A Guide to Practical Babooning: Historical, Social, and Cognitive Contingency

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As ecologically adaptable animals, baboons are distributed widely across Africa, and display a variety of morphological and behavioral differences that reflect both local ecology and a complex evolutionary history. As long-lived, slowly reproducing animals, baboons face numerous ecological challenges to survival and successful reproduction. As group-living animals, the social world presents an equally diverse array of challenges that require the negotiation of individual needs within the constraints imposed by others. Understanding how all these facets of baboon evolutionary history, life history, ecology, sociality, and cognition fit together is an enormous but engaging challenge, and despite one hundred years of study, it is clear there is a still much to learn about the various natural histories of baboons. What also is clear, however, is that an appreciation of contingency holds the key to understanding all these facets of baboon evolution and behavior. In what follows, I hope to illustrate exactly what I mean by this, highlighting along the way that history is not to be ignored, variability is information and not merely "noise", and that behavioral and cognitive complexity can be two very different things.

The *Papio* baboons have long been held up as models of behavioral plasticity and have played a large part in the establishment of hypotheses concerning how social behavior should vary in response to environmental conditions. This is because primate

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socioecology has been predicated on the assumption that the species is the arena of gene recombination, and that variability below the species level is best treated as plastic behavioral adjustment to current local conditions and not as indicative of differences in any underlying genetic influences on behavior. As such, the ecological plasticity that underpins the *Papio* baboons' wide distribution across Africa, in locations as varied as deserts and mountaintops, has made them the ideal model species.[1] The innovative time budget analyses by Robin Dunbar and his colleagues, for example, have capitalized on this assumption to explore how constraints of time influence the distribution, group size, and behavioral strategies of the taxon.[2–5]

HISTORICAL CONTINGENCY

As time has passed, however, we have begun to recognize a problem with this approach: there are behav-

ioral differences between baboons at the subspecific level (or species level, depending on how one chooses to classify the five "classic" baboon types of chacma, olive, yellow, Guinea, and hamadryas) that are clearly resistant to differences in local conditions.[1] In addition to the well-documented idiosyncrasies of the hamadryas baboon and the differences between them and olive baboons in hybrid zones, our own analyses have shown that while local ecology can account for troop size and sex-ratio differences between chacma and other East African baboons, it cannot explain the absence of coalition formation by male chacma baboons: large cohorts of male chacma are not observed to form reproductive coalitions despite apparent demographic opportunities whereas even small male cohorts of yellow and olive baboons will cooperate in this way.[1] What is even more problematic, however, is that different populations within each of the conventional subspecies also show as much morphological variation from one another as do the five subspecies themselves.[6] In addition, one cannot ignore these interpopulation differences in morphology when assessing environmental effects on behavior. Again, we can use chacma baboons as an illustration, specifically those living in the Drakensberg Mountains of KwaZulu-Natal. This habitat imposes high thermal demands on animals living there while also providing food that is difficult for baboons to both find and process. As the socioecological model predicts, the Drakensberg baboon population has a small mean group size and slow recruitment. As one moves fur-
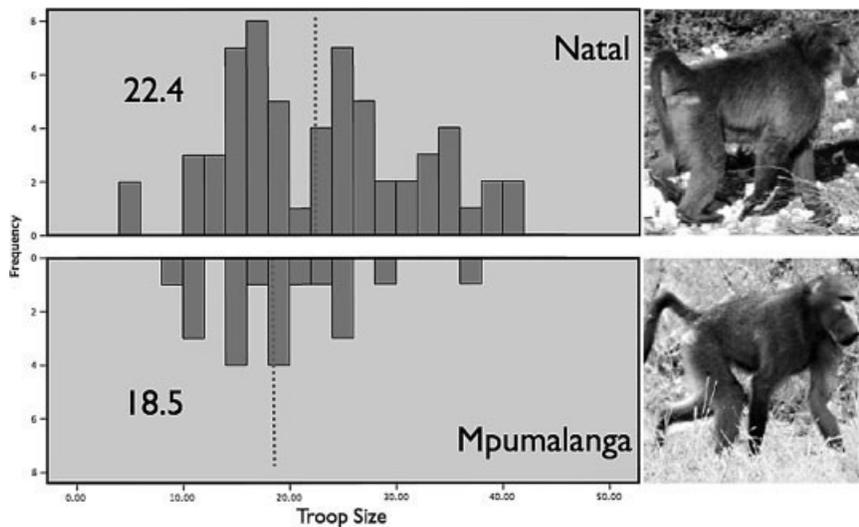
Figure 1. Comparison of baboon troop sizes and morphotypes found in the Natal Drakensberg in KwaZulu-Natal, South Africa and the northern Drakensberg, Mpumulanga, South Africa. Dotted lines represent the mean group size in each population.

ther north, however, although direct thermal demand remains high, resource quality and quantity improve, and predation risk also increases. According to the standard socioecological model, then, we should expect to see mean troop size to increase significantly. Oddly, though, this is not the case. Baboons living in the northern Drakensberg have a smaller mean group size than do those further south (18.5 vs. 22.4, respectively) (Fig. 1). Moreover, this occurs despite the fact that down the road (quite literally) at lower elevations, the baboons are found in much larger groups (mean group size = 37).[7]

The point here is that before we cast around for some unanticipated environmental influence that can explain these patterns, we need to notice that the two baboon populations differ in more ways than just their environments. Whereas those in the Natal Drakensberg are "Cape baboons," thought to have emerged from a montane refugium, and consequently are short, stocky, and hairy (Figure 1), those in the northern Drakensberg are noticeably more gracile, with shorter hair and longer limbs (clearly well adapted to the heat of the South African lowveld, but poorly suited to the cold winters of the mountains) (Figure 1). One chacma baboon is not like another,

and where they started out, evolutionarily speaking, has a large impact on where they have now ended up. In other words, history matters.

New analyses of baboon taxonomy and phylogeny based on mitochondrial DNA go further in revealing just how much history matters to baboon ecology and behavior. These analyses come primarily from two laboratories: Cliff Jolly and colleagues at New York University and, more recently, Dietmar Zinner and colleagues at the German Primate Centre (DPZ). Gratifyingly, their analyses show a high degree of consensus. Together, they confirm a basal split of *P. hamadryas* into a northern and southern clade around 2.4 million years ago[8–10] (C. Jolly, pers. comm.) (Fig. 2a–b). We see, in essence, that *Papio* emerges in Southern Africa (perhaps somewhere in modern-day Zambia) and then radiates in response to glacial and interglacial climate cycles. The northern clade then divides into eastern and western clades. While the western clade is made up of two olive and guinea baboon haplotypes, the eastern clade comprises a mixture of different morphotypes or taxonomic units.[8–10] Most strikingly, and surprisingly, the East and Northeast African taxa on which most work has been done (olive, northern yellow, and hamadryas) show very marked phenotype-mitochondrial discordance[8–11]

(C. Jolly, pers. comm.) (Fig. 2a). There is introgressive hybridization between northern yellow baboons and olive baboons, which is still continuing at Amboseli, and hamadryas and olive baboons also show a long and ongoing history of hybridization. Active hybrid zones also occur between northern chacma and kinda and southern yellow baboons. It also seems likely that western olive baboons hybridize with guinea baboons, throwing into doubt the status of the last remaining member of the conventional taxonomy as a "good" bio-species.[8–10] In other words, there is no such thing as "the" olive baboon or "the" yellow baboon: despite appearances, olive baboons in West Africa have a different evolutionary history to those in East Africa, and potentially different behavioral ranges; ditto the northern and southern yellow baboons. The morphological similarity between these baboons masks a great deal of variability at the genetic level, which represents the highly contingent nature of selection acting in both space and time on each population. The conventional taxonomy is really only a nod to broad phenotypic resemblance across populations, and in the case of chacma baboons, to geography. Consequently, there is no point at which we can assume that the behavioral responses we see in any baboon population are free of historical influence. This is not to say that we should privilege the history documented by mitochondrial haplotypes over that documented by the external phenotype, which reflects the influence of nuclear genes; both are important as sources of information (C. Jolly, pers. comm.). What these data show unequivocally is that history matters.

This realization should, for the socioecologists among us (if not the taxonomists), turn us away from the hunt for facts about "species" and towards a means of coming to grips with the fact that genes, histories, and environments are thoroughly entwined. In Cliff Jolly's words, "The population structure and dynamics of taxa at [the level below the species] exemplify crucial evolutionary processes…the evolution of phenotypic distinctiveness or reproductive
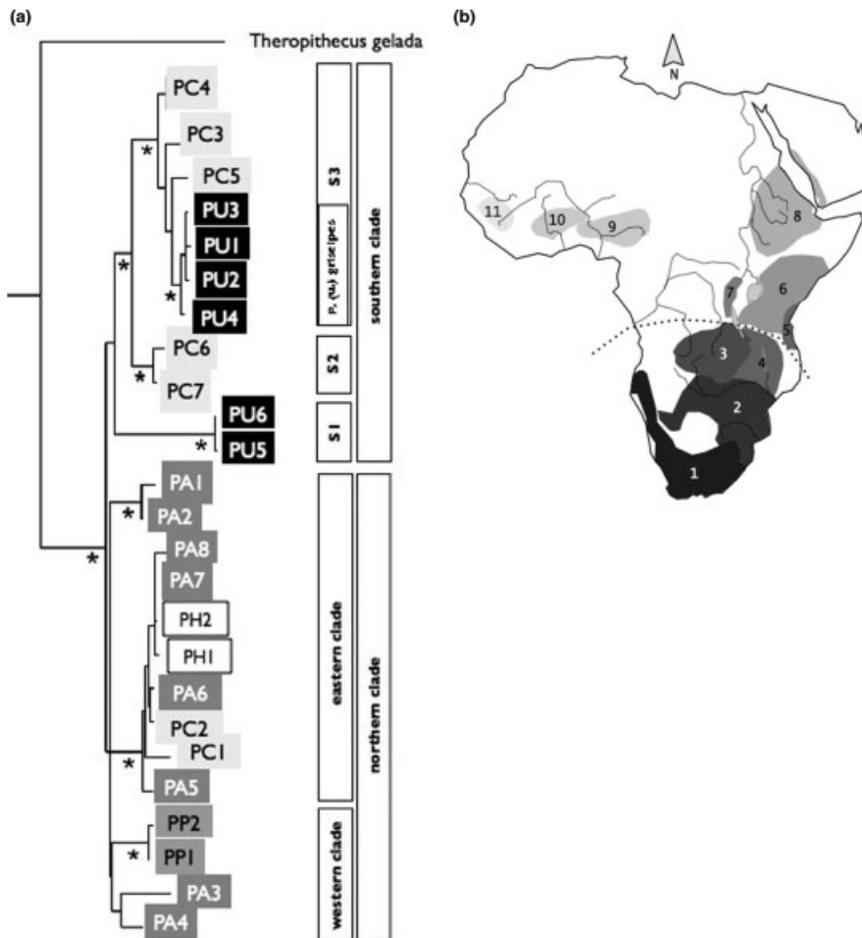
Figure 2. (a) Mitochondrial DNA phylogeny of baboons adapted from Zinner et al. (2009; in press).[8–10] The phylogram is based on the neighbor-joining algorithm and by applying the TrN + 1 + G model of sequence evolution. Marked* nodes yielded bootstrap values of ≥ 85% (for maximum parsimony, neighbor-joining and maximum likelihood algorithms as implemented in PAUP 4.0b10) or posterior probability values of ≥ 95% (Bayesian algorithm). Bars on the right side of the graph show the respective baboon clades. Letter codes in boxes indicate the traditional baboon taxonomic distinctions (PC = *Papio cynocephalus*; PU = *Papio ursinus*; PA = *Papio anubis*; PH = *Papio hamadryas*; PP = *Papio papio*). All taxa with the exception of *Papio papio* are para- or polyphyletic, and there is a strong geographical signal: local populations form monophyletic haplogroups irrespective of their species affiliations. The distinct subclade of *P. ursinus* within clade S3 is thought to represent grey-footed chacmas (*P. (u.) grisiepes*) and (b) Distribution of terminal savannah baboon mitochondrial haplogroups adapted from Zinner et al. (2009; in press).[8–10] 1. Southern chacma; 2. Northern chacma; 3. Kinda; 4. Southern yellow (not a monophyletic group); 5. Coastal yellow; 6. Eastern olive-northern yellow; 7. Hamadryas-north-eastern olive; 8. Cental olive; 9. Olive west 2; 10. Olive west 1; 11. Guinea. The dotted line indicates the division of the northern and southern clades.

isolation or both. Investigation of these processes is too biologically important to be sidetracked by the empty semantics of the 'species question'".[12:193] A quote that can be complemented, and completed, by another fine biologist who knew his evolutionary onions, Darwin himself stated: "In short, we shall have to treat species in the same manner as those naturalists treat genera, who

admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect....".[13:426] It is not cheering because, of course, it means our task is that much harder and the challenges that much greater. If we are up to meeting this challenge, however, an appreciation of historical contingency offers up a whole new generation of questions about how

baboons and their environments fit together, as we explore both the scope and limits of their ecological plasticity. As Dietmar Zinner (pers. comm.) suggested, we are on the verge of a "baboon Renaissance".

SOCIAL CONTINGENCY

As well as acknowledging the contingent effect of history in our phylogeographic and evolutionary ecological endeavors, an appreciation of contingency at other levels also can pay dividends. Moving down a level from the contingent responses shown by populations to prevailing climate and historical influence, we also can investigate how contingency influences the nature of individual relations within groups. Beginning with van Schaik's seminal paper on the ecology of female social relationships,[14] a good deal of interesting work has been conducted over the last twenty years on the manner in which food abundance, predation, and infanticide risk define the parameters of female social engagement. Baboons have once again, however, thrown a spanner in the works.

Baboon females are classified as a nepotistic, despotic species according to one of the most prominent socioecological models.[15] They are philopatric, form bonds with other females—especially kin, and show strongly linear dominance hierarchies. They are predicted to form coalitions, serviced by grooming, to reduce the impact of local resource competition on their reproductive success.[15] While baboons in other populations behave as expected,[16] the various populations of southern and northern chacma baboons that we have studied do not.[17] More precisely, they do not fit into the neat categorical distinctions offered by this model: chacma females can groom differentially in the absence of food competition or groom differentially in the presence of marked resource competition, but without forming coalitions.[18,19] Their individual patterns of grooming reciprocity can be strongly despotic and unbalanced when they form part of one dyad, but strongly egalitarian and balanced when part of another.[20,21]

They do not compete to groom high-ranking females,[21] and their rates of aggression and grooming reciprocity fluctuate across years,[19] as does the entire structure of their social network.[22]

In essence, what we are dealing with here is a "grain" problem: similar to the way in which morphological resemblance between different populations of baboons masks major differences in their evolutionary history (which, as noted earlier, will leave an indelible mark with respect to the behaviors shown in the present),[23] categorical socioecological models also mask the high levels of between- and within-population variability seen in both the size and structure of groups, and the nature of female–female relations, across chacma baboon populations. In other words, in the quest to explain the central tendency (which is, of course, an entirely sensible place to start), behavioral and social variation have been demoted from data to noise. It has been assumed that in a given species' population, under a given competitive regime, the optimal response set for all females would coincide. This heuristic, however, necessarily excises from consideration the prospect that the best strategy for one individual is often directly contingent on what others are doing. Fortunately for us, Ronald Noë, along with Carel van Schaik and Jan van Hooff, had, early on, developed a theoretical framework[24] (elaborated on subsequently by Noë and Peter Hammerstein[25]) that was able to address the kinds of flexible responses that we felt needed explanation. Biological market theory is built on the explicit assumption that an organism's responses are likely to be contingent and variable, not stable and monolithic. It expects variability not only across individuals in both time and space but also within individuals, as each responds to shifts in the value of potential social partners over time. Although it was not developed specifically as an alternative to existing socioecological models, the shift in emphasis entailed by the biological market framework made it a natural source of inspiration, providing us with a

means to extend socioecological thinking in ways that placed individual contingent response at the forefront, thus transforming "noisy" data into informative patterns of interindividual social interaction.

The elegant empirical demonstration of an "exchange economy" in chimpanzees[26] further highlighted the utility of a market-based view, and by adopting the same stance in thinking about our baboons, we were able to predict and confirm differences across populations in levels of grooming reciprocity,[20] demonstrate the dynamic interaction of grooming reciprocity, aggression, and partner choice within a population,[19] show that the law of supply and demand structures social interactions,[27] and more theoretically, reinterpret coalition formation as part of a suite of potential exchange commodities rather than as the organizing principle of female social engagement.[17]

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Market theory has opened the way to an investigation of temporal changes in the underlying, qualitative structure of female social networks,[22] and also has been adopted in studies of reconciliation as a means to a more effective explanation of the broad variability seen in this behavior across the primate order (and beyond).[28]

The value of Noë's recognition of contingency and variability as factors that determine partner choice and levels of engagement is now being realized in an increasing number of recent analyses. As for

baboons, long-tailed macaques have been shown to exchange grooming for infant handling in a way that abides by the laws of supply and demand (a study that does so more convincingly than ours since these analyses demonstrate that infant value is contingent on the infant–female ratio in the specific social context rather than merely on the general availability of infants).[29] Spider monkey females also have been shown to exchange embraces for the opportunity to handle infants,[30] an especially interesting result because it confirmed that social behaviors other than grooming could serve as commodities. One gratifying consequence of this is that where New World species had previously been excluded from analyses of social engagement due to the strong emphasis on grooming as a mediator of exchange, they are now firmly reincorporated.

Work on grey-cheeked mangabeys has extended the market approach to arboreal forest species, illustrating how future studies should incorporate factors relating to scramble as well as contest competition into the theory.[31] This study also draws attention to possibilities offered by other socioecological models that attempt to explain grouping patterns more broadly with respect to foraging efficiency and dispersal opportunities, and which can be used alongside a market-based approach[32,33] (L. Isbell, pers. comm.). Data from red-fronted lemurs have shown that like other primates, they are able to assess the social power of other group members and use grooming contingently to achieve their ends;[34] a neat demonstration that complex grooming relations are not dependent on anthropoid-size brains. Finally, work on long-tailed macaques also has identified mating markets where males and females trade grooming and sex.[35] Given similar findings on wood mice,[36] cleaner fish,[37] suricates,[38] red bishop birds,[39] and micorhyzza,[40] the predictive power of the market approach underscores the need to take contingency seriously, not only at the evolutionary level but also in the interpretation of real-time social dynamics.

Of course, as with any model, its assumptions need testing before application. Not everything, in other words, will be a market: highly stable, unchanging conditions (e.g., like those seen in captivity) are unlikely to generate market effects (at least without explicit experimental manipulation). Market effects also may be absent where constraints are placed on one or other potential trading partners. For example, the large size difference between male and female baboons, in combination with a strict priority of an access mating system, severely limits the ability of females to choose their mating partners, which undercuts any potential for the kind of interchange trading of grooming for sex seen in macaques. Consequently, while market effects are not seen in this system, the lack of interchange between males and females nevertheless has implications for market theory. Specifically, the ability of males not only to control their mating partners but also, and crucially, suppress their rivals and eliminate trade provides a clear validation of one of the core assumptions of market models: that commodities must be inalienable if trade is to flourish.[41]

COGNITIVE CONTINGENCY

If the value of different partners changes with variation in their reproductive state, health, rank, and the simple presence or absence of other individuals, then this contingency in the social marketplace must make primate groups tactically demanding places to live.[42] Selection for the ability to respond optimally in the face of constant variability is likely to account for the behavioral flexibility and plasticity that is so characteristic of the primates.[43] It has long been suggested—under the various guises of the social intelligence hypothesis, the Machiavellian intelligence hypothesis, and the social brain hypothesis—that the evolution of increased brain size within the primate order is driven by the demands of social life.[44–46] In each of these variants, an enlarged brain is taken to indicate the evolution of a more complex cognitive architecture that can deal with the specific problems thrown up by intense sociality. This architecture has, without exception, been specified in somewhat anthropocentric terms, not least because part of the social intelligence/social brain project has been to explain why our own brains are so inordinately large. Humphrey, for example, argued strongly in his seminal paper that primates must be "calculating beings,"[44:309] drawing a direct analogy between social life and that most cerebral of human pursuits, the game of chess. Here, predicting in advance what one's opponent is likely to do makes it possible to thwart such action before it can have a detrimental impact: "The social gamesman must be capable of a special sort of forward planning…, we and

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most other members of complex primate societies have been in this game since we were babies."[44:309] As a result of this particular perspective, we have a tendency to view the intellectual capacities of our primate cousins as representing the precursors of our own intelligence, using the evolutionary argument that our own cognitive skills did not spring forth fully formed, so that we can trace the emergence of advanced cognition by adopting a specifically "phylogenetic" approach. While this is, without question, an entirely reasonable research strategy, there are two reasons why we need to be cautious when using this approach, both of which arise through a failure to acknowledge the impact of contingent events.

First, our anthropocentric perspective obscures the fact that other species have followed their own unique evolutionary trajectories, and may have evolved their own unique skills that cannot be traced directly to our own. The parable of Cliff Jolly's Chimney illustrates this perfectly. During Cliff's talk at the recent Wenner-Gren Symposium in honor of his life and work, he told the story of how he had his chimney relined. Looking down the chimney from the roof, the builder was thoroughly satisfied that he had done a good job: the lining appeared smooth and all was well. As soon as a fire was lit, however, smoke began billowing out of the fireplaces all over the house. Looking up the chimney from the bottom, the reason became apparent: the lining plates had all been fitted upside down, leaving gaps that were not visible when gazing down from above. Drawing an analogy between these recent home improvements and the way we view evolutionary processes, Cliff noted that we are prone to the same mistake when we stand in the present and look down the chimney of evolution. We similarly fail to see the gaps, and instead see only a smooth, unbroken line leading inexorably to modern humans, where the precursors and building blocks are all neatly in place. Only if we decide to look up the chimney, towards the present from the past, do we see the true picture: the variety of different paths taken, the lines that went extinct, the chance events that bootstrapped the evolutionary process in various ways; the whole messy, highly contingent, nature of it all. A similar tendency to gaze down the evolutionary chimney to detect the precursors of our own cognition means that we run the risk of seeing other species only in terms of ourselves; if we discover a trait that was previously thought to be ours alone, we declare monkeys capable of "human-like" reasoning rather than making the equally valid inference that perhaps our reasoning is, in fact, rather monkey-like. This means, too, that the traits whose pre-

cursors we seek are those we have deemed particularly important in terms of their cognitive demands and consequent need for brain power by direct inference from what we, as humans, are capable of producing. Our failure to consider looking up the chimney means we run the risk of overlooking other, ostensibly less impressive (because not uniquely human) skills that may well form the true building blocks to our particular kind of social intelligence. In addition, we run the risk of forgetting altogether that other species have evolutionary trajectories all of their own and may, therefore, have evolved some skills of their own as well. For example, chimpanzees may have a superior working memory to ours as a consequence of positive selection over the last six million years, and not because this is a skill that has been lost from our own lineage. Scientists commenting on these findings, however, have tended to view them as a way to understand something of our own evolutionary heritage (e.g., "elaborate short-term memory skills may have had a much more salient function in early humans than is present in modern humans, perhaps due to our increasing reliance on language-based memory skills." http://news.bbc.co.uk/1/hi/7124156.stm); the possibility that chimpanzees may have gained these skills over the course of their evolutionary history rather than humans losing them was not considered.

Second, an emphasis on "higher" cognitive skills like forward-planning,[44] formal reasoning,[47] and propositional knowledge,[48] which place an emphasis on the internal manipulation of symbols performed entirely in the head, means that we fail to appreciate the extent to which our behavior is influenced by our specific physical interaction with the world (It is "embodied",) and by the environmental context in which it occurs (It is "embedded" or "situated").[49–51] We assume instead that complex, intelligent behavior must (can only) be the result of possessing an equally complex set of cognitive mechanisms. Given this assumption of a direct one-to-one mapping between the complexity of behavior produced and the complexity of the proximate mechanism that produces it, it follows that any animal capable of complex behavior also must be in possession of a complex cognitive architecture. Except, of course, that it does not. There is no necessary relation between the complexity of a behavior and the complexity of the proximate mechanism that produces it.[51] Simple mechanisms can produce highly complex behavior as a result of the interaction between organism and environment. Building a termite nest is an immensely complex behavior, but an individual termite is not a psychologically complex animal. All a termite needs to know is how to make a ball of dirt, impregnate it with pheromone, and carry it around until it encounters other similarly

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impregnated balls of dirt and drop it next to them.

It is easy to see this with termites, of course, but for other organisms such as baboons, for example, it can be more difficult. Let us briefly return to biological market theory. The idea of a biological market is, of course, a metaphor; one whose value lies in allowing us to generate predictions that can incorporate the dynamic nature of partner choice as well as the fluctuations in the benefits that one individual can derive from another. There is no sense in which a baboon needs to understand that it is in a market, or to appreciate either its own market value or that of others, or understand in any overt manner the nature of its trading interactions. Yet, I have been asked many times how, for example, mothers know why, and how much, they should be paid for infant handling, and exactly how they work out the market value of their infants. This kind of view unnecessarily complicates matters. All that is needed to account for the baboons' behavior at the proximate level is the simple use of grooming as a tension-reduction mechanism: fewer available infants = greater harassment = higher tension = longer grooming times before mothers are sufficiently relaxed to permit handling. Mothers may well behave "as if" they know their market value, but the actual proximate driver of their behavior can be satisfactorily explained by a process of "affect induction"[52,53] and probably involves no cognitive assessment whatsoever.

This is a point worth emphasizing because a similar tendency to use, and over interpret, a metaphorical "as if" argument is pervasive in studies of primate cognition;[53] animals that show particular behavioral responses are interpreted to be acting "as if" they can, for example, hierarchically structure their relations[47] or make spontaneous inferences about rational action.[54] The mechanisms proposed, however, are as wholly metaphorical as a biological market, and are rarely supported by strong evidence for an actual proximate, psychological (or even physiological) mechanism. The potential over interpretation of our explanatory metaphors (or worse, our failure to recognize that we are doing so), combined with a lack of attention to how proximate mechanisms play out in real environ-

ments,[55] means that we continually run the risk of mistakenly attributing more complexity to the animals than is warranted, as well as overestimating the cognitive requirements of certain tasks. Two extremely powerful demonstrations of this effect are provided by work in robotics, where simple self-organizing processes that reflect the dynamic coupling between the organism and its environment can produce complex behavioral patterns in the complete absence of any central (brain-like) control (see Box 1).

The lessons offered by robot behavior should give us pause when we attempt to attribute particular "goals," and their supporting cognitive mechanisms, to animals, including ourselves. They highlight beautifully that the proximate means by which a behavior is produced need bear no relation whatsoever to the form that behavior takes (with respect to the didabots, who, for example, would imagine that a rule for object avoidance would be a good way to produce object clustering) and completely destroys any notion that there is, by necessity, a simple one-to-one mapping between the complexity of a proximate mechanism and the complexity of the behavior that it produces. (As the biorobotic rats show, body–world coupling can be sufficient to rule out the need for any specific control process.) If we take all this on board, then it is clear that a focus on the kinds of emergent, contingent "mind" that brains, bodies, and environments can achieve in concert may prove more productive than persisting with the idea that intelligence is achieved solely by raw brain power.

Although the subtext of this message is often interpreted as "so monkeys are stupid"; this could not be further from the truth. I do not doubt that primates are smart, behaviorally flexible animals, just as many other people do. Where I differ is in agreeing with those theorists who suggest that this smart, flexible behavior is not a property of individual brains securely bound by "skin and skull"[50] but an emergent property of a cognitive system that extends into the body and out into the world.[50,51] Primates' cognitive

systems do not consist of brains alone, but brains inside bodies that act in the world as mutually coupled dynamic systems. Smart behavior emerges through interaction and engagement with the environment (including other animals), and is not generated by internal brain processes in isolation.[50,51,53]

Note that these are, in fact, old ideas. The view that cognition, and psychological processes in general, are emergent phenomena that depend crucially on the interaction of an animal with its world was recognized long ago by von Uexküll and his idea of the umwelt;[56] that an animal's representation of the world (if indeed it represents it at all) will be shaped by, and grounded in, the means by which it perceives and acts in it. These perception–action mechanisms, in turn, reflect the kind of body it has and the kind of ecological niche it occupies.

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More recently, J.J. Gibson took a similar approach, which he characterized as "ecological psychology", to get across the idea that psychological phenomena were to be found in organism–environment relations, and not in the organism alone.[57]

The most crucial and important component of an ecological approach is the idea that organisms regulate their behavior with respect to the "affordances" of the environment.[57]

Affordances are the opportunities and possibilities for action that particular objects and resources offer to an animal. For example, we do not see "chairs" as such but places to sit; a chimpanzee does not see a "tree" but a place to climb. My suggestion here is that a stronger, more ethological focus on the affordances that other individuals offer will pay real dividends in understanding how animals regulate their social relations, by allowing us to consider how brain, body, and world combine to produce flexible, contingent behavior.

Elsewhere, I have considered how the baby-handling interactions of female baboons can be understood in precisely this fashion.[53,58] While this behavior has been interpreted as a cognitively driven process of "tactical deception" on the part of the handler (who grooms to hide the ulterior motive of infant handling from a reluctant mother),[59] or, as noted earlier, an equally cognitive recognition of a mother's market value, an analysis of the sequence of events that occurs in these interactions reveals how grooming of the mother reflects the handler's response to the specific affordances offered by the mother. That is, as the mother turns away from the handler to avoid her gaze and prevent contact with the infant, her back affords grooming and so the handler grooms, perhaps as much to reduce her own level of arousal as that of the mother.[58]

Infant handling, then, is about two individuals "bringing their behavior into coordination"[60] in a real-time, dynamic fashion: both grooming and handling are contingent responses that emerge from the interaction rather than representing its "goal".[60] Similarly, some very recent work on grooming patterns within family groups of cotton-top tamarins suggests something similar with respect to cooperative infant care.[61] In this study, expectant parents actively maintained affiliative interactions with their adult sons as a function of the quality of the allo-parenting services the sons had provided previously. While breeding females groomed the son that had provided the most care, sires invested more grooming in those sons that had pro-

Box 1: Robots Illustrate How to Keep It Simple and Let Complexity Emerge

A didabot is a small, wheeled robot, shaped somewhat like a toy car (Fig. B1).[67–69] When placed into an arena in which small cubes are scattered randomly, these robots move around clustering the cubes so that eventually there are usually only two large heaps, with a few cubes left here and there against the walls (Fig. B1). The robots are therefore known as "Swiss robots", because their aim, apparently, is to tidy up the arena. At a minimum, then, one might suppose that the robots are provided with mechanisms for finding single cubes, detecting the nearest cluster of cubes, and then being able to push the former towards the latter so it can deposit the cube alongside all the others. In fact, the robots have only one kind of sensor—for proximity—and they follow one simple "rule" that results from the manner in which they are wired: if sensory information is received on the left, then turn right, and if sensory information is received on the right, turn left. In other words, the robots are designed exclusively to avoid obstacles[67–69]. Why then does clustering occur? To understand this,

we have to move beyond the robot's internal structure and consider the specific nature of its embodiment and its interaction with the environment.

A didabot is fitted with two proximity sensors at the front end of the body, positioned at an angle. Consequently, as the robots move forward, they detect cubes off to the side, but not straight in front of them. This means that although they turn away and avoid cubes on either side, a cube directly in front of them is pushed along because the didabot cannot "see" it (i.e., its sensors received no stimulation from it).[67–69] If the didabot then encounters another cube off to the side, triggering its sensor, it produces avoidance behavior, moving off to the left or right, and leaving the object it has just been pushing next to the object it has just avoided. In other words, the didabot clusters the two cubes. This alteration in the environment then increases the chance that another cube, being blindly pushed around, is deposited in the vicinity because the cluster of two cubes is more detectable than is a single cube; a simple self-organizing process

explains the didabots' behavior and results in the formation of ever-larger clusters as well as generating the abiding impression in a human observer that the didabots are "trying" their best to "clean up".[67–69] Were we to interpret the didabots' behavior as reflecting the operation of this kind of proximate "clustering" mechanism, reflecting their "goal" of cleaning the arena, the explanation would be entirely erroneous: both inaccurate and incomplete. It is also important to note that the clustering behavior is entirely dependent on the placement of the sensors on the didabots' body: move one of the sensors around to the front, and the clustering behavior disappears entirely because now objects directly in front of the robots are avoided in the same way as those off to the side, which means that no pushing behavior occurs.

If one should doubt that robot cars really have anything to offer the study of real animals, work on rat pups has used exactly the same kind of reasoning and a similar kind of robot to investigate the patterns of huddling shown over the first few weeks of life.[70] Robot rats with a random

Figure B1. Example of clustering behavior by didabots. (a) Initially, the cubes are randomly distributed over the arena. (b) Over time, clusters begin to form. (c) By the end of the experiment, there are only two large clusters, with the remainder of cubes aligned along the walls of the arena. Reproduced with the permission of Rolf Pfeifer and the Artificial Intelligence Laboratory, University of Zurich.

control architecture were found to display patterns of behavior that were either intermediate between, or the same as, 7- and 10-day-old real rat pups (Fig. B2). Again, the "goal-directedness" of the robots' behavior results from the interaction of the geometry of their bodies and that of the arena in which the robots are placed. When a wall is contacted, the tapering nose of the robot leads it to slide along it, with the direction determined by the angle of approach. The options for other kinds of movement (that will get it away from the wall) are constrained by this contact, resulting in a high probability of wall-following ("thigmotaxis"). If the robot encounters a corner, the effectiveness of any other movement bar backing up becomes even more limited. Even this option is limited if other robot rats randomly encounter the robot in this position. As other agents press in from the sides, "huddling" and "corner burrowing" are seen, just as in real rat pups. Of course, this does not mean that real rat pups have only a random architecture but it does mean that rat pups need not be equipped with any dedicated sensorimotor routine or specific neural processor that produces thigmotaxic behaviour[70]; rather, and as Brooks[49] has long suggested, body and environment may be so tightly coupled and mutually constraining that no cognitive control at all is required to produce the behaviors seen.

Figure B2. Rat pups and robotic rats forming aggregation patterns. (a) 7-day-old pups and (b) robots shortly after they are released or started in the arena, (c) 7-day-old pups and (d) robots forming a subgroup; (e) 10-day-old pups and (f) robots forming two subgroups in opposite corners; (g) 7-day-old pups and (h) robots forming a group in a single corner. Reproduced with permission from Wiley-Liss Publishers.

vided the least. As Ginther and Snowdon noted, while these data are consistent with the idea that tamarins are responding to the memory of past allo-parenting performance and allocating effort accordingly, it also is possible that a simpler explanation can account for the patterns seen where the parents' response is contingent on the tension levels of their sons. Specifically, they suggested that sons that had previously done more carrying simply may have been more comfortable when in physical contact with the parents. Reduced tension may afford more grooming between mother and son, which serves to further increase the son's comfort around mothers, and so facilitate further care. Fathers, by contrast, may groom nonhelping sons as a means of reducing the sons' tension levels around the parents, which may result in an increased likelihood of infant care as a by-product of this attention. While these behaviors serve both parents' functional aims of ensuring one reliable helper (in the case of mothers) and increasing the total number of helpers (in the case of fathers), there is no need for either parent to have any knowledge that this is necessary. Equally, they do not need to retain a memory of a son's previous helping effort: the body postures, latencies to act, and willingness to remain in proximity are all that are required for grooming to be allocated effectively.[61]

Finally, as the didabots and robot rats made clear, the affordances of the physical environment should not be overlooked either. Variation in male baboon consortship behavior (specifically, the manner in which males are usurped from consorts), for example, has been shown to be a function of differences in the physical affordances of sleeping cliffs, where movements and social tactics are restricted, versus open ground, where animals can move freely and exploit several social tactics.[62] What this means is that an animal's behavior may vary in contingent, unpredictable ways because its surroundings channel behavior in particular directions, and not because the animal itself is weighing its options and switching strategies accordingly. Exactly the same suite of tactics may play out in entirely different ways depending on the specific environment in which they are enacted.[62]

Once we take the physical environmental into account, then, or pay closer attention to the actual sequencing of interactions between animals, we can see that baboons and tamarins may be rather more like didabots or robot rats and rather less strategically "Machiavellian" than we have often assumed.[62] As such, we should at least entertain the idea that the complex and flexible social behavior we see may be the product of a dynamic interaction between a set of fairly simple perception–action routines and a particular social and physical environment. Similar sentiments are echoed in related work on self-organizing behavior.[63] This, in turn, means that although the social environment might well create some unique challenges for primates, it does not do so in the way we have traditionally assumed.[53]

A constantly changing social environment naturally affords a shifting landscape of opportunities upon which an animal can seize. But to do so, its responses need not result from internalized, strategic abstractions. Rather, they can exist in the moment-by-moment attunement and adjustment of movement and activity that bring actors into and out of various fields of engagement.

If so, then we can hypothesize further that the proximate basis for primate social engagement may be a form of non-analytic pattern recognition.[51,53] Specifically, the juxtaposition of particular individuals, particular behaviors, and particular contexts can form the basis of an association matrix from which individuals can distill higher order associations that enable them to respond appropriately to novel situations. This kind of process (singular value decomposition followed by dimension reduction) has been shown to produce neural networks that can comprehend the semantic content of written text.[64] If associative processing can produce language comprehension—that most exalted of human abilities—there seems to be no reason why similar associative processes should not give rise to behavior that has the functional appearance of sophisticated, strategizing representational cognition, but which is, in reality, driven wholly by the perception of concrete observables in an ongoing process of pattern recognition and completion.[53]

One of the problems with large-scale associative pattern recognizers, however, is that compared to representational mechanisms, they are tissue-intensive and require a lot of connectivity to implement. As noted elsewhere, this is, in fact, a strength of an associative pattern-recognizing hypothesis and not a weakness:[51,53,65] the empirical data to be explained are the vast amounts of neural tissue that primates possess compared to other mammals, not the complicated cognitive structures used to solve their problems. There are, in fact, no empirical data to support the existence of the latter; they are merely inferred from the vast quantities of brain tissue and the complexity of behavior seen. While evolution is cost-effective, as Humphrey[44] originally argued, this does not mean that it also must be an exceptionally efficient process, as we also assume. Convoluted, messy solutions may be both necessary due to inherent, physical constraints on neuronal functioning, and made possible by the fact that evolution is liberated by having the time in which

to come up with nonobvious, but effective, solutions.[42]

With this as a new working hypothesis, it becomes apparent that Humphrey's metaphor of the chess game does a poor job of characterizing the demands of primate social life. Instead, if one wishes to view life as merely a game, then a better option is the jigsaw puzzle.[53] There is almost no value in planning ahead or representing the completed picture when doing a jigsaw puzzle, and there is no need to check ahead for possible "downstream" effects. Instead, jigsaw puzzles are solved by a process of local pattern recognition and completion; one that is performed partly in the head and partly in the world, as one physically sorts, rotates, and moves the different pieces. One starts simply by joining complementary pieces and thereafter responds dynamically to the particular local patterns that appear. In the words of David Kirsh,[66:169] a jigsaw puzzle is "perceptually hard but intellectually simple…given a tile and an existing layout, the situation wholly determines whether or not the tile can be correctly placed." The irony here, of course, is that Grand Masters play chess like the rest of us solve jigsaw puzzles: they recognize patterns, having learned to distinguish those that require one kind of response from those that require another. They act both in the world and in the moment, needing no analysis or comparison of alternatives, and no looking ahead. Baboons may meet the challenges of their social world in a similar way, through dynamic contingent responses to an ever-shifting landscape of social perceptions that mirror the dynamic, contingent responses that baboons as a species have made to the ever-shifting landscape of natural selection. Contingency, then, is the key to baboons, and baboons, in turn, may be the key to a more fully rounded understanding of the contingent, dynamic nature of evolutionary, social, and cognitive processes.

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