

A socioecological perspective on primate cognition, past and present

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Received: 6 June 2005 / Revised: 1 February 2007 / Accepted: 2 February 2007 / Published online: 27 March 2007
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Abstract The papers in this special issue examine the relationship between social and ecological cognition in primates. We refer to the intersection of these two domains as socioecological cognition. Examples of socioecological cognition include socially learned predator alarm calls and socially sensitive foraging decisions. In this review we consider how primate cognition may have been shaped by the interaction of social and ecological influences in their evolutionary history. The ability to remember distant, out-of-sight locations is an ancient one, shared by many mammals and widespread among primates. It seems some monkeys and apes have evolved the ability to form more complex representations of resources, integrating “what-where-how much” information. This ability allowed anthropoids to live in larger, more cohesive groups by minimizing competition for limited resources between group members. As group size increased, however, competition for resources also increased, selecting for enhanced social skills. Enhanced social skills in turn made a more

sophisticated relationship to the environment possible. The interaction of social and ecological influences created a spiraling effect in the evolution of primate intelligence. In contrast, lemurs may not have evolved the ability to form complex representations which would allow them to consider the size and location of resources. This lack in lemur ecological cognition may restrict the size of frugivorous lemur social groups, thereby limiting the complexity of lemur social life. In this special issue, we have brought together two review papers, five field studies, and one laboratory study to investigate the interaction of social and ecological factors in relation to foraging. Our goal is to stimulate research that considers social and ecological factors acting together on cognitive evolution, rather than in isolation. Cross fertilization of experimental and observational studies from captivity and the field is important for increasing our understanding of this relationship.

Keywords Cognition · Foraging · Evolution · Comparative · Anthropoids · Lemurs

This contribution is part of the Special Issue “A Socioecological Perspective on Primate Cognition”.

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Introduction

Primate intelligence, in particular anthropoid intelligence, may have developed due to the interaction of social and ecological forces throughout primate evolutionary history, rather than to social or ecological factors acting in isolation. Relative neocortex size in anthropoid taxa appears to depend on diet and social structure (Barton 1996), perhaps reflecting their evolutionary relationship. Among living monkeys and apes, we see how social behaviors help meet ecological

challenges and how behaviors directed towards ecological problems make a more complex social life possible. Cognitive abilities from both social and ecological realms work together to increase chances of survival. In some cases it may distort or limit our view of primate cognition to consider social and ecological influences separately.

Although teasing apart individual versus social learning is difficult, there is a consensus among scientists that primates learn much about the environment from other members of their group. The subjects may be as basic as learning what is a predator or what is food or as complicated as learning traditional tool use. Young vervets learn from the behavior of older vervets to discriminate true avian predators from birds that are no threat in order to make effective predator alarm calls (Seyfarth and Cheney 1986). Young monkeys closely observe adults when foraging, learning which fruits and leaves to consider food (Janson and van Schaik 1993; Whitehead 1986). Juvenile chimpanzees learn the techniques involved in termite fishing (Lonsdorf 2006; McGrew 1977) or nut cracking (Boesch and Boesch 1990; Inoue-Nakamura and Matsuzawa 1997), at least in part, from adult chimpanzees. These skills allow them to access otherwise inaccessible food source. The juveniles may struggle for years before successfully extracting and ingesting termites or cracking a nut. Social learning about predators and foraging techniques are aspects of socioecological cognition.

The foraging decisions of primates that show sensitivity to their social environment are also examples of socioecological cognition. Depending on her rank and on the availability of resources, a primate may decide whether to follow another member of the group to food or to reduce scramble competition by avoiding other individuals (Bicca-Marques and Garber 2005; Di Bitetti and Janson 2001). Captive gorillas not only remember which foraging sites they have depleted (MacDonald 1994), but also which sites their foraging partners have depleted (Gibeault and MacDonald 2000). Primates can get information about the location of food from overt signals such as food calls (Hauser and Marler 1993), or subtle cues such as the odor of a conspecific's breath (Chauvin and Thierry 2005). Menzel's (1971) remarkable experiments indicated that, without any overt calls or gestures, chimpanzees were able to communicate to each other about the presence and quantity of hidden food. In nature, primate groups sometimes travel to more distant, more productive resources, instead of nearer, less productive ones (Cunningham 2003; Cunningham and Janson 2007; Garber 1989; Janson 1996, 2007). Traveling to more productive trees can reduce competition within the

group and facilitate group cohesion (Garber 1988; Janson 1988; White and Wrangham 1988; Whitten 1988).

As these examples demonstrate, social and ecological factors are inseparable in the daily lives of anthropoids. Although the focus of this issue is on primate cognition, highly encephalized animals in other taxa may also be distinguished by the degree of interaction between social and ecological challenges and solutions. Although primates generally have higher encephalization quotients (a measure of relative brain size) than other mammals, there is a substantial amount of overlap between the encephalization quotients of primates and cetaceans, elephants, and carnivores (Stephan et al. 1988).

Among carnivores, spotted hyenas have exceptionally large brains and complex social lives (Dunbar and Bever 1998). Tilson and Hamilton (1984) have suggested that sociality in the species might be an adaptation to capturing large prey. Elephants may benefit from the "ecological memory" of group members, especially older females, as they forage over a vast home range for limited resources such as water holes and mineral licks (Payne 2003). The communication system of elephants allows them to coordinate their foraging, even when miles apart, and to come to each other's defense when necessary (Payne 2003; Weilgart et al. 1996). Weilgart et al. (1996) compare elephants to less encephalized rhinoceros. Although rhinos inhabit the same environment as elephants and eat similar foods, their diet is less varied, their home range is smaller and they have a simpler social system. Ecological memory may be just as important for some cetaceans as for elephants or primates. During "el Niño" years when there is not enough food off the Galapagos Islands, sperm whales move directly and quickly to locations that may be thousands of miles away. Whitehead (1996) and Weilgart et al. (1996) have suggested that the benefits of an information pool in a variable environment could select for, and maintain, long-term social bonds in sperm whales. Social learning may also play an important role in the survival of cetaceans (Rendell and Whitehead 2001; Yurk 2003). For example, young killer whales learn from their mothers and other members of their group how to beach themselves to capture pinnipeds, a rewarding but dangerous practice (Guinet and Bouvier 1995). See de Waal and Tyack (2003) for a survey of social complexity in mammals.

Among birds, corvids have exceptionally large hyperstriatum ventrale and neostriatum, areas of the avian brain associated with integrative behaviors (Timmermans et al. 2000). When hiding and retrieving their caches, scrub jays not only consider where-what-when information (Clayton et al. 2001, 2003), but also take social factors into account by adjusting their

behavior to reduce the chances of their caches being taken by other jays (Emery et al. 2004). Similarly, ravens appear to take into account the knowledge of their social partners when deciding among foraging behaviors (Bugnyar and Heinrich 2005). The counter strategies of storing and pilfering corvids may involve mental attribution. See de Kort et al. (2006) for a review of the cognitive aspects of caching.

Among primates, there is a clear grade shift in neocortex size between strepsirhines and haplorhines. In strepsirhines, unlike haplorhines, neocortex size is not correlated with either group size or diet (Barton 1996). In the next section, we explore the possibility that cognitive limitations in lemurs' relationship to the ecological environment restrict the sophistication of their social relationships.

What-where-how much and when

The ability to “remember” important locations is found in many distantly related taxa: honey bees, birds, and mammals (Shettleworth 1998). Spatial memory is widespread among mammals, and is shared by most, if not all, primates (e.g., Garber and Hannon 1993; Gibeault and MacDonald 2000; Janson 1998; MacDonald and Wilkie 1990; Menzel and Juno 1985; Platt et al. 1996). Although little is known about the role of olfaction in primate ecology [but see Dominy et al. (2001) and Heymann (2006) for reviews of what is known], lemurs appear to use visual cues to remember the locations of parked infants, sleeping nests, and feeding sites (Kappeler 2000).

A survey of the foraging behavior of extant lemurs, however, is consistent with the notion that they do not have the ability to integrate “what-where-how much” information about resources. Among lemurs who travel in pairs, such as *Phaner furcifer* (Charles-Dominique and Petter 1980; Schülke and Kappeler 2003) and *Indri* (Pollock 1979), the male and female may maintain a distance between them, or the male may follow the female and wait until she is finished feeding in a tree before entering it. Some larger groups of lemurs break into small foraging units of 3–5 individuals. Frugivorous *Varecia variegata* is an example of this. Rigamonti (1993) reports that during the moist-cool period when fruit is scarce, subgroups may not see each other for weeks. Each subgroup tends to use a core area until the fruit is depleted. Core areas are separated only by a few hundred meters. We can speculate that if the group had mechanisms by which they could travel efficiently between the large trees in the core areas, they could remain cohesive. Larger groups of

lemurs that remain cohesive while foraging are relatively rare. The largest cohesive groups are found in *Lemur catta* (Jolly 1966, 2003; Sussman 1977). They may be able to maintain larger groups because they depend less on ripe fruit. Kappeler (1999) suggests that the low spatial cohesion of lemurs may be due to high within group competition for resources. If lemurs could use productivity measures in foraging decisions, competition would be reduced. Although cognitive constraints are certainly not the only possible explanation for the small size of lemur foraging parties, they are worth considering.

In contrast to lemurs, it appears that at least some monkeys and apes have the ability to represent multiple attributes of a feeding site. In 1973, Emil Menzel reported that juvenile chimps that were shown larger and smaller clusters of food visited larger clusters first. In his 1989 observational field study, Garber found that large crowned trees determined his tamarin study group's foraging route. In an experimental field study, Janson (1998) found that capuchins were willing to travel further for more productive sites. Janson (2007) presents experimental data that shows that capuchins will skip a smaller resource if visiting the smaller site adds too much travel time to reaching a larger site. Cunningham and Janson (2007) present observational data indicating that the travel path of saki monkeys is determined by highly productive trees.

The ability to remember multiple attributes of an experience is associated with episodic or episodic-like memory. Episodic memory binds together where, what, and when information in a recollection of a personal event [see Clayton et al. (2001) and Cunningham and Janson (2007) for a discussion of episodic memory]. So far, the ability to integrate all three aspects of episodic memory has been convincingly demonstrated only in food-caching jays (Clayton et al. 2001, 2003). Pigeons, however, have demonstrated that they can encode, but not bind together, information on identity, location and time (Skov-Rackette et al. 2006). Apes can recall “where and what” (reviewed in Schwartz and Evans 2001) and “what and who” (Schwartz et al. 2002) attributes of unique events. We know little, at this time, about the temporal characteristics of primate memories (Janson and Byrne 2007). A foraging primate would receive substantial benefit, however, from recalling “what” and “where” information from recent feeding bouts (particularly if “what” included information on food type, quantity, and stage of ripeness).

As a larger reward might involve traveling further, benefiting from the ability to consider size and location would often depend on an individual's ability to delay gratification. Monkeys seem to have more self control

than pigeons or rats (Tobin and Logue 1994; Tobin et al. 1996). Experiments with tamarins and marmosets (Stevens et al. 2005a, b) suggest the feeding ecology of these monkeys shaped the evolution of self control in those taxa. In the next section, we present an outline as to how the ensemble of traits that allow individuals to consider multiple attributes of a feeding site may have evolved and discuss the role it may have played in the evolution of primate cognition.

An evolutionary scenario

Recent findings [summarized in Covert (2004) and Fleagle (1999)] indicate that the Eocene prosimians were a diverse radiation that encompassed a wide range of body sizes (10 g–7 kg), diet (insectivory, frugivory, folivory), and activity cycles (nocturnal, diurnal). The substantial overlap in body size, dietary adaptation, locomotor behaviors, and activity cycle amongst omomyoids, adapoids, and the earliest anthropoids (Covert 2004) makes it impossible to confidently portray anthropoids as evolving from a small, solitary, insectivorous ancestor (Plavcan 2004). Nonetheless, it is estimated that 70% of omomyoids weighed less than 500 g and 40% of adapoids weighed less than 1 kg (Covert 2004). Many of these small (and often nocturnal) prosimian mothers would have left their infants parked in nests while they foraged (Nunn and van Schaik 2002). Obviously, after separating from their young, mothers would have to return to them. Although we cannot be sure how ancestral primates managed to locate their young, if we extrapolate from living prosimians, the ability to remember important locations—whether for parked infants or feeding sites—was probably present in Eocene primates.

At some point, or points, anthropoids, or their ancestors, most likely became diurnal [but see Tan et al. (2005) for divergent view] and, among early anthropoids, there was a trend towards increasing body size (Fleagle 1999). Diurnal medium-sized and large primates tend to live in groups to reduce the risk of predation (Janson and Goldsmith 1995; Nunn and van Schaik 2002). The canine dimorphism present in early anthropoids further suggests that they lived in groups (Plavcan 2004). Although monkeys have diversified their diets throughout their evolutionary history, early Oligocene anthropoids were highly frugivorous (Fleagle 1999). Based on relative size of the optic foramen of *Simonsius grangeri* it appears that Oligocene anthropoids had already developed keen eyesight (Kirk and Kay 2004). Sussman (1991) argues that early primates needed acute powers of visual discrimination and

precise coordination to manipulate small seeds and fruits. Trichromatic color vision may help primates distinguish fruit against a background of green leaves (Barton 2000) or may signal the nutritional value of fruit (Riba-Hernández et al. 2005), although other possible hypothesized reasons for trichromacy have been suggested (e.g., Dominy 2004). Improved vision would also facilitate the use of long-range landmarks to guide navigation between large, distant fruit trees.

For those early gregarious frugivores, the ability to travel efficiently to the highly productive fruit trees would have provided a distinct selective advantage. Brain size during this time was small (Simons 2004), however, implying that Oligocene anthropoids may not have been able to integrate information on the location and productivity of feeding sites. Barton (2000, 2004; Barton et al. 1995) attributes the large neocortex of monkeys and apes to the expansion of the visual system. He notes the finding of van Essen et al. (1992) that about half the neocortex of haplorhines is devoted to processing visual information. Barton (2000) suggests that integrative areas that are traditionally considered non-visual receive visual input and would be affected by the evolutionary enhancement of supporting, lower-level structures. Although the enhancement of the visual system may have primed the way for enlargement of not only primary sensory, but also higher integrative areas, the brain is energetically expensive (Armstrong 1983; Hofman 1983; Martin 1981). Therefore, without shifts in the environment favoring the ability to construct complex representations, it is unlikely that the genes necessary for this ability would spread through a population and persist.

The ability to construct more complex representations would have been useful for integrating “what-where-how much” information about resources. For groups of frugivorous primates, the ability to select more productive trees as destinations made it possible for more individuals to receive adequate nutrition and remain cohesive, reducing the chances of predation. As group size increased, however, competition for a limited clumped resource selected for increased communications skills and abilities such as anticipation, coalition formation, and reconciliation. These social skills, in turn, made a more sophisticated relationship to the environment possible. Apes, with their larger bodies and greater foraging challenges took this relationship to another level by relying heavily on social transmission of foraging information, as well as role-taking (theory of mind). Theory of mind, in particular, may be important in anticipating the competitive context of potential feeding opportunities in the presence of conspecifics (e.g., Hare et al. 2001). These cognitive

abilities are most developed in humans. Although social and ecological cognition is also present in other mammals, the development and feedback nature of the relationship may be unique in primates.

Strepsirrhines may never have evolved the ability to assign multiple attributes to feeding sites. Nocturnal strepsirrhines avoid predation through crypsis and small size rather than by increasing group size (van Schaik and van Hooff 1983). They have less need therefore, to integrate information on various attributes of feeding sites. In Madagascar, tree growth is slower, fruit productivity is lower, and periods of fruit scarcity are longer than in the rainforests of Africa and South America (reviewed in Wright 1999; Wright et al. 2005). Given the high energy requirements of the brain (Armstrong 1983), ecological conditions may have constrained the encephalization of diurnal lemurs, selecting rather for strategies that conserve energy: reduced activity, dense fur, small brains, small group size (Wright et al. 2005).

The papers in this issue

The papers in “A socioecological perspective on primate cognition, past and present” focus on monkeys and foraging behavior. Apes are neglected, not because socioecology does not apply to them, but because existing theories of ape evolution are already consistent with the idea that social and ecological factors have reinforced each other in selecting for greater intelligence. For example, Byrne (1999) suggests that ape planning and cultural learning abilities allow apes to gain access to novel foods. Potts (2004) proposes that habitat instability about 9.5 mya increased the difficulty of surviving on a ripe fruit diet and selected for cognitive and social means of finding food and is responsible for the higher intelligence of apes.

We have also focused on foraging behavior. In the past few decades there has been an explosion of research in social cognition. These studies, many of which were inspired by the book, *Machiavellian Intelligence* (Byrne and Whiten 1988), have fundamentally changed the way we view the social interactions of primates and the way cognition is studied. The studies have been broad and encompassed a wide range of behaviors and implied cognitive skills; for example communicating about the location of food, the formation of alliances, reconciliation, deceit, and announcing the arrival or predators. Some of these studies, we suggest, interpret social intelligence so broadly that they incidentally demonstrate the relationship between social and ecological intelligence.

In contrast, many discussions of ecological cognition seem to assume that the only foraging challenge facing primates is finding the closest fruit tree. The list of issues that monkeys could potentially consider, however, is staggering: will enough fruit on that tree have ripened since our last visit to make another visit worthwhile? Should we travel to a nearer, smaller resource or a more distant, larger one? Should we make a detour to a smaller resource on the way to a bigger one? Should we visit a big resource that carries with it a high risk of predation or a smaller, safer one? If this tree is fruiting, what other trees might be fruiting? What paths should we take to avoid other groups? What path should we take to meet other groups? Is this a good time of day to eat the leaves of that tree? Do I want to stay with the group today or forage independently? What can I learn about resources from others in my group? If I separate from the group, how will I find them?

In the past decade, several publications have delved into investigating the complexity of ecological cognition and its relationship to social cognition. In “Primate Cognition”, Tomasello and Call (1997) propose that both ecological and social theories of cognitive evolution are correct, but concern different cognitive abilities which evolved in different evolutionary periods. They suggest that many primate cognitive adaptations are not domain specific. An edited volume, “On the Move” (Boinski and Garber 2000), provides an in-depth and expansive look at primate movements, including decision-making and cognitive aspects. The *American Journal of Primatology*’s issue on “Primate Cognitive Ecology” (vol 62, 2004) examines cognition in social and ecological environments from a variety of perspectives. These publications are important precursors to this special issue. In spite of these important efforts, much remains unknown about the cognitive skills involved in foraging and impact of these skills on the social lives of primates.

In this issue, Janson and Byrne (2007) provide a methodological guide for researchers attempting to decipher what knowledge shapes primate travel decisions in the wild. They review the methods that have been used, what we have learned, and suggest directions for future study. Noser and Byrne (2007) and Di Fiore and Suarez (2007) investigate the mental representations that their study subjects use to navigate through their home ranges. Noser and Byrne describe the effect of chance encounters between baboon groups on their study group’s travel path. When other groups of baboons were in proximity, the study group traveled faster and their travel path was less direct. The detours that the group took suggest that they had

memorized sequences of landmarks from a tight network of routes with intersections, a “network map”. Di Fiore and Suarez analyze the travel paths of sympatric spider and woolly monkeys in Ecuador. They report that both spider and woolly monkeys travel on repeatedly used paths in a manner that is consistent with a route-based mental map. Di Fiore and Suarez propose that route-based travel allows monkeys to effectively monitor their resources and reduces the amount of information the monkeys need to remember, and it might also help subgroups of spider monkeys find each other.

Unlike the spider monkeys studied by Di Fiore and Suarez (2007), the spider monkeys studied by Valero and Byrne (2007) do not appear to use habitual routes. Is the difference in the behavior of the two groups due to difference in the terrain of the monkeys, or to differences in the resource distribution, or could they be due to cultural differences between the groups? The variation is intriguing and a possible topic for future study.

Valero and Byrne (2007), Cunningham and Janson (2007) and Janson (2007) look at the information that monkeys integrate when deciding on a foraging path. Valero and Byrne’s analysis of the foraging routes of their study subjects, suggest that the spider monkeys plan their routes more than one step at a time. Cunningham and Janson found that during periods of resource abundance, saki monkeys’ travel paths were not determined by the nearest trees, but by the most productive ones. The social benefit of traveling further for greater productivity was substantial. Although feeding party size was largest in more productive trees, aggression levels were lowest and the sakis were able to eat more seeds per minute. Janson’s field experiments offered capuchin monkeys a choice between a closer site with less food and a more distant site with more food. The smaller site functioned like a detour on the way to the larger site. The experiments show that capuchin monkeys appear to take into account the geometry and rewards of at least three possible goals at a time when deciding which food source to visit in a sequence.

Work with captive primates can play an important role in helping us understand the connections between social and ecological intelligence. Bonnie and de Waal (2007) present experimental evidence that brown capuchins learn by observing conspecifics, even without an extrinsic food reward. The results support the idea that primates find it intrinsically rewarding to do the same thing as conspecifics: a trait that may facilitate the social transmission of information.

Where we can go from here

The main goal of this issue is to stimulate research that considers social and ecological factors acting together, rather than in isolation, to influence the evolution of cognition. This is an area in which experimental and observational work from captivity and the field can cross-fertilize each other. Matsuzawa and his collaborators (2001, 2006) are pioneers in creatively synthesizing field and laboratory studies to shed light on cognitive questions. Although we have focused on primates, investigating distantly related taxa would determine whether an intimate relationship between social and ecological cognition is unique to anthropoids or is a major factor in selecting for neurobiological advancement in mammals and possibly birds [see Marino (1998) for comparisons of cetaceans and primates and Weilgart et al. (1996) for comparisons of cetaceans and elephants]. We did not include research on the cognitive skills primates use as predators or to avoid becoming prey, but this is another important area of investigation. We need information on cognition in strepsirhines. More information could disprove the evolutionary ideas presented here. Lemurs may be capable of more complex foraging calculations that we have given them credit for. Santos et al. (2005a, b) have found that lemurs have rudimentary math skills and perform comparably to capuchins in some tool-using experiments. Strepsirhines represent a link between anthropoid primates and other mammals (Martin 1990). They can offer unique insights into the evolution of cognition.

For all primates, the details of how social and ecological cognition interact have yet to be explored. There is abundant evidence that local availability of food may affect social decisions, including the tendency to form subgroups (van Schaik et al. 1983), number of animals in a feeding tree (Leighton and Leighton 1982), and levels of aggression (Cunningham and Janson 2007; McFarland Symington 1988). However, there is little evidence that actual foraging decisions differ under distinct social circumstances. For instance, Suarez (2003) found that the size of the next food tree used did not predict joining and leaving events in spider monkey foraging parties in Ecuador. Whether these monkeys are unaware of the expected productivity of future food trees or constrained in their ability to use this information is not clear, but similar work needs to be carried out for other species. Janson’s work (2007) suggests that capuchin monkeys may anticipate resource location and future rewards in their travel decisions, but does not demonstrate that different travel decisions are made by groups of different sizes or animals of different ranks. Such detailed study of foraging

decisions by animals of distinct social ranks is a compelling opportunity for future field studies.

Acknowledgments Most of the papers in this issue are from a Symposium on Socioecological Cognition presented at the XX Congress of the International Primatological Society, held in Torino, Italy, in August 2004. We thank all the participants in the Symposium on Socioecological Cognition for their contributions. We are grateful to Tatiana Czeschlik for collaborating with us on this special issue. We also thank Eric Delson and three anonymous reviewers for their thoughtful comments.

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