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Phil. Trans. R. Soc. Lond. B 1985 **308**, 203-214
doi: 10.1098/rstb.1985.0020

Phil. Trans. R. Soc. Lond. B **308**, 203–214 (1985) [203]
Printed in Great Britain

Conditions of innovative behaviour in primates

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Innovative behaviour achieved through exploration, learning and insight heavily depends on certain motivational, social and ecological conditions of short duration. We propose that more attention should be given to what these conditions are and where they are realized in natural groups of non-human primates. Only to the extent that such favourable conditions were frequently realized in a social structure or an extraspecific environment could selective pressures act on innovative abilities. There is hope that research into field conditions of innovative behaviour will help to identify its selectors in evolution.

Part 1 (H. Kummer)

Introduction

The motive of this paper is that we almost completely lack an ecology of intelligence. No other dimension of behaviour has so systematically *not* been studied in the field.

The major selection pressures that made the order of primates into specialists for mental flexibility have been the subject of some speculation. Chance & Mead (1953) seem to have been the first to develop the argument that the complexity of *social* life was the prime selective agent of primate intelligence. The group member is required to judge the skills and changing inclinations of others and to use them for intelligent predictions for its own benefit. The view was later and independently presented by Alison Jolly (1966) and by Humphrey (1976). The difficulty is that many non-primates live in large groups without having evolved particular intelligence levels. Social complexity is probably the effect as much as the ultimate cause of intelligence.

Katharine Milton (1981) plausibly argued that the necessity of predicting the few productive days of widely dispersed tree patches in tropical forests was a major factor in the evolution of primate mental abilities. Yet, resources dispersed in time and space are hardly a unique feature of primate environments; they are also mastered by predators of highly mobile groups of prey. The complex system of ultimate causes is likely to defy any one-factor explanation. While certain selective pressures may have been particularly formative, it is most probable that a whole *set* of primate characters were mutually preadaptive to each other's evolution, and that they evolved into a syndrome of which mental flexibility is a part. Foremost among these characters is the *a priori* lack of outstanding competence in any specific skill. Our inventive species probably emerged among the primates rather than from a different order *because* primates are remarkably ill-equipped with innate technologies. The termite is better than the chimp at nest-building by an incredible amount, but the chimp beats the termite by learning to tease him from his mound. Instinct is like a key fitting a single lock. A key is easy to use. The poor *a priori* competence of primates is comparable to a pick-lock. Its use requires and therefore promotes a kind of skill which eventually permits the opening of many locks.

If some selectors of primate intelligence were of outstanding importance, it should be possible to locate them empirically. The rationale is this: a behavioural character is tested by selection only in certain situations, those in which the behaviour is used to function. The critical assumption is that the situation that *selected* for a behavioural character in phylogeny also *trains* it in individual life. For example, the genetic basis of flying skill was selected only while the primeval birds were airborne; the learning of flying skill is restricted to the same context. An intelligence or learning disposition selected by the context of being socially subordinate would presumably be most proficiently developed by subordinates. The extent to which this assumption is correct must be ascertained for each behaviour. In general, it should be correct (i) if the behaviour with the higher fitness contribution were also the one with the greater reward – a very frequent case in all animals; (ii) if each individual were capable of several behavioural variants so that it could compare the rewards – a frequent case in primates; and (iii) if training could substantially improve on the uninstructed inherited ability – a condition fulfilled by definition in learning and intelligence.

From the above one may assume that innovative behaviour was selected primarily in the situations that now most effectively teach it. It would therefore be profitable to look systematically at the everyday situations in which present-day primates learn and invent most proficiently. These are the conditions by and for which their innovative dispositions must have been selected.

Time does not permit even a sketchy classification of the everyday conditions relevant to innovative performance. Instead a few examples from the field and the quasi-natural captive group will show the interest of the topic.

Intellectual training by group life

If the Chance–Jolly–Humphrey hypothesis is correct, that is, if complex social life selected primate intelligence *and* trained it to its greatest proficiency in natural life, we would expect the training effect to be most pronounced in those group members whom group life affects and constrains most, compared with solitaries. Most likely, these are the group members of low dominance rank. Subordinates should have made the most of the genetic disposition for intelligence and learning, since they most depend on the formation of alliances or need to lead their mate to where the dominant male cannot see them, and so forth.

Strayer (1976) and Bunnell *et al.* (1980; Bunnell & Perkins 1980) tested macaques that normally lived in captive groups on learning tasks. In Strayer's study, a buzzer sounded when a reward could be obtained. The subordinate monkeys made fewer time-out errors, that is, they did not press the lever when the buzzer was silent, whereas dominants pressed even with the buzzer off. Dominant macaques were more dependent on regular reinforcement. In Bunnell's study the subordinate macaques were faster to master a reversal learning task. Dominant animals that fell in rank improved their performance, which speaks against the possibility that subordinates performed better because they were younger. The subordinates in these studies were thus more attentive to the outside conditions of their actions as the test apparatus, and they were better at relearning and at persisting in spite of frustration. This is what we would expect if they had transferred abilities acquired in the highly conditional social life of a low-ranker.

Free time and energy

These are other candidate conditions of innovative behaviour. The reason is that environments are not stationary over time. Animals survive certain periods in which their maximized net energy intake is just sufficient to keep them alive. At other more favourable periods, survival may be so easy that the animal has time and energy to spare. It would be advantageous if it could somehow store them for worse times.

To hoard food in a cache is one form of storage, but the hoard is vulnerable to decay, to parasitism and to plundering by observant conspecifics. It is found in solitary rodents and in insects with hidden or defended nests. Non-human primates do not use hoards, probably because they have no dens and no organization for guarding and sharing. A second form of storage is fatty tissue, which is a well-defendable but burdensome hoard. It is particularly common in marine mammals, where part of the weight is carried by the water and where the fat is a useful insulator against hypothermia. Primates, being arboreal and a prey species, require agility and hardly use it.

By far the most elegant form of storage is new knowledge or skill in communication or ecological techniques. Here, the time and energy spent in exploratory behaviour is transformed into a light-weight unstealable commodity that can save time and energy in a harsher future.

Every zoo colony of primates is a rough experimental test of the hypothesis that free time and energy do indeed promote innovation. Kummer & Kurt (1965) quantitatively compared the behaviour of hamadryas baboons in the Zurich Zoo with the behaviour of wild troops in Ethiopia. Of 68 motor and vocal signals that the zoo baboons used in social communication, nine were not found in any wild troop, suggesting that they were innovations. (On the other hand, all social signals seen in the wild were also found in the zoo colony.) None of them looked pathological. Rather, they were functional elaborations, such as a new gesture that invited a youngster to be carried. In the case of 'protected threat', in which a female directs the attack of the dominant male against her opponent, the zoo version was technically improved and clearly more efficient than the crude hints at the same behaviour in the wild.

The best ecological invention of the zoo baboons was to obtain drinking water from a mound, otherwise unobtainable, by lowering the body, tail first, down a vertical wall and then to suck the water from the tuft (Schönholzer 1958). The tail-drinking also was an innovation. No wild baboon was seen to approach an incentive backwards.

Within the limits, free time and energy thus seem to further innovation.

Part 2. (Jane Goodall)

Introduction

The study of the chimpanzees at Gombe, in Tanzania, is now in its 24th year. The longitudinal records provide many anecdotes regarding innovative behaviour and the following discussion concerning conditions favouring (i) the appearance of novel patterns *per se*; and (ii) the transmission of such patterns through the social group, is centred around this information.

An innovation can be: a solution to a novel problem, or a novel solution to an old one; a communication signal not observed in other individuals in the group (at least at that time) or an existing signal used for a new purpose; a new ecological discovery such as a food item not previously part of the diet of the group. In some species of primates a new food becomes incorporated into the diet of a troop as a result of a whole series of independent individual discoveries; other novel behaviours, such as potato washing, are discovered by one individual only and acquired by other troop members through observational learning.

Some innovations derive from the ability of the individual to profit from an accidental happening. Thus when the chimpanzee Mike was afraid to take a banana from my hand he seized a clump of grasses and swayed them to and fro in the typical threat gesture. As he did so one of the grasses touched the fruit. Instantly he let go of the grasses, looked round, hastily broke off a slender, bendy twig, dropped it at once, reached for a thicker stick and hit the banana to the ground from where he took and ate it. Ten minutes later when I proffered a second fruit Mike unhesitatingly reached for a stick and repeated the performance. The first step in such a chance sequence is not always seen, but can sometimes be deduced. At Gombe, pots and pans are often washed at the edge of the lake. The anubis baboons of one study troop spend long periods of time digging in the gravel, searching for scraps. One day when the lake was rough and the successive breaking of large waves made drinking difficult, an adolescent male, Asparagus, was observed to dig a hole near the high water mark, wait for a wave to fill it, then quickly drink as the wave retreated. Subsequently he was observed to do the same thing on another occasion. Six years later eight-year-old Sage, of the same troop, was seen drinking in the same way on four separate occasions. It seems likely that the two males discovered the technique independently – probably by first drinking water that filled up holes dug by them when searching for food and subsequently profiting from that experience, digging the holes for the specific purpose of drinking. One year after he was seen drinking in this way Asparagus disappeared (he died or transferred to a new troop). Sage was three years old at that time, and might, therefore, have learnt the behaviour by watching the older male: if so it seems strange that he was not seen to drink in this way during the next six years.

Other innovations result from the ability of the higher primates to use existing behaviour patterns for new purposes. Chimpanzees at Gombe routinely use leaves to wipe their bodies when soiled: one female twice used handfuls of leaves to brush away stinging insects (once bees from a hive she was raiding, once ants from the trunk of a tree to which she was clinging as she raided their nest) and one male used leaves to wipe the inside of a baboon skull during a meat-eating session: he ate the leaf-brain wad (Wrangham 1975).

A third kind of innovation is the performance of a completely new pattern, such as the bizarre series of somersaults by which the polio stricken male, McGregor, managed to move from place to place after losing the use of his legs or the odd form of locomotion invented by one infant during lone play (to be described).

Conditions for the appearance of new behaviours

Innovations may be occasioned by sudden change in the environment such as when wild populations are provisioned or during an outbreak of disease (such as the polio at Gombe (Goodall 1983)). They may also, as has been described, appear during periods of environmental stability, particularly during periods of plenty which result in an excess of leisure and energy. This is exemplified in some captive situations.

A prerequisite for the solving of problems in novel ways, be they ecological, technical (involving the use of tools) or social (involving the manipulations of companions) is familiarity with the components of the situation. Chimpanzees have certain manipulative tendencies, which appear to be inborn – at a certain age an infant will reach out, grasp and brandish a stick (Schiller 1949). But he must become familiar with sticks during play if he is to use them successfully as tools to solve novel problems (figure 1) (Köhler 1925; Schiller 1952). Similarly, chimpanzees have certain inborn communications signals, but must have opportunity to interact with other chimpanzees to use these signals successfully (Menzel 1964). Social experience and familiarity with the other members of the group are essential if a chimpanzee (or other animal) is to invent novel methods of getting his own way in competitive situations.

FIGURE 1. Flint 'clubs' an insect, a behaviour not observed in the adult tool-using repertoire at Gombe.

(*a*) *Social innovations*

Much social skill emerges as a direct result of competition between group members. A subordinate individual A, to attain a particular goal *in spite of* the inhibiting proximity of a social superior B must either form a coalition with a third individual C (so that A and C are superior in strength to B) or follow a more devious route, such as moving out of B's sight, or persuading B to move away, or distracting B's attention. Some of the solutions to social problems of this sort represent novel ones on the part of the individual concerned. The following are examples of innovation of this sort observed among the chimpanzees at Gombe.

(i) One reproductive strategy of the male chimpanzee is to establish exclusive mating rights over a female by leading her away from the other males to the periphery of the community range (McGinnis 1973; Tutin 1979). A male wanting to establish a consortship of this sort faces obvious problems if there are higher ranking males in the group who are interested in the same female. One individual, Satan, was, on several occasions observed to keep very close to a sexually attractive female until she made her nest in the evening, rise before any other chimpanzee the next morning, shake branches at her (a signal for her to follow him) and lead her away before the others left their nests (Tutin 1979).

(ii) The charging display, when a male rushes over the ground or through the branches, swaying, dragging and throwing vegetation, branches and rocks is of major significance to his struggle for a higher position in the dominance hierarchy. Figan not only showed unusual timing and placing of his displays (Bygott 1974) but repeatedly got up before other chimpanzees in his group and performed wild arboreal displays while his companions were still in their nests. This caused great confusion and was one of the methods he employed during his successful bid for alpha position (Riss & Goodall 1977). Other males occasionally used this technique, but it seems that only Figan profited from the experience and made it a regular occurrence.

(iii) Adolescent males typically challenge older females with bristling, swaggering displays during which branches may be waved with which they may hit the females. Responses to such displays vary depending on the age of the male, rank of his victim in relation to that of his mother and so on, and range from fear and avoidance, through retaliation, to totally ignoring the youngster for as long as possible. Sometimes they hold onto the branches with which they are being flailed. One female, Winkle, twice terminated such displays in unusual ways. Once she firmly removed the branch from a young male even before he had begun to sway it, and once she reached out and vigorously tickled the swaggering youngster so that his aggressive display ended in *laughing*. Of interest was the fact that the same female used two quite different unusual patterns to achieve the same end.

Banana-feeding at Gombe created a new situation. Aggressive competition was greatly increased and the chimpanzees tended to aggregate in large numbers in camp as they waited for us to distribute the fruits. Among the innovations that appeared as a result of the new situation were the following.

(i) Before we had devised a way of distributing the bananas among the various individuals present it was often the case that youngsters got very few or none at all. One day, when the young adolescent male Figan was part of a large group and, in consequence, had not managed to get more than a couple of bananas, he suddenly got up and walked away with a purposeful gait. His mother followed and, as is often the case when one individual sets off as though with a goal in mind, the others followed. Ten minutes later Figan reappeared by himself, and was given bananas. We thought this was a coincidence as indeed it may have been on that first occasion. But when Figan repeated the performance on four subsequent occasions it became clear that he was following a deliberate strategy (Goodall 1971).

(ii) In the early sixties there were occasionally a few empty four gallon paraffin cans lying about my camp. At one time or another almost all of the 14 adult males had incorporated one of these into a charging display. One of them, Mike, profited from the experience and began to use the cans in almost all displays that he performed in camp. He even learned to keep three ahead of him as he charged towards his superiors. Within a four-month period he had become alpha male, having thoroughly intimidated all his rivals and, so far as we know, without taking part in a single fight (Goodall 1968, 1971).

Groups of chimpanzees in captivity show, as did the hamadryas, much innovation in the social sphere. With adequate food and drink provided, their health attended to, and most dangers and excitements removed from daily life, chimpanzees not only have more leisure time than their wild counterparts, they are also subjected to a new stress, over and above boredom and confinement. At Gombe, if the social environment becomes tense and hostile, an individual can, and often does, move off quietly by itself or with a small compatible group. In captivity, even in a large enclosure, this is not possible. The novel behaviours which zoo or laboratory chimpanzees show in their social interactions are undoubtedly, at least in part, a response to this new challenge. And, because they are forced to remain constantly in each other's company, chimpanzees in captivity are probably able to predict more accurately the responses of their companions so that their interactions can become increasingly sophisticated. One adolescent male, Shadow, in Emil Menzel's group, developed a unique courtship display during which he stood bipedally and flipped his upper lip back over his nostrils. Precisely how this strange performance originated is not known: it was clear, however, that the adult females, all dominant to Shadow, responded aggressively to the more usual male courtship (probably because this involves many aggressive elements). With the new display Shadow was able to convey his sexual interest devoid of aggressive overtones (C. Tutin & W. McGrew, personal communication). The chimpanzees of the large Arnhem colony have been carefully studied by de Waal (1982) who observed a great deal of extraordinarily astute social skill. Once, for example, when a subordinate male was surprised during a clandestine courtship by the arrival of the alpha male, he quickly covered his erect penis with his hands, effectively hiding the tell-tale signal. After an aggressive dispute between two of the adult males, a female sometimes showed behaviour which served to hasten reconciliation between the rivals: she would lead one towards the other, sit between them so that both groomed her, then step quietly away leaving the males grooming each other: harmony was restored. Each of the adult females was seen to act thus at one time or another; such incidents have never been observed in the wild.

(*b*) *Ecological and technical innovations*

While social innovations can only appear within the social environment, during interactions with other group members, ecological and technical innovations are more likely to appear during periods when an individual is, to some extent, freed from social distractions. In a hamadryas one-male unit the females have differing spatial positions: one stays close to the unit male; one spends much time at the periphery of a foraging group. While the central female is preoccupied with social interactions, particularly with the male, the peripheral female is alert to danger and is the individual most likely to discover a new food source. Sigg (1980) tested wild family units temporarily kept in field enclosures: he found that there was a marked difference in the abilities of peripheral versus central females in their ability to learn new ecological tasks. Thus peripheral females readily learned to discriminate between nails painted different colours that were used as markers for food buried in the ground. They also remembered the location of underground water several hours after being allowed to watch its burial. Central females seemed unable to learn these tasks, perhaps because their attention was almost totally absorbed in social interactions. In the Tai Forest of the Ivory Coast chimpanzees crack open nuts with stones or heavy pieces of wood. Adult females are more efficient in the hammering technique than males on several measures. This may be due, at least partly, to the fact that males appear to be more easily distracted by ongoing social events: they look around, away from the task in hand, more frequently than do hammering females (Boesch & Boesch 1981, 1983).

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. At Gombe, where female chimpanzees spend a great deal of time in association with her dependent offspring only, an infant may be without opportunity for playing with other youngsters for hours or even days at a stretch. With no social distraction the conditions are ideal for the emergence of novel behaviours in the ecological and technical sphere. This is particularly true for the first-born child who does not even have the opportunity to play with elder siblings. One infant invented a new method of locomotion, swinging her body forward through her arms (in the typical 'crutching' gait) while keeping one foot firmly tucked into the opposite groin. Another threw a round fruit into the air and caught it as it fell: he tried to repeat the performance many times but I did not see him succeed again. A third lay on his back with his legs in the air and rotated a large round fruit which he held on the soles of his feet. A fourth used stones and twigs to tickle her clitoris, continuing until she was laughing loudly. One infant spent many minutes playing with a butterfly, another with a frog. Occasionally an infant will taste a novel food object: behaviour which we have never observed in an adult chimpanzee in the wild.

Once an infant has mastered a newly acquired adult manipulative pattern this may be practised in a variety of contexts other than that in which it was learned. Thus one infant, Flint, used the termite-fishing technique on his mother's leg, pushing a blade of grass between the hairs and then sucking the end. And, on another occasion, Flint used a grass blade to 'fish' for water caught in the hollow of a tree stump. After sucking off the drops a few times the blade gradually became more and more crumpled until he had made a miniature *sponge* (Figure 2). This

FIGURE 2. (*a*) Flint dips a grass stem into a water bowl, using the termite-fishing technique. (*b*) After a few such dips the grass becomes crumpled and resembles a miniature *sponge*. (A sponge of crumpled leaves is traditionally used by the Gombe chimpanzees for drinking from water bowls.)

behaviour might have led to the typical leaf sponge used by the Gombe chimpanzees for soaking water from hollows of this sort (although it seems more likely that this originated for the removal of dead leaves that had accumulated in the water). At Gombe the chimpanzees open the large hard-shelled *Strychnos* fruits by banging them against the tree trunk or a rock. During one *Strychnos* season infant Flint picked up a rock and smashed an insect on the ground. This pattern might, one day, lead to the use of a hammer stone for cracking open nuts, as in West African chimpanzee cultures. On another occasion Flint hit an insect with a 'club' (figure 3).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

FIGURE 3. (*a*) Feeding traditions are passed from one generation to the next through mechanisms of social facilitation and observational learning. Here one-and-a-half-year-old Getty watches his grandmother's six-year-old son (his uncle), Gimble, feeding on leaves. (*b*) Getty then samples the same food, while Gimble, in turn watches him. This was not a new item in the diet, but the example illustrates the mechanisms for the passing on of information from one individual to another in chimpanzee society.

(*c*) *Innovation and tradition*

A comparison of the ecological, technical and social communication patterns of different groups of chimpanzees in different geographical localities reveals a wide variety of cultural traditions. Gombe and Mahale, 100 miles (160 km) apart, have many plant species in common: Mahale chimpanzees feed on some that are never used by the Gombe chimpanzees and vice versa, and some foods that *are* eaten at both localities are, nevertheless, prepared differently. Driver and Carpenter ants are present at both places: at Gombe the chimpanzees fish frequently for Driver but not Carpenter ants: at Mahale it is the other way round. Gombe chimpanzees use leaf sponges when drinking from water bowls: at Mahale this has not been observed. At Mahale two chimpanzees grooming often show a unique 'hand-clasp' posture never observed at Gombe (McGrew & Tutin 1978). Different traditions have been found in hamadryas baboons and various macaques (see, for example, Kummer 1971) and it seems certain that groups of almost all higher mammals will be found to show intergroup cultural variation. Traditions obviously began with the innovative performance of particular individuals in the past – performances that were subsequently incorporated into the repertoire of a group through processes of social facilitation and observational learning (figure 3.) Only in the Japanese macaques has this process been carefully documented (Kawamura 1954; Itani 1965), first in regard to the unwrapping and eating of candies and subsequently for the dramatic inventions of potato-washing and wheat-cleaning initiated by the gifted young female Imo (and which, as mentioned, led to other sea-related activities). It was young monkeys who were the first to perform the new behaviours, their peers and their mothers who were the first to follow their example. Siblings and other closely associating adults were next on the list. As new infants were born, they acquired the behaviours, in the normal learning process, from their mothers. In the case of the unwrapping and eating of candies the reward was immediate and obvious and it is undoubtedly significant that this behaviour was acquired by all members of the troop, whereas the washing and cleaning techniques were never learnt by some of the adult males.

The rhesus monkeys that were transferred from Santiago to a new island (Morrison & Menzel

1972) rapidly incorporated many new foods into their diet. There was no evidence that these new foods were consistently sampled by any individual monkey or category of monkey: each one tried each new food as he came across it and accepted or rejected it according (presumably) to its taste. When wheat was introduced to one group of Japanese monkeys the whole troop had acquired the new food habit within four hours (Itani 1965). Similarly, the baboons (of all ages and both sexes) at Gombe have always unhesitatingly tried new foods offered them. In chimpanzee society, however, both at Gombe and Mahale, it is only youngsters who experiment with new foods (Nishida *et al.* 1984). Moreover, the conservative attitude of mothers and elder siblings, who usually snatch or flick away a new food item from an infant, makes it unlikely that the infant will repeat the experiment, and even less likely that the food in question will be incorporated into the diet of the community as a whole.

One new behaviour that did spread through the community at Gombe was the use of sticks as levers to try to open banana boxes. Four and a half months after these boxes had been installed three adolescents began, independently, to use sticks to try to prize open the steel lids. Because a box was sometimes opened when a chimpanzee was working at it, the tool use was occasionally rewarded and, over the next year, the habit spread until almost all members of the community, including adult males, were seen using sticks in this way. That many individuals learnt as a result of watching their companions is suggested by the fact that one female was observed to behave thus on her very first visit to camp: before this she had had ample opportunity to watch what was going on from the surrounding vegetation (Goodall 1968).

Most of the innovative performances in the social sphere observed at Gombe were seen in single individuals only, and often only once, as when an adolescent male showed a submissive genital display (facing his aggressor with laterally positioned leg, hip and knee bent and an erection of the penis) exactly comparable to that of the squirrel monkey (Ploog 1967, plate 10.3). A juvenile female, Fifi, also showed a completely new pattern (at least at Gombe, though it was observed in Washoe (Gardner & Gardner 1969)) 'wrist-shaking'. This gesture, a rapid to and fro shaking of the hand, was directed at an adult female in an aggressive context. The following week Fifi repeated the gesture and continued to do so, on and off, for the next ten months, always in the aggressive context. A week after Fifi's first observed wrist-shake the new gesture appeared in a slightly younger female, Gilka, who was Fifi's most frequent playmate. For the next few months Gilka wrist-shook vigorously in many contexts. Then she, too, gradually dropped the gesture from her repertoire (Goodall 1973). Another new pattern was shown by infant male Flint when he inspected the genital area of a female with a small stick, instead of with his finger as is usual. He continued to stick-inspect occasionally over the next few weeks during which time another infant male imitated the behaviour. After this it was not seen again. Köhler (1925) reported a number of novel behaviours which became 'fashions' for a few weeks or months and then vanished from the repertoire of his colony.

Behaviours of this sort, which have no obvious practical reward, are unlikely to spread through a group unless they persist long enough, in one female, for her infant to acquire it during normal learning. The female, Madam Bee, developed a unique grooming pattern, vigorously scratching the skin of her partner before intently examining the skin at that place. The appearance of this behaviour followed the polio epidemic during which Madam Bee lost the use of one arm. At that time her elder daughter was about eight years old, the younger, one and a half years old. Subsequently the younger child was seen using the unique pattern on a number of occasions, but the older daughter was never seen to do so (Goodall 1973).

Twice the characteristic performances of individual males were incorporated into the repertoire of younger males. When Mike was enhancing his display by the use of empty four gallon cans Figan was an adolescent: on several occasions Figan was observed as he 'practised' with an empty can discarded by Mike in the bush. Figan himself, as described, developed a highly effective arboreal display when his companions were still in their nests. Young Goblin, who had associated closely with Figan from early adolescence onwards, and had watched Figan's rise in the hierarchy, subsequently began to perform early morning displays himself when he, at the age of 14, was making a determined bid for power.

In the social sphere, innovations are often designed to get the better of higher ranking companions. And, at least sometimes, they are quickly dropped when counter-strategies are developed. Thus Emil Menzel (1974) describes how a subordinate female, Belle, who had been shown the whereabouts of hidden food, tried, in various and ever more sophisticated ways to withhold this information from the dominant male, Rock (since, if she led him to the place he invariably took all the reward). But Rock quickly learnt to see through her various subterfuges. If she sat on the food, he learnt to search underneath her. When she began sitting half way towards the food, he learnt to follow the direction of her travel until he found the right place. He even learnt to go in the opposite direction when she tried to lead him directly *away* from the food. And, since she would sometimes wait until he was not looking, Rock learned to feign disinterest, but was ready to race after her once she began to head for the goal. This sequence of events is particularly interesting since it shows how one innovation during competitive interactions in the social sphere can stimulate the rival to make a novel response. Such competition between animals as cognitively advanced as chimpanzees can thus lead to an escalation in the development of new social strategies within a group.

Conclusion

More carefully documented 'anecdotal' reports from field studies should yield a wealth of information on innovative performances in the ecological, technical and social spheres. Of the many such behaviours observed, only a few will be passed on to other individuals, and seldom will they spread through the whole troop. However, systematic experimentation (such as the introduction of a variety of carefully designed ecological and technical 'problems' and long-term recording of reactions to them) both in free-living and captive groups would provide a new way of studying the phenomena of innovative behaviours and their transmission through and between social groups.

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GURE 1. Flint 'clubs' an insect, a behaviour not observed in the adult tool-using repertoire at Gombe.

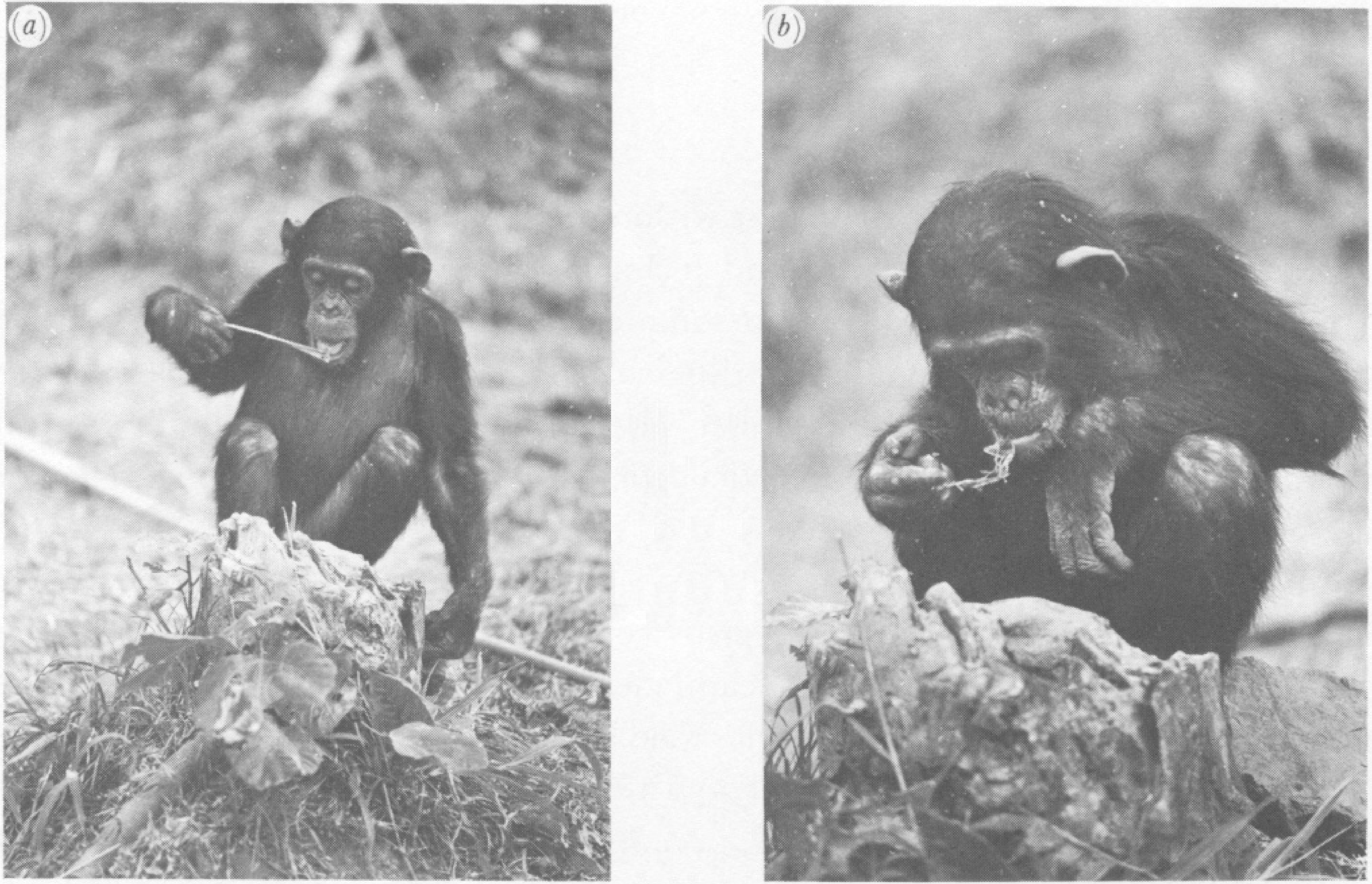

FIGURE 2. (*a*) Flint dips a grass stem into a water bowl, using the termite-fishing technique. (*b*) After a few such dips the grass becomes crumpled and resembles a miniature *sponge*. (A sponge of crumpled leaves is traditionally used by the Gombe chimpanzees for drinking from water bowls.)

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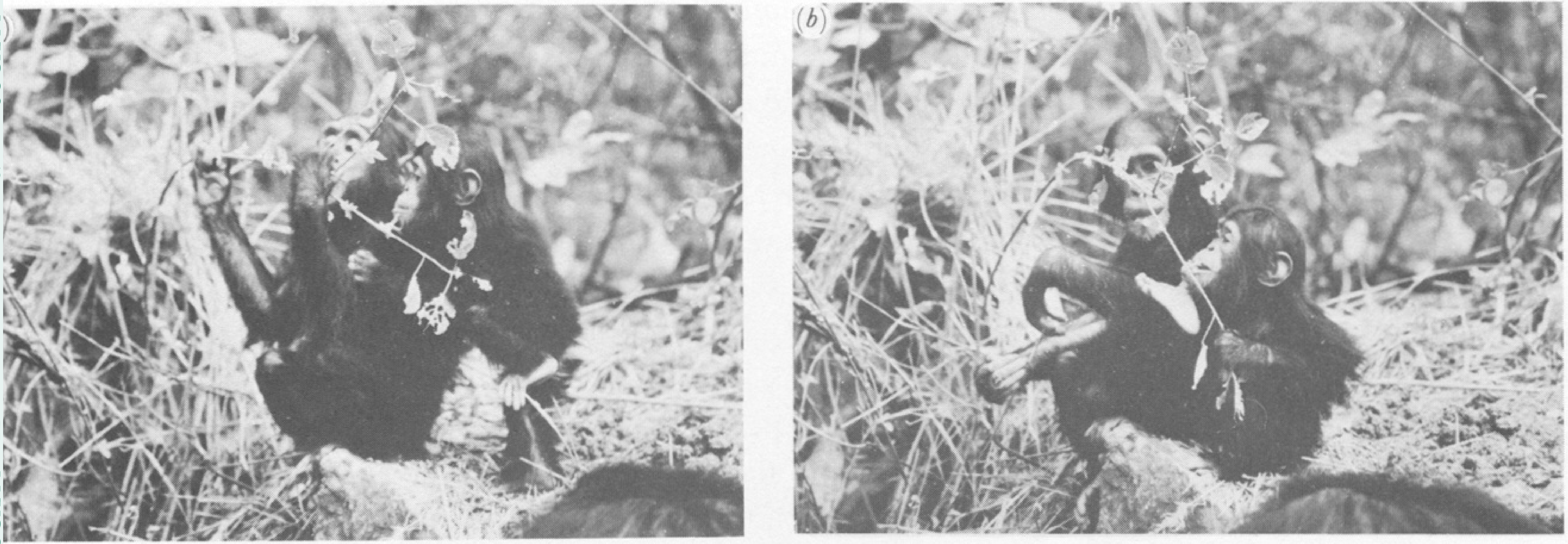

FIGURE 3. (*a*) Feeding traditions are passed from one generation to the next through mechanisms of social facilitation and observational learning. Here one-and-a-half-year-old Getty watches his grandmother's six-year-old son (his uncle), Gimble, feeding on leaves. (*b*) Getty then samples the same food, while Gimble, in turn watches him. This was not a new item in the diet, but the example illustrates the mechanisms for the passing on of information from one individual to another in chimpanzee society.