*Aotus azarae*), en Argentina: Resultados Preliminares. In *A primatologia no brasil–2*: 305–316. de Mello, M. T. (Ed.). Brasília: Sociedade Brasileira de Primatologia.

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