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Age-dependent mating tactics in male bushbuck (*Tragelaphus scriptus*)

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INTRODUCTION

Intra-specific variation in mating behaviour has been described for a number of taxa including arthropods, fishes, amphibians, reptiles, birds and mammals. Several mechanisms have been proposed to explain the various mating behavioural variations observed in mammals. For example, an individual's behaviour may be constrained by its **condition or status** (making-the- best of-a-bad-job strategy) or an alternative phenotype may be maintained by frequency-dependent selection influencing a genetic polymorphism (alternative strategies).

In the **majority of ungulates**, variation in mating tactics is most likely maintained as a **conditional strategy** influenced by multiple internal factors like **age**, health or **body size**, as well as external factors such as population density, number of competitors and social dominance rank.

In the present study, we investigated male mating tactics in a cryptic, bush-dwelling antelope from tropical Africa, the bushbuck, *Tragelaphus scriptus* (Figures.1, 2). Different mating strategies are expected to emerge, if variation in mating tactic is maintained as a **conditional strategy** influenced by **age** and / or **body size**:

1) Defending a territory when old and strong, what allows the owner to associating more frequently with females within the combined territory and home-range area.
2) No territory defence when young and weak, thereby associating with females less frequently and therefore sneak-mating with them.

Figure 1.
Adult male bushbuck.

Figure 2.
A group of female bushbuck.

MATERIAL and METHODS

We observed bushbuck in a free-ranging population on the Mweya peninsula and adjacent areas in **Queen Elizabeth National Park**, Uganda (study area: 8.7 km^2). We included 41 female and 27 male bushbuck, and cluster analysis was applied on **Cole`s coefficient of association** (CCA) to determine social vicinity between sexes. Home-range overlap was used to determine spatial vicinity between sexes using **fixed kennel density estimation**. Males from different social/age classes (adult, young-adult, sub-adult) were used for **row-wise matrix correlation** of social and spatial vicinity with females. Finally we used **mating behaviour** directed towards females (herding, monopolisation; Figure 3, 4) and **agonistic behaviour** (low horn presentation, attacks, escorting, intimidation; Figure 5, 6) to determine differences in mating success between male social/age classes.

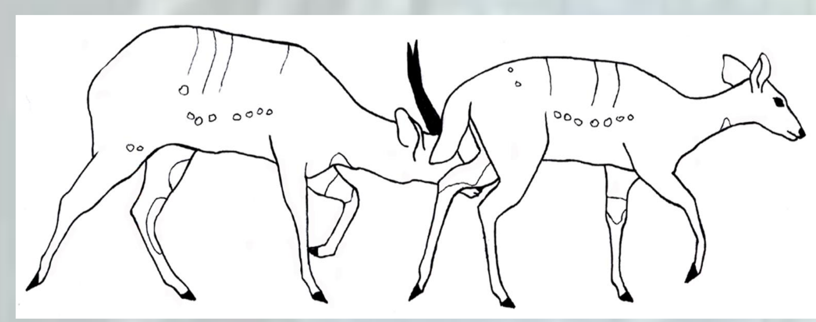

Figure 3.
Herding behaviour of an adult male bushbuck .

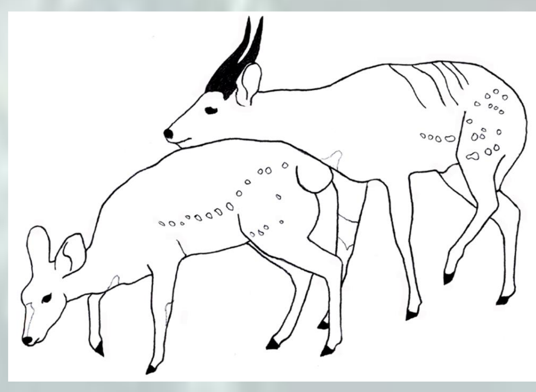

Figure 4.
Neck pressing, a typical pre-mating behaviour of male bushbuck.

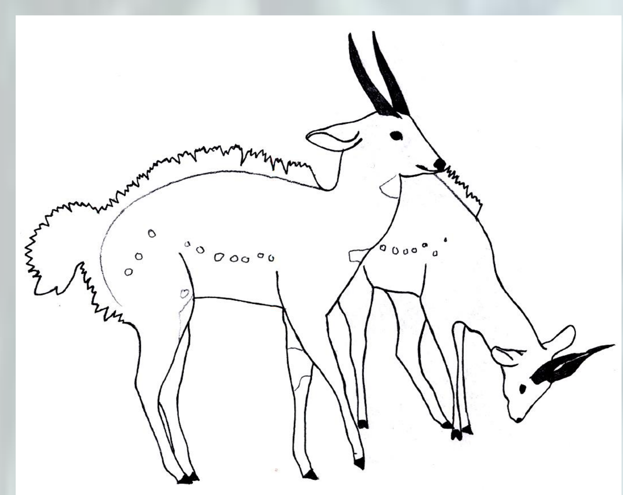

Figure 5.
Two adult males showing intimidation displays, the left performing low horn presentation.

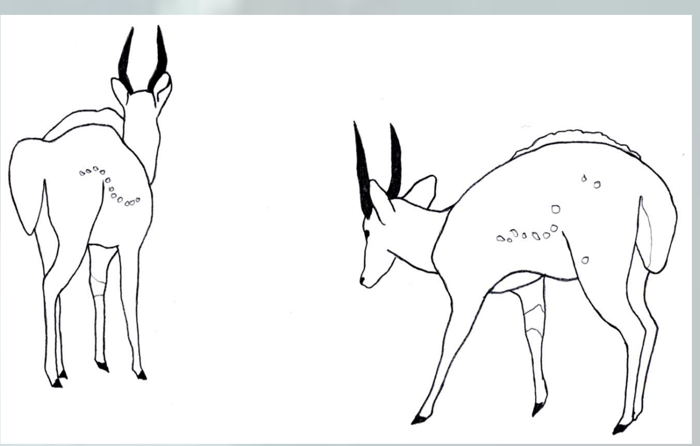

Figure 6.
An adult male bushbuck (left) escorting a young-adult challenger to the border of his territory.

We asked:

1a. Are adult males closer to females than young-adult or sub-adult males?
1b. Do males, living close to certain females, spend also more time with those females?
1c. Are young-adult males forced to associate with those females that receive less attention by territorial males?
2. Do male social/age classes differ in showing mating behaviours to females?
3. Do male social/age classes differ in performing agonistic interactions towards each other?

CONCLUSIONS

Our data indicated that the spatial distribution of bushbuck males and females directly predicts association patterns between males and females. Apparently, two alternative, age-dependent mating tactics exist in male bushbuck: territorial males show high rates of pre-mating behaviour, herd and monopolise females. Young-adult males, by contrast, show less pre-mating behaviour, herding and monopolisation behaviour, but frequently attempt to mate. Territorial bushbuck males responded to the constant challenge by the presence of young-adult males by showing intense agonistic behaviour on encounters with them.

RESULTS

1. Home range overlap and association patterns

a. Adult territorial males associated significantly more frequent with females than young-adult and sub-adult males (Kruskal Wallis ANOVA on ranks: $H_{2,26}$ = 24.55, P = 0.001).

b. The Cole's coefficient of association (CCA) between a male and a given female was significantly positively correlated with the home range overlap between them in all three social/age classes of males (adult, young-adult, sub-adult)as indicated by a row-wise matrix correlations. Correlation coefficients were largest in the case of adult territory holders and smallest for sub-adult males (Kendall's τ= 0.55 for adults, 0.30 for young-adults, 0.26 for sub-adults, in all cases p<0.05).

c. There was no significant correlation in the CCA of a given female between territorial males (sum of all territorial males for the respective female) and young-adult males (sum of all young-adult males; Kendall's correlation: τ = 0.004, z = 0.037, P = 0.97, n = 41). The number of territorial vs young-adult males that were observed in association with a given female (i.e., that had a CCA larger than zero for the respective female) tended to be positively correlated (Kendall's correlation: τ = 0.25, z = 1.94, p = 0.053, N = 41; Figure 7a, b). Therefore, the hypothesis of a negative correlation could be rejected with a one-sided p = 0.027.

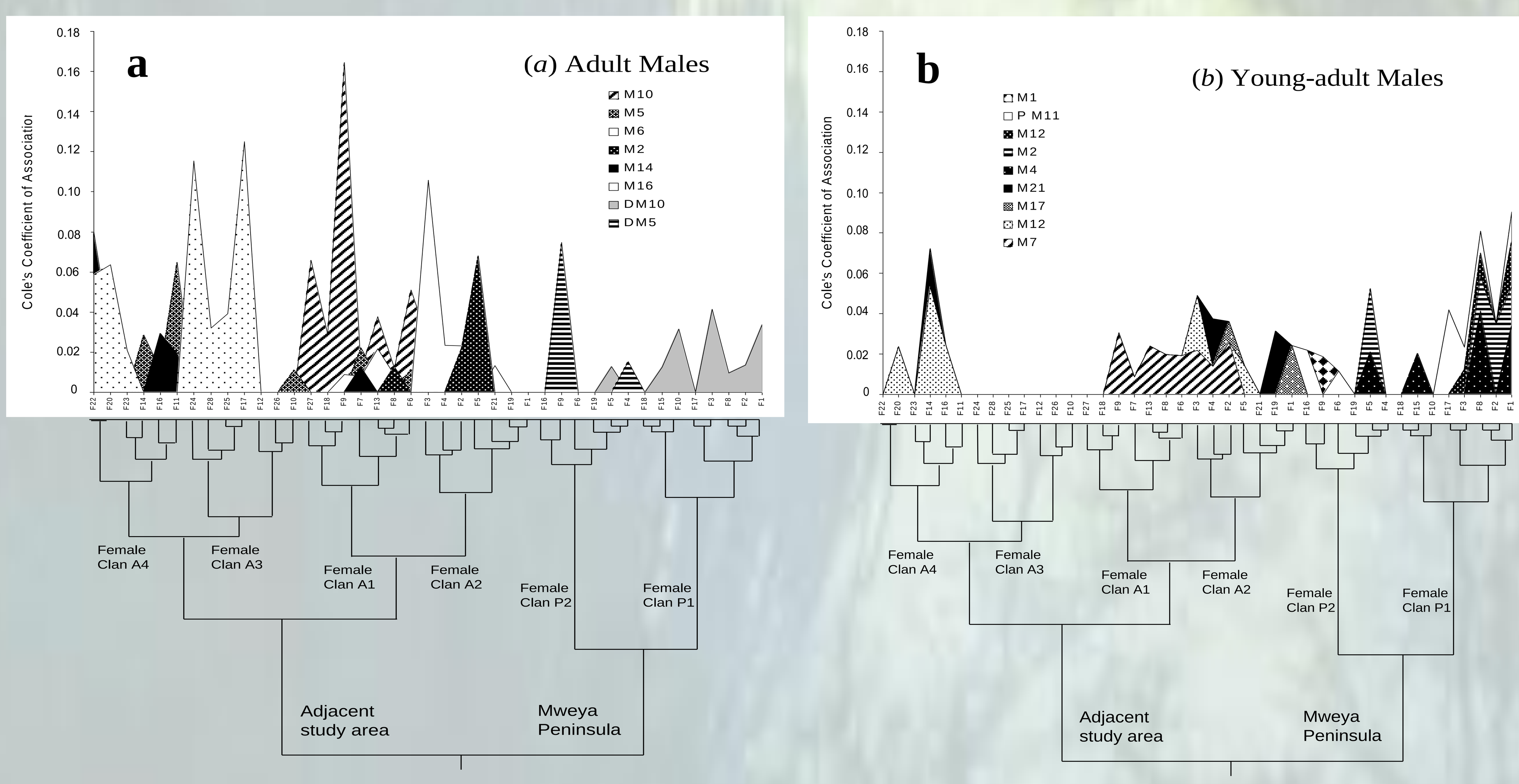

Figure 7. Cole's coefficient of association for all male/female dyads observed during this study for (**a**) territorial males and (**b**) young-adult, non-territorial males. The dendrogram depicts female clans as obtained from cluster analysis of spatial vicinity (home range centroids; Wronski & Apio, 2006).

2. Mating behaviour of different male social/age classes

Our analysis of mating behaviour in different male social/age classes showed that rates of herding of females were significantly higher in adult territorial males than in young adult non-territorial males (Kruskal-Wallis ANOVA on ranks: $H_{2,29}$ = 11.26, p = 0.004), while monopolization of females was significantly higher in adult territorial males than in young adult and subadult males (One-way ANOVA : $F_{2,29}$ = 13.21, p = 0.001).

3. Agonistic behaviour among males

A comparison of agonistic behaviour among three male social/age classes showed that adult territorial males showed significantly higher rates of low horn presentation (Kruskal-Wallis ANOVA on ranks: $H_{2,27}$ = 10.08, P = 0.006) and attacks (Kruskal-Wallis ANOVA on ranks: $H_{2,27}$ = 10.14, P = 0.006) towards young-adult and sub-adult males, than young adult males showed towards sub-adult males (Figure 8).

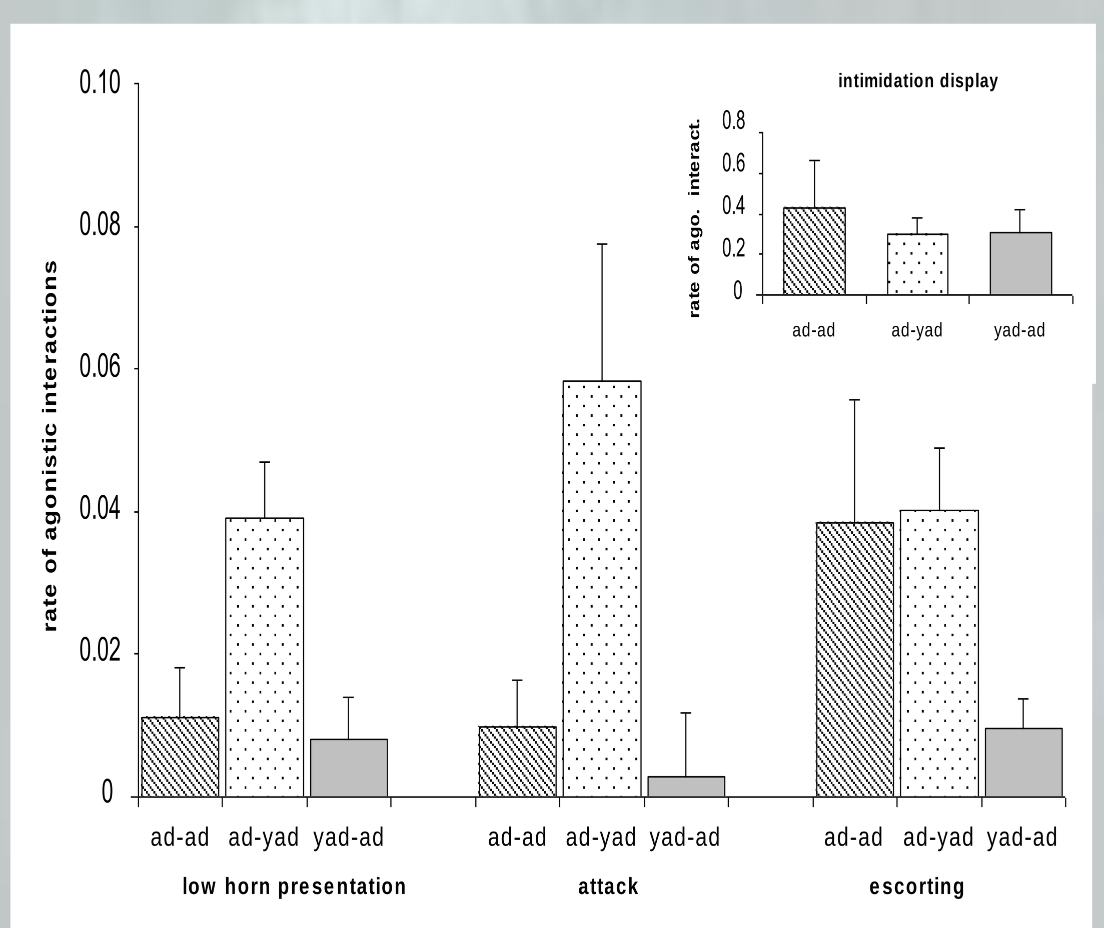

Figure 8.
Rate of aggressive behaviours (low horn presentation, attacks, escorting & intimidation displays) initiated by adult territory holders directed towards neighbouring territory holders (*ad-ad*), towards non-territorial young-adult bachelors (*ad-yad*) and aggressive interactions initiated by bachelors directed towards adult territory holders (*yad-ad*).

ACKNOWLEDGEMENTS

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