QUANTITATIVE STUDY OF COPULATORY BEHAVIOUR OF LARGE FELIDAE

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ABSTRACT


A total of 109 copulations was observed in six male-female pairs from four species of large Felidae. The mean intromission durations were 3.0 sec for Asian leopards (Panthera pardus), 12.9 sec for snow leopards (Uncia uncia), 3.3 sec for spotted jaguars (Panthera onca), 3.3 sec for black jaguars (Panthera onca), and 2.4 sec for Siberian tigers (Panthera tigris). Behavioural patterns were qualitatively similar across species; all displayed a copulatory pattern with no lock, no intravaginal ejaculation on a single insertion, and multiple ejaculations. Whereas domestic cats are reported to assume a neck grip and to tread prior to insertion, these larger Felidae usually did so after intromission had been achieved. After copulation, females of some species reacted at the male and displayed a rolling after-reaction.

INTRODUCTION

Despite the large number of breeding pairs of large Felidae in zoos and private collections, there are few complete descriptions of feline copulatory behaviour. Although there have been some excellent quantitative studies of domestic cats (e.g. Michael, 1961; Whalen, 1963), Dewsbury (1972) proposed a complete classification of the copulatory pattern could be determined.

Domestic cats show a copulatory pattern of no lock, no intravaginal thrusting, and on a single insertion and multiple ejaculations. While descriptions in large Felidae generally indicate that patterns are similar to those of domestic cats, previous reports of copulation in tigers (Sankhala, 1967; Sankhala, 1967; Gowda, 1968), jaguars (Stehlik, 1971), lions (Cooper, 1942; Coop, 1942; Stehlik, 1971; Eaton and York, 1971; Schaller, 1972; Rudnai, 1973), and leopards (Freeman, 1975) are lacking in sufficient detail to allow classification with regard to various qualitative characteristics.

The present study allows classification of four additional feline species in the system of Dewsbury (1972) and provides precise quantitative measures of copulation for these species.
**METHODS**

Observations were conducted at the Rare Feline Breeding Center in Center Hill, Florida, which was described by Baudy (1971). Observations were made between the hours of 08.00 h and 20.00 h, with most observations made between 12.00 h and sunset. Observations generally represent behavior after the first day of copulation for each pair.

A total of 109 copulations from six pairs of large Felidae was observed and recorded. The schedule was as follows: on January 3, 1973, 41 copulations in a pair of Asian leopards, *Panthera pardus*; January 4, 5 and 6, a total of 36 copulations in a pair of African leopards, *Panthera pardus*; January 16 and 17, 10 copulations in a pair of snow leopards, *Uncia uncia*; March 3 and 4, four copulations in a pair of spotted jaguars, *Panthera onca*; March 26, four copulations in black jaguars, *Panthera onca*; and on March 19 and 20, 16 copulations in Siberian tigers, *Panthera tigris*.

All copulations were observed by one observer (D.L.L.), with a second observer present on some occasions. Measures were derived from a running narration which was recorded on a portable tape recorder. A mono-syllabic code was used. These data were supplemented with and checked against records on both 16 mm and super 8 motion picture film and still photographs.

The frequency of two kinds of mount was scored: those with pelvic thrusting and intromission, which are presumed nearly always to include ejaculation, and those with pelvic thrusting, but no intromission. These are termed, respectively, mounts with intromission, intromissions or copulations, as opposed to mounts with thrusting. In addition, the occurrence or non-occurrence of each of the following behavioural patterns was recorded for each mount with intromission:

**Male approach** — instances where it was the male that approached the female and initiated the interaction leading to copulation.

**Female precopulatory vocalization** — instances where the female vocalized prior to being mounted. This was often a sort of moaning as in spotted leopards or a “purring-puffing” sound as in tigers.

**Female presentation** — instances in which the female solicited the male, typically by backing toward him, thus bringing her perineal region near to him.

**Female crouch** — instances in which the female displayed a crouching posture in front of the male prior to being mounted.

**Male vocalization** — instances where the male vocalized during copulation.

**Female swipe** — instances in which the female turned and swung a paw at the male at the end of a copulation.

**Female roll** — instances where the female displayed a rolling “after-reaction” within one minute following copulation.

The number of neck bites, instances in which the male bit at the nape of the female's neck, was recorded for each copulation.

The following latency measures were obtained:

**Interval from female crouch to male mount** — time from the female crouch of

**RESULTS**

All species observed display pattern recognition system, showing no lock, on a single insertion, and multiple ejaculations. The general sequence of copulation includes, tigers and snow leopards various subunits earlier reported for domestic cats (Hart, 1967).

The sequence typically begins with the male vocalizing. If the female may present her ano-genital region close to that of the male, crouching posture resting on her extended forelegs, the male may have her head raised and rectum close to that of the female. The female deflects her tail. The male makes one or two quick bites at the male's neck, which appears to function in leading to thrusting, and inserts the tip of his penis into her vagina, and the male makes three or four quick bites at the female's neck. The female often emits a low, growling sound, the more the male makes a "scream", presumably he usually turns toward the male and male thrusting. The female may show an anal swell on the ground.

While domestic cats are reported to use extra-vaginal thrusting and insertions, intromission has been achieved. The percentage of tests in which ejaculation was noted is presented.
The male stood over her oriented with forepaws on either side
his body and his genital region behind her.

Latency from male mount to male thrust — latency from the male’s mount,
above, to the onset of extra-vaginal pelvic thrusting.

Intromission mount duration — interval from the male’s mount until
penetration.

Intromission interval — time from the end of one intromission to the
onset of the next.

Intromission duration — the length of time that the male’s penis appeared
the female’s vagina. This measure was calculated both from the
record and through a single frame analysis of the 16 mm film.

All species observed display pattern number 15 in Dewsbury’s (1972)
system, showing no lock, no intra-vaginal thrusting, ejaculation
insertion, and multiple ejaculations.

The general sequence of copulation-related behaviour in these jaguars,
tigers and snow leopards varied little across species and closely re-
teled those earlier reported for domestic cats and tigers (Whalen, 1963;
Dewsbury, 1967).

The sequence typically begins with the male approaching the female,
calling she may vocalize prior to his approach, perhaps indicating receptivity.
The female may present her ano-genital region to the male by backing
with her tail deflected to one side. The female then assume a
resting posture resting on her extended forelimbs. In the snow leopard, the
may have her head raised and rest on her forepaws. The female’s hind-
are flexed and under her body. The male mounts by stepping over and
the female with forelegs straddling her on either side. He then brings
region close to that of the female by squatting on his hindlegs.
the female deflects her tail. The male then initiates extra-vaginal pelvic
which appears to function in detecting the vaginal orifice. The male
deep pelvic thrust after insertion is gained. During insertion, the
emit three or four quick bites at the nape of the female’s neck. The
then emits a low, growling sound. Near the end of the intromission,
ma a “scream”, presumably indicative of ejaculation. The female
turns toward the male and may swing a paw at him immediately after
mission. The female may show an after-reaction, consisting of vigorous
the ground.

Domestic cats are reported to assume a neck grip and to tread prior
eral thrusting and insertion, these large Felidae do so only after
mission has been achieved.

The percentage of tests in which each of the behavioural patterns
above was noted is presented in Table I. Males of all species vocalized
TABLE I

Percentage of mounts with intromission on which various behavioural patterns occurred as part of the sequence

<table>
<thead>
<tr>
<th>Behavioural pattern</th>
<th>Animals</th>
<th>Asian leopards</th>
<th>African leopards</th>
<th>Snow leopards</th>
<th>Spotted jaguars</th>
<th>Black jaguars</th>
<th>Siberian tigers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male approach</td>
<td></td>
<td>70</td>
<td>3</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>25</td>
</tr>
<tr>
<td>Female precopulatory vocalization</td>
<td></td>
<td>69</td>
<td>100</td>
<td>0</td>
<td>0</td>
<td>33</td>
<td>80</td>
</tr>
<tr>
<td>Female presentation</td>
<td></td>
<td>38</td>
<td>100</td>
<td>0</td>
<td>0</td>
<td>100</td>
<td>91</td>
</tr>
<tr>
<td>Female crouch</td>
<td></td>
<td>59</td>
<td>100</td>
<td>88</td>
<td>100</td>
<td>33</td>
<td>60</td>
</tr>
<tr>
<td>Male vocalization</td>
<td></td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>94</td>
</tr>
<tr>
<td>Female swipe</td>
<td></td>
<td>59</td>
<td>67</td>
<td>12</td>
<td>0</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Female roll</td>
<td></td>
<td>0</td>
<td>62</td>
<td>100</td>
<td>0</td>
<td>0</td>
<td>88</td>
</tr>
</tbody>
</table>

Number of observations: 41, 34, 10, 4, 4, 16

on nearly all copulations. Males generally appeared to initiate sequences in four of the six pairs. The frequencies of female precopulatory vocalization and female presentation generally appear inversely proportional to the frequency of male approach. Females in all pairs crouched prior to being mounted in at least one-third of the copulatory sequences. Differences between pairs on this measure may reflect individual receptivity rather than species differences.

One possible species difference appears in the absence of post-copulatory swiping and rolling in the two jaguar females. However, post-copulatory rolling in jaguars has been reported by Stehlik (1971).

As is shown in Table II, mounts with thrusting but no intromission were

TABLE II

Mean and standard error for the number of mounts with thrusting but no intromission, and neck bites per mount with intromission

<table>
<thead>
<tr>
<th>Measure</th>
<th>M or SE</th>
<th>Animals</th>
<th>Asian leopards</th>
<th>African leopards</th>
<th>Snow leopards</th>
<th>Spotted jaguars</th>
<th>Black jaguars</th>
<th>Siberian tigers</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of mounts with M</td>
<td>0.8</td>
<td>Asian leopards</td>
<td>0.1</td>
<td>0.4</td>
<td>0.3</td>
<td>0.3</td>
<td>0.6</td>
<td></td>
</tr>
<tr>
<td>thrust per intromission</td>
<td>0.4</td>
<td>African leopards</td>
<td>0.1</td>
<td>0.2</td>
<td>0.3</td>
<td>0.3</td>
<td>0.5</td>
<td></td>
</tr>
<tr>
<td>No. of neck bites per</td>
<td>3.5</td>
<td>Snow leopards</td>
<td>2.4</td>
<td>3.7</td>
<td>—</td>
<td>3.0</td>
<td>4.0</td>
<td></td>
</tr>
<tr>
<td>intromission</td>
<td>SE</td>
<td>Spotted jaguars</td>
<td>0.2</td>
<td>0.3</td>
<td>—</td>
<td>0.0</td>
<td>0.6</td>
<td></td>
</tr>
<tr>
<td>No. of observations</td>
<td>41</td>
<td>Black jaguars</td>
<td></td>
<td>4</td>
<td>4</td>
<td>16</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

INTRODUCTION

Temporal measures are presented in Table III. Intromission averaged 5–13 seconds. Intromission intervals ranged from six to 32 minutes.

TABLE III

Mean and standard errors (in seconds) for the duration of copulations and male recovery times

<table>
<thead>
<tr>
<th>Measure</th>
<th>M</th>
<th>SE</th>
<th>Asian leopards</th>
<th>African leopards</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intromission duration</td>
<td>3.4</td>
<td>0.3</td>
<td>3.4</td>
<td>2.3</td>
</tr>
<tr>
<td>Length of post-intromission</td>
<td>2.5</td>
<td>0.2</td>
<td>4.4</td>
<td>4.4</td>
</tr>
<tr>
<td>Male recovery time</td>
<td>3.58</td>
<td>2.1</td>
<td>5.7</td>
<td>13.1</td>
</tr>
<tr>
<td>Number of observations</td>
<td>41</td>
<td>34</td>
<td>34</td>
<td>5</td>
</tr>
</tbody>
</table>
rare. Fewer “mounts with thrusting and no intromission” than “mounts with intromission” were observed in all species. Means of 2–4 neck thrusts per intromission were observed.

Temporal measures are presented in Table III. Pre-intromission mount duration averaged 5–13 seconds. Intervals from the female crouch to the male

<table>
<thead>
<tr>
<th>Measure</th>
<th>Animals</th>
<th>Asian leopards</th>
<th>African leopards</th>
<th>Snow leopards</th>
<th>Spotted jaguars</th>
<th>Black jaguars</th>
<th>Siberian tigers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean or SE</td>
<td>M</td>
<td>0.6</td>
<td>2.9</td>
<td>1.0</td>
<td>—</td>
<td>0.3</td>
<td>1.5</td>
</tr>
<tr>
<td>Mount to male mount</td>
<td>SE</td>
<td>0.1</td>
<td>0.4</td>
<td>0.2</td>
<td>—</td>
<td>0.3</td>
<td>0.2</td>
</tr>
<tr>
<td>Time from female</td>
<td>SE</td>
<td>3.4</td>
<td>2.8</td>
<td>2.9</td>
<td>—</td>
<td>3.0</td>
<td>1.6</td>
</tr>
<tr>
<td>Mount to male thrust</td>
<td>M</td>
<td>1.1</td>
<td>0.5</td>
<td>0.7</td>
<td>—</td>
<td>1.2</td>
<td>0.5</td>
</tr>
<tr>
<td>Intromission</td>
<td>SE</td>
<td>13.1</td>
<td>5.7</td>
<td>5.1</td>
<td>—</td>
<td>7.0</td>
<td>6.8</td>
</tr>
<tr>
<td>Mount duration</td>
<td>SE</td>
<td>5.8</td>
<td>0.6</td>
<td>1.0</td>
<td>—</td>
<td>0.6</td>
<td>2.2</td>
</tr>
<tr>
<td>Intromission duration</td>
<td>M</td>
<td>259</td>
<td>782</td>
<td>696</td>
<td>3315</td>
<td>3325</td>
<td>1558</td>
</tr>
<tr>
<td>SE</td>
<td>32</td>
<td>108</td>
<td>346</td>
<td>2435</td>
<td>770</td>
<td>482</td>
<td></td>
</tr>
<tr>
<td>Intromission duration (mean record)</td>
<td>SE</td>
<td>3.0</td>
<td>3.3</td>
<td>12.9</td>
<td>2.3</td>
<td>3.3</td>
<td>12.4</td>
</tr>
<tr>
<td>Intromission duration (mean in analysis)</td>
<td>SE</td>
<td>0.2</td>
<td>0.2</td>
<td>1.0</td>
<td>0.3</td>
<td>0.3</td>
<td>0.8</td>
</tr>
<tr>
<td>Intromission duration (mean in analysis)</td>
<td>SE</td>
<td>2.5</td>
<td>4.4</td>
<td>13.0</td>
<td>—</td>
<td>—</td>
<td>13.1</td>
</tr>
</tbody>
</table>

Number of observations:
- Cases 1–3: 41 34 10 0 4 6
- Cases 4–5: 41 34 10 4 4 16
- Cases 6: 24 5 2 0 0 2

Intromission intervals ranged from six to 55 minutes. It is not clear whether this reflects true species differences, individual female receptivity levels, or individual male recovery times. Intromission durations were strikingly longer in tigers and snow leopards than in leopards or jaguars.

**Discussion**

There appears to be no information in the existing literature that is inconsistent with our classification of leopards, snow leopards, jaguars and tigers displaying no lock, no intra-vaginal thrusting, ejaculation on single insertions, and multiple ejaculations. While we have located no reports on leopards, the
reports on tigers (Sankhala, 1967; Schaller, 1967; Gowda, 1968), jaguars (Stehlik, 1971) and snow leopards (Freeman, 1975) generally concur with that in areas where they are explicit.

Lions, Panthera leo, share at least the characteristics of no lock, ejaculation on single insertions, and multiple ejaculation with the other species (Cooper, 1942; Guggisberg, 1963; Eaton and York, 1971; Schaller, 1972; Rudnai, 1977). While both Schaller and Rudnai describe pelvic thrusting in lions, it is not clear whether this is the pre-intromission, shallow, detection thrusting, or deep intra-vaginal thrusting.

Copulation in cheetahs, Acinonyx jubatus, appears to differ from the other species in several regards. There appears to be no lock, ejaculation on a single insertion, and multiple ejaculations (Eaton and Craig, 1973). However, Eaton and Craig (1973) write that “The male intromits and thrusts rapidly 20–80 times in succession” (p. 247). We interpret this to mean that the animals display intra-vaginal thrusting. However, as this does appear to differ from other species, confirmation of this would be desirable. While Tong (1954) reported a copulation lasting for about a minute, in a pair of cheetahs, thrusting was not noted. Cheetahs also contrast with other big cats in that they neck grip prior to mounting (Eaton and Craig, 1973).

Available literature is more difficult to interpret in regard to quantitative aspects than regarding pattern, because measures that are reported are not always clearly defined. For example, many authors report “copulation duration.” It is not clear whether this means the duration of actual intromission, as in our data, or the duration of some longer part of the sequence which might include approaching, mounting, and perhaps rolling. Thus, when other authors report copulation durations longer than ours, it is not clear whether this difference rests in the animals or the observers. In tigers, Sankhala (1967) reports “duration of copulation” of 10 seconds to 3 minutes, and Gowda (1968) writes “Copulation lasted for about two minutes” (p. 64). “The duration of coitus” in jaguars is reported to average 9 seconds, with a range of 2–35 seconds (Stehlik, 1971). Cooper (1942) writes that in lions, “Each actual copulation lasts from 20 to 25 seconds” (p. 30). In the Caracal lynx, Felis caracal, at the Mysore Zoo, Gowda (1967) reports that “Copulation lasted for about 10 minutes” (p. 128). Rabb (1959) reports that in pumas, Felis concolor, at the Brookfield Zoo, “Copulation was brief, less than a minute in the instances observed” (p. 615). It should be clear that these measures must be defined with greater precision if meaningful comparisons are to be made possible.

Inter-intromission intervals generally average from a few minutes to an hour. There are reports of inter-intromission intervals of 4–49 minutes in tigers (Sankhala, 1967), 10–100 minutes in tigers (Gowda, 1968), 2–3 minutes in jaguars (Stehlik, 1971) and about 5 minutes in lions (Cooper, 1942). Stehnal (1971) regards the short intervals he observed as abnormal because the pair was not left together continuously. Freeman (1975) observed that intromission occurred three times within a period of 15 minutes in a pair of snow leopards.

The present work has shortcomings, particularly in regard to the possibility of making broad generalizations from a few numbers of animals breeding in various species of animals and cross-validated.

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REFERENCES

generating broad generalizations from a few animals. However, there are sufficient
evidence of animals breeding in various zoos for many more data to be collected
and cross-validated.

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REFERENCES

Barrett, R.E., 1971. Notes on breeding felids at the Rare Feline Breeding Center. Int. Zoo
Yearb., 11: 121-123.


47: 1-33.


Barlow, R.L. and York, W., 1971. Reproductive biology, and preliminary observations on


Int. Zoo Yearb., 7: 133.

Mysore Zoo. Int. Zoo Yearb., 8: 63-64.

Bergius, C.A.W., 1963. Simba, the Life of the Lion. Chilton Book Co., Philadelphia,
304 pp.

Bell, R.P., 1961. Observations upon the sexual behavior of the domestic cat, (Felis

Bell, G.B., 1959. Reproductive and vocal behavior in captive pumas. J. Mammal., 40:
503-517.

Bennett, J., 1973. Reproductive biology of lions (Panthera leo massaica Neuman) in

Yearb., 7: 133-147.

370 pp.


Bennett, J. 1971. Breeding jaguars Panthera onca at Ostrava Zoo. Int. Zoo Yearb., 11:
118-118.

129-130.