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Evolutionary ecology of giraffes (*Giraffa camelopardalis*) in Etosha National Park, Namibia.

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1 INTRODUCTION

1.1 Aims

This project sought firstly to investigate the evolution of biogeographical variation in giraffe coat colour. In particular, we aimed to explain this variation in the context of natural and sexual selection. Our starting point was that darker colour coats should be costly due to an increased solar heat gain (e.g. Hutchinson & Brown 1969; Finch 1972; Finch & Western 1977; Finch *et al.* 1980; West & Packer 2002). Since environmental stress varies geographically, this would explain variation in colour between spatially distinct populations. It could also explain why males tend to be darker than females (e.g. Dagg 1968), if dark coat colour is functioning as a sexually selected costly signal of status (Zahavi 1975).

Secondly, we set out to explore the effects of limited resources, such as food and water, on male mating strategies and the potential for males to monopolise mates (Emlen & Oring 1977). We suggested that waterholes might serve as focal points for males to intercept females in their search for potential mates (e.g. Ritter & Bednekoff 1995). Thus, waterholes might drive male movements and determine spatial and temporal variation in levels of male competition.

1.2 The study species

The giraffe was chosen for this study firstly, because from a practical point of view, their large size, conspicuousness, and individually unique coat patterns make a study of them highly feasible (e.g. Foster 1966). Furthermore, giraffes exhibit a surprising diversity of coat markings, with variation in patch form, relative size and colour both between and within subspecies (Dagg 1962; Seymour 2001), which remains as yet unexplained.

And lastly, pilot work had suggested waterholes might serve an important role in male mating strategies. Giraffes make frequent use of water in Etosha NP and pilot observations (LM Gosling, unpublished) show that males often intercept, urine-test, and attempt to court females at waterholes when they come to drink. Large, dark-coloured males appear to dominate and exclude lighter coloured males from these mating interactions. This creates the potential for a small effective male population size, which is linked to the availability of water holes (e.g. Ritter & Bednekoff 1995).

Thus, the giraffe mating system could be susceptible to effects of waterhole management, if these influence the potential of males to monopolise females. This could determine the proportion of males that contribute genetically to the next generation, thus limiting the effective population size (e.g. Anthony & Blumstein 2000). These factors could lead to inbreeding and be detrimental to the viability of isolated giraffe populations (e.g. Lacy 1997; Frankham 2003). This effect may be absent or reduced where females are not spatially limited by water or preferred habitat patches.

2   METHODS

2.1   Coat colouration

Before the field work began, an analysis of giraffe coat colouration was carried out using photographs of wild giraffe. The aim was to identify possible environmental factors that may have driven the evolution of biogeographical variation in coat colouration. Each giraffe was scored according to patch darkness (1: very pale tan, 2: darker tan and russet; 3: chocolate-brown; 4: black; Figure 1). Patch density was measured using a MATLAB algorithm that binarises sections taken from images of giraffe and then records the number of black and white pixels (Figure 2).
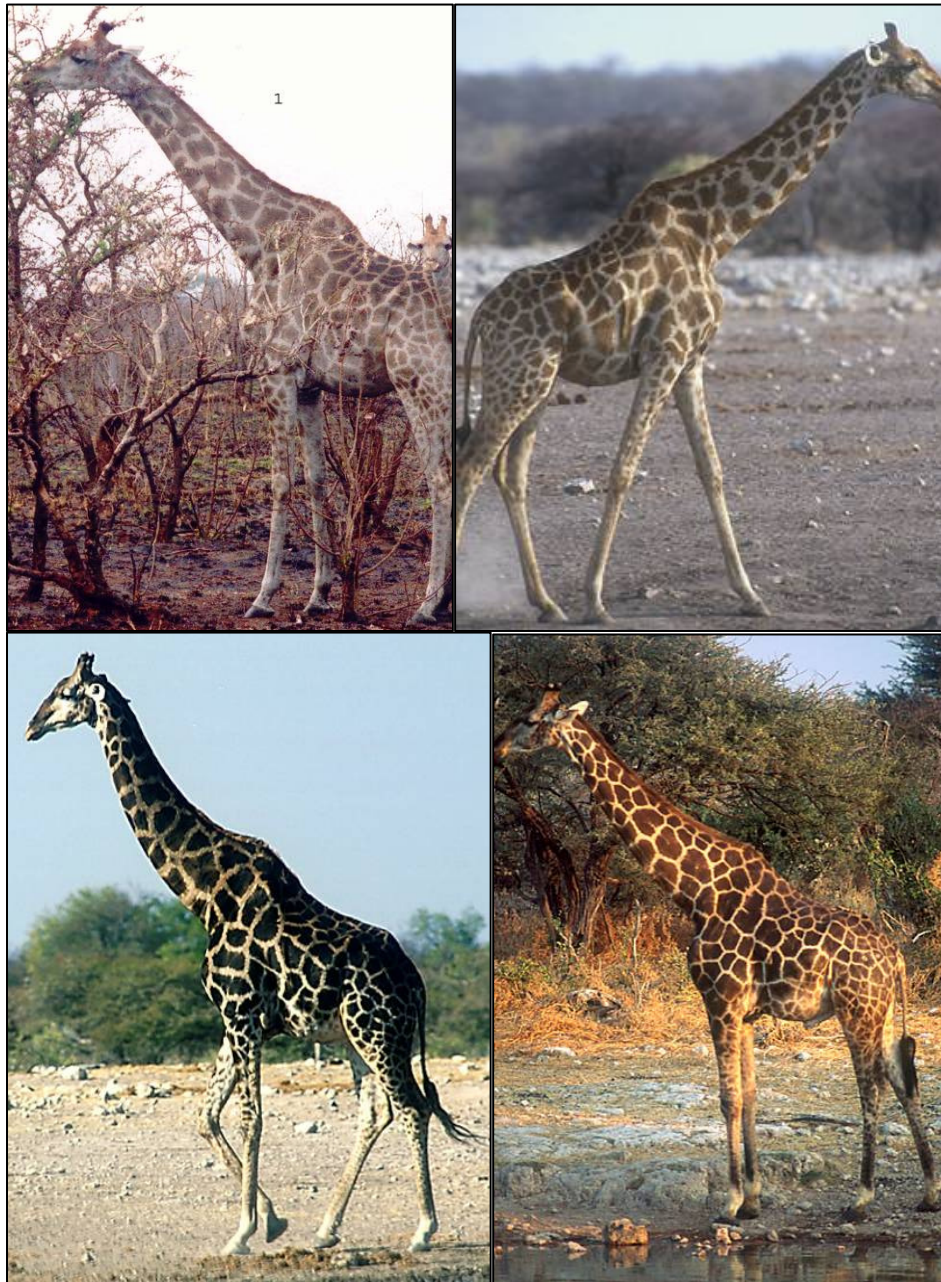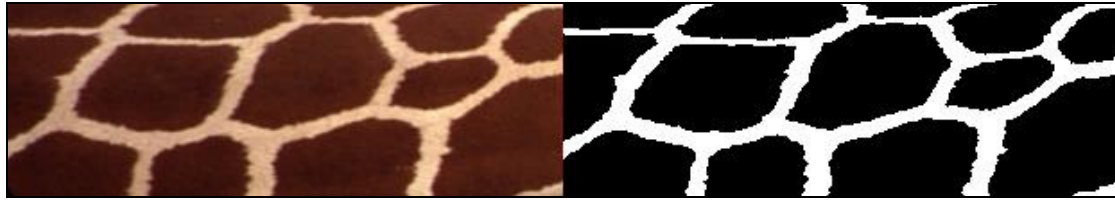

Figure 1. Examples of each of the 4 colour categories (1-4 clockwise starting from top-left).

Figure 2. Example of the MATLAB binarisation (transformation to black and white pixels only) of a section taken from a giraffe image

Population-specific patch colour and density were compared between the sexes and age classes, and compared to climatological variables. We used long-term climatological data (Meteorological-Office 1972) and focussed on variables that could affect environmental stress for giraffe (yearly maximum and minimum temperatures, relative humidity, yearly hours of bright sunshine, and yearly precipitation).

In the field, coat colouration of the study animals was scored in the same way. Behavioural data from agonistic interactions and male courtship attempts were also analysed to test the hypothesis that dark coat colouration in males functions as a signal of status.

2.2 Movements and male competition in relation to resource distribution

Fieldwork was carried out in Etosha National Park in Namibia, a hot, semi-arid area, with a high level of habitat heterogeneity and a well-defined network of waterholes. The majority of rain falls between January and April, with a little rain also between October and December. Surface 'veld water' remains in pits and depressions until the end of May or June. The selected study area included the nine perennial waterholes within 60km of Okaukuejo, which served as a base-camp. Approximately once a week, every waterhole was visited and every road was driven at least once. A database and photographic catalogue was produced for all the giraffe seen within the study area. A total of 431 individuals were identified, of which 90% were re-sighted at least once. On average, 255 giraffe were seen each month, and about 70% were recognised as known individuals.

Group composition, habitat type (species composition of the woody vegetation), and Global Positioning System (GPS) coordinates were recorded at all sightings of giraffe. These were used to examine variation in group composition, aggregation, individual movements relative to resources such as food and water, and home-ranges. Home-ranges were estimated using 95% Minimum Convex Polygons (MCPs) for all giraffe observed at least 10 times over a period of one year (e.g. Fennessy 2004).

Focal watches were carried out both at waterholes and away from waterholes to assess whether male competition for females is greater at waterholes. These were carried out from the vehicle, and lasted one hour, or until the focal subject was no longer visible. Behaviour was recorded instantaneously every five minutes. All occurrences of mating or agonistic behaviour were recorded and classed according to interaction type and intensity.

In order to determine paternity of calves, fresh faeces of known individual giraffe were collected for DNA extraction and microsatellite amplification. Faecal pellets from each giraffe sampled were initially stored in three tubes containing 90% ethanol, then the contents of two tubes were later transferred to silica gel beads (based on the methodology developed by Nsubuga *et al.* 2004).

3   RESULTS

3.1   Photographic analysis of patch density and colouration:

The analysis of photos revealed no significant overall sexual dimorphism in patch density (the proportion of the surface area of the pelage covered by patches). However, patch density was significantly greater in males than in females in the Etosha NP population.

Overall, males had significantly darker patches than females, but sexual dichromatism varied between subspecies and locations. Patch colour dichromatism was significant only in the Reticulated giraffe, *G. c. reticulata*, in Samburu GR, and the Angolan giraffe, *G. c. angolensis*, in Etosha NP. Dichromatism can be largely attributed to the darkening of males, but not females, with age.

There was a non-significant trade-off between patch colour and patch density. In populations with a higher mean patch density, the frequency of individuals with dark patches tended to be slightly lower than in those with a low mean patch density.

The climatological factors which most strongly predicted patch density were annual hours of bright sunshine and total annual rainfall. Between them, these factors accounted for 83% of the variation in mean patch density. Patches tended to be larger where rainfall was less, but size was limited in areas with greater hours of bright sunshine.

Bright sunshine also appeared to affect the optimum trade-off point between patch colour and patch density. Where bright sunshine is high (above the median of 2917 hours per annum), patches were paler than expected based on the mean patch size of the population, when compared to low insolarity habitats. This effect of bright sunlight on limiting patch colour was more prominent in females than in males (Figure 3). Consequently, in low-insolarity habitats the relationship between patch colour and patch density was similar for males and females. In high-insolarity habitats, females were paler, relative to their mean patch density, than males. This resulted in slight to extreme sexual dichromatism in patch colouration in most locations with high insolarity (e.g. Etosha NP, Namibia).

a)

Females: mean patch density

b)

Males: mean patch density
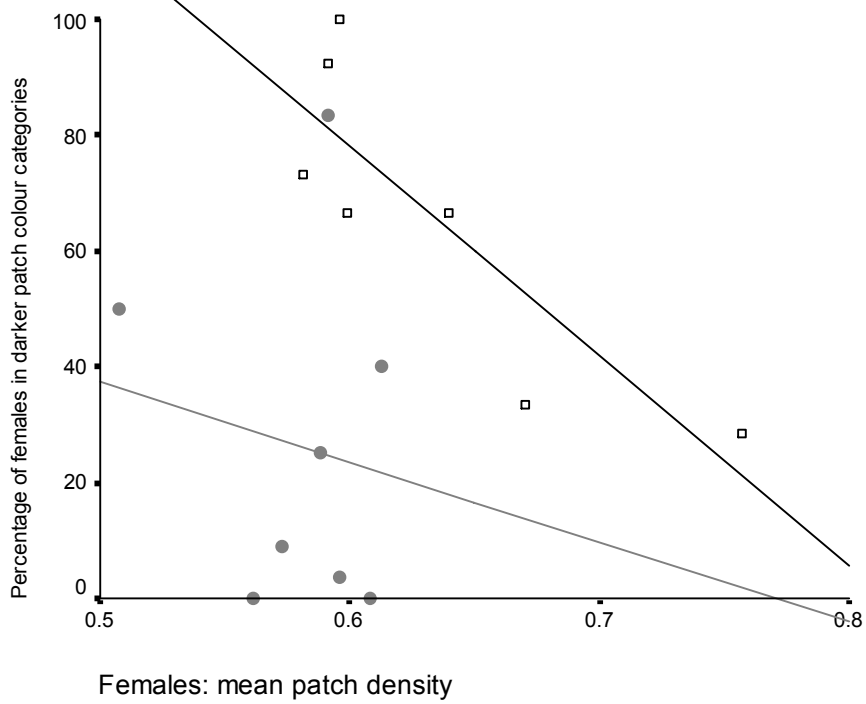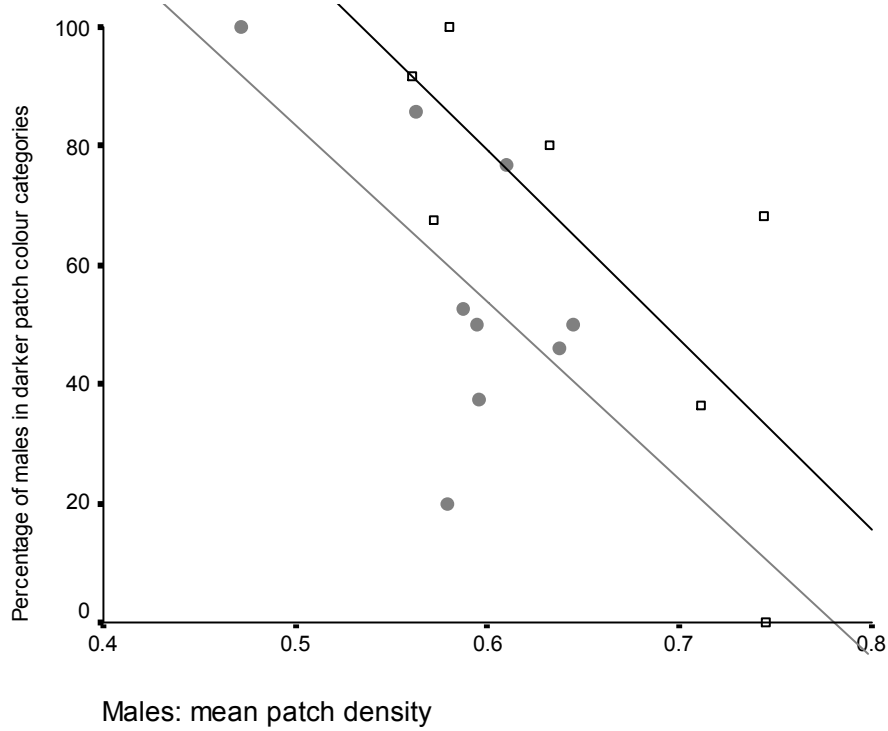
Figure 3. Relationship between patch density and percentage of giraffe with dark patches (dark brown and black) in a) females, and b) males. Empty squares = low-insolarity sites (<3000hrs p.a.), filled circles = high-insolarity sites.

3.2 Coat colour and male status in Etosha NP

Of the non-juvenile giraffe in the field study area, males were allocated to all patch colour categories, with almost half of the 191 males in the two darker categories, whereas only 17 females were darker than the typical category 2 ('tan') colouration and no females had black patches. This resulted in highly significant sexual dichromatism (Figure 4).
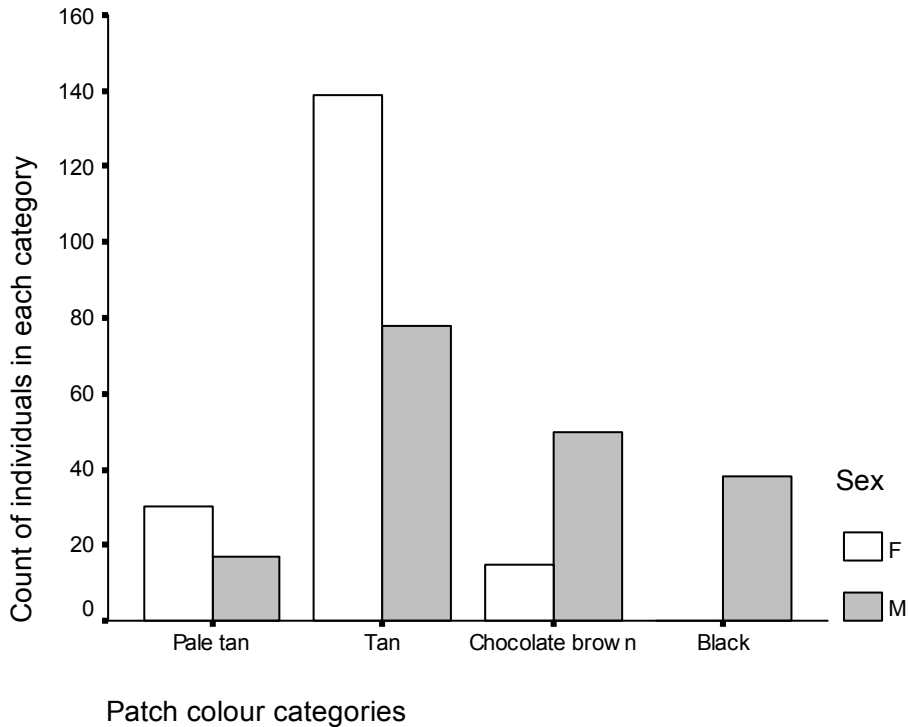
Figure 4. Distribution of study area giraffe in Etosha NP across the four patch colour categories. Numbers of non-juvenile males (M) and females (F) in the population are almost equal.

All sub-adult males (who are below adult height and whose horns still have hair protruding beyond the tips) were of colour categories 1 or 2. Conversely, all old bulls with very worn horns and bony exotoses on the skull are of colour category 3 or 4. Dark males were significantly taller than pale males, and heights of males of the darkest category (4) tended to be at the upper end of the height range for dark males (above 4.45 m). Thus male coat colour has a clear relationship with maturity.

Accordingly, there was a significant association between the type of agonistic interaction (displacement or intense necking vs. mild or moderate necking) and the coat colour of the participants (Figure 5). All but two displacements (demonstrations of dominance) involved adult males only. The majority (88%) involved at least one dark male, and half of these involved a pair of dark males. Conversely, all mild and moderate necking interactions involved at least one pale adult male, and 26% involved a sub-adult male. Violent necking interactions were observed only between dark, mature bulls.

Furthermore, the outcome of displacements and courtship attempts both corresponded well with male coat colour. The outcomes of displacement interactions and necking fights were significantly biased in favour of the darker male. The coat colour of the 'winner' was similar to or darker than that of the 'loser' in 91% of such interactions. The paler male was never the winner when more than 2 females were present.

There was also a highly significant association between male coat colour and success in eliciting female urination (Figure 6). The one sub-adult male that attempted to elicit urination was unsuccessful. Overall, pale adult males were successful 50% of the time, but very pale (category 1) males were never successful in eliciting urination, whereas category 2 males nearly always were. With the exception of one case, dark males were always able to elicit urination. The majority (81%) of the 27 observed consortships involved dark males, and all three observed attempted and successful matings involved dark mature males.
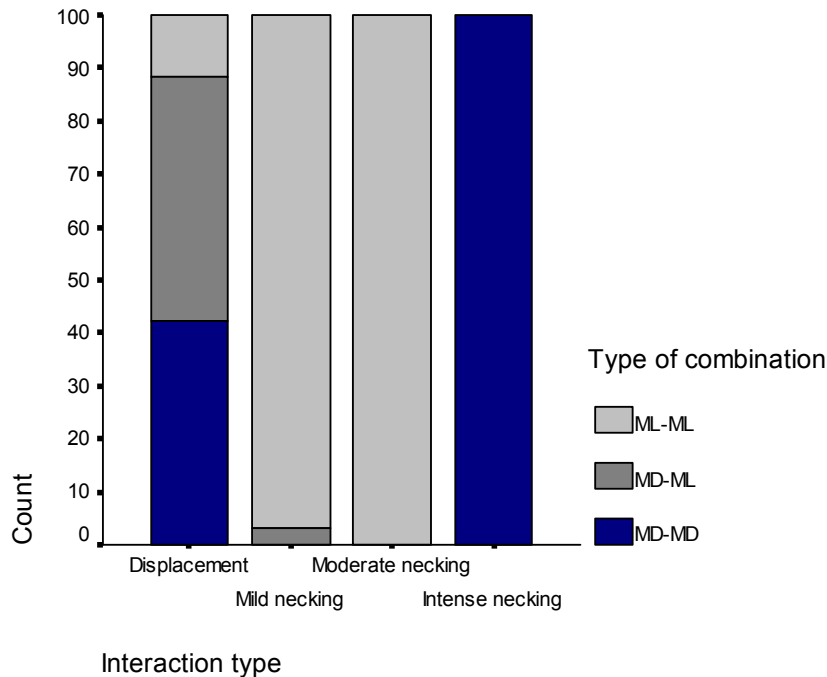

Figure 5. Combinations of bulls observed in the different types of agonistic interactions (MD = dark bull of patch colour category 3 or 4; ML = light bull of patch colour category 1 or 2).
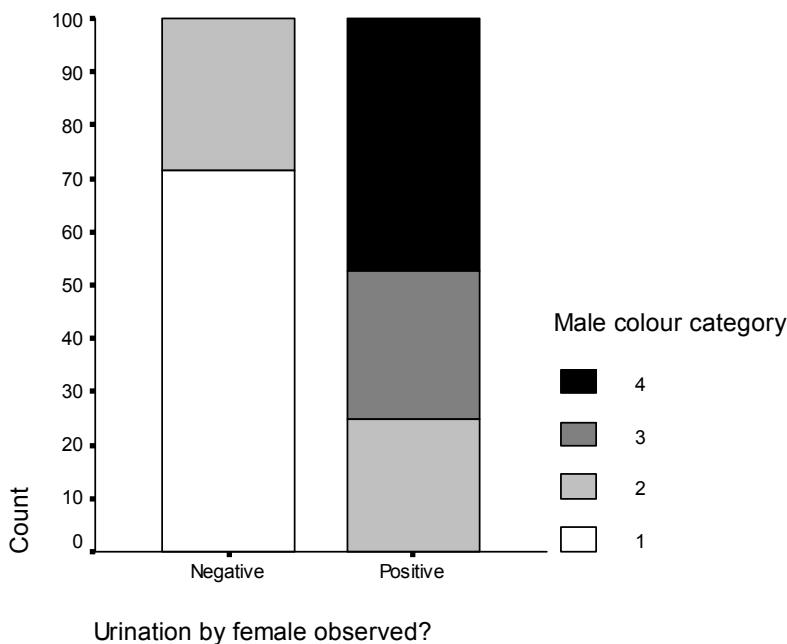

Figure 6. Outcome of urine-testing attempts by males, in relation to male patch colour (1-2 = pale bulls; 3-4 = dark bulls).

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A number of males, particularly young pale males, lost a degree of patch pigmentation towards the end of the dry season. In all, coat colouration of ten light males and of four dark males faded noticeably between one wet season and the end of the following dry season. In four cases, the male also experienced a noticeable loss of condition during the same period; in all other cases there was no clear change in condition. A disproportionately large number of giraffe deaths seem to occur towards the end of the dry season (B Kötting & W Versfeld, unpublished), suggesting that the colour loss could result from dry-season nutritional stress.

3.3 Feeding ecology and habitat selection

3.3.1 Feeding ecology

Giraffe were seen feeding on twenty species of woody plant, including seven Acacia species. *Acacia nebrownii* was the most important browse species for the giraffe of the Okaukuejo area of Etosha NP, making up 51% of all observed instances of giraffe browsing (Figure 7). It was the most frequently eaten species in at least eight out of ten months for both sexes.

Within specific habitat types, males and females made different selections from the browse species available. The main difference was that where such a choice of species was available, females were more likely to avoid *Colophospermum mopane* than males. Within-habitat feeding preferences did not differ between sub-adult and adult males, or between pale adult males and dark adult males, so sex differences do not appear to be due to different energy requirements associated with the larger size of mature males.

Seasonal variation in food selection corresponded largely with plant phenology (production of flowers, pods or fruit, and new leaves), especially for females (Figure 8). During the wet season, adult males were significantly less likely to be seen browsing than adult females (males: 36% of observations; females: 44%). In the dry season, males increased their browsing to match more closely that of females (43% and 41% respectively).
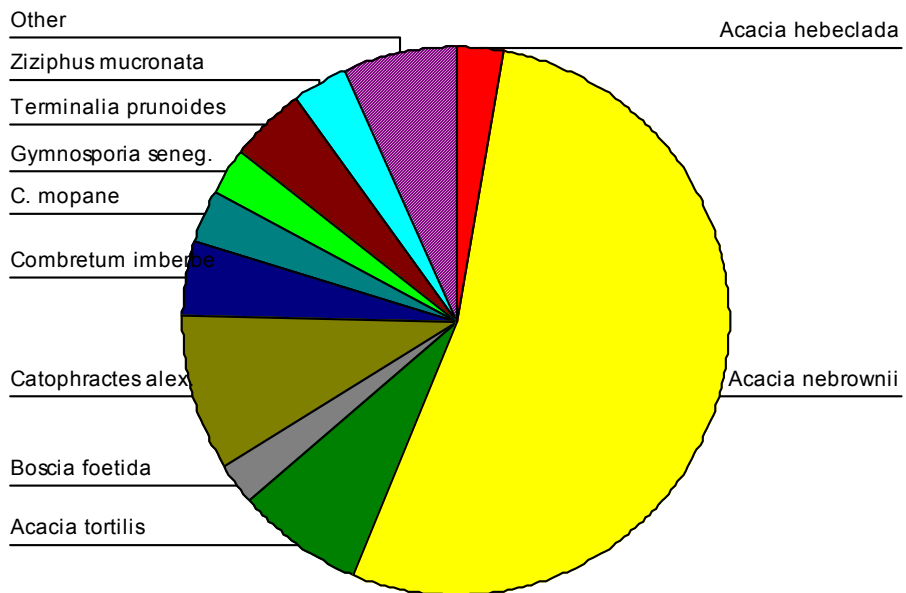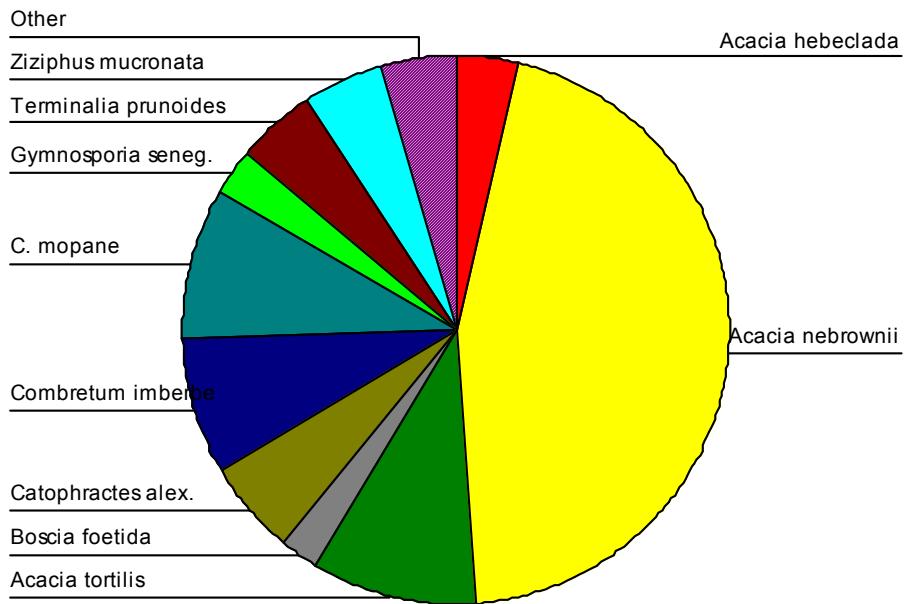
Figure 7. Representation of different browse species in feeding observations of males (above) and females (below) throughout the year.
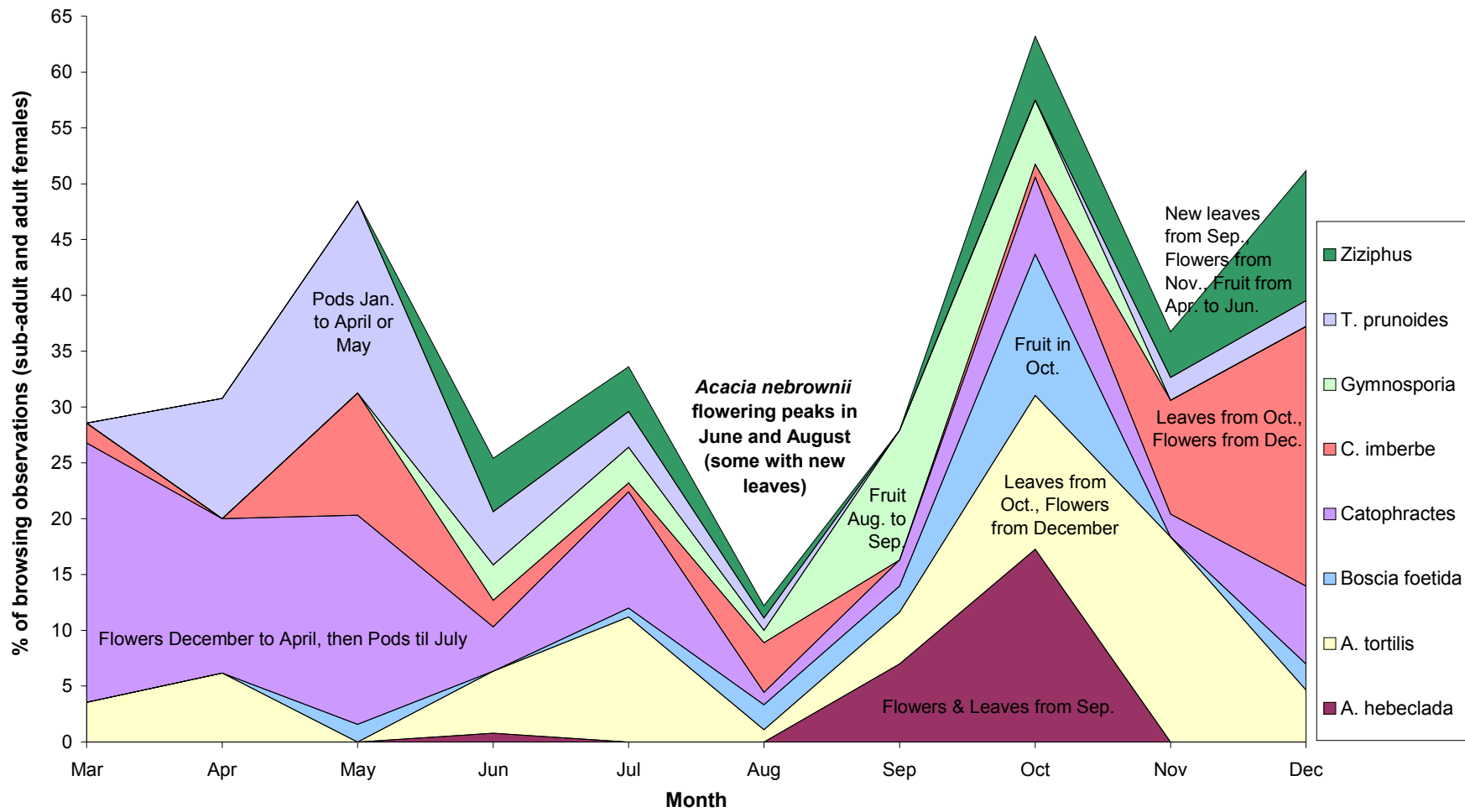
Figure 8. Variation in browse species selected by females throughout the year, omitting *A. nebrownii*, which accounts for the majority of the remaining observations.

3.3.2   Habitat selection

Giraffe were seen in all habitat types, including open, tree-less plains, which they traversed when walking to water, changing food patches, or when seeking mates (in the case of males). If giraffe use habitats in relation to availability, then ranks of sightings in the different habitat types should correlate with habitat availability ranks within the surveyed study area (within 1km of the roads). The most widely available habitats were open plains, mopane veld, mixed *C. mopane* and *Catophractes alexandrii* shrub savannah, then *Acacia nebrownii* bush veld. Preference indices (PI) were calculated as proportion of females sightings in a habitat divided by the proportion habitat availability.

Overall, female habitat selection ranks did not correlated with availability. Females showed strong preference indices for the spatially-restricted mixed broadleaf woodland (G: PI = 5.44), mixed thorn veld (F: 4.24) and Acacia veld (E: 3.08; Figure 3.8). Male habitat selection ranks also did not correlate with availability, and were significantly correlated with female selection ranks. Male preference indices were greatest for mixed broadleaf woodland (G: PI = 7.97) and mixed thorn veld (F: 6.96). Habitats containing high proportions of *C. mopane* were generally avoided by both sexes, but ranked highest for males in bachelor groups. Habitat selection ranks of solitary males correlated with those of females, whereas habitat selection ranks of males in bachelor groups did not.

3.3.3   Waterhole use

Giraffe not only used waterholes regularly in Etosha NP, but went out of their way to visit waterholes. Indeed, in the dry season, perennial water sources drew giraffe into habitats which they might not otherwise use (giraffe often walked 10 km across tree-less plains to reach one waterhole, Okondeka). Giraffe use of perennial waterholes was highly dependent on the rains and availability of surface water. Waterhole use was lowest in the months that heavy rain occurred, and increased steadily throughout the dry season (Figure 9). During the driest months in terms of water availability (July-Sept.), and in the later hot, dry season (Oct.-Dec.), female giraffe were significantly more likely to be found at perennial waterholes than at other sites. Overall, adults spent more time at waterholes than did sub-adults, and males spent more time at waterholes than females, with dark males staying the longest.
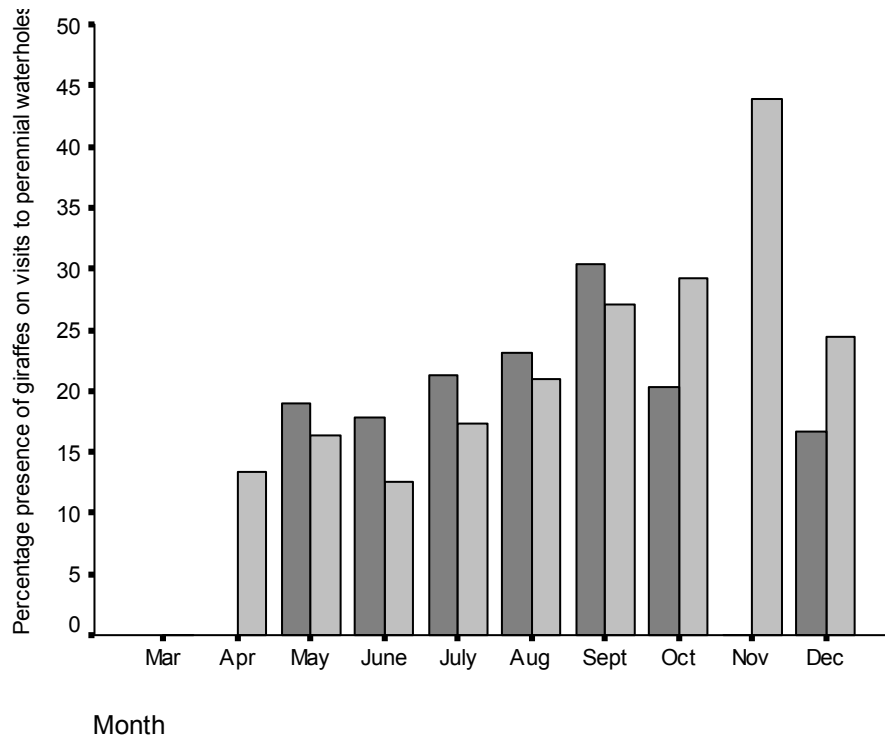
Figure 9. Occurrence of giraffe at perennial waterholes, as defined by the percentage of visits by the observer on which giraffe were present. Dark grey bars: 2004; light grey bars: 2005.

3.3.4   Group size and female aggregation

Group size averaged 3.56 (± 0.10) over the entire study period, but was largest during the 'wet' period from March to June, declined in size until September and then increased again toward the end of the year (Figure 10). Group size was significantly larger between March and June than during the drier, second half of the year. The largest observed group size was 23 individuals.

Based on tree phenology and feeding observations, female aggregations (with or without males) were expected in *Catophractes alexandrii* bush veld or mixed broadleaf woodland (containing *Combretum spp.* and *Terminalia prunoides*) from March to May, *Acacia nebrownii* bush veld between June and September, acacia veld from October to December, and mixed broadleaf woodland again in December. Females were not expected to aggregate in habitats comprising a large proportion of *Colophospermum mopane*.

Accordingly, females groups were generally smaller in *C. mopane*-rich habitats that did not also include Acacia species. Between March and May, the greatest numbers of large aggregations of females (>7 females) were seen in mixed broadleaf woodland, as predicted. However, mean female group sizes tended to be large in many habitats due to a widespread abundance of food and water, so mean group sizes in *C. alexandrii* bush veld and mixed broadleaf woodland did not significantly deviate from the overall mean group size.

Between June and September, the largest groups of females were seen predominantly in *A. nebrownii* thickets (B) and in open plains (A) surrounding waterholes. Females did aggregate significantly in *A. nebrownii* habitats, but only in the month of August. As predicted, significant aggregations of females formed in acacia veld between October and December, and in mixed broadleaf woodland in December.

Groups were not significantly larger at waterholes than away from waterholes, except during the driest month, September (Figure 10). Neither were female groups larger closer to perennial waterholes than further away, when all sightings were examined (comparison made at 2km). However, when analysed for each perennial waterhole separately, groups were found to be larger closer to certain waterholes, but not others. The clearest trend was for Ombika, where average female group size declined with distance from the waterhole (Figure 11). This trend was evident in both the wet and dry season, probably due to the preferred wet-season foods (e.g. *Terminalia prunoides*) located in close proximity of Ombika waterhole.
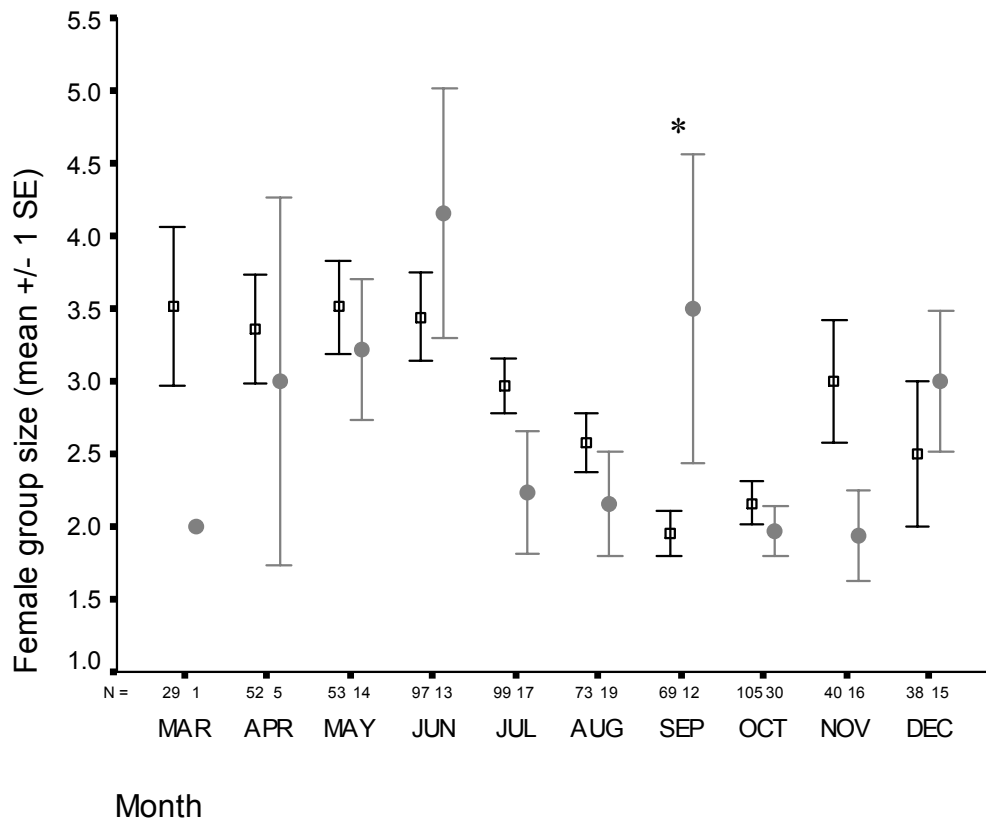
Figure 10. Mean monthly female group size (± 1 SE) in all groups that included females, at waterholes (filled grey circles) and away from waterholes (empty black squares).
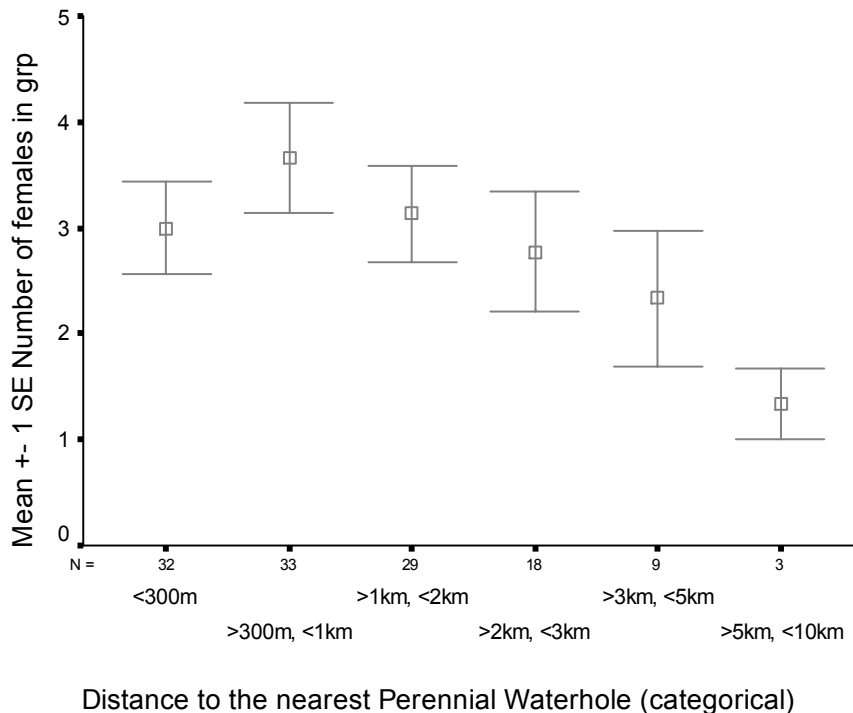
Figure 11. Mean female group size, for all groups that included females, in relation to distance from waterhole, for the waterhole Ombika.

3.4 Home ranges and movements

Male home ranges (95% MCPs) were typically slightly larger than female home ranges (213 km^2 and 135 km^2 respectively). Home ranges of dark mature males tended to be slightly larger than those of pale adult males, but were more variable in size and accounted for the three largest and three smallest male home ranges, suggesting a high degree of inter-individual variation in ranging behaviour.

Core areas were estimated for females using 50% fixed kernels (with smoothing factor calculated by the default least squares cross validation (LSCV) of locations (e.g. Kusak *et al.* 2005)), for 45 females that were sighted at least twelve times. The highest overlaps of female core areas occurred at or near perennial waterholes, and particularly at waterholes in proximity of preferred food sources (Figure 12).

As males mature they spend proportionately less time associating with females (Figure 13). The degree of association between mature males and females was also affected by male movements. Group composition varied with proximity to core areas of female use (degree of core area overlap). Lone males and bachelor groups were more likely to be seen in areas of low core overlap than a single male with females or mixed groups.

When males were in areas of high female usage (>5 core overlaps), they were more likely to be in a group with females than in areas of low overlap or where no core areas were identified. Furthermore, when males were in groups containing females, they tended to be with larger numbers of females in areas of greater core overlap. Individual males with smaller home ranges were seen within areas of high female core overlap on a greater proportion of sightings than males with larger home ranges (Figure 14). Solitary adult males were significantly more likely to be found standing resting or ruminating while outside the core female areas than within them.

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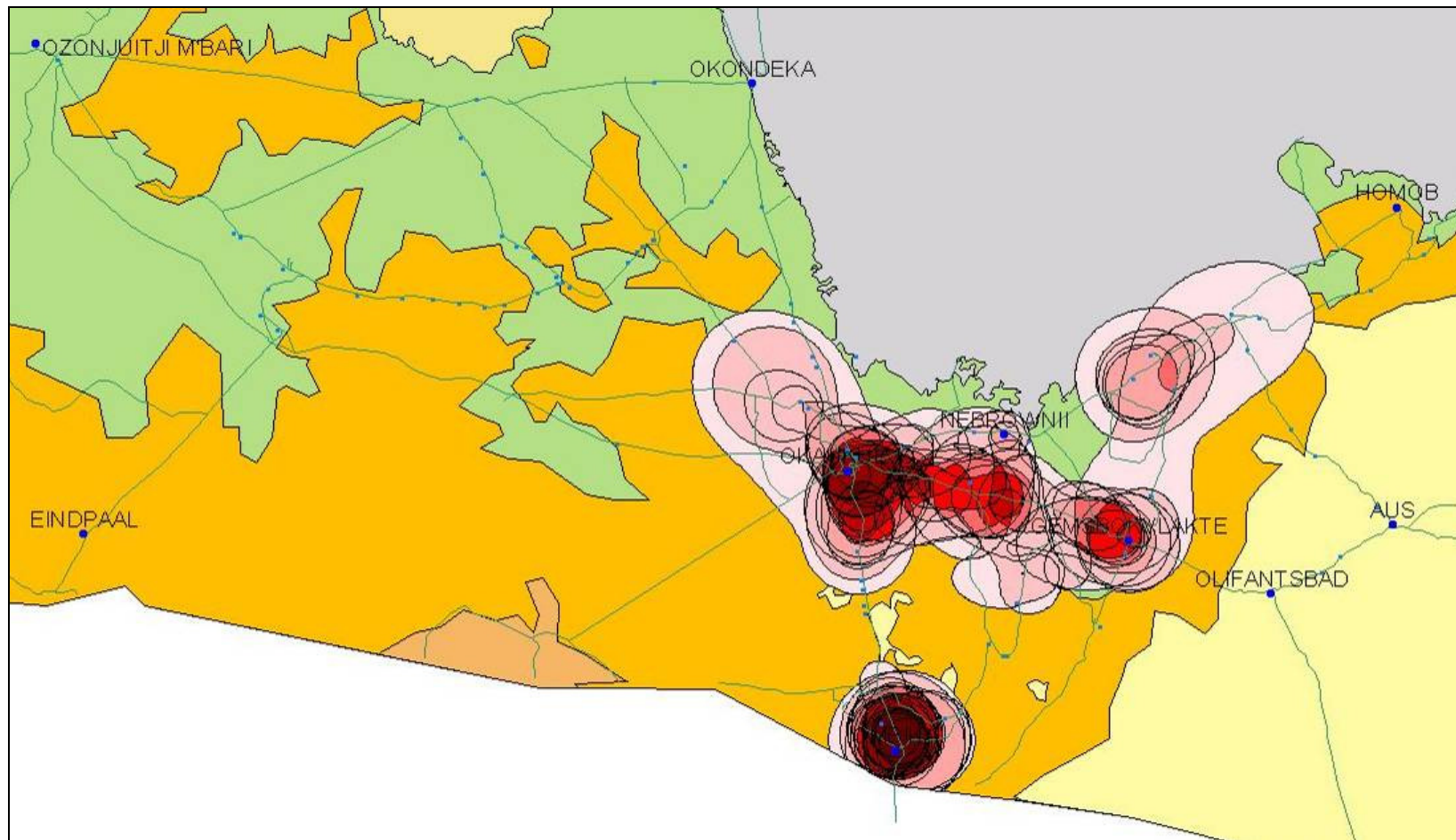
Figure 12. The entire study area, with female core areas in pink. Darker areas represent higher core area overlap. Grey areas are pans. Green areas represent predominantly open plains but include some shrub savannah (including *A. nebrownii*). Orange areas include some *A. nebrownii* and thorn veld close to the pan, but are predominantly mopane veld further from the pan (except around Ombika waterhole near the southern park boundary, which is in a patch of mixed broadleaf woodland). Pale yellow areas are mopane veld.

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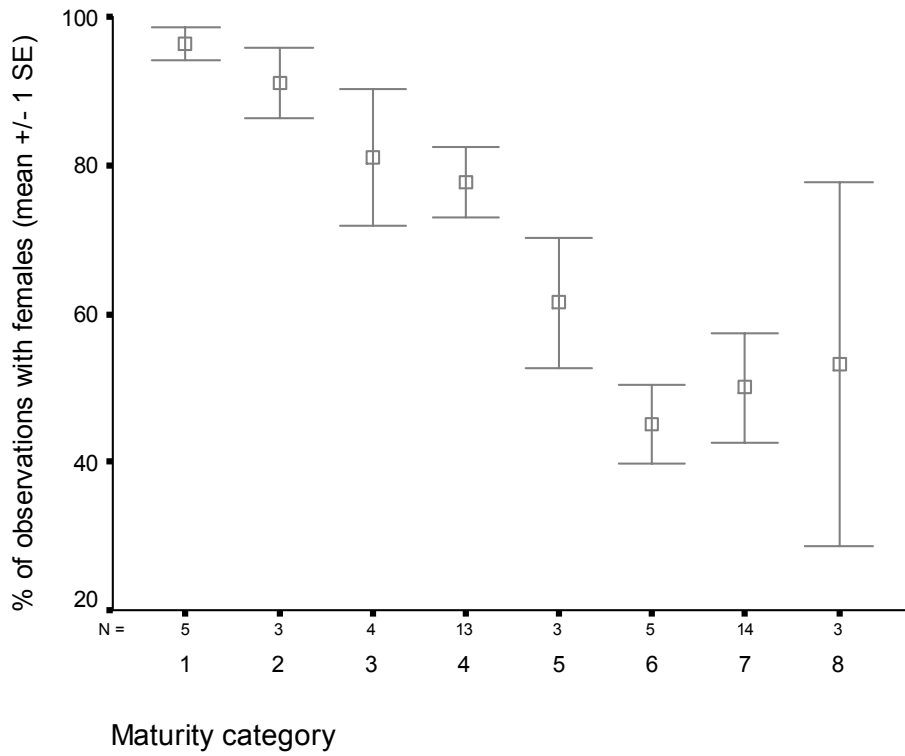
Figure 13. Percentage of observations with a female, for frequently observed males of different age classes (age classes ranged from: 1) juveniles to 8) old black males).
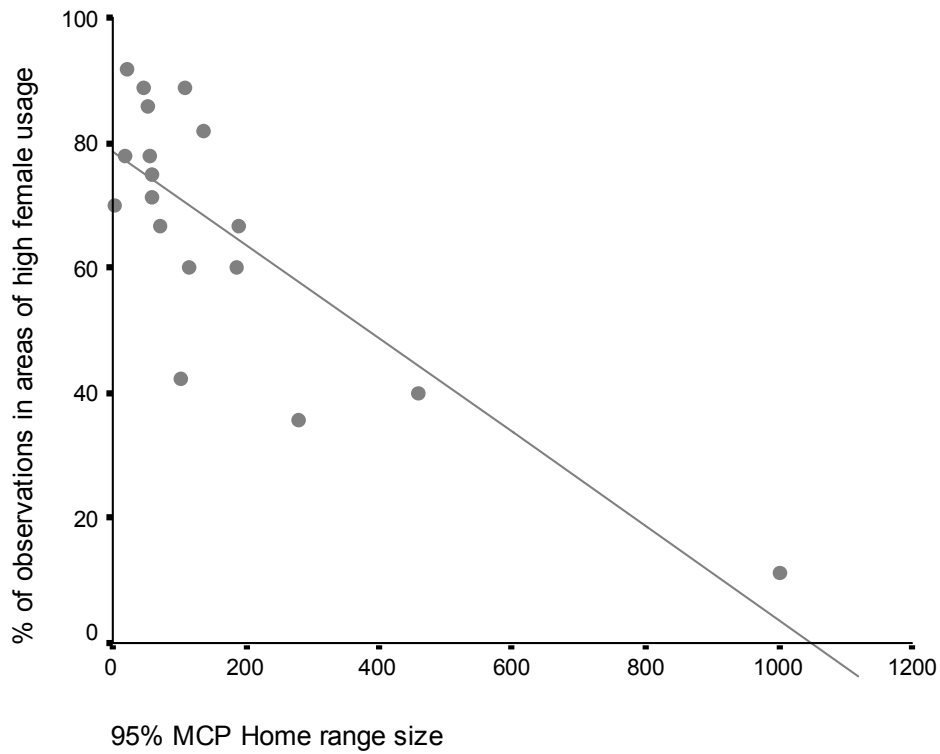
Figure 14. Proportion of observations of individual adult males in areas of high female usage (>5 female core area overlaps) relative to male home range size (95% MCPs). Males with smaller home ranges were seen more frequently with females than males with larger home ranges.

3.5 Breeding seasonality

It was predicted that within the study area, which has a similar seasonal rainfall pattern to the South African eastern Transvaal, there would be a comparable wet-season breeding peak to that found by Hall-Martin et al. (1975). Indeed, based on estimated birth-dates of calves (to the nearest month), a peak calving season was apparent from March to June, with the greatest number of births in May, and the fewest in September. Births occurred in all months of the year, but just over 50% of births were estimated to have occurred in the four peak months. Assuming a fourteen-and-a-half to fifteen month gestation period (Hall-Martin *et al.* 1975; del Castillo *et al.* 2005), this yields a conception peak between December and March, with the greatest conception rate in February, and a lull between June and September (Figure 15). The conception peak is very similar to that found by Hall-Martin et al. (1975), and also corresponds with the annual rainfall peak (data provided by W Versfeld and B Kötting).
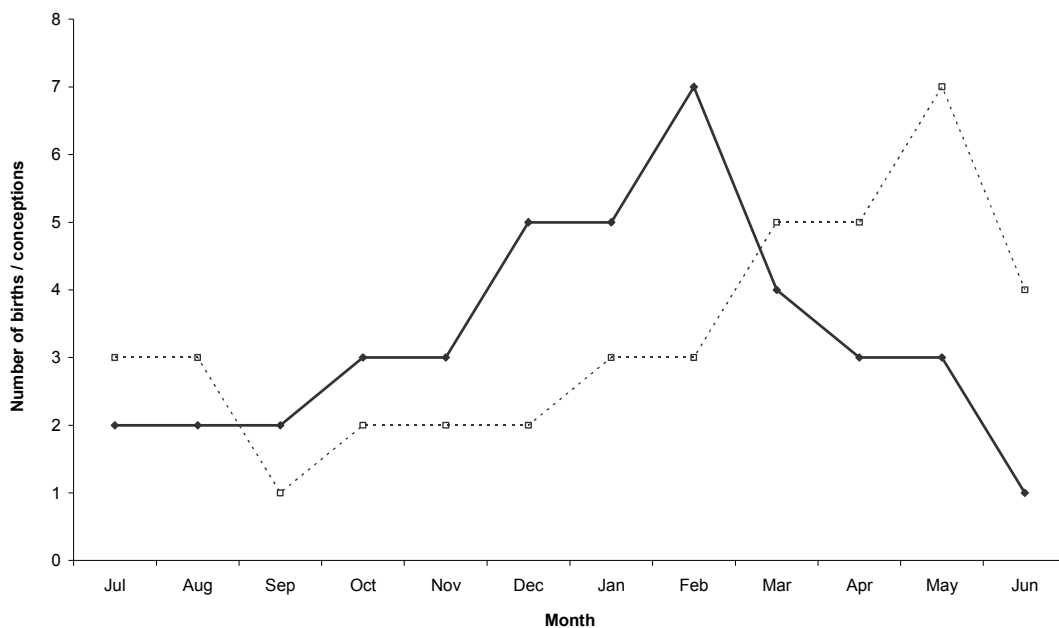
Figure 15. Estimated peaks in calving (dashed line) and conceptions (solid line) in the study area, based on forty estimated calf birth dates.

3.6 Seasonal and individual variation in movements and habitat use

Males of different age or social status may adopt different mating strategies, as only the most dominant males should have the potential to monopolise females. Therefore, it was predicted that dominant, darker males should move from habitats preferred by males into habitats where females were aggregating, and thus exhibit different habitat use to that of younger or subordinate adult males (who should remain in habitats preferred by males). In the study area, females were more aggregated and spatially clumped during the wet (high-conception-rate) than during the dry (low-conception-rate) season. Therefore, it was also predicted that male competition for females would be greater in the wet season.

In the wet season, habitat selection ranks for dark males, and for pale males and bachelor groups, did not correlate with female aggregation ranks (habitats ranked according to mean female group size), but both were highly correlated with female habitat selection ranks (habitats ranked according to proportion of female sightings).

In the dry season, habitat selection ranks for dark males (alone or with females) almost correlated with female aggregation ranks, and did correlate with female habitat selection ranks. On the other hand, habitat selection ranks for pale males and bachelor groups did not correlate with female aggregation or habitat selection ranks. Habitat selection ranks of dark males were highly correlated with those of pale males and bachelor groups in the high-conception-rate season, but not in the low-conception-rate season.

Overall, habitats in which females were aggregating ranked higher for habitat selection for dark males than for pale males and bachelor groups. The exceptions were mixed broadleaf woodland in the wet season, and *A. nebrownii* bush veld in the dry season. These were both the top-ranking habitat in terms of female occupation (after open plains) and held significant female aggregations for at least one month in their respective season.

On the individual level, there was a high degree of variation in habitat use among dark males. Some males were found almost exclusively in habitats preferred by females, whereas others were only seen in a wide diversity of less preferred habitats. It was also clear that some males used distinct seasonal home ranges, as they were only sighted within the study area during a short period in both years. These seasonal visitors had significantly smaller home ranges (all 95% MCPs less than 60 km^2) than year-round residents, tended to spend more time in areas of high female usage, and were more likely to be seen with females. Home ranges of all but one of the six seasonal visitors overlapped to some extent at Ombika waterhole, in the mixed broadleaf woodland.

3.7 Male competition

3.7.1 Waterholes as focal points for mate interception

Focal watches were carried out to establish whether competition between males for mates was indeed greater at waterholes because of the higher predictability of occurrence of females at waterholes. A total of 166 focal watches were carried out. Focal watches at waterholes were those that took place entirely within 300m of a waterhole, whereas those classed as away from waterholes were those that took place entirely beyond 300m of a waterhole.

The most important factor in determining the occurrence of social interactions, regardless of location, was the occurrence of new encounters. A new potential mating encounter was considered to form when, for example, a female arrived at a waterhole where a male was already present. For both mating and agonistic interactions, the occurrence of new encounters increased the likelihood of giraffes interacting during a focal watch (e.g. Figure 16 for mating interactions). New encounters were three times more likely to occur during focal watches at waterholes than away from them (e.g. Figure 17 for male-female encounters), and this difference was slightly greater during the dry than the wet season.

When interactions did occur, there was a slight trend for the rate of such interactions to increase as the number of potential interacting pairs present during the watch increased. Thus interactions tended to be more frequent when giraffe groups were larger. However, even when the number of potential interacting pairs was taken into account, interactions were still more frequent at waterholes.

A greater proportion of observed urine-testing attempts occurred at waterholes during the dry season and early wet season. Of the six consortships that were observed from the start (from the moment of the first encounter and urine-testing) five began at a waterhole.

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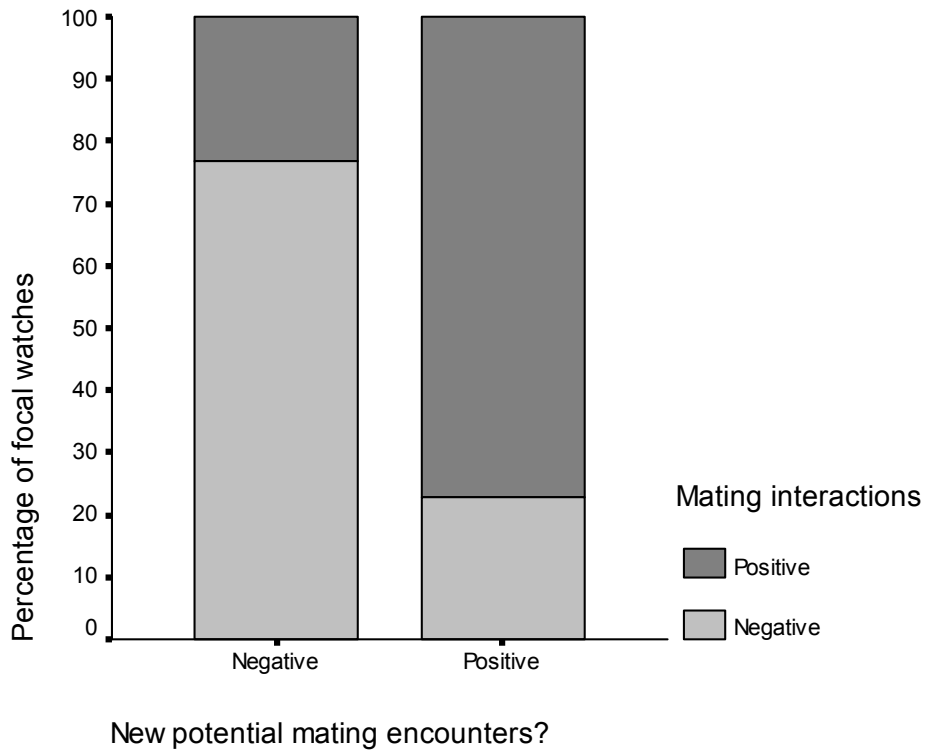
Figure 16. Association between the occurrence of new encounters forming, and the occurrence of mating interactions across all focal watches.
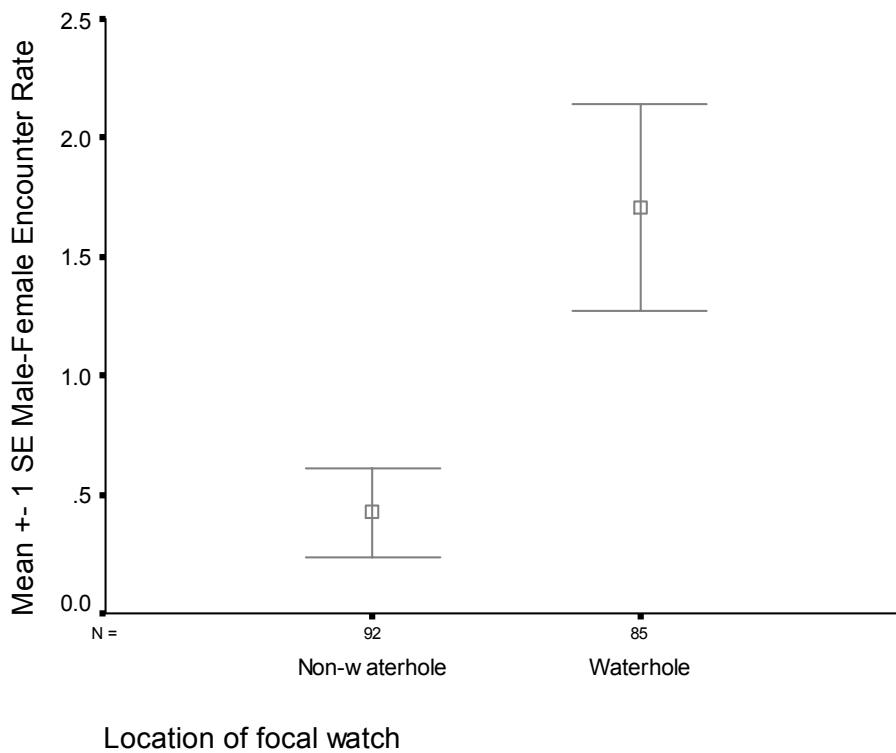
Figure 17. Mean frequency per hour of new male-female encounters at waterholes and non-waterhole locations.

3.8   Seasonal variation in intensity of male intra-sexual competition

There was a significant association between the colour of the male involved in urine-testing and the season .Very pale males were only observed attempting to elicit urination in the drier months (in June, and between August and November). Dark adults (cat. 3-4) made up the largest proportion of males urine-testing in December (100%), between March and May (at least 70%), and in September (69%).

Displacements of subordinates by dominant males (N = 55) were observed in all months except for November. Only three necking fights were observed, and these occurred in April, May and October. Overall, agonistic interactions between males, relative to total sightings of adult males, were most frequent in December, and between March and July.

Displacements in December and March involved only pairs of dark bulls, whereas pairs of pale bulls were only observed in displacement interactions in the dry season (between July and October; Figure 18). In August there were no interactions between two dark bulls.

During the late-wet, early-dry season (March-June), two dark bulls observed together were significantly more likely to be involved in an agonistic relationship (i.e. a displacement or necking fight) than a neutral one (Figure 19). In the dry and early-wet season, the majority (80%) of dark bull pairs observed did not demonstrate any sign of dominance, submission, or aggression towards each other.
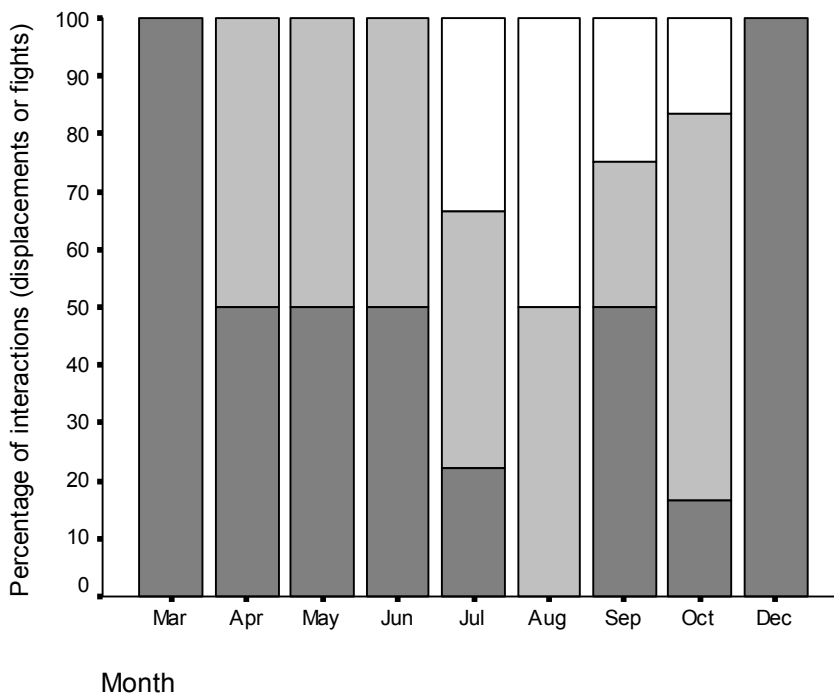
Figure 18. Pairs of males involved in displacement interactions across the months. Dark grey bars represent pairs of dark males (cat. 3-4); light grey bars represent pairs comprising one dark and one pale male (cat. 1-2); white bars represent pairs of pale males.

21
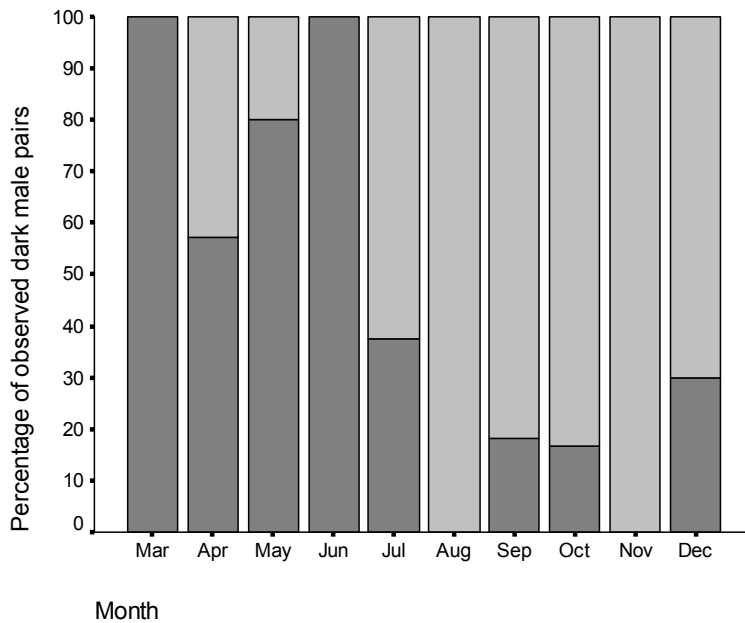
Figure 19. Relationships between two dark males observed together. Dark grey bars represent agonistic relationships (e.g. displacements, necking fights); light grey bars represent an absence of such agonistic interactions.

3.9   Paternity assignment

A total of 164 faecal samples were collected from 149 different giraffe, all but 32 of which were known individuals. In total, 147 of 241 DNA samples produced amplifiable PCR products, of which 120 could be scored for seven or eight microsatellites. A further 15 samples could be scored at five to six loci. These 135 samples represented 128 individuals. There was a slight effect of storage medium on the success of microsatellite genotyping. Time in storage had a significant effect on the number of loci successfully typed for samples stored in silica gel but not those kept in ethanol.

Unfortunately, the informativeness of the markers used was not sufficient for paternity assignment (mean PIC = 0.292, total exclusionary power (first parent) = 0.429, total exclusionary power (second parent) = 0.76). Two of the 16 available markers were not tested because one had previously been found to be monomorphic in the Etosha NP population (Rick Brenneman, pers. comm.), and the other amplifies microsatellite products over 300bp, which are generally considered too long to amplify reliably with faecal DNA (Frantzen *et al.* 1998). Three of the markers tested were monomorphic within the study population, and three markers were difficult to amplify or score reliably. The mean number of alleles for the eight remaining markers was 3.1.

These problems were further compounded by the lack of a known mother for the majority of calves (giraffe mothers often leave their calves with other females while they go to drink, for example), and the low proportion of candidate parents sampled (less than 30% of putative fathers and less than 40% of putative mothers). Even with relaxed confidence levels (80%) and conservative parameters, only one paternity could be assigned. Interestingly though, this was assigned to the male with the most extreme seasonal movements – he was seen in the study area only for two-three months each year, yet was the only male to be observed in four agonistic interactions and to win them all (three displacements and one necking fight), and was observed in the most mating interactions, including one of the two observed successful copulations.

### 3.10 Monopolisation of females and reproductive skew

Using the data from focal watches, the sex-age classes of nearest neighbours were compared for different types of focal subject, for mixed groups only. Away from waterholes, a dark male focal subject was significantly more likely than a pale adult male to have an adult female as a nearest neighbour. At waterholes, pale adult males were equally likely as dark adult males to have an adult female as a nearest neighbour.

There was also a significant association between male colour and the location where males were seen to urine-test females: paler males were significantly more likely than dark males to attempt to test females' urine at waterholes rather than away from waterholes. As a result, when urine-testing attempts occurred, the protagonist was a dark male in the majority of cases (70% of 74) away from waterholes, whereas at waterholes interactions were equally distributed among dark and pale males. Furthermore, when a pale adult male was urine-testing a female, a dark male was slightly, but not significantly, more likely to be present when the interaction occurred at a waterhole than when it occurred elsewhere.

When there were at least one pale male and at least one dark male present, dark males appeared more likely to concede access to females for urine testing to pale males when there were three or more pale males present. Very pale males (category 1) and sub-adult males had access to females for urine-testing predominantly when there were large numbers of pale males present

Despite frequent sexual interactions (urine-testing attempts) between pale males and females at waterholes when dark males were present, pale males were never seen to leave a waterhole in consortship with a receptive female when a dark male was present. All five observed consortships involving a pale male were in the absence of a dark male, including the two that were seen from the start (one at a waterhole, one away from a waterhole). In two of these cases, the female was subsequently observed in consortship with a dark male (four and seven weeks later). This suggests that the female was still unmated and the pale male had been unsuccessful in his attempt. If a dark male was present, regardless of the number of pale males also present and urine-testing females, the dark male always gained rights to the consortship (N = 4), following the female away from the waterhole.

Of the 25 observed consortships in the study area, 80% involved a dark male (Figure 20). Half of the dark males seen in a consortship were category three males, half category four. Two successful matings and one attempted mating were observed. All involved a dark, mature male, two of category four coat colouration, one of category three. Based on these behavioural data, it is estimated that pale adult males, which represent just under 50% of the known males in the study area, achieve between zero and 20% of matings. Among dark males, category four males are estimated to achieve a share of between 50% and 66.7% of matings.
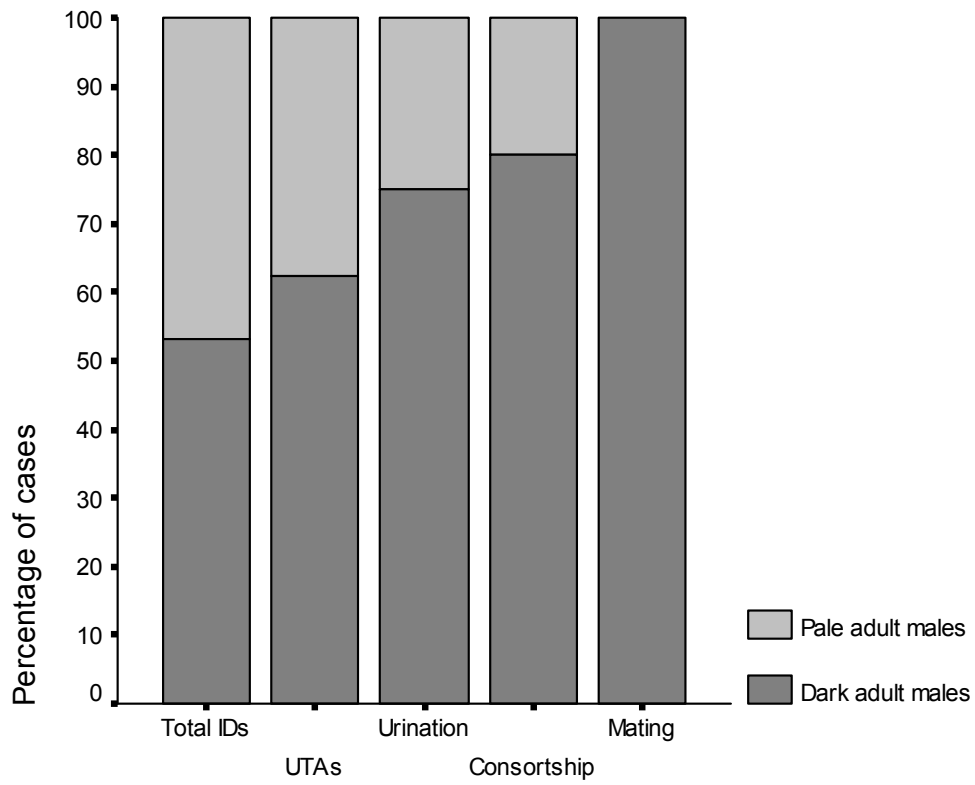
Figure 20. Relative share (%) of dark and pale adult males in: total known males in the study area, urine-testing attempts (UTAs), successful elicitation of urination, consortships, and attempted or successful matings.

4   CONCLUSIONS

4.1   Coat colouration

Solar heat gain in animals is influenced by coat colour, and is important in determining water consumption and survival in stressful conditions (Finch & Western 1977). The results of this study suggest that bright sunshine acts as a limiting factor in the evolution of giraffe coat markings: bright sunshine restricts patch density, or the frequency of certain types of colouration, in different environments.

It has been suggested that patches could help regulate heat balance by acting as "thermal windows through which giraffes dissipate heat" due to the arrangement of subcutaneous anastomotic blood vessels beneath patches (Skinner & Smithers 1990). Alternatively, patches could aid in the absorption of radiant heat on cold but sunny days (Mitchell & Skinner 2003). However, whether or not patches function as thermal windows, coat colouration will still affect heat gain considerably more than heat loss. So it is highly plausible that on hot and sunny days, large, dark patches may disrupt rather than enhance thermostatic control.

The stronger effect of bright sunlight on limiting patch colour in females than males results in sexual dichromatism in high insolarity locations. This suggests a thermoregulatory cost to being dark in areas of high insolarity; a cost which is important to females, but which is possibly outweighed in males by some benefit derived from being dark. This benefit could be that of a costly signal of status that only high quality males can afford to produce or maintain.

The results from the field, in a hot, semi-arid environment, provide support for a role of status signal for dark patch colour in males. A clear relationship was shown between colouration, social status and behaviour. Observations suggest that this status signal not only serves a role in male dominance interactions, but also in female mate choice.

A possible additional cost of producing dark pelage colouration was revealed by the observations that some males lost pigmentation in the height of the dry season. This could be due to a scarcity of nutrients (especially trace minerals) necessary to maintain pelage pigmentation (e.g. McGraw 2003). Thus, poor quality males, unable to obtain sufficient quantities of these nutrients, may be less able to sustain pigmentation of this secondary sexual trait. This observation is consistent with the idea that sexual selection should favour signals of quality that are costly and that cannot be imitated by poor quality individuals (Zahavi 1975).

4.2   Limited resources and intra-sexual competition

Giraffe movements were partly determined by the locations of perennial waterholes, but were in no way restricted by this limited resource. Although they did not gather in larger groups at waterholes overall, female groups were larger closer to waterholes that coincided with preferred food patches. Females also occurred more predictably at waterholes than elsewhere during the dry season, and particularly at waterholes near preferred foods. This would offer males an opportunity to reduce their search effort by focussing on perennial waterholes to intercept females.

As predicted, encounter rates and consequently interaction rates were greater at waterholes. As a result, waterholes appear to give pale males an increased opportunity to associate with and urine-test females. However, dark males did not appear to tolerate subordinates less at waterholes than elsewhere. It is proposed that this is due to increased intruder (competitor) pressure at waterholes. Dark males may tolerate subordinates, because reproductive access is

strictly determined by dominance, and as such the benefits to a dominant male of attempting to exclude subordinates, and the costs of allowing their presence, may both be low (Clutton-Brock 1989). Indeed, despite dark males' tolerance of subordinates, on occasions when a receptive female was investigated by both dark and pale males, it was invariably the dark male that gained the opportunity to court the female.

Although waterholes may serve as focal points for mating interactions, the seasonal availability of preferred foods also serves a key role in shaping the mating system and the potential for males to monopolise mates in the study area. Giraffe in the study area fed on different species at different times of year in relation phenological changes. Results suggested that males (e.g. bachelor groups) preferentially occupy different habitats to females, where food may be abundant but apparently unsuitable for females. In particular, females avoided *C. mopane* as a food species, and avoided mopane habitat. This has previously been observed by Dagg and Foster (1982) in South Africa, and may be due to a general avoidance of species that contain chemical components, such as tannins, that are difficult to digest, or which may be harmful if passed on through their milk to their calf (Caister *et al.* 2003).

Mature, dark males were found to move out of their preferred habitats into habitats preferred by females in their search for potential mates. A strong link was found between male movements and association with females. Firstly, association with females varied with male maturity. Mature males tended to spend less time associating with females than sub-adult or young adult males. Secondly, association with females related to differential use of the study area. Males were more likely to associate with females in certain areas (e.g. core areas of female use) than others. Males may leave female core areas to return to more optimum feeding or to rest and replenish energy reserves.

Lastly, use of the study area differed between individuals. Fully mature males that ranged over large areas and remained within the study area year-round spent a large proportion of their time in areas of low female usage, and were often seen alone. Other mature males were found to use the study area on a highly seasonal basis. These seasonal visitors had smaller home ranges, tended to spend more time in areas of high female usage, and were more likely to be seen with females. These seasonal visitors may in fact use home ranges of a similar size to those that remained within the study area year-round. This observation highlights the shortcomings of using field observations to collect GPS data versus using GPS collars (see Fennessy 2004 for benefits and limitations of GPS collars on giraffes).

These inter-individual differences in male ranging behaviour and social associations are suggestive of different mating strategies. Some males appear to adopt a year-round, but intermittent, following strategy. Others adopt a seasonally variable strategy with restricted movement and a high degree of association with females during the time they are in the study area. This points towards temporary, localised defence of females in areas of high and predictable female usage. This seasonal strategy might be favoured by the most dominant males, who can enter the female core areas temporarily with a high chance of encountering receptive females, and a high likelihood of being able to displace any potential competitors they encounter. Subordinate males adopting this strategy would face a high risk of not gaining any reproductive opportunities, if dominant males were already present in the female core areas on their arrival. Instead, subordinate males must occupy areas less favoured by females year-round, possibly gaining mating opportunities through chance encounters of undefended receptive females.

Male intra-sexual competition appeared to be greatest in habitats that were highly preferred by females (e.g. mixed broadleaf woodland in the wet season, *A. nebrownii* bush veld in the dry season), resulting in many mature males being excluded from them (although pale males seem to be tolerated, possibly because they do not represent a real threat). When the preferred habitat type was particularly spatially limited (e.g. mixed broadleaf woodland in the wet

season), this resulted in increased male competition. Indeed the intensity of male intra-sexual competition appeared to be greater in the wet than in the dry season.

4.3   Molecular analyses

The failure of the molecular analysis was extremely disappointing but the results will hopefully inform future work. Paternity assignment for a wild population of giraffe would be possible if a greater number of informative markers were available, if a larger proportion of candidate parents were sampled, and if a greater proportion of mother-offspring relationships could be identified *a priori*. If additional markers are to be developed for this purpose, they should ideally be developed using tissue samples (skin, muscle, or blood). These samples should also be taken from the population under investigation, as there appears to be considerable inconsistency between subspecies in the polymorphic information content (PIC) of the present markers (Rick Brenneman, pers. comm.).

In the absence of the genetic data, it can still be concluded that matings are largely restricted to fully mature dark males, as dark males are able to monopolise mating access to females even in the presence of large numbers of pale males. In addition, there is high variability among dark males in their degree of occupation of female core areas and association with females. Since these differences are not obviously related to maturity, they may be indicative of differences in male quality, and are likely to serve as moderately reliable indicators of reproductive success. Specifically, reproductive success is possibly highly skewed towards dominant males that enter the female core areas on a seasonal basis, excluding most competitors from these areas and likely monopolising access to receptive females.

5   ACKNOWLEDGEMENTS

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