Running title: Mother-offspring conflict in Ammotragus lervia
sahariensis

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**Mother-offspring conflict in the Saharan arrui,
Ammotragus lervia sahariensis: Relation to weaning
and mother's sexual activity**

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Abstract

Behavioural conflict between mother and offspring was investigated in a captive population of the Saharan arrui (Ammotragus lervia sahariensis, Artiodactyla: Bovidae). The frequency of agonistic behaviours (mother's aggressiveness and calf's retreats) and unsuccessful suckling attempts, Hinde's proximity index and the distances between mother and calf have been analysed in relation to weaning and sexual activity of the mother. Mothers that conceive in the following mating season accelerate the weaning process of their current offspring; furthermore, high-ranking females wean their male calves earlier. Behavioural conflict occurs during the resume of mother's sexual activity; however, no conflict appears to happen during weaning.

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Introduction

32 Parent-offspring theory postulates the existence of a behavioural conflict
33 between parent and offspring, because of a genetic conflict of interest
34 between them (TRIVERS 1974). Classically, this conflict has been
35 related to the weaning period and the amount of parental investment
36 allocated to the offspring (TRIVERS 1974; see also LAZARUS &
37 INGLIS 1986). Defining weaning and therefore establishing the period
38 in which conflict may arise is a controversial issue (see GREEN et al.
39 1993). MARTIN (1984) proposed that weaning be defined as the period
40 during which parental investment (sensu TRIVERS 1972) decreases
41 most rapidly, but in some species the investment decreases very slowly,
42 without a neat inflexion point (GREEN et al. 1993).

43 From a theoretical standpoint the evolution of a behaviour
44 demanding more investment by the offspring has been confirmed by
45 several authors (MACNAIR & PARKER 1978, 1979; PARKER &
46 MACNAIR 1978, 1979; STAMPS et al. 1978; PARKER 1985; ESHEL
47 & FELDMAN 1991), but, in spite of the great interest that parent-
48 offspring theory has generated, few empirical studies have been carried
49 out to test it, probably due to the lack of clear predictions. On the one
50 hand, conflict has been shown to occur in some species (see TRIVERS
51 1985; MOCK & FORBES 1992; GREEN et al. 1993), but on the other
52 hand, offspring that demand more care may obtain greater investment
53 from their parents (STAMPS et al. 1985).

54 Conflict may be manifested in agonistic behaviours, sometimes
55 clearly conspicuous, between parent and offspring (e.g. ALTMANN
56 1980; GAUTHIER & BARRETTE 1985; BABBITT & PACKARD
57 1990; BECKER & GINSBERG 1990; GOMENDIO 1991), and at other
58 times by more subtle behaviours, such as the mother's rejection of her

59 offspring or unsuccessful suckling attempts (e.g. GALEF 1981;
60 MARTIN 1986; KÖNIG & MARKL 1987).

61 In many studies, the existence of a conflict between parent and
62 offspring has been interpreted as a result of weaning or the cessation of
63 nursing (e.g. CLARK 1977; NASH 1978; TRIVERS 1985), but current
64 research also points to the existence of behavioural conflict which does
65 not coincide with a cessation of even a decrease in parental investment
66 (MARTIN 1986; KÖNIG & MARKL 1987; WORLEIN et al. 1988;
67 GOMENDIO 1991; SMITH 1991; see also OBREGÓN et al. 1992). It
68 has also been postulated that parent-offspring conflict is related to
69 maturation and socialization processes, as well as temporal events, such
70 as the mother's oestrus state (mating season), but not to weaning
71 (WORLEIN et al. 1988; GOMENDIO 1991; LEE et al. 1991; GREEN et
72 al. 1993). A recent study in bison (*Bison bison*) notes the lack of
73 behavioural conflict during weaning, but states that the mating season of
74 the mother may be a possible source of conflict (GREEN et al. 1993);
75 here this possibility has been tested in another ungulate. It is important,
76 therefore, to reconsider nutritional weaning as the main source of
77 behavioural conflicts. Furthermore, the assumption that conflict is
78 correlated with aggressive behaviours may not be justified (GODFRAY
79 1991; BATESON 1994). Examination of the timing of conflict may
80 clarify its role in the parent-offspring relationship (GREEN et al. 1993).

81 Studies of behavioural conflict should take into account both
82 agonistic behaviour (see e.g. ALTMANN 1980; GAUTHIER &
83 BARRETTE 1985; BABBITT & PACKARD 1990; BECKER &
84 GINSBERG 1990; GOMENDIO 1991) and behaviour that reflects the
85 mothers' rejection of their offspring in a more subtle way (see e.g.
86 GALEF 1981; MARTIN 1986; KÖNIG & MARKL 1987).

In this paper I investigate the behaviour of mother and offspring during the lactation period in a captive population of the Saharan arrui (*Ammotragus lervia sahariensis*, Artiodactyla: Bovidae). This North African ungulate is a poorly studied species, probably primitive to both *Ovis* and *Capra* (e.g. GEIST 1971). The Saharan subspecies has become more well-known recently. Females' social ranks, parental investment (CASSINELLO 1995; 1996) and females' reproductive success (CASSINELLO & ALADOS 1996) have already been investigated in the captive population studied here, so that this population is an excellent choice to carry out a study on mother-offspring relationships, focusing on the onset of any behavioural conflict.

Methods

A. The Study Population

The captive population of Saharan arrui living in the Estación Experimental de Zonas Áridas, EEZA (Higher Council for Scientific Research, CSIC), Almería, south of Spain, is descended from three founder individuals that were captured in Western Sahara in 1975, two males and one female (ALADOS & VERICAD 1993). The captive population has bred successfully (CASSINELLO & ALADOS 1996), despite a high degree of inbreeding (ALADOS et al. 1988). I focused my observations on herd number three, made up of 17 males and 26 females at the beginning of the study (density=0.05 individuals/m²), and of 33 males and 43 females at the end (density=0.08 individuals/m²). A total of 26 mother-calf pair bonds were sampled, including 8 twins and 18 single calves. 19 calves were followed until weaning, 5 died prematurely and 2 did not reach weaning during the sampling period.

B. Sampling Methods

116 I carried out this study in the largest herd of Saharan arruis at the EEZA,
117 and sampled all the females who gave birth during 1990 and 1991 and
118 their calves, until the latter were weaned. Data from every individual
119 born have been recorded at the EEZA since the captive population was
120 established: birth date, parturition type (single or twin), sex, weight,
121 identification of father and mother, and inbreeding coefficient (see
122 WRIGHT 1922; BALLOU 1983). A number is also assigned to every
123 animal using plastic ear tags, which differ in shape and colour. The
124 study herd was monitored from nearby high ground, so that the animals
125 were not disturbed. I used a telescope to identify the individuals and a
126 field computer Psion Organiser II to register behaviours (see
127 CASSINELLO 1996).

128 A previous analysis of the species' daily activity showed that night
129 activity is lacking or scarce, early in the morning the most active
130 individuals are the adult males, but from 9:00 h the arruis spend their
131 time mostly resting until late in the afternoon, when the main activity
132 starts to take place. Therefore, sampling was performed between
133 approximately 17:00 and 20:00 h, when the adult females and calves
134 were more active (D. MORGAN pers. comm., pers. obs.). Focal
135 sampling was used to record the behaviour of mothers and calves
136 (ALTMANN 1974; MARTIN & BATESON 1986), and consisted of the
137 observation of a mother-calf pair for 20 minutes. The focal animals were
138 sampled according to their numbers, in an increasing order. However,
139 because it was not possible to sample all the focal individuals in a
140 complete sampling period (from 17:00 to 20:00 h), the same animal was
141 never sampled in the same position in the observation order two days in
142 a row, and all the animals were equally sampled at different times. Every
143 focal female was sampled 4 times a week during the first two months of
144 her offspring's life. 1.5 samples per week were made during the

145 remainder of the lactation period (see CASSINELLO 1996). During the
146 same observation period as the focal sampling the distance between
147 mother and calf was recorded every five minutes, using a female adult
148 body length as a unit.

149 The most conspicuous agonistic behaviours were: horn display,
150 butting, horn pushing, horn clashing, rush-charge (together referred to as
151 "aggressive approach") and subsequent withdrawal. More subtle
152 behaviours included withdrawals provoked by non-aggressive
153 approaches or even "staring at", as well as unsuccessful suckling
154 attempts. In the analyses, all calf's withdrawals have been considered as
155 a single variable, regardless of the mother's behaviour. Most of the
156 behaviours are represented by frequencies, i.e. the number of times an
157 event occurs per minute, except the distances between mother and
158 calves, which are represented by the proportion of time spent at a
159 particular distance.

160 In relation to the study of proximity between mother and calves,
161 "approach" was defined as any movement which led to the distance
162 between two animals becoming one body-length or less and "departure"
163 was any movement that led to the distance becoming more than one
164 body-length (LICKLITER 1984; RALLS et al. 1987; CASSINELLO
165 1996). In defining which individual approached or left the other (see
166 RALLS et al. 1987; GREEN 1992), "staring at" behaviour resulted in an
167 individual being defined as the actor (see CASSINELLO 1996). Hinde's
168 proximity index (HINDE & ATKINSON 1970) was used to quantify
169 who was responsible for maintaining proximity, the mother or the calf.
170 This index estimates the difference between the proportions of
171 approaches and departures carried out by the calf and ranges from -1 to
172 +1, higher values denoting a more active role by the calf, and lower
173 values a more active role played by the mother in maintaining proximity.

174 In order to test whether mother-offspring conflict occurs during
175 mating I investigated when lactating females resumed their sexual
176 activity, since in the Saharan arrui matings may occur at any time in the
177 year (CASSINELLO & ALADOS 1996). Females' oestrus state was
178 easily detected by the conspicuous mating behaviour (HABIBI 1987;
179 pers. obs.), so that the mother's sexual state during lactation could be
180 divided into oestrus and non-oestrus. In this species male sexual activity
181 is very conspicuous (e.g. low-stretch approach, chasing, flehmen, etc.,
182 see HABIBI 1987), and females in oestrus also show a characteristic
183 permissive behaviour which eventually leads to mounting. A female
184 may be in oestrus for a few days, and the synchronisation observed in
185 the herd allowed the dominant male to mate with all the females in heat.
186 Daily sampling allowed me to monitor the study population without
187 missing any conspicuous interaction, such as sexual behaviour. Those
188 females which showed some sexual receptivity for a few days before and
189 after an effective mounting was recorded were considered as in oestrus
190 for analysis purposes. All the females conceived during their first oestrus
191 after parturition.

192 Finally, the mothers' social rank was calculated and monitored
193 throughout the whole sampling period, following the matrix method
194 established by SCOTT (1980) and LAMPRECHT (1986). The rank
195 given to a particular individual corresponds to the percentage of
196 individuals with a lower dominance status (see CASSINELLO 1995).

197

198 **C. Definition of Weaning**

199 Suckling in the Saharan arrui decreases markedly in calves older than
200 one month, declining gradually from then until weaning (see Fig. 1).
201 Weaning period is defined as the month before the last observed

successful suckling event by each individual. Behaviour during this period was compared with behaviour in the periods before and after.

D. Analyses

Analysis of Variance was used throughout, and when the variables did not follow the normal distribution they were transformed (see ZAR 1984). Specifically, the frequency of maternal aggression and calf's withdrawal were transformed into the form $\sqrt{(x+0.5)}$, and Hinde's proximity index into the form $\arcsin\sqrt{x}$. The proportion of unsuccessful suckling attempts and the proportion of time mother and calves spend within 1 body-lengths were normally distributed. Mother's mating behaviour and calves' weaning period may coincide in time, so that a two-way ANOVA was used to test for interaction.

Furthermore, data of different calves from the same mother were considered as independent because a previous analysis of the intra and inter-group variance showed for all the behavioural variables that the inter-group variance was not greater than the intra-group variance. Thus, the results for the most characteristic variables analysed here are: maternal aggression: $F(13,522)=1.35$, $p=0.18$; calf's withdrawal: $F(13,522)=1.03$, $p=0.42$; Hinde's proximity index: $F(13,238)=0.65$, $p=0.81$ (cf. GOMENDIO et al. 1995; CASSINELLO 1996).

Results

A. Weaning and The Causes for Its Variation

The age of weaning is extremely variable in the Saharan arrui (Fig. 2), ranging from 3.2 to 16.1 months. There is no difference in the age of

231 weaning of individuals with or without a living twin at one month of age
232 (unpaired t-test: $t=-0.72$, $df=15$, $p=0.48$), nor is there a relationship
233 between weaning age and mother's age ($r^2=0.002$, $n=15$, $p=0.89$).
234 However, weaning occurs earlier when the interbirth interval is shorter
235 ($r^2=0.88$, $n=16$, $p<0.0001$; Fig. 3). Finally, calf's age at weaning and
236 mother's rank are significantly correlated for male calves ($r_s=-0.66$,
237 $n=10$, $p=0.048$), but not for females ($r_s=-0.05$, $n=7$, $p=0.89$).

238

239 **B. The Analysis of Conflict**

240 In Table 1 a summary of the two-way ANOVA carried out for five
241 dependent variables is shown. Maternal aggressive approaches towards
242 her calf were more frequent when she was in oestrus; however, they did
243 not differ significantly between the three lactation stages (Fig. 4). Calf's
244 withdrawals did not vary significantly depending on the weaning period
245 or the mother's sexual state (Fig. 5). Hinde's proximity index does vary
246 significantly between the two mother's oestrus states, but it does not
247 between the three lactation stages (Fig. 6). On the contrary, the
248 proportion of unsuccessful suckling attempts is significantly higher after
249 weaning (Fisher's post-hoc test: before vs after: $p=0.0001$; during vs
250 after: $p=0.001$; Fig. 7). Finally, the proportion of time spent at 0-1 body-
251 lengths is the same whichever the weaning period or the mother's oestrus
252 state (Fig. 8).

253

254

255 **Discussion**

256 The present paper has studied behavioural conflict between mother and
257 offspring in the Saharan arrui. Firstly, the lactation period is shorter
258 when mothers conceive in the following mating season, and high-
259 ranking females wean their male calves earlier. A behavioural conflict

260 occurs when the mother resumes her sexual activity, being most evident
261 in the mother's agonistic behaviour towards her calves, which is more
262 frequent during this period.

263 Calf's age at weaning is very variable. The time of resumption of
264 sexual activity by the mother explains most of the variability in age at
265 weaning, as it also does in other species (CLUTTON-BROCK et al.
266 1982; DUNCAN et al. 1984; LEE 1984; LEE & MOSS 1986; HAUSER
267 & FAIRBANKS 1988; GREEN 1990; TANAKA 1992). Moreover, in
268 the case of male calves, age at weaning depends on maternal rank (cf.
269 e.g. WHITTEN 1983). No relationship between age at weaning and the
270 age of the mother was found. The increase expected on theoretical
271 grounds (see CLUTTON-BROCK 1991) probably does not occur in the
272 study population because no female is old enough for reproductive
273 investment to risk her survival chances. Finally, a recent study
274 (CASSINELLO & ALADOS 1996) found that the interbirth interval is
275 shorter in high-ranking females, so that a negative relationship is
276 expected between mother's rank and offspring age at weaning, consistent
277 with the observed relationship between the age at weaning of male
278 calves and mothers' social rank.

279 The results show the lack of a behavioural conflict between
280 mother and calf when the cessation of nursing is taking place. After
281 weaning, by definition, all of the calves suckling attempts are
282 unsuccessful, but this does not explain the onset of a conflict. There was
283 no variation in Hinde's proximity index and the proportion of time that
284 the mother and calf were within one body-length.

285 As found in other species (see WORLEIN et al. 1988; LEE et al.
286 1991; GOMENDIO 1991; GREEN et al. 1993), there was an increase in
287 maternal aggression during the resumption of sexual activity by the
288 mother, although the frequency of withdrawal by calves did not vary.

289 When the mother is in oestrus, she is also less active in maintaining
290 proximity with her offspring. Such conflict probably stems from the
291 differing priorities of mother and offspring, i.e. mating and being nursed,
292 during this period.

293 In this paper evidence of a sort of "agreement" between mother
294 and offspring when weaning is taking place is provided. It appears that
295 during this period no conflict arises, but, on the contrary, a gradual
296 process during which mother and offspring needs are progressively
297 diverging. Thus, the calves may be interpreting their mother's changing
298 attitude, while the mother is acquiring information regarding their
299 calves' maturation process, in order to determine when the cessation of
300 nursing should preferably take place (GODFRAY 1991). Eventually the
301 young calves become independent members of the herd, whereas the
302 mother focus her attention on a new generation to come. Finally, and on
303 the contrary, when the resumption of sexual activity by the mother is
304 taking place a behavioural conflict does happen, as a consequence of the
305 differing priorities which lead mother and calves' behaviour.

306

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314

315 **Literature Cited**

316 ALADOS, C.L.; ESCÓS, J. & VERICAD, J.R. 1988: Captive
317 populations of northwest African Antilopinae and Caprinae at the

- 318 Estación Experimental de Zonas Áridas. In: Conservation and
319 Biology of Desert Antelopes (DIXON, A. & JONES, D., eds.)
320 Christopher Helm Ltd, Kent, pp. 199-211.
- 321 — — & VERICAD, J.R. 1993: Aoudad. *Ammotragus lervia* from
322 Western-Sahara. International Studbook. Boletín del Instituto de
323 Estudios Almerienses. Ciencias **11/12**, 65-97.
- 324 ALTMANN, J. 1974: Observational study of behaviour: sampling
325 methods. Behaviour **49**, 227-267.
- 326 — — 1980. Baboon Mothers and Infants. Harvard University Press,
327 Cambridge.
- 328 BABBITT, K.J. & PACKARD, J.M. 1990: Parent-offspring conflict
329 relative to phase of lactation. Anim. Behav. **40**, 765-773.
- 330 BALLOU, J. 1983: Calculating inbreeding coefficients from pedigrees.
331 In: Genetics and Conservation: A Reference for Managing Wild
332 Animal and Plant Populations (SCHONEWALD-COX, C.M.;
333 CHAMBERS, S.M.; MACBRYDE B. & THOMAS L., eds.) Ben-
334 jamin/Cummins Publishing Co., London, pp. 509-520.
- 335 BATESON, P. 1994: The dynamics of parent-offspring relationships in
336 mammals. Trends Ecol. Evol. **9**, 399-403.
- 337 BECKER, C.D. & GINSBERG, J.A. 1990: Mother-infant behaviour of
338 wild Grevy's zebra: adaptations for survival in semi-desert East
339 Africa. Anim. Behav. **40**, 1111-1118.
- 340 CASSINELLO, J. 1995: Factors modifying female social ranks in
341 *Ammotragus*. Appl. Anim. Behav. Sci. **45**, 175-180.
- 342 — — 1996: High ranking females bias their investment in favour of male
343 calves in captive *Ammotragus lervia*. Behav. Ecol. Sociobiol. **38**,
344 417-424.
- 345 — — & ALADOS, C.L. 1996: Female reproductive success in captive
346 *Ammotragus lervia* (Bovidae, Artiodactyla). Study of its

- 347 components and effects of hierarchy and inbreeding. *J. Zool.* **239**,
348 141-153.
- 349 CLARK, C.B. 1977: A preliminary report on weaning among
350 chimpanzees of the Gombe National Park, Tanzania. In: *Primate*
351 *Bio-Social Development* (CHEVALIER-SKOLNIKOFF S. &
352 POIRIER, F.E., eds.) Garland Press, New York, pp. 235-260.
- 353 CLUTTON-BROCK, T.H. 1991: *The evolution of parental care.*
354 Princeton University Press. Princeton, New Jersey.
- 355 CLUTTON-BROCK, T.H.; GUINNESS, F.E. & ALBON, S.D. 1982:
356 *Red deer. Behaviour and ecology of two sexes.* Edinburgh Univ.
357 Press, Edinburgh.
- 358 DUNCAN, P.; HARVEY, P.H. & WELLS, S.M. 1984: On lactation and
359 associated behaviour in a natural herd of horses. *Anim. Behav.* **32**,
360 255-263.
- 361 ESHEL, I. & FELDMAN, M.W. 1991: The handicap principle in parent-
362 offspring conflict: comparison of optimality and population-genetic
363 analyses. *Am. Nat.* **137**, 167-185.
- 364 GALEF, B.G. 1981: The ecology of weaning: parasitism and the
365 achievement of independence by altricial mammals. In: *Parental*
366 *Care in Mammals* (Gubernick D.J. & Klopfer, P.H., eds.) Plenum
367 Press, New York, pp. 211-241.
- 368 GAUTHIER, D. & BARRETTE, C. 1985: Suckling and weaning in
369 captive white-tailed and fallow deer. *Behaviour* **94**, 128-149.
- 370 GEIST, V. 1971: *Mountain sheep. A study in behaviour and evolution.*
371 The University of Chicago Press, Chicago.
- 372 GODFRAY, H.C.J. 1991: Signalling of need by offspring to their
373 parents. *Nature* **352**, 328-330.
- 374 GOMENDIO, M. 1991: Parent/offspring conflict and maternal invest-
375 ment in rhesus macaques. *Anim. Behav.* **42**, 993-1005.

- 376 — —; CASSINELLO, J.; SMITH, M.W. & BATESON, P. 1995.
377 Maternal state affects intestinal changes of rat pups at weaning.
378 Behav. Ecol. Sociobiol. **37**, 71-80.
- 379 GREEN, W.C.H. 1990: Reproductive effort and associated costs in
380 bison (*Bison bison*): do old mothers try harder? Behav. Ecol. **1**,
381 148-160.
- 382 — — 1992: The development of independence in bison: pre-weaning
383 spatial relations between mothers and calves. Anim. Behav. **43**,
384 759-773.
- 385 — —; ROTHSTEIN, A. & GRISWOLD, J.G. 1993: Weaning and
386 parent-offspring conflict: variation relative to interbirth interval in
387 bison. Ethology **95**, 105-125.
- 388 HABIBI, K. 1987: Behaviour of aoudad (*Ammotragus lervia*) during the
389 rutting season. Mammalia **51**, 497-513.
- 390 HAUSER, M.D. & FAIRBANKS, L.A. 1988: Mother-offspring conflict
391 in vervet monkeys: variation in response to ecological conditions.
392 Anim. Behav. **36**, 802-813.
- 393 HINDE, R.A. & ATKINSON, S. 1970: Assessing the roles of social
394 partners in maintaining mutual proximity, as exemplified by
395 mother-infant relations in rhesus monkeys. Anim. Behav. **18**, 169-
396 176.
- 397 KÖNIG, B. & MARKL, H. 1987: Maternal care in house mice. I. The
398 weaning strategy as a means for parental manipulation. Behav.
399 Ecol. Sociobiol. **20**, 1-9.
- 400 LAMPRECHT, J. 1986: Structure and causation of the dominance
401 hierarchy in a flock of bar-headed geese (*Anser indicus*). Behaviour
402 **96**, 28-48.

- 403 LAZARUS, J. & INGLIS, I.R. 1986: Shared and unshared parental
404 investment, parent-offspring conflict and brood size. *Anim. Behav.*
405 **34**, 1791-1804.
- 406 LEE, P.C. 1984: Ecological constraints on the social development of
407 vervet monkeys. *Behaviour* **91**, 245-262.
- 408 — —; MAJLUF, P. & GORDON, I.J. 1991: Growth, weaning and ma-
409 ternal investment from a comparative perspective. *J. Zool.* **225**, 99-
410 114.
- 411 — — & MOSS, C.J. 1986: Early maternal investment in male and female
412 African elephant calves. *Behav. Ecol. Sociobiol.* **18**, 353-361.
- 413 LICKLITER, R. 1984: Mother-infant spatial relationships in domestic
414 goats. *Appl. Anim. Behav. Sci.* **13**, 93-100.
- 415 MACNAIR, M.R. & PARKER, G.A. 1978: Models of parent-offspring
416 conflict. II. Promiscuity. *Anim. Behav.* **26**, 111-122.
- 417 — — & PARKER, G.A. 1979: Models of parent-offspring conflict. III.
418 Intrabrood conflict. *Anim. Behav.* **27**, 1202-1209.
- 419 MARTIN, P. 1984: The meaning of weaning. *Anim. Behav.* **32**, 1257-
420 1259.
- 421 — — 1986: An experimental study of weaning in the domestic cat.
422 *Behaviour* **99**, 221-249.
- 423 — — & BATESON, P. 1986: *Measuring Behaviour. An Introductory*
424 *Guide*. Cambridge Univ. Press, Cambridge.
- 425 MOCK, D.W. & FORBES, L.S. 1992: Parent offspring conflict. A case
426 of arrested development. *Trends. Ecol. Evol.* **7**, 409-413.
- 427 NASH, L.T. 1978: The development of the mother-infant relationship in
428 wild baboons (*Papio anubis*). *Anim. Behav.* **26**, 746-759.
- 429 OBREGÓN, F.; ARIAS DE REYNA, L. & RECUERDA, P. 1992:
430 Nursing and suckling behaviour in the mouflon. *Ethol. Ecol. Evol.*
431 **4**, 285-291.

- 432 PARKER, G.A. 1985: Models of parent-offspring conflict. V. Effects of
433 the behaviour of the two parents. *Anim. Behav.* **33**, 519-533.
- 434 — — & MACNAIR, M.R. 1978: Models of parent-offspring conflict. I.
435 Monogamy. *Anim. Behav.* **26**, 97-110.
- 436 — — & MACNAIR, M.R. 1979: Models of parent-offspring conflict.
437 IV. Suppression: evolutionary retaliation by the parent. *Anim.*
438 *Behav.* **27**, 1210-1235.
- 439 RALLS, K.; LUNDRIGAN, B. & KRANZ, K. 1987: Mother-young
440 relationships in captive ungulates: spatial and temporal patterns.
441 *Zoo Biol.* **6**, 11-20.
- 442 SCOTT, D.K. 1980: Functional aspects of the pair bond in winter in
443 Bewick's swans (*Cignus columbianus bewickii*). *Behav. Ecol.*
444 *Sociobiol.* **7**, 323-327.
- 445 SMITH, E.F.S. 1991: The influence of nutrition and postpartum mating
446 on weaning and subsequent play behaviour of hooded rats. *Anim.*
447 *Behav.* **41**, 513-524.
- 448 STAMPS, J.A.; CLARK, A.; KUS, B. & ARROWOOD, P. 1985:
449 Parent-offspring conflict in budgerigars. *Behaviour* **94**, 1-40.
- 450 TANAKA, I. 1992: Three phases of lactation in free-ranging Japanese
451 macaques. *Anim. Behav.* **44**, 129-139.
- 452 TRIVERS, R.L. 1972: Parental investment and sexual selection. In:
453 Sexual Selection and The Descent of Man, 1871-1971 (Campbell,
454 B., ed.) Aldine, Chicago, pp. 136-179.
- 455 — — 1974: Parent-offspring conflict. *Am. Zool.* **14**, 249-264.
- 456 — — 1985: Social Evolution. The Benjamin/Cummings Publishing
457 Company, Menlo Park, California.
- 458 WHITTEN, P.L. 1983: Diet and dominance among female vervet
459 monkeys (*Cercopithecus aethiops*). *Am. J. Primatol.* **5**, 139-159.

- 460 WORLEIN, J.M.; EATON, G.G.; JOHNSON, D.F. & GLICK, B.B.
461 1988: Mating season effects on mother-infant conflict in Japanese
462 macaques, *Macaca fuscata*. Anim. Behav. **36**, 1472-1481.
- 463 WRIGHT, S. 1922: Coefficients of inbreeding and relationship. Am.
464 Nat. **56**, 330-338.
- 465 ZAR, J.H. 1984: Biostatistical Analysis. Second edition, Prentice-Hall,
466 Inc., Englewood Cliffs, New Jersey.

Table 1. Two-way ANOVA results for five dependent variables and the two factors weaning period and mother's oestrus state.

Dependent variable	Weaning period ¹	Mother's state ¹	Interaction
Maternal aggression ²	1.68(2,61)ns	8.34(1,61)***	0.89(2,61)ns
Calf's withdrawal ³	1.26(2,61)ns	1.51(1,61)ns	0.63(2,61)ns
Proximity index ⁴	0.02(2,55)ns	4.73(1,55)*	0.54(2,55)ns
Unsuccessful suckling	2.98(2,42)(*)	0.002(1,42)ns	0.03(2,42)ns
0-1 body-lengths	0.54(2,57)ns	0.89(1,57)ns	0.54(2,57)ns

1: F(df)p, where p: (*) 0.10>p>0.05; * p<0.05; ** p<0.01; *** p<0.001

2: $\sqrt{(\text{Maternal aggression} + 0.5)}$

3: $\sqrt{(\text{Calf's withdrawal} + 0.5)}$

4: $\text{Arcsin}\sqrt{(\text{Proximity index})}$

Figure Legends

Figure 1. Proportion of time suckling during the calves' first year in the Saharan arrui. Values are means $\pm$ SE and the sample size is shown.

Figure 2. Frequency distribution for the age of weaning (last suckling event registered) of 19 Saharan arrui calves.

Figure 3. Relationship between the interbirth interval and offspring age at weaning in the Saharan arrui. $Y = 103.63 + 1.10X$; $r^2 = 0.88$.

Figure 4. Maternal aggressive approaches before, during and after weaning, according to the mother's oestrus state, in the Saharan arrui. Sample size is shown. Values are means $\pm$ SE.

Figure 5. Calf's withdrawals before, during and after weaning, according to the mother's oestrus state, in the Saharan arrui. Sample size is shown. Values are means $\pm$ SE.

Figure 6. Hinde's proximity index before, during and after weaning, according to the mother's oestrus state, in the Saharan arrui. Sample size is shown. Values are means $\pm$ SE.

Figure 7. Proportion of unsuccessful suckling attempts before, during and after weaning, according to the mother's oestrus state (white: in oestrus; black: not in oestrus), in the Saharan arrui. Sample size is shown. Values are means $\pm$ SE.

Figure 8. Proportion of time per sample that mother and calf spend at 0-1 body-length before, during and after weaning, according to the mother's oestrus state, in the Saharan arrui. Sample size is shown. Values are means $\pm$ SE.

FIG. 1

FIG. 2

FIG. 3

FIG. 4

FIG. 5

FIG. 6

FIG. 7

FIG. 9