



Primate Innovation: Sex, Age and Social Rank Differences

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Analysis of an exhaustive survey of primate behavior collated from the published literature revealed significant variation in rates of innovation among individuals of different sex, age and social rank. We searched approximately 1,000 articles in four primatology journals, together with other relevant databases, for examples of innovation. The reported incidence of innovation is higher in males and adults, and lower in females and nonadults, than would be expected by chance given the estimated relative proportions of these groups. Amongst chimpanzees, the only species for which there are sufficient data to consider alone, there is a similar sex difference in the propensity to innovate, but no effect of age. Chimpanzees of low social rank are reported as innovators more frequently than high-ranking chimpanzees are. Male chimpanzees innovate more often than females in sexual, courtship, mating and display contexts; that is, in contexts likely to increase access to mates. The largest number of recorded observations are in the foraging context, wherein contrary to expectations, there is no evidence for female chimpanzees exhibiting more innovation than males. The study is the first extensive investigation of behavioral innovation in primates and provides evidence that much individual variation in the propensity to innovate can be explained in terms of sex, age, and social rank.

KEY WORDS: innovation; social learning; sex differences; social rank; behavioral plasticity.

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INTRODUCTION

Primates are renowned for behavioral innovation: the ability to respond to novel circumstances or stresses with new behavior patterns (Kummer and Goodall, 1985; Lee, 1991). Well-known examples include the washing of potatoes and wheat by Japanese macaques, (*Macaca fuscata*: Kawai, 1965), tail-drinking in ring-tailed lemurs, (*Lemur catta*: Hosey *et al.*, 1997), dipping Acacia pods to access tree exudate in vervet monkeys, (*Chlorocebus aethiops*: Hauser, 1988), and the use of empty cans by a male chimpanzee (*Pan troglodytes*) to augment his threat displays (Goodall, 1986). Innovation is an important component of behavioral plasticity, vital to the survival of individuals in primate species with generalist or opportunistic lifestyles, and potentially of critical importance to endangered or threatened species that are forced to adjust to changed or impoverished environments (Box, 1991; Lee, 1991; Lefebvre *et al.*, 1997). Moreover, the acquisition of information via innovation and the social transmission of innovations is widely assumed to have significant fitness consequences and ramifications for the invasion and construction of new niches, and so may have important evolutionary repercussions (Lee, 1991; Laland, 1992; Laland *et al.*, 1996; Sol and Lefebvre, 2000). Innovator identity may be an important determinant of the dynamics of social transmission (Laland and Reader, 1999b). Yet, in spite of its relevance to several research and conservation issues, virtually nothing is known about which individuals invent new behavior patterns and what ecological variables influence innovation (Kummer and Goodall, 1985; Box, 1991; Lee, 1991; Laland and Reader, 1999a).

We investigated which individuals are primarily responsible for innovation in the nonhuman primates, focusing on sex, age and social rank differences. We define innovation as the discovery of novel information, the creation of new behavior patterns, or the performance of established behavior patterns in a novel context. This definition is deliberately broad, as we regard research into animal innovation to be at too preliminary a stage to justify a more precise definition (Laland and Reader, 1999a). Nonetheless, we recognize that our use of the term may incorporate quite heterogeneous processes. Innovation and exploratory behavior may provide benefits such as novel food sources or more efficient foraging techniques, but are often energetically costly and may incur risks such as predation or exploiting poisonous foods (Bandura, 1977; Johnston, 1982; Hart, 1993; Milinski, 1993). Given the potential hazards, it is likely that innovators will commonly be individuals for which the current prevailing risk-averse foraging strategies are unproductive, and that are driven to search for alternatives, perhaps incurring some risk. The adage “necessity is the mother of invention” may apply

to animal innovation, with poor competitors driven to innovate (Laland and Reader, 1999a; 1999b).

Poor competitors may include low-ranking individuals, small individuals, nonadults, or females in species with a large degree of size dimorphism. Several authors have predicted or stated that young individuals are more likely to innovate than older individuals are (Kummer, 1971; Kummer and Goodall, 1985; Hauser, 1988). Social rank is positively correlated with foraging success and the ability to appropriate desirable food in several primate species (Goodall, 1986; Silk, 1987). Moreover, a small number of primate studies appear to indicate that innovators are frequently low in social rank, or poor competitors on the outskirts of the social group (Kummer and Goodall, 1985). For instance, Sigg (1980) found that peripheral female hamadryas baboons were significantly better at learning novel tasks than central females were.

In species where female but not male fecundity and reproductive success are closely linked to foraging success, females may show greater levels of foraging innovation than those of males, since innovation is likely to allow individuals to access new food sources or to obtain familiar food in new, or more efficient ways (Laland and Reader, 1999a; 1999b). Many primate species are sexually dimorphic in body mass, with males often larger than females, which may result in males being able to monopolize the most accessible food resources (Bean, 1999), and driving females to alternative tactics. For example, several researchers reported that female primates, particularly chimpanzees, use tools more than males do (Boesch and Boesch, 1981, 1984; Hannah and McGrew, 1987; Boesch, 1999). In capuchins, males can use their teeth to open nuts that females and juveniles cannot open without tools (Fragaszy and Visalberghi, 1989). However, different processes may underlie the initial invention of a tool-using skill, and their current utility in a population.

Conversely, in species where in male but not female reproductive success is limited by access to mates, males might show more innovation than females in contexts linked directly or indirectly to mating success, such as sexual or courting behaviors (Laland and Reader, 1999a). High social rank in many male primates could be linked to increased reproductive success, though conclusive proof is pending upon genetic paternity data (Nishida and Hiraiwa-Hasegawa, 1987; Silk, 1987). For example, Gombe chimpanzee Figan repeatedly monopolized matings with select females during their peri-ovulatory periods while he was the undisputed alpha male (Goodall, 1986). Male chimpanzees use display to establish dominance, and also display to females before leading them away from the group, where mating is presumably less likely to be disturbed (Goodall, 1986). Display in chimpanzees and in many other species may be more directly linked to increased

reproductive success in males than in females. Thus, we predict that in the display context, and the sexual, mating and courtship context, there will be a higher incidence of innovation in males, and a lower incidence in females, than that expected by chance.

As mating systems and ecology are highly variable among the primates (Smuts *et al.*, 1987; Dixson, 1998), they represent a useful taxonomic group for comparative studies on the relationship between individual differences in the propensity to innovate, the context of the behavior pattern, and life-history variables. Ideally, we would be able to make a specific set of predictions for the patterns of innovation in each species, depending on the idiosyncrasies of their ecology and life history, and so conduct a traditional comparative analysis (Harvey and Pagel, 1991). Unfortunately there are currently insufficient data to render such an analysis tenable. Instead, we tested hypotheses concerning the type of differences that might be expected across all primates, and examined more specific hypotheses on differences within contexts in the one species with a sufficiently large data set, *Pan troglodytes*.

In summary, we predict that in sexual, courtship, mating and display contexts, more instances of innovation will occur amongst males than females, while females will be more innovative than males in the foraging context. In general, low-ranking individuals will innovate more than high-ranking individuals, and nonadults will innovate more than adults; except in sexual and display contexts in which nonadults will be less innovative than adults are.

METHODS

We searched approximately 1000 articles in 4 primate journals for examples of innovation. We read the abstract of each article, and read the full text of all articles concerning the behavior of nonhuman living primates. The volumes examined were *Primates*, 32–38 (1991–1997), the *American Journal of Primatology*, 39–41 (1996–1997), *Folia Primatologica*, 15–68 (1971–1997) and the *International Journal of Primatology*, 17–18 (1996–1997). Where a complete set of issues were not available (*Folia Primatologica*), we simply examined available ones. We also searched our personal libraries of social learning literature for behavior patterns described as innovation. We included examples cited in the text of articles, with the final database carefully checked to remove redundancy. Like Lefebvre *et al.* (1997; 1998), we used keywords such as novel or never seen before to classify behavior patterns, so that the judgement of whether they qualified as examples of innovation was that of the author(s) of the article. This approach aims to avoid subjective bias by us during data collation. We noted data on the sex, age or social rank of the individual innovating when available, along with the context, e.g.

foraging, infant care, in which the behavior occurred. We recorded context via an overtly arbitrary categorization scheme which covered most of the innovations observed. When several species were noted to perform the same behavior, we scored it for each species. To maximize the size of the data set, we recorded all episodes, whether they occurred in captivity or in the field, as a result of experimental manipulations, or as a result of human intervention such as provisioning or habitat degradation. It was not our intention to make a complete survey of the huge primate literature, but instead to collect a representative sample of primate innovation. There probably are examples of innovation in other journals, though our rate of locating new instances of innovation decreased as our survey continued, as we found more innovations already cited in previously examined articles.

Whiten and Byrne (1988; Byrne and Whiten, 1992; Byrne, 1993) collected opportunistic observations of tactical deception, and advocated such an opportunistic approach when the behavior of interest is rarely performed. They emphasized that the reports were not uninformed casual observations or anecdotes but instead came from experienced scientists familiar with their subjects. A similar assertion applies to the methods described here. However, Byrne and Whiten (1992) cautioned that in such exercises there is no way to dissociate the tendency for scientists with particular interests, such as deception, to study groups that they consider appropriate. Thus the collected data may still be vulnerable to biases.

To determine whether particular groups were more likely to innovate than others were, we compared the data with observations expected if all individuals exhibited equal propensities to innovate. We calculated expected values for each species from the relative proportions of the population belonging to each class. We summed values across species and tested for significance via chi-square tests. Summing over species should result in a measure unaffected by phylogeny. When one species contributed a large number of observations to the data set, e.g. chimpanzees, we re-analysed the data with them removed. Usually we conducted no test when expected values were small (<5). Occasionally, we relaxed this conservative position, e.g. when a test was particularly interesting, since power, rather than inflated type I error rate, is likely to be a problem with small samples (Howell, 1997). Small samples meant it was typically impossible to analyze differences in individual species, except chimpanzees, for which the sample sizes were often large.

Authors typically described individuals as infant, juvenile, adolescent, subadult or adult, but we lumped infants, juveniles and adolescents as non-adults. Most researchers did not give details of group size or number in each age or sex category, so we estimated them from data on group composition. For example, data are available on the mean group size of monogamous primates (Dixon, 1998), so by assuming that their groups consisted of one

adult male and one adult female with the remainder of the group made up of nonadults (Dixson, 1998), we calculated the mean proportion of nonadults in the group. In species with polygynous mating systems, the group is typically made up of one adult male and ≥ 2 adult females. When data were available we calculated the mean number of nonadults in the group. Group composition data for species with multifemale-multimale mating systems are from Dixson (1998), and we used further data on sex ratios and group composition from chapters in Smuts *et al.* (1987). We collected data for 69 species, with the mean (\pm SE) proportion of nonadults calculated as 0.47 ± 0.02 .

We calculated adult sex ratio for each species as the mean of values in Dixson (1998), Mitani *et al.* (1996), Masters *et al.* (1982; 1993) and Smuts *et al.* (1987). When values for several subspecies or groups were available, we took the average as the mean value for the species. When data were available for a group over several years, we took the average as the group mean. Rowe (1996) presents sex ratio data for primates but does not specify whether they are adult sex ratios. We used this source to estimate missing values. In total, we gathered sex ratio data for 84 species. Mean (\pm SE) adult sex ratio is 2.30 ± 0.23 females per male. In most primate species, the birth sex ratio approximates parity (Dunbar, 1987), so birth sex ratio is often a poor guide to group composition (Goodall, 1986). We used the observed proportions of nonadult and adult innovators to estimate the numbers of each sex that would be expected to innovate by chance.

Amongst adults, we used the estimated adult sex ratio to calculate the expected values for males and females. For nonadults, we assumed the ratio of males to females was 1:1. Inspection of the data had shown this to be a more conservative position than assuming the nonadult sex ratio parallels the sex ratio among adults, an assumption that might underestimate the expected number of male observations. When chimpanzees were analysed separately, we used the observed proportions of chimpanzee nonadult and adult innovators to calculate expected values for each sex. In a few cases there were sufficient data on both the age and sex of individuals to conduct an analysis of sex differences amongst adults without the assumptions described above.

We calculated expected values for each species, summed them across species, and compared them with the summed observed value via chi-square tests. When a large number of statistical tests were conducted on one data set, we adjusted α per Howell (1997): set as the desired familywise error rate (0.05) divided by the number of comparisons. We considered data on age and sex separately for the purposes of setting familywise error rates because researchers frequently reported either the age or sex of the innovator but not both. We calculated power estimates when negative results would be particularly informative. We used two estimates of effect size for power

estimates: Cohen's (1988) medium effect size ($w = 0.3$) and the effect size in the most similar, independent analysis. For example, in analysis of the effect of rank, we used the effect size in chimpanzees to estimate the effect size for other primates. Accordingly, power estimates are presented as a range, representing the estimates of power calculated via the two effect sizes.

Interobserver Reliabilities

A second observer coded previously-examined issues of the journals *Folia Primatologica* and *Primates*. We calculated interobserver reliabilities for 241 records, i.e. approximately 10% of the total number of records examined, with agreement between the two observers calculated as an index of concordance (Martin and Bateson, 1986). The interobserver reliability for innovation is 0.83. The two observers agreed on the context of the behaviour 90.9 % of the time. The observers always agreed on the age category or sex of the innovating individuals.

RESULTS

In total, we recorded 533 instances of innovation from a total of approximately 2000 records and 1000 journal articles searched. Figure 1 reveals that

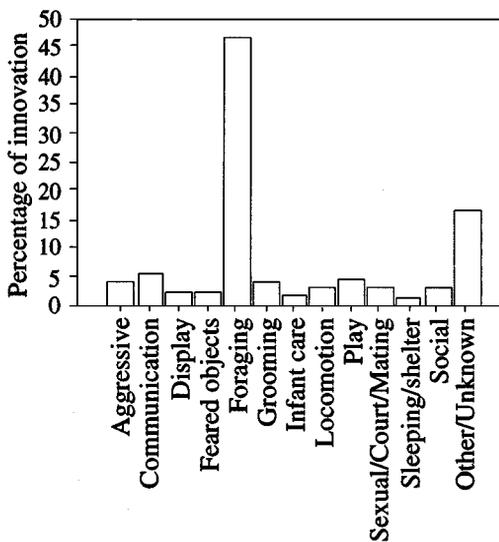


Fig. 1. The relative number of observations of innovation.

Table I. Examples of innovation with the species involved indicated in parentheses

Context	Example	Reference
Aggressive	Use of a club to attack a snake (<i>Cebus capucinus</i>)	Boinski, 1988
Communication	New gesture inviting infant to be carried (<i>Papio hamadryas papio</i>)	Kummer and Goodall, 1985
Display	Cans used to make noisy dominance display (<i>Pan troglodytes</i>)	Goodall, 1986
Feared objects	Special rattlesnake alarm call (<i>Macaca fuscata</i>)	Rowe, 1996
Foraging	Capture live fish from drying desert pools (<i>Papio hamadryas ursinus</i>)	Watanabe, 1989
Grooming	Rub peat into pelage (<i>Cebus capucinus</i>)	Ludes and Anderson, 1995
Infant care	Carrying infant by brother (<i>Hylobates pileatus</i>)	Geissmann and Braendle, 1997
Locomotion	Use nest as bridge to cross river (<i>Pongo pygmaeus</i>)	Galdikas, 1982
Play	Rolling snowballs (<i>Macaca fuscata</i>)	Eaton, 1976
Sexual/Courtship/Mating	Unique courtship display-flip upper lip over nostrils (<i>Pan troglodytes</i>)	Kummer and Goodall, 1985
Sleeping/Shelter	Roost in powerline masts (<i>Papio hamadryas anubis</i>)	Kummer, 1971
Social	Shows play face when being charged (<i>Pan troglodytes</i>)	Goodall, 1986

many more instances of innovation occurred in foraging contexts than any other; they constitute nearly half of all cases. Sex of the innovator is known in 178 instances, age in 110 instances and social rank in 42 instances. Table I illustrates the range of examples of innovation that we collected, with examples of each context.

Comparatively few researchers mentioned the ecological context in which innovation occurred, but innovation was prompted by ecological challenges, such as periods of food shortage, dry seasons, or habitat degradation, in 17 of the 36 cases where data are available. This raises the possibility that changes in the environment may precede much primate innovation (Hauser, 1988; Lee, 1991). There were also many examples of innovations in provisioned or captive populations, as predicted by Kummer and Goodall (1985).

Sex and Age Differences

Among the 42 species with examples of innovation, we could analyze 22 of them for sex differences, that is to say, data were available on both

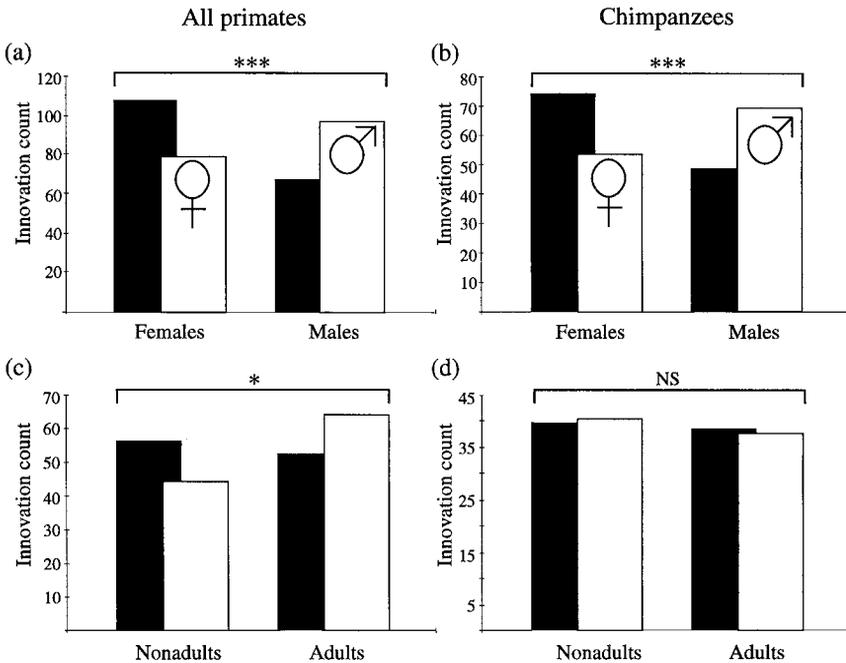


Fig. 2. Class differences in primate innovation. Solid bars indicate expected values, open bars indicate the observed innovation count. Sex differences for (a) all species combined (including chimpanzees) and (b) *Pan troglodytes* only. Age differences for (c) all species combined (including chimpanzees) and (d) *Pan troglodytes* only. Asterisks indicate the significance of the difference from the values expected by chance (NS not significant, * $p < 0.05$, *** $p < 0.005$).

the sex of the individuals innovating and the population sex ratio for the species. We analyzed 17 species for age differences and 16 species for sex and age together. We conducted 7 statistical tests on the innovation sex data, so alpha was set at 0.007. Tests examining sex differences with $p < 0.007$ are significant. Alpha remained at the usual value of 0.05 for other tests.

Figure 2a illustrates that across all primates there is a greater incidence of innovation in males and a lower incidence of innovation in females than would be expected by chance, given the sex ratio of the species studied (Chi-square test, $\chi^2_1 = 20.16$, $p < 0.005$). A similar sex difference occurs when adults are analysed separately (Chi-square test, $\chi^2_1 = 14.69$, $p < 0.005$). Analysis assuming an even sex ratio in the calculation of expected values results in a χ^2 value of 1.82, a nonsignificant difference, which emphasizes the importance of accurate sex ratio data. There was no interaction between sex and age (Chi-square test, $\chi^2_1 = 1.00$, $p > 0.1$). There is a similar sex difference in chimpanzees (Figure 2b), with more instances of innovation

in males and fewer instances in females than expected by chance, given the sex ratio of chimpanzees (Chi-square test, $\chi_1^2 = 15.12$, $p < 0.005$). The sex difference in the propensity to innovate across all nonhuman primates is weakened by the removal of chimpanzees from the data (Chi-square test, $\chi_1^2 = 2.98$, $p < 0.1$), but when adults are analyzed separately, the sex difference is significant, with a greater incidence of innovation in males and a lower incidence of innovation in females than would be expected by chance (Chi-square test, $\chi_1^2 = 9.83$, $p < 0.005$).

Figure 2c shows that across all primates there are more instances of innovation in adults and less in nonadults than expected by chance, given the proportions of adults and nonadults in populations of the species analyzed (Chi-square test, $\chi_1^2 = 5.11$, $p < 0.025$). There is no significant difference between the rate of innovation in adults or nonadults from that expected by chance in chimpanzees (Figure 2d, Chi-square test, $\chi_1^2 = 0.04$, $p > 0.1$, power = 0.76 to 0.99, effect size estimated from effect of age on innovation in non-chimpanzees, $\alpha = 0.05$), when the proportion of nonadults is 0.51. The effect of age is stronger after chimpanzees are removed from the all-primate analysis (Chi-square test, $\chi_1^2 = 21.18$, $p < 0.005$).

We also conducted analyses on a restricted data set, examining only instances of innovation from the field when there was no provisioning or experimental manipulation. We treated this set of analyses separately from those on the full data set for the purpose of setting alpha, which remained at 0.05. There is a similar pattern of sex differences in this restricted data set to that of the full data set, with more instances of innovation in males and fewer in females than would be expected by chance (Chi-square test, $\chi_1^2 = 7.71$, $p < 0.01$). This pattern persists when chimpanzees are analyzed separately (Chi-square test, $\chi_1^2 = 2.80$, $p < 0.1$), and with chimpanzees excluded from the analysis (Chi-square test, $\chi_1^2 = 3.12$, $p < 0.1$), though the tests do not reach statistical significance. We found no significant age difference in the reduced data set (Chi-square test, $\chi_1^2 = 1.80$, $p > 0.1$), which may reflect a bias in the full data set resulting from the skewed demography of captive populations. However, as for the full data set, the effect of age is stronger after chimpanzees are removed from the analysis, with more innovation in adults and less in nonadults than would be expected by chance (Chi-square test, $\chi_1^2 = 4.73$, $p < 0.05$). When we analyzed chimpanzees separately, we found more nonadult and fewer adult innovators than would be expected by chance (Chi-square test, $\chi_1^2 = 8.69$, $p < 0.005$), an age difference that is absent from the full data set. These findings suggest the age effect is probably robust in primates other than chimpanzees, with adults more innovative than nonadults are, but that a different pattern may be characteristic of chimpanzees.

Table II. Social rank differences in nonhuman primate innovation. Figures represent the number of observations where the social rank of the individual innovating was indicated

RANK	Chimpanzees	Other primates	All primates
High	7	5	12
Low	22	8	30
Total	29	13	42

Social Rank Differences

In all cases where the innovator rank was known, he or she was either referred to as dominant or high-ranking, or as subordinate or low-ranking, that is, there was no reference to mid-ranking individuals. The lack of reports of innovation by mid-ranking individuals is likely to reflect authors simply categorizing individuals as either of high or low rank, rather than a lack of innovation amongst mid-rankers, though we address this issue below. Table II shows the number of incidences of innovation among the social ranks of chimpanzees, other primates, and all primates combined. Social rank is often confounded with age, particularly among male primates, with younger individuals typically lower in the dominance hierarchy (Goodall, 1986). We could not eliminate this confound.

Social rank in primates is commonly defined so that equal numbers of individuals are classified as high-ranking and low-ranking, though there is no consensus as to how these terms should be employed, and usage varies across species. If we assume that individuals of low versus high social rank might be expected to be responsible for half of the incidents of innovation, more low-ranking chimpanzees and fewer high-ranking chimpanzees innovated than expected by chance (Chi-square test, $\chi_1^2 = 7.76$, $p < 0.01$). Among other nonhuman primates there is no significant effect of rank (Chi-square test, $\chi_1^2 = 0.69$, $p > 0.1$). However, the power of the latter analysis is extremely low (power = 0.20 to 0.48, effect size estimated from effect of social rank on innovation in common chimpanzees, $\alpha = 0.05$) so conclusions on social rank effects amongst them should be drawn with caution.

Alternatively, we could assume that one third of reported innovations would be expected in each of the three categories of high, middle and low social rank. That is, we assume that authors did not report mid-ranking innovators because there is no observation of them innovating. We then found a significant effect of social rank in both chimpanzees (Chi-square test, $\chi_1^2 = 26.15$, $p < 0.005$), and in the other primates (Chi-square test, $\chi_1^2 = 7.54$, $p < 0.025$). In both chimpanzees and other primates, there are more reports of innovation amongst individuals of low social rank, and fewer among mid-rankers, than would be expected by chance.

The Context of Innovation

We were only able to conduct an analysis of the context of innovation in chimpanzees, in which the female-to-male adult sex ratio is 2.38:1 and the proportion of nonadults is 0.51. Sample sizes are small, but by summing across contexts in which the same prediction was made, some analyses were possible. Contrary to predictions, in the foraging context there are more instances of innovation in males and fewer in females than expected by chance, though the difference is not statistically significant (Chi-square test, $\chi_1^2 = 5.76$, $p < 0.025$). We summed the data for display, sexual, courtship and mating contexts since in all cases males were predicted to show a higher propensity to innovate. As predicted, males innovated more than expected by chance (Chi-square test, $\chi_1^2 = 11.34$, $p < 0.005$). Sample sizes for sex differences in other contexts and for age differences are too small to allow statistical analysis.

DISCUSSION

We describe variation between sex, social rank and age classes in the propensity to innovate among nonhuman primates. In summary, there were more recorded observations of innovation in adult and male primates and fewer in nonadults and females, than would be expected by chance given their relative proportions. These findings are contrary to predictions, given that the largest number of observations are in the foraging context. There is a similar sex difference in the propensity to innovate among chimpanzees, but there is no significant effect of age. A greater than chance incidence of innovation occurs in low-ranking chimpanzees. As predicted, there are more reported instances of innovation in sexual and display contexts in male chimpanzees, and fewer in female chimpanzees, than expected by chance. Contrary to expectations, there is no evidence that female chimpanzees are innovators in the foraging context more frequently than would be expected by chance.

We emphasize the results can only be as good as the data set on which they are based. Classifications of behavior patterns such as innovation were made by the primary observers, which should minimize the likelihood of subjective bias imposed by us during data collection. However, reporting biases on the part of the original investigators cannot be controlled for. Equally, the findings rest upon accurate estimates of the specific demographics that we used to calculate the distribution of observations between age and sex classes that would be expected by chance. Biases in these estimates, such as an under-reporting of males in group compositions, would also affect the

findings. With these considerations in mind, perhaps the most interesting aspect of the findings is that, in several cases, the results run contrary to predictions and to the typical stance of the very literature from which the data were gathered. We will discuss possible reasons for these discrepancies.

Between-Sex Variation

A surprising theme to the results is the higher than expected incidence of innovation among male versus female primates. At first glance, the primate literature gives the impression that innovators are more likely to be females than males. It is possible that this impression is misleading, and based on a small number of high profile cases. Perhaps the most famous nonhuman primate innovator, Imo, a potato-washing macaque, was female (Kawai, 1965), and several heavily cited examples of cultural transmission in macaques describe behavior patterns that initially spread to the peers and mothers of the innovators, leading to more adult females acquiring the behavior than adult males did (Kawai, 1965; Kummer and Goodall, 1985). Hauser (1988) described how the eldest, highest-ranking female was the first to use a pod-dipping technique to access exudate in a time of drought, and Tsumori (1967) found that adult female Japanese macaques paid more attention to a buried-peanut task than males did. Box (1991; 1997) provided examples of increased investigation by females, noting that females of some species appear more adaptively responsive to environmental change than males do. However, Box (1997) also noted that captive adult female marmosets and tamarins demonstrate priority of access to food over males, which may lead to the false impression that female callitrichids are more investigative than males are. Female chimpanzees use tools more frequently and more efficiently than males (McGrew, 1979; Hannah and McGrew, 1987; Boesch, 1991), even after carefully accounting for female-biased adult sex ratios (Boesch and Boesch, 1981; 1984), though in a recent survey of published literature Reader (1999) found no evidence for sex differences in primate tool use. Famous male innovators and tool users, such as Kanzi the stone tool-making bonobo (Toth *et al.*, 1993; Lewin, 1995) and Sultan the box-stacking chimpanzee (Köhler, 1925), were presented with tasks in captivity, and so do not contribute to the impression that innovation in the wild tends to be carried out by females. In several cases, females are thought to be innovative because a larger proportion of females than males have acquired the novel behavior, not because a female was seen to invent the technique. The sex difference responsible for greater female use of tools and novel skills may be more related to capacity for social learning, motivation to acquire tasks from the innovator, or some other factor, than innovation itself.

If male primates do indeed exhibit more innovation than that of females this might suggest that innovation is more beneficial, or less costly, to male primates. Male primates are often larger than females (Bean, 1999). This may provide them with a foraging advantage over females because they can displace smaller individuals during feeding competition or exploit food sources that require physical strength to access, but males may require more food than females do, and foraging activities, such as climbing trees, may be constrained in heavier-bodied animals (Bean, 1999). Accordingly, male primates may be more induced than females to access food in novel ways. An additional possibility is that males might be generally less risk-averse than females are, and so more likely to exhibit novel, unusual or untried behaviors. Sex differences in personality traits could evolve if a risk-taking strategy has greater marginal fitness payoffs in males than in females. The benefits of innovation may be one such example of a fitness payoff, but other selective pressures for risk-taking among males could also be responsible.

We should bear in mind that there are biases in the data that could be responsible for the finding of proportionally more innovation in males than in females. For example, males may be more easily observed than females (Boesch and Boesch, 1981), researchers may attend to male behavior more per individual in the population because females typically outnumber males, male innovation may be more obvious, captive studies may be biased towards the study of males, or estimates of sex ratios may be inaccurate. Pooling results across species may obscure sex differences within each of them (Bean, 1999). A sufficiently large data set would allow the question of the influence of sex on innovation to be addressed more adequately, by examining the relationship between specific lifestyles and innovation frequencies via comparative approaches such as independent contrasts or maximum likelihood (Harvey and Pagel, 1991; Pagel, 1999).

We do not believe we have the data necessary to extrapolate from our findings to humans, in whom we expect additional processes may be operating. It would be both premature and injudicious to generalize from our early findings and to speculate about patterns of innovation in *Homo sapiens*. In fact, such speculations are unnecessary, as there already exists a comprehensive literature on technological and behavioral innovation in humans (Rogers, 1995; Sulloway, 1996). Rogers (1995) argued that technological innovators have a characteristic personality type. Innovators constitute approximately 2.5% of the population, and they are typically well-educated, risk-loving nonconformists. Sulloway (1996) argued that much of the variance in receptivity to novel ideas can be explained by birth order, suggesting that most innovations in science, especially radical ones, have been initiated and championed by laterborns. In humans, males show more risk-taking and thrill-seeking behavior than females do (Daly and Wilson, 1983), perhaps

leading to apparently innovative acts. Contrarily, we found few examples of innovative behaviors that we would describe as thrill-seeking in our survey of nonhuman primates.

Variation Between Social Ranks

Social rank differences in the propensity to innovate are fairly intuitive. We predicted that animals would be more innovatory in contexts that are closely linked to reproductive success, where established risk-averse behavior patterns are unsuccessful. For example males whose position in the dominance hierarchy restricts their access to mates may be expected to use novel methods to elicit matings. As predicted, low-ranking chimpanzees performed the majority of innovations. There is no report of innovation by mid-ranking primates, which is likely an artefact of researchers broadly categorizing innovators as either high or low, with no medium social rank. We urge future collection of precise field data on innovator identity, since this would avoid confusion over whether the missing reports of mid-ranking innovation are an artefact. We could be neglecting the interesting finding that among chimpanzees and other primates, mid-ranking individuals innovate less than expected by chance. Group life affects and constrains subordinates most, so low-ranking primates might have been forced to ‘make the most of the genetic predisposition for intelligence and learning’ (Kummer and Goodall, 1985, p. 204). Kummer and Goodall (1985) cite experimental studies of macaques as evidence for the greater learning abilities of low-rankers, where subordinates made fewer errors learning a buzzer task or mastered a reversal learning task quicker than dominants did (Strayer, 1976; Bunnell *et al.*, 1980; Bunnell and Perkins, 1980). Sigg (1980) also found that peripheral female hamadryas baboons, which tend to be low-ranking, outperformed central females in learning to use painted markers to locate food and in remembering the location of water that they had observed being buried in the ground. Such studies support the argument that necessity drives animals to innovate (Laland and Reader, 1999a).

Age Differences

Our finding that innovation is more common in adults and less common in nonadults than would be expected by chance runs counter to contemporary thinking. Several authors have presented anecdotal evidence or have suggested that young individuals are more likely to be innovatory. For example, Kummer and Goodall (1985, p. 209) state that ‘many innovations

appear during childhood when a youngster is cared for and protected by its mother and thus has much time for carefree play and exploration', and Hauser (1988) reported that newly observed behaviors are first recorded in young animals in most cases of invention and transmission in nonhuman primates. Whiten and Byrne (1988) suggested that social play is important in the discovery of deceptive techniques, and Laland and Reader (1999a; 1999b) argued that individuals of poor competitive ability, which may include juvenile primates in some species, may be forced to access resources in novel ways. Surprisingly we found no support for these views.

The greater than expected extent of adult innovation may be because innovation frequently builds on other skills, and requires a degree of experience or competence that is more common in adults than in younger primates. Hauser (1988) also suggested that older individuals innovate because they are most experienced and that experienced individuals are sources of knowledge for the group that are potentially important in times of stress. There has been little experimental work in this area, but Cambefort (1981) demonstrated experimentally that in chacma baboons new foods were discovered by juveniles and transmission throughout the group was rapid, whereas in vervet monkeys all age classes participated in the introduction of new habits into the troop, but transmission was slower. In both species most transmissions were among juveniles and from juveniles to adult females. Cambefort (1981) related these age class differences to social structure, with young baboons, but not vervets, foraging separately from the remainder of the group. Cambefort (1981) argued that strong group cohesion appears to promote fast propagation.

In conclusion, our study is the first extensive comparative investigation into behavioral innovation in primates, and provides evidence that sex, age, and social rank may account for much individual variation in the propensity to innovate. However, it is clear that much more work needs to be done if the sometimes surprising findings that emerge from our analyses are to be confirmed, in particular, to allow innovation to be considered on a broad comparative basis. We hope that our study will spur other researchers to record further data on the perpetrators, context, and functions of primate innovation.

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