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DOMINANCE RELATIONSHIPS IN CAPTIVE MALE BARE-TAILED WOOLLY OPOSSUM (*CALUROMYS PHILANDER*, MARSUPIALIA: DIDELPHIDAE)

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RÉSUMÉ

Au cours de ce travail nous avons voulu tester en captivité l'importance du poids corporel dans l'établissement de relations de dominance chez les mâles *Caluromys philander*, chez qui des compétitions inter-mâles ont été étudiées. Les comportements et l'évolution de différents paramètres physiologiques ont été observés durant 18 expérimentations effectuées respectivement sur 6 groupes de deux mâles et sur 12 groupes de deux mâles et une femelle. Des relations de dominance-subordination se mettent en place même en l'absence de femelle, mais la compétition est plus forte dans les groupes comprenant une femelle. Dans ces conditions expérimentales, le rang social est basé principalement sur le poids et l'âge. Lorsque la relation de dominance est mise en place, le rang social des mâles est bien défini et il reste stable jusqu'à la fin de l'expérimentation. Ces relations de dominance stables pourraient profiter aux dominants et aux dominés en minimisant les risques de blessures sérieuses. Les mâles montrent des signes typiques caractérisant un stress social : une baisse du poids et de l'hématocrite, les dominés étant plus stressés que les dominants. Chez les mâles dominants, la baisse de l'hématocrite est plus faible que chez les dominés, et la concentration de testostérone dans le sang diminue plus que chez les dominés. Au niveau comportemental, les dominants effectuent la plupart des interactions agonistiques « offensives » et plus d'investigations olfactives de leur environnement (flairage-léchage) que les dominés. De plus, leurs interactions avec les femelles sont plus nombreuses et moins agressives que celles des dominés.

SUMMARY

In this study, we test the hypothesis that body size is a key factor in determining dominance relationships during agonistic encounters between captive males *Caluromys philander*, and male-male competition was experimentally tested. Physiological and behavioural parameters were investigated during 18 experimental trials including two males alone (6), and two males with a female (12). A dominance-submission relationship exists even with no female, although competition is stronger when a female is present. Dominance is based on age and body mass in *C. philander* under experimental conditions. When dominance was settled, dominance rank was clear cut and consistent during all the experimentation. Stable dominance-subordination relationships may benefit both dominants and subordinates by minimizing the incidence of serious wounds. Males show typical signs of social stress: both body weight and hematocrit rate decrease, but subordinates are more stressed than dominants.

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Dominant males exhibit a lower decrease in hematocrit rate and a higher decrease in testosterone concentration in blood. They display most of the "aggressive" behaviours, scan more actively the experimental cages and engage in fewer aggressive interactions with females in comparison with subordinate males.

INTRODUCTION

Competition among males for access to females is often characterized by combats and aggressive interactions. These aggressive interactions are expected to play a major role in determining reproductive success of males (Krebs & Davies, 1997). But, under certain ecological conditions, mate searching by males could supersede combat as the primary mode of competition. This "scramble competition" polygyny has been first demonstrated in insects (Alcock, 1980) and seems important in some species of asocial mammals (Schwagmeyer, 1988). Even if combat and mate searching seem to be two contradictory modes of competition, in some species these two competition modes could coexist. For example, in some species searching is a prerequisite for acquiring mating opportunities. However, if numerous males accumulate around the same female before the onset of the œstrus, aggressive interactions can determine final success in mating (review in Schwagmeyer, 1988).

Didelphids in general retain numerous ancestral morphological and physiological traits (Charles-Dominique, 1983; Atramentowicz, 1986; Holmes, 1987). For these reasons, many authors have proposed that their social behaviour is more or less identical to that of their ancestors (Holmes,1987). Social interactions have been well investigated in only one didelphid species: *Didelphis virginiana* (Holmes, 1987; Ryser, 1990). In this species Holmes (1987) and Ryser (1990) determined that captive and wild animals perform a stable social hierarchy, with male social status associated with body mass and testosterone concentration in plasma. Various features are associated with dominance in *D. virginiana*, including access to resources (food and mate) and scent marking (Holmes, 1987). In nature, females *D. virginiana* are followed by numerous males (up to five males; Ryser, 1990) from several days to several hours before the œstrus. This precopulatory accumulation of males around a female have also been recorded in the wild for another didelphid species: *Philander opossum* (Charles-Dominique, pers. obs.).

The Bare-tailed Woolly Opossum (*Caluromys philander*) is a polygynous species. This nocturnal, arboreal and solitary species is widely distributed in the northern and eastern regions of South America (Atramentowicz, 1988). Animals do not defend a territory, and male and female home range largely overlaps (Charles-Dominique, 1983; Julien-Laferrière, 1995). Individuals communicate through olfactory and auditory pathways, as in most nocturnal species (Russell, 1984). In the Bare-tailed Woolly Opossum social bonds are limited and hierarchy is not obvious. As in the other didelphid species, interactions between conspecifics are few, often aggressive, except during mating or mother/offspring relationships. Nevertheless, *Caluromys* occupies a special place among didelphid species, with a higher encephalisation quotient, related to arboreality (Eisenberg & Wilson, 1981), and extended mother-offspring relationships (Atramentowicz, 1986). Evidence of inter-male competition to gain access to œstrous females has not been experimentally demonstrated, although it has been observed in the field (Charles-Dominique, 1983).

In this study, we test the hypothesis that body size is a key factor in determining dominance relationships during agonistic encounters between captive males *C. philander.* Experimental trials were performed in testing cages using paired males including, or not, a female. Morphological and hormonal correlates of dominance were assessed and we postulated that subordinate males would exhibit lower levels of testosterone and poorer physical conditions at the end of the encounter compared to dominant males.

MATERIAL AND METHODS

ANIMALS

In this study, 12 females and 15 males *Caluromys philander* were used. All of them were sexually mature (more than seven months) and born in captivity at the laboratory of Écologie Générale, M.N.H.N. (Brunoy, France). Owing to the little number of animals in our breeding colony, males were used in more than one experiment. These males, used in more than one experiment, were individually housed for at least four weeks between two experimental trials. The diet consisted in fruit (apples, bananas and oranges) and a mixture of milk, baby cereal and protein-rich powder. Water was available *ad libitum.* Temperature (25 °C), hygrometry (50 %) and light period (12 h) remained constant throughout the year. In order to facilitate observations, animals were maintained in a reverse daylight.

EXPERIMENTAL DESIGN

Animals were housed in three adjacent cages (149 × 64 × 58 cm), each provided with a wooden nest-box and branches to allow locomotion activity for this arboreal species. Cages could be connected together, by opening doors. Doors were opened 48h each week during a four-week period. Therefore, the animals of an experimental trial could meet each other only during two consecutive days by week. Three experimental trials were monitored simultaneously in three separate rooms.

Males were paired according to body mass differences. Both males were either about the same body mass (on average a 25 g difference, maximum = 50 g difference) or of different body mass (on average a 100 g difference, minimum = 80 g difference). In this species where adult body mass in males ranges from 300 to 500 g, these differences represented from 8 to 20 % of total body mass.

Reference experiments were monitored with two males alone, and later on, another with two males and a female. Eighteen groups were tested: six groups with males alone, including four groups of different body mass and two groups of similar body mass; and 12 groups with two males and a female, including eight groups with males of different body mass and four groups with males of similar body mass.

PHYSIOLOGICAL MEASUREMENTS

Body mass was recorded weekly, two days before the beginning of the experiments. Blood sample of males was taken by puncture of the saphenous vein.

After centrifugation, hematocrit was measured and testosterone plasma concentration was determined by radioimmunoassay. We used samples of 50 µl plasma and the procedure described by Perret & Atramentowicz (1989). The mean intra-assay coefficient of variation based on all samples tested in duplicate was 6.3 % (± 4.2) and the mean inter assay coefficient was 8.5 % (± 5.9) based on 25 samples with testosterone concentrations averaging 5 ng/ml. Uro-genital smears were collected in females twice a week, to detect œstrous occurrence.

BEHAVIOURAL OBSERVATIONS

Animals were observed in their cage for one hour following daylight switch off, with a dim red light suitable for nocturnal species. To allow sequential observations in three rooms, daylight was switched off delayed successively in each room. Observations were conducted for two consecutive days each week, when experimental cages were connected together.

All individual behaviours were recorded: eating, drinking, excreting, grooming, scent-marking (urine deposit or rubbing the penis along branches) and smelling-licking (the animal smells the air or a branch with slight head movements or lick the branches). Interactions between individuals, described in table I, were noted as follow:

— neutral or affiliative (indifference, approach, close proximity, licking or smelling)

TABLE I

Social behaviour patterns in the Bare-tailed Woolly Opossum (Caluromys philander).

Behaviour	Description
Neutral or affiliative	
Indifference	An animal stays motionless or carries on his behaviour when a conspecific makes any type of active social behaviour such as an approach or a threat
Approach	Walking towards another animal
Close proximity	Staying close to a conspecific (less than 0.1 m)
Licking or smelling	Olfactory investigation of the body or of the ano-genital area of a conspecific
Antagonistic	
offensive	
Threat	Emission of a "hiss" often associated with the typical opened mouth posture
Aggression	An animal jumps on its opponent and tries to bit him
Chasing	An animal runs after its opponent
defensive	
Escape	Running away from the opponent
Avoidance	Walking away from another animal
Distress calls	Loud distress call varying from a weak "hiss" to a loud "ki-hein", emitted in situation of pain or intense aggression
Sexual	
Sexual chasing	The male follows, or runs after, the female
Mating attempt	The male tries to immobilize the female using his fore legs and mouth

— antagonistic (threat, aggression, chasing, escape, avoidance, distress calls)
— sexual (sexual chasing, mating attempt)

A dominance index $\mathbf{I_d}$ and an activity rate **A** were calculated for each male.

$\mathbf{I_d}$ = number of offensive behaviours (chasing, threatening, physical aggression)/total number of agonistic behavioural acts (offensive + defensive).

A = total number of behavioural acts per hour (individual behaviours and interactions).

The dominance index, calculated for each individual of a dyad, corresponds to the hierarchical index established by Coulon (1975, in Yahyaoui *et al.*, 1995). This index varies from 0 in animals which exhibit only defensive behaviours to 1 in animals which exhibit only offensive behaviours. The differences between the $\mathbf{I_d}$ of the two males are calculated for each experiment. In dyads where this difference was 0.5 or more we considered that a dominance-subordination relationship was settled. In these groups, the male with the greatest $\mathbf{I_d}$ was considered as the dominant and the other male as the subordinate.

Statistical procedures

All values are means ± standard deviations. To compare different groups we used Kruskall-Wallis tests and multiple comparisons. Comparisons between two groups were made with Mann-Whitney and Wilcoxon tests. Spearman tests were used to evaluate correlations between specific parameters.

RESULTS

Dominance-subordination relationships between males

Female presence was not necessary to enhance a dominance relationship since it was observed in reference groups (two males alone, Table II). In only two groups $\mathbf{I_d}$ was below 0.5, meaning a lack of established dominance-submission relationship between males (Table II). These four males appeared significantly less active compared to other males (**A** = 32 ± 17 and **A** = 79 ± 34 respectively; U test, $p < 0.01$; Table II). Male-male interaction rate was 15 ± 11 interactions per hour and mainly included agonistic interactions (84 %).

In nine groups, since the beginning of the experiment, one male exhibited essentially offensive behaviours whereas the other behaved as a subordinate and dominance took place without any fight. In seven groups a dominance relationship took place after 1 to 62 fights (total observed per groups). In these groups, both males exhibited, firstly, as many offensive behaviours (threat, chasing, attack) as defensive ones (escape, run away, distress calls). Fights usually occurred on the ground or both males hanging under a branch using their prehensile tail. Serious wounds may result, especially biting. Then fights briefly ceased and afterwards only the dominant male displayed offensive agonistic behaviours, the other male exhibiting defensive behaviours. Thus we considered that the dominance-submission relation was established. In any case, once the relationship was

TABLE II

*Dominance index (I_d) and activity rate (**A**) calculated for each male in experimental groups. The total number of agonistic behavioural acts are noted into parenthesis. In two groups, noted in shaded areas, the dominance-submission relationship was not established (I_d 1 - I_d 2 < 0.5).*

	A) Reference group: two males alone				
	male 1		male 2		
	I_d 1	**A**	**I_d** 2	**A**	**I_d** 1 - **I_d** 2
males of different body mass **N = 4**	0.80 (44)	63	0.30 (62)	18	0.50
	1.00 (31)	62	0.00 (89)	66	1.00
	1.00 (58)	50	0.00 (154)	88	1.00
	0.60 (28)	45	0.37 (8)	8	0.23
males of similar body mass **N = 2**	0.96 (81)	138	0.02 (220)	103	0.94
	1.00 (103)	185	0.06 (274)	63	0.94
	B) Two males and a female				
	male 1		male 2		
	I_d 1	**A**	**I_d** 2	**A**	**I_d** 1 - **I_d** 2
males of different body mass **N = 8**	1.00 (3)	86	0.00 (6)	86	1.00
	0.80 (34)	71	0.00 (99)	103	0.80
	0.84 (19)	7	0.00 (23)	47	0.84
	0.65 (17)	67	0.00 (69)	58	0.65
	0.86 (61)	102	0.05 (136)	56	0.81
	0.97 (138)	119	0.01 (193)	83	0.96
	1.00 (83)	135	0.45 (138)	69	0.55
	1.00 (33)	60	0.00 (90)	73	1.00
males of similar body mass **N = 4**	0.85 (7)	33	0.12 (7)	9	0.73
	1.00 (38)	56	0.12 (65)	95	0.88
	0.97 (69)	64	0.19 (92)	62	0.78
	0.40 (5)	42	0.00 (4)	34	0.40

fulfilled, no more fights occurred and males kept their status until the end of experiment. Since the dominance relationship was never reversed it could be considered as "stable" under these experimental conditions.

A flow diagram of antagonistic behaviours between two males that occurred once the relation was established is shown in figure 1. This figure specifies behavioural sequences between a dominant and a subordinate male *C. philander*. Whereas the dominant male is indifferent to the approach of the other male, the latter exhibits a spontaneous escape behaviour, sometimes followed by distress calls when the dominant male comes too close. Threatening pattern is typical in this species: a wide-open mouth and emission of loud vocalization often in a raised posture. Threats are few, but very efficient and lead the subordinate male to look for a shelter on the ground, in an empty nest-box or an empty cage.

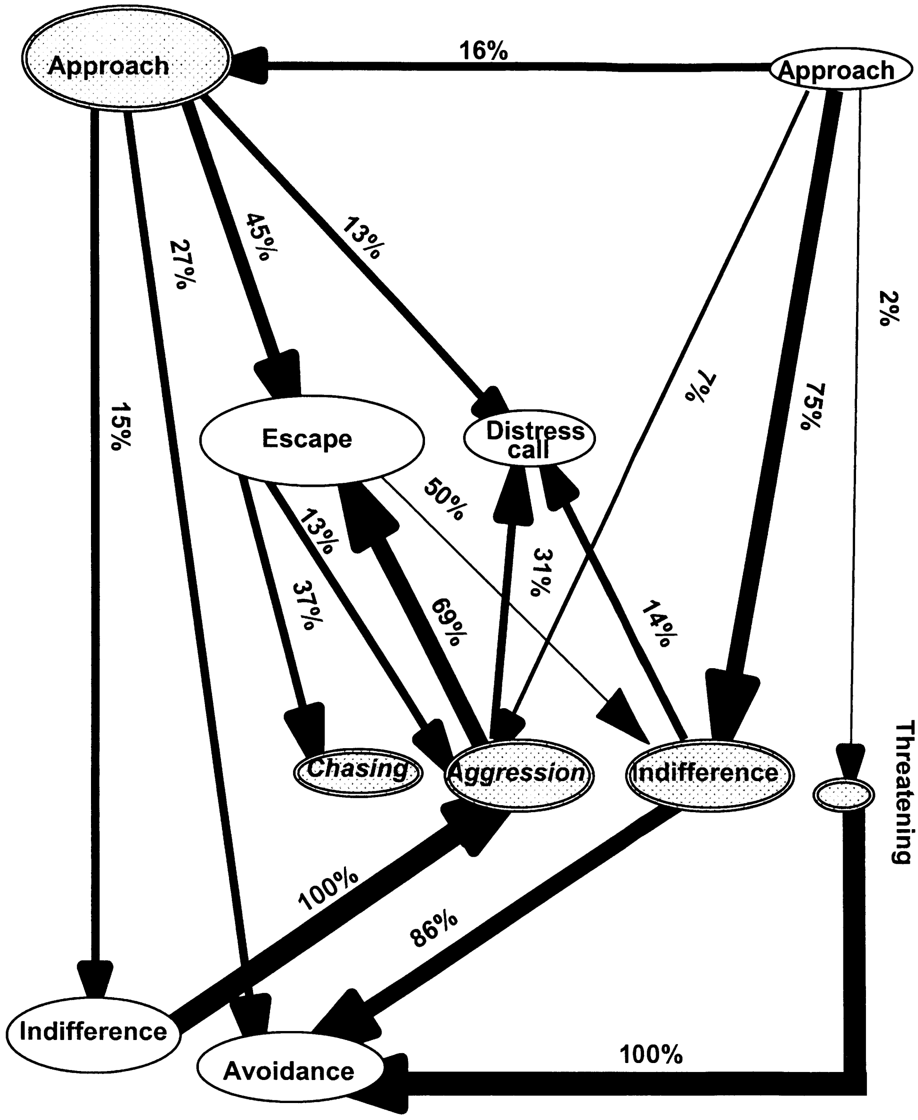


Figure 1. — Flow diagram of the antagonistic male/male interactions occurring when a dominance-submission relation was established. Frame size is proportional to the number of acts performed and arrow size is proportional to % of interaction. Dominant male ⬭, Subordinate male ⬭ (% of the total number of interactions observed between males in all groups, N = 16)

NUMBER OF FIGHTS AND TIME BEFORE DOMINANCE SETTLEMENT

In 16 groups a dominance-submission relationship was considered as established (difference in $\mathbf{I_d}$ between the two competing males ≥ 0.5). We compared four groups: males alone of similar and different body mass, and males of similar and different body mass with a female.

Time before settlement of the dominance relationship was different between groups (Kruskall-Wallis, $\chi^2 = 7.8$, $p = 0.05$). The relationship was settled after a longer period of time in male/female groups compared to groups with males alone (multiple comparison, $p < 0.05$). This period varies from 1 to 4 weeks in male/female groups and is of 1 week in groups of males alone.

The number of fights was not significantly different between groups (Kruskall-Wallis, $\chi^2 = 3.8$, $p = 0.28$), the total number of fights observed vary from 0 to 62 in the 16 different groups.

INFLUENCE OF MALE BODY MASS AND PLASMA CONCENTRATION OF TESTOSTERONE ON SOCIAL RANK

As in other didelphid species, growth in body mass and body length is continuous (Atramentowicz, 1986), and older individuals are mainly heavier. In this study, body mass and age were significantly correlated in males ($n = 15$, $r_s = 0.59$, Spearman test $p = 0.02$).

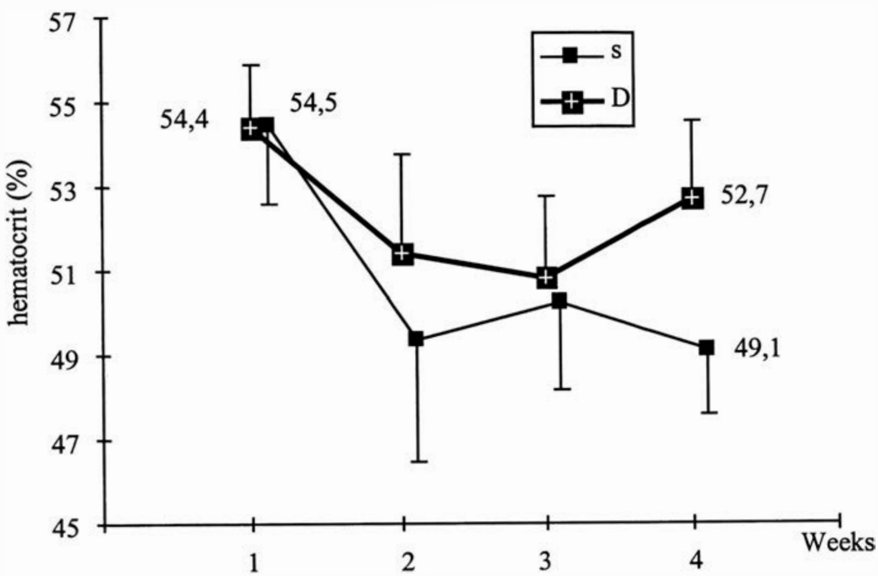
Relation between dominance index ($\mathbf{I_d}$) and body mass and plasma concentration of testosterone (measures recorded two days before the beginning of the first experiment) was tested with a Spearman rank correlation.

In male groups with similar body mass, no significant correlation emerged between dominance index ($\mathbf{I_d}$) and plasma concentration of testosterone ($r_s = 0.3$, $n = 12$). In male groups with different body mass, the dominance index was not significantly correlated with testosterone concentration in blood plasma, but positively correlated with body mass ($r_s = 0.66$; $n = 24$; $p < 0.001$) and age ($r_s = 0.5$; $n = 24$; $p < 0.05$). Heavier and older males exhibited a higher dominance index.

INFLUENCE OF MALE SOCIAL RANK ON PHYSIOLOGICAL AND BEHAVIOURAL PARAMETERS

The influence of social status on physiological and behavioural parameters was compared between dominant and subordinate males in four groups: males alone of similar and different body mass, and males of similar and different body mass with a female. As no significant difference was found (Kruskall-Wallis, p = ns), the influence of social status was then investigated for all individuals: dominant males ($n = 16$) were compared to subordinate males ($n = 16$).

To test the influence of social status on body mass, blood hematocrit and testosterone concentration (Fig. 2), we recorded variations between the first and the fourth week. Most males lost weight from the onset to the end of each experiment, without any significant difference between dominant and subordinate males (-12 ± 19 g and -11 ± 31 g). Individual variations of hematocrit and testosterone concentration in blood were very important. Despite these important individual differences, the evolution of these physiological parameters was significantly different for subordinate and dominant males. The decrease in hematocrit, between the first and the fourth week of experiment, was higher in subordinate males than in dominant ones (-1.7 ± 4.2 % and -5.4 ± 3.9 % respectively; U test, $p = 0.02$). During the first week, dominant males exhibited a sensible though not significant higher testosterone blood concentration than subordinate males (4.0 ± 2.7 ng/ml and 2.6 ± 1.3 ng/ml; U test n.s.). Testosterone level diminished significantly more in dominant males during the experiment compared to subordinate males (– 1.8 ± 2.8 ng/ml and – 0.2 ± 1.1 ng/ml respectively; U test, p = 0.05).



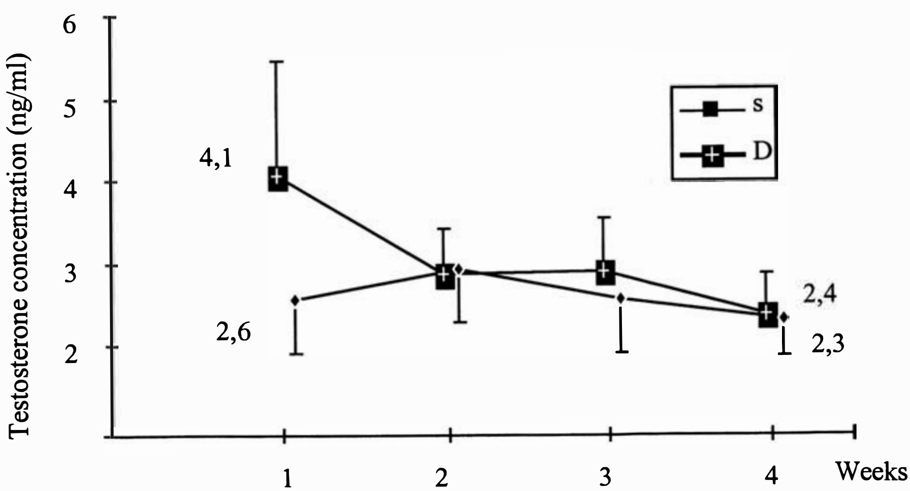


Figure 2. — Variation in hematocrit and testosterone concentration in blood in dominant (D) and subordinate (s) males (N pairs of males = 16). Mean ± s.d. are given for the four weeks of experimental encounters.

Activity rate and scent-marking frequency were similar in dominant and subordinate males (**A** = 86 ± 40 and 68 ± 27, Fig. 3, and scent-marking/hours = 0.40 ± 0.48 and 0.35 ± 0.29 respectively). Nevertheless smelling-licking, which represents 73 % on average of the individual behaviours, was significantly more frequent in dominant males than in subordinate ones (48 ± 28 and 32 ± 20/hour; U test, $p < 0.05$; Fig. 3). The number of other behaviours (eating, drinking, excreting, grooming) was too low to perform separate calculations.

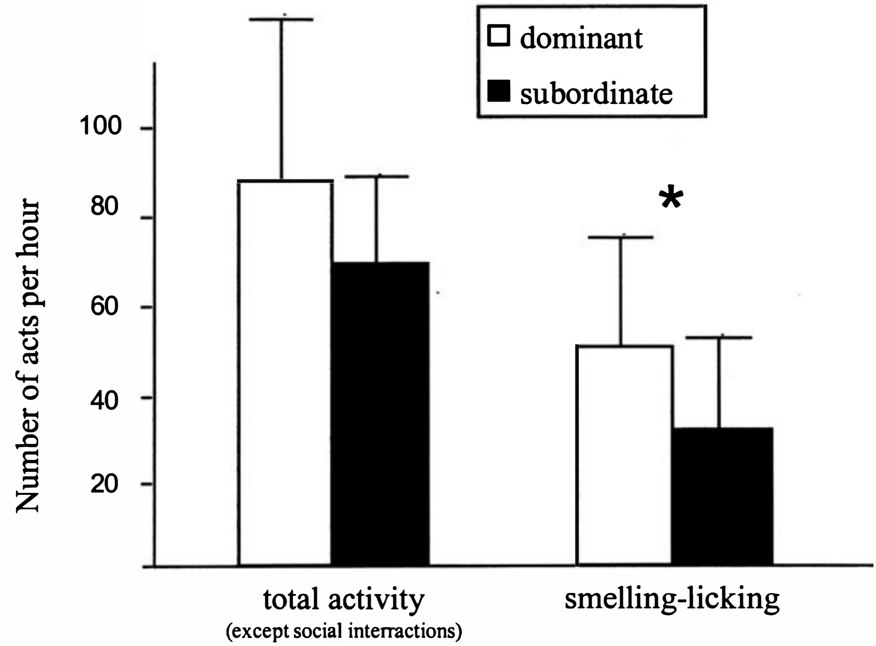


Figure 3. — Influence of social status on behavioural parameters (in number of acts per hour). Dominant males (N = 16), subordinate males (N = 16); U-test ★ = $p < 0.05$.

Twelve females were placed in male groups: eight with males of different body mass and four with males of equivalent body mass. All females lost weight during the four-week experiment: mean body mass decreased significantly from 368 ± 44 g during the first week, to 348 ± 44 g during the last week (Wilcoxon test, $p < 0.05$). Only two females did not exhibit cytological œstrus during the experiment. Moreover, no difference in female activity was obvious when œstrus occurred.

Male-female interaction occurrence was 11 ± 9 interactions per hour and most of these interactions were aggressive 73 ± 25 %. Males frequently initiated interactions with females and they rarely threatened or aggressed females even when they are attacked repeatedly. Most of the male-female interactions ended by female avoidance or threat. Interactions between the dominant male and the female were less aggressive, compared to those against the subordinate male (Wilcoxon test, $p < 0.05$). Unfortunately, probably due to captivity conditions, only two females exhibited typical sexual interactions: sexual chase and mounting attempt by the dominant male exclusively, and only during occurrence of œstrus.

DISCUSSION

It is apparent in this study that dominance is based on age and body mass in *Caluromys philander* under experimental conditions. Dominant males exhibit a lower decrease in hematocrit rate and a higher decrease in testosterone concentration in blood; they display most of the offensive antagonistic behaviours, scan more actively the experimental cages and are engaged in fewer aggressive interactions with females compared to subordinate males. Caution must be used in extrapoling from the behaviour of captive to wild animals, particularly when using data from observations of small groups of individuals, because some phenomena may occur only under unnatural constraints. Nevertheless, these informations are particularly useful for nocturnal, arboreal, small bodied neotropical species like *C. philander* for which direct observation of interactions in the wild is virtually not possible.

In captive Woolly Opossum, body mass and age are important parameters to establish hierarchy and heavier and older males were dominant in groups of different body mass. This observation fits well with many others performed on mammalian species (marsupials: Braithwaite, 1974; Bradley *et al.*, 1980; Ganslosser, 1989; Ryser, 1990; Mallick *et al.*, 1994; rodents: Militzer, 1995; elephants: Poole, 1989; Grey Seal: Anderson & Fedak, 1985 and Elephant Seal: Haley, 1994). The existence of a settled dominance between males of similar body size show that other indicators of dominance, as experience or aggressivity for example, should play a role in the probability of winning contests. In this species it is not possible to isolate confounding effects of age and body size since growth goes on throughout adulthood (Atramentowicz, 1986). Nevertheless, data collected on a natural population of *Didelphis virginiana* in Florida, a relatively close species, show that "outcome of fights was strongly influenced by body mass, but there was no influence of age" (Ryser 1992). In *Caluromys philander*, dominance-submission relationships exist between males even without females. Nevertheless, inter-male competition is stronger when a female is present at close vicinity as in macropodid marsupials (Ganslosser, 1989).

When dominance was settled, dominance rank was clear-cut and consistent during all the experimentation. Stable dominance-subordination relationships may benefit both dominants and subordinates by minimizing the incidence of serious wounds (de Waal, 1982). Display, as territorial marking or threat, could also avoid potentially dangerous fighting. In *Caluromys philander*, as in *Didelphis virginiana* (Ryser, 1992), no limits to wounds occur, on the opposite to macropodid marsupials where animals test their strength in ritualized fights without risking severe injuries (Ganslosser, 1989).

In our experiment, males showed typical signs of social stress as described by Von Holst (1977) in *Tupaia belangeri* (Scandentia, Tupaiidae): both body weight and hematocrit rate decrease. This could be due to a density effect associated with a psychological effect tied-up with social status or loss of aggressive interactions. Psychological effect could explain that hematocrit of subordinate males decreases more than in dominant ones. In *Didelphis virginiana* (Holmes, 1987), subordinates are more stressed than dominants. During our experiment, the physical condition of males declined but none died, as it may happen in other marsupial species as *D. virginiana* (Ryser, 1990) and *Antechinus stuartii* (Braithwaite, 1974; Bradley *et al.*, 1980). The decrease in testosterone concentration observed in all males probably resulted from stress (Von Holst, 1977) and inter-male inhibition (Atramentowicz, unpublished data).

Small differences occur in behaviour between dominant and subordinate males. No differences were found in global activity, or scent-marking, but dominant males scan more the experimental cages and exhibit more smelling-licking behaviours than subordinates. In other marsupial species, *D. virginiana* or *Petaurus breviceps*, the social status had a marked influence on behaviour. In these species, dominant males scent-mark more, are more active and mobile (Holmes, 1987; Ryser 1990; Mallick *et al.*, 1994; Stoddart *et al.*, 1994).

In the Woolly Opossum, males and females show principally indifferent and avoidance behaviours, and mating rarely occurs if they are in continuous contact. Therefore, intermittent contact was chosen in our experimental procedure (48 h each week). A stress due to a density effect could explain the lack of mating and pregnancy, as in mice (Bronson, 1989). Furthermore, females exhibited a reduced physical condition (weight loss) which is characteristic of stressed animals. Even if an influence of dominance upon mating success could not be demonstrated in our study, in the two groups where sexual interactions were performed, these happened only between a female and a dominant male. Interactions are less aggressive between females and dominant males than with subordinates. This difference in females aggressivity should be an important factor in determining access to mate in opossum species. In *Caluromys philander*, as in *Didelphis virginiana* (McManus 1970, Holmes 1987), females indicate copulatory readiness only by a lack of aggression toward males.

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