Sexual Behaviour of Group-living Adolescent Chimpanzees

C. E. G. TUTIN AND W. C. McGREW
Department of Psychiatry, Stanford University School of Medicine, Palo Alto, California and Department of Zoology, University of Edinburgh, Edinburgh, Scotland

ABSTRACT
This paper reports a study of the heterosexual behavior of three male and four female captive adolescent chimpanzees living a semi-natural life style in a large field enclosure. Observations made with binoculars from an overhead deck were balanced over the daylight hours and the seven weekdays. We recorded 213 copulations in 741.25 hours of observation between February 14 and July 21, 1972. Analysis of the observations suggests that group-living chimpanzees in a large field enclosure behave more like free-living chimpanzees than like other captive chimpanzees paired in small cages. In this group, copulations were non-randomly distributed throughout the day, a finding in agreement with results on wild-living chimpanzees but not previously reported for captive chimpanzees. In this group, moreover, copulations were highly concentrated within each female's period of maximum tumescence, as are those of free-living chimpanzees; and individual differences in sexual attractiveness among females were apparently based on a maturational threshold of swelling size, a phenomenon that has also been reported for wild chimpanzees.

This paper reports a study of the heterosexual behaviour of captive adolescent chimpanzees living a semi-natural life style. The most complete previous reports of chimpanzee sexual behaviour were based on captive animals housed in pairs in small cages (e.g., Yerkes and Elder, '36) or, more recently, on wild populations (van Lawick-Goodall, '68). Previous studies of chimpanzee sex in group situations in captivity are largely non-quantitative and generally descriptive (e.g., Kollar et al., '68). By studying in detail group-living chimpanzees in a large field enclosure, we hoped to achieve an ideal compromise between the types of studies cited. We hoped to remove the artificial and sometimes distorting limitations of the bare cell and limited companionship situation, while at the same time retaining the advantages of uninterrupted, unimpeded observation not available in the wild. Results of a detailed ethological study of the elements of sexual interaction and their frequencies and sequences will be presented elsewhere.

MATERIAL AND METHOD
Three male and four female wild-born chimpanzees (Pan troglodytes) at the Delta Regional Primate Research Center, Covington, Louisiana, participated in the study. Five individuals formed the basis for the findings presented here: the male Shadow (age 9), and the four females Gigi (10), Polly (9), Belle (8) and Bido (8). A female infant was born to Gigi in the enclosure on May 1, 1972, and is being reared in the group. The chimpanzees arrived at Delta when between one to four years of age and have lived in a group or as subgroups since then.

From September, 1969, to September, 1972, the chimpanzees were housed together (except for temporary absences) in a 30 x 120 m outdoor enclosure. It was open overhead, had walls 5 m high of sheet metal above and chainlink fence below, and was surrounded by pine forest. The enclosure was carpeted with natural vegetation and contained three elevated platforms, numerous upright and fallen poles and tree trunks, and a plentiful sup-
ply of small movable objects. Fresh woody foliage for roughage and nest building was supplied weekly. By captive standards it was a spacious and stimulating environment.

For one hour daily the chimpanzees were locked into a smaller, closed cage adjacent to the enclosure while cleaning and maintenance took place. Otherwise they were left to their own devices to move and interact freely. Thus, all our observations were made on a group living in continuous mutual access, minimally interfered with by man. Observations were made from an overhead deck using 7 x 35 binoculars. These were balanced over the daylight hours (from 06.30–18.30) and the seven weekdays.

RESULTS

We recorded 213 chimpanzee copulations in 741.25 hours of observation between February 14 and July 21, 1972. A copulation was defined as an interaction between a male and a female which included at least one intromission. Some copulations included multiple intromissions; to be classified as separate copulations, two intromissions had to be separated in time by more than five minutes of non-interaction between the two individuals.

Table 1 gives the distribution of the copulations over the four females listed at the left in order of sexual development. (Shadow was the male in all but one of the copulations). Up to four cycles of sexual swelling for each female are given in chronological order across the top (I-IV). Day 1 of a cycle was the day when the first tumescence occurred after a period of no swelling. The total number of copulations divided by the total hours of observation gives the overall rate of copulations for each female. Individual differences are obvious. Even discounting the partial inflation of Gigi's total, the difference between Gigi's overall frequency and Bido's is many-fold; Polly and Belle are equally intermediate.

Although we did not know it at the time, Gigi was pregnant when observations commenced. Consequently, we only saw most of her last full cycle and after that one isolated copulation before she ceased swelling altogether. Her copulation rate during that cycle was the highest we observed and more than double that of any other. A gap of ten days ensued during which Gigi remained unswollen before the last odd copulation. She gave birth to her first infant 41 days later. The assumption that it was a full-term infant means that Gigi engaged in coitus during more than 80% of the pregnancy. Some pregnant chimpanzees in the wild show cyclic sexual swellings and periods of receptivity up to 75% of the course of pregnancy (van Lawick-Goodall, '68: 217).

We observed Polly's sexual behaviour through four complete sexual cycles. Three of them (I, III, IV) showed a fairly regular rate of copulation, but in II it was low, possibly because it coincided with Belle's first adult swelling, which provided Shadow with a novel sexual alternative. Preliminary results from Cycle V indicate that her frequency is increasing and will

<table>
<thead>
<tr>
<th>Cycle</th>
<th>Total</th>
<th>Total hours</th>
<th>Total frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>copulations recorded</td>
<td>observed</td>
<td>frequency</td>
</tr>
<tr>
<td>Gigi</td>
<td>30 1</td>
<td>1 31</td>
<td>68.5 0.5 2</td>
</tr>
<tr>
<td>(0.4)</td>
<td></td>
<td>(0.1)</td>
<td></td>
</tr>
<tr>
<td>Polly</td>
<td>18 0.2</td>
<td>7 0.04</td>
<td>10 0.1 38</td>
</tr>
<tr>
<td>Belle</td>
<td>1 0.01</td>
<td>20 0.1</td>
<td>31 0.2 46</td>
</tr>
<tr>
<td>Bido</td>
<td>0 0</td>
<td>0 0</td>
<td>11 0.1 0</td>
</tr>
</tbody>
</table>

1 Number of copulations
2 (Frequency/observation hour).
3 Recording of cycle began in mid-tumescence, so frequency is an over-estimate.
likely soon approach that of the experienced Gigi. Although Belle had shown cycles of sexual swelling for over four months prior to the study, she was first observed to copulate during her Cycle I. It was an isolated copulation, but 27 days later in Cycle II, her participation increased to its current frequency. The raw totals have increased with each cycle, so that Belle's transition from virginity to experience has been very rapid. Like Polly and Belle, Bido was observed through four complete sexual cycles. However, she was seen to copulate during only one of these (III). Her rate during that cycle (0.1/ hour) resembled those of the more experienced Polly and Belle, although her initial copulation in this cycle was probably also her first one. The absence of copulations during Bido's other cycles considerably depressed her overall frequency relative to the other females. (One additional copulation occurred between Bido and Shadow, during her Cycle V).

The rise and fall of each female's sex skin is shown graphically in figure 1. Initially we only interpolated between significant turning points, such as when the swelling reached a plateau or when swelling decreased to a minimal flatness for several days running. Thus, the early results on the left side of the figure were schematic and rather crude. After two months, we felt confident enough to substitute the more refined interval system of fractional assessment: zero, one-fourth, one-half, three-fourths, one. This resulted in more accurate but less smooth vicissitudes in the right half of the figure. The four records coincide, so that instances in which two animals were simultaneously maximally tumescent can be derived.

The females' different stages of sexual development are indicated by their cycling patterns in figure 1. In her only cycle, the experienced Gigi showed both the typical swelling pattern and time course for the mature female chimpanzee. Polly also

![Fig. 1 Sexual swelling cycles of the four chimpanzee females.](image-url)
showed the typical pattern, although there was still some variability in the lengths of her cycles (29–42 days). Physically, both Gigi's and Polly's swellings resembled those described for adult female chimpanzees in size and shape. Polly's periods of menstrual bleeding increased in length with each swelling cycle. Belle's pattern of cycling was more irregular: two short cycles (24 days) followed by three long ones (as long as 48 days). Her only observed menstrual bleeding (probably her menarche) occurred during detumescence of one of these prolonged cycles, and her swelling never disappeared completely between that cycle and the next. Menstrual bleeding while at least partially swollen is rare but has been recorded previously (Graham, '70: 187). Belle's swelling size blossomed over the observation period from small swellings restricted to the vulvar lips (typically adolescent) to full swellings of the entire perineum. At the younger end of the spectrum, Bido's sexual cycling was that of a young adolescent. Her cycles showed the greatest variability in length (18–43 days) and the greatest irregularity from day-to-day. It was not always easy to delineate her swelling into cycles, e.g., the one-day drop to no swelling between Cycles II and III. Bido has not been seen to menstruate, and her swellings remain adolescent in size and shape. It should be noted that the only cycles in which she copulated were those during part of which both Polly and Belle were non-swollen. At other times her maximum tumescence overlapped with one or both of them, but during parts of her Cycles III and V she represented Shadow's only heterosexual outlet.

Table 2 gives the distribution of the observed copulations for the four phases of the females' swelling cycles. For each individual, copulations were markedly concentrated in maximum tumescence. Copulations occurred in the three other phases of the cycle but less frequently. Belle restricted her copulations almost entirely (96%) to maximum tumescence. Gigi and Polly exhibited more copulations outside this phase: 39% and 26% respectively. Their copulations occurred with approximately equal frequency during tumescence and detumescence but only rarely during the no swelling phase. This dispersion may have been related to their greater sexual experience and cooperativeness. Also, Belle may have been relatively less attractive to Shadow when not maximally swollen since her swellings were fairly small. Bido's position in this ranking was intermediate (82% of copulations during maximum tumescence), but she only participated in 11 copulations overall. The concentration of copulations during maximum tumescence agrees with both van Lawick-Goodall's ('68: 216) findings on free-living chimpanzees and Yerkes and Elder's ('36: 22) on captive ones. However, our high overall concentration during maximum tumescence (83%) and

TABLE 2

<table>
<thead>
<tr>
<th>Phases</th>
<th>Tumescence</th>
<th>Maximum tumescence</th>
<th>Detumescence</th>
<th>No-swelling</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gigi</td>
<td>2 (0.2)</td>
<td>19 (0.6)</td>
<td>9 (0.3)</td>
<td>1 (0.01)</td>
<td>31 (0.5)</td>
</tr>
<tr>
<td>Polly</td>
<td>6 (0.1)</td>
<td>54 (0.3)</td>
<td>11 (0.1)</td>
<td>2 (0.1)</td>
<td>73 (0.1)</td>
</tr>
<tr>
<td>Belle</td>
<td>3 (0.02)</td>
<td>94 (0.2)</td>
<td>11 (0.01)</td>
<td>1 (0.1)</td>
<td>98 (0.1)</td>
</tr>
<tr>
<td>Bido</td>
<td>2 (0.02)</td>
<td>9 (0.1)</td>
<td>11 (0.0)</td>
<td>11 (0.02)</td>
<td>213 (0.1)</td>
</tr>
<tr>
<td>Total</td>
<td>13 (0.03)</td>
<td>176 (0.25)</td>
<td>20 (0.05)</td>
<td>14 (0.05)</td>
<td>213 (0.1)</td>
</tr>
</tbody>
</table>

1 Number of copulations (Frequency/observation hour).
2 Observations of Gigi began during tumescence, thus the frequency in this phase is exaggerated. Due to pregnancy Gigi showed no further swelling, and thus a no-swelling phase could not be delimited in this cycle. These factors combine to exaggerate Gigi's overall frequency.
TABLE 3

*Daily periodicity in occurrence of copulations by four female adolescent chimpanzees. Chi-square one-sample test, df = 1*

<table>
<thead>
<tr>
<th></th>
<th>Morning</th>
<th>Afternoon</th>
<th>Total</th>
<th>( x^2 )</th>
<th>( p )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gigi</td>
<td>23</td>
<td>8</td>
<td>31</td>
<td>4.69</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td></td>
<td>(17)</td>
<td>(14)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Polly</td>
<td>43</td>
<td>30</td>
<td>73</td>
<td>0.23</td>
<td>&lt; 0.70</td>
</tr>
<tr>
<td></td>
<td>(41)</td>
<td>(32)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Belle</td>
<td>65</td>
<td>33</td>
<td>98</td>
<td>4.18</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td></td>
<td>(55)</td>
<td>(43)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bido</td>
<td>8</td>
<td>3</td>
<td>11</td>
<td>1.47</td>
<td>&lt; 0.30</td>
</tr>
<tr>
<td></td>
<td>(6)</td>
<td>(5)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>139</td>
<td>74</td>
<td>213</td>
<td>7.62</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td></td>
<td>(119)</td>
<td>(94)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^1\) Observed. (Expected)

virtual absence during no swelling (2\% ) resembled the former's findings (87\% and 1\% ) more than the latter's (60\% and 9\% ). The latter divergence occurred probably because Yerkes's chimpanzees were housed in pairs in small cages. Thus, the male had no alternative sexual partners available, and the female had insufficient space to escape his advances. The wild-living animals and ours faced neither of these abnormal restrictions.

Table 3 presents a preliminary analysis of daily periodicity in copulatory behaviour. All four females copulated more frequently than expected by chance in the mornings rather than the afternoons. This reached statistical significance for Gigi and Belle and for the pooled group. Van Lawick-Goodall’s (‘68: 219) found similar periodicity in free-living chimpanzees in Tanzania: over two-thirds of copulations over a two and one half year period occurred in the mornings.

**DISCUSSION**

The results suggest that group-living chimpanzees in a large field enclosure behave more like free-living chimpanzees than like other captive chimpanzees paired in small cages. In this group copulations were non-randomly distributed through the day, a finding in agreement with results on wild-living chimpanzees. This observation has not previously been reported for captive chimpanzees, probably because short-term cohabitation schedules and rotating sex partners effectively prevent stable adjustments to long-term stimuli. In this group copulations were highly concentrated within each female’s period of maximum tumescence, as are those of free-living chimpanzees. The similar but far less clear pattern reported for chimpanzee pairs in small cages probably reflects an opportunistic attitude forced upon the male by the limited access schedule to only one sexual partner. In this group, individual differences in sexual attractiveness existed among females, and these were apparently based on a maturational threshold of swelling size. A similar phenomenon has been reported for wild chimpanzees (van Lawick-Goodall, ‘68: 216).

**ACKNOWLEDGMENTS**

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**LITERATURE CITED**


Exceptions to Promiscuity in a Feral Chimpanzee Community

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Introduction

It has become clear in recent years that the sexual behaviour of feral chimpanzees is more complex than the freely promiscuous (i.e. random mating) system described by early field workers. VAN LAWICK-GOODALL [1968] and McGINNIS [1973] have reported the formation of temporary consort relationships between pairs of chimpanzees in the Gombe National Park, Tanzania. This paper reports on data collected during 15 months of observation at the Gombe Stream Research Centre and describes consort behaviour and other examples of non-promiscuous sexual behaviour shown by a community of feral chimpanzees. It attempts to assess the relative frequencies of the different types of mating systems and to determine what factors are responsible for maintaining the observed proportions. The mating systems observed in the study community ranged from promiscuity at one extreme to the formation of temporary monogamous consorts at the other. Consistent dyadic differences in the frequencies of copulations, indicating partner preferences, and the exhibition of possessive behaviour in group situations fall between the two extremes.

Methods

The Kasakela community (the unit group whose range centres on the artificial feeding station, Camp) numbers 38 individuals of whom 8 females and 17 males contributed to the data. In addition, 3 females from other communities were observed during temporary visits to the Kasakela community. In the 15-month period from November,
1972, to February, 1974, 1,000 h of data was collected on females showing cycles of sexual swelling. Observations were tape-recorded in the field and subsequently transcribed onto checksheets and supplemented with written notes.

Results

Over 1,000 copulations were observed during the study. From these it was possible to compute copulation rates per hour for the 61 dyads who were observed in contact (i.e. simultaneously present in a group) for at least 5 h. Mean copulation rates for each male with all females, and vice versa, were also calculated [this data is presented elsewhere, Tutin, in preparation]. Dyadic copulation rates ranged from 2.18 per contact hour to 0, and the observed variability indicates that sexual partner preferences exist. An arbitrary index of partner preference was arrived at by comparing dyadic copulation rates with the mean copulation rates for the male and female involved. A positive index was established if

\[
\frac{\text{dyadic rate}}{\text{mean male rate}} \geq 2, \text{ or } \frac{\text{dyadic rate}}{\text{mean female rate}} \geq 2.
\]

Similarly a negative index was established if

\[
\frac{\text{dyadic rate}}{\text{mean male rate}} \leq 0.5, \text{ or } \frac{\text{dyadic rate}}{\text{mean female rate}} \leq 0.5.
\]

A negative preference was also inferred if a dyad had 5 or more contact hours but was never seen to copulate.

Eight positive and 16 negative indices emerge. Only one male (of 14) and one female (of 6) show no indices of partner preference. This indicates that while promiscuous mating does occur in the chimpanzee it is the exception rather than the rule. It is not possible here to discuss in detail the diverse factors which contribute to partner preferences, but age, degree of relatedness and a number of personality factors all appear to be important.

The existence of partner preferences emerges during post hoc analysis, and as no characteristic behaviour patterns were involved they are not identified in the field at the time of observation. On the other hand, possessive behaviour was categorised during observation on the basis of behaviour shown by males to females. A male is described as acting possessively towards a female if he shows persistent special attention to her beyond the
bounds of normal courtship. The male initiates possessive behaviour by maintaining close proximity to a female by either leading or following her over a minimum period of 2 h. In addition to maintaining proximity, a possessive male may interfere in copulations between ‘his’ female and other males.

During the 15 months of the study 30 incidents of possessive behaviour were observed. In 22 of these the female was maximally tumescent. Seven females were involved, 2 of whom were not resident members of the Kasakela community. Six of the 8 adult males showed possessive behaviour on at least one occasion as did the 2 adolescent males. In 11 of the 32 records of possessiveness (30 incidents, 2 of which involved joint possessiveness by 2 brothers) the male made no attempt to interfere in copulations between the female and other males. In 7 other cases no opportunity to interfere arose, either because no other males were encountered or because males made no attempt to mate the female as she was not tumescent. In 14 cases, effective interference was seen and in one of these cases the male also made ineffective attempts to interfere. An interfering male was always of higher dominance status than the male whose mating he terminated. In the one case where interference was ineffective the mating males were of higher dominance status than the possessive, interfering male.

There is nothing a possessive male can do to prevent more dominant males from copulating with ‘his’ female whilst in a group. Faced with this situation the possessive male may do one of 3 things: (1) remain inactive; (2) ‘redirect’ his interference by chasing or attacking an uninvolved lower ranking male; or (3) take the female away from the group and once alone avoid further contact with other chimpanzees, i.e. form a consort relationship. While consorting, the pair cease all loud vocalisations and if they hear other chimpanzees vocalising, the consort pair appear to take avoiding action. This avoidance often results in the pair’s moving to the edge or even outside the normal range of the community. The maintenance of both possessive and consort behaviour depends on the female’s cooperation. With female cooperation, a consortship will last for several days; possessive behaviour is more transient, only rarely persisting for more than a day.

13 consortships occurred during the study period, their lengths ranged from 3 h to 28 days with a mean length of 9.5 days. In the majority (9 of 12; 1 unknown) of cases the female was maximally tumescent for at least part of the consortship. Six of the 8 females who were regularly observable were involved in consorts. All consorting males were fully adult and 4 of the 8 adult males in the community were responsible for the 13 consorts.
Discussion

Both males and females are involved in possessive and consort behaviour at different frequencies. Parous females are involved at higher frequencies than are nulliparous females. Nulliparous females cycle for several years ($x = 26$ months, $N = 4$) before conceiving whilst parous females usually conceive within a few months of resuming cycling. Thus, the probability of impregnating a parous female will be greater than that of impregnating a nullipare, in any one cycle. However, the immediate cause of parous females being involved in possessive incidents and consortships at higher frequencies than nullipares could be related to differential pheromonal cues or to a novelty effect of the parous females' relatively infrequent cycles. The frequencies of male involvement in possessive and consort behaviour do not correlate with age, dominance or the amount of agonistic behaviour males directed at females. However, the amount of time males spent grooming tumescent females in group situations does correlate positively with the frequencies of possessive and consort behaviour ($r_s = 0.63$, $N = 10$, $p < 0.05$). There is also a positive relationship between the amount of time males spent grooming females and their generosity to females in food-sharing situations [McGreW, personal commun.].

Both possessive and consort behaviour would seem to have obvious selective advantage to male chimpanzees in that they increase chances of impregnating females and hence passing on genes to the next generation. As previously mentioned, female cooperation is essential for the maintenance of these special relationships and they thus present an opportunity for females to exercise choice. If female choice is involved, it is of interest to note that the selection criteria appear to be social and caretaking abilities of the males and not their dominance status.

Consort relationships maximise the advantages outlined above as it is virtually impossible for even the dominant male to monopolise a female in a group situation. However, although in consort situations the male does not have the problem of other males, he does have to contend with the dangers encountered while avoiding other members of the community. Probably the greatest of these dangers is the increased risk of intercommunity encounters. Such encounters often involve extremely severe attacks and when a number of males of one community meet an isolated member of another community the attacks can result in fatal injuries [ByGott, 1972]. To minimise the possibility of both intra- and intercommunity encounters, the consort pair may be forced to move into an undesirable area where there
may be less food available or where they are in relatively close proximity to humans. Despite these risks, consortships do occur and during the study period 3 females were impregnated whilst consorting.

Consort behaviour and other exceptions to promiscuity have rarely been reported for wild chimpanzees in other localities. REYNOLDS [1963] indicated that similar phenomena might exist in the Budongo Forest chimpanzee population, but he saw only 4 copulations. The possibility remains that cultural variations in sexual behaviour exist in different isolated populations of chimpanzees, such as the one in the Gombe National Park. STEPHENSON [1973] has described similar troop-to-troop differences in sexual behaviour of relic populations of Japanese macaques.

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References


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Chimpanzee Copulatory Behaviour

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Abstract. Observations were made of a group of adolescent chimpanzees (Pan troglodytes) living in one-acre field enclosure. In 1,200 h of observation, we observed 341 copulations involving six individuals. 34 elements of copulatory behaviour were described and recorded, including facial expressions, vocalisations, gestures, postures and locomotion. Frequencies, combinations and sequences of the elements were extracted in analysis. The results emphasise individual differences and the rapid ontogeny of copulatory behaviour elements.

Key Words
- Pan troglodytes
- Sexual behaviour
- Adolescence
- Ontogeny of behaviour

Introduction

This paper reports an ethological study of the copulatory behaviour of adolescent chimpanzees living a semi-natural life style. Previous reports of chimpanzee sexual behaviour were based on captive animals housed in pairs in small cages [YERKES and ELDER, 1936; Riesen, 1971] or, more recently, on wild populations [VAN LAWICK-GOODALL, 1968]. A few exceptions to these extremes exist in which chimpanzee sexual behaviour was studied in group situations in captivity [KOLLAR et al., 1968; ROGERS and DAVENPORT, 1969], but these papers include only general descriptions of the behaviour. By studying group-living chimpanzees in a large field enclosure, we hoped to achieve an ideal compromise between the previously cited types of studies. We hoped to remove the artificial and sometimes distorting limitations of the bare cell and limited companionship situation, while at the same time retaining the advantages of uninterrupted, unimpeded observation not available in the wild.
The development of sexual behaviour in individual chimpanzees of both sexes has been previously reported only anecdotally [Bingham, 1928] or briefly [Van Lawick-Goodall, 1968]. Yet sexual behaviour in higher primates is an extremely sensitive and complicated phenomenon, and knowledge of its ontogeny is crucial for its full understanding. Adolescence is a time of rapid physical and behavioural growth with great individual variation, so a careful longitudinal approach is preferable to a cross-sectional one.

Material and Method

Three male and four female wild-born chimpanzees (Pan troglodytes) at the Delta Regional Primate Research Center, Covington, La., participated in this study. The oldest male, age 11, was in the group for only 24 days during the observation period and was seen to copulate once. The youngest male, age 7, showed no interest in social sex throughout the study, although his behaviour was otherwise typical. The remaining male, Shadow (age 9), and the four females, Gigi (10), Polly (9), Belle (8), Bido (8), formed the basis for the findings given here. A female infant was born in the enclosure on May 1, 1972, to Gigi, and is being reared in the group. The chimpanzees arrived at Delta when between 1-4 years of age and have lived in a group or as subgroups since then.

From September, 1969, to September, 1972, the chimpanzees were housed together (except for temporary absences) in a 30 × 120-m outdoor enclosure. It was open overhead, had walls 5-m high of sheet metal above chain-link fence, and was surrounded by pine forest. The enclosure was carpeted with natural vegetation and contained three elevated platforms, numerous upright and fallen poles and tree trunks, and many small moveable objects. Fresh woody foliage for roughage and nest building was supplied weekly. By captive standards, it was a spacious and stimulating environment.

For one hour daily the chimpanzees were locked into a smaller closed cage adjacent to the enclosure while cleaning and maintenance took place. Otherwise they were left to their own devices to move and interact freely. All findings are based on a group living in continuous mutual access, minimally interfered with by man. Observations were made from an overhead deck using 7 × 35 binoculars and a 35-mm camera with a 300-mm telephoto lens.

Initially we took longhand descriptive notes on the chimpanzees' behaviour. Later, we devised a checksheet of behavioural elements from which frequencies, combinations, and sequences of these elements could be extracted. Observations were balanced over the daylight hours (from 06.30 to 18.30) and the seven weekdays.

Results

We recorded 341 chimpanzee copulations in 1,200 h of observation between February 14 and September 6, 1972. A copulation was defined as an
interaction between a male and a female which included at least one intromission. Some copulations included multiple intromissions, and to be classified as separate copulations, two intromissions had to be separated by more than five minutes of non-interaction between the two individuals.

Table I gives the distribution of the copulations over the four females, listed at the left in descending order of sexual development. (Shadow was the male in all but one of the copulations.) Up to six cycles of sexual swelling for each female are given chronologically across the top (I–VI). Individual differences in the rate of copulations are apparent: the greater the sexual experience, the higher the copulation rate.

Gigi was in her sixth month of pregnancy when observations commenced. We saw most of her last full cycle before she ceased swelling altogether. We observed Polly's sexual behaviour through six cycles. Her copulation rate dropped during cycle II, possibly because this cycle coincided with Belle's first adult swelling, which provided Shadow with a novel sexual alternative. Although Belle had shown cycles of sexual swelling for at least four months prior to the study, she was first observed to copulate during her cycle I. It was an isolated copulation, but 27 days later in cycle II, she began to copulate regularly. The low rate in Belle's cycle V is probably partially due

Table 1. Distribution of copulations of four adolescent female chimpanzees through up to six cycles of sexual swelling. Cycle begins on the first day of swelling in each new cycle

<table>
<thead>
<tr>
<th></th>
<th>Cycle</th>
<th>Total copulations recorded</th>
<th>Total hours observed</th>
<th>Total frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I</td>
<td>II</td>
<td>III</td>
<td>IV</td>
</tr>
<tr>
<td>Gigi</td>
<td>31</td>
<td>68.5</td>
<td>0.5²</td>
<td></td>
</tr>
<tr>
<td>Polly</td>
<td>18</td>
<td>7</td>
<td>10</td>
<td>38</td>
</tr>
<tr>
<td>Belle</td>
<td>1</td>
<td>20</td>
<td>31</td>
<td>46</td>
</tr>
<tr>
<td>Bibo</td>
<td>0</td>
<td>0</td>
<td>11</td>
<td>0</td>
</tr>
</tbody>
</table>

¹ Number of copulations (frequency/observation hour).
² Recording of cycle began in mid-tumescence, so frequency is an over-estimate.
³ Animals anaesthetised during maximum tumescence of this cycle, no observations on one day and effects probably lasted 2–3 days.
to the animals being anaesthetised for a medical check-up. This occurred during her maximum tumescence; one day’s observation was lost and several days elapsed before the chimpanzees’ behaviour returned completely to normal. *Bido* only copulated in two of the five cycles observed. She had never been seen to copulate prior to cycle III, and the absence of copulations in three of her cycles considerably depressed her total frequency relative to the other females.

The rise and fall of the sex skins is given graphically in figure 1. Initially, we interpolated between significant turning points, such as when swelling reached a plateau, or when swelling decreased to a minimum flatness for several days consecutively. Thus, the left side of the figure is schematic and rather crude. Later, we substituted the more refined interval system of fractional assessment: 0, $\frac{1}{4}$, $\frac{1}{2}$, $\frac{3}{4}$, 1. This resulted in the more accurate but less smooth vicissitudes in the right half of the figure. The four records coincide, so that occasions on which animals were simultaneously maximally tumescent can be derived.

The females’ cycling patterns indicate their differing stages of sexual development. The normal sexual cycle of a mature female chimpanzee lasts 37 days [YERKES and ELDER, 1936] and in her only cycle, the experienced *Gigi* showed the typical swelling pattern and time course. *Polly*’s swellings

---

*Fig. 1.* Sexual swelling cycles of the four chimpanzee females. Ordinate gives the standard gradient of sexual swelling from 0 (no swelling) to 1 (maximum tumescence). Abscissa measures time in three-day intervals chronologically from left to right. The six instances of observed menstruation are indicated by solid horizontal bars beneath each graph.
were similar but varied more in length (29–42 days). Menstrual bleeding occurred regularly between each of Polly's cycles. Belle's cycles varied irregularly in length, her cycle V being the only one typical of the mature chimpanzee female. We observed menstrual bleeding only once (almost certainly her menarche), during detumescence of cycle III. Belle’s swelling size blossomed dramatically over the observation period from small swellings restricted to the vulvar lips (typically adolescent) to full swellings of the entire perineum. At the younger end of the spectrum, Bido's sexual cycling typified young adolescence: small swellings showing irregular fluctuations from day to day. We never saw Bido menstruate. She only copulated when both Polly and Belle were non-swollen, i.e. when she was the only heterosexual outlet available to Shadow. All four females showed a high concentration of copulations during maximum tumescence and tended to copulate more frequently in the mornings than in the afternoons [TuTIN and McGREW, 1973].

**Table II.** Behavioural elements exhibited in copulatory behaviour of adolescent chimpanzees

<table>
<thead>
<tr>
<th></th>
<th>Male</th>
<th>Female</th>
<th>Either</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pre-intromission</strong></td>
<td>bipedal display</td>
<td>female posture</td>
<td>advance</td>
</tr>
<tr>
<td></td>
<td>‘branch’ shake</td>
<td>present</td>
<td>approach</td>
</tr>
<tr>
<td></td>
<td>gaze</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>glance</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>hair erect</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>lip-flip</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>male invite</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>manhandle</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>nest build</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>penis erect</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>penis manipulate</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>quadrupedal bounce</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>rock</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>sex display</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>stick wave</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Post-intromission</strong></td>
<td>leanback</td>
<td>grin</td>
<td>end intromission</td>
</tr>
<tr>
<td></td>
<td>mount</td>
<td>hit out</td>
<td></td>
</tr>
<tr>
<td></td>
<td>number of thrusts</td>
<td>squeal</td>
<td></td>
</tr>
<tr>
<td><strong>Either</strong></td>
<td>bumpprump</td>
<td>follow</td>
<td></td>
</tr>
<tr>
<td></td>
<td>inspect</td>
<td>groom</td>
<td></td>
</tr>
<tr>
<td></td>
<td>male ‘frustration’</td>
<td>leave</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>play</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>self-inspect</td>
<td></td>
</tr>
</tbody>
</table>
Table III. Definitions of copulatory behaviour elements

Advance: Individual moves toward another but stops outside of arm's reach.
Approach: Individual moves toward another and stops within arm's reach.
Bipedal display: Male stands, walks or runs bipedally. Usually incorporates slight hair erection and side to side swaying.
Branch' shake: Male repeatedly jerks a tree branch (or substitute) back and forth.
Bumprump: Rubbing of the perineal areas of two individuals. The active participant (male or female) backs toward the passive, usually prone recipient (always a somewhat swollen female), crouches quadrupedally, then repeatedly moves its perineum vertically against the other's, making contact on both upward and downward motions.
End intromission: Animal responsible for male's penis leaving female's vagina.
Female posture: Female may adopt the following postures during copulation:
  flat prone: lies on venter, arms usually at side of body, legs either straight back or pulled forward and flexed at knee, grasshopper-style;
  flat supine: lies on back, legs flexed at knee and jack-knifed against body;
  crouch: 'normal' copulatory posture. Body supported on all four partially flexed limbs;
  upright quadrupedal: body supported on all four extended limbs;
  side: body supported on either side, leg and arm positions variable;
  kneel: body primarily supported on knees and shins with arms partially flexed.
Follow: Individual orients locomotion and trails behind another moving animal.
Gaze: Male stares at female for two or more seconds.
Glance: Male looks at female for less than two seconds.
Grin: Individual exhibits full closed grin face: mouth corners retracted, upper and lower teeth together and exposed.
Groom: Manipulatory movements of fingers and/or lips directed to body surface (except for perineum) of self or others, characterised by:
  (a) focus of attention on spot being groomed;
  (b) often accompanying vocalisations, for example lip-smacking, teeth-clapping, or spluttering;
  (c) transfer between site of grooming and mouth;
  (d) relative immobility and passivity of groomee.
Hair erect: Male's hair is abducted from his skin.
Hit out: Female extends arm horizontally toward male in sudden movement, sometimes striking him with forearm or hand.
Inspect: Face and/or hands are brought close (usually within 20 cm) or into contact with perineum of self or others. The female's vaginal opening is socially inspected. The inspecting individual parts the lips of the vagina and uses fingers, mouth or nose to poke, lick or sniff. The self inspecting individual inserts a finger (female) or dabs with a finger (male).
Intromission: Penis enters vaginal canal.
Leanback: Male squats behind female during intromission with both hands on the ground and leans back slightly.
Liplip: Male manually everts his lower lip and hooks it below his chin.
Leave: Individual moves beyond arm's reach of another.
Male 'frustration': Combination of elements: full open grin, whimper, hand extended toward female without touching her.

Male invite: Male sits with legs partially flexed and spread apart, feet close together, revealing his erect penis.

Manhandle: Male pulls, pushes, or otherwise manipulates female into a posture permitting copulation.

Mount: Part of the mounter’s ventral surface contacts part of the other’s back, and mounter appears to rest weight on the other.

Nest build: Animal manipulates and interlaces sticks, grass, twigs, etc. in area next to and around his body.

Number of thrusts: Number of rhythmical back and forth pelvic movements.

Penis erect: Male's penis is fully distended.

Penis manipulate: Male briefly fingers or strokes his erect penis without looking at it.

Play: Vigorous non-agonistic interaction in which two or more participants exhibit a similar set of behaviour patterns [van Hooff, 1971; van Lawick-Goodall, 1968; LoiZos, 1969].

Present: Female crouches in front of male with her swelling oriented toward him.

Quadrupedal bounce: Male stands with rounded back and head lowered, repeatedly pushes his body up and down by flexing and extending limbs but not leaving ground.

Rock: Male oscillates torso forward and backward from hips in slow, rhythmic motion.

Sex display: Male stands bipedally with penis erect and hair down, often with flip-lip. He raised one or both arms vertically overhead while leaning slightly backward, thus maximally exposing his erect penis.

Squeal: Clear, high-pitched sound of variable length accompanying grin.

Stick wave: Male swings stick or branch to and from in low, looping horizontal motions while standing bipedally.

Table II lists the behavioural elements recorded in the study. They are divided by sex (whether exhibited by male or female or either) and time (whether before or after intromission or either). Table III lists brief definitions of the categories. Many of the definitions correspond to those in the unpublished glossaries of van Lawick-Goodall and McGinnis. Figures 2-8 illustrate selected elements.

The distribution of the elements of copulatory behaviour by time and sex in table II indicates the nature of the interaction. Almost half the patterns are performed by the male before intromission and constitute a complex of courtship behaviour. The female performs few exclusively sex-specific behaviours at any point in the interaction. The elements in table II exhibited by either sex are mostly general behaviours related to the participants' spacing or incorporated secondarily from other types of behaviour.
Fig. 2. Shadow gives sex display (note erect penis and lipflip) to females Belle (left) and Bid (right).

Fig. 3. Shadow sits in male invite posture with erect penis and lipflip.

Fig. 4. Shadow and Belle copulate during her cycle II. Belle is in flat prone posture with legs extended; Shadow almost completely covers her body.
Legends see p. 246.
Ontogenetic Changes

A pair of animals showed significant changes in copulatory behaviour from cycle to cycle. Figures 9 and 10 illustrate this by comparing Shadow and Polly’s copulatory behaviour in her cycles I and IV. Behavioural sequences are summarised in flow chart form. In the figures, the three type sizes indicate three degrees of frequency of the behavioural elements. (The number of intromissions rather than the number of copulations represents 100%). The smallest type size gives elements occurring in 11–33% of cases, the middle type those occurring in 34–67% of cases, and the largest type those occurring in over 68% of cases. The lines between the elements represent transitions from one element to another in the direction indicated. The four line thicknesses from the narrowest to widest represent 6–25, 26–50, 51–75, and 76–100% of cases, respectively. These percentages were cal-
Fig. 9. Sequence of copulatory behaviour elements exhibited by Shadow and Polly, during her cycle I.

culated from the proportion of the total occurrences of element A which were immediately followed by element B. If element A occurred 20 times and was immediately followed by element B on 15 occasions the percentage for the transition from A to B was 75%. Elements occurring in 10% or less of cases and transitions occurring in 5% or less of cases were omitted. Also omitted for the sake of diagrammatic clarity were cases in which transitions occurred only once but the relative rarity of the first element produced a transition occurrence of more than 5%.
Fig. 10. Sequence of copulatory behaviour elements exhibited by Shadow and Polly during her cycle IV.

The flow chart in figure 9 is based on the 18 copulations of Polly’s cycle I (all had a single intromission). The typical sequence began when Shadow, with penis erect, showed a sex display accompanied with the lipflip (fig. 2). Polly responded to this by moving to Shadow and presenting; alternatively, Shadow approached her and she responded by presenting. Shadow then effected intromission from a mount or leanback posture and commenced pelvic thrusting. The mean number of pelvic thrusts per intromission was 11.3 (n = 13, range 2–35). Either animal might end intromission but usually it was Polly. Genital inspection, self or social, often followed intromission. Polly usually ended the interaction by leaving, but sometimes they played before parting. The behavioural sequence was relatively consistent: Shadow
showed much idiosyncratic behaviour before intromission, and Polly responded like a mature female chimpanzee.

Figure 10 is a flow chart for Shadow and Polly based on 37 intromissions in 35 copulations of her cycle IV. The typical copulatory sequence is depicted down the centre of the figure. Shadow usually glanced repeatedly at Polly, who then followed him as he walked away. He then performed a bipedal display accompanied by hair erection, sometimes incorporating other displays such as sex display, male invite, or rock. When Shadow had an erect penis, Polly advanced, approached and presented to him, and he effected intromission from a mount or leanback posture. During intromission he averaged 9.3 pelvic thrusts (n = 35, range 2–20). Polly commonly ended intromission, then either or both chimpanzees inspected their genitals and she left.

Four months separated Polly's cycles I and IV (mid-February to mid-June) and striking differences existed between the pair's behaviour in the two cycles. Table IV lists the behaviour patterns seen predominantly in one cycle or the other.

Lipflip and sex display, both significantly more frequent in cycle I than in cycle IV, were idiosyncratic patterns not previously reported for the chimpanzee. Branch shake, follow, glance, hair erect and bipedal display were all significantly more common in cycle IV than in cycle I, and these patterns have previously been described for adult male chimpanzee courtship. It appears that Shadow's courtship developed over these four months from idiosyncratic, adolescent to more typical adult male courtship.

During this time Shadow showed no marked physical development. He gained some weight and his upper canines lengthened but these happened gradually. Onset of spermatogenesis had occurred earlier; Shadow impregnated Gigi in August, 1971. However, a dramatic change occurred in the social relations of the group which was probably linked to his changed sexual behaviour. At the beginning of the study, Shadow was clearly subordinate to Polly and Gigi. (Dominance–subordinance was judged on three criteria: object possession, displacement from specific locations, and outcome of agonistic encounters. Gigi and Polly were very close and often acted in concert against Shadow.) Then followed a turbulent period during which the adult male Rock re-entered the group and, although clearly subordinate to Rock, Shadow's dominance relations to Gigi and Polly were difficult to assess. From early May when Rock left the group, Shadow gradually became more assertive over the others, including Gigi and Polly. By early June he was unquestionably the dominant animal in the group.
Table IV. Frequencies of behaviour patterns seen in Shadow–Polly copulations, differences between Polly’s cycles I and IV

<table>
<thead>
<tr>
<th>Behaviour pattern</th>
<th>I</th>
<th>IV</th>
<th>Total</th>
<th>$\chi^2$</th>
<th>p$^1$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n = 18</td>
<td>n = 37</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lipflip</td>
<td>12</td>
<td>0</td>
<td>12</td>
<td></td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Male advance</td>
<td>8</td>
<td>0</td>
<td>8</td>
<td></td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Sex display</td>
<td>9</td>
<td>5</td>
<td>14</td>
<td></td>
<td>&lt; 0.02</td>
</tr>
<tr>
<td>Male approach</td>
<td>8</td>
<td>7</td>
<td>15</td>
<td>2.7</td>
<td>n. s.</td>
</tr>
<tr>
<td>Leanback</td>
<td>9</td>
<td>13</td>
<td>22</td>
<td>1.1</td>
<td>n. s.</td>
</tr>
<tr>
<td>Penis erect</td>
<td>18</td>
<td>31</td>
<td>49</td>
<td>0.3</td>
<td>n. s.</td>
</tr>
<tr>
<td>Male ends intromission</td>
<td>6</td>
<td>9</td>
<td>15</td>
<td>0.3</td>
<td>n. s.</td>
</tr>
<tr>
<td>Female self-inspect</td>
<td>3</td>
<td>5</td>
<td>8</td>
<td></td>
<td>n. s.</td>
</tr>
<tr>
<td>Intromission</td>
<td>18</td>
<td>37</td>
<td>55</td>
<td>0</td>
<td>n. s.</td>
</tr>
<tr>
<td>Thrusting</td>
<td>18</td>
<td>37</td>
<td>55</td>
<td>0</td>
<td>n. s.</td>
</tr>
<tr>
<td>Female leaves</td>
<td>17</td>
<td>36</td>
<td>53</td>
<td>0</td>
<td>n. s.</td>
</tr>
<tr>
<td>Mount</td>
<td>17</td>
<td>37</td>
<td>54</td>
<td>0.1</td>
<td>n. s.</td>
</tr>
<tr>
<td>Female ends intromission</td>
<td>12</td>
<td>28</td>
<td>40</td>
<td>0.2</td>
<td>n. s.</td>
</tr>
<tr>
<td>Male self-inspect</td>
<td>9</td>
<td>22</td>
<td>31</td>
<td>0.2</td>
<td>n. s.</td>
</tr>
<tr>
<td>Present</td>
<td>9</td>
<td>23</td>
<td>32</td>
<td>0.4</td>
<td>n. s.</td>
</tr>
<tr>
<td>Male invite</td>
<td>4</td>
<td>14</td>
<td>18</td>
<td>0.9</td>
<td>n. s.</td>
</tr>
<tr>
<td>Female approach</td>
<td>6</td>
<td>31</td>
<td>37</td>
<td>4.7</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Bipedal display</td>
<td>3</td>
<td>22</td>
<td>25</td>
<td>5.1</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Female advance</td>
<td>6</td>
<td>34</td>
<td>40</td>
<td>5.9</td>
<td>&lt; 0.02</td>
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<tr>
<td>Glance</td>
<td>0</td>
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<td></td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Follow</td>
<td>0</td>
<td>13</td>
<td>13</td>
<td></td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Branch shake</td>
<td>0</td>
<td>17</td>
<td>17</td>
<td>8.4</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Hair erect</td>
<td>0</td>
<td>21</td>
<td>21</td>
<td>10.3</td>
<td>&lt; 0.01</td>
</tr>
</tbody>
</table>

$^1$ When the total $\geq$ 15, $\chi^2$ test is used; when the total $< 15$, binomial test is used.

Some behaviour patterns are common to adult male courtship and agonistic interaction, for example bipedal display, hair erect, branch shake and rock. It is possible that while Shadow was competing for dominance with the females, his use of these behaviour patterns in courtship may have elicited an aggressive response. This may explain why Shadow showed idiosyncratic behaviour in this context during cycle I. The patterns lipflip and sex display have apparently not been reported previously for the chimpanzee in any context. They appear to be arbitrary signals devised by Shadow to obtain a
goal unobtainable by conventional methods. A similar interpretation may explain the appearance of patterns such as glance and follow in the later cycle. Although these patterns have no agonistic connotations it seems likely that they require dominant, or at least equal, status to be effective. It is unlikely that a subordinate animal could induce a dominant one to follow him, sometimes for distances of several hundred feet, merely by glancing or gazing.

*Fig. 11. Sequence of copulatory behaviour elements exhibited by Shadow and Belle during her cycle IV.*
We conclude that Shadow was initially inhibited from displaying the behaviour patterns of an adult male chimpanzee because of his subordinate status relative to the available females. With his newly acquired dominance he was able to adopt more typical behaviour patterns and to abandon his early idiosyncracies.

**Individual Differences**

Figure 11 is the flow chart for Shadow and Belle based on the 63 intromissions in 46 copulations in her cycle IV. The overall pattern was less consistent than either of Shadow's or Polly's and no single typical sequence of copulatory behaviour emerged. Initially Shadow frequently engaged Belle in a non-sexual activity, for example play, grooming, and gradually manhandled her into intromission. He always used a mount posture during intromission with her, apparently in order to prevent her breaking away. The number of pelvic thrusts resembled that in Shadow–Polly copulations; \( x = 10.9, n = 61, \text{range } 2-25 \). After intromission they often returned to their pre-copulatory activity or exhibited some other non-sexual associative behaviour. This frequently led to another intromission.

Shadow's tactics obviously differed between the two females. Belle's cycle IV was in late June-early July, just after Polly's cycle IV. But Belle's level of experience in this cycle was closer to Polly's in cycle I (although not equivalent, as Polly had been copulating for over six months prior to the present study). Shadow and Belle exhibited four elements not seen in Shadow–Polly copulations: groom, bumpump, manhandle and male 'frustration'. Conversely, bipedal display, sex display, male invite, rock, hair erect and leanback were never or rarely seen in Shadow–Belle copulations. Although Shadow was dominant to Belle, he showed no typical adult male courtship patterns to her, although these were common in his copulations with Polly at this time. With Belle, Shadow probably had to incorporate many non-agonistic, general behaviour patterns since she was a non-cooperative, passive partner. The usual adult male courtship would have been ineffective with Belle as it requires an active response from the female.

At least, two alternative explanations exist for the differences in the copulatory behaviour of the two females. Perhaps Belle exhibited an unpracticed, adolescent form of behaviour while Polly showed a more typical adult female form because of differing degrees of sexual experience and physical maturation, with Belle lagging behind. Or, perhaps individual differences based on personality and past experiences existed, and Belle's behaviour may never come to resemble Polly's. Only continued observations
to maturity will provide an answer. That the two females are at different stages of sexual development in physiological terms was shown earlier, but they also experienced different rearing conditions in early life. Belle arrived at Delta at approximately 12 months of age and was always housed with at least two males of a similar age. She always lived in large enclosures and was cared for by one person for five years. Polly was probably between 18 and 24 months of age upon arrival at Delta and lived alone for her first 2½ years, having only limited contacts with a series of similarly aged males and females. She lived in a small cage and was cared for by a series of human attendants. Thus, Belle had a more socially stimulating early upbringing, but her younger age at capture and the formation of a strong emotional relationship with a single human caretaker may have detrimentally affected the development of her sexual behaviour [ROGERS and Davenport, 1969].

Belle was probably a virgin at the study's beginning. In her first cycle during our observations (when she still exhibited small adolescent swellings), we saw her copulate once with Shadow. In her next cycle, her swelling was noticeably bigger and Shadow showed great sexual interest in her, and at least 19 copulations resulted. She behaved similarly in both cycles, appearing totally passive and allowing Shadow free license in his actions. She appeared oblivious to his activities and sometimes lay and self-groomed during intromission. In her cycle II, 40% of copulations occurred with Belle lying prone or supine. In her cycle III, only 8% of copulations involved lying either prone or supine, while 74% occurred with Belle crouched in the normal position or standing quadrupedally with legs extended. By cycle IV Belle crouched in the normal posture for 80% of copulations and only 5% occurred with her lying prone or supine. Belle became no more actively involved in copulations, but she gradually made it easier for Shadow.

Gigi copulated for over a year before the study began. In the 31 copulations we observed, she was cooperative and efficient. The copulations averaged less than five minutes in length. Shadow–Gigi copulations were almost behaviourally identical to Shadow–Polly ones in Polly's cycle I, although Gigi was the only female who regularly vocalised and grimaced during intromission. Gigi and Shadow rarely indulged in non-sexual associative interaction, except for his occasionally grooming her.

Bido was probably also a virgin before her 11 copulations in her cycle III. Contact play preceded all her copulations and they all involved manhandling. She was more active than Belle but not cooperative; she frequently attempted to restart play during intromission. The duration of copulations were not systematically recorded, but Shadow and Bido had long copulations
with bouts of non-sexual associative behaviour, such as play, grooming or nest building, interspersed with sexual interaction. Their longest copulatory sequence lasted 47 minutes and included two intromissions.

Thus, the four females represented a spectrum of sexual experience: Gigi, now a mother; Polly, experienced and cooperative; Belle, relatively experienced but still passive; and Bido, behaviourally inexperienced and physically immature.

Discussion

The results suggest that group-living chimpanzees in a large field enclosure behave more like free-living chimpanzees than like other captive chimpanzees paired in small cages. This is not surprising, but it illuminates some of the distortions of the typical captive chimpanzee's incarceration. Several behaviour patterns recorded in this study could not have occurred in the usual caged situation. Lack of space would preclude elements involving long distance locomotion, such as prolonged following by the female or glancing-and-leading by the male. Lack of suitable or even moveable objects would preclude other elements such as branch shaking, stick waving or nest building. In addition to being significant in this group, such behaviour patterns are commonly shown by free-living chimpanzees [Van Lawick-Goodall, 1968].

In general, our group's sexual behaviour resembled descriptions given for free-living populations. However, Shadow's copulatory repertoire showed more variability and eccentricity than those of his wild-living counterparts. This may have resulted from Shadow's being reared exclusively in a peer group lacking adults on whom to model 'normal' copulatory behaviour. Or, because this group was not forced to spend long periods daily foraging for food, its members had ample time for experimentation and innovation. When Gigi and later Polly became sexually receptive Shadow was subordinate to them both. One can imagine the usefulness of a signal pattern such as lip-flip, being visually obvious from a distance and having no intrinsic agonistic meaning. A long range, sex-specific behaviour pattern would be useful to a young subordinate male temporarily faced with only more dominant females available for copulation. Later, after achieving dominance, he could abandon the idiosyncratic elements and adopt the more normals chimpanzee courtship patterns.

The greatest difference between this group's constituency and wild chimpanzee populations is its abnormally uniform age structure. This seems to
have affected the males more than the females. In a wild mixed-age-sex population, the development of male sexual behaviour is long and probably intimately tied with male-male dominance. Shadow's development seems to have been accelerated and diversified by the lack of this. The females' behaviour was closer to that of their wild-living counterparts. Because their sexual development was closely linked to physiological events such as the first adult swelling, it appeared less susceptible to effects of the social and physical environment.

Chimpanzees brought up artificially, either in nurseries or under deprivation conditions, commonly show abnormal or inadequate sexual behaviour (Riesen, 1971; Rogers and Davenport, 1969). Effects are more pronounced in males, at least partly, because a copulation does not require compliance by the female. Competent male sexual behaviour appears to develop more as a response to the presence of a receptive female than to physiological maturation. The appearance of male sexual behaviour precedes the onset of spermatogenesis. In the wild, male infants from five months onwards show interest in swollen females and are able to mount and show pelvic thrusting with intromission by one year of age (van Lawick-Goodall, 1968). However, it seems that without the stimulus of a receptive female before maturity, male sexual behaviour may never develop. In the Holloman Air Force Base consortium, all adolescent and juvenile males introduced into the group showed normal sexual behaviour, but only two of the five adult introduced did so (one of the adequate males is reported to have had experience with a receptive female while adolescent) (Kollar et al., 1968). Lemmon (1971) reports that if artificially raised chimpanzees are given an adequate surrogate mother, i.e. they are home raised with full-time attention from at least one human, sexual behaviour will appear normally when they have access to a receptive female. (In all cases the access has been provided prior to maturity.) It seems that the crucial factors for producing sexually competent males is to give them an adequate social environment in early life and, equally important, access to a receptive female before they are fully mature. None of our females had any prior sexual experience, and Lemmon (1971) also reports that a receptive inexperienced female can elicit sexual behaviour from an inexperienced male. Most males on whom data are available were wild-born, but most were only a year old or less when captured. It is possible that some sexual behaviour was learned at this tender age. However, the evidence suggests that learning by imitation is not crucial to sexual development but that the important factors are an adequate social environment and exposure to a sexually receptive female before maturity.
Summary

Observations of the copulatory behaviour of group-living, adolescent chimpanzees (*Pan troglodytes*) in a large field enclosure revealed large individual differences in behaviour, and the rapid ontogeny of some behavioural elements. Each female elicited different courtship patterns from the same male. These differences apparently stemmed from differing levels of experience and influences of personality differences. The male changed his courtship of the females over the study period, probably in relation to his rise to dominance within the group.

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