Evolutionary Ecology of Giraffes
(*Giraffa camelopardalis*)
in Etosha National Park, Namibia

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ABSTRACT

The giraffe (*Giraffa camelopardalis*) occupies a variety of habitats across sub-Saharan Africa. It is characterised by a loose social organisation, and a dominance-driven polygynous mating system. This project sought to explain biogeographic and inter-sexual variation in pelage colouration in the context of natural and sexual selection. I also sought to test the hypothesis that in a semi-arid environment, limited resources (food and water) would predictably concentrate females, increasing the potential for dominant males to monopolise matings.

I analysed photos from across Africa, and reveal that where yearly bright sunshine is greater, female giraffe in particular tend to be lighter, resulting in sexual dichromatism in high insolarity locations. I hypothesised that dark pelage colour is maintained in males through sexual selection for a costly status signal.

Field work was carried out in Etosha NP, Namibia. Using photographic records, I identified 431 individual giraffe. I surveyed the study area regularly and collected data on group composition and behaviour upon locating giraffe. I carried out focal watches, and recorded all observations of agonistic and mating behaviour.

Darker males tended to be older and more dominant than lighter males, associated less with females, but had greater success in courting females. Food and water affected female movements on both a spatial and temporal scale. At waterholes, encounter rates were increased and consequently mating and agonistic interactions more frequent. Paler males had a greater chance of interacting with females at waterholes because of higher intruder pressure, but when present, darker males always monopolised courtship opportunities.

Mature males demonstrated a diversity of ranging strategies that affected association with females. These individual differences are assumed to relate to status and probably affect individual reproductive success. Evidence suggests male reproductive success is skewed towards mature dark males, but may also vary among dark males, with some potentially being excluded from mating.

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1 GENERAL INTRODUCTION

1.1 Introduction

This study aimed to investigate mammalian intra-sexual male competition, specifically the potential role of intra-specific variation in external colouration as a status signal, and the effect of local variation in ecology on male mating strategies. The giraffe (*Giraffa camelopardalis*) was chosen for this study firstly because from a practical point of view, giraffes have a number of characteristics which make a study of them highly feasible, including their large size, conspicuousness, and individually unique coat patterns (Foster 1966; Pratt & Anderson 1985). Their feeding ecology and general biology are quite well known, but important aspects of giraffe evolutionary ecology and sexual selection remain unexplored.

The giraffe constitutes an ideal model system for investigating the role of mammalian coat colouration in a social context. There is a high level of variation in coat colour between the sexes and between males (Lydekker 1904; Dagg 1968). Intra-sexual male competition can be intense, and anecdotal reports suggest that male colouration develops with age (M. A. McDonald, personal communication), and a preliminary study suggested that dark coloured males may be dominant to pale coloured males in competitive interactions (L. M. Gosling, unpublished data). Therefore it is highly plausible that male coat colour may function as a sexually selected status signal. This would provide an explanation for sexual dimorphism in external colouration in giraffes and other ungulates, as has already been suggested for a number of bird and primate species (e.g. Senar & Camerino 1998; McGraw & Hill 2000a; Gerald 2001; Setchell & Dixson 2001b; Mennill *et al.* 2003; Pryke & Andersson 2003).

Furthermore, like many large mammals, giraffe live at low densities, occur in relatively small, mostly isolated populations that are increasingly restricted to protected areas. It would appear that aspects of their ecology and mating system may render this species vulnerable to effects of park management on male mating strategies, and potentially a population's genetic viability. A study of a wild giraffe population therefore also carries the potential of revealing information relevant to wildlife conservation and management.

1.2 Mating strategies and intra-sexual competition

Although males and females are subject to similar pressures to secure resources and survive, the factors that determine their reproductive success differ between the two sexes (Clutton-Brock *et al.* 1982c). In most mammals, the female is the higher investing sex, with males investing almost nothing in offspring. Thus, according to sexual selection theory, male intra-sexual competition should be greater than female intra-sexual competition, as males must compete for access to receptive females (Trivers 1972). This theory can be best explained by Bateman's principal (Bateman 1948), which was restated by Trivers (1972) as follows:

1. "In any closed population, the total number of offspring produced by one sex is equal to the total produced by the other.
2. The sex whose typical parental investment (energetic and otherwise) is greater will become a limiting resource for the other sex.
3. Therefore individuals of the sex investing less will compete among themselves to breed with members of the sex investing more.
4. Individuals of the limited sex can increase reproductive success (RS) by investing successively in offspring of several members of the limiting sex."

1.2.1 Intra-sexual female competition and reproductive success

If a female can only have one offspring per gestation, as in the giraffe, her reproductive success depends on her ability to secure sufficient nutritional resources to successfully produce and rear each offspring with minimum risk to herself or to her offspring (Clutton-Brock *et al.* 1982c; Gosling 1986). Therefore female intra-sexual competition should usually take the form of indirect scramble competition for access to resources such as food supplies and habitats where predation risk is minimised (Mysterud *et al.* 1999). As a result, the spatial distribution of females is usually determined primarily by the distribution of these resources (Clutton-Brock *et al.* 1982c).

1.2.2 Intra-sexual male competition and reproductive success

Male reproductive success, on the other hand, depends primarily on their ability to maximise the number of matings they achieve (Clutton-Brock *et al.* 1982c). In order to maximise their reproductive success, males must respond to female movements, and out-compete other males in securing access to females (Trivers 1972; Emlen & Oring 1977). They can achieve this by investing relatively more in growth, defence of territory or of females, searching for females, and fighting (Trivers 1972; Gosling 1986). Furthermore, because they do not bear the costs of gestation and lactation, males are not as constrained by the distribution of high quality habitat and food (Clutton-Brock *et al.* 1982b). The potential for individual males to secure multiple matings depends largely on the environmental and social factors that drive the distribution of breeding females (environmental potential for polygyny, Emlen & Oring 1977). This distribution can be described in terms of three parameters (Trivers 1972):

1. The extent to which females are clumped or dispersed in space;
2. The extent to which they are clumped or dispersed in time;
3. The extent to which their exact position in space and time is predictable.

1.2.3 Temporal distribution of females and the operational sex ratio

The lower the female-bias in operational sex ratio (OSR; the average ratio of available oestrous females to sexually active males at any given time (Emlen & Oring 1977)), the greater the potential for monopolisation of females, the greater the intensity of competition and sexual selection, and the greater the resulting variance in male reproductive success (Emlen & Oring 1977). For example, continuous long periods of sexual activity in males, combined with brief, asynchronous receptivity in females leads to a strong skew in OSR, and a strong potential for multiple matings by some males (e.g. Ims 1988a). Conversely, highly synchronous breeding (lasting only a matter of days) prohibits sequential polygyny (e.g. Coltman *et al.* 1999) as individual males may not be able to defend and mate with more than a small number of females before the breeding period is over (Emlen & Oring 1977; Ims 1988a; Isaac & Johnson 2003).

1.2.4 Spatial distribution of resources and females, and resulting mating systems

As well as being defined by the reproductive interactions between males and females (e.g. monogamy, polygyny, polyandry), mating systems can also be differentiated in terms of the competitive strategies employed by males that result from female (and resource) distribution and predictability (Owen-Smith 1977). Within a species, the mating system may differ between populations because of differences in the distribution of resources and thus females (e.g. topi, Gosling 1991; red deer, Carranza *et al.* 1996; roe deer, Thirgood *et al.* 1999; blackbuck, Isvaran 2005).

1.2.4.1 Resource defence polygyny

If there is a high degree of spatial clumping of high quality food or another essential resource (e.g. nesting or birthing sites), then females are likely to aggregate into groups and remain in the same area for extended periods of time, resulting in predictable female movements and concentration areas (Gosling 1986; Ims 1987). Such high predictability in female spatial distribution often leads to males competing to establish exclusive territories, where they defend the resources essential to females (Emlen & Oring 1977; Carranza *et al.* 1996). Females may choose territory holders as mates directly, based on the quality of the male, or indirectly, based on the quality of the resource he is defending (Emlen & Oring 1977; Andersson & Iwasa 1996). Encounter rates with females, and the potential for increasing reproductive success (RS) by obtaining more mates, should be highest for males that control the areas that attract most females (Trivers 1972; Emlen & Oring 1977; Owen-Smith 1977; Gosling 1986; Ims 1990). Thus, the greater the degree of resource clumping, the greater the potential for a small proportion of males to monopolise a large proportion of resources, and thus females (Emlen & Oring 1977).

Territoriality will be favoured only when the benefits of increased numbers of matings achieved outweigh the costs of territory defence (Owen-Smith 1977; Gosling 1986; Thirgood *et al.* 1999). Costs of defence may be minimised by the existence of a spatial reference for dominance, whereby the territory holder has an 'owner's advantage' over any intruders, resulting in intruders generally behaving submissively, and agonistic interactions being consistently won by the territory holder (Parker 1974; Owen-Smith 1977; Gosling 1986).

Resource defence may involve a sit-and-wait strategy, whereby males wait in a part of the female range where there is a high chance of females being intercepted, even though females may be absent at the time the male establishes the territory (Gosling 1986). The effectiveness of this strategy will depend on the predictability of female ranging behaviour, as males must select a location that has a high probability of being visited by receptive females (Gosling 1986). At one extreme of this strategy, males aggregate and defend leks: high concentrations of very small territories or display areas containing insignificant resources (e.g. Gosling 1991; Isvaran 2005). Leks may be placed at 'hotspots' so as to intercept females as they move to and from a valued resource, or may attract females simply by offering an opportunity to choose a mate from among a large number of males (Gosling 1986; Clutton-Brock 1989; Krebs & Davies 1993; Bro-Jorgensen 2002; Hayes *et al.* 2006)

1.2.4.2 Following of females

If food resources are distributed more evenly, then female spatial distribution is likely to be more unpredictable, and female home ranges larger (Forchhammer & Boomsma 1998). Under such conditions, it can become uneconomical to control access to females through resource defence. Instead, male competition may take the form of direct intra-sexual competition, resulting in differential dominance relationships between males, which in turn determine differential access to females (Altmann 1962; Emlen & Oring 1977). Dominance-based polygyny may also arise if intruder (competitor) pressure is too high for males to be able to successfully defend a territory (Gosling 1986; Ims 1988a; Gosling 1991).

Dominance relationships generally rely on individuals remembering past encounters with particular individuals, resulting in what has been termed an 'individual reference for dominance' (Gosling 1986). This is typically coupled with following and defence of one or a group of females over part or all of their foraging movements, for variable periods of time (Gosling 1986; Forchhammer & Boomsma 1998). If they employ such a strategy, males are faced with decisions about when to join and leave a group of females (Gosling 1986).

- At one extreme, males will adopt a roving strategy, spending the majority of time moving between groups, searching for receptive females, only defending a female when one in oestrus is located, and then forming only a brief 'tending bond' for as long as it takes to court and mate with the female (Clutton-Brock *et al.* 1982b; Forchhammer & Boomsma 1998). This is most likely where females are relatively evenly and unpredictably dispersed in space and time, as male mobility will be crucial to encountering a large number of females (Trivers 1972). This strategy will likely result in an increase in male home range size relative to female home range size (Trivers 1972). This could be a more optimal strategy for males of high competitive ability. They would acquire control of female groups more easily and would be less likely to face rejection by oestrous females, so they would be able to move between groups more frequently (Forchhammer & Boomsma 1998).
- At the other extreme, the most time will be spent in direct defence of one or more females (i.e. harem-defence). This can involve a single male defending one or more females, or a stable dominance ranking within a set of males associated with a group of females, where the dominant male has priority of access to females (Altmann 1962; Owen-Smith 1977; Clutton-Brock 1989; Cowlishaw & Dunbar 1991; Thirgood *et al.* 1999). The time spent with each group of females is likely to increase as female group density decreases (i.e. distance between groups increases), as female group size increases, as the OSR decreases, and as the time spent on environmentally or socially enforced non-mating activities (e.g. foraging, migrating) increases (Krebs & Davies 1993; Forchhammer & Boomsma 1998).

1.2.5 Water as a limited resource that concentrates females and affects sexual selection

Wildlife distribution and movements within parks are often determined by the location of water, particularly in the dry season in arid and semi-arid environments (Western 1975; Auer 1997). This often results in a seasonal concentration of many species near water-sources in the dry season and dispersion away from them (to preferred food sources and habitats) during the wet season (Ayeni 1975; Western 1975; Knight 1995). This movement pattern tends to be clearer for water-dependent species (mostly grazers) than for water-independent species (mostly browsers (Western 1975)).

Artificial provisioning of water is now widespread in national parks and game reserves across Africa (Ayeni 1977; Ritter & Bednekoff 1995). In most cases, provisioning of water became necessary as a result of the erection of fences around the reserves, which prevented migratory species from leaving the reserves in times of drought (Cloudsley-Thompson 1990; Knight 1995; Gaylard *et al.* 2003). Artificial water provision can also be used to open up areas to animals that were previously unavailable during the dry season, and to disperse wildlife (Ritter 1993). Waterholes serve the additional purpose of providing tourists with improved wildlife viewing opportunities (Ayeni 1975; Cloudsley-Thompson 1990; Ritter 1993).

Water provision can result in larger populations of common water-dependent species, high densities of large mammals in the vicinity of waterholes, and smaller dry-season ranges restricted to areas near permanent water (Ayeni 1975; Western 1975; Knight 1995; Ritter & Bednekoff 1995; Auer 1997; Gaylard *et al.* 2003). This usually results in increased grazing and browsing pressure on vegetation in the area surrounding waterholes, often resulting in long-term habitat degradation (Ayeni 1975; Cloudsley-Thompson 1990; Gaylard *et al.* 2003).

The number, distribution and density of water-sources are all important considerations for sustainable wildlife and park management (Ayeni 1975; Auer 1997). The issue of the ideal density of water sources has long been one of contention, with policies on water provision changing quite significantly over the years (Ayeni 1975; Ayeni 1977; Auer 1997; Gaylard *et al.* 2003). In both Etosha NP, Namibia and Kruger NP, South Africa, many waterholes have been closed within the last few decades (Gaylard *et al.* 2003, Shayne Kotting, personal communication). This was carried out primarily with the intention of locally relieving grazing and browsing pressure, especially in ecologically sensitive areas, and to reduce the effect of high waterhole density on the homogenisation of habitats (Gaylard *et al.* 2003, Shayne Kotting, personal communication). As a result, in Etosha and the Kruger, water tends to be a greater limiting factor on animal movements currently than in the past.

It has been suggested that artificial waterholes may have subtle effects on wildlife social behaviour as a result of influences on dispersion (Ritter 1993). Conflicts between members of the same species are common at waterholes when water is a limited resource (du Toit 1996). Furthermore, as described above (section 1.2.4), the effect of the distribution of resources on both male and female distribution can influence male mating strategies, with clumped, patchy resources resulting in locally high concentrations of females. Where water is a scarce resource, isolated waterholes will likely play an important role in predictably clumping females, thus increasing the efficiency with which males can locate females, and consequently increasing the potential for mate monopolisation (Emlen & Oring 1977; Ims 1987; Ims 1990).

Accordingly, Ritter and Bednekoff (1995) observed that in the Nxai Pan National Park in Botswana, artificial dry-season water provision appeared to influence sexual selection in springbok. Specifically, they noted that female springbok (*Antidorcas marsupialis*) were concentrated in a limited area around the single waterhole in the Park, enabling a few dominant males to gain a monopoly on territories around the waterhole and thus on females. This could potentially increase the skew in male mating success and reduce the number of males contributing to the next generation, which can be detrimental to population viability through its effect on the effective population size. The authors concluded that several, smaller waterholes would be preferable to a single large waterhole, as it would allow females to be distributed more evenly throughout the park (Ritter & Bednekoff 1995).

1.3 Roles of surface colouration

The surface colouration of an animal can affect its fitness by both determining its conspicuousness and modifying the thermal effects of solar radiation (Louw & Seely 1982; Walsberg & Wolf 1995b). Therefore the actual colour of an animal's coat will be the result of a balance of a number of sexual and natural selection pressures, including camouflage (reduced conspicuousness), aposematism and social communication (enhanced conspicuousness), and optimisation of radiative heat gain. Coat colour will thus be dependent on the environment and the relative importance to survival and reproduction of different selection pressures (Walsberg *et al.* 1978; Louw 1993; Cloudsley-Thompson 1999; Ortolani 1999).

1.3.1 Signals of status and sexual dichromatism

Sexual selection theory has traditionally been used to explain the evolution of exaggerated traits, ornaments or other secondary sexual characters that are used in competition for mates and which are possessed only by mature males (e.g. Darwin 1871; Zahavi 1975; Andersson 1982; Petrie *et al.* 1991; Andersson 1992; Andersson & Iwasa 1996). Sexual selection of traits not directly involved in combat (e.g. purely visual ornaments) can operate through female mate choice or male-male competition (Andersson 1982). For example, females may choose mates based on male phenotypic traits that honestly indicate genetic viability, qualities that are likely to confer fitness benefits to their offspring (Zahavi 1975; Emlen & Oring 1977; Kirkpatrick & Ryan 1991). Numerous studies of secondary sexual traits have produced evidence for trait variation relating reliably to age, status or genetic quality, and as such predicting male interaction outcomes or individual reproductive fitness (e.g. Folstad *et al.* 1994; Petrie 1994; Senar & Camerino 1998; McGraw & Hill 2000b; Siitari & Huhta 2002; Mennill *et al.* 2003; Pryke & Andersson 2003; Siefferman & Hill 2003).

In male intra-sexual competition, signals of status enable males to reliably assess the competitive ability of adversaries (including unfamiliar opponents), and potentially avoid escalated agonistic interactions (e.g. Rohwer & Rohwer 1978; Parker & Ligon

2002). It has been proposed that status signals should evolve where there is aggressive competition for resources, variability in individual male competitive ability (or Resource Holding Power, RHP (Parker 1974)), and repeated agonistic interactions between individuals as well as large or unstable group composition (which precludes efficient recognition of adversaries (Rohwer 1982)).

Furthermore, if signals of status are to function as evolutionarily stable honest signals of quality, then, it is argued, their development and maintenance should carry costs, or 'handicaps', or else they would be subject to corruption by 'cheaters' (Zahavi 1975; Andersson 1994). Higher quality individuals should gain greater marginal fitness returns, and should experience a lower marginal increase in cost, from an incremental increase in the signal intensity, than lower quality individuals (Andersson 1982; Smith 1991; Zuk & Johnsen 2000; Getty 2002). For visual signals, potential costs that could prevent cheating include an increased risk of predation-related mortality due to enhanced conspicuousness (e.g. Godin & McDonough 2003), metabolic or immunological costs accrued through developing and maintaining the trait (e.g. Folstad & Karter 1992), or increased physiological stress due to less than optimum absorption of solar radiation (e.g. West & Packer 2002). Alternatively, there may be social mechanisms for maintaining signal honesty, whereby 'cheats' are repeatedly challenged and exposed to high fighting risks (e.g. Gerald 2000; Parker & Ligon 2002)

Among mammals, sexual dichromatism, where dark or bright colouration is unique to or more pronounced in mature males, is most evident in primates, but also common in pinnipeds and artiodactyls (Ortolani & Caro 1996; Ortolani 1999). The males of many artiodactyl species darken progressively, or otherwise develop more striking colouration, with age. Examples include the blackbuck *Antilope cervicapra* (Isvaran 2005), many of the Tragelaphine antelopes (Jarman 1974) and giraffe *Giraffa camelopardalis* (e.g. Dagg 1968). These species also generally exhibit sexual size dimorphism (Jarman 1974; Owen-Smith 1992), and mature males of certain species, such as ibex (*Capra ibex*), darken only during the breeding season (Nowak 1995). This suggests that sexual selection might have played a part in the evolution of this trait. Darker males could be at a selective advantage either through direct choice by females, or with the intermediary of direct male-male competition, whereby coat colouration functions as a status signal indicating male dominance or competitive status (e.g. Senar & Camerino 1998; Parker & Ligon 2002), which in turn determines priority of access to females (Altmann 1962).

Recent studies on primates have found evidence for the development of male colouration being determined by and conveying social status through the intermediary of testosterone. As a result, coat colouration influences the outcome of agonistic interactions and potentially determines reproductive success (Wickings *et al.* 1993; Gerald 2000; Gerald 2001; Setchell & Dixson 2001a; Setchell & Dixson 2001b; Setchell & Dixson 2002). Similarly, lion mane darkness appears to indicate testosterone levels, and influences both female choice and male intra-sexual competition when tested using models (West & Packer 2002). However, in artiodactyls, functional and comparative studies of external features have generally focussed either on body size dimorphism and weaponry (e.g. Roberts 1996), or on surface colouration but not in the context of sexual or status signalling (e.g. Stoner *et al.* 2003).

1.3.2 Coat colour and thermoregulation

Darker coat colouration can result in increased heat gain in large mammals, particularly at low air speeds (Cena 1966; Hutchinson & Brown 1969; Finch 1972; Finch & Western 1977; Finch *et al.* 1980; West & Packer 2002). In hot arid conditions with high insolarity, such gains in heat can be metabolically costly, especially in terms of water turnover, as animals must dissipate not only their own metabolic heat but also heat gained from the environment (Taylor 1970; Finch 1972; Walsberg 2000). Finch and Western found that due to its effect on heat stress, dark coat colouration in cattle increased both water consumption and mortality during droughts (Finch & Western 1977).

If dark colouration functions as an honest signal of status (e.g. Zahavi 1975) in male artiodactyls, the cost that renders it honest could therefore be a thermoregulatory cost. If dark coat colouration is costly, then it should only be exhibited by high quality, sexually mature males. Colouration of females (who must undergo increased metabolic stress during gestation and lactation (Pellew 1984b)) should be selected to provide optimal absorption or reflection of solar radiation.

1.4 The ecology and mating system of the giraffe

1.4.1 Temporal distribution of receptive females

Giraffes breed throughout the year, with slight calving peaks in the more seasonal southern latitudes (Hall-Martin *et al.* 1975; Dagg & Foster 1982; Pratt & Anderson 1982). On average, adult female giraffe reproduce every 19-24 months (Foster & Dagg 1972; Leuthold 1979; Dagg & Foster 1982; Pellew 1983b), and are pregnant for 15 of these (Innis 1958; Dagg & Foster 1982). During the remaining months, from as early as the second month post-partum, females are fertile for approximately four days every two weeks (Bercovitch *et al.* 2006). Therefore, it can be estimated that at any one time, only about 6-11% of adult females are potentially receptive, producing a highly skewed OSR. The chance of males encountering receptive females by chance will be low (Bercovitch *et al.* 2006), but due to the high level of reproductive asynchrony, when they do locate females, the potential for monopolisation of mating opportunities by dominant males should be high (Trivers 1972; Emlen & Oring 1977; Ims 1988a).

1.4.2 Spatial distribution of females

Because of the giraffe's large body size, and the sparse and seasonally variable availability of their food, both sexes must cover large distances in search of food (Sinclair 1983). Giraffe generally respond to seasonal changes in the distribution of food sources by local small-scale movements within their home range, rather than large-scale migrations (Pellew 1983b; Fennessy 2004). Giraffe group composition is fluid, changing from one day to the next, but at any one time, herd size is usually small, averaging approximately 4-6 individuals (Innis 1958; Foster 1966; Leuthold 1979; Pratt & Anderson 1985; Le Pendu *et al.* 2000). However, herd size and composition, population density, home range size and mobility all tend to vary in relation to the range of habitats in which giraffes are found (van der Jeugd & Prins 2000).

1.4.3 Male mating strategies and intra-sexual competition

Since giraffe herd composition changes so frequently, and females in oestrus are so few and far between, it would be uneconomic for males to attempt to defend a herd or harem. Instead, the predominant male mating strategy is to rove between groups and identify oestrus females by testing their urine (Leuthold 1979; Dagg & Foster 1982; Pratt & Anderson 1985). Upon locating a receptive female, the male follows her, and over a period of many hours, or even days, he attempts to defend her and eventually mate with her (Dagg & Foster 1982). However, with a large variation in ecological conditions across their range, male giraffe may adopt different mating strategies in different areas, possibly even demonstrating resource defence polygyny where resources and females are most clumped and predictable (van der Jeugd & Prins 2000).

There is a high potential for mate monopolisation in giraffe because of the year-round breeding, the high OSR, an ability in males to discern when females are receptive, and male dominance relationships that probably determine priority of access to mates (Altmann 1962; Pratt & Anderson 1985; Bercovitch *et al.* 2006). This potential for monopolisation by a few dominant males, to the exclusion of all others, will be greatest where female concentrations are most predictable (Emlen & Oring 1977).

This raises a potential conservation issue, in that management of protected areas, and particularly of limited resources, may restrict the distribution and movements of giraffe. Consequently, the preferred mating strategies of males could be artificially altered, such that reproductive skew and effective male population size may be adversely affected in the context of long-term genetic viability (e.g. Ritter & Bednekoff 1995).

1.4.3.1 Intercepting of females by males at waterholes

Giraffes make frequent use of water in Etosha NP and pilot observations (LM Gosling, personal communictaion) show that males often intercept and attempt to mate with females at waterholes when they come to drink. Large, dark-coloured males appear to dominate and exclude lighter coloured males from these mating interactions. If relatively few dominant male giraffe succeed in monopolising matings at waterholes, then this creates the potential for the effective male population size to be driven down by a limited availability of waterholes (e.g. Ritter & Bednekoff 1995). This effect may be absent or reduced if females are not spatially limited by water.

If waterholes do enhance the potential for mate monopolisation, then levels of male intra-sexual competition are likely to differ between the wet season and the dry season. Giraffe tend to frequent waterholes most often in the dry season, when the water content of vegetation is at its lowest and sources of free water are most scarce (Ritter 1993). As a result, during the dry season, females should concentrate more predictably around waterholes, increasing the chances of males encountering receptive females. This may result in more frequent and potentially more intense competition between males for dominance, in order to monopolise access to females. Conversely, in the wet season, females should be more widely dispersed because of a widespread availability of food and water.

Alternatively, localised and ephemeral preferred food patches may have a stronger effect on predictably concentrating females than waterholes. In this case, the seasonal variation in male competition and potential for monopolisation will depend on which foods have the greatest potential to cause females to aggregate.

1.4.4 The evolution of giraffe coat colouration

The coat markings of the giraffe are broadly heritable (Dagg 1968) and camouflage the animal effectively among tall trees, blending with the dappled effect of light and shade (Dagg & Foster 1982). Camouflage is likely to be of particular importance for young giraffes, which face high mortality rates due to predation in their first year

(Foster & Dagg 1972; Mitchell & Skinner 2003). However, although this may explain the origin of the giraffe's unique spotted pattern, it does not provide an adequate explanation for the observed biogeographic variation in patch form, relative size and colouration. Examples of this variation are the Masai giraffe *Giraffa camelopardalis tippelskirchi*, which have small, dark brown, stellate patches of colour on a pale background, with a total area of patches approximating 60%, whereas Reticulated giraffe *G. c. reticulata*, have comparatively large, tightly-packed russet-coloured patches covering approximately 80% of the surface area (Dagg 1968; Dagg & Foster 1982).

However, the different subspecies cannot be distinguished solely on the basis of coat patterns as there is marked variation between populations of the same subspecies and also between individuals within populations (Dagg 1962b; Seymour 2001). Abundant anecdotal evidence would suggest that colouration varies with sex, and, in the case of males, also with age (Mary Ann McDonald, pers. comm., Dagg 1968).

Male giraffe can fight intensely for dominance (Dagg & Foster 1982; Pratt & Anderson 1985) and sexual selection has already been proposed as an explanation for the evolution of the giraffe's long neck (Simmons & Scheepers 1996). It is therefore surprising that this selective force has not yet been evoked as an explanation for sexual dichromatism in the giraffe. Giraffe are believed to rely heavily on visual signals, as they appear to have excellent distance vision (Innis 1958), their colour vision is probably dichromatic, as in other artiodactyl species (Jacobs *et al.* 1998), and their extreme height gives them a very good vantage point (Foster & Dagg 1972). It has been observed that bulls in particular react to one another at a considerable distance (Estes 1991). In contests, dark males appear to be dominant to paler males (Innis 1958, LM Gosling personal communication), and although such colour-related dominance may be partly age-related, it appears possible there may be variation in colour within age classes.

In light of the fact that dark colouration should be costly in terms of thermoregulation in hot environments (section 1.3.2), it is also surprising that so few proposed explanations for the evolution of giraffe coat colouration have yet referred to a potential thermoregulatory function or cost (although a link has been proposed between patch shape and a thermoregulatory function, Mitchell & Skinner 2005). It is hypothesised here that 1) biogeographical variation in patch colouration and density results from an adaptation to minimise heat stress; and 2) dark colouration in males functions as a sexually selected signal of status.

1.5 Aims of study and thesis structure

This thesis aims to provide further detailed description of giraffe behaviour and ecology, and also to test a number of hypotheses relating to the evolution of sexually selected traits and giraffe mating systems. Specifically, the initial aims of this study were:

1. To examine how the spatial and temporal distribution of resources drive the mating system of a wild population of giraffe. Specifically, to test the hypothesis that resources, including spatially restricted foods and artificially provisioned water, may predictably concentrate females (spatially and temporally) and thus increase the potential for dominant males to monopolise females for mating.
2. To examine whether actual biogeographical and local variation in giraffe pelage colouration can be explained by natural and sexual selection pressures, with particular reference to factors relating to potential environmental costs of dark coat colouration.
3. To test the hypothesis that dark colouration is maintained in males through selection for a reliable signal of status, by examining male behaviour, intra-sexual competition, and female mate choice in relation to colouration.

The thesis begins with an overview of the methodology used, the study species and the study site (Chapter 2). I then establish how giraffe respond to variation in food and water availability in the study area, and examine how the sexes differ in their selection of foods and habitats (Chapter 3). Next, I address the issue of reproductive seasonality, with the aim of identifying the seasonal peak in breeding (if one exists) in Etosha NP, and comparing the timing of any such peak with environmental factors such as food availability (Chapter 4).

In Chapter 5, I explore giraffe movements and home ranges within the study area. I focus on male movements in relation to areas of greatest female use, and relate these movements to how often males associate with females. I also highlight seasonal effects, and explore differences in movements and association with females between males of different age classes.

In Chapter 6, I consider the subject of male competition for mates. I first compare male pelage colouration with male age class, behaviour, dominance, success in competition and success in courtship of females, to assess the hypothesised relationship between coat colouration and male status. I then examine the effect of waterholes on encounter and interaction rates, and the potential for males to monopolise mates. I also examine evidence for seasonal variation in the intensity of intra-sexual competition. Finally, I explore reproductive skew in males, and propose a surrogate measure of potential male mating success for the giraffe.

In Chapter 7, I seek an evolutionary explanation for some of the observed biogeographic variation in coat colouration and sexual dichromatism, with a focus on a possible thermoregulatory cost of dark coat colouration. I also test the hypothesised relationship between coat colour and solar heat gain by investigating giraffe thermoregulatory behaviour, comparing the behaviour of adults of different coat colours. Lastly, I highlight a possible nutrition-related cost of dark pigmentation.

I end, in Chapter 8, by reviewing the results and conclusions detailed in the previous chapters and discussing their implications, addressing the limitations of this research project, and highlighting possible areas for further investigation.

2 FIELD METHODOLOGY AND STUDY SPECIES

2.1 Field study area, study species and study population

2.1.1 Etosha National Park

2.1.1.1 History, location and dimensions

Etosha National Park (hereafter also referred to as Etosha) is situated in north-central Namibia (18°30’-19°28’S, 14°20’-17°10’E), about 120 km south of the Angolan border. It was originally established as a game reserve in 1907, and was officially designated as a National Park in 1958, by which time it encompassed 99,530 km^2, including a section of the Skeleton Coast (Cloudsley-Thompson 1990). However, by 1970 the park was again reduced in area, this time to its present size of 22,270 km^2. The park is currently under the jurisdiction of the government’s Ministry of Environment and Tourism (M. E. T.), Directorate of Environmental Affairs. Etosha National Park is elongate in shape (290 km by 108 km at the widest points), with about one quarter of the park (about 5,500 km^2) occupied by one large and several small pans (Figure 2.1). For most of the year, the pans are dry and barren, but following good wet-season rains, water drains from the north to cover the pans with a very shallow layer of water. The eastern, southern and western boundaries of the park are delimited by game fences (220 cm), although these are occasionally breached by elephants; the northern boundary game fence is incomplete.

2.1.1.2 Climate

Annual rainfall averages 320 mm to 400 mm in the central part of the park (ranging over 29 years from 173 mm to 685 mm), with a gradient from west to east of increasing rainfall (Auer 1997, Wilferd Versfeld, M. E. T., unpublished data). Three seasons are generally recognised in the year: the cold, dry season from May (or June) to September (or August), the hot, dry season from October (or September) to December with local rains, and the hot, wet season from January to April (or May), during which time most of the rain falls (Scheepers 1991; Fennessy *et al.* 2003; Fennessy 2004; Leggett 2006). Maximum daytime temperatures average 34°C in the peak summer months (October to March) and 27°C in the peak winter months (May to August), whereas minimum temperatures average 18°C in the peak hot season and 9°C in the peak cold season, and only very rarely descend to freezing in the winter (Birgit Kötting, M. E. T., unpublished data).

2.1.1.3 Flora and fauna

The dominant vegetation type in the park is savannah plains, particularly in proximity to the pans, tending towards broad-leaved mopane, acacia or mixed savannah (short bushveld and more open tree savannah) away from the pans (Cowling *et al.* 1997; Burke *et al.* 2002). In contrast to the majority of other areas inhabited by giraffe (e.g. Berry 1978; Leuthold & Leuthold 1978b; Ginnett & Demment 1999), there is no riverine woodland habitat within Etosha. Woody vegetation in the park is predominantly made up of *Acacia nebrownii* thickets on the plains near the pans, acacia veld and rattle bush (*Catophractes alexandrii*) thickets further from the pans, and mopane shrub and woodland consisting predominantly of mopane *Colophospermum mopane*, but also including in some areas *Terminalia prunoides* and various *Combretum* species. As well as the giraffe *Giraffa camelopardalis angolensis*, the park supports many other medium-sized and large herbivore species including a large population of elephants *Loxodonta africana*. Many of the common African carnivores are also present, including leopard *Panthera pardus*, lion *Panthera leo*, cheetah *Acinonyx jubatus*, and spotted hyena *Crocuta crocuta* (Cloudsley-Thompson 1990).

2.1.1.4 Water availability

Since much of Etosha National Park is surrounded by boundary fences, animals are largely confined to the park and natural migration patterns are disrupted. Nonetheless, the distribution and movements of animals within the Park are still largely driven by the seasonal variation in availability of water and browse. There are no permanent rivers or water-courses in the park (du Preez & Grobler 1977), but there are over 100 perennial and near-perennial waterholes, of which about 35 can be accessed by tourists (about 80% of the park is closed to tourists). These consist of natural springs, fountains and artificial boreholes, many of which are assisted by solar- or wind-powered pumps. There are also numerous rain-provisioned seasonal waterholes, artificial gravel pits, and natural depressions and pans. These hold water during the peak rainy season (January to April) and for many weeks after the last rains, as well as occasionally between October and December (Auer 1997).

In the dry season, water sources are limited, and as a result most animals concentrate in large numbers in proximity of perennial waterholes (du Preez & Grobler 1977). During the wet season, there is a widespread availability of water and accordingly animals can disperse away from perennial waterholes and move to areas where their preferred foods are in abundance (vegetation surrounding perennial waterholes is often degraded).

2.1.2 Study area

The selected study area was situated in the east-central part of Etosha, centred on Okaukuejo, and extending from Ozonjuitji M'Bari in the west to Homob and Charachas in the East; from M'Bari and Okondeka in the North to Ombika in the South (Figure 2.2). This constituted an area of approximately 1900 km^2, spanning 70 km west to east and 35 km north to south. About one tenth of this area was occupied by the salt pan, and the area included over 500 km of roads.

The selected area was open to tourists, so there was a well-maintained network of roads, and the animals were habituated to vehicles. The study area incorporated 10 perennial waterholes, over 50 artificial gravel pits close to the roads, as well as numerous, scattered natural depressions. The average distance from each of the perennial waterholes to the next nearest waterhole was 10.4 km (range: 6.3 to 21.0 km). The selected area included examples of all of the most significant habitats in Etosha: pans, grassland, mixed low trees and tall mopane savannah.

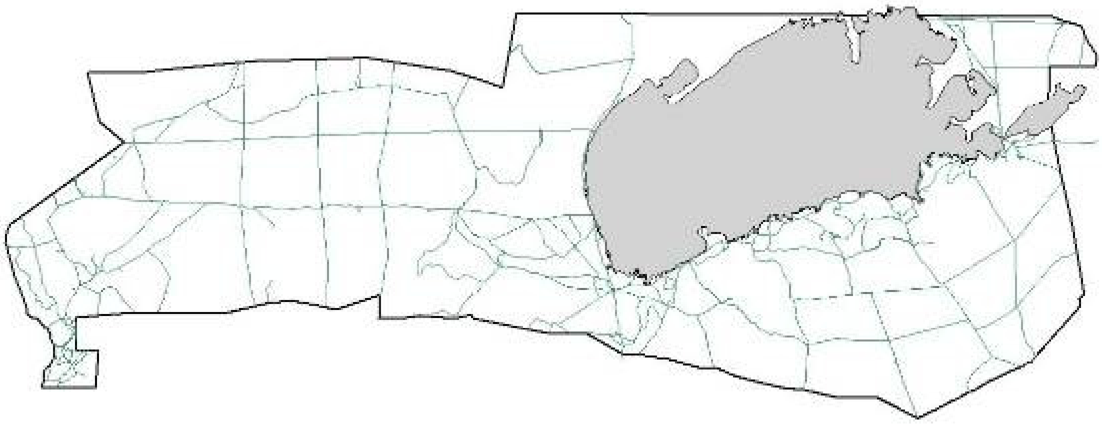

Figure 2.1. The entire Etosha National Park, with the boundary, roads and main salt pan (grey area) indicated.

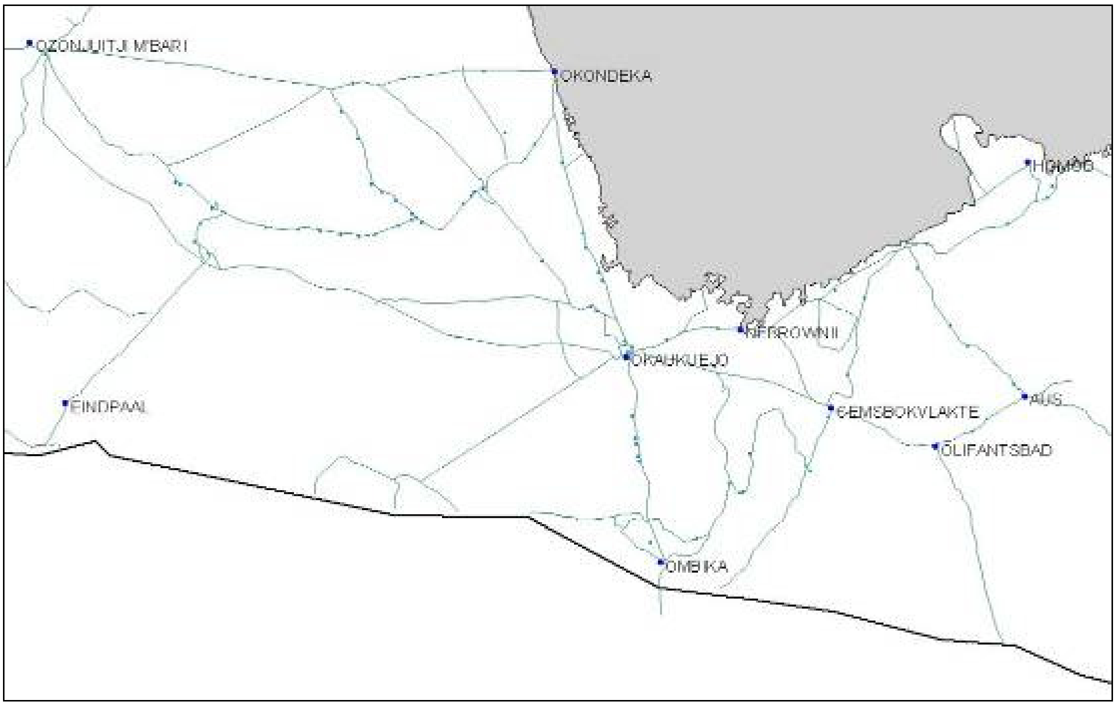

Figure 2.2. The study area in the south-central part of Etosha NP. The southern boundary is indicated (heavy black line), as is the pan (grey area). All other lines indicate roads. Waterholes are marked with their name. Seasonal waterholes in regularly-driven areas are also indicated by small markers. The waterhole to the south-west, Eindpaal, and surrounding area was not visited due to poor quality of roads. The greater density of perennial waterholes to the south of the pan than to the south-west is evident.

2.1.3 Study species

Giraffe (*Giraffa camelopardalis)* are found throughout Africa, in sub-Saharan countries such as Niger in western Africa, through Chad and Sudan to Uganda, Kenya, and Tanzania in eastern Africa, and also in Zambia, Zimbabwe, Botswana, Namibia, Angola and South Africa in southern Africa (Figure 2.3). A total or nine extant subspecies are currently recognised, all of which appear to be able to interbreed (Dagg & Foster 1982). Subspecies classifications have until recently been based on geographical range and morphological features (Dagg 1971; Dagg & Foster 1982; Skinner & Smithers 1990; East 1998; Seymour 2001; Mitchell & Skinner 2003). More recently, genetic information has shed new light on the phylogeny of the southern African subspecies (Seymour 2001, Brenneman *et al.* unpublished data; Fennessy 2004). Although there is still no complete consensus on giraffe subspecies phylogeny, certain inter-subspecies differences or relationships have now been elucidated. For example, morphologically (as well as geographically), there is a clear divide between the northern and the southern subspecies, with the southern Zambian population the most northerly of the southern clade (Seymour 2001).

Previously, the giraffe in northern Namibia had been assigned both to the Southern subspecies of South Africa, Zimbabwe and Botswana, *G. c. giraffa* (formerly *G. c. capensis*, Dagg 1962a; Dagg 1971), and to the Angolan subspecies *G. c. angolensis* (Skinner & Smithers 1990; Scheepers 1991). A recent taxonomical analysis of skull morphology, pelage pattern variation and mitochondrial DNA added weight to the former designation (Seymour 2001). However, giraffe from Angola were only represented by one sample in this study, so the relationship between Namibian and Angolan giraffe could not be properly born out. A more recent study of microsatellite genotypes (Fennessy 2004, Brenneman *et al.* unpublished data) revealed that the genetic distance between sampled Namibian giraffe and giraffe from Kruger NP, South Africa was sufficient to distinguish them at the subspecies level, thus placing the giraffe in Namibia, *G. c. angolensis,* apart from *G. c. giraffa*.

The range of *G. c. angolensis* would thus extend from northern Namibia to southern Angola, southern Zambia, north-western Botswana and probably north-western

Zimbabwe, and that of *G. c. giraffa* from eastern South Africa and south-western Mozambique up to southern Zimbabwe. The current natural occurrence of giraffe within Namibia is only a fraction of the historical range, and is now limited to the north and north-west of the country (including Etosha NP), and part of the Kavango region in the north-east (Fennessy *et al.* 2003; Fennessy 2004). The largest giraffe population in Namibia, approximating 3500 individuals, is found in Etosha National Park (Werner Kilian, pers. comm.). Unknown numbers of giraffe also occur in smaller private parks and farms, and communal farmlands, including many in the desert region of the Kunene in the north-west of Namibia (Dagg & Foster 1982; Fennessy 2004, Figure 2.3).

Although their numbers are relatively stable as a whole, approximately half of the nine subspecies and many isolated populations, particularly in the northern and north-western parts of the giraffe's geographical range (e.g. Niger), are very restricted in size and range, or declining in numbers (Table 2.1). The species' status in the IUCN Species Survival Commission Red List is listed as Lower Risk / Conservation Dependent (criteria version 2.3, IUCN 2006). The greatest threat to the persistence of these populations is loss or degradation of habitat, mostly as a direct result of human population encroachment, and particularly in areas of political unrest, where illegal hunting of animals adds to the problem (Dagg & Foster 1982; East 1998).

Table 2.1. Giraffe subspecies names, current ranges and status. Adapted from East (1998) and Fennessy (2004).

Subspecies	Common name	Range	Status
G. c. angolensis	Angolan giraffe	Southern Angola, Northern Namibia, North-western Botswana, Southern Zambia	Increasing overall, especially in Namibia, but virtually extinct in Angola.
G. c. antiquorum	Kordofan giraffe	Sudan	Possibly extinct
G. c. camelopardalis	Nubian giraffe	Western Ethiopia	Decreasing; very small population.
G. c. giraffa	Cape or Southern giraffe	Southern Zimbabwe, Northern and eastern South Africa, South-western Mozambique, Swaziland	Stable / Increasing. Extinct in Mozambique but may re-colonise from Kruger NP.
G. c. peralta	West African or Nigerian giraffe	Mali, Niger, Nigeria, Northern Cameroon, Southern Chad, Central African Republic	Decreasing, and limited to small, isolated populations.
G. c. reticulata	Reticulated giraffe	Northern Kenya, Southern Ethiopia	Stable / Decreasing
G. c. rothschildi	Rothschild's or Baringo giraffe	Western Kenya, North-eastern Uganda	Decreasing; very small population.
G. c. thornicrofti	Thornicroft's or Rhodesian giraffe	North-eastern Zambia (Luangwa valley)	Stable
G. c. tippelskirchi	Masai giraffe	Southern Kenya, Tanzania, Rwanda	Decreasing, but the most numerous subspecies.

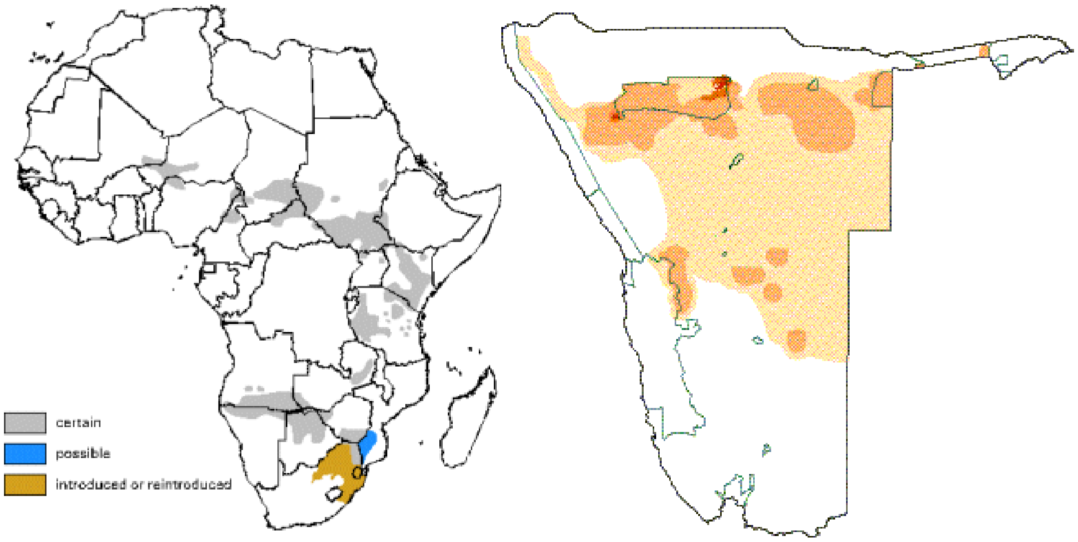

Figure 2.3. Estimated current ranges of giraffe across Africa (left, African Mammals Databank, 1998, Institute of Applied Ecology) and within Namibia (right, courtesy of the Atlas of Namibia Project (Burke *et al.* 2002)).

2.1.4 Study population

The giraffe population in Etosha NP is not completely isolated. In particular, movement is likely between Etosha and the desert to the west of the Park, and the communal farmlands to the north. The most recent aerial surveys of Etosha National Park suggested the following population sizes and densities (calculated excluding the pan from the total area of the park) for giraffe in the Park (Werner Kilian, pers. comm.):

Date	**Estimated population**	**Estimated density (per km^2)**
September 2000	2740	0.15
September 2002	3060	0.17
May/June 2004	3550	0.20

These estimates suggest an increasing, or at least stable population (taking into account possible differences in surveying techniques). The greatest concentration of giraffe in Etosha NP occurs in the eastern extremity of the park, around the Namutoni rest camp. However, it was not practical to attempt an individual-based study on such a large number of giraffe, and for this reason it was decided to base the study area at Okaukuejo, where the population density is lower. Furthermore, the giraffe in the tourist areas of Etosha are habituated to vehicles so are not greatly disturbed by their presence. For this reason, the study was restricted to areas east of the tourist boundary (situated just west of Ozonjuitji M'Bari waterhole).

Distance sampling (e.g. Hounsome *et al.* 2005) was carried out throughout the study area over three days in July 2004, by driving a known distance along each of the main roads in the study area, with two observers, recording all sightings of giraffe whilst noting the distance of the observed animals from the road. These data were entered into the program Distance 3.5 (Research Unit for Wildlife Population Assessment, University of St Andrews, UK), which assumes that all sightings located at zero metres from the road are detected with certainty, and calculates a probability of detection as the distance from the road increases. Thus giraffe density within the study area was estimated as 0.2/km^2 (95% Upper Confidence Limit = 0.38; LCL = 0.11), based on 70 giraffe seen along 430 km of road and an effective detection strip width (calculated by Distance) of 400 m. This corresponds very closely with the overall estimate for the park based on an aerial survey (see above).

2.2 Field methods

2.2.1 Field seasons

Data were collected over two field seasons, the first running from the end of May 2004 until the middle of December 2004, and the second running from the start of March 2005 until the end of December 2005. The first field season focussed on the identification process (below), as well as on collecting data that would permit an understanding of waterhole use and seasonal movements within the study area. The second field season focussed on collecting genetic material (in the form of faecal pellets) and building on the spatial and behavioural data collection.

2.2.2 Definition of the wet and dry seasons

Berry (1980) identified three seasonal periods in Etosha, the hot, wet season from January to April, the cold, dry season from May to August, and the hot, dry season from September to December. However, for the purposes of investigating the effects of perennial waterholes on giraffe movements and aggregation in this study, the seasons needed to be defined not by the same time period each year, but by the actual seasonal availability of water. A delimitation of the wet season based on rainfall was proposed by Hulme and Walsh (1983), for use in the similarly semi-arid habitat of the Sudan. The wet season onset was taken as the first daily rainfall of at least 10 mm that was followed by at least 10 mm more rain in the next ten days. The end of the wet season was defined as the last day on which rain fell.

These definitions produce wet season dates as follows:
23rd October 2003 – 25th April 2004
20th October 2004 – 30th April 2005
10th December 2005 – 1st May 2006
Thus the 2005-2006 rains fell considerably later than in the previous two years.

If water availability in food is also taken into account, then a more appropriate definition would be that of Leuthold and Leuthold (1978b), who defined the ‘green’ season as the period during which deciduous, water-dependent plants bear leaves. This season begins one week after the first substantial rains, when new shoots are first produced, and ends about two months after the last rains, when deciduous plants have lost their leaves and available browse biomass has begun to decline (Leuthold & Leuthold 1978b; Pellew 1983a). Leaf water content tends to decline sharply after June (Sauer 1983), and surface water remains available in some dams and gravel pits in Etosha NP until two months after the end of the rains. For all these reasons, the ‘wet’ season was taken to begin with the first substantial rains, as defined above, and to end two months after the last rains (i.e. the last week of June in both 2004 and 2005).

2.2.3 Identification of individuals

Giraffe pelage patterns are unique to each individual, and aside from colour changes, these patterns do not change with age. Individual giraffe photographed as calves can therefore be identified throughout their life (Innis 1958; Foster 1966). Following the basic methodology used by Foster (1966), photographs were taken of both sides, where possible, of any new giraffe encountered within the study area. Photographs were taken of the whole body, or failing that, at least the whole neck. Photos were taken using a Fuji Finepix S5000 digital camera with a 10x optical zoom, and then uploaded to a laptop computer at the end of each day. At this point, each individual was allocated a unique identification number: M# for males, F# for females, U# for juveniles or sub-adults of unknown sex (young giraffe can be difficult to sex in their first two years as the navel may remain as a visible bump resembling the penis sheath (Foster 1966)). In the case where the two sides of an individual were photographed on different days, and initially given different identification numbers, then once the two sides were matched through observation, the second identification number was discarded (and not re-used), and all data was transferred to the first identification number.

2.2.3.1 Age classes

Ages of giraffe in the study area were not precisely known, so giraffe were attributed to one of three approximate age-classes, in relative keeping with previous studies of giraffe (Le Pendu & Ciofolo 1999; Cameron & du Toit 2005). Immature giraffe were considered juveniles up to the age of about 18 months, by which time they have generally stopped suckling and have left their mother (Leuthold & Leuthold 1978b; Leuthold 1979). Giraffe older than 18 months, and up to about four years were classed as sub-adults (e.g. males that still had a fringe of hair around the horn tips were considered sub-adults (Leuthold & Leuthold 1978b)). All individuals over four years, of approximately adult height, were considered potentially sexually active (Dagg & Foster 1982) and thus classed as adults, although it was noted that females continue to gain height until the age of five years, and males until at least the age of seven years (Foster & Dagg 1972).

The age classification of many giraffe changed between the start and end of the period of data collection. For this reason, more illustrative 'maturity' classes (0-8) were also developed for males that described their maturity, or change in maturity, over the course of the study period (Table 2.2).

Table 2.2. Classification of maturity classes of males using changes in height, coat colouration and horn class.

	Start of study period	End of study period	Colour category	Horn class
0	Juvenile	Juvenile	Any	1
1	Juvenile	Sub-adult	Any	1 to 2
2	Sub-adult	Sub-adult	Any	2
3	Sub-adult	Pale adult	1 or 2	2 to 3
4	Pale adult	Pale adult	1 or 2	2 or 3
5	Pale adult	Dark adult	2 to 3	3
6	Dark adult	Dark adult	3	3
7	Dark adult	Dark adult	3 or 4	4 or 3
8	Very dark adult	Very dark adult	4	4

Horns were classed into four categories representative of age (Figure 2.4), as follows:

1) Horns typical of juveniles: slender from base to tip, with a full tuft of black hair on the tip (these resemble adult female horns; although female horns are typically longer and more slender).

2) Horns typical of sub-adults: thickening from base to tip, but still with a circle of black hair on the tip.

3) Horns typical of young adult males: thick from base to tip, with the black hair worn away from the tip, but skin still covering the entire length of the horns; additional skull ossifications are still few or absent.

4) Horns typical of older adult males: thick from base to tip, with the black hair worn away from the tips. Skin may also be worn away from the periphery of the uppermost few centimetres of the horns. Additional skull ossifications are many, such that the profile of the head is distorted relative to that of a younger male (Pratt & Anderson 1985).

Identification sheets were printed out with black-and-white images of both sides of each individual giraffe, as well as a record of the location and date of the first sighting of the giraffe. These were ordered in a catalogue by area (north, south, east or west), sex, approximate age class, and colour, to facilitate the recognition process. Other notable features that would aid in recognition were noted on the identification sheets, including scars, conspicuous spot shapes, broken or skewed horns, bob-tails and known mother-offspring relationships. These details were also included in a MS Excel database of all the giraffe identified.

Figure 2.4. Examples of the horn classes used to estimate relative male maturity. Top row: category 1; second row from top: category 2; third row from top: category 3; bottom row: category 4.

2.2.3.2 Height measurements

Heights of individual giraffe were measured using a photographic technique. Photos were taken at full zoom (10x) of giraffe in a stationary, upright, relaxed posture, preferably with good visibility at ground level so that the hooves could be seen. At the same time, the distance from observer to animal was measured in metres using a Bushnell Yardage Pro 400 Compact laser rangefinder. Once the photos had been uploaded to a computer, the height of the giraffe, from the base of the hooves to the top of the head (not including the horns) was measured in pixels using a photo editing programme. The digital camera had previously been calibrated using structures of known height and distance to the observer, in order to establish a ratio of photographic pixels to actual metres. The approximate height of the photographed giraffe was calculated using the following formula: height (m) = [distance (m) x pixels] / [pixels per meter]. Since giraffe height is heavily dependent on posture (adult giraffe may carry their neck at anything from a 15° to a 50° angle from the vertical), analyses were restricted to giraffe photographed holding their neck at approximately a 25 - 35° angle from the vertical.

When dead giraffe were encountered, their identity was confirmed (if the skin was still intact), and their age estimated based on dentition and tooth wear (Hall-Martin 1976).

2.2.3.3 Patch darkness categories

Each giraffe was allocated a patch darkness score at each sighting. Four categories were established for patch darkness. Category one included only very pale tan patches, category two darker tan patches, category three chocolate-brown, and category four black patches (Figure 2.5). Category two was considered as the typical colouration of sub-adults and adult females. Males in categories one and two were termed “pale males”, and those in categories three and four were referred to as “dark males”.

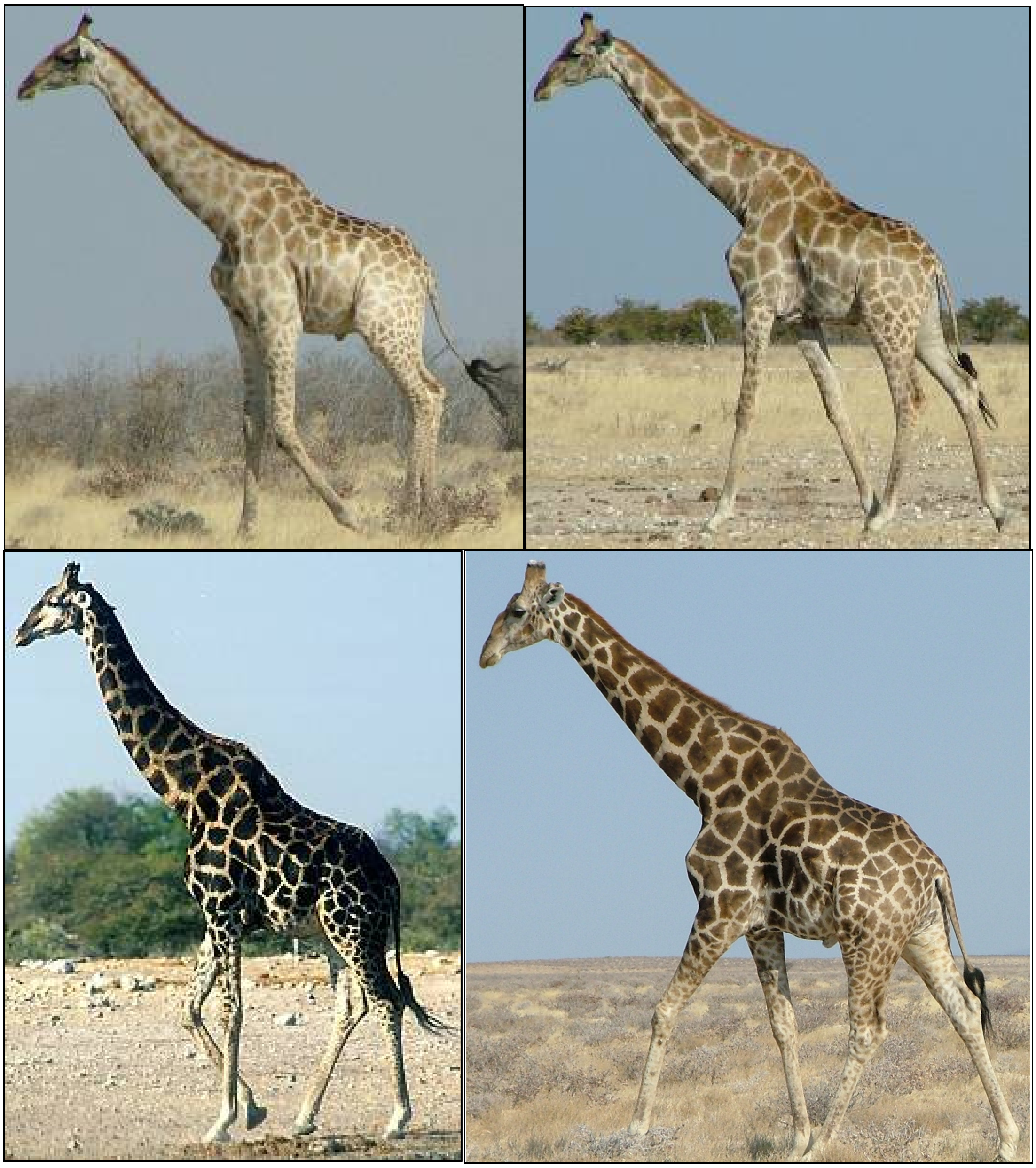

Figure 2.5. Examples of each of the 4 colour categories (1-4 clockwise starting from top-left)

2.2.4 Waterhole visits and driving of roads

The study area was divided into four parts, each of which could be reasonably covered in a day’s driving. These four areas were the North area (up to Okondeka waterhole via the pan-edge road from Okaukuejo, and also the loop including the dry waterholes Leeubron, Natco and Adamax), the South area (Okaukuejo to Ombika, the two detours near Ombika, and ‘W-drive’ – the detour that passes Gaseb), the East area (east to Homob, plus Aus, Olifantsbad, Gemsbokvlakte and Nebrownii, with the two detours from the main pan-edge road down to Gemsbokvlakte), and the West area (west to Ozonjuitji M'Bari via the Leeubron road, and including the road to the dry waterhole at Grunewald).

A systematic rather than a random survey of the waterholes and roads in the study area was chosen, firstly because by surveying the waterholes systematically, using a four-day rotation of the four regions of the study area (N, S, E and W), travel was minimised and the project was thus more cost- and time-efficient. Furthermore, this method ensured a systematic coverage of the roads in the study area, with all roads being driven at least once every cycle. Some staff roads in poor condition were excluded (hence Eindpaal and Gonob waterholes were excluded) as visibility on these was low due to dust during the dry season, and they were often impassable in the wet season. Some of the tourist roads also proved to be impassable during the height of the rainy season, so had to be excluded from March to April 2005.

On arriving at a waterhole, the following data was recorded on a datasheet: time of arrival at the waterhole; whether the waterhole held water; presence/absence of giraffe; if present, how many, individual identities, the dominant activity (scan sample), and whether any were drinking; presence/absence of other game; time of departure from the waterhole.

2.2.5 Giraffe sightings: GPS data collection and behavioural observations

At each giraffe sighting, their Global Positioning System (GPS) location was recorded using a Garmin eTrex Vista, regardless of whether the giraffe were recognised as known individuals or not. If the group was very large, the distance from the road, as well as the bearing in relation to the vehicle, of each individual giraffe was noted in order to improve the individual GPS coordinates when later plotting them on a Geographic Information System (ESRI's ArcView was used for this purpose).

All sighted individuals were identified where possible. Individuals that could not be identified were nonetheless recorded in terms of age/sex/colour category (e.g. male, adult, dark), and photographed if possible. All individuals within 1 km of each other, and not moving in opposing directions, were assumed to belong to the same social group at that instant (Foster 1966; Leuthold 1979; Pratt & Anderson 1985; Le Pendu *et al.* 2000). However, it is important to note that in areas of particularly dense vegetation, the distance at which giraffe were visible to the observer was often reduced to less than 300 m (e.g. Leuthold 1979). An individual giraffe who was not possibly within visible distance of any other giraffe, or who, upon first sighting, was approaching from at least 500 m a group of giraffe that were either stationary or were approaching from the opposite direction, was considered to be alone (solitary) at the instance of first sighting.

By instantaneous scan-sampling on arrival at each group (including groups of one), the behaviour of each giraffe in the group was recorded, as well as the tree species on which they were browsing, if relevant. At each location where giraffe were sighted, the habitat type was noted based on the dominant species of woody vegetation present. If a giraffe was immobile and undisturbed upon sighting, then additional data was recorded regarding thermoregulatory behaviour. If the immobile giraffe was standing in the shade, then this was noted. Otherwise, the orientation of the giraffe's body in relation to the sun was noted, using the most appropriate of the following three categories (after Kuntzsch & Nel 1990): Lateral (long axis of giraffe at right angles to the sun); Anterior (facing towards the sun); Posterior (facing away from the sun).

2.2.5.1 Behaviour class definitions

The behaviour classes used in the instantaneous scan samples were as followed:

Br = Browsing: actively feeding on vegetation (removing parts of trees, shrubs or forbs with the teeth, lips or tongue).

Dr = Drinking: at a water-source and with head lowered to water, drinking.

St = Standing: immobile; not browsing, drinking, grooming or involved in a social interaction; includes standing while ruminating, resting, or vigilant.

Wa = Walking: mobile; does not include moving a single step while browsing if feeding is uninterrupted.

Ly = Lying: body in contact with the ground, legs folded up under or beside the body; neck erect or resting on body.

Gr = Grooming: including scratching body with the hooves, licking with the tongue, scratching with the teeth, or rubbing against a tree or other fixed object.

Ag = Agonistic interaction: social interaction involving two non-juvenile males, with or without body contact; see below for details.

Ma = Mating interaction: social interaction involving a non-juvenile male and a non-juvenile female, with or without body contact; see below for details.

Mo = Mother-offspring interaction: interaction involving an adult female and a juvenile, with body contact; includes allogrooming and suckling.

Un = Not visible: focal animal no longer visible, or unable to determine activity of focal animal. In the case of an animal being 'Un' for 2 subsequent intervals, the focal watch of that animal was abandoned.

Bo = Chewing a bone: giraffe has a bone in its mouth which it is not ingesting but is masticating; includes bending down to pick up a bone.

Ee = Geophagy: includes licking, picking up, and masticating soil or salts from the ground.

Further qualifiers used:

If browsing:

Hi = Browsing with nose above level of base of neck.

Lo = Browsing with nose below level of base of neck.

Gr = Feeding on vegetation at ground-level, such that the front legs must be splayed or the knees bent in order to reach the food-source.

The browse species was also recorded.

Other:

Al = Alert: when standing; not masticating or carrying out any other activity; vigilant, watching or looking fixedly in one direction; not disturbed (see below).

Di = Disturbed: when standing; not masticating or carrying out any other activity; looking towards a specific human disturbance; alert and flighty in response.

Ru = Resting/Ruminating: while standing or lying, not alert or disturbed, may be masticating (ruminating only), but not browsing on vegetation.

2.2.6 Focal watches

Focal watches were carried out both at and away from waterholes wherever giraffe were encountered. A focal watch was classed as being at a waterhole if it took place entirely within 300 m of a waterhole, whereas those that took place entirely beyond 300 m of a waterhole were classed as being away from waterholes (or ‘non-waterhole’ watches). For all the waterholes in the study area, this distance was sufficiently far to encompass the entire bare area around the waterhole as well as the vegetation edge, but beyond this distance individuals were not clearly visible from the waterhole (the exception being Okondeka, at which the nearest giraffe browse was more than 500 m). If a watch began further than 300 m away from a waterhole, but the focal subject then walked to the waterhole, the watch was split in two at the point where the focal subject arrived within 300 m of the waterhole; conversely if a watch began at a waterhole and the focal subject then walked more than 300 m from the waterhole. Insofar as possible, focal watches were distributed evenly across times of day and locations within the study area, but were ultimately influenced by the location of giraffe.

The focal subject type (dark male, pale male, female) was selected according to a pre-determined random-order list, in an attempt to equalize the total number of observations of adult males and females, and of dark and pale adult males. The focal individual was then randomly selected from those giraffe of the selected subject type that could be clearly seen from the vehicle. Focal watches were carried out from within the vehicle cab, or from a hide built onto the vehicle, using 8x40 binoculars or a spotting scope secured onto the vehicle with a clamp. Behaviour was recorded by instantaneous sampling every five minutes, as were the number of other giraffe visible, the identity of the nearest neighbour of the focal subject, and the distance between these two animals.

If an individual was out of sight of the observer for one sampling instant, that data point was excluded from later analyses. If the focal subject was out of sight for two sampling instances, the focal watch was terminated. Thus, each focal watch lasted one hour, or until the focal subject was no longer visible, whichever was shorter. Successive focal watches were only carried out at the same location if group composition had changed between the start of one focal watch and the start of the next. Each individual was included no more than once in focal watches at waterhole locations and no more than once in focal watches at non-waterhole locations so as to avoid pseudoreplication (e.g. Sanchez-Prieto *et al.* 2004). Ultimately, from the focal watches, only the nearest neighbour data and the *ad-libitum* recordings of mating and agonistic interactions (see below) were used in analyses.

2.2.6.1 Mating interactions

All occurrences of mating (male-female) interactions were recorded *ad libitum*, both during and outside of focal watches, and classed according to type and intensity.

1 = Testing of female reproductive condition only: male sniffing or nudging the female's anogenital area with or without urination by the female and flehmen by the male.

2 = Courtship behaviour: with a female found to be in oestrus; includes behaviours such as: the male in erect posture, normally behind and close to the female; the male pursuing the female closely by following her whenever she moves, frequently nosing the female's rump and back; laufschlag.

3 = Attempted mounting: mounting of female by male with penis unsheathed, but without successful intromission.

4 = Copulation: mounting with successful intromission and ejaculation; usually not followed by any other mounting attempts.

During the last six months of the second field season, the success of a male in eliciting urination by a female was recorded. This information was collected whenever it was possible to unequivocally determine whether the female had urinated subsequent to the male nudging the female's rump or tail. On occasion this was not possible, for example if the interaction occurred in dense shrub savannah, at a large distance from the observer, or if the female was facing the observer. The performance of flehmen by the male (or lack thereof) was also recorded.

Consortships were defined as male-female pairs, where the male was pursuing and seeking to mate with the female, who, from the male's behaviour, was assumed to be in oestrus (e.g. Forchhammer & Boomsma 1998). Consortships were taken to include the entire period subsequent to a male having identified an oestrus female, up until successful copulation (mounting with successful intromission and ejaculation).

Consortships were identified by one or more of the following behaviours (derived primarily from Pratt and Anderson (1985)):

- Male adopting the 'erect' or 'proud' posture (standing stiff with neck and head stretched upwards and slightly arched), normally behind, and close to, the female (Figure 2.6);
- Male pursuing the female closely by following her whenever she moves, and ceasing to walk whenever she stops, often circling trees, and sometimes with his head held low and out towards the female as if attempting to smell her.
- Frequent and prolonged nosing of the female's rump by the male. N.B. this is distinct from the single nosing of a female's rump associated with inducing urination and urine testing);
- Female holding her tail out and deflected to one side for extended periods without urination;
- Laufschlag-like foreleg kicks by the male aimed at the female's hind legs;
- Small jumps, or slight raising of both front legs by the male while positioned immediately behind the female;
- Unsheathing of the penis, while the male is in close proximity to the female.

Figure 2.6. Dark male in consortship with a female. Note the female's deflected tail, and the male's 'proud' posture.

2.2.6.2 Agonistic interactions

All occurrences of agonistic (male-male) interactions between males, whether involving contact or not, were recorded and classed according to the type and intensity of interaction. This term was taken to include all offensive and defensive, dominant and submissive behaviours, as well as more ambiguous interactions between males.

1 = Display and displacement: includes standing or walking in erect posture with legs and neck rigid or arched and head up; may result in the other individual being displaced (Pratt & Anderson 1985; Estes 1991).

2 = Light necking: little or no straddling of legs, light contact of shoulders and flanks, with rubbing, curving and swinging of necks with the horns angled towards opponent, but with no significant blows. Corresponds with Coe's 'low intensity necking' (1967) and Innis's 'necking' (1958).

3 = Moderate necking: legs firmly straddled (participants parallel or reverse-parallel), both participants leaning against and pushing each other, with blows delivered by both participants, with the horns aimed at and striking the opponent's body, and avoidance of blows by swinging neck over and above that of opponent. Corresponds with Coe's 'high intensity necking' (1967) and Innis's 'sparring' (1958).

4 = Intense necking fight: very heavy, clearly audible, rapid blows and jabbing of horns that threaten to knock participants off-balance or cause injury; often preceded by 'proud' posturing by both males and parallel walking (Dagg & Foster 1982; Estes 1991). Corresponds with Innis's 'serious fights' (1958).

Only the highest level of interaction was noted for each mating or agonistic event. Thus, if two males were observed necking mildly and then necking moderately, only one incidence of moderate necking was finally recorded. Each occurrence of interaction was noted for each pair of individuals, so if a male smelt the same female's rump twice it was counted as one event, but if two males smelt the same female, it was counted as two events.

2.2.7 Collection and processing of faecal pellets in Etosha NP

In order to attempt to determine parentage of calves, DNA samples were acquired from faecal pellets of known individual giraffe. This is a non-invasive technique, which does not require immobilisation of the animal or any disruptive intervention (e.g. Reed *et al.* 1997; Taberlet *et al.* 1999; Constable *et al.* 2001).

Fresh faecal pellets, free of insects and relatively free of soil, were picked up using disposable laboratory gloves following observed defecation by an identified animal. All samples were collected within thirty minutes of defecation. The pellets were placed in three labelled 50 ml plastic centrifuge tubes, with at least 3 pellets in each. Faecal pellets were immediately covered with 90% ethanol and stored upright at ambient temperature. Ethanol has been shown to be an effective long-term storage medium for faecal DNA (Murphy *et al.* 2002). After 24 to 48 hours, in the Etosha Ecological Institute lab, the ethanol was tipped off two of the three tubes. These faecal pellets were then air-dried on a clean sheet of foil for 10 minutes and then placed back in the two tubes this time with silica gel beads, in accordance with the two-step storage method recently developed by Nsubuga *et al.* (2004). The pellets were then stored in silica gel beads first at room temperature and later at 4°C. This second storage method was chosen because of the risk of ethanol leakage in transit.

A total of 164 faecal samples were collected from 149 different giraffe, all but 32 of which were known individuals. These samples were packed in boxes and sent to Newcastle by plane at the end of the second field season (after obtaining a Namibian MET export licence and a UK Home Office import licence). Subsequent DNA extraction, PCR, fragment analysis and parentage assignment were carried out at the University of Newcastle (see Appendixes 8 to 10 for molecular methodology).

2.2.8 Data analysis

Wherever possible, interval or ratio data have been analysed using parametric statistics (e.g. Student's t-test, ANOVA, linear regression, Pearson's correlation coefficient), after transformation of the data to approximate a normal distribution where necessary. If the data could not be normalised (i.e. a Kolmogorov-Smirnov test revealed a significant deviation from a normal distribution at $P < 0.05$), the equivalent non-parametric tests were chosen (e.g. Mann-Whitney U test, Wilcoxon signed rank test, Spearman's correlation coefficient). Nominal and ordered categorical data have been analysed using Pearson's chi-squared tests, except where expected counts were too low (less than five in more than 20% of cells, or less than one in any cell), in which case the contingency coefficient was calculated.

3 FEEDING ECOLOGY AND HABITAT SELECTION IN RELATION TO RESOURCES

3.1 Introduction

To investigate male mating strategies and the environmental potential for monopolisation (Emlen & Oring 1977), it is vital to first understand how resources drive or restrict female movements and aggregation. The environmental potential for monopolisation of mates depends on the degree to which multiple mates (in this case females), or the resource critical to gaining multiple mates (e.g. food, water), are clumped, predictable and economically defendable (Emlen & Oring 1977). If there is high quality food is predictably clumped, then females are more likely to aggregate in groups and remain in the same area for extended periods of time, resulting in predictable female movements and concentration areas (Gosling 1986). Males can thus reduce their search effort and increase their chances of encountering and securing access to receptive females by focussing on, and possibly defending, these concentration areas (Gosling 1986; Ims 1990). Individual males that can exclude other males from these areas can thus enhance their chances of achieving a significant proportion of all mating opportunities (Owen-Smith 1977; Gosling 1986). Conversely, if resources are distributed more unpredictably, then female spatial distribution is also likely to be more unpredictable. As a result, males will have to spend more time locating females, will be more likely to adopt a following strategy of mate competition, and the potential for monopolisation by dominant males may be reduced.

It is also important to determine how the feeding ecology of males and females differ, in order to be able to distinguish male movements that are driven by the need to locate mates, from those that are driven by the need to forage. This chapter explores giraffe resource use within the study area, and aims specifically to identify food preferences, sex differences in feeding strategy and habitat use, and the effect of artificial water provision on female aggregation. The effects on male movements will be explored in Chapter 5.

3.1.1 Giraffe food preferences and habitat use

Giraffe are generalist browsers and eat a diversity of shrub and tree species, as well as forbs, taking leaves, fruit, pods, flowers, shoots and twigs (Innis 1958; Pellew 1984a; Skinner & Smithers 1990; du Toit 2003). Their diet is diverse and includes a large number of trees and shrubs belonging to the family Fabaceae (or Leguminosae), many of which are acacias (Innis 1958). In most areas, giraffe will sample nearly all species of tree and large shrub available, but show clear species preferences (Dagg & Foster 1982). For example, species from the genera *Acacia*, *Albizia*, *Boscia*, *Combretum*, *Commiphora*, *Terminalia*, *Ziziphus* are usually cited among the preferred foods wherever they are found (Innis 1958; Leuthold & Leuthold 1972; Berry 1973; Pellew 1984a). All of these are represented by at least one species in Etosha NP.

Typically between one-third and two-thirds of the day is spent in feeding, depending on the aridity and productivity of the environment (Innis 1958; Leuthold & Leuthold 1978a; Pellew 1984a; van der Jeugd & Prins 2000; Fennessy 2004). A previous study has suggested that feeding is greatly reduced at night, with ruminating being the dominant night-time activity (Pellew 1984a). In the dry season, giraffe spend relatively more of the day-time time foraging, and less time resting, lying and ruminating, than in the wet season (Dagg 1971; Ciofolo & Le Pendu 2002; Fennessy 2004). Giraffe tend to forage most actively at the coolest times of the day, in the early morning and the late afternoon (Innis 1958; Ginnett & Demment 1997; Fennessy 2004), and reduce feeding activity during hotter days (Leuthold & Leuthold 1978a).

Male and female giraffe foraging strategies tend to differ, but both are directed at maximising reproductive success. Male giraffe increase their reproductive fitness by adopting an ‘energy minimiser’ or ‘time minimiser’ strategy (Schoener 1971; Ginnett & Demment 1997; Fennessy 2004), whereby they seek to minimise the time and energy required to obtain the necessary nutrients to meet their metabolic needs. This allows them to dedicate more time each day to seeking potential mates and competing with other males (Pratt & Anderson 1985; Ginnett & Demment 1997). Conversely, female giraffe increase their reproductive fitness by adopting an “energy maximiser" strategy, whereby they maximise the time they spend browsing, thus maximising their total energy and nutrient intake (Schoener 1971; Geist 1974; Pellew 1984b; Ginnett & Demment 1997). Because of the metabolic demands of gestation and lactation, females are also more selective in their choice of browse, generally feeding on higher quality foods (higher protein content) than males, who instead prefer greater forage biomass (Pellew 1984a; Pellew 1984b). Consequently, males typically spend less time each day foraging than females, even though they are larger than females (mean adult body mass of 1200 kg for males, 800 kg for females (Dagg & Foster 1982)) and would thus be expected to have greater absolute energy requirements (Ginnett & Demment 1997). Males are able to do this by tolerating a lower-quality diet, by dedicating more foraging time to food ingestion as opposed to movement between patches, by feeding longer on taller browse patches that contain potentially higher biomass, and by feeding with an increased bite size (Ginnett & Demment 1997; Ginnett & Demment 1999).

Giraffe generally respond to seasonal changes in the distribution of food sources by local small-scale movements within their home range, rather than large-scale migrations (Pellew 1983b; Fennessy 2004). Seasonal variation in food selection can be explained by plant phenology, which is driven primarily by rainfall (Scholes *et al.* 2003), and generally reflects selection for food species with high quantities of new leaf and shoot material (Pellew 1984a). Seeds and fruits are usually rich in protein (Jarman 1974), so should also be selected as they become available.

This chapter does not seek to explain the food choices of giraffe in relation to nutrient value or digestibility (e.g. Fennessy 2004). Rather it aims to present a more general understanding of seasonal variation in food and habitat choices in relation to availability, differences between the sexes in the choices they make, and how these choices affect giraffe aggregation and movements. Changes in female habitat use in the study area should therefore be driven by the location of new vegetative growth. Where preferred food sources are spatially or temporally restricted, females using these resources are predicted to aggregate (e.g. Ims 1987).

3.1.2 Artificial water provision and use of water sources by giraffe

Wildlife distribution and movements within parks are often determined by the location of water, particularly in the dry season, when movements are restricted and population densities tend to be higher in proximity of perennial water sources (Auer 1997). This often results in a seasonal movement of many species towards artificial water points in the dry season and a dispersion away from them during the rains (Ayeni 1975; Western 1975). Accordingly, in riverine environments, seasonal movements of giraffe are generally characterised by a concentration in areas near rivers during the dry season, and a dispersion into areas away from the rivers in the wet season (Ayeni 1975; Leuthold & Leuthold 1978b). However, it is difficult to separate the influence of the availability of drinking water from that of vegetation on these movements, since riverine vegetation is distinct from vegetation further away from rivers (Ayeni 1975; Leuthold & Leuthold 1978b).

Their selection of moisture-rich food types, combined with physiological adaptations that reduce water loss, enables giraffe to go for long periods without water (Sidney 1965; Dagg 1971). This allows giraffe in arid and semi-arid habitats to extend their range further away from free water sources than more water-dependent species (Ayeni 1975). In the most arid region of the species' range, in north-western Namibia, the arid-adapted populations of giraffe have been observed to go for months without drinking and may even be entirely independent of free water (Fennessy 2004). In other areas, giraffe have also been recorded to drink only very rarely (Dagg & Foster 1982). Nonetheless, giraffe will often drink freely if water is available (Berry 1973; Ayeni 1975; du Preez & Grobler 1977), especially during the dry season, when the water content of vegetation is at its lowest (Ritter 1993). Western (1975) classed giraffe in Amboseli, Kenya, as non-water-bound based on their distribution relative to water, but suggested that under more heat-stressed environments they might show water-dependent distributions. In the Kruger NP, South Africa, where the density of water points is particularly high, giraffe are generally found within 0.5-1 km of water when feeding (Gaylard *et al.* 2003).

In Namibia, formerly water-independent desert-dwelling giraffe have been seen to change their habits and movements once water is artificially provisioned (Fennessy

2004). Fennessy *et al*. (2003) also observed that movement into a game park to the east of the desert region was increased during the hot-dry season, due to the presence of reliable water sources within the park. If water can affect giraffe movements in this way, then artificial water provision may have the potential to locally increase giraffe sexual competition, if it increases the predictability of occurrence of female giraffe. As seen in the introduction, predictable concentrations of females increase the ability of males to defend and monopolise females or the resources that concentrate them (e.g. Ritter & Bednekoff 1995). It was predicted that perennial waterholes in Etosha NP would predictably concentrate females, especially during the dry season. This would provide males that could dominate others at the waterholes with an opportunity to encounter, urine-test and potentially monopolise access to a large number of females, with reduced effort required in locating these females.

3.2 Aims

This chapter aims to test the following hypotheses and predictions:

Hypothesis 1: Male and female giraffe differ in their food and habitat preferences as a result of different foraging strategies. Thus, I predict that:

- Females will spend relatively more time foraging than males.
- Food plant selection will differ between males and females.
- Females will be more selective in their food choice than males, and seasonal changes in food selection will reflect phenological changes in food plants.

Hypothesis 2: Limited resources cause females to aggregate predictably. Thus, I predict that:

- Females will occur more predictably at waterholes and in larger groups close to waterholes during the dry season than during the wet season.
- When preferred foods and habitats are spatially limited, larger aggregations of females will form in these habitats.

Hypothesis 3: Reproductively active males will need to leave their preferred habitats to search for potential mates. Thus, I predict that:

- Solitary males (assumed to be seeking mates) will occur in the same habitats as females. Habitat selection of males in bachelor groups will differ to that of females and to that of solitary males.

3.3 Methods

3.3.1 Tree phenology

In order to interpret the effects of seasonal and spatial variation in food availability on giraffe movements, an understanding was necessary of the phenology of the tree and shrub species in the study area used by giraffe. Turning of leaves, leaf-fall, start of new leaf growth, and appearance of flowers, pods and fruits were all noted for the following species (preceded by an abbreviated form):

Ac he: *Acacia hebeclada*
Ac ki: *Acacia kirkii*
Ac lu: *Acacia luederitzii*
Ac me: *Acacia mellifera*
Ac ne: *Acacia nebrownii*
Ac re: *Acacia reficiens*
Ac to: *Acacia tortilis heteracantha*
Al an: *Albizia anthelmintica*
Bo fo: *Boscia foetida*
Ca al: *Catophractes alexandrii*
Co ap: *Combretum apiculatum*
Co he: *Combretum hereroense*
Co im: *Combretum imberbe*
Co mo: *Colophospermum mopane*
Gy se: *Gymnosporia senegalensis*
Rh br: *Rhigozum brevispinosum*
Te pr: *Terminalia prunoides*
Zi mu: *Ziziphus mucronata*

For common names, see Appendix 1.

3.3.2 Identification of habitat types

Existing data on Etosha vegetation (e.g. Mendelsohn *et al.* 2000; Burke *et al.* 2002) generally highlight twelve different habitat types in Etosha, six of which occur in the study area (two of these habitats, *salt pans* and *Etosha turf clay pans*, are largely devoid of vegetation). However, the vegetated areas are in reality more heterogeneous than this classification suggests. Each of the four remaining categories includes a number of habitat sub-types of varying significance for giraffe. For example, the category *Etosha grass and dwarf shrubland* comprises open grassland, *Acacia nebrownii* thickets, open mopane veld, and tall acacia veld.

Therefore a finer level classification was developed for this study that focussed on distinct tree and shrub communities. The habitat categories defined were as follows:

A: Open plains: grass or low scrubland with less than 5% tree or shrub-cover

B: *Acacia nebrownii* shrub savannah: with less than 5% other species

C: *Catophractes alexandrii* shrub savannah: with less than 5% other species

D: Mopane veld: *Colophospermum mopane* tree or shrub savannah with less than 5% other species

E: Acacia veld: mixed *Acacia* tree and shrub species with less than 5% non-*Acacia* species

F: Mixed thorn veld: including almost exclusively *Ziziphus mucronata*, *Gymnosporia senegalensis*, *Acacia hebeclada* and *A. tortilis*

G: Mixed broadleaf woodland: including *Colophospermum mopane*, *Combretum imberbe* or *C. apiculatum* or *C. hereroense*, and *Terminalia Prunoides*. May also include some *Catophractes alexandrii*, but *C. mopane* and *C. alexandrii* together should constitute less than 50% of woody vegetation.

H: *C. mopane* and *Catophractes alexandrii* shrub savannah: with both plants presenting similar coverage, and with less than 5% of other species

I: *C. mopane*, *C. alexandrii* and mixed *Acacia* shrub savannah: with at least one third *Acacia spp.* (including *A. nebrownii)*, and less than 5% of other species

J: *C. mopane* and *A. nebrownii* shrub savannah: with both plants presenting similar coverage, and with less than 5% of other species

K: Other distinctive but rare habitats: includes tree or shrub savannah dominated by *Boscia foetida*, *Albizia anthelmintica* or *Moringa ovalifolia*

Of these habitat classes, H to J generally constituted wide ecotones between two different habitats from the list B to G. Only 1.6% of giraffe locations could not be allocated to one of the above categories.

3.3.3 Feeding behaviour and preferences

An instantaneous scan sampling record of the species upon which all browsing giraffe were feeding was noted at each sighting, and occasionally every half hour or hour thereafter if giraffe were followed. An estimate of the proportion of the day spent feeding for each sex-age class was calculated using the percentage of scan samples for each sex-age class that were recorded as browsing (data from all individuals of each sex-age class were pooled due to low individual re-sightings (median for females = 7, for males = 3)). To limit the effect of any possible observer effect on giraffe behaviour, the analyses of feeding behaviour were limited to those that occurred further than 5 m from the observer (as these were almost exclusively giraffe on the road, and hence the majority of these were walking away from the observer). Beyond 5 m, vigilance and walking behaviour were not increased closer to the observer than further away.

Selection of the different browse species for each sex were defined as percentages (for each species) of all feeding observations. Analyses of sex differences in browse species selection were also carried out on a within-habitat basis, in those habitats where a choice of browse species was available. This was to eliminate the effect of potential constraints on feeding choices imposed by habitat selection, which may have also be driven by predator-avoidance, shade, or mate-seeking requirements (Mysterud *et al.* 1999). All analyses of sex-differences in feeding behaviour and within-habitat food selection were carried out using the Chi-square test for independence.

3.3.4 Habitat selection

3.3.4.1 Habitat availability

An analysis of individual-level habitat selection within home ranges was not possible, as large parts of the study area could not be visited. Thus analyses were restricted to habitat selection among areas available to sampling (alongside roads). Thus, availability of habitats (for sampling) was estimated using a set of randomly created coordinates, restricted to those 160 that fell within the maximum distance from the road at which giraffe could be seen in each habitat (this maximum distance was based on observations during the study and thus varied among habitat types). The habitat type at each of these random points was noted, and the proportion of these points attributed to each habitat type calculated.

3.3.4.2 Habitat selection ranks

Habitat selection ranks of (non-juvenile) males and females were constructed by totalling the number of giraffe of each sex-age class seen in each habitat type. Data were pooled for sex-age classes, as re-sightings for most individuals were very low (see above). Only data collected during the first survey of each road in each cycle were used, so as to avoid biases towards areas that were surveyed more often (e.g. some roads had to be driven twice, once on the outward, and once on the return journey). These selection ranks were compared (using Spearman's rank correlation coefficient, rho) between males and females in order to detect differences in habitat use.

3.3.4.3 Preference indices

Preference indices were also calculated to assess the degree of selection or avoidance of habitats relative to availability, using the methodology described in Ntumi *et al.* (2005). To calculate the preference index (PI) for each sex-age class and each habitat, the proportion of all pooled sightings for that sex-age class that occurred within that habitat was divided by the proportional availability of that habitat (derived by the method described above, section 3.3.4.1). Thus, the PI for each sex-age class in each habitat was equal to:

PI = percentage of sightings / percentage habitat availability

Therefore a PI of one indicates neither habitat selection nor avoidance relative to availability. The greater the PI index above a value of one, the greater the habitat preference. The smaller the PI index (below one), the greater the avoidance.

3.3.5 Measures of female aggregation

Aggregations of females should form through females coming together in response to an abundant or spatially limited resource. Dispersal and aggregation of females within the study area was assessed firstly by looking at variation in the number of females in all observed groups that included females (hereafter called ‘female group size’). If a resource was causing females to aggregate significantly, then this could result in larger female groups. Therefore, habitat-specific aggregations of females were revealed firstly by identifying large female groups (those larger than the upper quartile value for the season).

Habitat-specific aggregations were also identified by estimating female densities in each habitat type using distance sampling. For this purpose, transects were established along roads (Etosha has a strict policy of limiting off-road driving, due to a fragile topsoil in many places) wherever one of the designated habitat types (see Section 3.3.2) occurred along both sides of the road without variation in habitat type in relation to distance from the road. Sharp bends in roads were excluded from transects to eliminate surveying the same area twice. The immediate areas around waterholes (300 m) were also excluded from transects. Only data collected during the first survey of each road in each week-cycle were used, so as to avoid re-counting the same giraffe group twice.

Due to very low sightings within the transects, data from each cycle were pooled for each habitat and each season, and approximate densities estimated using the software Distance 3.5 (Research Unit for Wildlife Population Assessment, University of St Andrews, UK). A number of habitats (e.g. *Catophractes* shrub savannah (C), mixed thorn veld (F), and other distinctive but rare habitats (K)) had to be excluded from this analysis due to the short total length of these transects (< 3 km). Data for some of the other more spatially restricted habitat types were also very few, so, for example, all *A. nebrownii* habitats (B, I and J) were combined for this analysis.

A number of models for density estimation were compared, and the model with the lowest AIC (Akaike’s information criterion) was chosen to fit the detection function (e.g. Hounsome *et al.* 2005). This resulted in selection of the uniform key function model with one cosine adjustment term for habitat-specific estimates, and the half-normal key function model with one cosine adjustment term for overall (all habitats combined) estimates. All uniform and half-normal function models produced similar estimates and very similar AIC values. The recommended minimum of 80 observations (for reliable modelling of the detection function (e.g. Hounsome *et al.* 2005)) could not be achieved in any habitat, so these density estimates must be considered as approximations only.

3.3.6 Measures of waterhole use

Seasonal and spatial variations in waterhole use were assessed by examining data on the presence or absence, and number if present, of giraffe at waterholes upon arrival of the observer at each waterhole. All perennial waterholes were visited approximately once a week, in a different sequence and at different times of day each week. For comparison, seasonal waterholes (man-made gravel pits and natural depressions) were also visited; these were widespread throughout the study area, occurred in all habitat types, and were also located near (usually about 50-200 m) to tourist roads, but only held water during the wet season. Differences between seasons and locations (perennial versus seasonal waterholes) in the predictability of occurrence of giraffe at waterholes (presence versus absence) were analysed using the Chi-square test for independence.

Female group sizes were also compared between waterhole and non-waterhole locations, and relative to the distance to the nearest perennial waterhole, to test the prediction that larger groups would assemble at or near waterholes, particularly during the dry season. All analyses of group size were carried out using non-parametric statistics (e.g. Mann-Whitney U test) due to the data being highly skewed to the right.

3.4 Results

3.4.1 Study population and data collection

A total of 431 individuals were identified within the study area, of which 90% were re-sighted at least once. On average, 255 giraffe were seen each month, of which about 70% were recognised as known individuals, although this percentage was greater when in the centre of the study area and lower when on the periphery. Of the known individuals, 72% of the 188 females and 81% of the 190 males were classed as adults throughout the study period. Although the sex ratio for all non-juveniles was almost even (male to female ratio = 1:1.06), females made up 60% of sightings of non-juveniles of known gender. Thus, of those seen more than once, females were re-sighted more often than males (females: mean re-sightings = 8.42, maximum = 32; males: mean = 4.68, maximum = 23).

The sex ratio for juveniles was difficult to determine as the umbilical bump often remained for many months after birth, and could be confused with the penis sheath. The majority (94%) of the 53 individuals of unknown gender were thus juveniles (less than 18 months old) throughout most, if not all, of the study period.

Solitary individuals made up one third (33.9%) of all observations, while herds of two individuals accounted for 18.7%, and herds of three 10.7% of all sightings. The largest herd size observed was 23 individuals. Just over 50% of solitary individuals were dark mature males.

Repeat sampling of individuals was negligible: re-sampling of an individual within one hour made up just 4.4% of all scan sample behavioural records of known non-juveniles, and those re-sampled within 30 minutes just 1.1% of scan sample records. Furthermore, subsequent records of behaviour were largely independent of one another (re-sampling within one hour: Cohen’s kappa = -0.044, N = 126, P = 0.460; re-sampling within 30 minutes: kappa = -0.008, N = 32, P = 0.938). There were only seven occurrences of repeat sampling of a giraffe browsing, and in five of these cases, the giraffe was feeding on a different species in the second browsing record to the first record. Therefore, repeat sampling was not considered likely to bias results.

3.4.2 Tree phenology

Most tree and shrub species bear leaves only during the wet season, with fruit or pods being produced during the latter part of the wet season, and leaves being shed at the start of the dry season (Figure 3.1). Flower and leaf flushes, particularly of most *Acacia* species, generally occurred independently of actual rainfall, although leaf-flushes of some species were timed to coincide with the likely start of the rains in October or November (e.g. leaf production of the semi-deciduous broadleaf *Colophospermum mopane*).

However, certain broadleaf species, such as *Catophractes alexandrii* and *Terminalia prunoides*, did not produce flowers or new leaves until after the first heavy rains, which in 2005 occurred only in December. A few species showed atypical flowering phenology, in that they produced flowers, and leaves, in the middle of the dry season. These included the very common and widespread *Acacia nebrownii*, and the much rarer *A. mellifera*, *Gymnosporia senegalensis* and *Albizia anthelmintica*.

The phenology of *A. nebrownii* plants was not consistent across the study area: although all plants produced flowers between June and August, the start date of flowering differed by many weeks between locations as little as 3 km apart. However, there was a slight trend for more easterly thickets to begin flowering earlier those more to the west (in accordance with the rainfall gradient). There was also inconsistency in whether the plants produced only flowers, or both flowers and new leaves (Figure 3.2).

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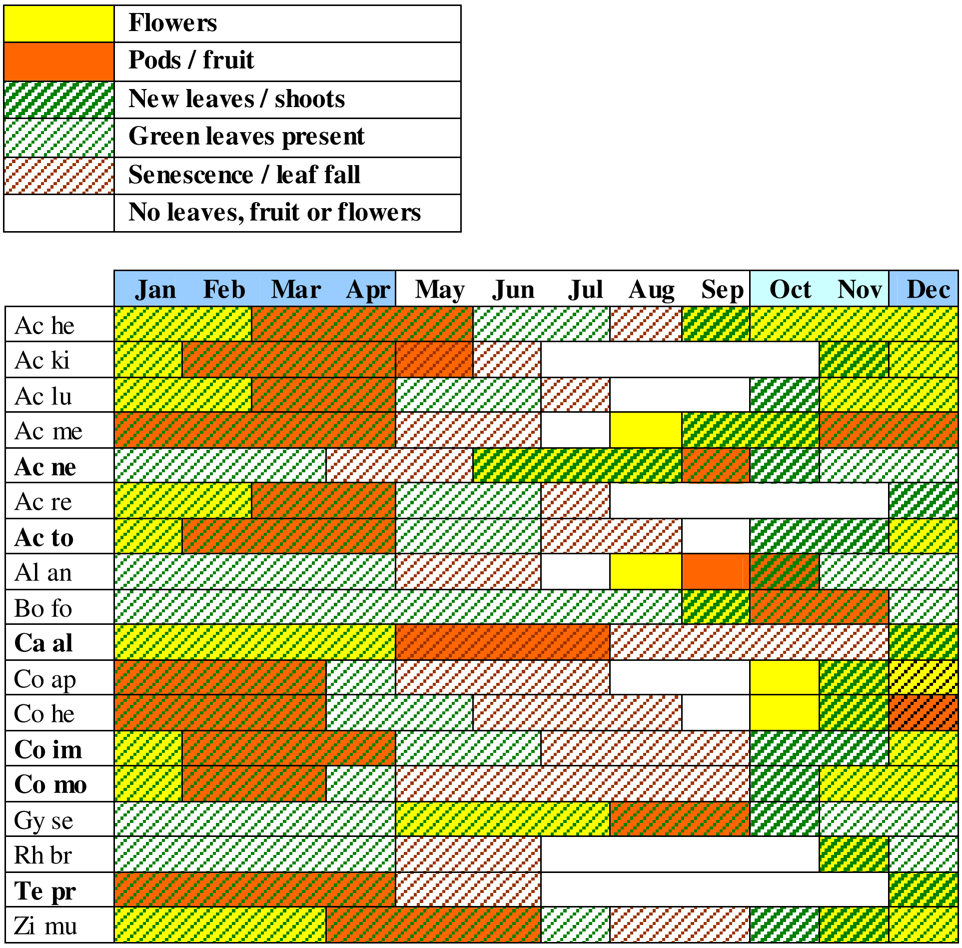


Figure 3.1. Approximate phenology for the tree and large shrub species occurring in the study area. The most important and widespread species are highlighted in bold type. For explanations of abbreviations, see Methods.

Figure 3.2. *Acacia nebrownii* flowers, produced simultaneously as leaves (left), and independently of leaf production (right).

3.4.3 Feeding ecology, habitat use and female aggregation

3.4.3.1 Feeding behaviour

Instantaneous scan sampling observations of individual behaviour showed that sub-adult females and sub-adult males spent the greatest proportion of their day-time (away from waterholes) browsing (47.7% and 46.6% respectively), followed by adult females and pale adult males (42.9% and 42.4% respectively), then dark adult males (32.0%). If waterhole sightings are included, these percentages decrease to 39.8% for sub-adult females, 33.6% for sub-adult males, 37.2% for adult females, 35.7% for pale adult males, and 29.4% for dark adult males. These relative decreases in time spent browsing are due to increases in walking, standing and drinking at waterholes.

During the wet season, adult males (pale and dark) were significantly less likely to be seen browsing than adult females (males: 38.1% of non-waterhole observations; females: 49.0%; $X^2 = 6.094$, N = 622, df = 1, $P < 0.05$). In the dry season, males increased their browsing to match more closely that of females (males: 48.4%; females: 46.6%; $X^2 = 0.305$, N = 895, df = 1, P = 0.581). The wet season difference was limited to adults, as there was no significant difference between sub-adult males and sub-adult females in the wet season (males: 41.5%; females: 45.0%; $X^2 = 0.172$, N = 162, df = 1, P = 0.678). These results all remain if waterhole sightings are also included.

These sex-differences could not be attributed to a time-of-day bias in observations, as there was no sex-difference in the distribution of observations of adult giraffe across the hours of the day within the wet or dry season, for all sightings or just for those away from waterholes, either for all observations or for only those of giraffe browsing (Kolmogorov-Smirnov Z tests, all $P > 0.25$).

3.4.3.2 Feeding preferences

Giraffe were seen feeding on twenty species of woody plant, including seven *Acacia* species. On less than ten occasions, giraffe were also seen to browse on a number of unidentified small shrubs or forbs. Chewing of bones was also observed, predominantly by females (13 of 19 observations), but only during the late wet / early dry season (April – July). Geophagy was also observed on one occasion.

Acacia nebrownii was the most important browse species for the study area giraffe. Over the entire study period, *A. nebrownii* made up 50.5% of observed instances of (non-juvenile) giraffe browsing (from instantaneous scan samples). It was the most frequently eaten species in nine out of ten months for females (in May it ranked equal with *Terminalia prunoides*), and in eight out of ten months for males (in May and December, *Combretum imberbe* was the more frequently browsed species). It accounted for 83.3% of observations of females feeding in August, at the height of the *A .nebrownii* flowering season.

The next most important species for females (adults and sub-adults; Figure 3.4), largely because of relatively high observations of them being browsed in certain months, were *Catophractes alexandrii* (8.5% overall; 23.2% in March, 18.8% in May), *A. tortilis* (7.1% overall; 18.4% in November), *Combretum imberbe* (4.3% overall; 23.3% in December), and *Terminalia prunoides* (4.1% overall; 17.2% in May).

The next most important species for males (Figure 3.5) were *A. tortilis* (9.1% overall; 15.3% in October), *Colophospermum mopane* (8.4% overall), and *C. imberbe* (7.7% overall, 33.3% in December, 29.6% in May). *C. mopane* made up at least 5% of males' diets in seven out of ten months, but only figured so highly in females' diets in March and April. Thus, taller trees (e.g. *A. tortilis*, *C. mopane*, *C. imberbe*) were browsed upon more by males than by females, who browsed more on the shrubby tree species (*A. nebrownii*, *C. alexandrii*).

3.4.3.3 Seasonal variation in food selection

As seen above, peaks in browsing on different species were evident in certain months. These peaks corresponded largely with plant phenology, and particularly with the production of flowers, pods or fruit, and to a lesser extent, new leaves. For example, both sexes showed a sharp increase in feeding on *A. hebeclada* in

September and October, when this uncommon species produced flowers and new leaves (at a time when most other species were bare). Similarly, feeding on *Boscia foetida* peaked for both males and females in October, when it was in fruit. However, for other species, this correspondence was clearer for females than for males, with females feeding more selectively throughout the year. For example, as soon as *A. nebrownii* began producing flowers in June, females switched to feeding predominantly on this species (Figure 3.6), whereas males only began concentrating on *A. nebrownii* in August (Figure 3.7).

Although *T. prunoides* constituted less than 5% of browsing observations overall, it was as frequently consumed by females at the end of the wet season as *A. nebrownii*. Because its distribution in the study area was spatially very restricted, this resulted temporarily in very high browsing pressure, which was evident in both its effect on tree form, and the height to which pods were browsed off (Figure 3.3).

Figure 3.3. Example of the effect of high giraffe browsing pressure on a spatially-limited tree species, Terminalia prunoides. Pods still remain on the top-most branches, which are out of reach of even the tallest males.

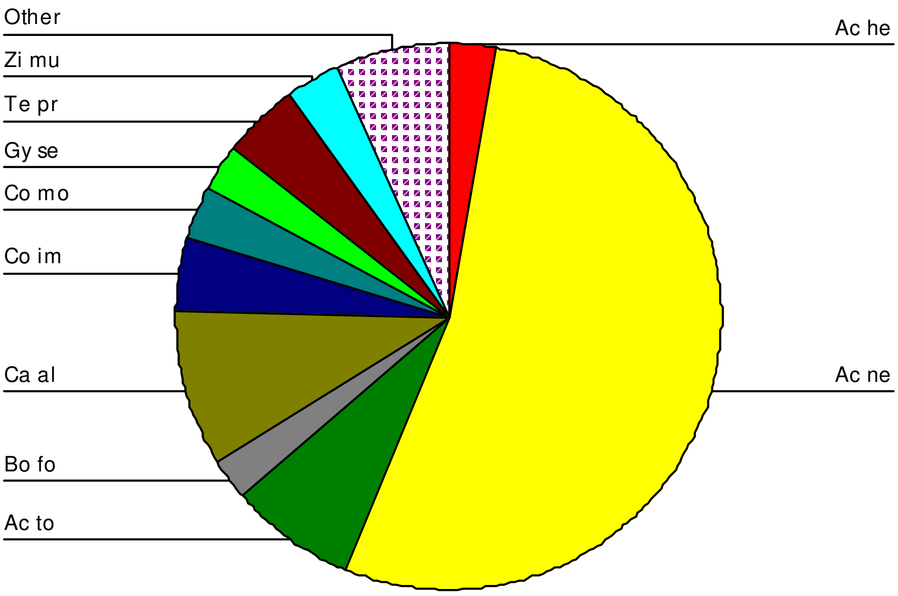


Figure 3.4. Representation of different browse species in feeding observations of females throughout the year. For explanations of species abbreviations, see text (section 3.3.1).

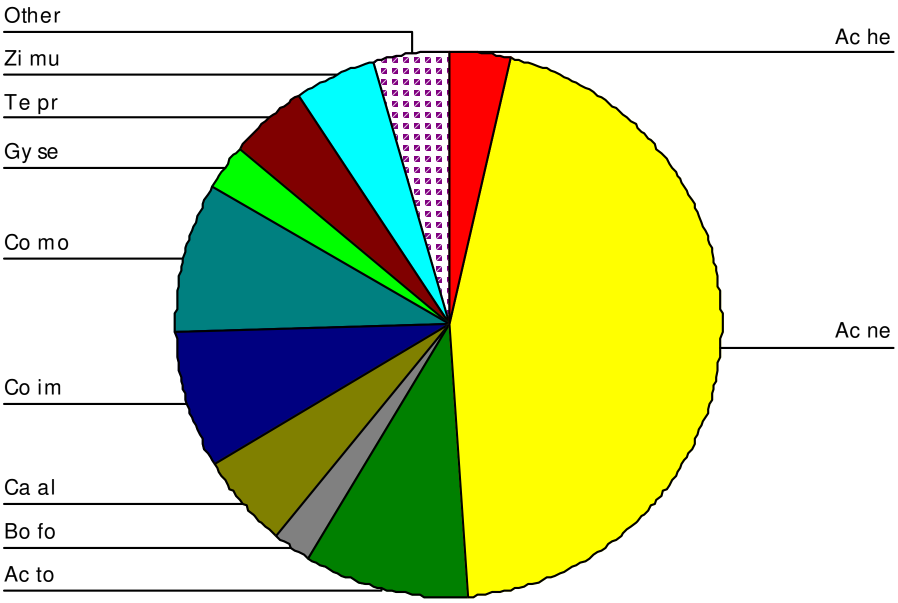


Figure 3.5. Representation of different browse species in feeding observations of males throughout the year. For explanations of species abbreviations, see text (section 3.3.1).

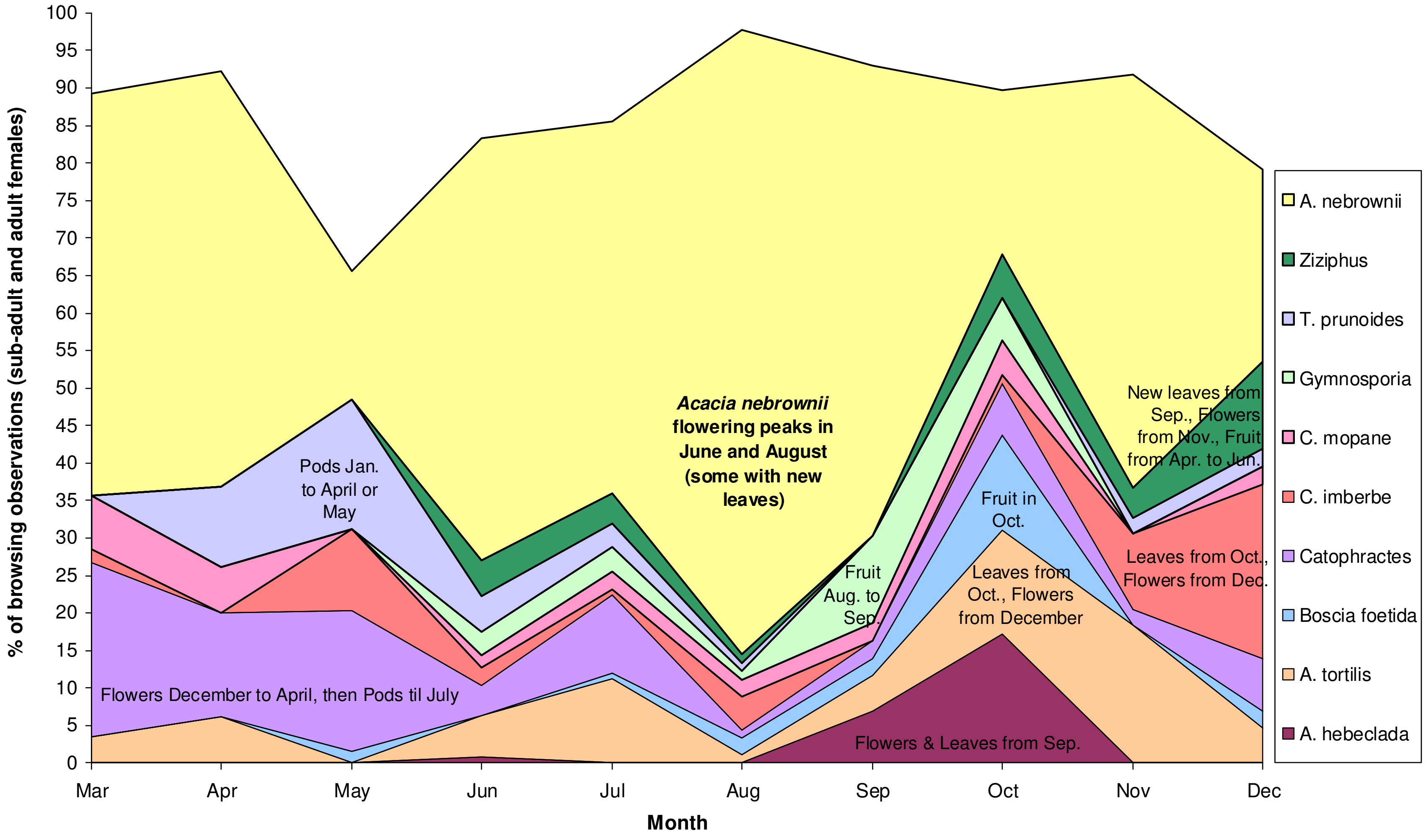


Figure 3.6. Variation in browse species selected by females throughout the year, for the 10 most frequently browsed species. The remaining browse plants were uncommon species (e.g. other *Acacia spp.*, *Combretum spp.*), or were unidentified.

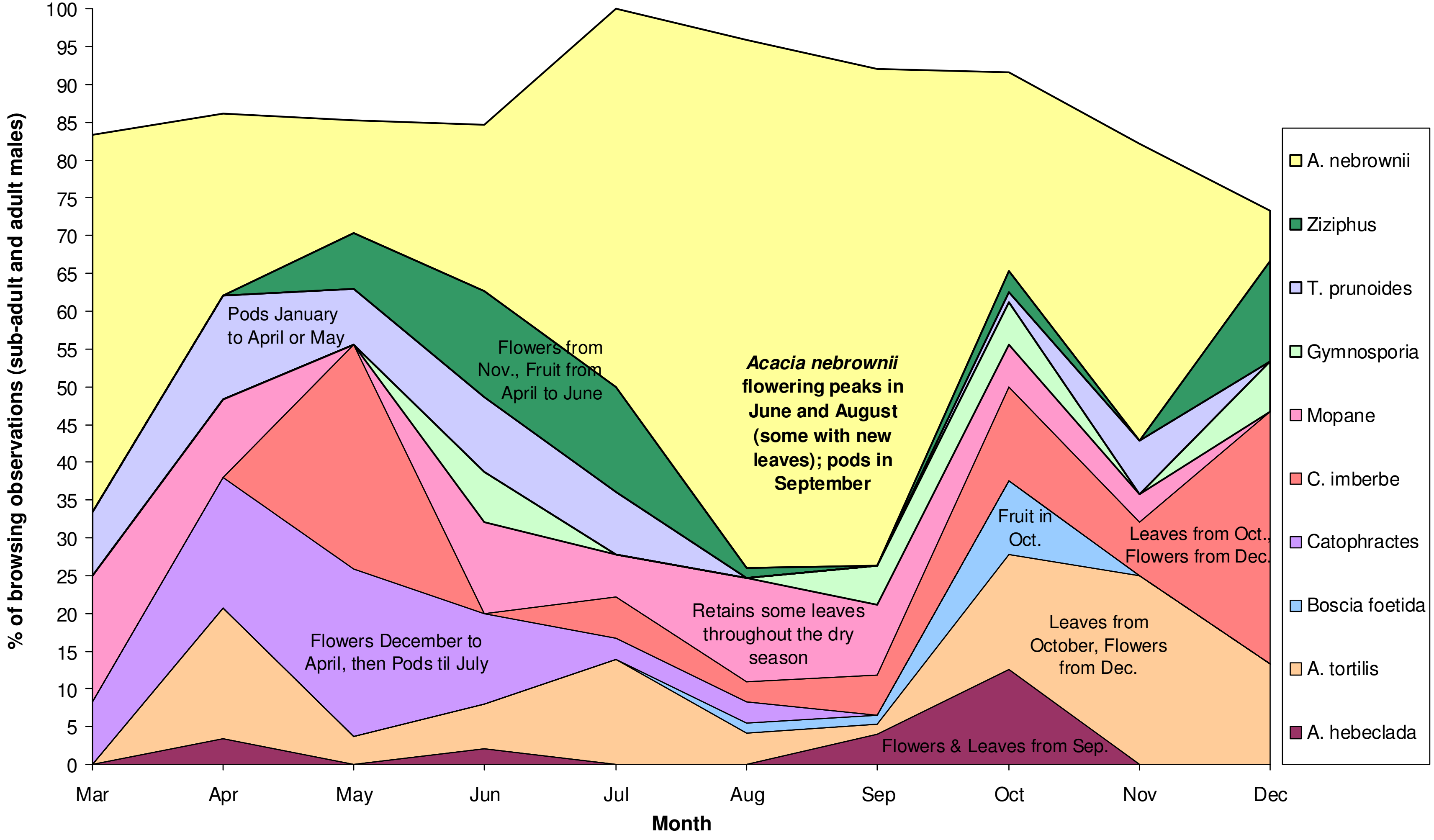


Figure 3.7. Variation in browse species selected by males throughout the year, for the 10 most frequently browsed species. The remaining browse plants were uncommon species (e.g. other *Acacia spp.*, *Combretum spp.*), or were unidentified.

3.4.3.4 Differences in feeding preferences between the sexes

Within-habitat comparisons using the instantaneous scan sampling data revealed that males and females made different selections from the browse species available. Within habitats B (*A. nebrownii*), F (mixed thorn veld) and G (mixed broadleaf woodland), food preferences were very similar, although males browsed on a wider diversity of species in the broadleaf woodland. In habitat C, males were slightly, but not significantly, more likely to select species other than *C. alexandrii* than females (females: 24.0% of observations, males: 37.5%; $X^2 = 1.11$, $N = 66$, $P = 0.291$).

In habitats H and J (combinations of *C. mopane* and either *C. alexandrii* or *A. nebrownii*), males were significantly more likely to feed on *C. mopane* than females (females: 16.1% of observations, males: 36.0%; $X^2 = 8.44$, $N = 162$, $P < 0.005$), whereas females were more likely to select the other species available. In acacia veld (habitat E), males were significantly more likely to select *A. tortilis* than females (females: 39.1% of observations, males: 73.5%; $X^2 = 11.61$, $N = 121$, $P < 0.001$); females had a higher preference for the shorter *Acacia* species, possibly because the branches of many of the *A. tortilis* trees were beyond their reach. Indeed, males were significantly more likely to browse 'high' than females in acacia veld ($X^2 = 4.205$, $N = 93$, $P < 0.05$).

Overall, where such a choice of species was available, females were more likely to avoid *C. mopane* and feed on other species such as *C. alexandrii*. 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.

3.4.3.5 Habitat availability and use

Giraffe were seen in all habitat types, including open, tree-less plains, which they traversed when walking to water, changing food patches, feeding on forbs (only 0.6% of feeding observations), or probably when seeking mates (in the case of males). Giraffe were not seen to walk out onto the pan, but were observed walking along the pan-edge. The availability of the main habitat types for sampling along roads are presented in Table 3.1, below.

Table 3.1. Availability (%) of habitat types for sampling along roads, with the maximum distance from the road at which giraffe could be seen in each habitat type. For an explanation of the method used to estimate habitat availability, see section 3.3.4.1.

Rank	Habitat type	Max. distance to road (m)	% availability
1	A: Open plains	1000	41.9
2	H: *C. mopane* and *C. alexandrii*	800	16.9
3	B: *A. nebrownii* shrub savannah	1000	13.1
4	D: Mopane veld	300	6.3
4	C: C. *alexandrii* shrub savannah	1000	6.3
6	J: *C. mopane* and *A. nebrownii*	350	5.0
6	E: Acacia veld	900	5.0
8	F: Mixed thorn veld	600	2.5
9	I: *C. mopane*, *A. nebrownii* and other *A. spp.*	400	1.9
10	G: Mixed broadleaf woodland	400	0.6
10	K: Other habitat types (inc. *Boscia* and *Albizia*)	300	0.6

If giraffe were using the different habitat types randomly, one would expect, for example, almost half of giraffe to have been located in open plains (A), and a very small proportion of sightings to have occurred in the rarer habitat types (e.g. F, I, G, K). However, based on observed feeding preferences, one would expect giraffe to show a preference for *A. nebrownii* habitats, acacia veld and mixed broadleaf woodland, and also for females to show a greater preference than males for habitats including *C. alexandrii* and *A. nebrownii,* and a greater avoidance of habitats including *C. mopane*.

For females in female-only groups, after open plains (A: 28.4% of observations), *A. nebrownii* shrub savannah (habitat B) was the most frequented habitat (15.2%). This was followed by acacia veld (E: 13.2%) then mixed thorn veld (F: 10.7%). Overall, habitat selection ranks for females in female-only groups did not correlated with habitat availability ranks (Spearman's rho = 0.430, N = 11 habitats P = 0.187). Preference indices were strongly positive for the spatially-restricted mixed broadleaf woodland (G: PI = 13.06), mixed thorn veld (F: 4.24) and acacia veld (E: 2.78;

Figure 3.8). As predicted, females showed the strongest avoidance of mopane veld (habitat D: PI = 0.13), as well as mixed *C. mopane*-*C. alexandrii* shrubland (H: 0.34).

For males in male-only groups, after open plains (A: 19.6%), mixed thorn veld (F: 17.4%) was the most frequented habitat, followed by *A. nebrownii* shrub savannah (B: 14.1%), then mixed broadleaf woodland (G: 12.0%). Habitat selection ranks for males in all-male groups (including loners) also did not correlate with availability (Spearman's rho = 0.438, N = 11 habitats, P = 0.178), and were significantly correlated with female habitat selection ranks (Spearman's rho = 0.793, P <0.005). Overall, males showed a strong preference for mixed broadleaf woodland (G: PI = 19.13) and for mixed thorn veld (F: 6.96). Males also strongly avoided mopane veld (habitat D: PI = 0.61), but males in bachelor groups showed the highest preference indices for habitats containing high proportions of *C. mopane* without acacias (D: 1.04 and H: 1.03). Habitat selection ranks of solitary males significantly correlated with those of females (Spearman's rho = 0.907, P < 0.001), whereas habitat selection ranks of males in bachelor groups did not (Spearman's rho = 0.485, P = 0.130). As well as showing a greater relative preference for habitats containing *C. mopane*, males in bachelor groups had lower preference indices for open plains (A), *Catophractes alexandrii* shrub savannah (C) and acacia veld (E) than either females or solitary males (Figure 3.8).

Evidence suggested that females did not select habitats for foraging purposes only. Between March and May, females seen in mixed thorn veld (F) were almost exclusively (>80%) standing resting or ruminating (this habitat provides abundant shade), whereas during the rest of the year, about 50% of females in this habitat were browsing (it includes two evergreen species). Conversely, between March and May, 50% of females sighted in mopane veld (D) were browsing, whereas during the rest of the year, females in mopane veld were almost never seen browsing (only one out of 35 observations). Mopane is one of the few tree species to retain its leaves (albeit senescent) during the dry season, and consequently continues to provide shelter from the sun when many other tree species cannot.

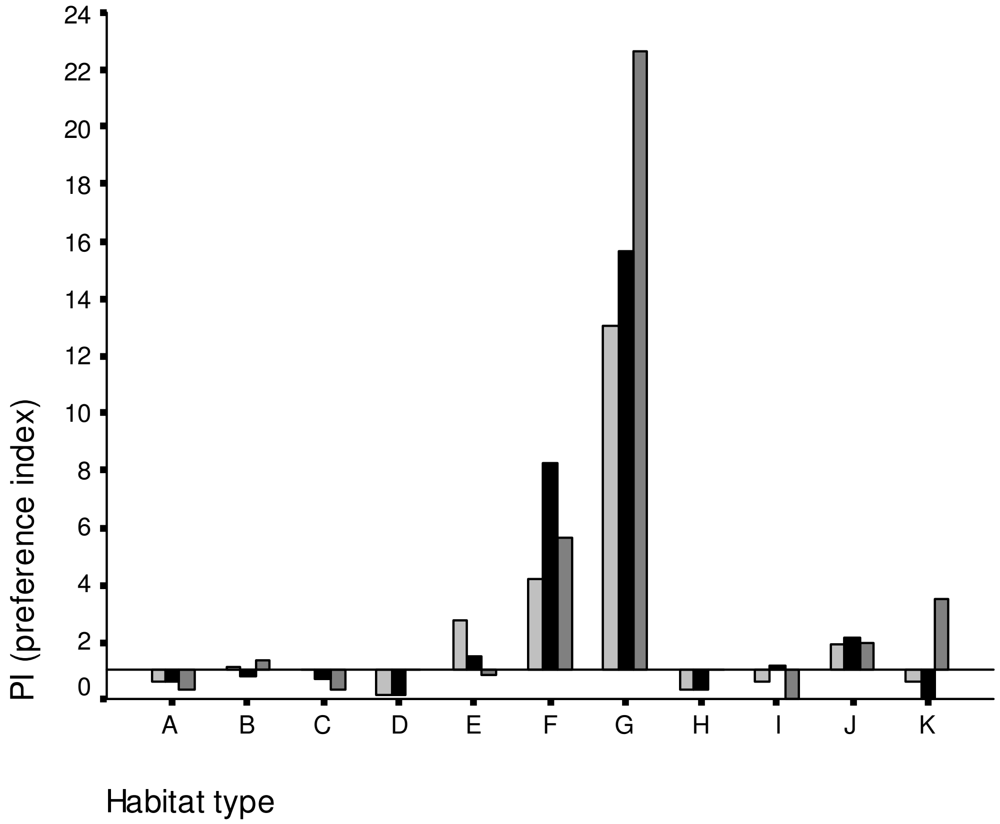
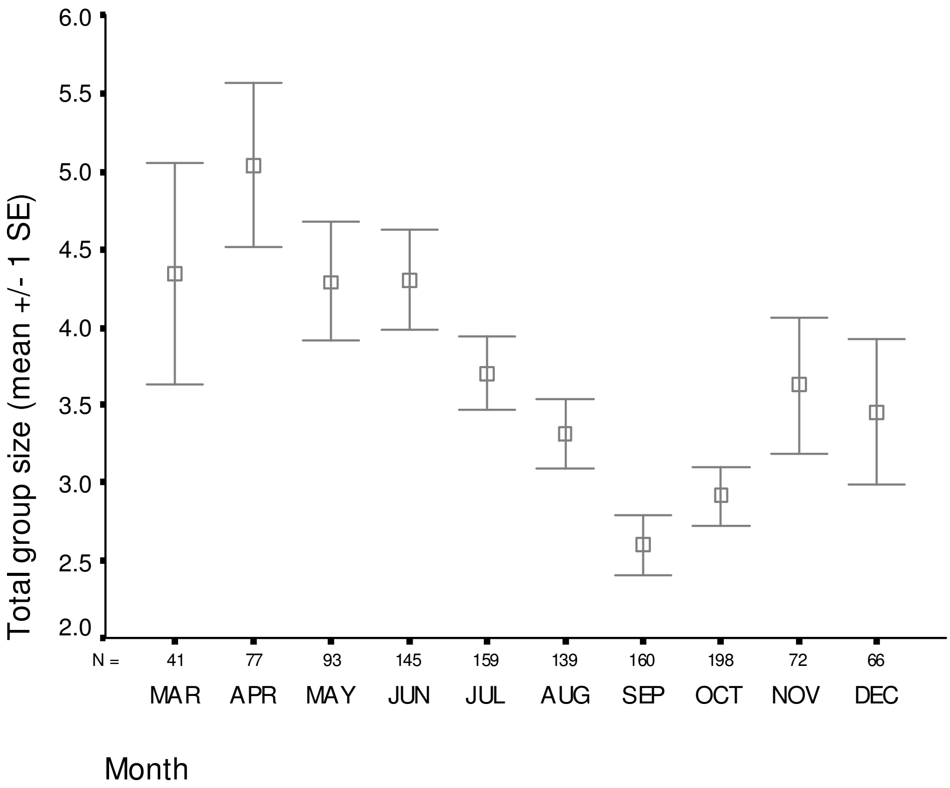


Figure 3.8. Habitat preference indices for females (pale grey bars), lone males (black bars), and males in bachelor groups (dark grey bars). For description of calculation of preference indices, see text. Axis line at PI = 1 corresponds to no preference or avoidance; bars above the line represent preference, bars below represent avoidance relative to availability.

3.4.3.6 Group size and female aggregation

Mean group size over the entire study period was 3.58 ± 0.10 (one standard error; median = 2.0), but varied across the seasons (Figure 3.9). Only five groups were seen with twenty or more individuals (in March, April, June, November and December), and the largest observed group size was 23. Groups tended to be largest during the 'wet' period from March to June, declined in size until September, and then increased again toward the end of the year. Mean group size was 4.46 ± 0.22 between March and June (median = 3.0), and was significantly less, at 3.19 ± 0.10, during the drier, second half of the year (median = 2.0; Mann-Whitney U = 114067, N = 1148, P < 0.001). This seasonal disparity is equally apparent in the number of females found in female-inclusive groups, with a mean of 3.46 ± 0.17 females between March and June (median = 3.0), and 2.47 ± 0.08 between July and December (median = 2.0; Mann-Whitney U= 54385, N = 795, P < 0.001).



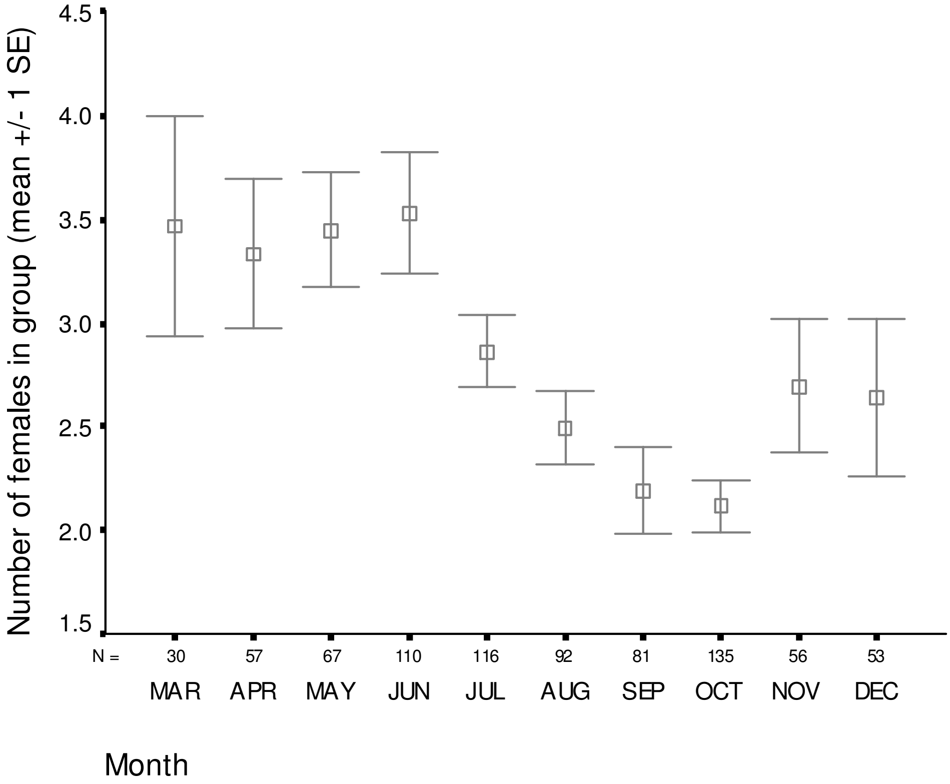


Figure 3.9. Variation across the months in mean total group size (top), and in mean number of females in female-inclusive groups (bottom). Bars represent 1 standard error of the mean.

Based on tree phenology (section 3.4.2) and feeding observations (section 3.4.3), female aggregations were predicted to occur as follows:

- Aggregations in *Catophractes alexandrii* shrub savannah (C) or mixed broadleaf woodland (G) between March and May; possibly in habitats including large proportions of *Acacia nebrownii* (B, I and J) in March and April.
- Aggregations in *A. nebrownii* habitats (B, I and J) between June and September, particularly in June and August; possibly in mixed thorn veld (F) in September.
- Aggregations in acacia veld (E) from October to December, but also in mixed broadleaf woodland (G) again in December.
- No aggregations in habitats comprising a large proportion of *Colophospermum mopane*.

The largest groups observed were in mixed broadleaf woodland (G) between December and June (five groups of 19, one of 23), in *A. nebrownii* shrub savannah (B) in June (one group of 19, one of 23), in acacia veld (E) in March and November (one group of 20, one of 22), and walking across open plains (A) to a waterhole in December (one group of 20).

Large groups of females were defined as those larger than the upper quartile value for the season. Between October and December, the majority of large groups of females (> 3) were seen in mixed broadleaf woodland (G; N = 11), and to a lesser extent in acacia veld (E; N = 7), mixed thorn veld (F; N = 6) and *A. nebrownii* thickets (B; N = 6). Between March and May, the greatest numbers of large groups of females (> 5 females) were seen in mixed broadleaf woodland (G; N = 8).

Thus, throughout the wet season, as predicted, female densities were greatest in mixed broadleaf woodland (G: 2.3/km^2, Table 3.2, Figure 3.10), and were also higher than the overall female density of 0.14/km^2 in *A. nebrownii* habitats (B, I, J: 0.31/km^2). Densities were negligible (<0.05/km^2) in the other habitat types for which data were collected during this time (open plains (A), acacia veld (E)). Female density could not be calculated for *Catophractes* shrub savannah (C), but females were not found in larger groups in this habitat type than in other habitats during the same period (March-May; Mann-Whitney U = 754, N = 144, P = 0.776).

Between June and September, the largest groups of females (> 4) were seen predominantly in *A. nebrownii* thickets (B; N = 23) and in open plains surrounding waterholes (A; N = 21). Female densities were again greatest in mixed broadleaf woodland (G: 0.45/km^2) and, as expected (Table 3.3), in *A. nebrownii* habitats (B, I, J: 0.30/km^2). Densities were negligible (<0.07/km^2; overall female density during this period = 0.13/km^2) in all other habitats for which data were collected during the dry season (open plains (A), acacia veld (E), mopane-*Catophractes* shrub savannah (H)). Female density could not be calculated for mixed thorn veld (F), but females were not found in larger groups in this habitat than in others in September (Mann-Whitney U = 312, N = 81, P = 0.510), possibly due to the very small size of mixed thorn veld clumps (< 400 m in diameter, hence the lack of density estimation).

Despite comprising the second and third largest total transect distances (after open plains), females were never recorded within mopane-veld (D) transects, and only at very low densities (0.02/km^2) in mopane-*Catophractes* shrub savannah (H). Female groups were significantly smaller in mopane-rich habitats (without *Acacia spp.)* than in other habitats year-round (Mann-Whitney U = 19205, N = 780, P < 0.05).

Table 3.2. Estimated female densities, with confidence limits, for the wet and dry season.

Habitat	**Females seen**	**Density (per km^2)**	**95% LCL**	**95% UCL**	**CV (%)**	**Effective strip width (m)**
Wet season (October-May)						
Open plains (A)	14	0.03	0.01	0.11	54.5	607
A. nebrownii habitats combined (B, I, J)	35	0.31	0.13	0.78	42.0	180
Acacia veld (E)	11	0.05	0.01	0.22	57.6	900
Mixed broadleaf woodland (G)	33	2.27	1.05	4.94	36.0	136
Overall (all transects)	95	0.14	0.09	0.22	24.2	248
Dry season (June-September)						
Open plains (A)	16	0.04	0.01	0.13	47.2	500
A. nebrownii habitats combined (B, I, J)	31	0.30	0.15	0.62	35.6	192
Acacia veld (E)	10	0.06	0.01	0.37	60.8	1000
Mixed broadleaf woodland (G)	6	0.45	0.08	2.61	60.1	167
Overall (all transects)	78	0.13	0.08	0.20	22.6	245

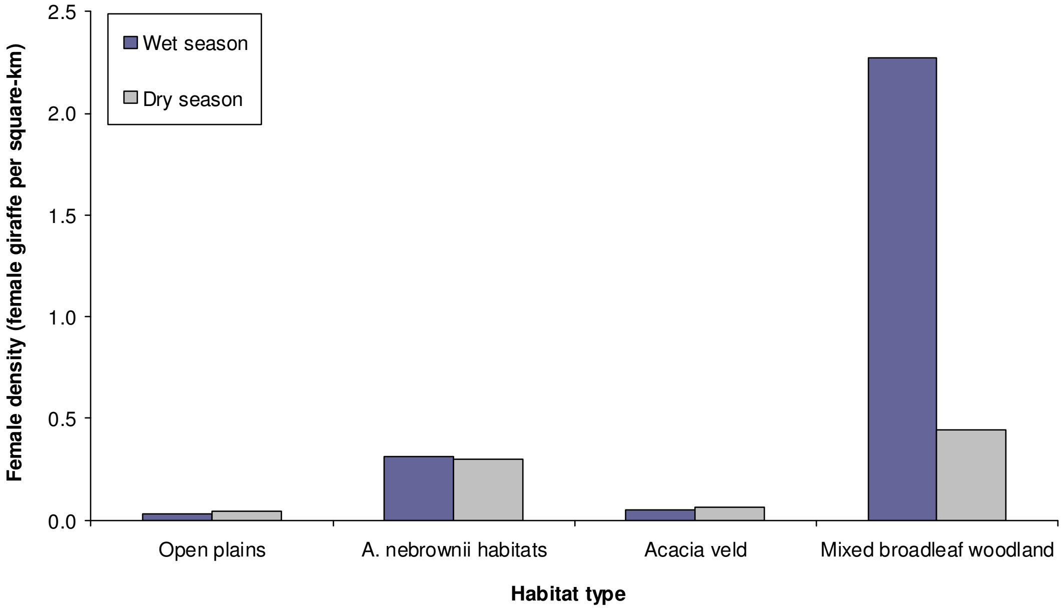


Figure 3.10. Estimated female densities (per km^2) in habitats for which data were available in both the wet season (Mar-May and Oct-Dec) and dry season (Jun-Sep). Overall female density for the study area was about 0.14/km^2 in the wet season and 0.13/km^2 in the dry season.

Table 3.3. Summary of results, relating observed female group sizes and estimated densities to predictions.

Aggregations expected:		**Observed?**
Wet season (Oct-May)	*C. alexandrii* shrub savannah (C)	-
	Mixed broadleaf woodland (G)	Large groups and high density
	A. nebrownii habitats (B, I, J)	Large groups in B; high density
	Acacia veld (E)	Large groups, but low density
Dry season (Jun-Sep)	*A. nebrownii* habitats (B, I, J)	Large groups in B; high density
	Mixed thorn veld in September (F)	-
No aggregations expected:		
Year-round	*Colophospermum mopane* habitats (D, H)	Small groups and low density
Not predicted, but observed:		
Wet season (Oct-May)	Mixed thorn veld (F)	Large groups
Dry season (Jun-Sep)	Open plains (A) near waterholes	Large groups

3.4.4 The effects of water availability on female movement and water use

3.4.4.1 Rainfall and waterhole use

Giraffe use of perennial waterholes was found to be 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. The monthly percentage presence of giraffe at perennial waterholes differed between the two field seasons (N = 8 months, Pearson's r = -0.591, P = 0.123) because of differing rainfall patterns. In particular, there was a much higher presence of giraffe at perennial waterholes in October, November and December in 2005 than in 2004, due to the later start to the rains in 2005 (Figure 3.11).

In March, when giraffe were never seen at perennial waterholes, their presence at seasonal waterholes was at its greatest, at 17.6% of observer visits, whereas in months without rain or any remaining surface water (July-September), giraffes were present at seasonal waterholes on only 1-5% of visits (Figure 3.12). It is assumed that waterhole use in January and February resembles that of March, as rainfall in these two months usually exceeds or matches that of March.

3.4.4.2 Predictability of occurrence of females and males at perennial waterholes

Females were almost twice as likely to be present at waterholes during the dry season as during the wet season (16.1% presence and 8.9% presence respectively). In 2005, during the driest months in terms of water availability (July-September) and in the early summer months (October-December), female giraffe were significantly more likely to be found at perennial waterholes than at dry seasonal waterhole sites (X^2 = 10.525, df = 1, P < 0.0001; X^2 = 16.448, df = 1, P < 0.0001, respectively). During the drier months, occurrence at dry seasonal waterholes should reflect the chance of encountering females at any random location in the study area. From March to June, this difference was not statistically significant (X^2 = 0.506, df = 1, P = 0.48): females were equally likely to be encountered at seasonal waterholes as at perennial waterholes.

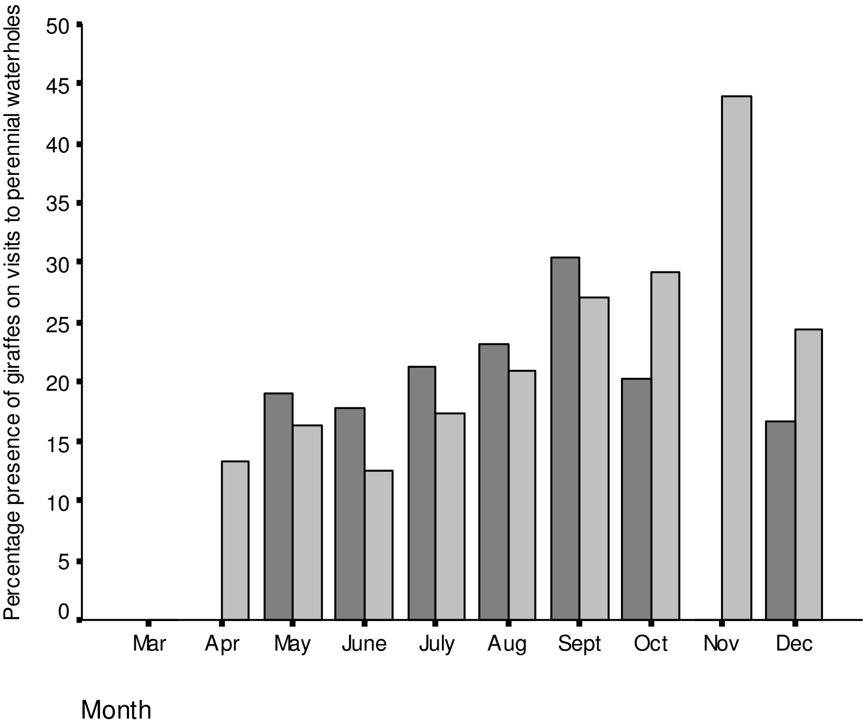


Figure 3.11. Occurrence of giraffe at perennial waterholes, as defined by the percentage of visits by the observer on which giraffe were present. Dark grey bars: 2004; light grey bars: 2005.

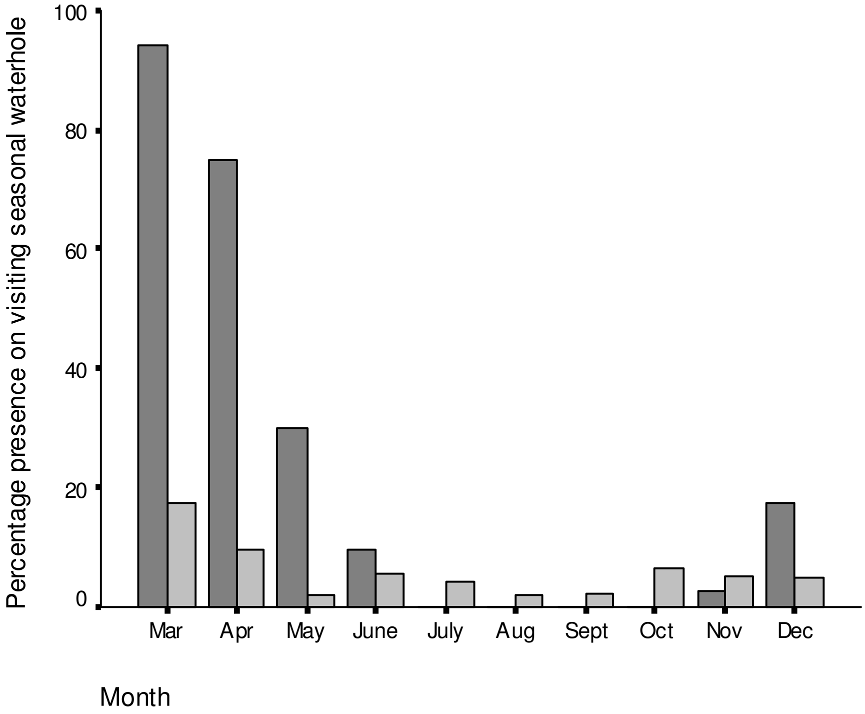


Figure 3.12. Presence of giraffe and water at seasonal waterholes in 2005. Light grey bars: percentage of visits by observer on which giraffe were present; Dark grey bars: percentage of visits on which water was found in the seasonal waterhole.

When females were present at perennial and seasonal waterholes holding water, dark males were no less likely to be present during the wet season, when water availability was widespread (dark male present on 26% of occasions when females present), than during the dry season when water availability was more restricted (dark male present on 25% of occasions when females present; $X^2 = 0.572$, N = 100, df = 1, P = 0.45).

3.4.4.3 Group size in relation to waterholes

Mean female group size at perennial waterholes did not correlate with mean female group size away from waterholes, month for month (Spearman's rho = 0.251, N = 9, P = 0.515). However, there was no significant difference in female group size between groups seen at perennial waterholes and groups seen elsewhere over the whole year (Mann-Whitney U = 45473, N = 801, P = 0.586), or during any single month of the year (after a Bonferroni correction for multiple tests: P > reduced alpha value of 0.005 for each of the ten months; Figure 3.13).

Neither were female groups larger closer to perennial waterholes than further away, when all sightings were examined (comparison made at 2 km). However, once sightings were divided up according to the nearest perennial waterhole, groups were found to be larger closer to certain waterholes, but not others. The clearest trend was for Ombika, where female group size was slightly, but not quite significantly, larger closer to the waterhole (Mann-Whitney U = 1087, N = 124, P = 0.053), and declined with distance from the waterhole (Figure 3.14). This trend was evident in both the wet and dry season, probably due to the presence of preferred foods (e.g. *Combretum imberbe* and *Terminalia prunoides*) in the broadleaf woodland that is restricted to within about 2 km of Ombika waterhole.

Female group size was actually significantly smaller within 2 km of Okaukuejo waterhole (Mann-Whitney U = 3889, N = 211, P < 0.05). Okaukuejo is surrounded by important patches of *A. nebrownii* and Acacia veld, but unlike Ombika these preferred habitats are not restricted to the immediate area surrounding the waterhole.

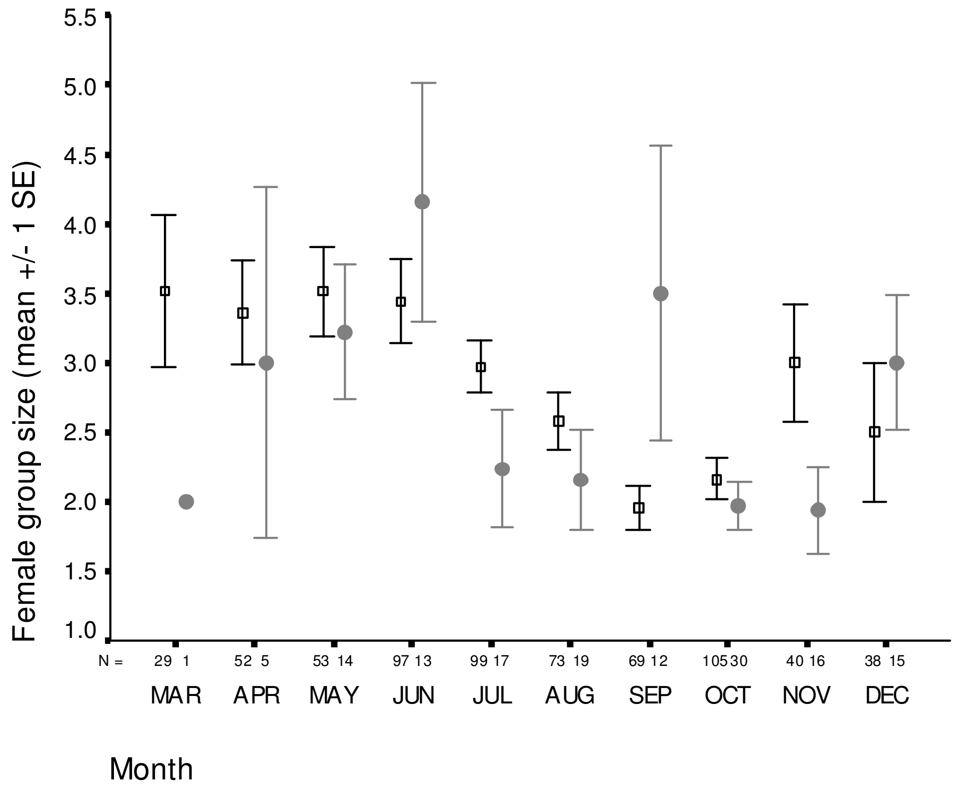


Figure 3.13. Mean monthly female group size (± 1 SE) in all groups that included females, at waterholes (filled grey circles) and away from waterholes (empty black squares).

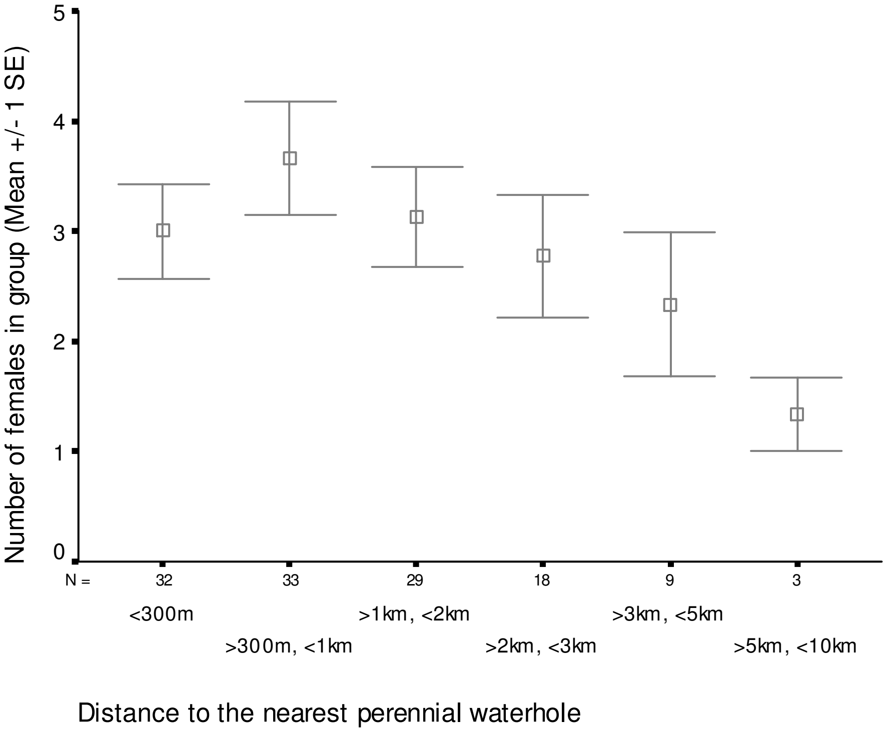


Figure 3.14. Mean female group size (± 1 SE) in female-inclusive groups at different distances from Ombika waterhole.

3.4.4.4 Drinking, and time spent at waterholes

Typically, giraffe took about 20 minutes to reach the water's edge after arriving within the vicinity of a waterhole (within 300m of the water's edge, or within the clearing around the waterhole). Among adults, this time was shortest for females (median = 16.0, range: 1.0 – 142.7, N = 23), slightly longer for pale males (median = 22.0, range: 4.0 – 49.0, N = 18), and slightly longer still for dark males (median = 23.8, range: 3.5 – 127.5, N = 12). Once they were at the water's edge, they began to drink within a few minutes (median = 1 minute), and typically left the water's edge less than 10 minutes later (median = 8 minutes). In all, they spent just over half-an-hour (median = 34 minutes) in the vicinity of a waterhole, although this time was considerably shorter if the giraffe did not drink (median = 29 minutes). Overall, adults spent more time at waterholes than did sub-adults, and males spent more time at waterholes than females, with dark males staying at waterholes the longest (Figure 3.15).

On ten occasions, all in mixed groups, individual giraffe were observed to leave the water's edge, only to return again later. Adult females invariably drank the second time, and three of five had drunk on the first visit as well. Their return is suspected to have been necessary because they were harassed by males during their first visit. Four of five adult males did not drink on at least one of their two visits to the water's edge. Their repeat visits to the waterhole seemed to have been driven by the presence of females, and the opportunity to test their oestrus condition.

Giraffe appeared to occasionally use waterholes at night, but with a much lower frequency. During two 24-hour waterhole watches, only one adult male giraffe was seen at night, compared to twelve giraffe during the daylight hours. This male was also even more wary than during the day. He was first seen at 21:30, but did not approach the water's edge (possibly because a hyena was present) and left 15 minutes later. He only drank after returning to the waterhole two hours later, and then waited 40 minutes before approaching the water to drink. He left only six minutes after he started drinking.

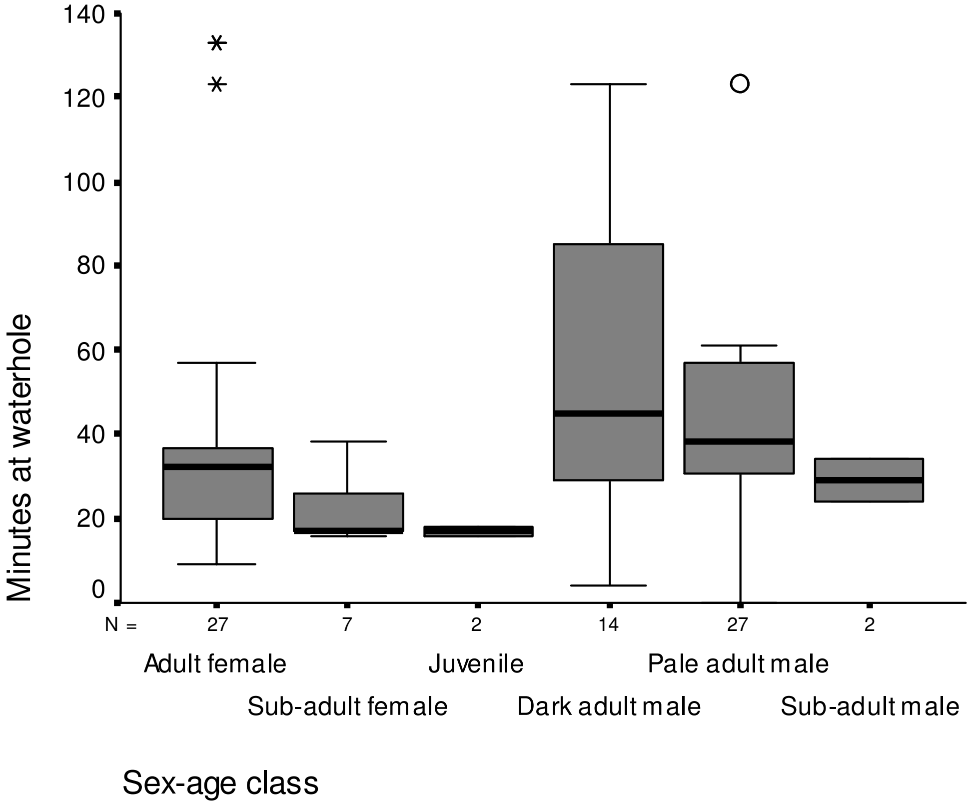


Figure 3.15. Duration in minutes (boxes represent the median and upper and lower quartiles) spent at a perennial waterhole in a single visit by giraffe of different sex-age classes (from arrival within 300m of the waterhole, to leaving beyond 300m).

3.4.4.5 Evidence from waterhole use of sex differences in habitat use

Different age and sex categories of giraffe do not frequent the different waterholes equally. For example, juveniles were never seen at Aus or Charachas although they made up 3-10% of sightings at other waterholes. Furthermore, Olifantsbad and Charachas diverged significantly from the overall distribution of observed sex and age classes at waterholes ($X^2 = 19.88$, df = 6, $P < 0.005$, $X^2 = 113.05$, df = 6, $P < 0.001$, respectively), due to fewer adult females and more adult males using these two waterholes.

3.5 Discussion

3.5.1 Food resources and habitat selection

The widespread *Acacia nebrownii* constituted the most important browse species throughout most of the year for both sexes. Seasonal variation in food selection reflected tree phenology, and particularly production of flowers, pods or fruit and new leaves. Females were more selective in their choice of food plant than males, who browsed more uniformly on a wider diversity of species. During the wet season, species browsed included a large proportion of deciduous broadleaf species, such as *Combretum imberbe*, and for females *Terminalia prunoides* and *Catophractes alexandrii* as well. At the end of the dry season, when food was otherwise scarce, the newly-produced shoots and leaves of *Acacia tortilis* became an important food source.

Female groups were generally larger overall when food was more widely abundant, in the wet season, as has also been noted by Ginnett and Demment (1997) in a Tanzanian population. Maximum group sizes may have been limited by restricted food availability in the dry season (Jarman 1974). Densities of females were greatest in one of the most spatially restricted habitats, mixed broadleaf woodland, throughout the year, but especially in the wet season. Large groups of females also occurred in acacia veld toward the end of the year and in *A. nebrownii* thickets at the height of the *A. nebrownii* flowering season in the dry season. Densities were not as high in these habitats as in mixed broadleaf woodland, as they occur more widely throughout the study area. However, female densities were higher than the overall study-area density throughout the year in habitats comprising both mopane and *Acacia* species. In mopane habitats that did not include *Acacia* species, female densities and group sizes were always very low.

These mopane habitats were avoided by both sexes, but most by females, and least by males in bachelor groups. *Colophospermum mopane* was generally avoided by females as a food plant when a choice of food was available, and this represented the clearest sex difference in food selection. The avoidance of *C. mopane* as a browse species if other food plants are available, and of mopane veld habitat, has previously been noted by Dagg and Foster (1982), Oates (1972), and Fennessy (2004).

Differences in feeding preferences between size-classes of males were not evident, although samples sizes were small. Thus, observed sex differences in choice of food could not be attributed to differences in energy requirements associated with the larger size of mature males (e.g. forage selection hypothesis for sexual segregation (Ruckstuhl & Neuhaus 2002)). However, differences in choice of food may have reflected differences in feeding strategy (e.g. activity budget hypothesis (Ruckstuhl & Neuhaus 2002)). Instantaneous behavioural observations suggested differences in diurnal activity budgets during part of the year. Results indicated that while food is scarce in the dry season, adult males and females must spend similar amounts of time browsing. But when high quality browse is abundant in the wet season, females make the most of the abundance by continuing to dedicate the same proportion of the day to browsing and thus maximising their intake, whereas adult males can afford to reduce their browsing time and dedicate more time to other activities (e.g. Ginnett & Demment 1997). The same seasonal pattern was found by Pellew (1984a; 1984b) in the Serengeti NP. This corresponds with males adopting a ‘time minimiser’ strategy when food abundance permits (Schoener 1971; Ginnett & Demment 1997; Fennessy 2004), while females maximise their total energy and nutrient intake year-round (Pellew 1984b; Ginnett & Demment 1997).

With reduced browsing time, males could still optimise their energy intake by feeding in taller patches, on tree species with higher leaf biomass; available biomass density tends to increase with canopy height, and is greater for broad-leaf species than for the compound-leaf acacias (Pellew 1983a; Woolnough & du Toit 2001). Furthermore, there is some evidence to suggest that giraffe feeding efficiency increases with height, particularly for males (Young & Isbell 1991). *C. mopane* may satisfy these height and biomass criteria better than other available species: *A. nebrownii* and *C. alexandrii*, for example, are shrubby trees about 2-3 m in height, with small leaves and thorns or spines (which increase handling time and reduce bite size (Pellew 1984b)), whereas *C. mopane* can form medium-size trees of 3-5 m, with large leaves and no thorns. Males fed low (below the height of the base of the neck) more than 50% of the time in all habitats with substantial proportions of *A. nebrownii* or *C. alexandrii*, but only 16.7% of the time in mopane veld. Males also showed a greater preference for the taller tree species overall (*A. nebrownii* was consumed less often by males than by females, and the second most frequently browsed species was *A. tortilis* for males, and C. *alexandrii* for females).

Sex differences in food and habitat selection could also be explained by additional constraints on females (e.g. predation risk hypothesis (Ruckstuhl & Neuhaus 2002)). Females not only avoided feeding on *C. mopane*, but also avoided habitats comprising a large proportion of *C. mopane*, and females and juveniles were seen less at waterholes in areas dominated by mopane veld (Aus, Olifantsbad and Charachas waterholes).

Sex differences in giraffe habitat use are usually characterised by a preference by females for more open habitats with shorter trees (Foster 1966; Foster & Dagg 1972; Pratt & Anderson 1982; Young & Isbell 1991; Ginnett & Demment 1999). This has been attributed to a female reproductive strategy explained by the predation risk hypothesis, whereby females trade off foraging benefits for habitats with reduced predation risk for their offspring (Young & Isbell 1991; Ginnett & Demment 1999; Ruckstuhl & Neuhaus 2002). Giraffe juvenile mortality can be very high, exceeding 50% within the first year in some areas (e.g. Foster & Dagg 1972; Pellew 1983b).

Visibility is reduced in mopane veld, and accordingly adult females spent a greater proportion of time vigilant in mopane-rich habitats than in other habitat types (5.5% of 163 observations in D, H and J habitats, vs. 2.5% of 1083 observations in all others). When accompanied by juveniles, adult females were most vigilant in mopane veld and mixed thorn veld, and were least vigilant in Acacia veld, which was often very open, and *Catophractes* shrub savannah. However, the predation risk to giraffe in Etosha seems to be very low. During a four-year study during which lions were followed closely for a total of 3134 hours, they were observed to hunt 833 plains ungulates, of which they killed 117, but hunted only 5 giraffe and killed none (Stander 1992). During this study, only two giraffe carcasses were found within the study area that appeared to be killed by lions.

Alternatively, pregnant or lactating females might avoid feeding on species high in secondary chemical components such as tannins and polyphenolics, which disrupt digestion and may be harmful if passed on through their milk to their calf (Macala *et al.* 1991; Styles & Skinner 1997; Caister *et al.* 2003). This might explain the avoidance of *C. mopane* by females in their choice of food. This hypothesis is supported in this study firstly by the observation that *C. mopane* only figured as highly in female diets as in males' during the months of March and April, when the protein content of mopane leaves is highest and condensed tannin levels are lowest (Styles & Skinner 1997). During the rest of the year, when females were seen in mopane veld, they appeared to be using it for shade rather than as a source of food. Furthermore, on examining feeding observations of mothers of calves of estimated birth-date (see Chapter 4), *C. mopane* only constituted more than 5% of feeding observations for these females after six months post-partum, by which time calves should be feeding regularly on solid foods (Dagg & Foster 1982).

The observed sex differences in habitat use would explain the discrepancy in numbers of sightings of the two sexes (males: 1528; females: 2329). The study area was centred on the more open and species-rich habitats favoured by females (*A. nebrownii* shrubland, *Catophractes* shrubland, acacia veld, mixed broadleaf woodland), while mopane veld, which females tend to avoid, was located predominantly on the south-western and south-eastern edges of the study area. Foster (1966) also found that the preference of males for less open habitats tended to skew the apparent sex-ratio in favour of females, even though the sex-ratio of 'known' individuals was almost even.

Habitat selection ranks of lone males correlated with those of females, whereas those of males in bachelor groups did not. This suggests that individual males leave bachelor groups to search for females. In doing so, they move out of habitats avoided by females into habitats preferred by females. This is further supported by the greater use of open plains by lone males than males in bachelor groups. Because of a lack of food resources on open plains, giraffe should traverse the plains primarily as a means of getting from one resource patch to another, and males actively seeking potential mates would have the greatest need to travel between resource patches. Furthermore, visibility (i.e. the ability to locate giraffe from a distance) is greater on open plains, relative to those habitats preferred by males in bachelor groups.

3.5.2 Waterholes

Where surface water is not available throughout the year, giraffe can be almost completely independent of drinking water (e.g. Fennessy 2004). However, as the recent installation of artificial water points in north-western Namibia has demonstrated, even desert-adapted giraffe will switch to drinking regularly when water becomes readily available (Fennessy 2004). In Etosha, where water is provided throughout the year, giraffe were seen not only to use waterholes regularly, but to go out of their way to access them, especially in the dry season. One waterhole, Okondeka, is on the edge of the pan and is surrounded by extensive grass and low-shrub plains almost entirely devoid of trees. On one occasion, a group of females were seen to walk 10 km across these open plains to Okondeka. They later walked the same distance back across the plains to the tree savannah they had left over five hours earlier.

In the rainy season (especially March and April), the abundance of water in seasonal waterholes (man-made gravel pits and natural depressions), puddles on the roads, and in new vegetative growth enabled giraffe to be largely independent of perennial waterholes. During the wet season giraffe still drank, but preferred seasonal water sources to perennial waterholes. Auer (1997) also found that during the rainy season, wildebeest and zebra in Etosha drank exclusively from seasonal waterholes. In both cases, this may have been because they were more widespread and readily available than perennial waterholes and generally held water of good quality (low salinity (Auer 1997)), or possibly because predation risk was lower at seasonal waterholes; while lions were observed at perennial waterholes on 2% of 750 visits (approximately one visit to a perennial waterhole each month), they were never seen at seasonal waterholes (452 visits).

During the wet season, giraffe were no longer seen in the vicinity of Okondeka waterhole, although they were still seen in the Acacia veld beyond the plains.

Similarly, in Botswana, giraffe have been found to avoid the Nxai Pan during the wetter months, due to the widespread availability of surface water and food elsewhere, whereas grazing species (e.g. gemsbok, zebra) were drawn to the pan during the same period (Ritter 1993).

During the drier months (June to September), large groups of females were relatively common in open plains surrounding waterholes. However, a perennial waterhole only had a significant concentrating effect on females if its location coincided with that of another spatially limited resource (e.g. mixed broadleaf woodland at Ombika), resulting in female groups being larger closer to the waterhole. Therefore, although giraffe movements were not restricted by water availability, their use of certain areas (specifically open plains in the dry season), and their distribution within a spatially restricted habitat (mixed broadleaf woodland), was affected by the limited availability of permanent water.

3.5.3 Potential for mate monopolisation

Overall, females were found in the smallest groups during the late dry season, from August to October. Female densities were highest in mixed broadleaf woodland throughout year, and especially during the wet summer months (October to May). Females also concentrated to a lesser extent in *A. nebrownii* habitats throughout the year, but especially during the *A. nebrownii* flowering season. Habitats containing *A. nebrownii* were widespread, accounting for over 20% of the surveyed study area, whereas mixed broadleaf woodland was more spatially restricted, accounting for less than 2% of the study area.

Therefore, female spatial predictability should be greater in the wet season, when females concentrate in the small patch of mixed broadleaf woodland, than in the dry season. The profitability for a male of searching for females in broadleaf woodland should therefore be high throughout the year, but especially between October and May. Male potential for monopolisation also increases as females become more spatially clumped and predictable (Emlen & Oring 1977), so is predicted to be greater during the wet season, when females are spatially more clumped and predictable, than during the dry season. Potentially, it could be profitable for males to attempt to defend areas (i.e. resource defence) within the mixed broadleaf woodland, as female densities, and thus predictability, are consistently high.

Although they do not generally gather in larger groups at or near waterholes, females occur more predictably at waterholes than elsewhere during the dry season, and large groups are common near waterholes in the dry season. This could offer males an opportunity to reduce their search-effort by focussing on perennial waterholes to intercept females, potentially resulting in temporary defence of waterholes (as a resource that concentrates females). It was predicted that this would result in dominant males consistently excluding subordinates from mating opportunities at waterholes, through an increased likelihood of successfully intercepting females as they congregate to drink, and displacing any subordinate males present.

However, it was assumed that perennial waterholes would only be able to fulfil this function in the dry season, as water is no longer a limited resource in the rainy season. In the wet season, water is widely available in hundreds of seasonal waterholes and natural depressions (over 70 were identified, but no doubt many exist away from the roads). As a result, female aggregations will be less likely to occur at any one water source, and dominant males may no longer be able to maintain a monopoly on matings by locating female groups and excluding subordinate males. For example, it was expected that subordinate males would have a greater chance of encountering undefended females at water during the wet season. Surprisingly though, it was found that dark males were no less likely to be present when females were at water-holding waterholes in the wet season than in the dry season.

4 GIRAFFE BREEDING SEASONALITY

4.1 Introduction

In most parts of their range, giraffes do not have a clearly delimited breeding season (e.g. Pratt & Anderson 1982). Indeed, an absolute seasonal breeding peak in giraffe is unlikely, because gestation is longer than twelve months, and females usually conceive between three and nine months after giving birth (Foster & Dagg 1972; Pellew 1983b; Bercovitch *et al.* 2006). In order to benefit from calving synchrony (e.g. Estes 1976), females would have to trade off the cost of further delaying reproduction (resulting in a consistent nine-month interval between parturition and subsequent conception), which might reduce their reproductive potential (Sinclair *et al.* 2000).

As it is, parturition occurs during all months of the year, although more or less distinct peaks in calving have been recorded (Foster & Dagg 1972; Berry 1973; Hall-Martin *et al.* 1975; Nje 1983; Pellew 1983b; Scheepers 1991). Calving is relatively evenly distributed in equatorial latitudes, where there are two rainfall peaks, but a calving peak is more pronounced in the more seasonal southern latitudes where it coincides with the rainfall peak (Hall-Martin *et al.* 1975). For example in a population of giraffe in the eastern Transvaal in South Africa, a peak in conceptions (60% of 123 calves) was noted between December and March, during the wet period, which resulted in a calving peak from March to June, immediately after the peak rainy season (Hall-Martin *et al.* 1975). Hall-Martin *et al.* (1975) attributed this correspondence between rainfall and conceptions to a stimulus acting on female giraffe via the high nutritional value of the vegetation. Berry (1973) also observed a calving peak near the end of the rains in Luangwa Valley in Zambia. In the northern Namib desert, Scheepers (1991) found a calving peak in the warm wet period (January-March), but this was based on only twelve calves born during his study.

These patterns in calving suggest that giraffe are able to obtain sufficient dietary nutrients and energy for reproduction throughout the year (Pellew 1984b), but that there may be benefits in calving at certain times of year where rainfall is more seasonal. Pellew (1984b) estimated female energy requirements in relation to reproductive condition. He envisaged energy expenditure being greatest immediately post-partum due to the complete dependence of the calf on rich milk during the first couple of months, decreasing steadily as the calf grows and lactation declines. He estimated that females should only experience a deficit in their energy balance if the immediate post-partum lactation phase coincides with a period of food scarcity, such as the dry season (Pellew 1984b).

Therefore, where rainfall and food production are seasonal, those females that calve during a period of sustained abundance of high quality food should be at a selective advantage; they would experience relatively smaller costs of lactation, and would be better able to provide milk of sufficient quantity and quality to sustain their calf’s rapid growth (Pellew 1984b). Indeed, giraffe breeding phenology (monthly distribution of calf births) in the Serengeti NP, Tanzania, has been demonstrated to be in phase with varying protein availability rather than total browse biomass (Sinclair *et al.* 2000).

Consequently, with a fourteen-and-a-half to fifteen month gestation period (448 days (del Castillo *et al.* 2005), 457 days (Hall-Martin *et al.* 1975)), females should ideally conceive fifteen to seventeen months (which corresponds to three to five months) before the peak in high quality food availability. High quality food should also be available, at a sufficiently low height, for calves beginning to wean, a few months after birth. Calves have been recorded as starting to taste solid food at about three weeks, beginning to consume solid food regularly and to ruminate at between three weeks and four months, and as being fully weaned at around eight months (Dagg & Foster 1982).

4.2 Aims

This chapter aims to test the following hypothesis and predictions:

Hypothesis: Giraffe breeding seasonality is driven by seasonality in rainfall and food availability. Thus, I predict that:

- A similar seasonal breeding peak will be found in Etosha NP as in the South African Lowveld (Hall-Martin *et al.* 1975).
- The peak in conceptions will also correspond with the rainfall peak.
- The peak in births will resultantly correspond with a peak in availability of high quality (protein-rich) foods.

4.3 Methods

4.3.1 Estimates of calf age and birth-dates

Ages and birth-dates of calves were estimated to the nearest month. Calves with horns still bent forward or flattened against the head, and tail still not straightened, were taken to be less than one month old (Dagg & Foster 1982; Skinner & Smithers 1990). Calves with the umbilical cord still attached were taken to be up to four months old (Hall-Martin *et al.* 1975). In addition, heights of calves were measured using the photographic technique described in Chapter 2. These estimated heights were compared to an age-height chart derived from Pellew (1983b), scaled, for males, to the maximum height estimation from the study population (the maximum female height encountered in Etosha did not differ from Pellew's, at 4.21m compared to his 4.22m, whereas the maximum male height was only 4.76m compared to his 5.06m). Ages of calves for which heights were not available were estimated based on general appearance relative to that of calves of known or estimated age (using mane length, coat texture, and body proportions).

4.4 Results

Young calves were seen all year round, but only six were seen within one month of birth. Birth-dates (to the nearest month) were estimated for 40 calves first seen when younger than one year old. Based on only those calves estimated to have been born in the 24-month period from October 2003 to September 2005, 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 more than 50% of births (21 of 40) were estimated to have occurred in the four peak months. Assuming a fourteen-and-a-half to fifteen month gestation (448 days (del Castillo *et al.* 2005), 457 days (Hall-Martin *et al.* 1975)), this yields a conception peak between December and March, with the greatest conception rate in February, and a lull between June and September (Figure 4.1). This distribution is significantly different from an even distribution across the year (Dec-Mar versus Apr-Nov: $X^2 = 6.613$, df = 1, $P < 0.02$).

The conception peak corresponds with the annual rainfall peak (about 80% of the year's rain falls between December and March), and the lull in conceptions corresponds with the driest time of year (less than 1.5% of annual rainfall falls between June and September; Figure 4.2). Indeed, monthly conceptions were significantly correlated with mean monthly rainfall for the area (averaged over the two years; Spearman's rho = 0.853, N = 12, $P < 0.001$). Monthly mean female group size (Chapter 3) correlated with the estimated monthly share of yearly births (Spearman's rho = 0.803, N = 10, $P < 0.01$), both being greatest between March and June before decreasing towards the end of the year.

Calves were seen to browse occasionally from the age of two months (N = 3), and to browse regularly from seven months, predominantly on *A. nebrownii* (55% of 22 feeding observations of calves aged 7-12 months). Mothers of calves whose age had been estimated were found to be browsing on the largest percentage of observations (56% to 75% of 15 to 18 sightings per month) during the period one to three months after parturition (browsing accounted for between 27% and 47% of observations in all other months from zero to twelve months post-partum). This three-month period may represent the time during which energy demands, due to lactation, are greatest.

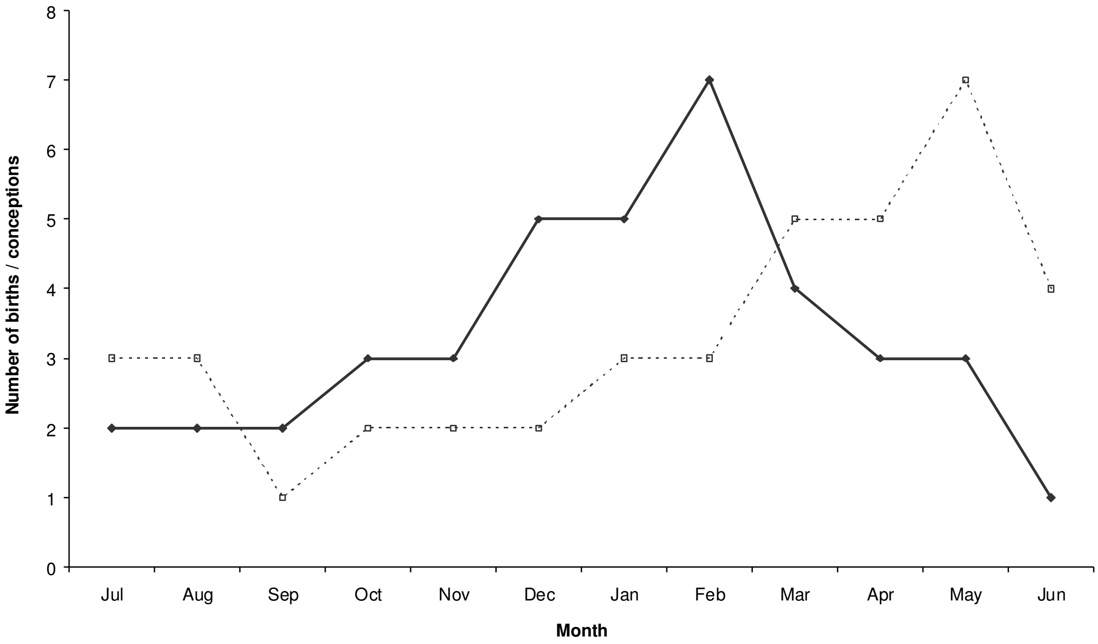


Figure 4.1. Estimated peaks in calving (dashed line) and conceptions (solid line) in the study area, based on forty estimated calf birth dates.

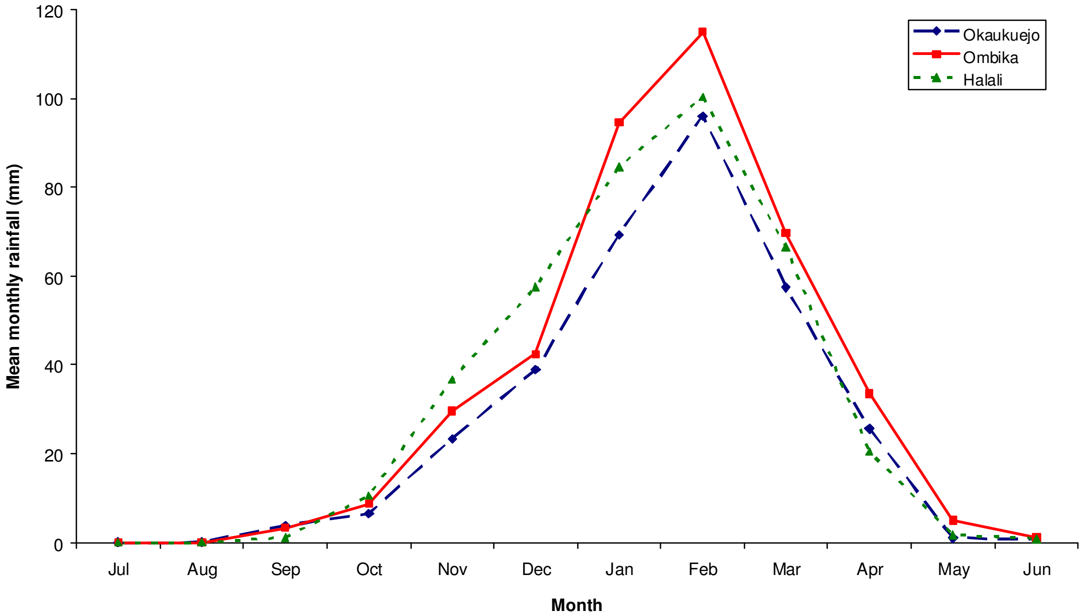


Figure 4.2. Monthly rainfall, averaged over a 29-year period for three weather stations in or near the study area (data provided by W. Versfeld, Etosha Ecological Institute, Okaukuejo, Namibia).

4.5 Discussion

The observed calving peak does not match that found by Scheepers (1991) in the northern Namib desert (calving peak between January and March), but corresponds very closely with that described by Hall-Martin *et al.* (1975) in the giraffe population in the eastern Transvaal in South Africa. The mismatch with findings from elsewhere in Namibia may be due either to Scheepers' relatively small sample size (12 calves, Scheepers 1991), or to differences in tree phenology and seasonality of key nutritional resources in the two areas.

The observed correlation between monthly mean female group size and monthly proportion of annual births suggests that females may form larger groups between the months of March and June partly as a predator defence strategy to protect their young calves while they are at their most vulnerable (e.g. Jarman 1974).

4.5.1 Possible explanations for the observed breeding seasonality

4.5.1.1 Explanation 1: Lactation costs driving calving seasonality

If post-partum lactation costs (e.g. Pellew 1984b) are driving breeding seasonality, then the first few months after calving (or months one to three post-partum, based on feeding observations, see above) should coincide with a peak in food quality or quantity (e.g. Sinclair *et al.* 2000). The observed calving peak suggests that females may face the greatest costs of lactation between April and September. Thus, many females would face high energy demands at the very end of the period of peak food availability and quality; in southern Africa, the protein content of giraffe browse is greatest during the rainy season, between November and March (Hall-Martin & Basson 1975), when all trees are in leaf, and many also have flowers, fruit or pods (see also Chapter 3, Figure 3.1). Specifically, fruiting of trees generally occurs two months after either flowering (Scholes *et al.* 2003) or the peak rainfall (Mduma *et al.* 2006), which in the study area usually occurs in February (W Versfeld, personal communication), and *Acacia* pods, for example, are highly nutritious, often fed to livestock as a supplement in the dry season (Sikosana *et al.* 2002) or to increase milk yields.

Therefore, a large proportion of females would be facing the greatest costs of lactation at a time when most tree species' leaves were starting to senesce and fall (late-April to early June), and the protein, water and energy content of remaining browse was beginning to decline (Sauer 1983; Fennessy 2004). However, from late-June, another reliable source of food becomes available. Flowers of *A. nebrownii* were abundant across the study area from mid-June to late-August (the much rarer *Gymnosporia senegalensis* also flowered from mid-May to July, and from August, *A. mellifera* and *Albizia anthelmintica* came into flower).

Possibly, *A. nebrownii* flowers are sufficient to sustain females through lactation. Compared with all other tree species in the study area, the flowers of *A. nebrownii* were the single most abundantly produced crop, produced at a time when other foods were scarce or nutritionally of poor quality (e.g. Sauer 1983; Owen-Smith 1992). Habitats including large proportions of *A. nebrownii* were also widespread, accounting for 20% of the surveyed study area (over one third, if open plains were excluded). Moreover, since flushes of flowers occurred at different times in different patches, there was always a new and un-depleted source of flowers for giraffe to move to.

Unfortunately, there is no available information on the nutritional value of *A. nebrownii* flowers. However, since giraffe and other species (e.g. springbok *Antidorcas marsupialis*) feed so keenly on *A. nebrownii* flowers, it can be assumed that their overall nutritional value is favourable; they probably contain relatively high quantities of water and protein, low quantities of fibre, and may contain less tannin than the leaves. In South Africa, flowers of *A. nigrescens* are also produced in the dry season, and giraffe feed prolifically them, despite high tannin levels, possibly because this cost is outweighed by the benefits of the otherwise high nutritional value of the flowers: they contain about 50% more water than leaves, almost twice as much protein and less fibre (Fleming *et al.* 2006). Flowers of *A. tortilis* also contain more water than leaves, but contain *less* condensed tannin (Wrangham & Waterman 1981; Sauer 1983).

Therefore, although the high-cost lactation period for many females would not correspond with the greatest abundance of food in terms of biomass (the peak rainy season), it would coincide with a period of reliable, widespread and sustained abundance of a potentially protein- and water-rich food source. *A. nebrownii* is also a food source that would be available to (and is indeed browsed by) young, weaning calves, as it is a shrubby, multi-stemmed tree, usually only about 2-3m in height.

Conversely, females that calved in the later dry season (August to October) would be at a selective disadvantage, as during these months only a few, rare tree species bear flowers or produce new vegetative growth (e.g. *A. hebeclada*). Water and protein content of giraffe browse plants are lowest during this time (Hall-Martin & Basson 1975; Sauer 1983), and it is at this time of year that some giraffe in the study area appeared to lose condition (see also Chapter 7). Some tree species began to flourish again in October or November, independently of the start of the rains (e.g. *Colophospermum mopane*), but certain preferred browse species (e.g. *Catophractes alexandrii*, *Terminalia prunoides*) did not produce new leaves and flowers until after the first heavy rains (which often do not fall until December or January).

Since a seasonal breeding peak has now been identified in both the South African Transvaal and northern Namibia, it is likely that a seasonal peak in breeding occurs throughout the giraffe's range in southern Africa. Although the geographic range of *A. nebrownii* is limited to the far-north and central-south of Namibia (Curtis & Mannheimer 2005), other *Acacia* species are prevalent throughout the giraffe's southern African range, some providing pods in the late wet season, and others flowering prolifically during the dry season (e.g. Milton 1987; Dudley 1999; Scholes *et al.* 2003). Thus, high quality food sources may be available for females calving during the late wet and early dry season across southern Africa.

In conclusion, the study area calving peak occurs at the end of the productivity peak, but near the start of production of a single alternative source of food that is probably rich in protein and water (*A. nebrownii* flowers). Thus, there is evidence for a calving peak that coincides with the start of a secondary, but reliable peak in food availability, or possibly selection *against* calving just before a period of food shortage or unpredictable food availability (i.e. the late dry season).

4.5.1.2 Explanation 2: Condition-dependent conception driving mating seasonality

Alternatively, it is possible that conception is triggered by the physiological condition of females; females may only be able to conceive when their diet comprises sufficient high quality food, as suggested by Hall-Martin *et al.* (1975). Scheepers (1991) also observed that conceptions in desert-dwelling giraffe in north-western Namibia seemed to coincide with the first flush of new vegetation in the late dry season (October to December) in that region. In the study area, the conception peak (December to March) was found to correspond very well with the rainy season (November to April) and the probable peak in protein content of browse (November to March, Hall-Martin & Basson 1975).

4.5.2 Implications of the peak conception period

According to traditional mammalian socio-ecological models, the potential for polygyny is lowest when females are receptive briefly and in unison, and increases with more asynchronous breeding patterns, although it may decline again as breeding becomes absolutely asynchronous (Trivers 1972; Emlen & Oring 1977; Ims 1988a). With a large proportion of conceptions in the Etosha giraffe population occurring in the wet season, female receptivity will probably remain asynchronous throughout the year, but there will be a greater potential overlap in female receptivity during the wet, high-conception-rate season (Nunn 1999). Therefore, the operational sex ratio (the number of potentially mating males divided by the number of fertilizable females (Emlen & Oring 1977)) will be slightly reduced in the wet season relative to the dry season. As a result of this temporal effect, the potential for polygyny may be greater in the dry, low-conception-rate season (Emlen & Oring 1977).

However, this effect may be counteracted by the spatial effect of female distribution on the ability of dominant males to monopolize females. In non-synchronously breeding populations, spatial effects are often more important in driving variance in male mating success than temporal effects (Nunn 1999). In the study area, females are more aggregated and predictably spatially clumped during the wet (higher-conception-rate) than during the dry (lower-conception-rate) season. As well as increasing the potential for dominant males to monopolise mates, this will also lead to higher encounter rates with females and competitors for all males (Ims 1990). Consequently, it is predicted that in spite of the increased OSR in the dry season, the potential for monopolisation, and frequencies of mating and agonistic interactions, may be increased during the wet (higher-conception-rate) season.

To test for seasonal effects in the subsequent chapters, the year was divided up into two periods, of relatively higher and lower conception rates (though these differ only in degree), based on the estimated conceptions per month:

1) Higher-conception-rate season: October to May (at or above the median of three). This corresponds closely with the wet season (see figure 4.2).

2) Lower-conception-rate season: June to September (below median), which corresponds with the dry season.

5 MALE MOVEMENTS AND MATING STRATEGIES

5.1 Introduction

5.1.1 Giraffe home ranges and movements

Giraffe home ranges generally are non-exclusive, overlapping, and show no evidence of territoriality (Leuthold 1979; van der Jeugd & Prins 2000). Average home range sizes are large, but depend on vegetation structure and food availability, and thus vary widely across the geographic range of the giraffe. Smaller home ranges, as well as higher giraffe densities, lower mobility and more stable groups, are generally found in more heavily vegetated and productive habitats (van der Jeugd & Prins 2000). Sex differences in range size are also less pronounced in such habitats than in more arid environments (Fennessy 2004). The largest mean and individual home ranges have been found in desert environments, where giraffe densities are lowest (largest recorded home ranges: 1,559 km^2 in Niger (Le Pendu & Ciofolo 1999), and 1,950 km^2 in north-western Namibia (Fennessy 2004)). In Tsavo East National Park, where the giraffe density was similar to that found in Etosha NP during this study (0.2 animals/km^2), home ranges averaged 160 km^2, with a maximum of 655 km^2 (Leuthold & Leuthold 1978b).

Male and female mean ranges are often similar within a location, but where giraffe are not restricted in their movements, the maximum male range can be much larger than the maximum female range (e.g. 145 km^2 vs. 82 km^2 in Luangwa Valley NP, Zambia (Berry 1978); 655 km^2 vs. 484 km^2 in Tsavo East NP, Kenya (Leuthold & Leuthold 1978b)). This sex difference in range size is consistent with male roving as the predominant male mating strategy, and a polygynous-promiscuous mating system (Trivers 1972; Clutton-Brock 1989; Schwab 2000).

Range sizes and locations may vary seasonally, as giraffe respond to seasonal changes in food availability by local small-scale migrations (Pellew 1983b; Fennessy *et al.* 2003; Fennessy 2004). For example, in Niger, the mean home range size of the last remaining population of western giraffe (*G. c. peralta*) was 90.7 km^2 in the dry season, but only half that size in the rainy season (Le Pendu & Ciofolo 1999). These seasonal movements often result in clumped distributions and locally high densities of giraffe (Leuthold & Leuthold 1978b).

Male home range size also appears to vary with age. As males mature, they tend to spend progressively less time in mixed groups, less time with individuals of their own age class, and more time wandering alone (Pratt & Anderson 1985). This can result in larger home ranges for mature than for immature males, although home ranges of older adult males may be smaller than those of younger adult males (Leuthold & Leuthold 1978b). However, recent studies of giraffe home range have not explored these individual differences in home range size in any detail, or their potential association with differences in mating strategy.

The majority of giraffe home range estimates have been determined using just field observations of individuals, although more recently, GPS satellite collaring has enabled more accurate home range measures for a very limited number of individual giraffe (Fennessy 2004). However, for studies of range-use of a large number of giraffe, the recording of GPS locations during field observations remains the most practical method.

5.1.2 Giraffe mating strategies

The giraffe mating system is polygynous or possibly promiscuous, with males attempting to obtain as many matings as possible, but with females also occasionally mating with more than one male within an oestrus cycle (Bercovitch *et al.* 2006). Since giraffe group composition changes so frequently, groups are relatively small and home ranges large, it would be uneconomic for males to attempt to defend a herd or harem. Instead, males generally adopt a roaming strategy, whereby they wander over large distances, visiting female and mixed herds in search of potential mates, and temporarily mate-guarding females in oestrus (Dagg & Foster 1976; Leuthold 1979; Pratt & Anderson 1985; Bercovitch *et al.* 2006). Thus, males may converge on areas where females are concentrated by a food resource (e.g. Berry 1978). On locating a receptive female, a male will attempt to court and defend her, following her closely for up to two days until mating is achieved (Leuthold 1979; Pratt & Anderson 1985).

Bercovitch *et al*. (2006) recently summarised the male giraffe mating strategy as one that maximises time spent with receptive females whilst minimising time spent with non-fertile females and searching for females. An individual's mating strategy should be whatever best fulfils the ultimate function of achieving maximum lifetime reproductive success (Thirgood *et al.* 1999). The optimal strategy may differ depending on environmental and social conditions, such as habitat type, resource distribution and female densities (e.g. Dunbar 1982; Gosling 1986; Thirgood *et al.* 1999), and as such may vary across the giraffe's range (van der Jeugd & Prins 2000). For example, it has been proposed that 'pseudo-territorial' resource defence polygyny might occur under special circumstances (van der Jeugd & Prins 2000). It is also possible that where females exhibit seasonal peaks in breeding, such as South Africa (Hall-Martin *et al.* 1975) and Etosha NP (this study), the intensity of mating competition, and the potential for mate monopolisation, varies across the year. Therefore this chapter explores how males respond to changes in female aggregation, and tests whether male movements are driven more by the location of females (rather than food) when the potential for mate monopolisation is higher.

5.1.3 Predictions

5.1.3.1 Home ranges and movements

Because rainfall is relatively low (about 350 mm per annum) and highly seasonal, and food resources thus rather scarce and variable, it is predicted that giraffe home ranges in Etosha will be large relative to those recorded elsewhere (van der Jeugd & Prins 2000; Fennessy 2004). It is predicted that female home ranges will all be of a similar size, regardless of age, and will all encompass a similar range of habitat types, since females move to take advantage of high quality foods as they become available (see Chapter 3). Male home ranges are expected to vary in size with age and social status: home ranges of fully mature males are expected to be larger overall than those of adult females or younger males (e.g. Leuthold & Leuthold 1978b; Cederlund & Sand 1994; Schwab 2000; Fennessy 2004).

Where females are spatially clumped, male success in locating females should be high for all males (Ims 1990), but the potential for monopolisation of mating opportunities will also be high if dominant males can successfully exclude subordinates (Emlen & Oring 1977). Therefore, at times when females are aggregating predictably, dominant males (it was assumed that these would be darker in colouration; this will be verified in Chapter 6) should move from habitats preferred by males into female concentration areas (Gosling 1986), and thus exhibit different habitat use to that of younger or subordinate adult males, who should remain in their preferred habitats.

The habitat in which females aggregate in the wet, higher-conception-rate season (mixed broadleaf woodland; October to May) is more spatially restricted than *A. nebrownii* shrub savannah, in which females aggregate in the dry, lower-conception-rate season (June to September). It is predicted that due to this relatively higher spatial clumping of receptive females, male competition will be greater in the higher-conception-rate season; the potential for monopolisation will be increased, and dominant males should compete to control the female aggregation areas by excluding subordinates from herds and from mating opportunities.

5.1.3.2 Mating strategies

Individuals of different age or social status may adopt different mating strategies, as the potential for mate monopolisation, and possibly reproductive effort, is likely to vary with age and social status (Clutton-Brock *et al.* 1982d; Dunbar 1982; Mysterud *et al.* 2003; Plaistow *et al.* 2004). Firstly, mature males could adopt a year-round roving strategy (Gosling 1986; Forchhammer & Boomsma 1998), whereby they search throughout the year for potential mates by moving to whichever habitats are concentrating females. As such, male home ranges should be large to encompass all of the habitats in which females aggregate throughout the year, but may also include habitats avoided by females if males return periodically to other food sources (e.g. *C. mopane*). Males not actively following females (e.g. young males and bachelor groups) should spend relatively more time in habitats avoided by females, and thus show different habitat selection to females and to dark males throughout the year.

Alternatively, it may only be profitable (in terms of potential matings gained relative to the energy expenditure and risks associated with searching for females and excluding competitors (e.g. Dunbar 1982)) for mature males to compete for receptive females when they are most predictably clumped and easiest to locate (i.e. during the higher-conception-rate wet season, see Chapters 3 and 4). In this case, male home ranges might still be relatively large, to encompass the areas in which females aggregate during the peak reproductive season (i.e. mixed broadleaf woodland). However, dark males should use different habitats to females during the rest of the year when they return to their preferred food sources. Thus, dark males should utilise different habitats to pale males during part of the year (the wet season), but show similar habitat choices to pale males during the rest of the year.

Alternatively, at times when females are most predictably clumped, it may be economical for sexually active males to adopt a temporary resource defence strategy (Owen-Smith 1977; Gosling 1986; Clutton-Brock 1989). In this scenario, seasonal ranges of those males successful in defending temporary 'territories' should be small, and should be centred on female concentration areas (Gosling 1986; Ritter & Bednekoff 1995; Carranza *et al.* 1996). During the rest of the year, these males should range over a much larger area encompassing a greater proportion of habitats in which females do not aggregate. If the defended male ranges are not exclusive, then males that hold them should at least show space-specific dominance (Owen-Smith 1977). Males that adopt this strategy might have the greatest potential to monopolise matings (e.g. Heckel & von Helversen 2002; Hayes *et al.* 2006).

5.2 Aims

This chapter aims to test the following hypotheses and predictions:

Hypothesis 1: Males and females preferentially use different foods and habitats (see Chapter 3), and have different means of maximising reproductive success, with male reproductive success being determined largely by the ability to locate females and compete for mating rights, which involves larger scale movements than the search for resources alone (e.g. food and water). Thus, I predict that:

- Home ranges of mature, dark males will be larger than home ranges of adult females or sub-adult and young adult males.

Hypothesis 2: Dominant males that have a chance of securing access to females for mating leave their preferred habitats to follow females to locate, defend and court those that are receptive. Thus, I predict that:

- Male association with females will be determined by their movements relative to female concentration areas, and will vary in relation to male maturity.
- Males will spend less time browsing and more time in other activities (e.g. walking) when within areas of high female usage than when outside them (e.g. Turner *et al.* 2005).

Hypothesis 3: Due to seasonal variation in resource availability (and thus time spent foraging), female group size and aggregation (see Chapter 3), and in the proportion of females that are receptive (due to a slight breeding season peak, see Chapter 4), the relative costs and benefits of searching for and competing for females will also vary seasonally. As a result, mature males may benefit from seasonally varying their strategy for locating and competing for mates. Thus, I predict that:

- Mature, dark males will be more likely to associate with females when they are aggregating more predictably and receptive females are easier to locate (i.e. during the wet season, when a high proportion of conceptions occur).
- During the wet, higher-conception-rate season especially, dominant males will select habitats where females are aggregating, whereas younger, pale males will show different habitat preferences to both females and dark males.

5.3 Methods

5.3.1 Home range estimations

5.3.1.1 Minimum convex polygons

In keeping with previous studies of wild giraffe, home ranges were estimated using minimum convex polygons (MCPs). This method has fewer assumptions as to how the areas are used by the animals, and generally work better with small sample sizes, when compared to other methods (Ferguson & Elkie 2004). The greatest number of sightings of a female giraffe was 33, and of a male, 22 (due to fewer sightings of males in general).

Previous studies have estimated home ranges based on as few as six (Foster 1966) or nine (Leuthold & Leuthold 1978b) sightings of individual giraffe. Here, I selected giraffe for home range estimation on the same basis as Fennessy (2004) in his recent study of desert giraffe in the north-west of Namibia. After converting coordinates to UTM, 95% MCP home ranges were estimated using all sightings for each individual seen at least 10 times over at least one year (95% MCPs require a minimum of 10 points). For these individuals, sightings from across the entire study period were included, rather than just those within one year, due to small samples sizes (total sightings per individual). Analyses were carried out using 95% MCPs as these are generally considered to better represent the ‘normal’ home range, as peripheral outliers that may represent exceptional excursions outside of the usual range are excluded (Broomhall *et al.* 2003; Lent & Fike 2003; Fennessy 2004).

MCPs were calculated using the Animal Movement extension of Arcview 3.1 (Environmental Systems Research Institute, Hoodge & Eichenlaub, 1997). Parts of a home range that fell on the saltpan were excluded from the home range size since giraffe were never seen beyond the edge of the pan. MCPs that were extremely elongate in shape (long axis more than ten times the short axis) were considered unrealistic and excluded from any analyses. Home range values were logarithm-transformed to permit the use of parametric statistics (t-tests) in analyses of sex and maturity differences in home range size.

5.3.1.2 Female core areas

Core areas (50% fixed kernel areas, with smoothing factor calculated by the default least squares cross validation (LSCV) of locations, (e.g. Kusak *et al.* 2005)) were created for all adult females with at least twelve sightings, to examine male movements relative to approximate areas of greatest female use. It was decided to use a 50% kernel rather than a 50% MCP, despite the small number of sightings, as the latter often resulted in unrealistic (highly elongated) shapes, often along roads, and the kernel method has the benefit of being able to identify multiple core areas (Ntumi *et al.* 2005).

Female core areas that exceeded 50% of their 100% MCP home range were excluded as these were considered to be least informative about actual core areas of use (nine of 54 possible core areas were thus excluded). The remaining female core areas were combined using the Union Intersect function of the Geoprocessing Wizard in ArcView. This produced a single graded core area, with class values representing the number of core overlaps. Since sample sizes (individual re-sightings) were low, and inaccuracies in the calculation of core areas thus inevitable, classes of core overlaps were further pooled into three classes describing area usage by females:
0) Low usage: zero female core areas,
1) Moderate usage: 1-5 female core areas overlapping,
2) High usage: >5 female core areas overlapping.

For all males seen within the study area on more than five days, each observation (the first observation of them each day) was allocated a value indicating the degree of female use at that location (0, 1, or 2, as described above). Differences in group composition, and particularly the number of females that males were associating with, were assessed relative to these values for different age-classes of males. If these core areas are truly representative of areas of intense female use, then males should be found to associate more with females when in areas of high usage, and less when in areas of low usage.

5.3.2 Male habitat selection and female aggregation ranks

If dominant males seek to monopolise access to females, then they should move out of their preferred habitats into habitats in which females are concentrating at times when they are predictably aggregated. To test this idea, male habitat preference indices (PIs, see Chapter 3) were compared to those of females. Solitary dark males and dark males with females were predicted to be found in greater numbers (and thus have higher PIs) in habitats preferred by females, particularly during the wet, higher-conception-rate season. Conversely, PIs of solitary pale males and bachelor groups (including pale and dark males) were predicted to be independent of female habitat-specific densities and PIs, and to also differ from dark male PIs.

Habitat preference indices of dark males (solitary or with females) were also predicted to be greater than habitat preference indices of pale males and males in bachelor groups for those habitats with high female densities (see section 3.4.3.6). Male habitat use and association with females was also explored on an individual level, to highlight possible differences between movements of dominant and subordinate males, using only dark adult males that were seen on more than five days each (N = 24).

It should be noted that preference indices resulted from the division of sightings in each habitat (during the first survey of each road in each cycle) by habitat availability. Thus, any possible inaccuracy in the estimation of the availability of the different habitats for sampling will have been applied equally to all sex-age groups, so will not have affected between-sex comparisons.

5.4 Results

5.4.1 Hypothesis 1: Large male home ranges

5.4.1.1 Cumulative identifications

Differences between male and female movements were first assessed by comparing cumulative identifications of new male and female giraffe within the study area. If females were more sedentary than males, as predicted, then cumulative identifications of new females should have reached an asymptote faster than cumulative identifications of males. Indeed, the rate of increase of new female IDs began to decrease sooner than that for male IDs (Figure 5.1). By the end of the first four months of the study, 75% of all identified females had been sighted for the first time. Larger numbers of new males continued to be encountered throughout the second field season, and 75% had been first sighted only after six-and-a-half months of the field period.

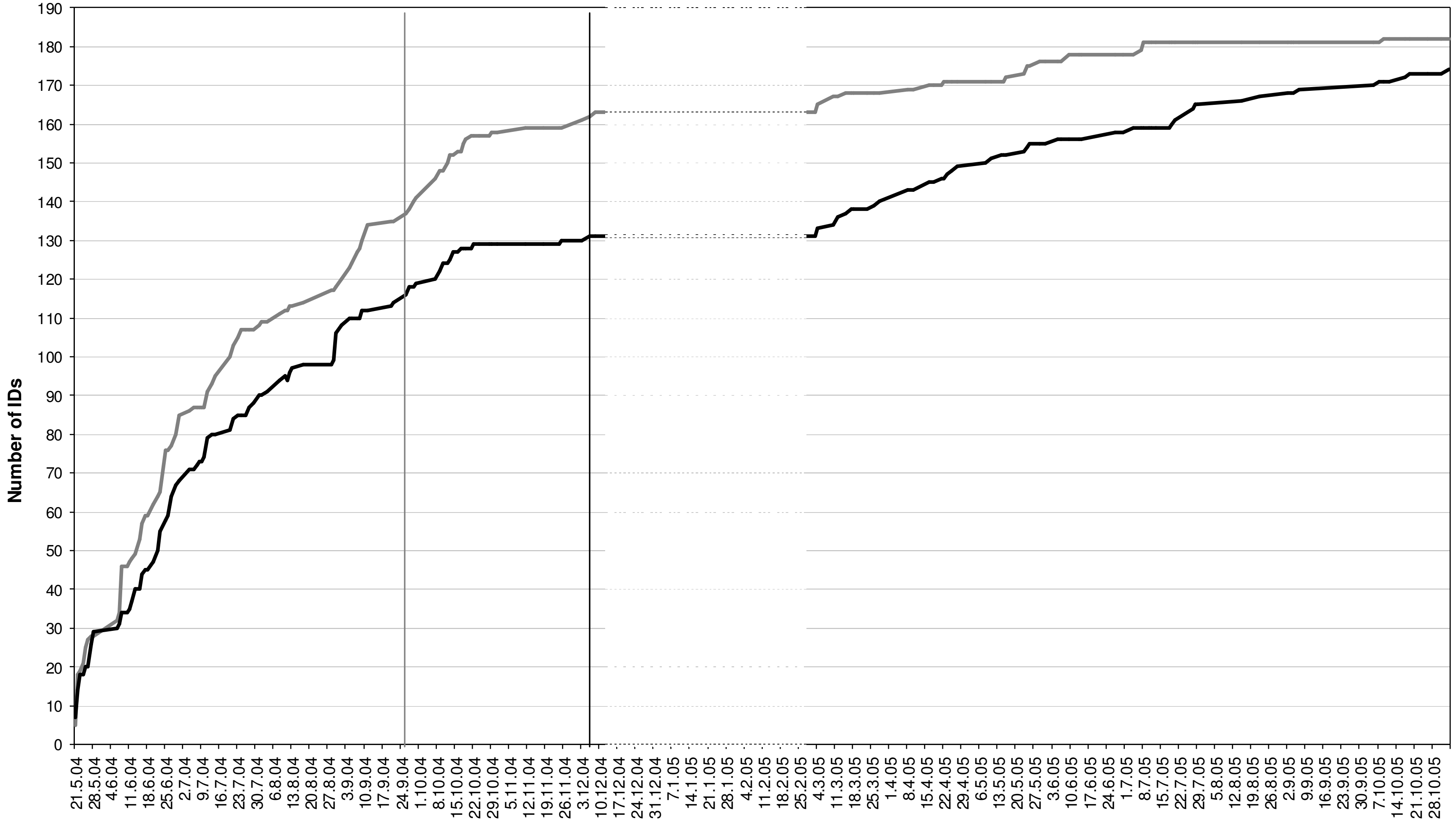


Figure 5.1. Cumulative identifications of new giraffe in the study area. Black line = males; Grey line = females. Vertical lines indicate when 75% of identified individuals had been first sighted. Opaque section indicates period of absence from the study area.

5.4.1.2 Minimum Convex Polygon home ranges

There was no correlation between the number of sightings and MCP size (95% MCPs: r = 0.178, N = 99, P = 0.077). Mean home ranges (95% MCPs) for non-juvenile females were 96.2 km^2 (range: 12.7-352.6 km^2, N = 68), and those of males were typically larger at 148.0 km^2 (range: 2.49-1000.5 km^2, N = 21; Table 5.1). However, the difference between non-juvenile male and female mean home range size was not significant (Student's t = 0.158, df = 87, P = 0.833), nor was the difference between range sizes of adult males and adult females (t = -0.091, df = 65, P = 0.928). Mean and maximum home ranges, particularly of males, were much smaller than those estimated for the desert-adapted giraffe in the nearby Kunene region of Namibia (Fennessy 2004).

Table 5.1. Sample size, mean, minimum and maximum estimated home range sizes (95% MCPs) for this study (Etosha NP), and for comparison, Fennessy's (2004) study of the desert-dwelling giraffe in north-western Namibia.

Study site	Sex-age class	N	Mean	Min.	Max.	SD
Etosha NP, Namibia	**Juveniles**	**10**	**113.8**	**21.0**	**362.4**	**100.7**
	Sub-adult females	19	112.4	28.8	240.8	65.6
	Adult females	49	89.9	12.7	352.6	60.1
	Females	**68**	**96.2**	**12.7**	**352.6**	**62.1**
	Sub-adult males	3	116.4	24.9	254.8	121.9
	Pale adult males	6	87.9	57.9	115.4	27.8
	Dark adult males	12	186.0	2.49	1000.5	288.5
	Males	**21**	**148.0**	**2.49**	**1000.5**	**222.6**
Kunene desert region, Namibia	Juveniles	2	14.5	10.3	18.7	
	Females	16	100.0	8.33	702.1	
	Males	44	355.5	11.5	1773.0	

As predicted, home ranges of sub-adult (maturity classes 2-3) and adult females (maturity class > 3) did not differ in size significantly (t = 1.373, df = 66, P = 0.174), but nor did those of sub-adult and adult males (t = 0.032, df = 19, P = 0.975), nor those of dark and pale adult males (t = 0.282, df = 16, P = 0.781). However, home ranges of males were more variable in size than those of females (see Table 5.1, above). Those of dark males were also more variable than those of pale males, and accounted for the three largest and three smallest male home ranges, suggesting a higher degree of inter-individual variation in ranging behaviour in fully mature males.

Both female and male home ranges overlapped extensively within and between sexes. Every 95% MCP male home range was contained within the combined area covered by all 95% MCP female home ranges (a total area of 898 km^2), with the exception of four dark, mature, but not old males. Between 38% and 48% of their home ranges fell outside the area used by females. Of all the males in their age category, these four were seen with females the least often (less than 33% of sightings), and included the three largest home ranges. Fully mature males (maturity category 5 and above) with small home ranges (less than the non-juvenile male median of 69.4 km^2) were generally seen in larger groups (median = 4) than males with large home ranges (median = 1; Mann-Whitney U = 1550.5, N = 152, $P < 0.001$).

5.4.2 Hypothesis 2: Male movements and activity in relation to areas of high female usage

5.4.2.1 Female core areas

Female core areas (50% kernels) comprised either one (N = 26), two (N = 13), or three (N = 6) parts. In the majority of cases (84.4% of the 45 females), at least one part of the core area included a minimum of one perennial waterhole. In ten cases, the core area encompassed two or more waterholes. All but two of these ten females were not known to have young calves during the study period, whereas the majority of females (eleven of thirteen) known to have a young calf had core areas incorporating only one waterhole or none at all.

The highest overlap of female core areas occurred at or near perennial waterholes, and particularly at waterholes in proximity of preferred food sources. Specifically, ten female core areas overlapped at Gemsbokvlakte, and over fifteen overlapped at both Okaukuejo and Ombika. Ombika waterhole (to the south) is surrounded by mixed broadleaf woodland, Okaukuejo waterhole (in the centre of the study area) is surrounded by acacia veld and mixed thorn veld. *A. nebrownii* thickets extend from east of Okaukuejo to Gemsbokvlakte waterhole to the south-east, and also occur near the dry waterhole, Ondongab (to the east, near the pan, see Figure 5.2 below). Fewer overlaps occurred at Nebrownii waterhole, possibly because, although it is located in an area of *A. nebrownii* thickets, it is near the pan edge and thus on the periphery of most females' home ranges.

No female core areas were found in the mopane veld either on the south-eastern edge of the study area, or south of Okaukuejo and Gemsbokvlakte waterholes (except within 5 km of Ombika waterhole), or to the south-west or west of Okaukuejo. Neither were any core areas recorded on the open plains to the east of Nebrownii waterhole or to the north and far north-west of Okaukuejo.

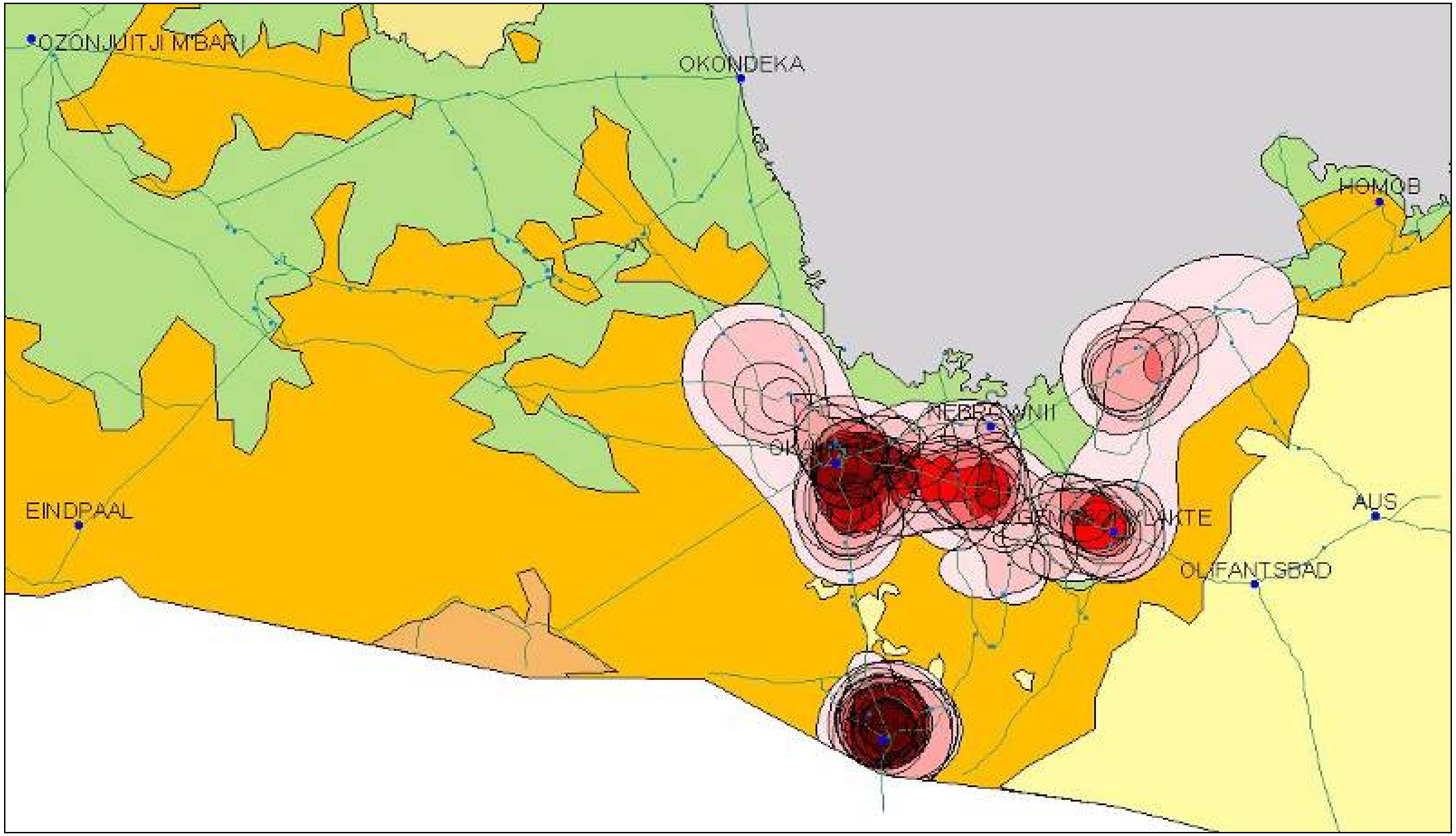


Figure 5.2. The entire study area, with female core areas in pink. Darker areas represent higher core area overlap. Grey area is the pan. Green areas represent predominantly open plains but include some shrub savannah (including *A. nebrownii*). Orange areas include some *A. nebrownii* and thorn veld 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 (map data from Burke *et al.* 2002).

5.4.2.2 Male movements relative to female core areas, and association with females

As expected, male association with females varied with male maturity. More mature males associated relatively less with females than younger males (Figure 5.3). Males below maturity category six (dark colouration throughout the study period; expected to be fully sexually mature) were all seen with females on at least 50% of observations. In older males, there was a higher degree of inter-individual variation, with a range from zero to all sightings with females.

As predicted, 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; Figure 5.4). Solitary 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 (contingency coefficient = 0.311, N = 470, $P < 0.001$).

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 (Spearman's rho = 0.264, N = 470, $P < 0.001$; Figure 5.5). Furthermore, when males were in groups containing females, they tended to be with larger numbers of females in areas of greater core overlap (categories 0, 1-5. and >5 core overlaps; ANOVA: $F_{2,316} = 3.080$, $P < 0.05$; Figure 5.6). Adult males with smaller home ranges were seen within areas of high female core overlap (> 5 overlaps) on a greater proportion of sightings than males with larger home ranges (Pearson's r = -0.605, N = 19, $P < 0.01$; Figure 5.7).

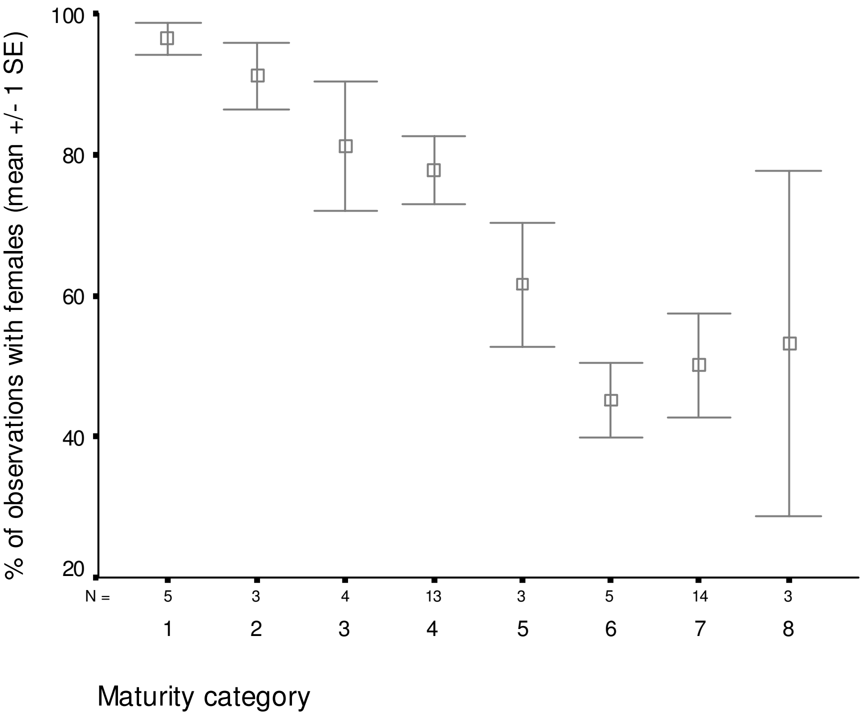


Figure 5.3. Percentage of observations with a female, for males of different age classes seen more than five times (age classes ranged from: 1) juveniles to 8) old black males; for full details of age class definitions, refer to Table 2.2, Chapter 2).

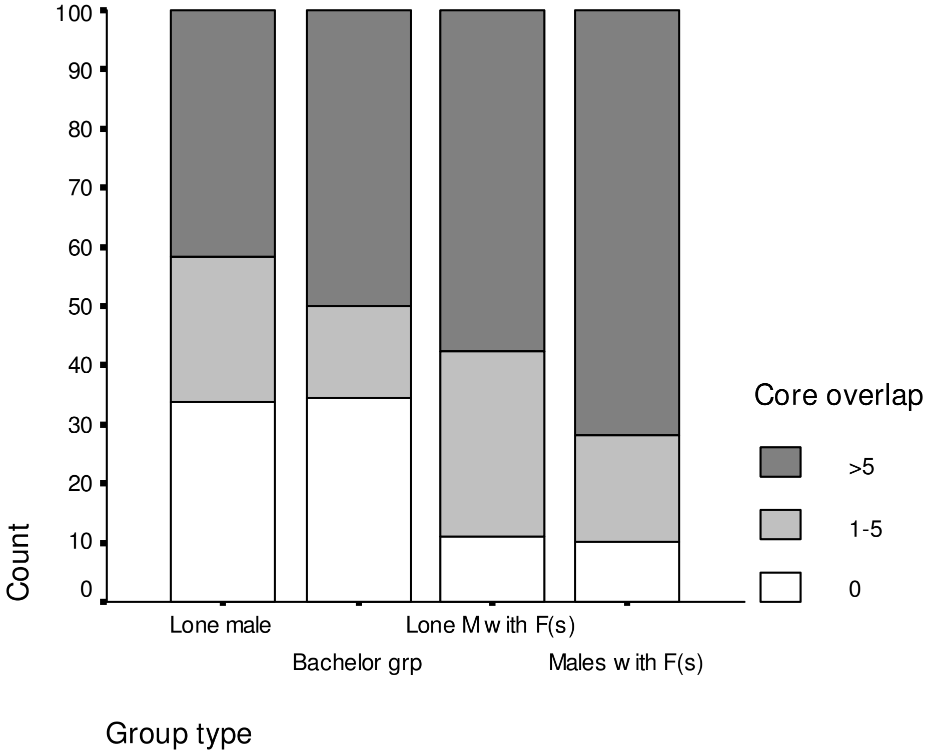


Figure 5.4. Relationship between group type and female core area overlap.

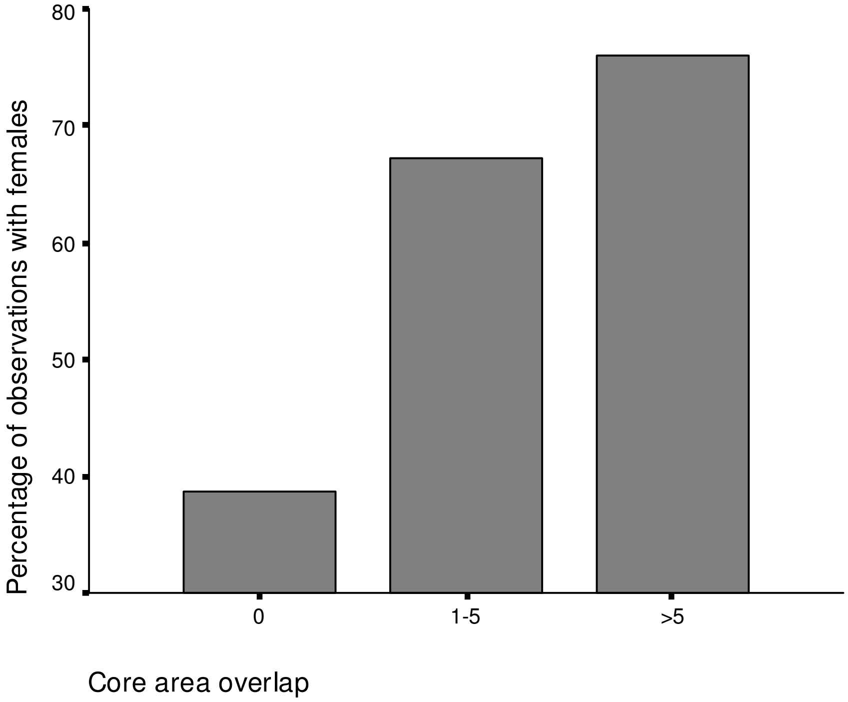


Figure 5.5. Association of males with females, relative to the male's location in terms of female core area overlap.

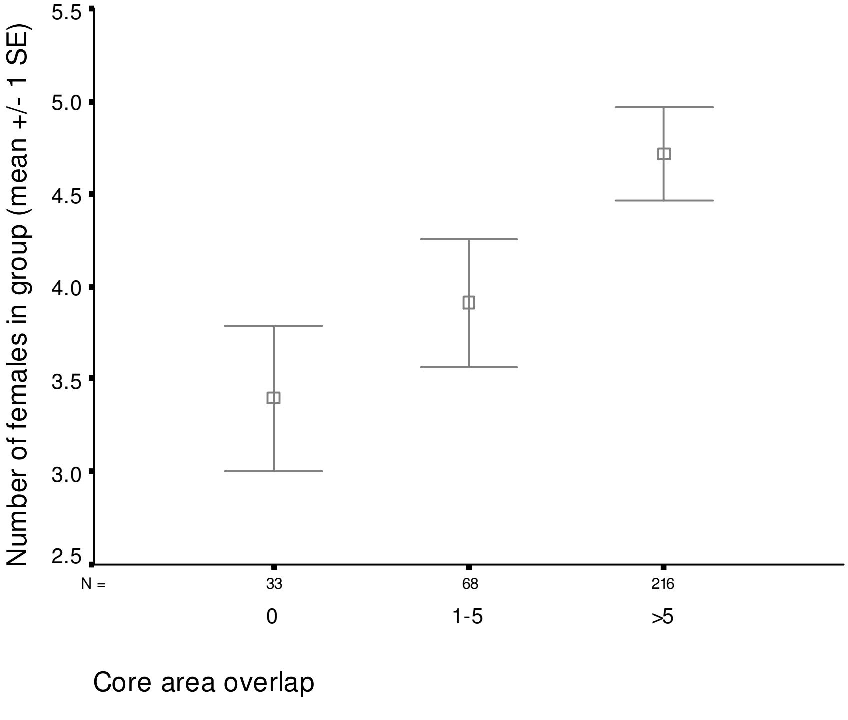


Figure 5.6. Mean number of females that were in a group, on occasions when males were seen with at least one female, relative to female core area overlap

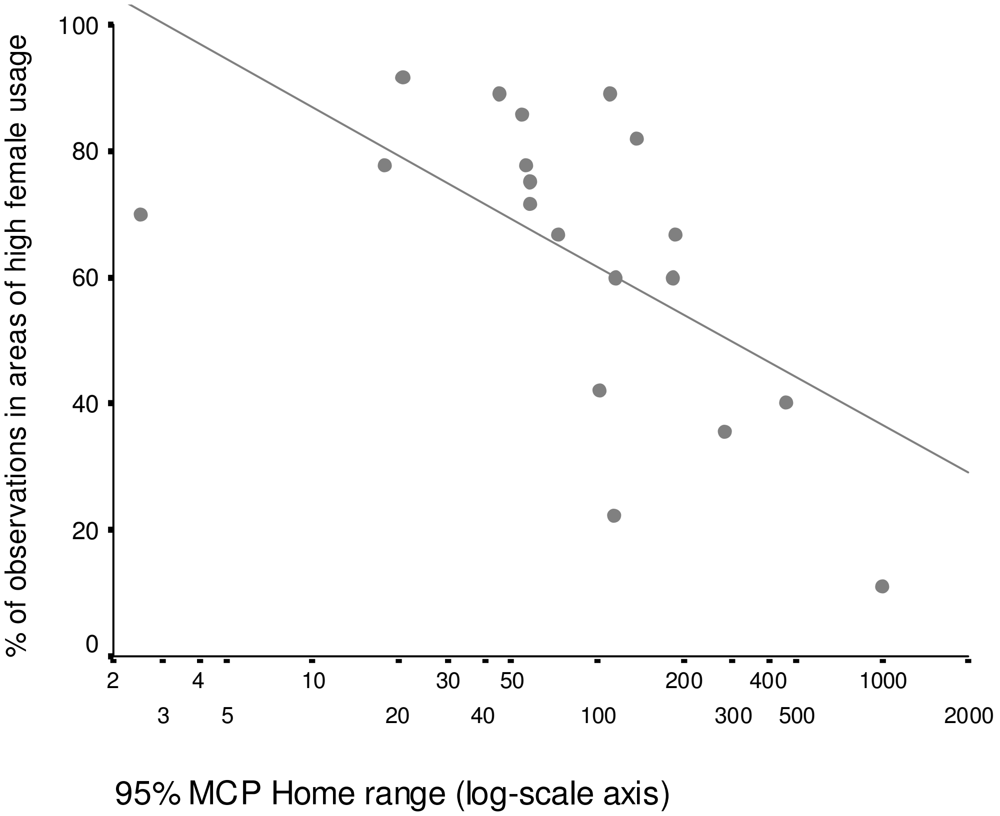


Figure 5.7. Proportion of observations of individual adult males that were in areas of high female usage (>5 core area overlaps) in relation to male home range size (95% MCPs).

5.4.2.3 Male activity relative to core areas

To test the prediction that males would spend more time browsing outside female core areas than within them, the proportion of observations on which males were seen browsing was compared between areas of low, and moderate or high female usage (all sightings for males of each class were pooled). The prediction was not supported, as neither dark nor pale adult males were more likely to be found browsing whilst outside female core areas than within them (dark males: $X^2 = 0.064$, N = 216, df = 1, P = 0.800; pale males: $X^2 = 2.383$, N = 216, df = 1, P = 0.123). Nonetheless, pale, but not dark, males were more likely to be found browsing when alone or in a bachelor group than when with females (pale: $X^2 = 4.26$, N = 444, df =1, P < 0.05; dark: $X^2 = 0.125$, N = 566, df =1, P = 0.723). Interestingly though, solitary adult males (pale and dark combined) were significantly more likely to be found standing resting or ruminating while outside the core female areas than within them ($X^2 = 5.12$, N = 98, df = 1, P < 0.05; Figure 5.8).

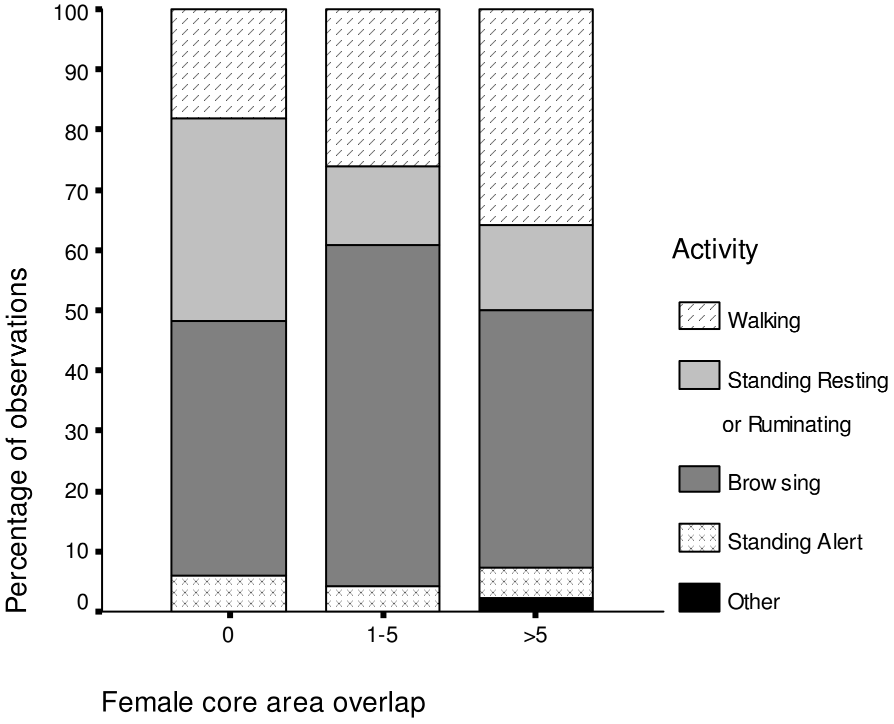


Figure 5.8. Activity of solitary males relative to female core area overlap.

5.4.3 Hypothesis 3: Seasonal variation in male movements and habitat use

5.4.3.1 Home ranges

Female home ranges did not differ significantly in size between the wet season (when a high proportion of conceptions occurred) and dry season (twelve adult females seen at least eight times in each season; 100% MCPs: $t = 0.130$, $df = 11$, $P = 0.899$); both averaged about 80 km^2 despite one season being longer than the other (October to May versus June to September; Figure 5.9). Seasonal ranges overlapped for some females, but not others (mean = 0.32, N = 12, range in overlap coefficient: 0 – 0.78); females that had smaller total home ranges had significantly greater overlap coefficients (100% MCPs: Spearman's rho = -0.581, N = 12, $P < 0.05$), and significantly smaller distances between the arithmetic centres of their seasonal ranges (Spearman's rho = 0.648, N = 12, $P < 0.05$). Notably, three females that were known to have young calves during the study period had relatively high seasonal range overlaps (31, 47, and 78%), and short distances between the arithmetic centres of their seasonal ranges (mean for these three = 3.8 km, versus a mean of 6.7 km for all 12 females).

Due to fewer sightings of males overall, there were insufficient data to compare seasonal range sizes for males in the same manner. Only one adult male was seen at least eight times in both seasons. However, five other adult males were seen on a sufficient number of occasions between October and May, and four others between June and September (Figure 5.10). Based on these data, male home range sizes also did not differ significantly between the two seasons ($t = -0.282$, $df = 9$, $P = 0.784$), and were similar in size to those of females (wet season mean = 77.4 km^2, dry season mean = 85.8 km^2).

It was also not possible to measure seasonal range overlap for males. However, within a season, there was considerable overlap between just the five or six male seasonal home ranges mapped, especially in the vicinity of waterholes (Figure 5.10). 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. Of the 18 adult males seen at least ten times over the study period, six were seen only in two to four months of each year and only in three to five different months over the whole study period (the median for the number of different months in which individuals were seen was seven for females and six for males). These 'seasonal visitors' had significantly smaller home ranges (all 95% MCPs less than 60 km^2) than year-round residents (mean = 210 km^2; $t = 2.778$, $df = 16$, $P < 0.02$).

The ranges of each seasonal visitor were similar from one year to the next, and all had one waterhole in common between the two years; five of the males used Ombika waterhole both in 2004 and 2005, and one used Gemsbokvlakte in both years, suggesting some sort of site-fidelity. Seasonal visitors with home ranges that overlapped spatially at Ombika were only seen there during five months of 2005 (April-May and September to November), but did not all overlap temporally. More than one seasonal visitor was seen near (within 2 km of) Ombika during two of these months (May and October); whereas during three of these months, only one seasonal visitor was seen there (April, September, November). However, when at least one seasonal visitor was present in the area around Ombika, there were other dark males (two to eight individuals) present in four out of the five months, and pale adult males present (one to eleven individuals) in every month. In the months that no seasonal visitor was present near Ombika, there were also very few (no more than three) other adult males present.

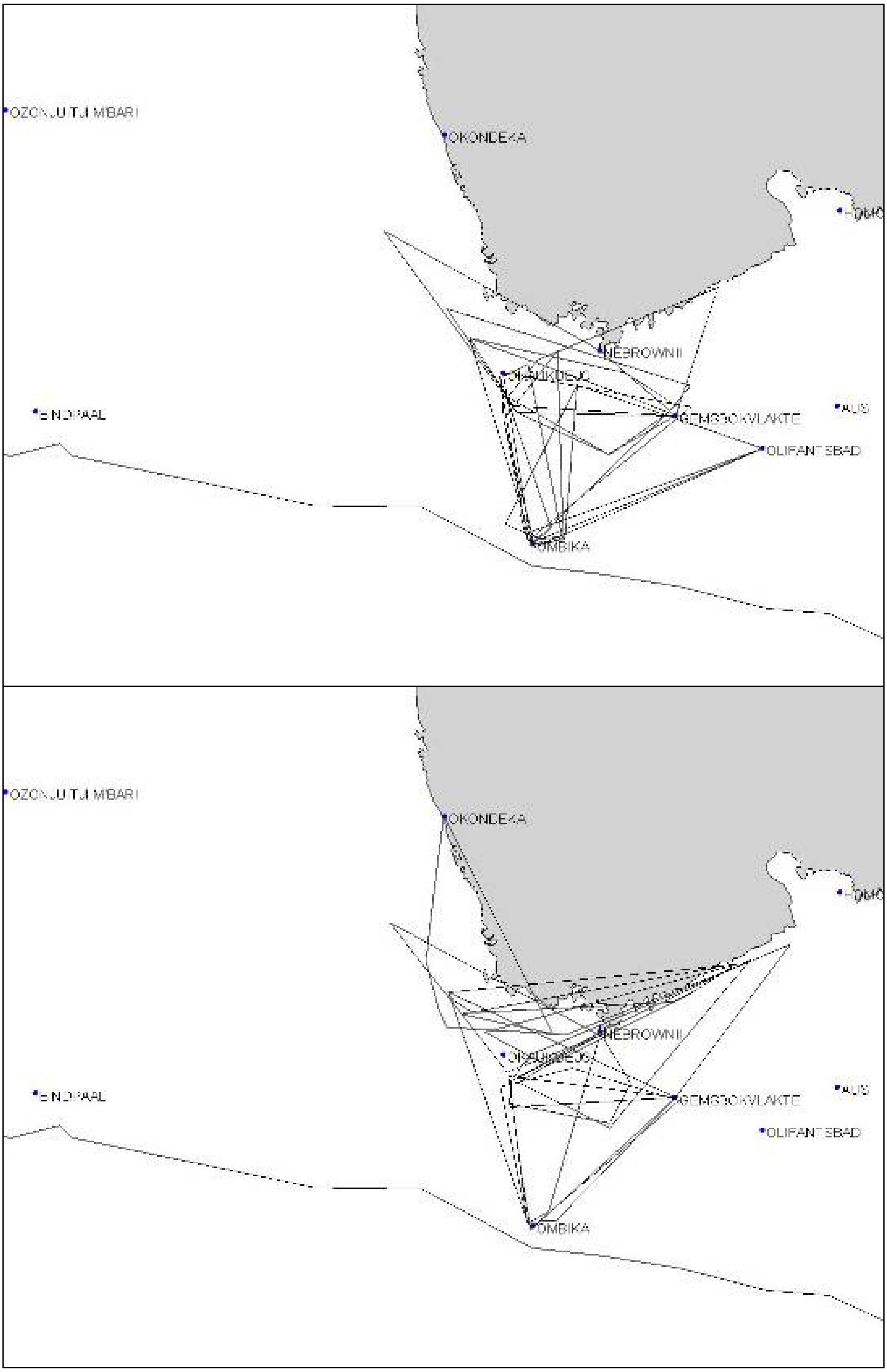


Figure 5.9. Female seasonal ranges (100% MCPs) for the same 12 females in the wet, higher-conception-rate season (October-May, top), and the dry, lower-conception-rate season (June-September, bottom).

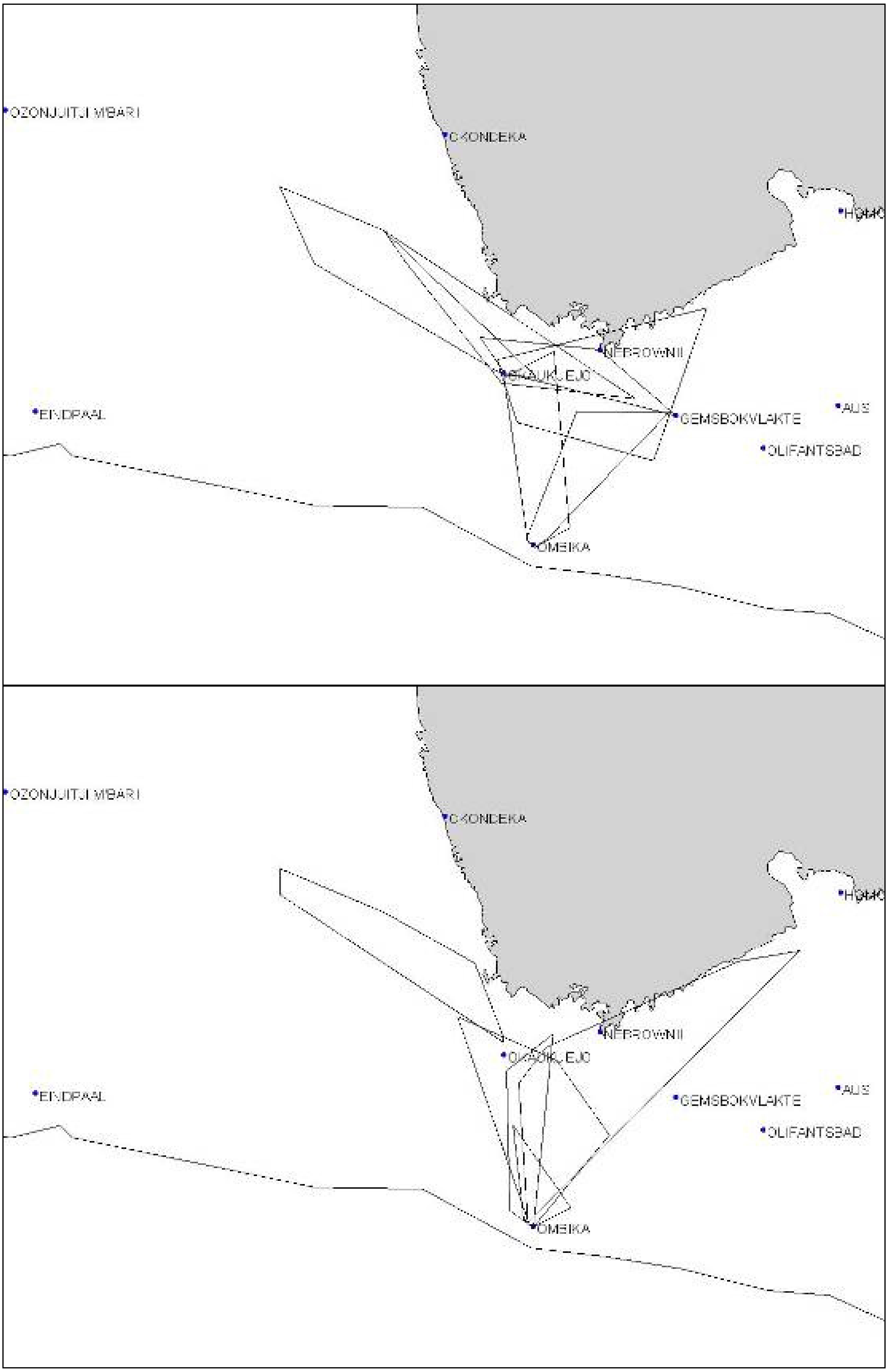


Figure 5.10. Male seasonal ranges (100% MCPs) for six males in the wet, higher-conception-rate season (top), and five males in the dry, lower-conception-rate season (bottom).

5.4.3.2 Habitat use and association with females

Fully dark, sexually mature males (maturity class 6 and above) were significantly more likely to be with females during the wet, higher-conception-rate season than during the dry, lower-conception-rate season, whereas there was no significant difference for younger adult males (classes 4-5: N = 142 sightings, X^2 = 1.565, df = 1, P = 0.211; classes 6-8: N = 205 sightings, X^2 = 7.977, df = 1, P < 0.005; Figure 5.11).

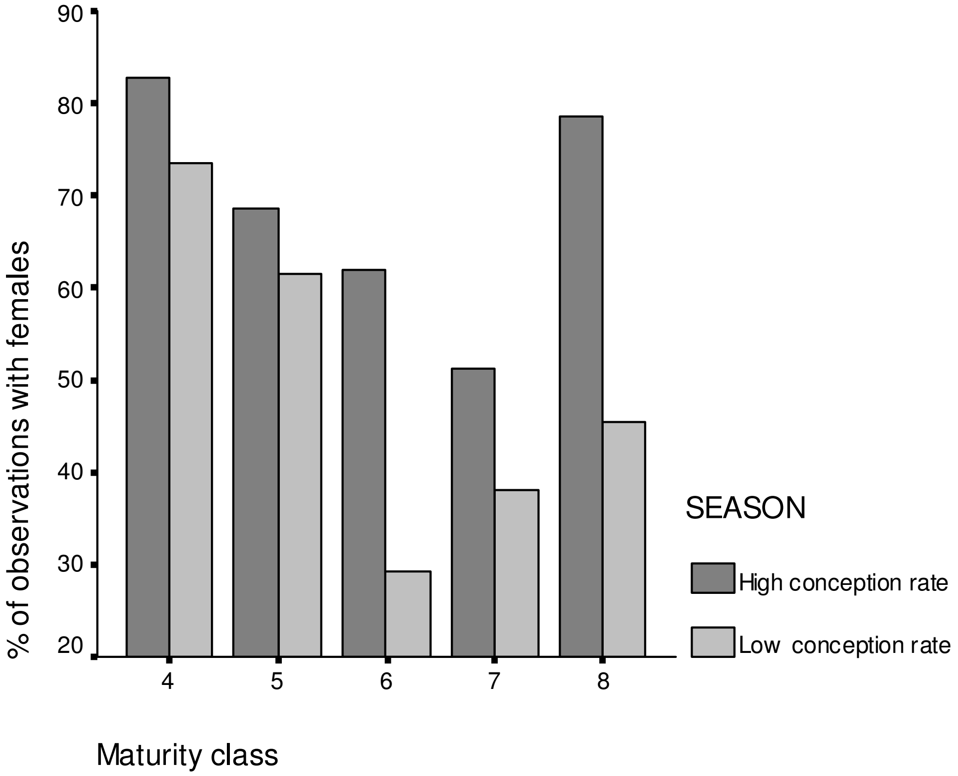


Figure 5.11. Degree of adult male association with females (% of observations) relative to maturity class, for both the higher-conception-rate season (Oct-May) and lower-conception-rate season (Jun-Sep).

Dark males were also significantly more likely to be in areas of high female usage (>5 overlaps) during the wet, higher-conception-rate season (October to December, and March to May), than during the dry, lower-conception-rate season (June to September: N = 217 sightings, X^2 = 6.615, df = 2, P < 0.02). This relationship was less important for pale adult males (N = 130 sightings, X^2 = 3.430, df = 2, P = 0.064). Although this relationship could be accounted for by males and females converging on the same preferred foods and habitats within these core areas during the wet season, this would not explain the difference between dark and pale males.

In the wet season (October to May), preferences indices (PI) for pale males and bachelor groups correlated with PIs of females in female-only groups (rho = 0.846, N = 11 habitats, $P < 0.005$), whereas PIs for dark males did not (rho = 0.405, P = 0.216). Dark males were occupying the different habitats more uniformly (fewer habitats with a $PI < 1$) during this time than either females or pale males.

In the dry season (June to September), habitat preference indices (PI) of dark males (alone or with females) did correlate with PIs of females in female-only groups (rho = 0.727, N = 11 habitats, $P < 0.05$), whereas PIs of solitary pale males and males in bachelor groups did not (rho = 0.386, N = 11, P = 0.241).

Habitat preference indices of dark males (alone or with females) did not correlate with those of pale males and males in bachelor groups in either the wet season (rho = 0.413, N = 11, P = 0.207), or the dry season (rho = 0.391, P = 0.234). Specifically, in both seasons, lone pale males and males in bachelor groups avoided mopane-*Catophractes* shrub savannah (H) less than dark males or females. They also used mopane-*Acacia nebrownii* shrub savannah (J) less than dark males or females in the wet season (Figure 5.12), and mopane veld (D) more and acacia veld (E) less than dark males or females in the dry season (Figure 5.13).

5.4.3.3 Individual variation and possible exclusion of subordinate males

Contrary to predictions, preference indices for dark males (alone or with females) were not equal to or greater than those of lone pale males and males in bachelor groups for all of the habitats with high female densities in each season. Specifically, PIs for dark males were considerably lower than those of pale males for mixed broadleaf woodland (G) in the wet, higher-conception-rate season (14.81 versus 26.67), and for *A. nebrownii* habitats (B and J) in the dry, lower-conception-rate season (1.09 and 1.43 respectively, versus 1.66 and 3.19).

These discrepancies may have been due to a high degree of individual variation among dark males. For example, of ten dark adult males seen on at least five days each during the wet season, three were seen in mixed broadleaf woodland (G) on the majority of sightings (60-73%), while five were never seen in this habitat. Those seen rarely (N = 2) or never in mixed broadleaf woodland were found in a wider range of habitats, including mixed thorn veld (F), open plains (A), *A. nebrownii* thickets (B), and acacia veld (E).

Similarly, of nine dark adult males seen on at least five days each during the dry season, only one was seen regularly in *A. nebrownii* habitats B and J (86% of sightings), five were seen in these habitats occasionally (14-40% of sightings), and three were never seen in these habitats. Those seen rarely or never in *A. nebrownii* habitats, tended to be found predominantly in open plains (A), mixed thorn veld (F), or mixed broadleaf woodland (G). Certain males were consistently not found in preferred female habitats. For example, one dark male was never seen in mixed broadleaf woodland in the wet season or in *A. nebrownii* habitats in the dry season, whereas another was never seen in mixed broadleaf woodland in the wet season, and was only once seen in *A. nebrownii* habitats (one of five sightings) in the dry season.

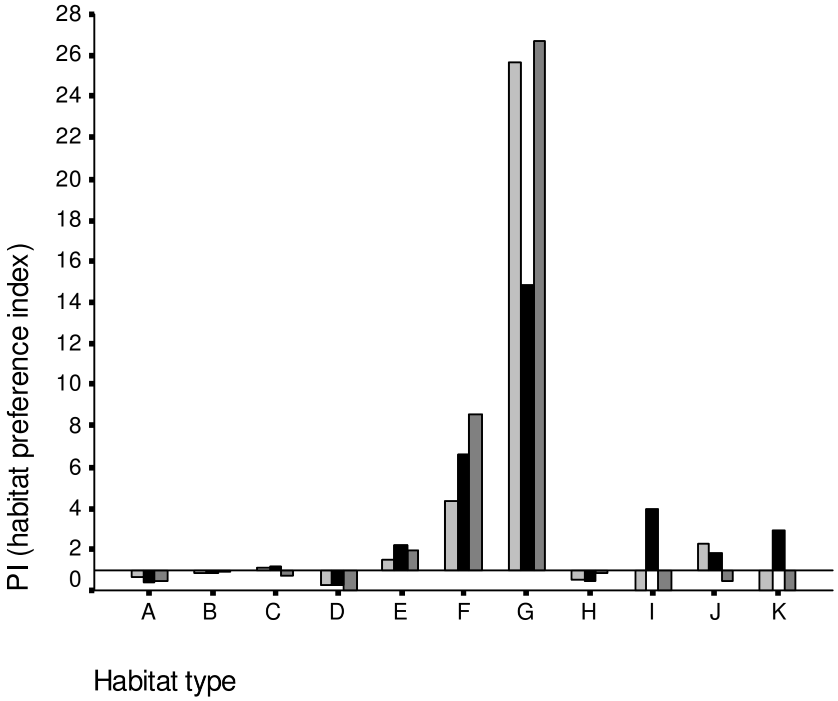


Figure 5.12. Wet, higher-conception-rate season habitat preference indices (PIs) for females (light grey bars), dark males alone or with females (black bars), and pale males alone or males in bachelor groups (dark grey bars). For a description of the calculation of PIs, see Chapter 3. Axis line at PI = 1 corresponds to no preference or avoidance; bars above the line represent preference, bars below represent avoidance relative to availability.

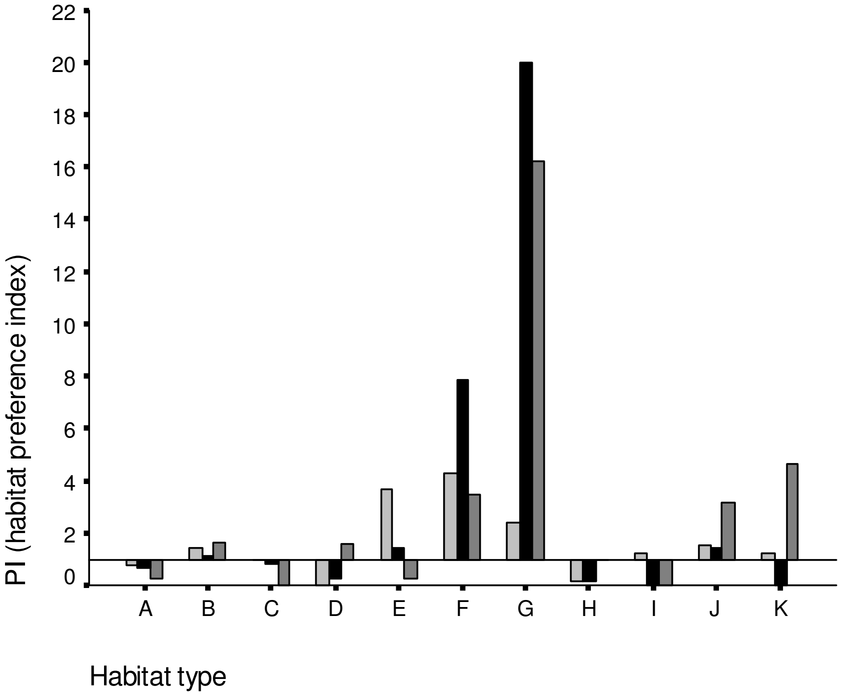


Figure 5.13. Dry, lower-conception-rate season habitat preference indices for females (light grey bars), dark males alone or with females (black bars), and pale males alone or males in bachelor groups (dark grey bars). Axis line at PI = 1 corresponds to no preference or avoidance; bars above the line represent preference, bars below represent avoidance relative to availability.

5.5 Discussion

5.5.1 Hypothesis 1: Large male ranges

Estimated home ranges for giraffe in central Etosha NP resembled those recorded in Tsavo East NP (Leuthold & Leuthold 1978b), where giraffe densities and typical group sizes were similar. Home ranges in Etosha were smaller than those measured in the northern Namib desert to the west (Fennessy 2004). This was most likely due to the combined effects of the less patchy availability of food, the artificial provision of water, and the greater ease with which males were likely to be able to locate mates in Etosha when compared to the desert region (Fennessy 2004; Ntumi *et al.* 2005). It must be noted, however, that some home range values may have been slight underestimates because they were based on relatively few sightings (Lent & Fike 2003).

Male home ranges overlapped considerably. Evidence from cumulative identifications supported the prediction that females are more sedentary than males, who must range further due to their need to search for mates (see also Fennessy 2004). As predicted, home ranges of dark adult males were also found to be slightly larger, and more variable in size, than those of adult females or pale adult males. Furthermore, known males were sighted less frequently than known females, suggesting that males may move in and out of the study area more often than females.

These observations were further supported by the seasonality of sightings of individual males. Smaller male home ranges were associated with extended periods of absence from the study area (but not fewer sightings). These ‘seasonal visitors’ tended to be present in a similar part of the study area at a similar time of year in each of the two years. Because they were not sighted throughout the year, it is possible that seasonal visitors 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 compared to using GPS collars (e.g. Fennessy 2004).

5.5.2 Hypothesis 2: Male movements and activity in relation to areas of high female usage

5.5.2.1 Male movements relative to female core areas, and association with females

As predicted, a strong link was found between male movements and association with females. Firstly, association with females varied with male maturity, as was expected. 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 (core areas of female use) than others. 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. Conversely, seasonal visitors and males with smaller home ranges tended to be found in larger groups, spent more time in areas of high female usage, and were more likely to be seen with females.

These inter-individual differences in male ranging behaviour and social associations are suggestive of within-population variation in mating strategies, as has been found in a number of other ungulate species (e.g. Gosling 1991; Carranza *et al.* 1996; Coltman *et al.* 1999; Thirgood *et al.* 1999; Isvaran 2005). Variation in mating strategies usually suggests that there are different costs and benefits of adopting the different strategies, and thus different optimal trade-off points, which may vary with environmental and social conditions, or with male age or social dominance (Dunbar 1982; Gosling 1986). For example, according to life-history theory, older males, nearing the end of their reproductive life, may be more likely to adopt a high-risk, high-benefit (i.e. high reproductive success) strategy, whereas young males should prefer a low-risk, low-benefit strategy that does not reduce their potential for reproduction in later life (Dunbar 1982; McElligott & Hayden 2000). Alternatively, young or lower ranking males may be forced to adopt more opportunistic strategies with a low probability of reproductive success due to competitive exclusion by mature, dominant males (Dunbar 1982; Thirgood *et al.* 1999; McElligott *et al.* 2002). In these cases, their mating strategy can be described as ‘making the best of a bad job’ (Dunbar 1982).

Some males appear to adopt a year-round, but intermittent, following strategy, covering a large area. Others appear to 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 toward an area-restricted search strategy (Ims 1990), and possibly temporary localised defence of females (e.g. van der Jeugd & Prins 2000), in areas of high and predictable female usage. This seasonal strategy might be favoured by the most dominant males, who could enter areas of high female density with a good chance of encountering receptive females, and high likelihood of being able to displace any potential competitors they encounter (e.g. Parker 1974; Ims 1990; Forchhammer & Boomsma 1998; Isaac 2005). However, these males would probably have to trade off the benefit of encountering greater numbers of potentially receptive females with an increased risk of encountering and competing with other dominant males (Ims 1988b).

Males of low competitive ability 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 might benefit from a low-risk, low-benefit, opportunistic strategy, involving more extensive roving in and out of female core areas year-round, attempting to gain mating opportunities upon chance encounters with undefended receptive females (e.g. Fisher & Lara 1999). These different strategies likely constitute two extremes of a continuum (Gosling 1991; Thirgood *et al.* 1999). Unfortunately, data on dominance interactions between males for which home ranges could be estimated were insufficient to test whether males with smaller or seasonal ranges were indeed more dominant.

5.5.2.2 Male activity relative to core areas

Consortship and mate guarding have been reported to reduce male foraging time (Leuthold & Leuthold 1978a; Pratt & Anderson 1985). Therefore, it was predicted that males would spend less time browsing, and more time in other activities (e.g. walking) within areas with high densities of females (e.g. Turner *et al.* 2005). Whilst the evidence did not directly support this prediction, lone adult males did appear to spend less time standing ruminating whilst inside the core areas, and slightly more time walking. This may be due to higher levels of male competition within these areas, which forces sexually active males to keep moving, either to avoid competition or to seek out other undefended females. Therefore, periodically leaving the core areas might provide males with an opportunity to rest and regain body condition (Turner *et al.* 2005). It is assumed that many of the males that appeared to leave the study area may have moved into the surrounding mopane veld (found to the east, south-east, south-west and west of the study area), a habitat used more by males, particularly bachelor groups.

5.5.3 Hypothesis 3: Seasonal variation in male movements and habitat use

Male movements and habitat use were expected to differ between the high and low-conception-rate seasons, as a result not only of differences in food availability, but also as a result of differences in the detectability, and potential for monopolisation, of females. It was predicted that female habitat preferences would affect the movements of dark males most, under the assumption that mate-searching and reproductive effort should be greater in more mature males than young adult males (e.g. Mysterud *et al.* 2003). Therefore, it was expected that dark males would select habitats where females were aggregating, but pale males would not.

During the wet, higher-conception-rate season, habitat preferences of dark males differed to those of pale males and males in bachelor groups, as predicted, but solitary pale males and males in bachelor groups were showing similar habitat preferences to females, whereas dark males were not. Furthermore, during this season, the preferred female habitat (mixed broadleaf woodland) actually ranked lower for dark males than pale males. This was contrary to expectations, and could possibly be explained by the considerable variation among habitat preferences of individual males, with some mature (dark) males predominantly using mixed broadleaf woodland, where female densities were greatest, while others were found in a wider diversity of habitats.

It is proposed that these individual differences correspond with differences in male status, with dominant dark males restricting their search efforts to female concentration areas, and subordinate dark males avoiding these habitats, possibly to avoid the risk of increased encounters and conflicts with other dark males in these areas (e.g. Sanchez-Prieto *et al.* 2004). As a result, these dark males are more likely to be found in habitats less favoured by females. Younger, pale males, on the other hand may continue to use these habitats as they are tolerated by dark males, maybe seen to pose a relatively low ‘threat’, and as such do not face high levels of challenges from dark males (e.g. Senar & Camerino 1998; Parker & Ligon 2002). As such, whereas dominant males would have a high chance of encountering large numbers of females and monopolising mating opportunities within female concentration areas, subordinates would have to rely on chance encounters with smaller groups of females in less preferred habitats, away from competitors (e.g. Fisher & Lara 1999).

In the dry, lower-conception-rate season, solitary pale males and males in bachelor groups were again selecting different habitats (e.g. habitats rich in mopane) to dark males, and to females, whereas dark males were showing similar habitat preferences to females. This suggests that, as expected, dark males leave their preferred habitats and move into habitats preferred by females in order to follow them throughout the year. In the dry season, there was also variation between individual dark males, with one dark male being seen almost exclusively in *A. nebrownii* habitats, where estimated female densities were high, and some dark males avoiding these habitats entirely. Consequently these habitats ranked lower, in terms of habitat selection ranks, for dark males than for pale males.

Males clearly follow females and compete to exclude competitors from mating throughout the year, with a few dark males being apparently successful in maintaining access to female aggregation areas, others being consistently unsuccessful. It is predicted that levels of intra-sexual competition will be greater during the wet, higher-conception-rate season than during the dry season: during the wet season, female densities were very high in a highly spatially restricted habitat (mixed broadleaf woodland). Such a predictably clumped spatial distribution of females, throughout the wet season, means that searching for potential mates in this habitat should be very profitable for males as there will be a high likelihood of encountering a receptive female (Ims 1990). As a result, sexually active males are likely to face increased intruder pressure (Ims 1988a), probably resulting in increased levels of competition (Sanchez-Prieto *et al.* 2004), and potentially only the most dominant males securing access to mates ('priority of access' model, Altmann 1962). Effects of female spatial distribution on male intra-sexual competition will be explored in the following chapter.

6 MALE INTRA-SEXUAL COMPETITION AND MONOPOLISATION OF FEMALES

6.1 Introduction

6.1.1 Competitor assessment and signals of status

On encountering an adversary in competition for a limited resource (e.g. mates), a male must make a strategic decision based on the behaviour of the opponent and any asymmetry that may exist between the two males. Specifically, in response to a display by an opponent, a male must decide whether to 'retreat' or to 'escalate' to combat (Smith 1982). Since escalated contests can be costly (in terms of possible injuries), it would benefit participants of agonistic interactions to avoid unnecessary escalated contests (Smith 1982).

Most agonistic interactions are asymmetric, where the probability of each male winning depends on existing differences between the competitors (Parker & Rubenstein 1981). For example, one male may have greater competitive ability (or resource holding power, RHP, Parker 1974; Smith 1982) due to greater age or size, or might have more to gain from winning (or more to lose from losing) the contest (i.e. pay-off asymmetry, Smith & Parker 1976). If such asymmetries can be perceived at the start of an agonistic interaction, for example during the initial display, then they should inform the decision to retreat or to escalate (Smith 1982). This competitor assessment may result in a strategy involving the rule of the type: 'display if larger; retreat if smaller' (Smith 1982).

However, if the available information regarding relative competitive ability is imperfect, or if one male misjudges his status relative to that of his opponent (e.g., both assume they are the larger male as they are very closely matched), then an escalated contest is likely to occur (Smith & Parker 1976; Parker & Rubenstein 1981; Smith 1982). Where competitor assessment is reliable, and injury risks associated with escalated fights high, then escalated contests should be rare (Smith & Parker 1976). However, contests may also escalate if there are contradictory effects of differences in RHP and differences in pay-offs, for example if the smaller male is the current resource-holder, and therefore values the resource more than the ‘intruder’ (Parker & Rubenstein 1981).

Males that are known to each other may also be able to rely on an individual reference for dominance, based on prior experience, to avoid escalated contests (Parker & Rubenstein 1981; Gosling 1986). However, since males may not always be familiar with their opponent, it should generally benefit males to convey information about their competitive ability, and to respond to the information they receive (Smith 1982). This should result in selection for reliable signals of status, so long as it is costly to acquire high RHP and to convey false information (i.e. produce a false status signal) (Smith 1982). One means of preventing ‘cheating’ is a social mechanism, whereby ‘cheats’ are repeatedly challenged and exposed to high fighting risks (e.g. Rohwer & Rohwer 1978; Gerald 2000; Parker & Ligon 2002). Consequently, the outcome of dyadic contests should reflect differences between the two males in the strength of the status signal (e.g. Gerald 2000).

The evolution of giraffe body size and shape, and horns and bony exotoses on the head have been attributed to sexual selection (Simmons & Scheepers 1996). Specifically, giraffes fight using their neck and head, so a larger male giraffe, with more developed neck musculature and skull weaponry would have a distinct advantage over a less endowed male in intra-sexual competition. Here, I postulate that although it may not confer any direct benefit in combat, dark coat colouration may be selected as an honest signal of male status to both potential competitors and potential mates. Since male giraffe have large home ranges, group composition is fluid, and the study population large, encounters are likely to frequently involve unfamiliar males. Furthermore, escalated necking fights can potentially be very costly (see Section 6.1.2). Therefore, male giraffe would benefit from being able to assess adversaries’ potential competitive ability using a reliable signal of status, in order to avoid escalating to costly fights (e.g. Rohwer & Rohwer 1978; Smith 1982).

6.1.2 Male intra-sexual competition in giraffe: displacements and necking

6.1.2.1 Necking

The behaviour most commonly associated with male competition in the giraffe is generally known as "necking". This term was first used by Innis in her early, extensive paper on giraffe behaviour to describe the gentle rubbing of the neck of one animal against that of another (Innis 1958). The term has since been extended to include more violent usage of the neck and head in male-male interactions (Coe 1967). Necking is often preceded by and interspersed with posturing, including standing tall, arching the neck and pointing the head towards the sky, walking stiff-legged, or both giraffe parallel-walking (Innis 1958, LM Gosling pers. comm.; Estes 1999). Submission during or following a bout of necking may be demonstrated by the subordinate male jumping aside, yielding to the opponent and moving away, lowering its head and ears, or pulling the jaw in towards the neck (Estes 1999). Necking is usually observed at all times of the day, and throughout all months of the year (Innis 1958). Two types of necking behaviour may be distinguished, albeit somewhat arbitrarily (Innis 1958; Pratt & Anderson 1985).

6.1.2.2 Sparring

The first, "sparring", has been described as occurring only in all-male herds between males of similar or of different age (Coe 1967), though most frequently between young, immature males (Leuthold 1979; Pratt & Anderson 1985). Le Pendu *et al.* found that young males exchanged agonistic interactions with peers 23 times more than expected assuming an equal distribution of interactions between classes, and that sparring was particularly characteristic of young adult males of around 5 years of age (Le Pendu *et al.* 2000). Sparring is comparatively ritualised and slow, and is rarely violent. Sparring has been described as a sexuo-social bonding mechanism (Coe 1967) as it has often been seen in association with males attempting to mount other males (Innis 1958; Le Pendu *et al.* 2000). It has also been described as play-fighting, possibly as a mechanism for developing skills that will be needed later in life to determine the right to breed (Pratt & Anderson 1985). However, more commonly, the role of necking is attributed to the establishing of dominance relationships between individuals (Dagg & Foster 1982; Pratt & Anderson 1982). More specifically, these low-risk sparring contests are likely to serve maturing males as a means of testing their own strength and competitive ability, relative to that of others (e.g. Parker & Rubenstein 1981).

6.1.2.3 Necking fights

The second, rarer type of necking behaviour, "fighting" (Dagg & Foster 1982; Pratt & Anderson 1985) is most likely to occur in direct competition for a resource (e.g. females), where the competitive asymmetry between mature males cannot be accurately assessed by one or both opponents, or where there is a conflict between asymmetries in competitive ability and pay-offs (see Section 6.1.1 above). Such high intensity necking is often initiated when a mature male approaches a herd of females accompanied by another mature male, and neither male immediately defers by running off (Leuthold 1979). Escalated fights tend to begin and end abruptly, and involve heavy and frequent blows, often delivered simultaneously by both contestants (Pratt & Anderson 1985). Although neither Foster (1966), Coe (1967) nor Leuthold (1979) observed any violent fights, intense necking contests have been reported where the losing male was knocked to the ground or killed (Dagg & Foster 1982; Simmons & Scheepers 1996).

6.1.2.4 Displacements

Where there is a clear competitive asymmetry between two competing mature males, the dominant male is able to displace the subordinate male through display only: the dominant male walks towards the subordinate male while adopting a threatening 'proud' posture, causing him to retreat (Pratt & Anderson 1982). By observing such dyadic interactions (displacements) between males, Pratt & Anderson (1985) were able to establish that the success of one male in displacing another reflected differences between the males in "class", as determined by age, neck and horn size and the presence or absence of bony exotoses on the skull.

6.1.3 Courtship of females

Male giraffe are physically sexually mature from the age of about four years (Dagg & Foster 1982) but are unlikely to be reproductively active until the age of about seven (Estes 1991). At any one moment, male giraffe have a relatively low probability of encountering a sexually receptive female (Bercovitch *et al.* 2006). Despite breeding peaks in some populations, female giraffe breed all year round, but are pregnant for 15 out of every 19 to 24 months and are receptive for at most four days every two weeks (Dagg & Foster 1982; Bercovitch *et al.* 2006).

Moreover, as for roving, polygynous males of other species, searching for and courting females is likely to be energetically expensive, reduces time available for foraging, and in addition, competition between males for mates can be risky (Isaac 2005; Bercovitch *et al.* 2006; Pelletier *et al.* 2006). Therefore, it is important that males are able to accurately identify females in oestrus and restrict their mating efforts to receptive females only, and also that females can signal their receptivity to potential mates (Fisher & Lara 1999; Bercovitch *et al.* 2006). In giraffe, this information may be conveyed by changes in the hormone composition of the urine of females with the oestrus cycle (Innis 1958; Bercovitch *et al.* 2006).

Although observations of giraffe matings are very rare (Berry 1973; Leuthold 1979), urine-testing is a commonly observed courtship behaviour throughout the year (Innis 1958; Pratt & Anderson 1985). It involves the female volunteering to produce urine in response to investigation of her anogenital region by the male (Figure 6.1), and the subsequent tasting of the urine by the male with flehmen, characterised by raising of the head and curling back of the lips (Innis 1958; Pratt & Anderson 1985). Females may choose whether or not to produce urine for the male to test, so this behaviour can be used as an indicator of female mate choice (Pratt & Anderson 1985). Pratt and Anderson (1985) found that mature males were more attentive of females and more successful at eliciting urination by females than the younger males. Specific females were also observed to preferentially urinate for large males relative to young males (Pratt & Anderson 1985). However, Bercovitch *et al.* (2006) suggested that female choice might not be a major factor influencing male reproductive success, because of the potential risks to a female of missing a mating opportunity and postponing reproduction.

Figure 6.1. Young adult male sampling urine of a female.

Priority of access to receptive females is likely to be determined by individual male competitive status (Altmann 1962; Leuthold 1979; Dagg & Foster 1982; Simmons & Scheepers 1996). A male successful in securing access to a female in oestrus will focus his attention on her and proceed to court her, following her closely for up to two days until mating is achieved (Leuthold 1979; Pratt & Anderson 1985). Male foraging time is reduced during these consortships, which could be considered as tests of male endurance (Leuthold & Leuthold 1978b; Pratt & Anderson 1985; Bercovitch *et al.* 2006). The prolonged courtship period also provides the opportunity for a more dominant male to displace the current 'suitor' and take over the consortship before mating has been achieved, thus potentially increasing the relative importance of direct conflict between males (Pratt & Anderson 1985; Fisher & Lara 1999).

Thus, male reproductive success will be affected by a combination of indirect male competition (mate searching, or ‘scramble competition’ (e.g. Schwagmeyer 1988)), direct male competition involving contests for dominance that in turn determines reproductive access (i.e. ‘priority of access’ (Altmann 1962)), and possibly endurance rivalry during consortships (Bercovitch *et al.* 2006).

If the courted female is receptive to being mated, she will eventually stand still and braced, enabling the male to mount her (Innis 1958; Estes 1999). If she is not receptive to being mated, she will continually move away from the male when he tries to mount her (Dagg & Foster 1982). Thus, female cooperation is essential for a female to be successfully courted and mated. Larger, mature males also appear to be more successful than younger males in this stage of courtship (Pratt & Anderson 1985).

6.1.4 Waterholes as focal points for encountering potential mates

As has already been demonstrated (Chapter 3), waterhole use is driven by rainfall and field water availability. Perennial waterholes were used rarely while field water was available (November or December to May or June), and waterhole use increased from the end of the wet season (May) to the end of the dry season (October or November).

When perennial waterholes are used regularly, they will likely play an important role in determining the predictability of female movements. Predictable clumping of females at, or near, waterholes should enhance male ability to locate females (e.g. Ims 1990). Dominant males may use this to their advantage by restricting their search behaviour to areas near waterholes (Ims 1990), and competing to monopolise access to females at waterholes. For example, Ritter and Bednekoff (1995) observed that in the Nxai Pan National Park in Botswana, artificial dry-season water provision appeared to influence sexual selection in springbok. Specifically, they noted that female springbok (Antidorcas marsupialis) were concentrated in a limited area around the single waterhole in the Park. This enabled a few dominant males to gain a monopoly on territories around the waterhole and thus on females.

Artificial provisioning of food can produce a similar effect, as shown by Carranza *et al.* (1995) and Sanchez-Prieto *et al.* (2004) in red deer. Highly clumped provisioning of supplemental food caused increases in local density of females and in female group size. This led to local increases in male-male interactions (Sanchez-Prieto *et al.* 2004), and in one experiment even resulted in defence of territories at or near the supplemental food resource by males that previously defended harems (Carranza *et al.* 1995). Perennial waterholes in Etosha may serve a similar role in predictably concentrating females, and locally affecting the form and intensity of male intra-sexual competition. Therefore, they are expected to serve as a focal point for males to intercept and compete for females, especially during the dry season, when predictability of occurrence of females at waterholes is greatest.

6.1.5 Reproductive skew

Reproductive skew, or differential reproductive success, can be defined as "the unequal distribution of reproductive opportunities across individuals in a population, with a disproportionate share of matings being acquired by a small subset of individuals" (Alberts *et al.* 2003). This variance in mating success, combined with the breeding sex ratio, generally defines the mating system of a population (Parker & Waite 1997).

The degree of reproductive skew among each sex is determined by the type and intensity of intra-sexual competition for mating opportunities. In mammals, male variance in reproductive success tends to be greater than that of females, because females are restricted in their reproductive output by the energetic and time costs of gestation (Trivers 1972; Clutton-Brock *et al.* 1982c). In monogamous and truly promiscuous mating systems, both sexes experience very low variance in reproductive success (Parker & Waite 1997). In a highly polygynous mating system, female variance in reproductive success is also low, but male reproductive success is highly skewed as a few males mate with many females and some males do not mate at all (Parker & Waite 1997; Anthony & Blumstein 2000). The environmental potential for mate monopolisation (Emlen & Oring 1977) is determined primarily by the distribution of receptive females in space and time (Trivers 1972, see also Chapter 1). Specifically, male variance in reproductive success tends to increase with increasing asynchrony in female receptivity, and an increasingly clumped and predictable spatial distribution of females (Emlen & Oring 1977; Ims 1988a).

In polygynous species with dominance hierarchies, male reproductive success may be extremely skewed in favour of the most dominant males. For example, in a small group of black rhinos in Zimbabwe, 52% (10 of 19) of young born in the study area over 10 years could be attributed to a single male (Garnier *et al.* 2001). Similarly, genetic evidence of highly skewed male reproductive success was also demonstrated for a large population of fallow deer by Say *et al*. (2003). Their study revealed that the most dominant of 21 males sired between 34% and 60% of fawns in each season (a total of 321 fawns over 3 years).

The difference between the sexes in variance in reproductive success, which is particularly characteristic of polygynous mating systems, is clearly demonstrated by the results of a study of wood bison (*Bison bison athabascae*) in Canada (Wilson *et al.* 2002). This study reported that for 317 calves born over a period of four years, males sired from zero to 24 each, with a mean of 3.5 and a variance of 14.9, whereas female reproductive success ranged from 0 to 4 calves, with a mean of 2.7 and a variance of only 1.0 (Wilson *et al.* 2002).

The giraffe mating system consists of dominance-driven polygyny with probable promiscuity among females (Bercovitch *et al.* 2006). Female variance in reproductive variance should be very low, as at most they can produce one calf every 18 months, whereas male reproductive success should be skewed in favour of the more dominant males. The greater the ability of the dominant males to monopolise access to receptive females, the greater will be the reproductive skew. Differential male reproductive success will depend on a number of abilities:

- mate detection success: the ability to locate and identify receptive females with minimum search cost (i.e. scramble competition),

- ability to dominate other males in order to gain access to potentially oestrus females, and secure mating opportunities with oestrus females (direct contest competition),
- reproductive tenure: the duration that a male is able to remain dominant and monopolise mating opportunities (endurance rivalry),
- ability to gain the cooperation of the female to produce urine for testing and to mate (female mate choice, possibly also coercion),
- male fecundity (possibly including sperm competition)
- male survivability (reproductive life-span)

(Altmann 1962; Clutton-Brock *et al.* 1982a; Smith 1982; Ims 1988a; Ims 1990; Andersson & Iwasa 1996; McElligott *et al.* 2002; Bercovitch *et al.* 2006; Engelhardt *et al.* 2006).

It is assumed that all of these should increase with male maturity, dominance, and genetic or phenotypic quality (e.g. Ims 1988a; McElligott *et al.* 2002).

6.1.6 Surrogates of reproductive success

When assessing differential reproductive success, it is often possible to estimate, approximately, individual male mating success from the level of participation in copulations (e.g. Wickings *et al.* 1993; Hirotani 1994; Say *et al.* 2003), unless alternative ‘sneaky’ mating tactics or female promiscuity are in operation (e.g. Coltman *et al.* 1999). However, in species where copulations are rarely seen, it may be necessary to derive surrogates of reproductive success from behavioural traits such as dominance status, behaviour patterns such as tending bonds, or the number of females a male associates with (Owen-Smith 1977; Clutton-Brock *et al.* 1982a). It is extremely rare to observe copulations in giraffe (Pratt & Anderson 1985). Therefore, to estimate the potential for monopolisation of mates (and thus reproductive skew) in the study population, without relying on genetic information alone, it will be necessary to generate an indicator of probable male potential for mating success using behavioural and social indicators based on the traits outlined above (section 6.1.5).

6.2 Aims

This chapter aims to test the following hypotheses and predictions:

Hypothesis 1: Dark coat colour in males functions as an honest signal of status and potential competitive ability. Thus, I predict that:

- Dark coat colouration should develop with maturity, and only in males.
- Differences in male coat colouration should be biologically significant and correspond to different stages of social maturity.
- If coat colour is a reliable indicator of competitive ability, then darker adult males should be larger than paler adult males.
- Differences in male coat colouration should reliably predict the outcome of dyadic agonistic interactions.
- Changes in coat colouration should correspond with changes in male status.
- Females should respond to differences in male coat colouration when choosing whether to provide urine upon solicitation by males for receptivity testing.
- Darker males should experience greater success in courtship and mating.

Hypothesis 2: Perennial waterholes serve as focal points for encounters, and consequently interactions between males and females (mating interactions) and among males (agonistic interactions). The predictability of occurrence of females at perennial waterholes offers dominant males an opportunity to monopolise access to females, and possibly temporarily defend waterholes. Thus, I predict that:

- The rate of new encounters will be greater at perennial waterholes than at locations away from waterholes.
- The rate of mating and agonistic interactions will also be greater at waterholes than at locations away from waterholes.
- These effects will be greater during the dry than during the wet season, as females occur more predictably at perennial waterholes during the dry season (see Chapter 3).
- Consequently, consortships will be observed closer to waterholes during the dry season, as they are more likely to be initiated at waterholes during the dry season than the wet season.
- During the dry season, dominant males will compete with greater intensity to monopolise access to females at waterholes.

Hypothesis 3: Male competition varies seasonally as a result of seasonal variation in size and predictability of female aggregations, and seasonal variation in the proportion of females that are receptive (due to the peak breeding season, see Chapter 4). Thus, I predict that:

- Intensity of competition between dark males will differ in degree between the wet, high-conception-rate season (October to May) and the drier, low-conception-rate season (June to September).

Hypothesis 4: Due to a relatively predictable occurrence of female aggregations in certain habitats, and at waterholes, at least during part of the year, dominant males can potentially monopolise access to receptive females, excluding subordinate males from mating, resulting in reproductive success skewed towards a relatively small number of dominant (dark) males. Thus, I predict that:

- Access to females for courtship and mating will be highly skewed towards dark males, and will also vary considerably among dark males.

6.3 Methods

6.3.1 Relationship between coat colour and behaviour

Differences in coat colour between participants of different social interactions, and between successful and unsuccessful males in attempts to elicit urination by females, were all tested using the Chi-square test for independence, or where expected values were too small (<5), the contingency coefficient was used instead. The relationship between participant coat colour and the outcome of displacements was tested using the Mann-Whitney U test, by comparing the differences in coat colour between the winner and loser (three categories: darker, similar or lighter) with a random distribution of outcomes based on the actual coat colour differences of all the pairs of males interacting. Seasonal differences in the coat colour of participants in agonistic or mating interactions, and the type of interaction that males were involved in, were also tested using the Chi-square test for independence, or the contingency coefficient where expected frequencies were low.

6.3.2 Definition of 'new encounter' and interaction rates

A 'new encounter' was defined as a pair of giraffe that were previously more than 1 km away from each other and not visible to one another, which subsequently came together, through the movement of one or both individuals, to at least within visual range of each other, often approaching the encounter location (e.g. a waterhole) from different directions. It was assumed that such pairs of individuals were not associating in a group prior to the encounter. These new encounters were further divided into new male-male encounters (two males coming together) and new male-female encounters (a male and a female coming together). Thus if a group of three males approached a male and female at a waterhole, three new male-male encounters and three new male-female encounters would be recorded, as all three new males could potentially interact with the male already present and with the female. The new encounter rate was defined as the number of such new encounters per 100 hours of observation.

The rates of agonistic and mating interaction (see sections 2.2.6.2 and 2.2.6.3 for classification of interaction types) were defined as the number of interactions (the total, or sub-totals of each interaction class) recorded per 100 hours of observation during focal watches. All analyses of focal watch data were carried out after pooling focal watches by focal subject type (female, dark adult male, pale adult male), location (waterhole, non-waterhole), or season (dry, wet). Differences between waterhole and non-waterhole focal watches in new encounter and interaction rates were tested using the Chi-square test for independence, or the contingency coefficient where expected frequencies were low. Spatial (waterhole versus non waterhole) differences in nearest neighbour type were also tested using the Chi-square test for independence. Differences between waterhole and non-waterhole watches in potentially confounding variables, such as focal watch duration, group size and visibility (mean number of giraffe seen divided by total number of giraffe known to be present) were tested using the Mann-Whitney U test.

6.4 Results

6.4.1 Hypothesis 1: Dark male coat colour as a status signal

6.4.1.1 Coat colour and age

Male giraffe continue to grow beyond sexual maturity (Foster & Dagg 1972; Pellew 1983b). Therefore height gives a rough idea of relative age, and renders it possible to distinguish sub-adults from young-adults, and young adults from mature adults. Among fully mature adults, however, height is likely to become a less reliable indicator of age, as male height tends towards an asymptote (Foster & Dagg 1972; Pellew 1983b).

To investigate whether there was a relationship between male coat colour and maturity classes, heights were compared to coat colour category for those males measured using the photographic technique. For this sample of males (N = 26), age, maturity and colour categories corresponded with estimated heights (rounded to the nearest 5 cm) as follows:

Age category	Colour category	Maturity class	Min. height (m)	Max. height (m)
Juvenile	Any	0	1.95	3.15
Sub-adult	1 or 2	1-2	3.15	3.75
Pale adult	1 or 2	3	3.75	4.15
Pale adult	1 or 2	4	4.15	4.75
Dark adult	3	5-7	4.45 (one 4.20)	4.65
Dark adult	4	7-8	4.45	4.60

Thus, on the basis of the age-class classification used here, sub-adults measured less than 3.75 m, young (pale) adults at least 4.15 m, and dark adults generally at least 4.45 m. Due to the small variation in height among fully mature males, there was no significant difference in height between males of colour category three and category four (Kolmogorov Smirnov test: Z = 0.798, N = 11, P = 0.548). Heights of males of category three and four covered similar ranges (category 3 range: 4.45 - 4.62, N = 4; category 4 range: 4.46 - 4.66, N = 7), with the exception of one category three male of 4.18 m. Estimated heights of pale adult males overlapped with heights of dark males. However, as expected, dark males were significantly taller than pale adult males (Z = 1.706, N = 22, P < 0.01; Figure 6.2).

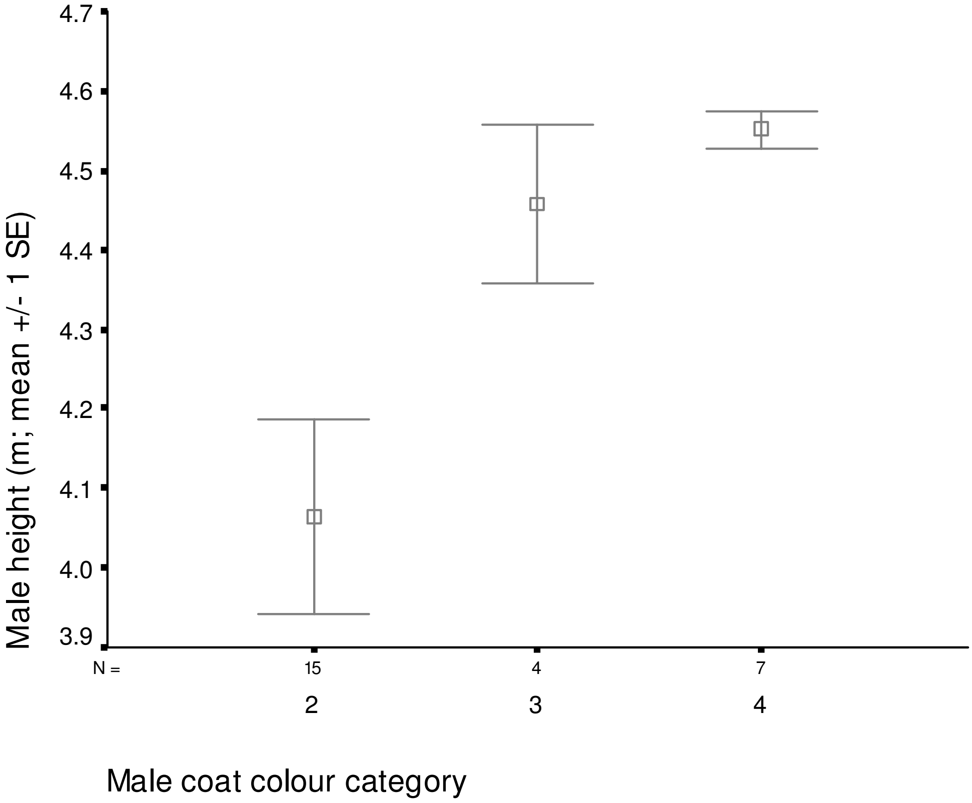


Figure 6.2. Mean estimated heights for adult males of the different colour categories.

Males in Etosha can acquire dark (category 3) colouration by the age of eight or nine years (based on the estimated age of a deceased dark male, aged according to dentition (Hall-Martin 1976)). However, a few pale males appeared at least this old (e.g. M205). The transition from pale to dark colouration was observed in several adult males during the two field seasons, and based on horn development these appeared slightly younger than the deceased male. So development of dark colouration seems to begin typically once males have reached adult height (c. 4.15 m), after sexual maturation and near the age at which males become reproductively active (six or seven years), although it may occur later in some males than in others.

The few dark-coloured adult females were all at least 4.0 m in height, whereas estimated heights of pale adult females ranged from 3.65 m up to the maximum female estimate (4.20 m). One of the three giraffe carcasses found during the field period was of a dark female. Based on dentition (Hall-Martin 1976), her age was estimated to be over 20 years.

6.4.1.2 Coat colour and social behaviour

Displacements were the most commonly observed type of agonistic interaction (N = 55) followed by mild necking (N = 30), then moderate necking (N = 8). Mild necking often led to moderate necking (in which case an observation of moderate necking was recorded), but neither led to intense necking fights. Only three such fights were observed (see Appendix 2 for details). These all began in the same manner as many displacements, with one male approaching another in a ‘proud’ posture, only instead of retreating, the second male responded in kind. Once within ten metres of each other, the males commenced a parallel walk, then approached each other close enough to lean against one another, then abruptly began swinging very heavy blows at each other while attempting to push each other sideways.

These necking fights ended with the winner walking briskly in a ‘proud’ posture behind the retreating loser. In all three cases, the fight took place in the presence of females, and the ‘winner’ succeeded in securing access to females that were previously with the ‘loser’ of the interaction. One third of mild necking interactions occurred in the absence of females, whereas females were present on all eight instances of moderate necking. Mild and moderate necking sometimes lasted up to 20 minutes, with frequent pauses, whereas the contact part of each necking fight was very brief, lasting less than one minute, with blows delivered almost without pause.

To test the predicted relationship between coat colour and social maturity, agonistic interactions were related to the coat colour of the participants. There was a highly significant association between the type of agonistic interaction and the coat colour of the participants (Contingency coefficient = 0.665 N = 185, P < 0.0001; Figure 6.3). All necking fights involved pairs of dark adult males. All but two of the 56 observed displacements 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. With one exception, dark males were never seen to partake in mild or moderate necking.

Necking was not restricted to male-only groups (e.g. Coe 1967); females were absent in less than a quarter of cases of mild or moderate necking, and outnumbered males on almost one-third of occasions. Necking tended to occur in groups with relatively large numbers of pale males when compared to all sightings of groups comprising at least two pale males (median for interactions = 3.0, median for all sightings = 2.0, Mann-Whitney U = 2644.5, N = 246, P < 0.005). Males were never observed to mount one another during this study (e.g. Innis 1958), although this behaviour was seen once between two adult females apparently competing over access to a small water source.

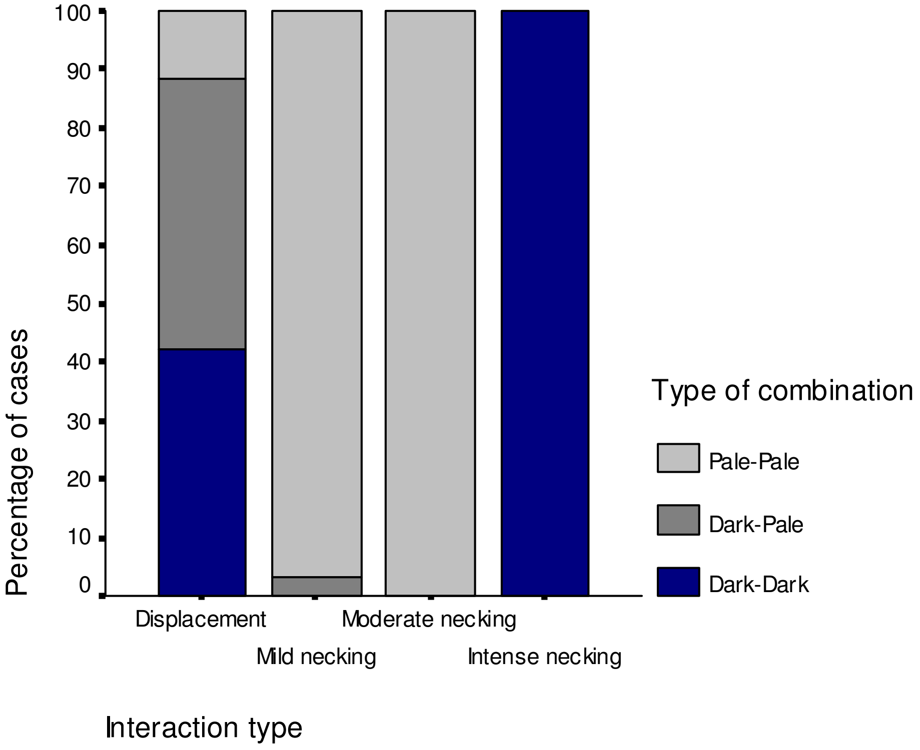


Figure 6.3. Combinations of bulls observed in the different types of agonistic interactions (Dark bull = patch colour category 3 or 4; Pale bull = patch colour category 1 or 2).

6.4.1.3 Coat colour and success in agonistic interactions

To test whether coat colour is a reliable indicator of competitive ability, I examined the difference in coat colour category, and in relative discernable coat colour darkness, between the winner and loser of all dyadic interactions with a clear directional outcome. It was almost always possible to determine the directional outcome of displacements, as the subordinate male always turned or moved away from the dominant 'aggressor'. The directional outcome of mild or moderate necking interactions was more difficult to judge as the interaction often ended with neither male moving away, or both moving away simultaneously. Unfortunately, it was impossible to control for the effects of age in this analysis, due to the difficulties of accurately ageing fully mature, dark giraffe (see section 6.4.1.1).

As expected, the outcomes of displacement interactions and necking fights were significantly biased in favour of the darker male (Figure 6.4). The coat colour of the 'winner' was similar to or darker than that of the 'loser' in 85% of such interactions (comparison with a random distribution of outcomes; Mann-Whitney $U = 794.5$, $N = 48$, $P < 0.005$). The paler male was never the winner when more than four females were present. When restricted to interactions involving only dark males, the winner was still similar to or darker than the loser in 90% of displacements (Mann-Whitney $U = 135$, $N = 20$, $P = 0.057$).

The winner of the three observed necking fights was also the darker of the two males, although in all three cases, both males were assigned to the same colour category. However, the winner was not the older male in two out of these fights (based on horn wear in all cases, and also height in one case).

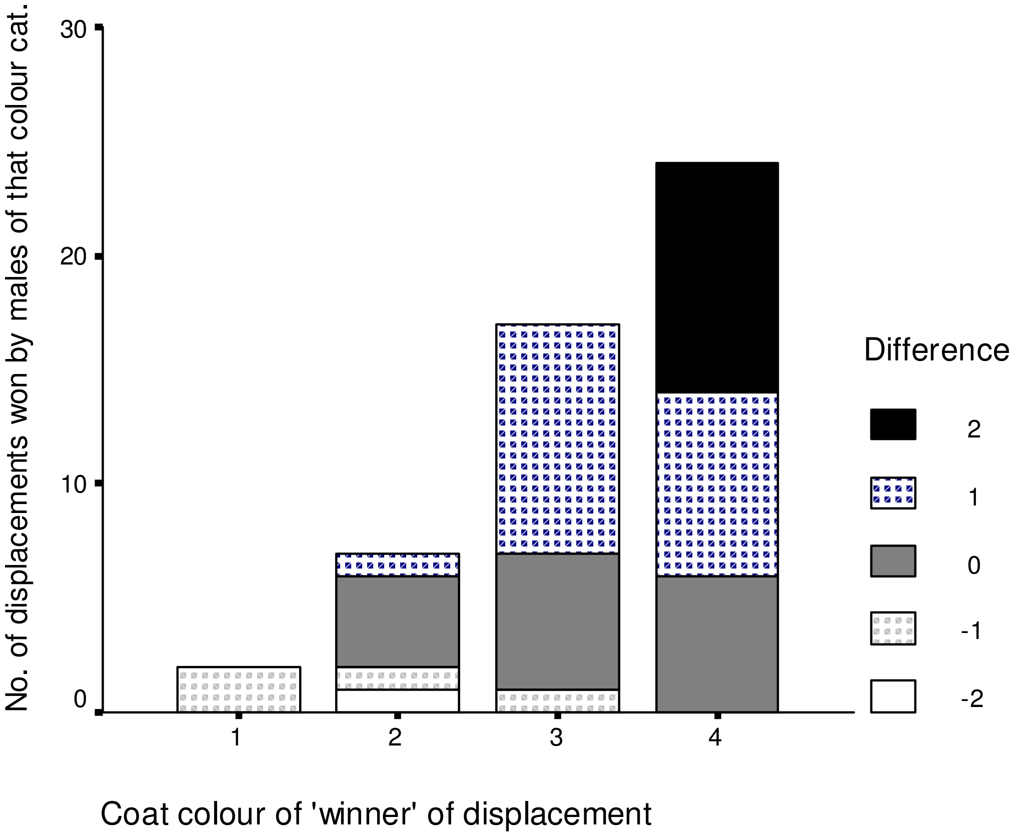


Figure 6.4. Outcomes of displacements, in relation to coat colour of interaction 'winner', and the difference in coat colour category between winner and loser (Difference). Positive values (2, 1) are instances where the loser was paler, negative values (-1, -2) where the loser was darker. Zero indicates no difference in colour category between the winner and loser.

6.4.1.4 Changes in male colouration

It was noted that five pale adult males darkened (to become 'dark males') over a period of more than six months, irrespective of season. An increase in pigmentation was also observed in four dark bulls, over varying periods and seasons. It was predicted that such changes in male coat colour would correspond with changes in male social maturity or competitive ability. Evidence to support this prediction can be drawn from agonistic interactions involving the most frequently observed of these males before and after their colour change (Table 6.1). After the increase in pigmentation, males were unlikely to partake in mild necking (e.g. M97 and M98), and were more likely to challenge very dark males (e.g. M97). They were also more likely to successfully displace other males, whereas before they were more often seen to be displaced (e.g. M98, M238).

Table 6.1. Details of interactions involving males that exhibited changes in coat colouration, with interactions after the change in colour highlighted in bold type.

ID (male 1)	Coat colour category	Other male ID	Other male colour and age class (colour cat.)	Type of interaction	Outcome for male 1
M98	2	M97	Dark adult male (3)	Mild necking	Loser?
	2	M97	Dark adult male (3)	Displacement	Loser
	3	**M297**	**Pale adult male (2)**	**Displacement**	**Winner**
M99	2	N/A			
	3	**M92**	**Dark adult male (3)**	**Displacement**	**Winner**
	3	**M238**	**Dark adult male (4)**	**Displacement**	**Loser**
M97	3	M98	Pale adult male (2)	Mild necking	
	3	M98	Pale adult male (2)	Displacement	Winner
	3	M95	Sub-adult male (2)	Displacement	Winner
	4	**M296**	**Pale adult male (2)**	**Displacement**	**Winner**
	4	**M295**	**Dark adult male (4)**	**Violent fight**	**Loser**
M238	3	M239	Dark adult male (3)	Displacement	Loser
	3	unknown	Dark adult male (?)	Displacement	Loser
	4	**M92**	**Dark adult male (3)**	**Displacement**	**Winner**
	4	**M99**	**Dark adult male (3)**	**Displacement**	**Winner**

6.4.1.5 Female mate choice in relation to male coat colour

Females were predicted to respond to male colour when choosing whether to produce urine for testing by a male when stimulated. It was expected that darker males would be more successful in eliciting urination. Urine-testing was observed in all months, by both dark and pale males in every month (except for December when only pale males were seen attempting to urine-test females). During the last six months of fieldwork, the occurrence of urination or flehmen was recorded on 75% of urine-testing attempts. Flehmen was only observed following urination by the female, but urination was only followed by flehmen 78% of the time. Only dark males were observed not to flehmen when testing female urine.

As predicted, there was a highly significant association between male coat colour and success in eliciting female urination (contingency coefficient = 0.611, N = 32, P < 0.001; Figure 6.5). The one sub-adult male that attempted to elicit urination was unsuccessful. Pale adult males were successful nearly half (46%) of the time, and their success depended on their coat colour: very pale (category one) males were never successful in eliciting urination, whereas category two males often were (75%). Dark males were always able to elicit urination, with the exception of one case: immediately prior to this, the unsuccessful male had been involved in a necking fight with a dark male, and appeared to have defeated him.

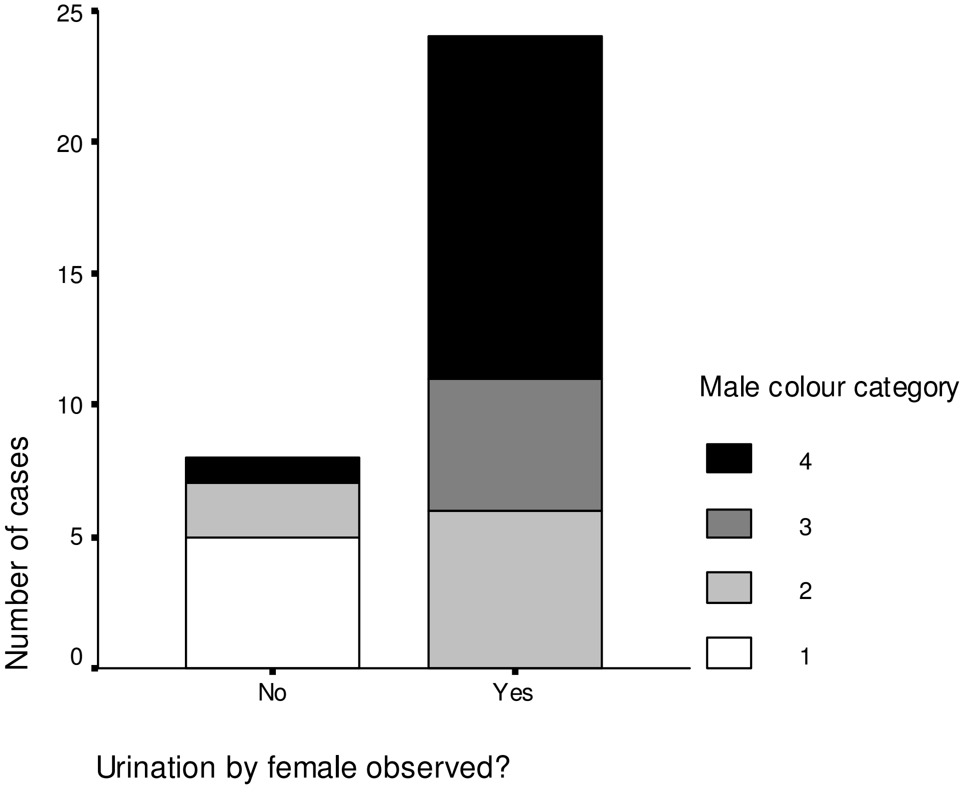


Figure 6.5. Outcome of urine-testing attempts by males, in relation to male coat colour (1-2 = Pale bulls; 3-4 = Dark bulls).

6.4.1.6 Male courtship and mating success in relation to male coat colour

Of the 25 observed consortships in the study area, 80% involved a dark male. This is significantly different from the distribution across dark and pale males that one would expected by chance (dark males made up 53% of known adult males seen in the study area; $X^2 = 7.27$, df = 1, $P < 0.01$). 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 (but with well developed skull ossifications).

6.4.2 Hypothesis 2: Waterholes as focal points for intercepting females

6.4.2.1 Summary of focal watch data collection

A total of 166 focal watches were carried out, with the following composition of locations and focal subject types:

	Females	**Pale males**	**Dark males**	**Total**
Waterhole (WH)	40	21	19	**80**
Non-Waterhole (NWH)	37	26	23	**86**
Total	**77**	**47**	**42**	**166**

The average focal watch duration was 48 minutes. Potentially confounding variables were tested for differences between waterhole and non-waterhole watches. There was no significant difference in the duration of the focal watch (Mann-Whitney U-test: U = 3011, P = 0.140), the total giraffe group size (U = 3340, P = 0.745), or the mean number of giraffe visible throughout the watch (square-root transformed, t = 1.021, P = 0.309). However, visibility was significantly better at waterholes, as indicated by the ratio of the mean number of giraffe visible during the watch to the known total group size (median WH ratio = 0.93; median NWH ratio = 0.83; U = 2600, N = 166, P < 0.01).

6.4.2.2 Likelihood of encountering new giraffe at waterholes

Rates of formation of new encounters between previously un-associated giraffe were predicted to be greater at perennial waterholes than away from waterholes. In support of this prediction, it was found that giraffe were significantly more likely to have new encounters with other giraffe during focal watches at waterholes than at locations away from waterholes. Overall, for every 100 observation hours, 54 new male-female encounters and only 9 new male-male encounters occurred at non-waterhole sites, whereas at perennial waterholes this rate was 215 new male-female encounters and 151 new male-male encounters. These new encounter rates deviate significantly from those expected assuming a uniform distribution of new encounters across the two types of location (new male-female encounters: $X^2 = 96.26$, df = 1, P < 0.001; new male-male encounters: $X^2 = 126.03$, df = 1, P < 0.001).

6.4.2.3 Comparison of social interaction rates at waterholes versus other locations

As a consequence of the relationship between waterholes and increased rates of new encounters, it was predicted that interactions between giraffe should occur at an increased rate at waterholes. This prediction was also supported by the data: for both mating and agonistic interactions, the increased occurrence of new encounters was associated with an increase in the likelihood of giraffes interacting during a focal watch (mating interactions: $X^2 = 29.97$, df = 1, $P < 0.001$; agonistic interactions: contingency coefficient = 0.367, df = 1, $P < 0.001$; Figure 6.6). For agonistic interactions, this relationship still holds true if the analysis is restricted to displacements only (i.e. excluding necking; contingency coefficient = 0.266, df = 1, $P < 0.001$).

As a result, both mating and agonistic interactions were more likely to occur during focal watches at waterholes than during watches away from waterholes: for every 100 hours of observations, 35 mating interactions and 13 agonistic interactions occurred at non-waterhole sites, whereas 108 mating and 59 agonistic interactions occurred per 100 hours at perennial waterholes. Again, these frequencies deviate significantly from a uniform distribution (mating interactions: $X^2 = 37.37$, df = 1, $P < 0.001$; agonistic interactions: $X^2 = 29.39$, df = 1, $P < 0.001$). If agonistic interactions are restricted to displacements only, they were still more likely to occur at waterholes (30 displacements at waterholes, 7 elsewhere; $X^2 = 14.30$, df = 1, $P < 0.001$).

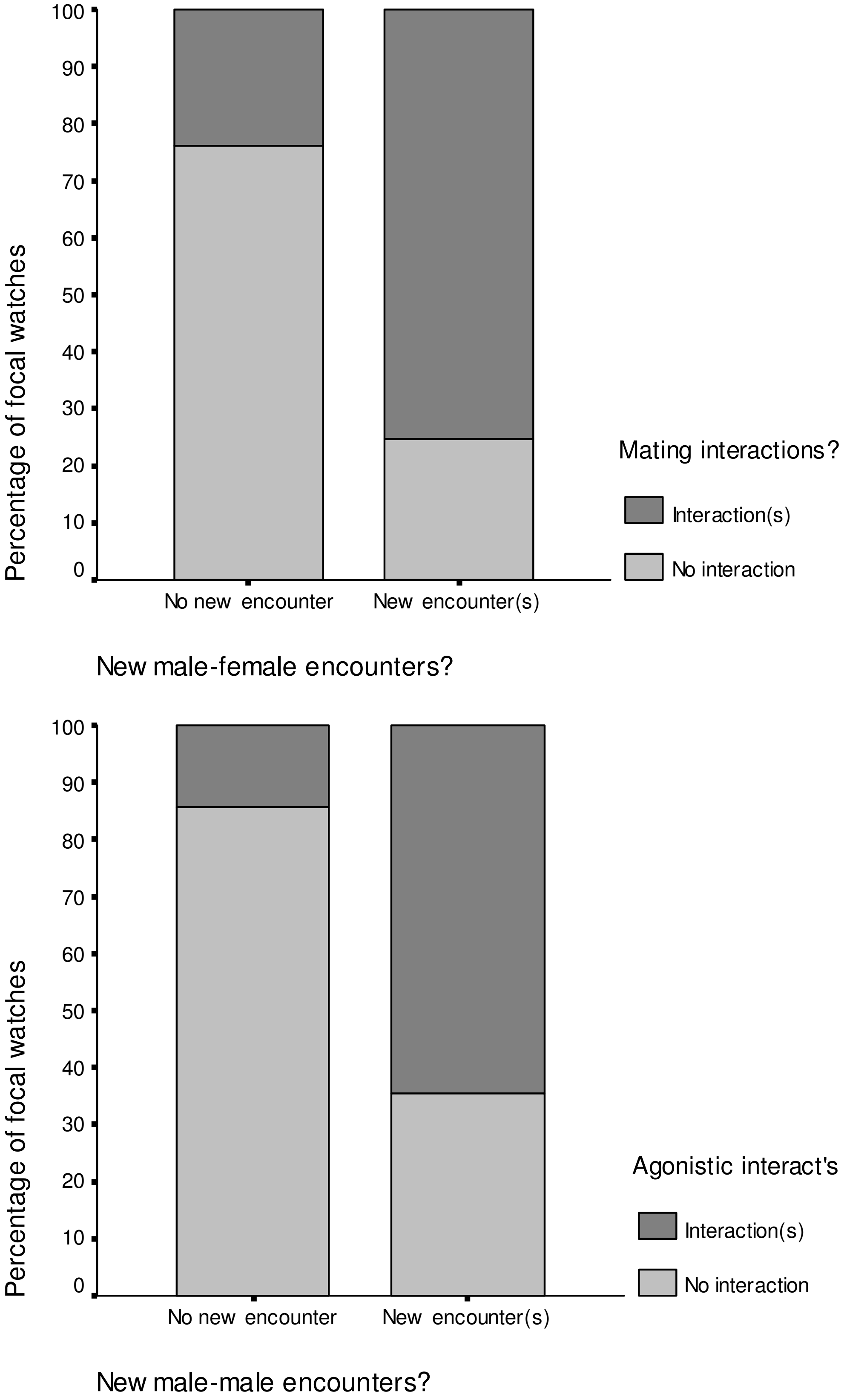


Figure 6.6. Occurrence of social interactions relative to occurrence of new encounters during focal watches, for mating interactions and male-female encounters (top) and agonistic interactions and male-male encounters (bottom).

Furthermore, during focal watches when new male-female encounters and mating interactions did occur, the rate of interactions per hour increased as the number of potential interacting pairs (total males multiplied by total females) present during the watch increased (variables log-transformed, $F_{1,23} = 10.58$, $P < 0.005$, $R^2 = 0.5325$; Figure 6.7). Thus interactions tended to be more frequent in groups with large numbers of males and females. There was not as clear a trend for male-male encounters and agonistic interactions, partly because of a smaller sample size. However, the rate of agonistic interactions per hour did increase with an increasing new male-male encounter rate per hour (variables log-transformed, $F_{1,10} = 5.971$, $P < 0.05$, $R^2 = 0.399$).

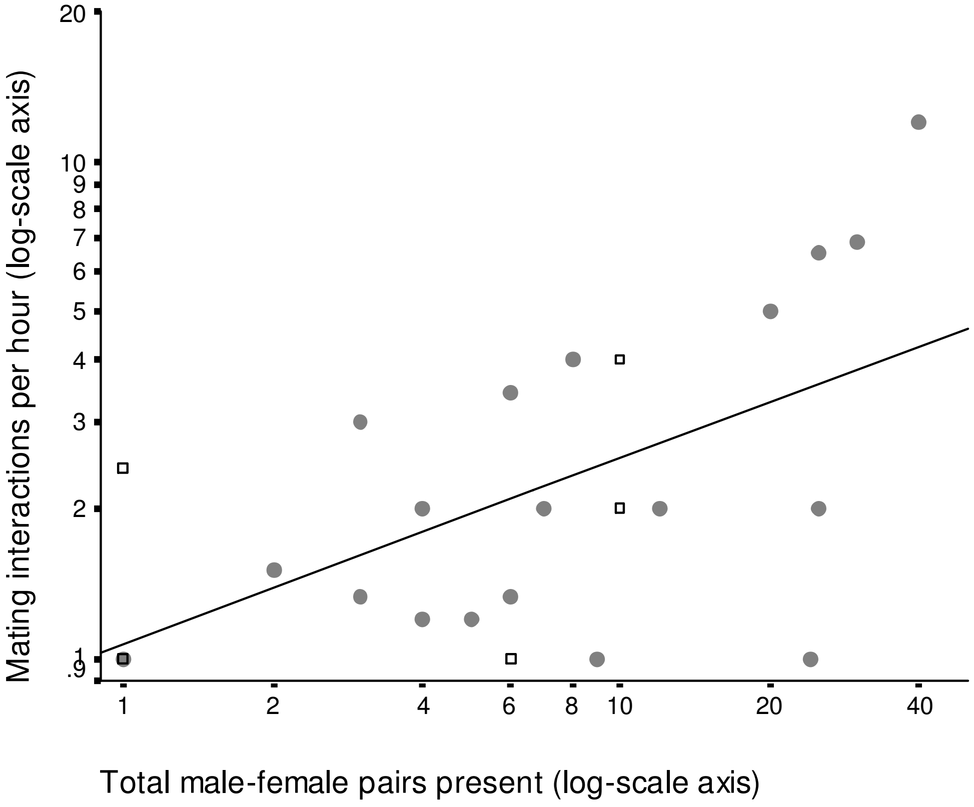


Figure 6.7. Relationship between mating interaction rate and the total number of potential male-female pairs (total males multiplied by total females) present during the focal watch. Grey circle markers indicate waterhole watches; empty black squares indicate non-waterhole watches.

6.4.2.4 Effect of seasonal water availability on encounters and interactions at waterholes

It was predicted that the effect of waterholes on increasing rates of new encounters and social interactions would be greater in the dry season (as defined in Chapter 2), when water is a more limited resource, than during the wet season. New male-female and male-male encounter rates (per 100 hours observation) were significantly greater at waterholes than at non-waterhole locations in both the wet and dry season (wet season: male-female: $X^2 = 64.93$, $P < 0.001$, male-male: $X^2 = 50.97$, $P < 0.001$; dry season: male-female: $X^2 = 106.51$, $P < 0.001$, male-male: $X^2 = 148.97$, $P < 0.001$), even after application of a Bonferroni correction for multiple tests (alpha value for each test reduced to 0.0125).

Mating interaction rates also were significantly greater at waterholes than away from waterholes in both seasons, although at a seasonal level, mating interactions occurred at a greater relative rate at waterholes in the dry season ($X^2 = 140.70$, df = 1, $P < 0.001$) than during the wet season ($X^2 = 6.90$, df = 1, $P < 0.01$). Agonistic interactions remained significantly more frequent at waterholes during both seasons (wet season: $X^2 = 35.63$, $P < 0.001$, dry season: $X^2 = 25.33$, $P < 0.001$). Thus, the predicted seasonal effect was not substantiated.

Nonetheless, a greater proportion of observed urine-testing attempts occurred at waterholes during the dry season and early wet season (at least 50% each month from July to December compared to no more than 40% each month from March to June; Figure 6.8). In fact, there was a highly significant relationship between the predictability of female giraffe at waterholes each month (percentage of visits to waterholes on which females were present), and the proportion of urine-testing events that were observed at waterholes (Spearman's rho = 0.796, N = 10, $P < 0.01$; Figure 6.9).

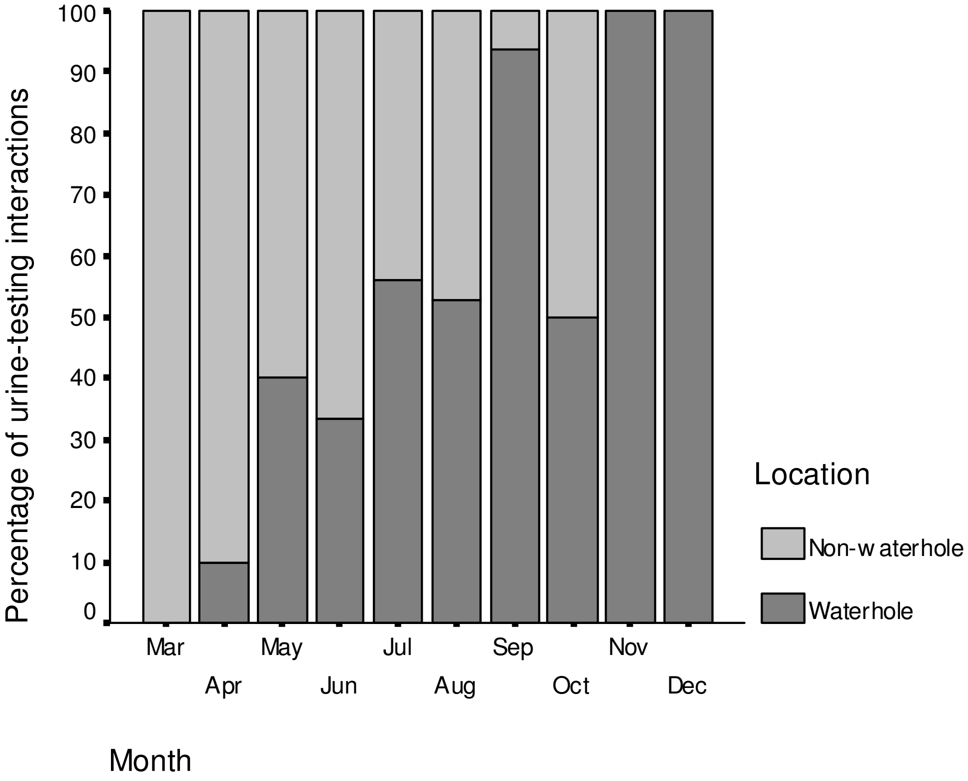


Figure 6.8. Location (waterhole vs. non-waterhole) of urine-testing attempts across the months.

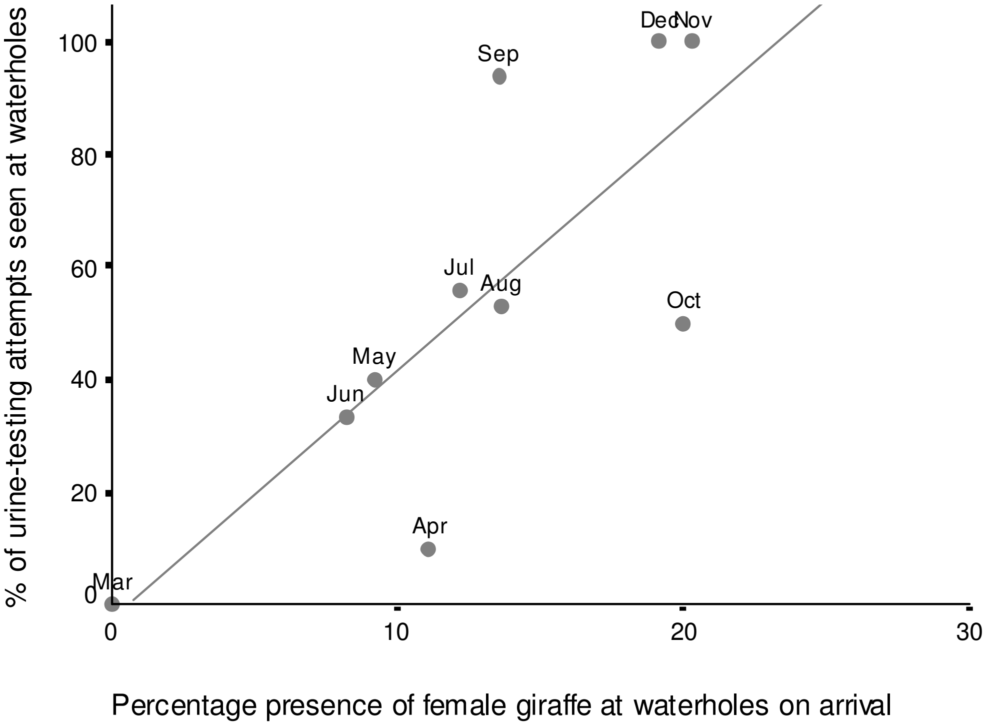


Figure 6.9. Relationship between location of urine-testing events and monthly predictability of female giraffe at waterholes.

6.4.2.5 Locations of consortships in relation to waterholes and water availability

It follows from the above findings (i.e. a higher proportion of urine-testing events occurring at waterholes in the dry season) that consortships should be expected to begin in closer proximity of waterholes during the dry season. Of the six consortships that were observed from the start (from the moment of the first encounter and urine-testing), the majority (N = 5) did indeed begin at a waterhole; all but one consortship observed away from waterholes were ongoing interactions. However, the prediction did not hold up when the distance of all consortships to water was examined: overall, consortships were not observed any closer to perennial waterholes during the dry season than during the wet season (wet season median distance = 0.285 km; dry season median distance = 0.550 km; Mann-Whitney U = 56, N = 25, P = 0.311).

6.4.2.6 Competition between dark males at waterholes versus away from waterholes

It was predicted that during the dry season (as defined in Chapter 2), competition between dark males would be more intense at waterholes than away from waterholes, because of the more predictable occurrence of females at waterholes during this time. However, on all occasions when two dark males were observed already associating in the same group (N = 30), whether at a waterhole or not, they did not demonstrate any sign of dominance, submission, or aggression towards each other, and were generally both browsing, both resting, or both walking. When two dark males were seen to encounter each other, they did participate in an agonistic interaction on both occasions that this was seen away from waterholes, whereas at waterholes, there was no evidence of an agonistic interaction (no demonstration of dominance or submission by either male) on five out of twelve occasions. Therefore, contrary to the predicted effect, dark males actually appeared to be more tolerant of each other at waterholes than at locations away from waterholes, although this association was not significant (contingency coefficient = 0.291, N = 14, P = 0.255). These results were not affected by limiting the analysis to occasions when females were present.

6.4.3 Hypothesis 3: Seasonal variation in the intensity of male intra-sexual competition

It was predicted that intra-sexual competition would differ in intensity between the wetter, high-conception-rate season, and the drier, low-conception-rate season, due to differences in spatial distribution and predictability of females. Specifically, it was predicted that the prolonged, predictable high concentration of females in mixed broadleaf woodland throughout the wet season would provide dominant males with an opportunity to exclude subordinates and monopolise access to females. I tested this prediction firstly by examining seasonal variation in rates of mating and agonistic interactions, and by testing for seasonal differences in the social class of participants in urine-testing attempts and directional agonistic interactions (displacements).

6.4.3.1 Seasonal variation in mating interactions

Urine testing was observed in all months, by both dark and pale males in every month (except for December when only dark males were seen attempting to urine-test females). When compared to either the number of mixed-group sightings each month, or the number of field-hours, the rate of urine-testing attempts and consortships were greatest in March and lowest in November and December. The only three attempted and successful copulations were seen in May, July and November (for detailed descriptions of mating interactions, see Appendix 3).

Very pale males (cat. 1) were only observed attempting to elicit urination in June and between August and November (Figure 6.10). Dark adults (category 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%). As predicted, there was a significant association between the colour of the male involved in urine-testing and the season (wet, higher-conception rate versus dry, low-conception rate season; contingency coefficient = 0.293, N = 146, $P < 0.005$), with more pale males involved in urine-testing attempts in the dry season.

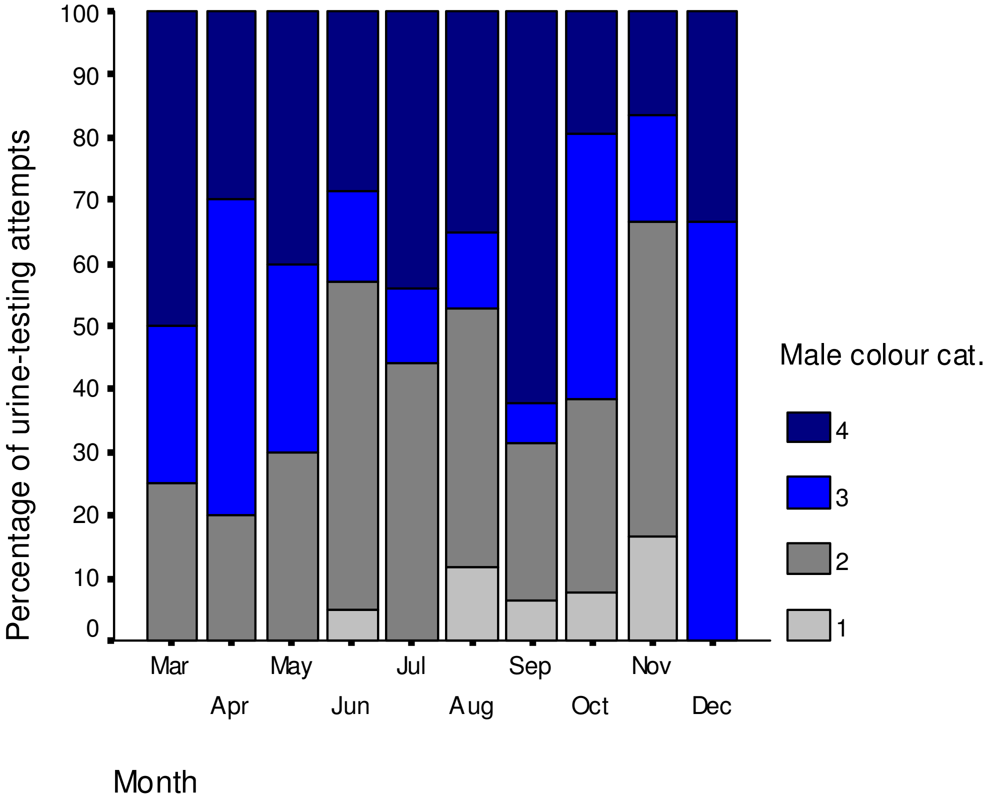


Figure 6.10. Colour category of males observed attempting to urine-test females across the months.

6.4.3.2 Seasonal variation in agonistic interactions

Displacements (N = 55) were observed in all months except for November. Mild necking (N = 30) was observed in all months except March, and moderate necking (N=8) in May, June, July, November and December only. Only three necking fights were observed, and these occurred in April, May and October. Overall, agonistic interactions between males, relative to monthly sightings of adult males, were most frequently observed between March and July, and in December.

Displacements in March and December involved only pairs of dark bulls, whereas pairs of pale bulls were only observed in displacement interactions between July and October (Figure 6.11). In August, no agonistic interactions were observed between two dark bulls. However, there was no association between breeding season (wet, higher-conception-rate versus dry, lower-conception-rate season) and the type of participants in displacements (contingency coefficient = 0.225, N = 52, P = 0.250).

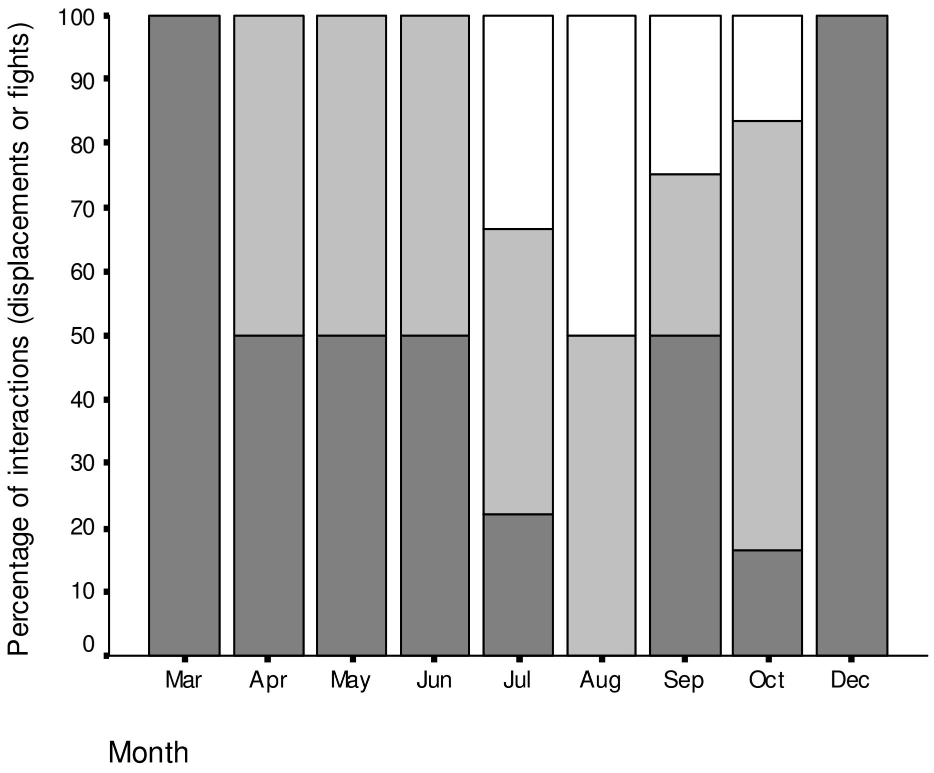


Figure 6.11. Pairs of males involved in displacement interactions across the months. Dark grey bars represent pairs of dark males (cat. 3-4); light grey bars represent pairs comprising one dark and one pale male (cat. 1-2); white bars represent pairs of pale males.

6.4.3.3 Seasonal variation in the relationship between associating dark males

Next, I tested for seasonal differences in the type of relationship (agonistic or neutral) between two dark males seen in close proximity (<500 m) of one another (N = 65). There was clear seasonal variation in the type of association between two bulls: between March and June, two dark bulls together were significantly more likely to be involved in an agonistic interaction (i.e. a displacement or necking fight) than a neutral relationship (i.e. no interaction; $X^2 = 21.06$, df = 1, P < 0.001), whereas between July and December, the majority (80%) of dark bull pairs observed did not demonstrate any sign of dominance, submission, or aggression towards one another (Figure 6.12). However, this seasonal difference was not associated with seasonal variation in conception rate (higher-conception-rate versus lower-conception-rate season; $X^2 = 0.157$, df = 1, P = 0.692).

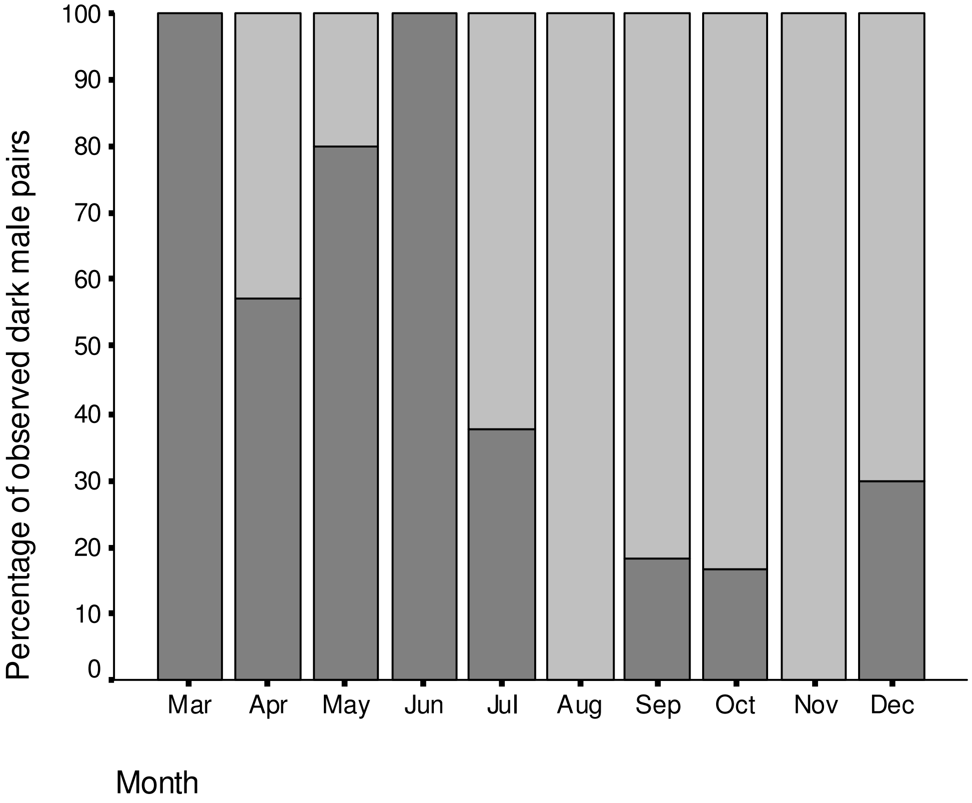


Figure 6.12. Relationships between two dark males observed together across the months. Dark grey bars represent agonistic relationships (e.g. displacements, necking fights); light grey bars represent an absence of such agonistic interactions.

However, there was a highly significant association between the season (higher-conception-rate versus lower-conception-rate season) and whether females were present when dark males were associating (X^2 = 8.991, df = 1, P < 0.005; Figure 6.13). There was no direct relationship, though, between the presence of females and whether males were associating in an agonistic or neutral relationship (X^2 = 0.969, df = 1, P = 325).

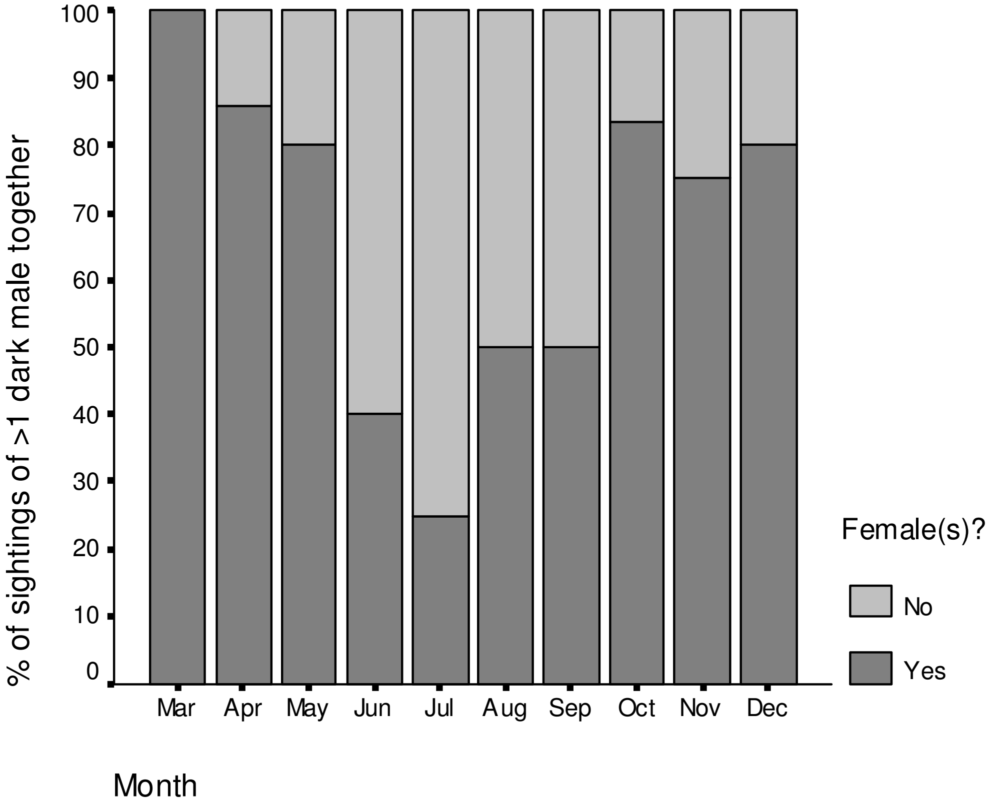


Figure 6.13. Presence or absence of females when two dark males were observed together. The wet, higher-conception-rate season covers March to May and October to December.

6.4.4 Hypothesis 4: Monopolisation of mates by dark males to the exclusion of pale males

It was predicted that dominant males would compete most intensely to exclude subordinates when females were most predictably concentrated and potentially economically defendable (at least in the short-term). In the longer term, it was predicted that the most dominant males would consistently monopolise access to females, and a large proportion of males, specifically pale, subordinate males, would be excluded from mating.

6.4.4.1 Exclusion of pale males from mixed groups by dark males

Mixed groups without a dark male contained slightly more males in months when mean female group size was also larger (March - July versus August - December: t = 1.856, df = 178, P = 0.065). But when a dark male was present, mixed groups contained slightly fewer males in those months when mean female group size was largest (March - July versus August - December: t = -1.936, df = 220, P = 0.054), particularly in March, when dark males appeared to almost exclude pale males from mixed groups (Figure 6.14).

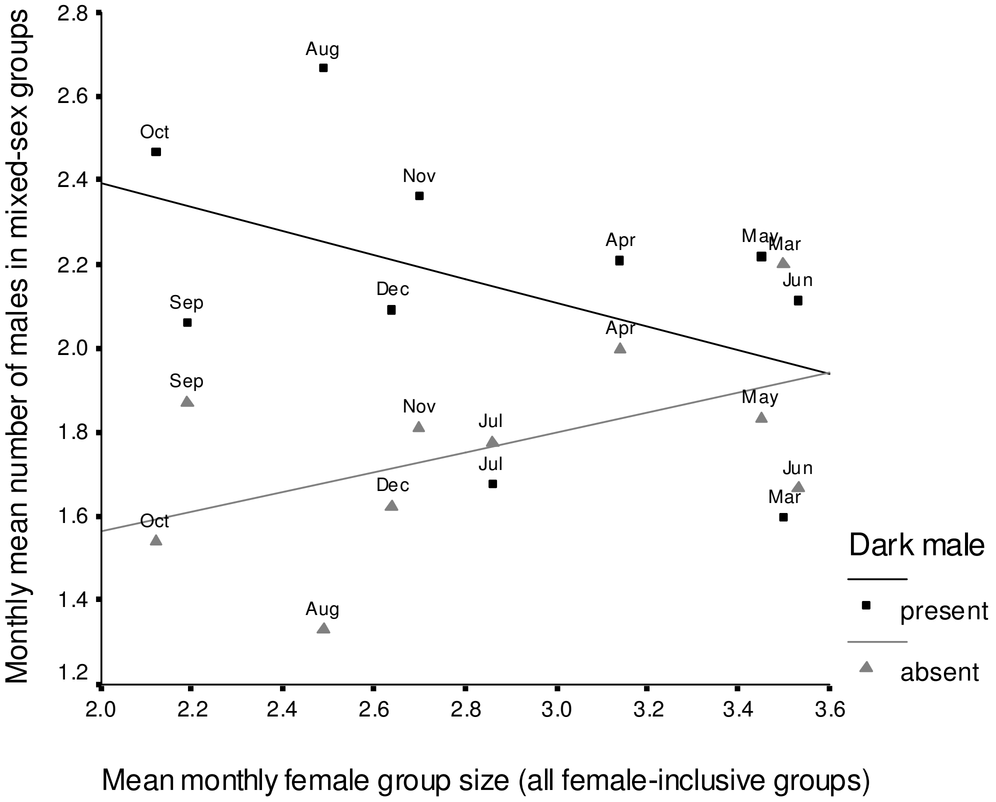


Figure 6.14. Monthly mean number of males in mixed-sex groups, relative to monthly mean number of females in all female-inclusive groups, for groups with a dark male (black squares), and groups without a dark male (grey triangles).

6.4.4.2 *Effect of location and group size on the ability of dominant males to exclude subordinates*

Pale males were more likely to associate closely with females at waterholes than away from waterholes. Using the data from focal watches, the sex-age classes of nearest neighbours (when identified) were compared for different types of focal subject in mixed groups. A dark male focal subject was significantly more likely than a pale adult male to have an adult female as a nearest neighbour when not at a waterhole (69% versus 43%; X^2 = 16.056, N = 237, df = 1, P < 0.001; Figure 6.15). At waterholes, however, pale adult males were equally likely as dark adult males to have an adult female as a nearest neighbour (49% and 55% respectively; $X^2 = 0.422$, N = 146, df = 1, P = 0.516). Similarly, female focal subjects were twice as likely to have a pale male as a nearest neighbour at waterholes as away from waterholes (analysed with three categories of nearest neighbour: dark adult male, pale adult male, or other: $X^2 = 9.81$, N = 430, df = 2, P < 0.01).

Between dark males of different coat colour category (3 and 4), there was no significant association between coat colour and the proportion of occasions on which an adult female was the nearest neighbour at waterholes ($X^2 = 1.92$, N = 51, df = 1, P = 0.166). Away from waterholes, males of colour category 3 were significantly more likely to have an adult female as nearest neighbour than males of category 4 (82% and 55% respectively; $X^2 = 10.09$, N = 122, df = 1, P < 0.005).

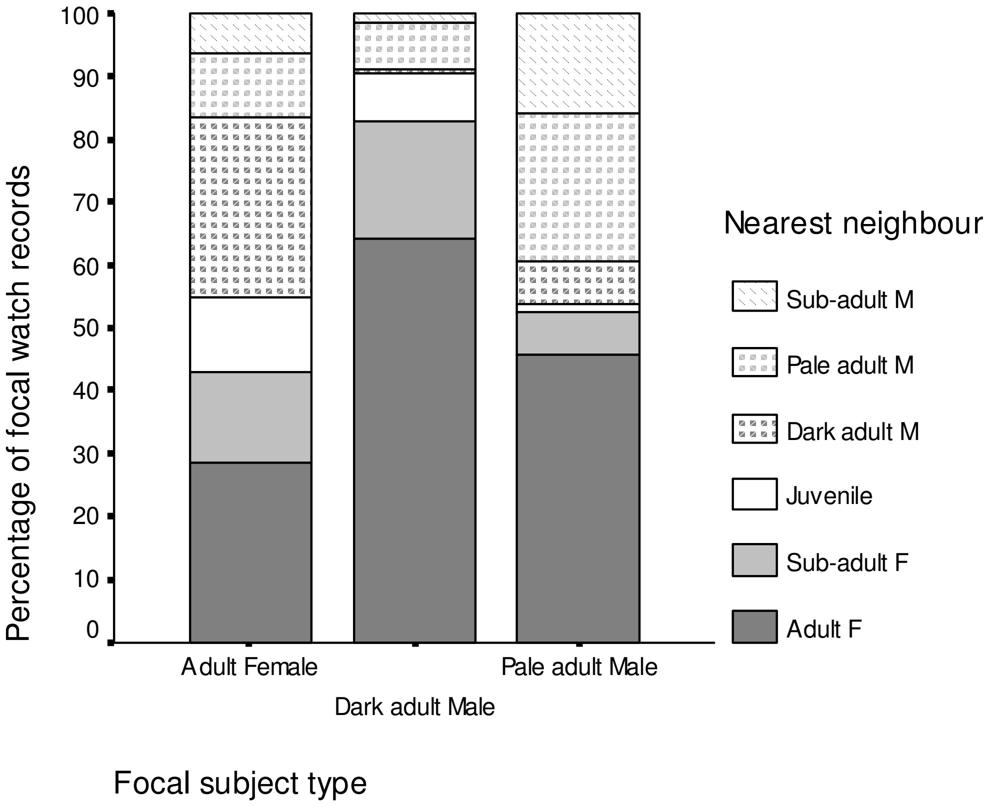


Figure 6.15. Nearest neighbour type for adult focal subjects (adult female, dark adult male, pale adult male) during focal watches both at waterholes and away from waterholes.

Paler males were also significantly more likely to attempt to test females' urine at waterholes than away from waterholes, when compared to darker males (contingency coefficient = 0.239, N = 146, $P < 0.05$; Figure 6.16). 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 (49%) and pale males (51%). 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 (dark male present on 70% of occasions at waterholes, 45% away from waterholes; $X^2 = 3.03$, N = 51, df = 1, P = 0.082). Among interactions involving dark males, 60% involved a male of colour category 4 both at waterholes and away from waterholes.

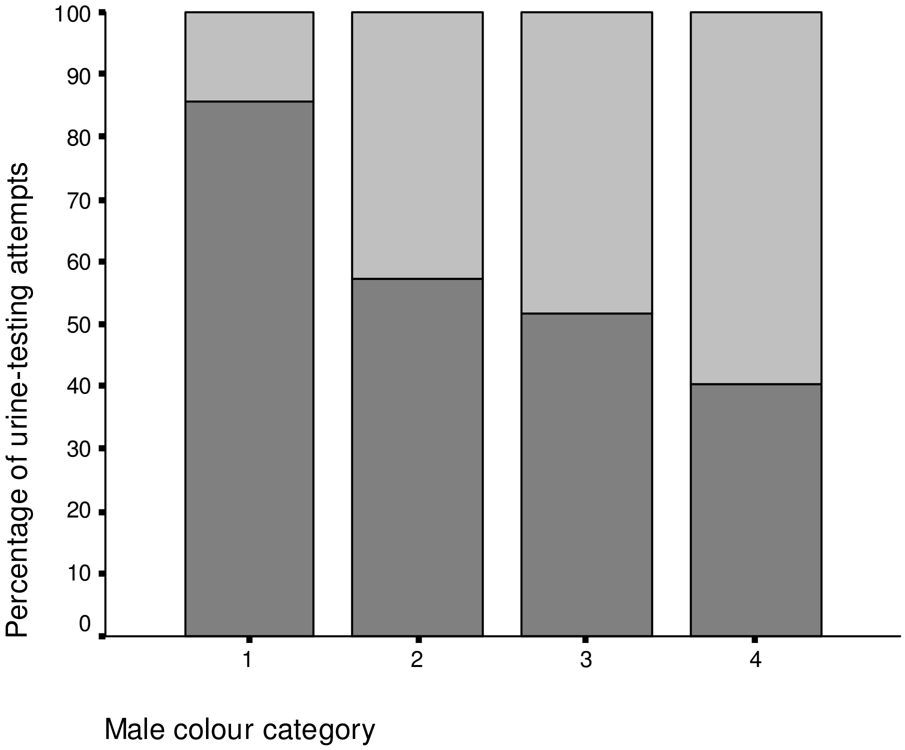


Figure 6.16. Location of urine-testing attempts in relation to male coat colour category. Light grey bars represent non-waterhole observations; dark grey bars represent observations at perennial waterholes.

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. Thus very pale adult males (category 1) and sub-adult males had access to females for urine-testing predominantly when there were large numbers of pale males present (Figure 6.17).

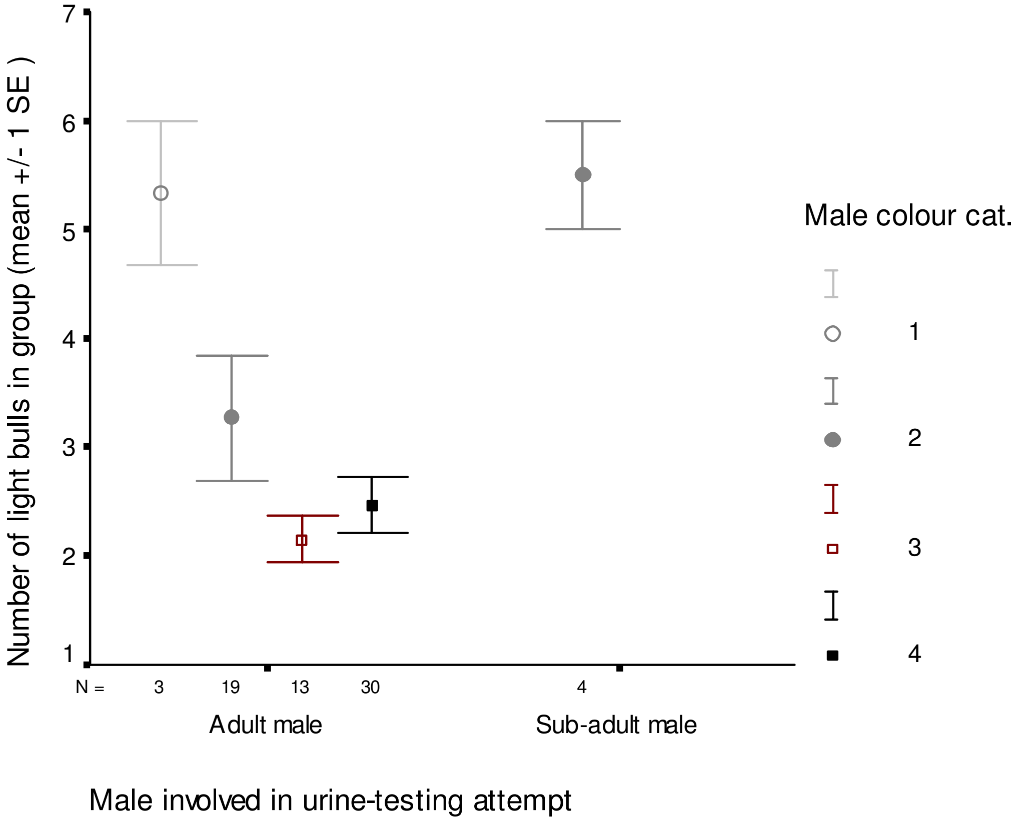


Figure 6.17. Number of pale males present during urine-testing attempts by males of different coat colouration categories, in groups with at least one pale male and at least one dark male.

6.4.4.3 Reproductive skew and surrogates of potential reproductive success

Of the 25 observed consortships in the study area, 80% involved a dark male. Half of the dark males seen in a consortship were category three males, half category four. Category four males were involved in a smaller proportion of consortships in the dry season (29%) than in the wet season (63%). Nonetheless, pale males were not seen in a greater proportion of observed consortships in the dry season (wet season: 25%, dry season: 16%): not more than one observed consortship per month involved a pale adult male, even in July, when nine consortships were observed.

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. Thus, the dark male always gained rights to the consortship (N = 4), regardless of the number of pale males also present and urine-testing females. Consequently, all five observed consortships involving a pale male were in the absence of a dark male, including the two seen from the start (one at a waterhole, one away from a waterhole). However, in two of these five 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 mating attempt.

Two successful matings and one attempted mating were observed. All involved a dark, mature male (Figure 6.18), two of category four coat colouration, one of category three (but with well developed skull ossifications). Based on these behavioural data, it is estimated that pale adult males, which represent just fewer than 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.

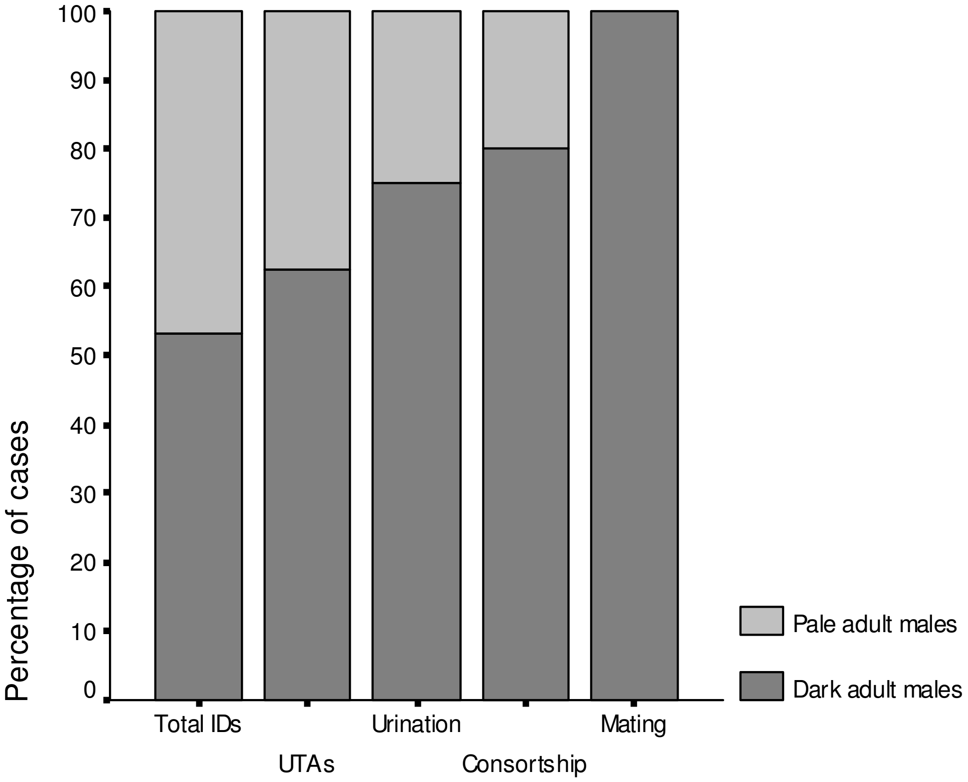


Figure 6.18. Relative share (%) of dark and pale adult males in: total known males in the study area, urine-testing attempts (UTAs), successful elicitation of urination, consortships, and attempted or successful matings.

It was evident from the findings in this chapter that both mate detection (or scramble competition (Schwagmeyer 1988; Ims 1990)) and 'priority of access' (Altmann 1962; Cowlishaw & Dunbar 1991) were important in determining male access to potential mates. Therefore, it was predicted that two key factors in determining current individual mating success would be the relative amount of time a male spent with females (to maximise his chances of encountering a receptive female), and the number of times a male had priority of access, in other words, when he was in a position to monopolise access to any receptive females. From observations of consortships (section 6.4.8.4), it was evident that this potential for monopolisation was greatest when a male was the only male or the most dominant male in a group with females. Unfortunately, dominance interactions were too few to permit an unambiguous determination of relative dominance among males present in each group, but it was assumed, based on results cited above, that an adult male would always be dominant to a sub-adult, and a dark male always dominant to a pale male.

Thus, males that were sighted most frequently (on at least 5 days) were plotted on a graph in relation to two variables relating to association with females, which were predicted to affect potential mating success:

- percentage of observations on which the male was in the presence of females;
- percentage of these observations on which the male was undoubtedly the dominant, or only, male (i.e. the only adult male for pale adult males, and the only dark male for dark males).

By highlighting on this graph the three males that had been observed in an attempted or successful copulation, and the one male that had been observed in two separate consortships, a clear pattern arose: these males were all located in the upper right-hand corner, corresponding to a high proportion of time with females, and a high proportion of time as the only, or dominant, male (Figure 6.19).

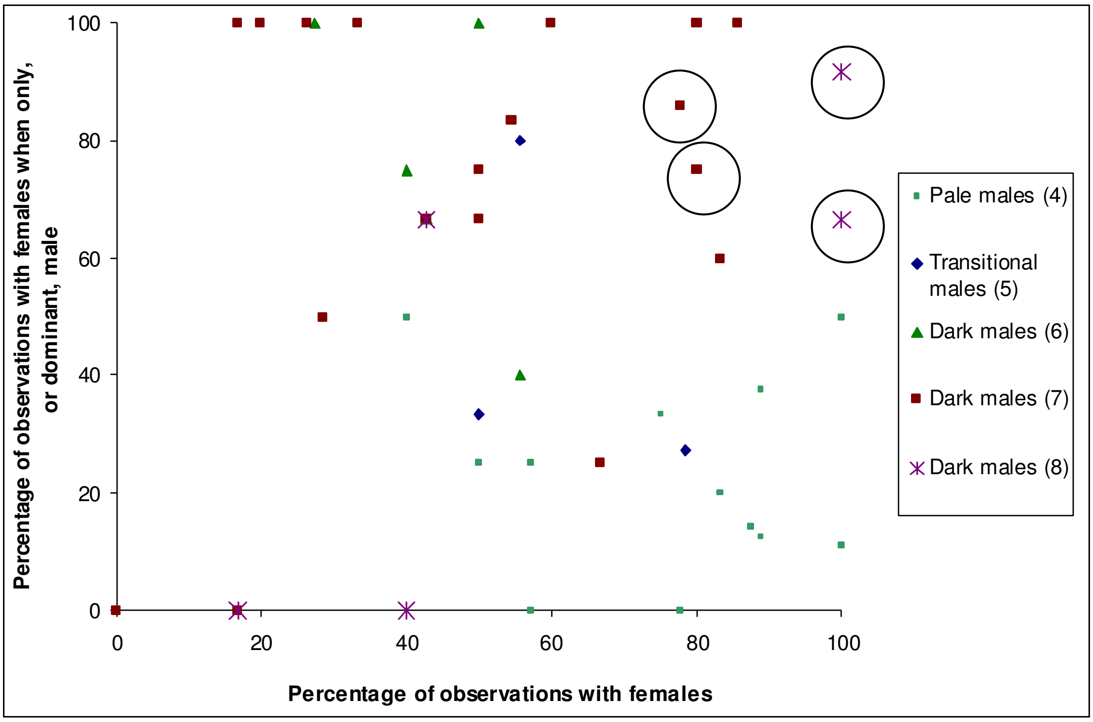


Figure 6.19. Plot of individual male association with females (percentage of observations with females), and potential for monopolisation of females, as measured by the percentage of sightings with females when the male was the only, or most dominant, male in the group. Points representing males that were seen in an attempted or successful copulation, or multiple consortships, are highlighted by a circle. Figures in brackets in the legend are maturity classes.

Subsequently, the two variables were multiplied together to obtain one single value taken to represent the male's monopolisation potential, or potential mating success. All males seen in an attempted or successful mating, and the one male seen in two separate consortships, had values of 0.6 or greater (Figure 6.20). From this, it was evident that a few dark, mature males of maturity categories 7 and 8 had the greatest potential mating success, whereas pale adult males (maturity category 4), transitional males (category 5), and young dark males (category 6) had the lowest probable chance of securing matings. However, many older dark males (category 7 and 8) also had low expected mating opportunities, so mating success may not be strictly age-dependent, and may indeed be highly skewed in favour of a small number of mature, dominant, dark males.

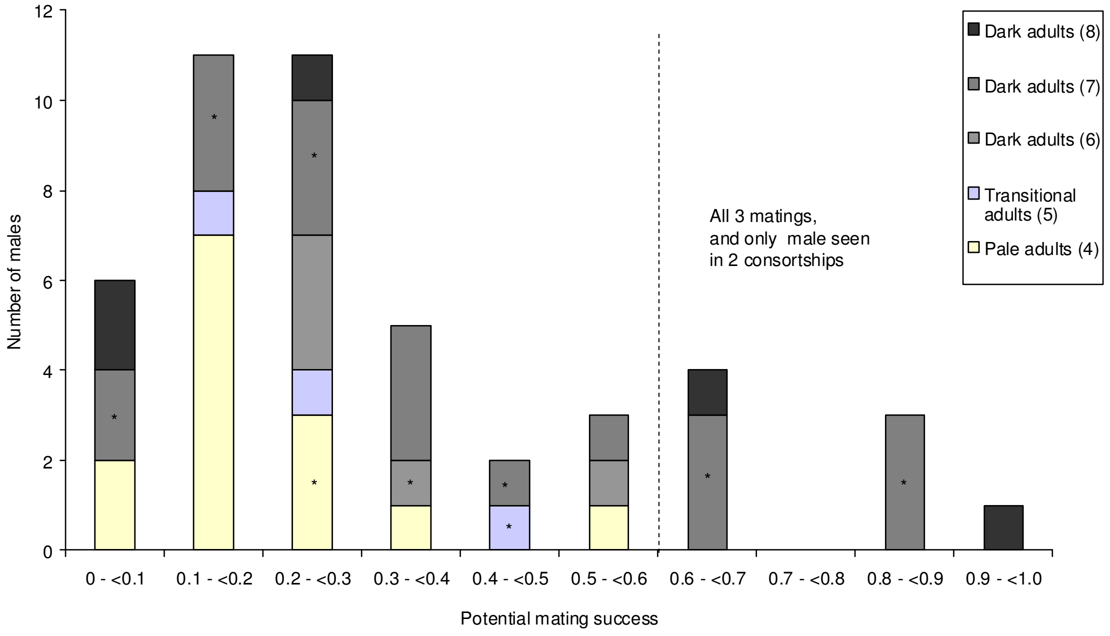


Figure 6.20. Individual male potential mating success, based on a value representing the combined effects of male association with females and male potential for monopolisation (the percentage of observations with females that the male was the only or most dominant male). All males observed in an attempted or successful copulation, and the one male observed in two separate consortships, are located to the right of the dashed line. Asterisks represent all other observed consortships. Colour break-down represents male coat colour (and maturity classes).

Unfortunately, the molecular assignment of paternity, and thus estimation of actual reproductive success, was unsuccessful, largely due to insufficient variability in the genetic markers used (the molecular methodology and results are treated in detail in

Appendices 8 to 12). It was also not possible to use behavioural measures to gauge longer-term differences between individuals in key factors that would affect lifetime reproductive success, such as tenure of dominance status.

6.4.5 Summary of results

The main findings of this chapter, in relation to the predictions made in the Aims section (6.2) at the start of this chapter are summarised in the table below.

Table 6.2. Summary of the results of chapter 6, in relation to the hypotheses and predictions outlined at the start of the chapter.

	Prediction supported by data?
Hypothesis 1 predictions:	
Male coat colour corresponds to maturity and behaviour	Yes
Darker males taller than paler males	Yes (largely)
Darker males win displacements	Yes
Changes in colour correspond with changes in status	Possibly
Darker males more successful in eliciting urination by females	Yes
Darker males more successful in consortships and matings	Yes
Hypothesis 2 predictions:	
Rate of new encounters greater at waterholes	Yes
Rate of mating and agonistic interactions greater at waterholes	Yes
Effects greater in dry season	No
Consortships closer to waterholes in dry season	No
Greater intensity of competition at waterholes (in dry season)	No
Hypothesis 3 predictions:	
Seasonal variation in intensity of male-male competition	Maybe (greater participation of pale males in dry season)
Hypothesis 4 predictions:	
Exclusion of pale males from mixed groups by dark males	Yes
Exclusion of pale males from associating with females	Yes (but not at waterholes or when many males)
Mating success skewed in favour of dark males	Yes
Variation among dark males in probable mating success	Yes

6.5 Discussion

6.5.1 Hypothesis 1: Male coat colouration as a status signal

Here, I have presented evidence in support of the hypothesis that dark male coat colouration functions as a signal of status, indicating social maturity, competitive ability, and consequently probable reproductive success.

6.5.1.1 Coat colour and maturity

Dark colouration (versus pale colouration) is a clear indicator of males having reached sexual maturity: dark colouration was observed only in fully mature adult males, and all old males (with advanced secondary skull ossifications) were very dark in colour. Darker males generally tended to be taller than paler males. However, some pale males were found to be as large as, or even larger than, dark males. Thus, within middle-aged males there may not be a direct relationship between age (as indicated by height) and colour. The relationship between colour and age in older males could not be assessed because of the unreliability of height as a measure of age in fully mature males.

It has been shown that in mature male fallow deer, dominance is more important than age in determining reproductive participation, suggesting that achievable dominance status and reproductive success are not entirely age-dependent (Komers *et al.* 1997; Thirgood *et al.* 1999). If this is also true for giraffe, then if male colouration is a true indicator of status, it may develop in relation to male quality and status rather than directly in relation to age (e.g. Setchell & Dixson 2002). Pratt and Anderson (1985) also found that certain morphological traits, such as neck thickness, were better predictors of male success in pair-wise interactions than male height.

It is proposed here that all males should eventually achieve dark colouration (excepting premature mortalities), but that the age at which such colouration is achieved, and the degree of darkness achieved, may vary among males in relation to male status. Since height varies so little among fully mature males, coat colour could potentially be a more informative signal of competitive ability (maybe assessed in conjunction with height), especially if it relates to other traits that affect competitive ability, such as body condition, or fighting experience and testosterone levels (e.g. Setchell & Dixson 2001b; McGraw *et al.* 2002; McGraw *et al.* 2003).

Consequently, the observed transitions from light to dark in some males may correspond not only with physical maturation, but rather with a substantial increase in status and competitive ability (e.g. Setchell & Dixson 2001b). These transitional males would therefore be potentially reproductively active adult males, who have begun to be able to compete with dark bulls for access to mates. The increase in pigmentation seen in males that already had dark brown patches may also represent a further increase in competitive status.

6.5.1.2 Coat colour and competitive ability

Only displacements and violent necking fights were clearly directional forms of competition over a resource. Pratt and Anderson (1985) also failed to find any indication of dominance or submission in necking bouts among young males. Thus, it is likely that this activity serves primarily to test one's own strength and competitive ability relative to that of others (Parker & Rubenstein 1981), and possibly as an opportunity to practice an activity that will later be used in more serious contests (Pratt & Anderson 1985). Information gathered from such interactions will likely form a basis of competitor assessment (e.g. Parker 1974) in agonistic interactions in later life.

As expected, dyadic interactions (displacements) among adult males were more likely to be won by the darker male than by the paler male in each pair of competitors. Thus, relative coat colour quite reliably predicts the relative dominance of males in dyadic interactions. Males may be using the colour of their opponent as a signal of status, to inform their decision to display, retreat or escalate (Smith 1982; Senar & Camerino 1998; Gerald 2000); where there was no perceivable colour difference to the observer, the giraffe may have been nonetheless able to perceive a difference, or may have relied on other cues.

Escalated contests were very rare, which is consistent with high potential injury costs and a high degree of resource holding power (RHP) disparity among competitors (Parker 1974). In the three escalated fights, both males were attributed to the same colour category but the winner was always noticeably darker than the loser. In one case, the winner also appeared older (based on horn wear), whereas in two cases the winner appeared to be younger (based on horn wear, and in one case relative height). This further reinforces the suggestion that dominance is not directly related to age, and that colour is a reliable indicator of competitive ability. All of the observed escalated contests were preceded by parallel walking, which probably provided the participants with an additional opportunity to obtain information about each other's competitive potential before committing to escalated fighting (Smith 1982).

6.5.1.3 Coat colour and female choice

As predicted, male coat colour was also a clear indicator of potential success in eliciting urination in females, a probable indicator of female choice (Pratt & Anderson 1985); very pale males were rarely successful in eliciting urination, whereas dark males nearly always were. Although many pale males were able to urine-test females, dark males experienced far greater courtship success than pale males, participating in a greater proportion of consortships and all mating attempts. Among dark males, courtship success appears to be similar regardless of male coat colour, but the few observations of actual matings would suggest that the reproductive success of very dark males may be greater.

6.5.2 Hypothesis 2: Competition in relation to a limited resource: waterholes

As predicted, encounter rates and consequently interaction rates were greater at perennial waterholes than at locations away from waterholes. Waterholes were more important for the occurrence of urine-testing during the dry season than the wet season, as females were occurring more predictably at perennial waterholes during the dry season (see also Chapter 3). However, despite the importance of waterholes as focal points for intercepting females, there was no evidence for dark males tolerating less the presence of other dark males or pale males at waterholes than elsewhere, and they did not always prevent pale males from gaining access to females at waterholes.

It is proposed that this was due to the 'swamping effect' of increased intruder pressure at waterholes (e.g. Ims 1988a; Cowlishaw & Dunbar 1991), as evidenced by the higher encounter rates at waterholes. This greater competitor pressure appeared to limit the ability of dominant males to deny subordinates access to females (Cowlishaw & Dunbar 1991). As a result, pale males had a greater likelihood of gaining at least temporary access to females at waterholes than at other locations. This was demonstrated both by a greater proximity of pale males to females at waterholes (nearest neighbour analysis) and by the greater relative participation of pale males in urine-testing attempts at waterholes.

However, dark males may tolerate subordinates in this way because reproductive access is strongly determined by dominance status (e.g. Altmann 1962), and as such the benefits to a dominant male of excluding 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. Thus, although the predictable concentrations of females at waterholes increase the ability of all males to locate potentially receptive females (Ims 1990), they also increase the relative importance of direct male competition and 'priority of access' relative to scramble competition in determining male reproductive success (Altmann 1962; Schwagmeyer 1988).

Consequently, dark males appeared to benefit most from the predictable occurrence of females at waterholes, especially in the dry season. Despite increased intruder pressure at waterholes, and the increased contact between females and pale males, dark males still succeeded in monopolising mating rights without recourse to escalated contests. Therefore, using waterholes to intercept females would be a relatively low cost, high benefit strategy for dominant males.

Younger, or more subordinate males, on the other hand, are unlikely to gain reproductive opportunities at waterholes because of the high likelihood of being displaced by more dominant males. Individuals of low competitive ability (or RHP) generally have to search longer for an undefended resource (e.g. females) than individuals of high RHP (Parker & Rubenstein 1981). Therefore, males of low competitive potential might instead adopt a strategy that makes the 'best of a bad job' (Dunbar 1982; Smith 1982). For example, away from waterholes and other concentration areas, the likelihood of encountering females is reduced, but females are less likely to be defended by a dominant male. Indeed, dark males were less likely to be present when pale males were urine-testing females away from waterholes than at waterholes. Thus, males of low competitive ability should search for potential (undefended) mates predominantly away from waterholes and other concentration areas. This conclusion supports the prediction that limited artificial provision of water (versus provision at numerous sites) could increase the potential for a relatively small number of dominant males to monopolise matings (e.g. Ritter & Bednekoff 1995).

Unfortunately data on consortships were too few to test whether pale males were also more likely to establish consortships with receptive females away from waterholes, as only six consortships were observed from the start. Overall though, consortships appeared more likely to begin at waterholes than elsewhere, which would further benefit dominant males. However, contrary to the prediction, consorting pairs were not encountered any closer to waterholes in the dry than in the wet season. This can probably be explained by the prolonged duration of consortships (up to 24 hours), during which time consorting pairs may move away from the site where the male first encountered the female. Regardless of whether the consortship began at a waterhole, their location at any later moment during the consortship is likely to be determined primarily by the location of food (since consorting pairs must pause in their mating activities to browse (Pratt & Anderson 1985)), and possibly the location of potential competitors that the consorting male may seek to avoid.

6.5.3 Hypothesis 3: Seasonal variation in male intra-sexual competition

As predicted, evidence was found to suggest that male competition was greater during the wet, high-conception rate season (October to May, see Chapter 4) than during the rest of the year. Between October and May, dark males appeared to be brought together almost exclusively by the presence of females, whereas between June and September dark males often associated with one another in the absence of females. More pale males were involved in urine-testing attempts in the dry, low-conception-rate season, but this can probably be attributed to the greater use of waterholes at this time, and the resulting decrease in the ability of dark males to exclude pale males from interacting with females (as described above).

Competition between dark males was generally greatest in months when mean female group size was largest (March to June) and in December, when females were aggregating in a highly spatially restricted habitat (mixed broadleaf woodland). The dry season (July to October) seemed to be a period of respite for courtship and competition for dark males. It is highly likely that dark males were seen to tolerate each other more during this time because there was less often a receptive female in their vicinity, due to the slightly lower conception rate during the dry season.

Furthermore, during the late dry season in particular, water and food are more difficult to obtain, so giraffe must visit waterholes more frequently, and males in particular must spend more time feeding (see Chapter 3). Seeking out the remaining reserves of food, and returning regularly to water, will likely result in larger daily movements than during the wet season (e.g. Le Pendu & Ciofolo 1999), potentially requiring greater energy expenditure in resource acquisition (Hall-Martin & Basson 1975). Thus, males may have less energy to invest in competition, and if they are already in poor condition due to nutritional stress, may be ill able to afford committing to a fight.

Conversely, the peak in intra-sexual competition coincides with a time of year when, because of the abundance of high quality food, males are in good condition and are able to reduce their foraging behaviour (see Chapter 3). They can thus dedicate a larger proportion of their time and energy to competing for females (Pratt &

Anderson 1985; Ginnett & Demment 1997). This is comparable to the trend in ungulate species with seasonally territorial males for territories to be held only in the summer or wet season, when food is most abundant (Owen-Smith 1977).

Males that restrict their reproductive effort to the season when a greater majority of females are receptive, and food and water are more abundant, will be better able to maintain good condition year-round. They would also be better able to invest in growth (males continue to grow in bulk, especially in neck thickness, even after they have stopped growing in height (Simmons & Scheepers 1996)) and secondary sexual characters, and as a result more likely to achieve and maintain a high dominance status. Those that currently have a low competitive ability (e.g. smaller, younger, or poor quality males) may have a better chance of obtaining a few mating opportunities by competing year-round (i.e. 'making the best of a bad job' (Dunbar 1982); see also Chapter 5). Nonetheless, despite the apparent increased intensity of mating competition among dark males in the wet season, the likelihood of a pale male encountering undefended females at waterholes, and the reproductive participation of pale males (in consortships), did not appear any greater in the dry season.

6.5.4 Hypothesis 4: Monopolisation of females, and reproductive skew

As seen above, dark males were unable to prevent pale males from associating with and urine-testing females when they were present in large numbers, especially at waterholes. Although females did show some choice in producing urine for testing (refusing very pale adults), they produced urine quite readily for many pale males, even when a dark male was present. However, it was always the most dominant male in the group (either a pale adult male if only pale males were present, or a dark male if both dark and pale males were present), that later secured access to a female for consortship. At any one time only 5-10% of females are likely to be receptive (see Chapter 1), although this percentage will be slightly higher in the wet season, and slightly lower in the dry season (see Chapter 4). Thus, any group of females encountered by males, even a large aggregation at a waterhole, is unlikely to contain more than one receptive female, and thus unlikely to offer more than one mating opportunity. Therefore, when present, dark males do not monopolise access to females for urine-testing, but do appear to be able to monopolise mating opportunities, as predicted by priority of access and mate monopolisation models (Altmann 1962; Emlen & Oring 1977; Cowlishaw & Dunbar 1991; Setchell *et al.* 2005).

Consequently, measures of association with females and opportunities to urine-test females cannot serve as realistic indicators of differential reproductive success (e.g. Fisher & Lara 1999), as these will tend to inflate the reproductive contribution of pale males (as seen in Chapter 5, older males actually tend to associate less with females than younger males). If observations of consortships were used as measures of the relative reproductive success of dark and pale males, these may also tend to inflate the relative reproductive contribution of pale males, as females seen to be courted by pale males were later courted by a dark male, suggesting that the pale males were unsuccessful in their mating attempts. Therefore, since 20% of observed consortships involved pale males, it can be concluded that pale males probably achieve less than 20% of all matings.

However, by combining both male associations with females, and male potential for monopolisation of females (measured by the proportion of observations with females that a male was the only, or most dominant, male), a value was created that appears to represent, at least crudely, potential current mating success, or at least the potential for monopolisation of matings. Because matings are observed so rarely in giraffe, it was not possible to verify the reliability of this surrogate of male mating success. In addition, because the molecular parentage analysis was unsuccessful, predicted individual success in mating with females could not be compared to actual male reproductive success. Nonetheless, evidence has been outlined here to suggest that male reproductive success in this population of giraffe may be highly skewed in favour of a relatively small proportion of dominant, mature dark males, and may be highly variable among mature males, with many potentially being excluded from mating.

It is important to note that the tenure of dominance status may vary between males, and as such, individual males may switch between alternative strategies as their dominance status, and thus competitive ability, changes (Smith 1982; Coltman *et al.* 1999; Thirgood *et al.* 1999). As a result, the observed current variance in reproductive success between males may not equate to such variance in long-term reproductive success, unless the reproductive tenure of dominant males lasts throughout a large part of their life (Dunbar 1982). Individual differences in overall dominance status, reproductive tenure and lifetime reproductive success do occur, for example in fallow and red deer (Clutton-Brock *et al.* 1982a; McElligott & Hayden 2000). Some male fallow deer consistently gain higher social dominance status and greater reproductive success year-on-year, and furthermore, these more successful reproducers consistently survive better than non-reproducing males (McElligott & Hayden 2000; McElligott *et al.* 2002). Thus, males that obtain greater lifetime reproductive success appear to be of higher phenotypic quality than those that fail to reproduce (McElligott *et al.* 2002).

It may also be the case in giraffe that some males never achieve high competitive ability (possibly due to historical factors such as poor nutrition or juvenile growth (Parker 1974; Dunbar 1982)), and thus experience low lifetime reproductive success, whereas other males succeed in monopolising matings over many years. Unfortunately, measuring reproductive tenure, lifetime reproductive success and the degree of polygyny in a long-lived animal such as the giraffe remains possible only through a long-term behavioural (and genetic) study (Clutton-Brock *et al.* 1982a; Coltman *et al.* 1998).

7 GIRAFFE COAT COLOURATION AND ENVIRONMENTAL STRESS

7.1 Introduction

The aim of this chapter was to investigate biogeographic variation in patch colour in giraffe, with reference to natural and sexual selection. In Lydekker's original descriptions of the giraffe subspecies, he noted clear differences in pelage markings and colouration between the subspecies (Lydekker 1904). For example, he described the colour of the patches of *Giraffa camelopardalis thornicrofti* as "light brown", but those of *G. c. camelopardalis* as "chestnut coloured", of *G. c. giraffa* as "chocolate brown, or almost black", of *G. c. reticulata* as "orange-red to red-chocolate", and those of *G. c. rothschildi* as "reddish-chestnut, or reddish-fawn, darkening to deep blackish brown". He also noted differences between the sexes in some, but not all, subspecies. He described the sexes as alike in *G. c. camelopardalis* and *G. c. tippelskirchi*, but reported that the sexes differed markedly in *G. c. giraffa* (the old bulls being much darker), and in *G. c. rothschildi*. In the latter, he recorded the patches of the sexes as differing in both form and colour, with the patches of adult bulls "large and very dark, almost blackish, compared to the reddish colouring of females".

Lydekker (1904) noted that where males acquired dark colouration, the change in colour was "apparently coincident with advancing age". This darkening with age was also noted by Berry (1973) in *G. c. thornicrofti* in the Luangwa Valley Zambia. He described the patches of males in their prime as darkening almost to black, whereas females did not usually attain the same degree of darkening. However, Lydekker (1904) also noticed that some full grown bulls were "decidedly lighter than type", thus demonstrating variation at an individual level, as well as at the level of the sexes and subspecies.

7.1.1 Coat colour and thermoregulation

The surface colouration that an animal presents to its environment can affect its fitness both by determining its conspicuousness and by modification of the thermal effects of solar radiation upon the animal (Louw & Seely 1982; Walsberg & Wolf 1995a). The actual colour of animal's coat will be the result of a balance of the following selection pressures (Walsberg et al. 1978; Louw 1993; Ortolani 1999):

1. Thermoregulatory function: optimisation of radiative heat gain.
2. Visual functions:
    a. Camouflage (reduced conspicuousness)
    b. Social communication (enhanced conspicuousness; see also Chapter 6)

For example, the colour of most savannah animals is assumed to be a compromise of the need to be camouflaged against the background savannah vegetation, and the need to reflect incident solar radiation (Louw 1993).

7.1.2 Absorption and reflection of solar radiation

Heat is absorbed from direct solar radiation at all wavelengths (Louw 1993), but radiation is emitted by surfaces in the long-wave (far infrared) spectrum only and is proportional to the temperature of the emitting body (Gates 1980). Radiative emissivity of a surface is equal to absorptivity but only at the same wavelength, so a difference in surface absorption characteristics with respect to the visible part of the spectrum does not necessarily mean that there is an emissivity difference in the far infrared (Hamilton & Heppner 1967; Gates 1980).

With changes in animals' skin and fur colour and structure, absorptance of incident shortwave radiation can vary between 30 and 85% (Gates 1980), whereas long-wave absorptance varies only between 95 and 98% (Gates 1980). So although there is a high degree of variation in the amount of heat absorbed from direct incident solar radiation by pale and dark coloured animals, there is a relatively negligent level of variation in the amount of heat re-radiated by pale and dark animals.

The dependence of absorptance and reflectance of solar radiation on coat colour was clearly demonstrated in a study by Cena (1966) using cattle and horses with different colour coats. He found that in the spectral range of 280-900 nm, black cattle coats absorbed twice as much radiation as white coats, and in horses, black coats absorbed almost twice as much radiation as grey coats. He also found that increased absorptance resulted in an increased heat gain and heat load (Cena 1966). This has since been confirmed in other studies, at least at low air speeds (Hutchinson & Brown 1969; Finch 1972; Finch & Western 1977; Finch et al. 1980; Brosh et al. 1998; West & Packer 2002).

Furthermore, Cena (1966) observed that all cattle and horse coats provided effective protection against ultraviolet radiation, regardless of colour. Finch and Western (1977) also pointed out that protection against deleterious effects of UV is generally related to skin rather than pelage colour. Giraffe colouration is determined by the hairs rather than by skin colour, which is heavily pigmented and uniformly dark grey in appearance (Dagg & Foster 1976; Dimond & Montagna 1976; Mitchell & Skinner 2003).

7.1.3 Thermoregulatory adaptive colouration in mammals

Optimisation of solar heat gain should be most important for survival where thermoregulatory stress is greatest, or where resources crucial to maintenance of heat balance, such as food and water, are most limited (e.g. Dawson & Brown 1970). For example, light colouration should be selectively favoured over dark colouration in hot, arid environments, where animals face a combination of high ambient temperatures, high solar radiation and limited water (Walsberg 2000). In these conditions they must dissipate through evaporative cooling not only their own metabolic heat but also heat gained from the environment (Taylor 1969; Taylor 1970).

Finch and Western (1977) found that black cattle in Kenya had a higher inward heat flow and a higher water requirement than brown or white cattle. Their study also revealed that the proportion of dark-coloured cattle in herds in different locations, and the relative survival of dark and light-coloured cattle in each herd, could be explained by differences in predicted heat stress. They also noted a proportionally higher mortality of black cattle during droughts in low-lying areas. Their findings suggest a selective advantage of light over dark-coloured animals where heat stress is greatest, and an increasing selective advantage of dark over light-coloured animals as heat stress decreases (Finch & Western 1977).

7.1.4 Thermoregulatory adaptations in giraffe

For giraffe, the major climatic influences on body temperature regulation are high solar radiation, high ambient temperature, low relative humidity and restricted water availability (Sinclair 1983). In a study of physiology in the giraffe, Langman et al. (1982) observed a fluctuation in body temperature (Tb) between 35.7ºC and 39ºC. Changes in Tb correlated strongly with ambient temperature (Ta), with a phase lag of about 2 hours (Langman et al. 1982). Thermolability has also been observed in other savannah ungulates, such as the camel (*Camelus dromedarius*), eland (*Taurotragus oryx*), oryx (*Oryx gazella*) and hartebeest (*Alcelaphus buselaphus*) (Harthoorn et al. 1970; Taylor 1970).

As in camels, thermolability in giraffe may limit the need for evaporative cooling (respiratory and cuticular), and as a result, minimise water loss (Schmidt-Nielsen et al. 1957; Taylor 1970). However, if darker animals gain heat quicker than paler individuals of the same size, they will have to start dissipating heat by evaporative cooling sooner, and continue to do so for a larger part of the day (Taylor 1970). Therefore any reduction in water loss resulting from thermolability will be greater for pale than for dark animals. Giraffe are able to survive increases in body temperature by use of a carotid rete and cavernous sinus system, which enables blood passing to the brain to be cooled by a heat exchange system with cool venous blood from the nasal mucosa (Langman et al. 1979; Mitchell & Skinner 2005). This nasal heat exchange also further minimises water loss (Langman et al. 1979).

Thermal stress potentially places an upper limit on the time that large mammalian herbivores can devote to foraging, as this behaviour increases the thermal load generated by muscular activity and increases exposure to solar radiation (Owen-Smith 1998). Indeed, giraffe become slow in the heat of the day (Innis 1958) and the activity levels of females in particular are reduced when Ta exceeds 32ºC (Leuthold & Leuthold 1978a). Giraffe feeding activity tends to be biphasic, with increased activity early morning and late afternoon (Leuthold & Leuthold 1978a; Pellew 1984a; Fennessy 2004), and giraffe are more likely to be seen lying down at the hottest time of day, early afternoon (Innis 1958). To counter radiative heat stress, giraffe should seek to minimise their solar heat-load. In a study in Etosha NP, Namibia, Kuntzsch and Nel (1990) found that as ambient temperatures increased, giraffe oriented themselves to minimise the body surface exposed to direct sunlight, or sought shade.

It has been suggested that giraffe pelage patches may act as "thermal windows" that facilitate heat transfer (Skinner & Smithers 1990). This hypothesis is supported by the finding that subcutaneous vasculature varies, with a rete mirabile located underneath each patch, and that the subcutaneous temperature between patches and non-patches differs (Mitchell & Skinner 1993; Mitchell & Skinner 2005). However, the conditions under which these measurements were made are unclear, and the influences of environmental conditions and patch colour on this effect are unknown.

Nonetheless, it is also possible that in giraffe, pelage colouration is the result of natural selection for optimal coat colouration under varying environmental conditions. Giraffe colouration is determined by the hairs that cover the skin (Dagg & Foster 1976), and as in humans and other mammals, giraffe hair colour is assumed to be determined by varying levels and ratios of the two distinct hair pigments, phaeomelanin (for yellow to reddish-brown and buff colouration) and eumelanin (for dark-brown to black colouration (Ito & Wakamatsu 2003; Jawor & Breitwisch 2003)).

7.2 Aims

This chapter aims to test the following hypotheses and predictions:

Hypothesis 1: The possession of dark patches should be costly in hot, arid conditions in terms of increased solar heat gain, and should be selected against in such environments. Thus, biogeographical variation in giraffe coat colouration could result from an adaptation to minimise heat and water stress, and as such can be explained by geographical variation in environmental selection pressures. Thus, I predict that:

- Variation in giraffe coat colour and patch cover can be explained by geographical variation in climatic factors that would influence environmental heat stress.

Hypothesis 2: If dark coat colouration is maintained in males by sexual selection for an honest signal of male status (see Chapter 6), then I predict that:

- Any relationship between predicted environmental stress and biogeographic variation in colouration will be stronger in females than in males.

Hypothesis 3: If dark coat colouration is costly in terms of increased solar heat gain, then males with dark coats facing this additional cost should demonstrate different thermoregulatory behaviour to adult females or pale adult males. Thus, I predict that:

- Dark males will preferentially select shade over body orientation (i.e. presenting the smallest body surface possible to the sun's rays) as a form of reducing exposure to the sun, when compared with adult females and pale adult males, who should demonstrate similar thermoregulatory behaviour.

7.3 Methods

7.3.1 Photographic analyses

7.3.1.1 Photographs

Photos of giraffe from throughout Africa were obtained from wildlife photographers from locations where giraffe are known to be native (Table 7.1). A unique identifier, independent of sex or location, was given to each photo and to each individual. Where possible, individuals were sexed by referring to characteristics such as visible genitalia, the size, shape and condition of the horns and skull ossifications, and body shape (male neck musculature often appears highly developed relative to that of a female (Pratt & Anderson 1982)). Each individual was also classed according to approximate age class (5 categories: juvenile, sub-adult, young adult, fully adult and old; derived from Leuthold (1979)), based on body proportions, relative length of the mane, profile of the head, overall condition, horn and skull development and wear, and size relative to other individuals in the same photograph.

Table 7.1. Numbers of images (excluding duplicates of the same individual) included in the dataset for each location. The total for each location includes individuals of unknown gender.

Country	Location	Assumed subsp.	Males	Females	Total
Botswana	Chobe NP	*G. c. angolensis*	8	5	16
	Okavango Delta	*G. c. angolensis*	8	11	29
Kenya	Aberdare NP	*G. c. reticulata*	11	3	20
	Lake Nakuru NP	*G. c. rothschildi*	3	6	18
	Meru NP	*G. c. reticulata*	2	0	2
	Nairobi NP	*G. c. tippelskirchi*	12	12	30
	Samburu NR	*G. c. reticulata*	47	21	88
	Tsavo NP	*G. c. tippelskirchi*	13	12	32
Kenya / Tanzania	Masai Mara GR / Serengeti NP	*G. c. tippelskirchi*	63	41	150
Namibia	Etosha NP	*G. c. angolensis*	65	26	131
	Kunene region	*G. c. angolensis*	15	6	37
Niger	Koure region	*G. c. peralta*	7	2	15
South Africa	Kruger NP	*G. c. giraffa*	38	20	84
Tanzania	Arusha NP	*G. c. tippelskirchi*	5	13	22
	Lake Manyara	*G. c. tippelskirchi*	9	0	9
	Selous GR	*G. c. tippelskirchi*	1	1	8
	Tarangire NP	*G. c. tippelskirchi*	0	2	2
Uganda	Murchison Falls	*G. c. rothschildi*	6	1	10
Zambia	Mosi-Oa-Tunya	*G. c. angolensis*	2	0	3
	South Luangwa	*G. c. thornicrofti*	3	2	5
Zimbabwe	Hwange NP	*G. c. angolensis*	19	8	37
		Total:	**337**	**192**	**748**

7.3.1.2 *Patch colour categories*

Each giraffe was scored according to patch darkness using the same categories as in the field study (see Chapter 2: 1 = very pale tan patches, 2 = darker tan and russet, 3 = chocolate-brown, 4 = black). It was decided to score patch colour by eye rather than using image analysis software, because of varying ambient light conditions, camera types and image qualities. These could not be controlled for due to the variety of image sources used. It is assumed that human raters take some of these factors into account when judging actual colour (e.g. Hurlbert 1999; Golz & MacLeod 2002). The four categories were based on an evaluation of gross darkness, rather than variation in hue (Sumner & Mollon 2003). The categories were assumed to correspond to incrementally different levels of melanin (predominantly eumelanin) pigmentation (Ito & Wakamatsu 2003; Jawor & Breitwisch 2003), and consequently different levels of absorption/reflection of solar radiation (Cena 1966).

7.3.1.3 Patch cover

A MATLAB algorithm was used to analyse sections (Figure 7.1) taken from 432 images of giraffe. This algorithm served to binarise the JPEG image (Figure 7.2), then count and record the number of black and white pixels produced. Patch cover values (the proportion of the total number of pixels in the binarised image that are black) were recorded for sections both of the body and of the neck that were free from obvious scars, oxpeckers, folds of skin or strong shadows.

Figure 7.1. Example of rectangular neck and body sections (white outlines) taken from images of giraffe to be analysed for patch cover.

Figure 7.2. Example of a section taken from a giraffe image, and of the MATLAB binarisation (transformation to black and white pixels only) used to assess patch cover.

7.3.1.4 Validation tests

To test for inter-scorer reliability, the patch colour of 100 randomly selected images were independently scored by two additional scorers who were first shown examples of the four categories, but who were naïve to giraffe sex or origin (images were trimmed to show only the neck and body, excluding the head and genital region). It was also assumed that any individual recording or scoring errors would not be biased in favour of any one sex or location.

A total of sixty images were also analysed manually by overlaying a transparent grid on printed out sections of the body and of the neck, and then counting the proportion of intercepts falling on patches relative to the total The size of the grid (i.e. the distance between points) was varied according to the size of the image, such that a minimum of 250 points were always counted. These patch cover values were compared to those obtained by computer analysis for the same giraffes to test the validity of the algorithm.

Where the same individual appeared in two different images, a patch cover value was obtained from both, where possible. These scores from the same individual in different images were compared to test for repeatability, and averaged to produce overall scores for that individual. Where both body and neck values were available for the same individual, the average of the two was also calculated to produce an overall body score. After checking that body and neck scores for the same individual correlated well, where only one of the two values (body or neck) for an individual was obtained, then that value was used as the overall body score.

Sexual dichromatism was also tested using a method that did not rely on the categorisation of colour, but instead involved assessment of 33 occurrences of different male-female pairs in an image. A score of 1 was given if the male in the pair was darker, -1 if the female was darker, and 0 if there was no perceptible difference. This was independently scored by four people, three of whom were naïve to the sex or origin of the giraffes.

7.3.1.5 Population means

For each distinct population, the mean patch cover was calculated for all individuals sampled, and for males and females separately. The overall ‘darkness’ of a population was defined as the percentage of individuals (or of males or females) in each area allocated to the two darker patch colour categories (three and four; see Appendix 4). Patch cover data were logarithm-transformed at the level of analysis to reduce skewness.

7.3.1.6 Climatological data

Climatological data were obtained from the ‘Tables of temperature, relative humidity, precipitation and sunshine for the world’ (Meteorological-Office 1972), which were based on data collected over about 30 years. Data were noted from the nearest one, two or three weather station sites, and averaged where necessary (see Appendix 5). Since the major climatic influences on body temperature regulation for giraffe are high solar radiation, high ambient temperature, low relative humidity and restricted water availability (Sinclair 1983), the following climatological variables (see Appendix 6) were selected:

- Average yearly maximum temperature: daily maximum temperature, averaged over the whole year, and over all years.
- Average yearly minimum temperature: daily minimum temperature, averaged over the whole year, and over all years.
- Relative humidity at 13h30 or 14h30.
- Average yearly precipitation: this was obtained from the UNEP-WCMC World Database on Protected Areas, an online resource that provides data on reserves and national parks. Where data for a site was not available in this database, it was substituted with data from the aforementioned tables. Information on rainfall in the Kunene region of north-west Namibia was taken from Fennessy (2001).
- Average yearly hours of bright sunshine.

Differences in colouration between the sexes were assessed using the Mann-Whitney U test. The relationships between climate, patch cover and patch colour for each location were examined using regression analyses, with data points weighted by the original sample size from which the means were calculated. Only pairs of climatological variables that were not significantly inter-correlated were tested as potential covariate predictors.

7.3.1.7 Phylogenetically-controlled subspecies-level analyses

To control for phylogenetic constraints (e.g. Felsenstein 1985; Garland et al. 1992; Freckleton et al. 2002; Martins et al. 2002) on the evolution of patch cover and colour, the analysis was replicated at the subspecies level using the Comparative Analysis by Independent Contrasts (CAIC) program for the Macintosh (Purvis & Rambaut 1995). The phylogeny used (Figure 7.3) was based on morphological and genetic analyses carried out by Seymour (2001) and Fennessy (2004). Phylogenetic tree branch lengths could not be reasonably estimated, so equal lengths were assigned to all the branches of the phylogenetic tree. All climate stations in the above-mentioned tables (Meteorological-Office 1972) that fell within the assumed recent-historical range of the different subspecies (Sidney 1965) were used to calculate mean values for each climatological variable (see Appendix 7). Evolutionary assumptions of the CAIC model were satisfied (e.g. absolute values of the standardised contrasts were independent of the estimated nodal values), after appropriate transformations of some of the variables (Purvis & Rambaut 1995). Regression analyses, forced through the origin, were carried out using the standardised linear contrasts produced by CAIC.

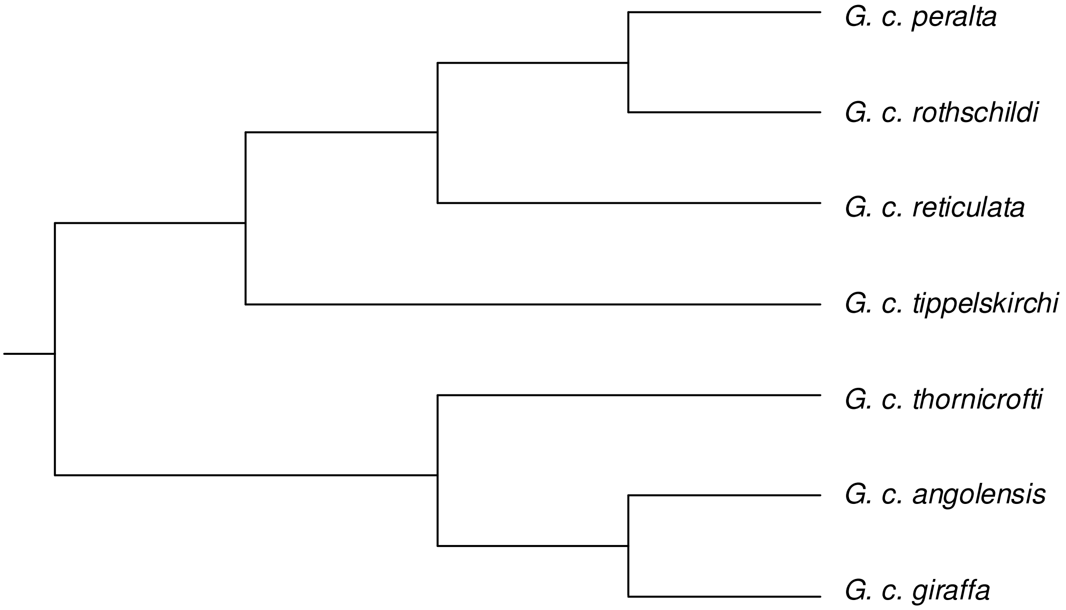


Figure 7.3. *Giraffa camelopardalis* subspecies phylogeny used in the phylogenetically-controlled analysis, based on previous morphological and genetic work (Seymour 2001; Fennessy 2004).

7.3.2 Field data collection: Thermoregulatory behaviour in wild giraffe

Based on the study of giraffe body orientation and use of shade by Kuntzsch and Nel (1990), a similar investigation was carried out to look at the effects of sex-age class and coat colour on thermoregulatory behaviour on the study population. The aim was to establish if there was an apparent thermoregulatory cost to the dark coat colouration observed in mature male giraffe. When a giraffe was observed standing resting or ruminating, it was noted whether the giraffe was standing in the shade (4), and if not, then whether the body was oriented facing towards the sun (1), away from the sun (2), or with the long axis of the body perpendicular to the sun's rays.

Thermoregulatory behaviour was compared between different sex-age and coat colour classes, as well as between the summer and winter seasons. The cooler winter months were defined by monthly mean minimum temperatures (calculated from four years of daily data from Okaukuejo, Etosha NP). These are lowest (below 15°C) between May and September (Birgit Kötting, M.E.T., unpublished data). Monthly mean maximum temperatures are also lowest (below 30°C) between May and August.

7.4 Results

7.4.1 Photographic analyses

7.4.1.1 Validation tests

Relative coat colour rankings correlated extremely well between all pairs of scorers (Spearman's rho = 0.696, 0.769 and 0.789, all $P < 0.001$). The correlation between patch cover values obtained by computer analysis and those obtained by manual analysis was highly significant for body, neck and overall values (bodies: Pearson's r = 0.817, N = 24, $P < 0.001$; necks: r = 0.907, N = 44, $P < 0.001$; overall: r = 0.814, N = 56, $P < 0.001$).

Values obtained for the same giraffe occurring in different images correlated highly with each other. This result was significant whether only body values were included (Pearson's r = 0.927, N = 34, $P < 0.001$) or only neck values (r = 0.916, N = 37, $P < 0.001$), but was most significant for values that were an average of both body and neck score (r = 0.963, N = 22, $P < 0.001$).

There was also a highly significant correlation between values obtained for body sections and those obtained for neck sections (r = 0.902, N = 356, $P < 0.001$). Some variability existed due to actual differences in patch cover between the neck and the body. However, the high overall correspondence lent support to the decision to use body, neck or overall scores, depending on availability.

7.4.1.2 Sexual dimorphism in patch cover, and patch dichromatism

No significant overall sexual dimorphism in patch cover was found (Students t = 1.18, df = 351, P = 0.238), although there was a very slight trend for males to have relatively greater patch cover than females (mean male percentage cover = 63.0%, mean female patch cover = 61.7%). At the population level, patch cover was significantly greater in males than in females in just one population, that from Etosha NP (mean male patch cover = 63.7%, mean female patch cover = 59.1%, Students t = 2.761, df = 60, $P < 0.01$).

With regards patch colour, males were generally darker than females (Mann-Whitney $U = 26156$, $N_m = 339$, $N_f = 189$, $P < 0.001$ for all non-juvenile age classes; Figure 7.4). Sexual dichromatism varied between populations from different locations. Patch colour dichromatism was significant only in Etosha NP (Mann-Whitney $U = 408$, $N_m = 63$, $N_f = 25$, $P < 0.001$) and Samburu GR ($U = 285$, $N_m = 47$, $N_f = 21$, $P < 0.005$). Dichromatism can be attributed to the darkening of males, but not females, with age; male patch colouration was significantly associated with age, with older males tending to be darker than younger males (Kendall's tau-b = 0.369, $N = 339$, $P < 0.001$), whereas there was no such association in females (tau-b = 0.096, $N = 189$, $P = 0.152$).

The test of sexual dichromatism performed independently of colour categories confirmed the above result. A sign test showed a significant deviation from parity, with males tending to have darker patches than females (sign-test P-values for the four scorers were < 0.005, < 0.01, < 0.05 and 0.064; Figure 7.5). Agreement among the scorers was good, with an average concordance for all possible pairs of scorers of 0.82, and an overall agreement for all four scorers of 0.70. Only 4 reversals were noted among the 33 pairs, where one scorer disagreed with at least one of the other scorers regarding the direction of dichromatism.

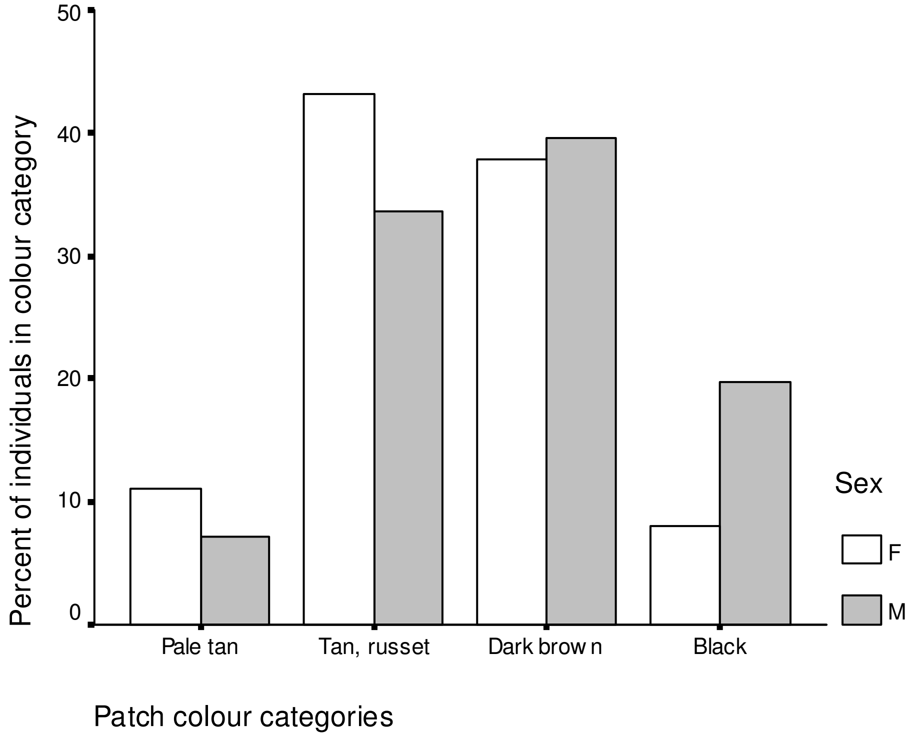


Figure 7.4. Frequency of different patch colour categories in the two sexes (filled bars = males, empty bars = females). A greater proportion of males are classed in the darker categories, and a greater proportion of females are classed in the lighter categories.

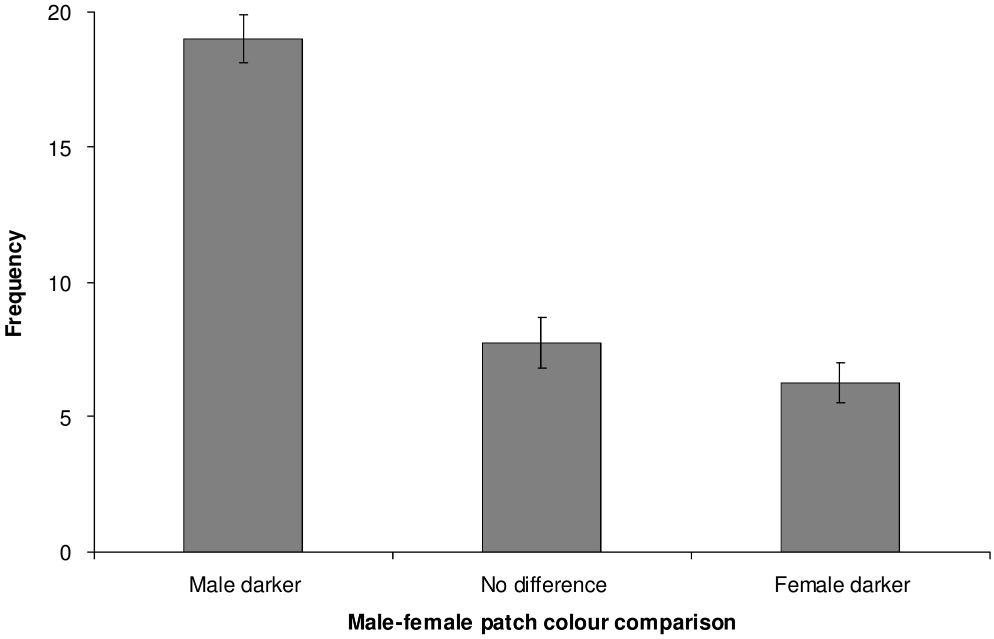


Figure 7.5. Assessment of patch colour differences of male-female pairs of giraffe in the same image, judged by 4 independent scorers. Bars represent the mean frequency, across the 4 scorers, of male-female pairs allocated to each category (male darker, female darker, or no difference) and error bars represent 1 standard-error of the mean.

7.4.1.3 Relationships between patch cover, patch colour and climate

The climatological factors which most strongly predicted patch cover were annual hours of bright sunshine (a result of the combined effects of latitude, depth of atmosphere and cloud-cover) and either mean yearly minimum temperature ($F_{2,19}$ = 10.09, P<0.005) or total annual rainfall ($F_{2,18}$ = 36.67, P < 0.001; Table 7.2). These pairs of factors accounted for 57% and 83%, respectively, of the variation in mean patch cover across the locations (the r^2 value was not improved by including all three predictors in the model). Patch cover tends to be greater in cooler, drier sites, but patch cover is limited in areas with greater hours of bright sunshine (Figure 7.6). These results remained highly significant if the analysis was restricted to just females (rainfall and minimum temperature: $F_{2,15}$ = 9.372, P < 0.005; rainfall and bright sunshine: $F_{2,15}$ = 29.852, P < 0.001) or just males (rainfall and minimum temperature: $F_{2,16}$ = 8.744, P < 0.005; rainfall and bright sunshine: $F_{2,16}$ = 20.936, P < 0.001).

Table 7.2. Inter-correlation of pairs of potential predictors (*italics*), and predictive ability of non-correlated pairs (heavy outline) for variation in mean patch cover at the different sites. The two combinations of predictors that are significant after a Bonferroni correction (a P-value of less than 0.0083 was considered significant, accounting for six tests) are highlighted in bold type.

	Yearly min. temp. (°C)	Relative Humidity at 14:30 (%)	Annual rainfall (mm)	Annual hours bright sunshine
Yearly max. temp. (°C)	*Inter-correlated: r=0.752, P<0.001*	*Inter-correlated: r=-0.628, P<0.005*	F=5.348, P=0.017, r^2=0.401	F=6.063, P=0.012, r^2=0.447
Yearly min. temp. (°C)	-	F=2.719, P=0.096, r^2=0.254	F=3.843, P<0.05, r^2=0.325	**F=10.090, P<0.005, r^2=0.574**
Relative humidity at 14:30 (%)	-	-	*Inter-correlated: r=0.607, P<0.005*	*Inter-correlated: r=-0.891, P<0.001*
Annual rainfall (mm)	-	-	-	**F=36.666, P<0.001, r^2=0.830**

Values for total hours bright sunshine variable were not available from the nearest meteorological stations to Tsavo NP, Arusha NP and Hwange NP. For these locations, values were taken from the nearest station at which this information was available. The results remained largely unchanged if these three points were not included in the analysis (minimum temperature and sunshine: $F_{1,14}$ = 9.501, P < 0.005; rainfall and sunshine: $F_{1,15}$ = 29.733, P < 0.001).

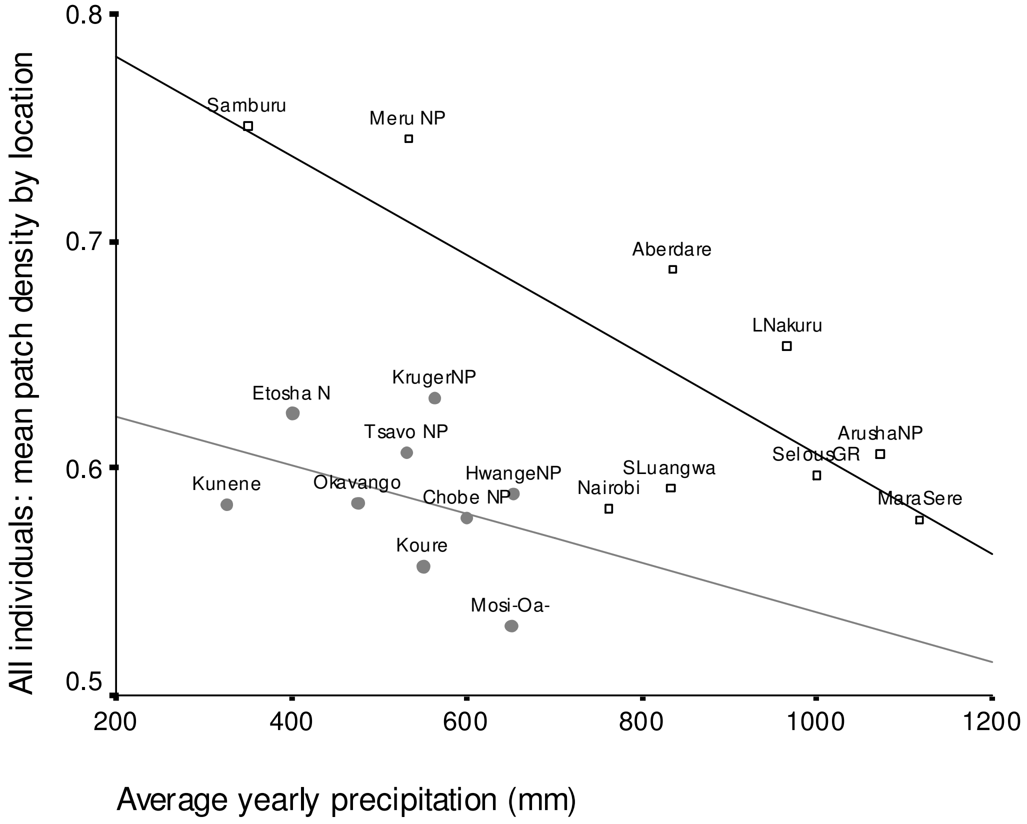


Figure 7.6. Relationship between mean patch cover in a population and mean annual precipitation, for all individuals. Empty squares = low-insolarity sites (<2917 hrs p.a.), filled circles = high-insolarity sites.

Bright sunshine also appeared to limit patch colouration, especially in females. For locations where the sample size was greater than two individuals for both males and females, there was a significant relationship between yearly hours of bright sunshine and the percentage of individuals with dark patches for males ($F_{1,14} = 6.213$, $P < 0.05$), and almost for females ($F_{1,12} = 3.576$, $P = 0.085$). However, the regression slope was noticeably steeper for females than for males (Figure 7.7). This resulted in a trend for increasing sexual dichromatism with increasing insolarity (as mentioned above, this was significant in Etosha NP, Namibia). Overall, dichromatism was significant in high insolarity locations (Mann-Whitney $U = 5225$, $N_m = 169$, $N_f = 89$, $P < 0.001$) but not in low insolarity locations ($U = 6818$, $N_m = 146$, $N_f = 98$, $P = 0.494$).

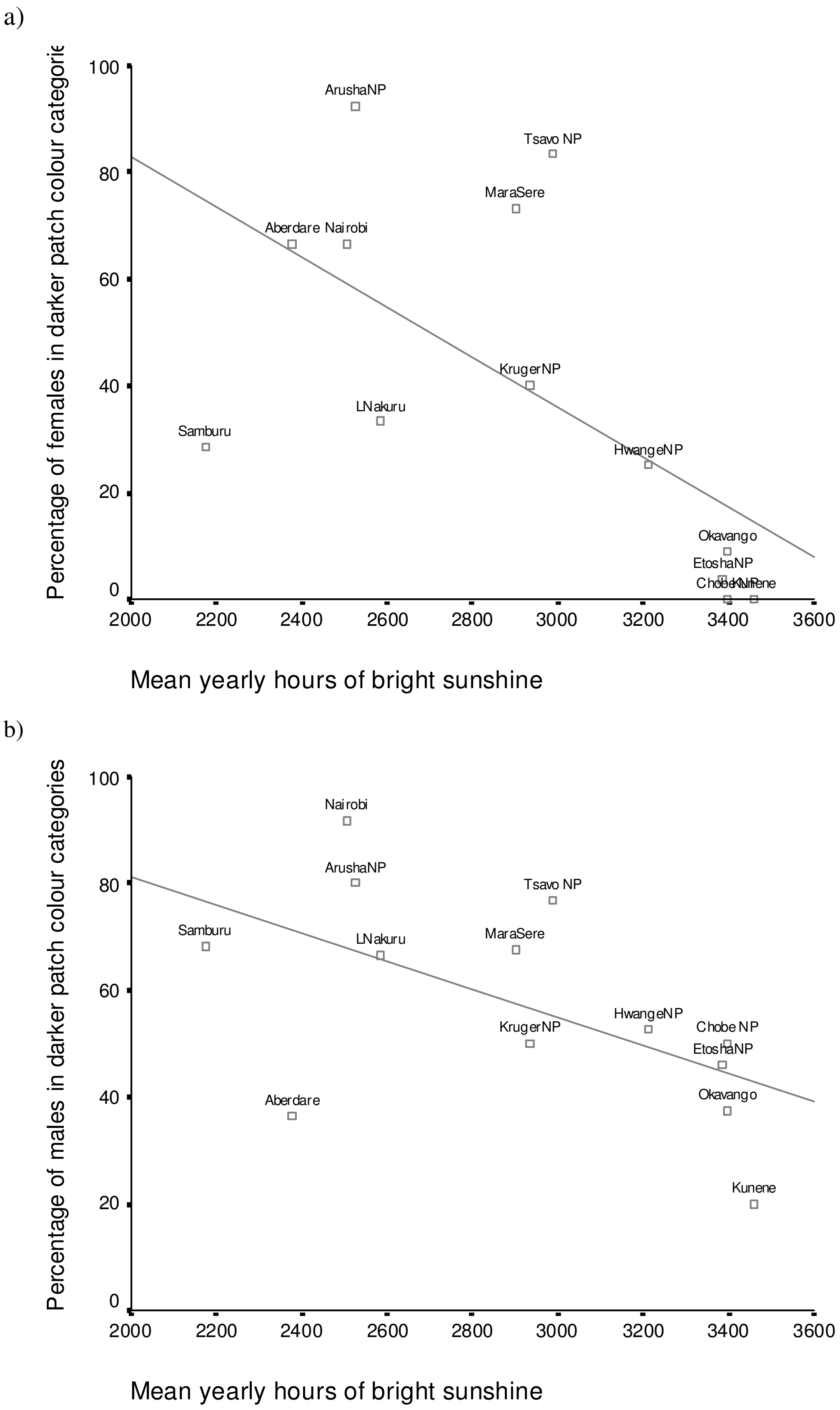


Figure 7.7. Relationship between yearly hours of bright sunshine and the percentage of individuals with dark brown or black patches in a) females, and b) males, for sites where sample size was greater than two for both males and females .

7.4.1.4 Phylogenetically-controlled subspecies-level analyses

None of the climatological variables significantly predicted patch cover once subspecies relationships were controlled for. However, there was a trend for decreasing patch cover with increasing annual rainfall for females (regression through the origin: $F_{1,6} = 4.985$, $P = 0.076$; Figure 7.8), and for males if the effect of yearly hours bright sunshine was also taken into account ($F_{2,5} = 7.841$, $P = 0.064$), as found in the population-level analysis, above. There was also a slight trend for decreasing proportions of females with dark patches as yearly hours of bright sunshine increased ($F_{1,6} = 2.378$, $P = 0.184$; Figure 7.9), which also lends some support to findings of the population-level analysis. No such trend was found for male patch colour ($F_{1,6} = 0.749$, $P = 0.426$).

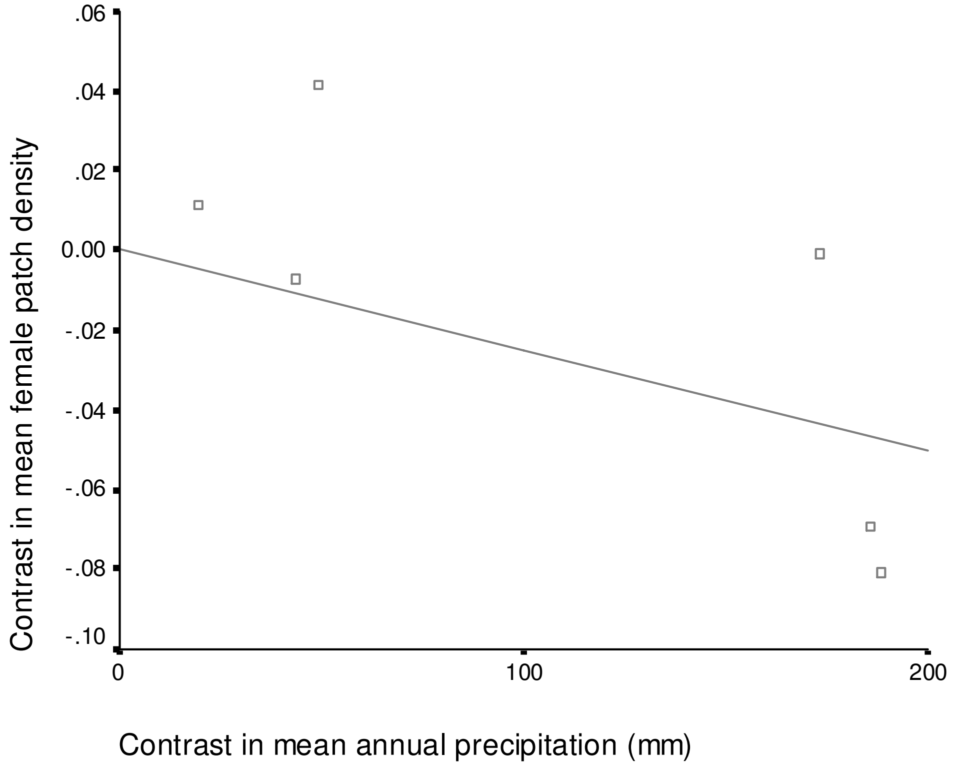


Figure 7.8. Relationship between contrasts (calculated by CAIC) in mean female patch cover and contrasts in mean annual precipitation (trend line is forced through the origin).

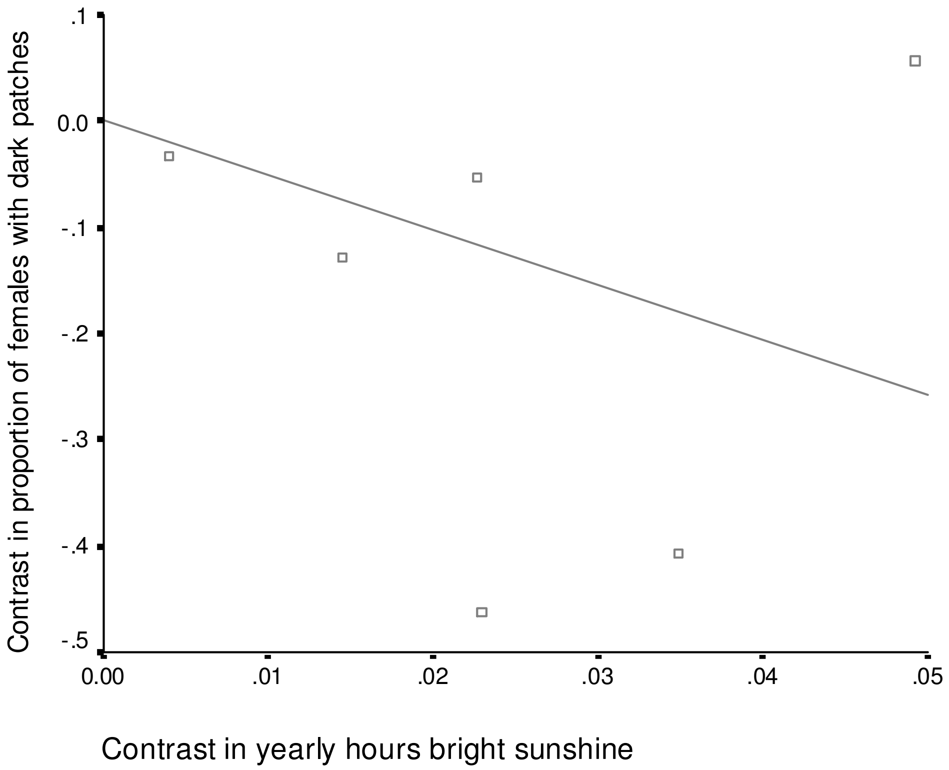


Figure 7.9. Relationship between contrasts (calculated by CAIC) in the proportion of females with dark patches and contrasts in mean yearly hours bright sunshine (trend line is forced through the origin).

7.4.1.5 Within-subspecies analyses

The observed association between patch cover or colour and climatological variables for females was further reinforced by analyses carried out at lower taxonomic levels using the subspecies with the largest sample sizes (numbers of sites sampled). Specifically, the observed trend between female patch cover and the combined effects of bright sunshine hours and annual rainfall also held if the analysis was restricted to either just *G. c. angolensis* and the most closely related subspecies *G. c. giraffa* ($F_{2,5}$ = 6.744, P = 0.078; Figure 7.10), or to all of the southern African subspecies (the two mentioned as well as *G. c. thornicrofti*; $F_{2,6}$ = 8.208, $P < 0.05$).

There was also a significant relationship between female patch cover and just annual rainfall for the four most western *G. c. angolensis* populations, which experience the highest yearly hours of bright sunshine ($F_{1,3}$ = 23.70, $P < 0.05$), but a more highly significant relationship between female patch cover and mean annual minimum temperature ($F_{1,3}$ = 187.0, $P < 0.01$). In these locations, rainfall and minimum temperature were correlated (Spearman's rho = 0.90, $P < 0.05$). For males, the relationship between patch cover and climatological variables did not hold among all southern African populations ($F_{2,7}$ = 1.219, P = 0.370), or among just *G. c. angolensis* populations ($F_{2,7}$ = 0.812, P = 0.523).

This relationship was not significant among males of *G. c. tippelskirchi* ($F_{2,4}$ = 0.290, P = 0.775), but there was still a non-significant trend for decreasing female patch cover with increasing rainfall for *G. c. tippelskirchi* ($F_{1,4}$ = 3.319, P = 0.166; Figure 7.11).

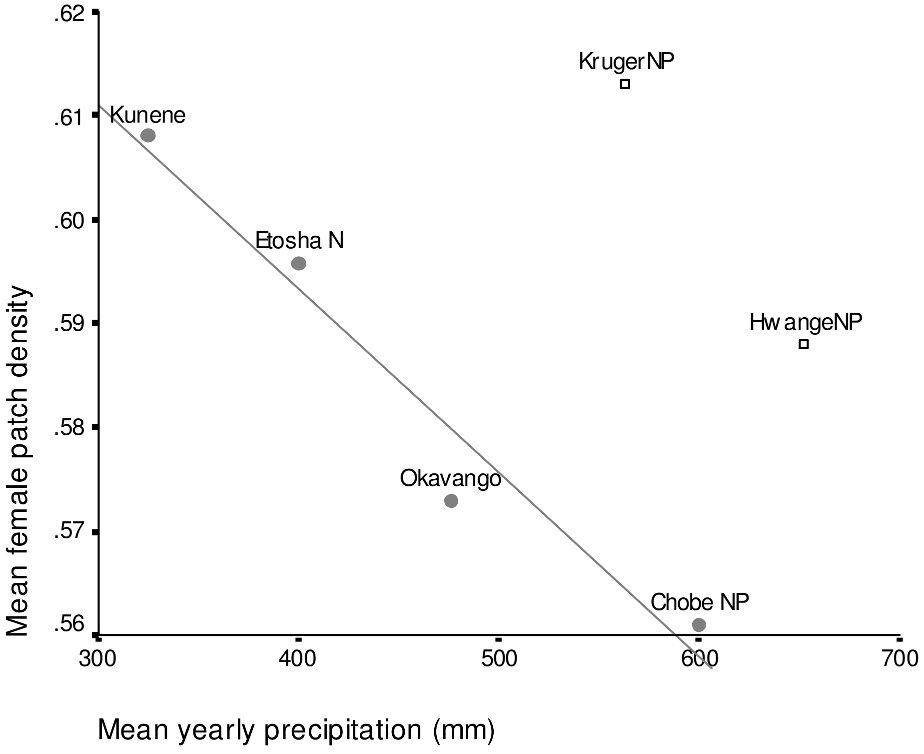


Figure 7.10. Relationship between mean female patch cover in a population and mean annual precipitation, for populations of *G. c. angolensis* and *G. c. giraffa* only. Empty squares = lower-insolarity sites (<3300 hrs p.a.), filled circles = higher-insolarity sites.

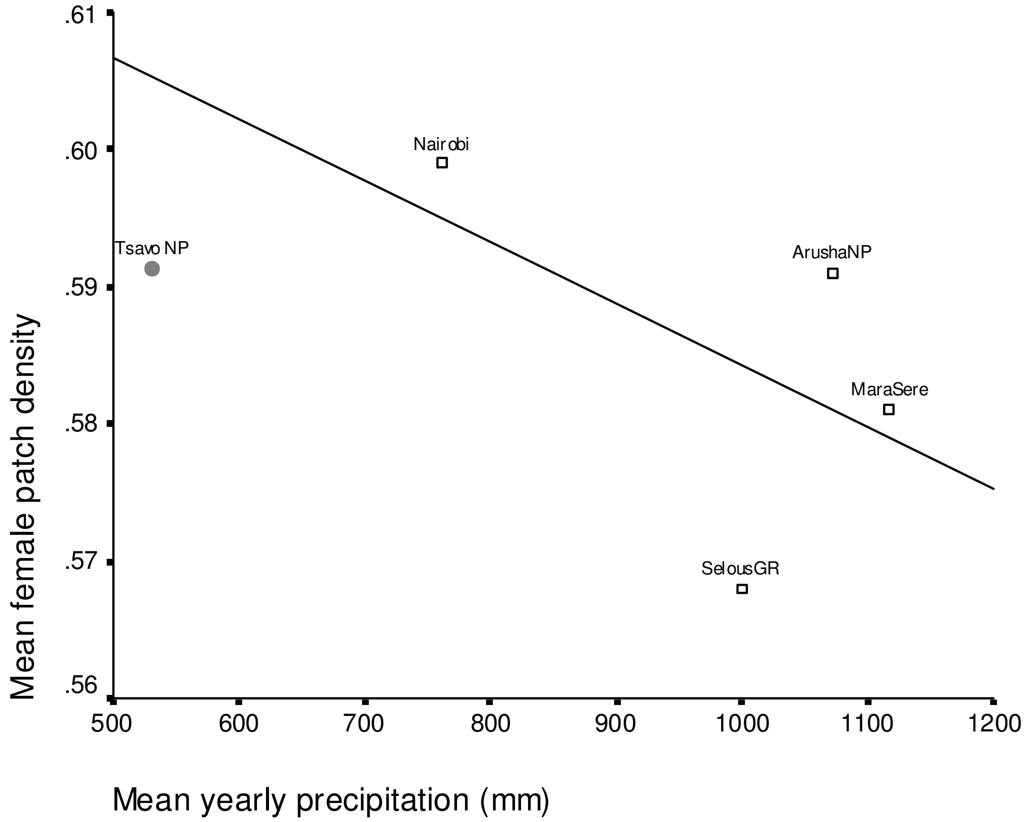


Figure 7.11. Relationship between mean female patch cover in a population and mean annual precipitation, for populations of *G. c. tippelskirchi* only. Empty squares = lower-insolarity sites (<2917 hrs p.a.), filled circles = higher-insolarity sites.

There was also a significant relationship between the proportion of females that had dark patches and the mean yearly hours of bright sunshine, both within *G. c. angolensis* ($F_{1,4}$ = 19.785, P < 0.05), and among all southern African populations ($F_{1,6}$ = 49.201, P < 0.001; Figure 7.12). Above about 3300 hours of bright sunshine per year, nearly all females (<10%) have pale patches (though these populations vary in mean patch cover; see above). This relationship was also evident, though not significant, among *G. c. angolensis* for males ($F_{1,5}$ = 5.457, P = 0.08). This relationship also did not hold for males or females of *G. c. tippelskirchi* populations (males: $F_{1,3}$ = 6.310, P = 0.129; females: $F_{1,3}$ = 0.452, P = 0.571).

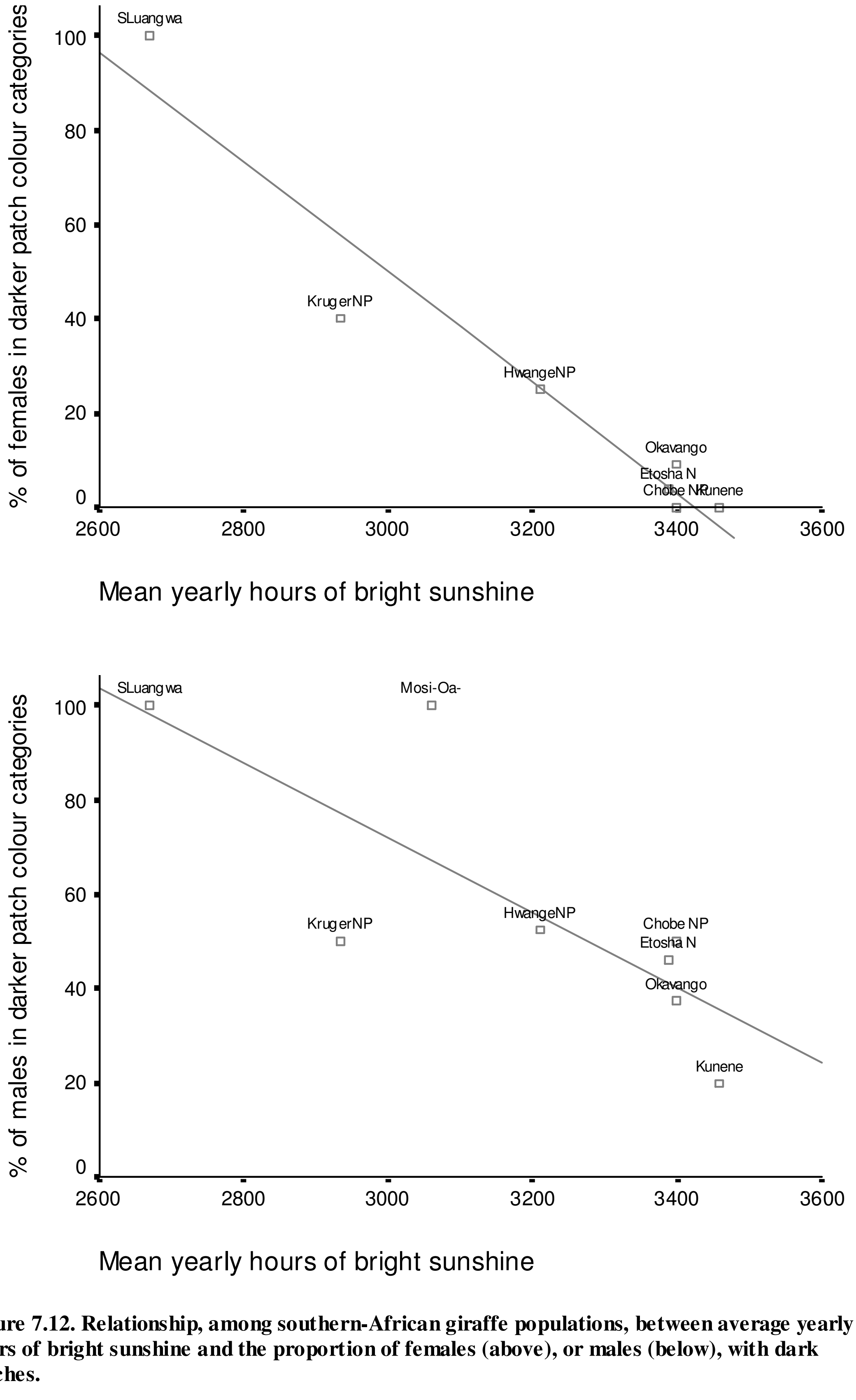


Figure 7.12. Relationship, among southern-African giraffe populations, between average yearly hours of bright sunshine and the proportion of females (above), or males (below), with dark patches.

7.4.2 Field data

7.4.2.1 Sexual dichromatism in Etosha NP giraffe

There was highly significant sexual dichromatism among fully adult giraffe (adult throughout the study period) in the study area population in Etosha National Park (Mann-Whitney U = 4743, N = 278, $P < 0.001$), with only 16 of the 135 fully adult females classed in colour category three (chocolate brown), and none with very dark brown or black spots (Figure 7.13). Most of the darker females appeared to be elderly; one dark female that died of apparently natural causes was estimated to be aged over 20 years (based on dentition (Hall-Martin 1976)). Although a few juveniles had dark tan colouration, this was generally lost as they reached independence (around 18 months), and all sub-adults were of category one or two colouration. All dark males were fully adult, and just over 60% of adult males were classed in the darker two categories.

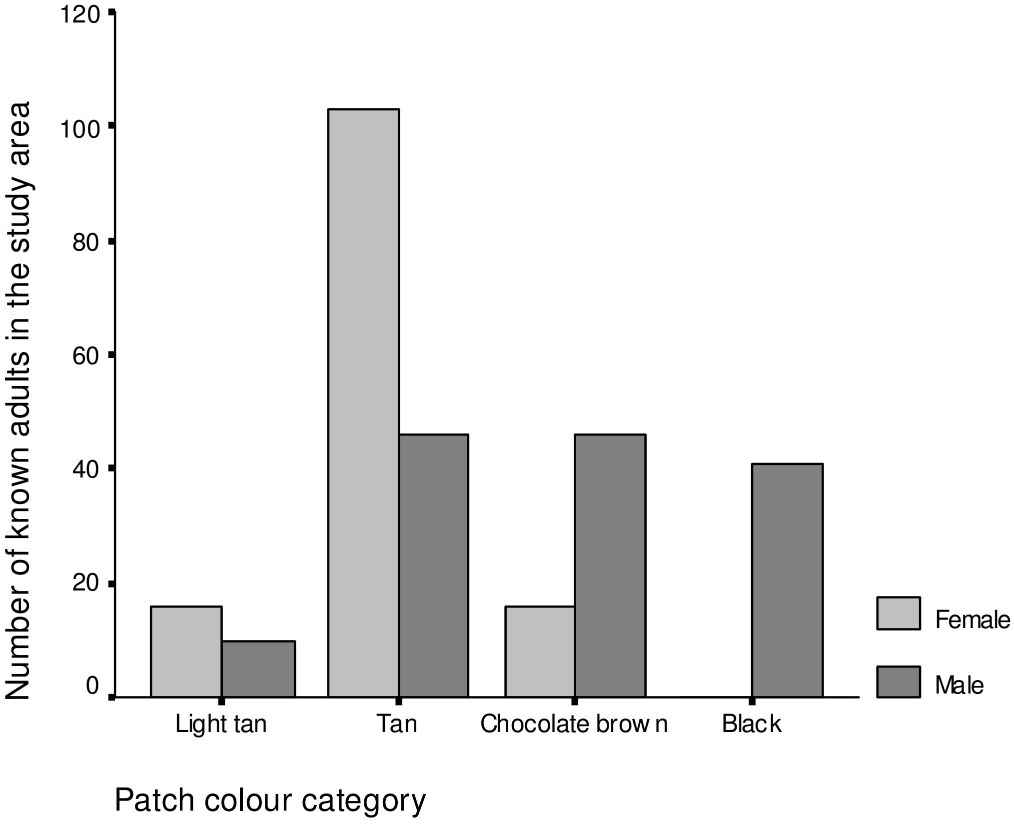


Figure 7.13. Distribution of known, fully adult giraffe in the study area across the four patch colour categories.

7.4.2.2 Thermoregulatory behaviour in relation to coat colour

As expected, giraffe did appear to use body orientation as a means of thermoregulatory behaviour, but only when cloud cover was minimal (one quarter cover or less). When cloud cover was greater (in October), giraffe exclusively sought shade as a means of reducing exposure to sunlight, possibly because of the reduced directionality of incident sunlight (or skylight). For this reason, all subsequent analyses were restricted to days when cloud cover was one quarter or less.

Thermoregulatory behaviour was associated with time of day and season. For all adults, behaviour (four categories) was significantly associated with time of day during the cooler winter months (May to September; contingency coefficient = 0.623, N = 77, P < 0.001; Figure 7.14), but not during the warmer months (March to April, October to December; contingency coefficient = 0.315, N = 78, P = 0.198). Indeed, with one exception, all the observations of giraffe standing with the long axis of their body perpendicular to the sun were on winter mornings (the exception was one dark bull seen standing perpendicular to the sun at 13:00, when the sun was almost at its azimuth and the effect of body orientation would have been reduced.).

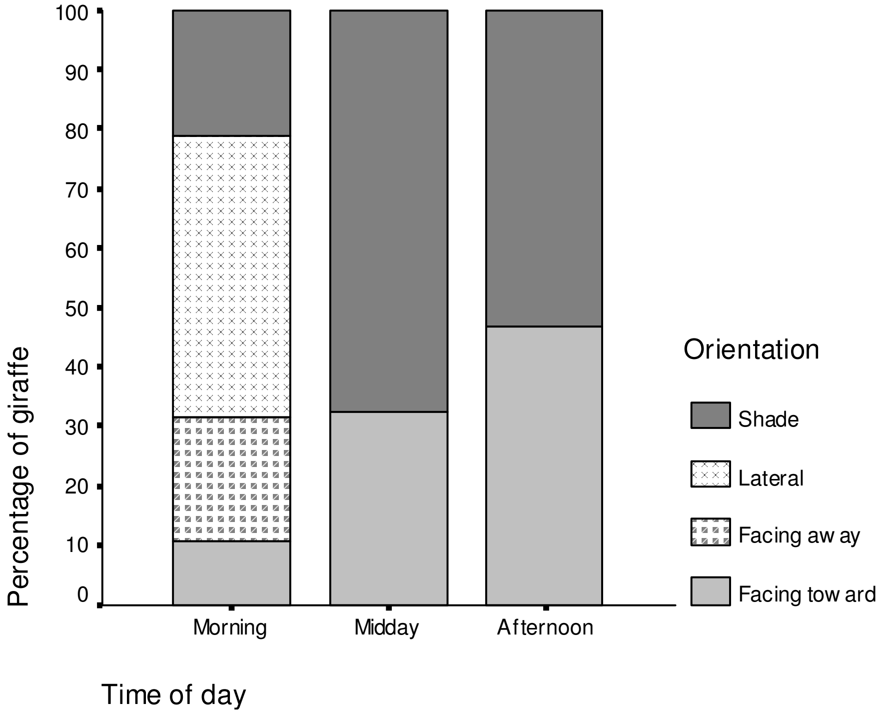


Figure 7.14. Relationship between time of day and giraffe thermoregulatory behaviour in the cooler months (June to September). Morning includes any daylight time up until 11:00; Midday includes times after 11:00 until 14:00; Afternoon includes any daylight time after 14:00.

There was a slight but not significant association between adult male colouration and behaviour (four categories) in the cool season only, at the level of pale adult males compared to dark males (cool season: contingency coef. = 0.396, N = 26, P = 0.090; warm season: contingency coefficient = 0.301, N = 29, P = 0.410); only pale males were found resting with their body perpendicular to the incident sunlight. There was no significant association between behaviour and coat colour among dark adult males (category three versus category four patch colouration, cool season: contingency coef. = 0.311, N = 10, P = 0.301; warm season: contingency coef. = 0.354, N = 18, P = 0.463). The few darker (category three) females that were observed resting, all did so in the shade (N = 6), whereas paler-than-normal females (category one) were equally likely to be resting in the open as in the shade throughout the year (N = 14). This association between adult female coat colour (category one and three only) and thermoregulatory behaviour was significant (contingency coef. = 0.433, $P < 0.05$).

Use of shade relative to body orientation by dark males did not differ significantly from that of females during the warmer months ($X^2 = 0.029$, N = 83, df = 1, P = 0.864), whereas that of pale males did slightly, but not significantly ($X^2 = 3.324$, N = 70, df = 1, P = 0.068; Figure 7.15). Specifically, light adult males always sought shade to rest in the warmer months (March to April and October to December), whereas 16% of females and 14% of dark males were resting in the open in the early hot wet season (October to December) and 59% of females and 57% dark males in the later warm wet season (March, April). Use of shade by dark males also reflected that of females in the cooler months (May to September; Figure 7.16), with about 45% of females and 40% of dark males selecting shade. Pale males, on the other hand, more often rested in the open (64% of observations), during the winter months.

Females used shade more in certain habitats, possibly in relation to the availability of shade-trees. In particular, they rested in the open at least 50% of the time (N = 38) when in certain habitats (A, B, C, D, J; see Chapter 3 for habitat codes), whereas they primarily used shade (at least two-thirds of the time) when in some of the more wooded habitats (E, F, G, H; N = 61). In the warmer months, pale males were only observed standing resting or ruminating in the more wooded habitats E, F, G and H, whereas, like females, dark males were also seen resting in the more open habitats.

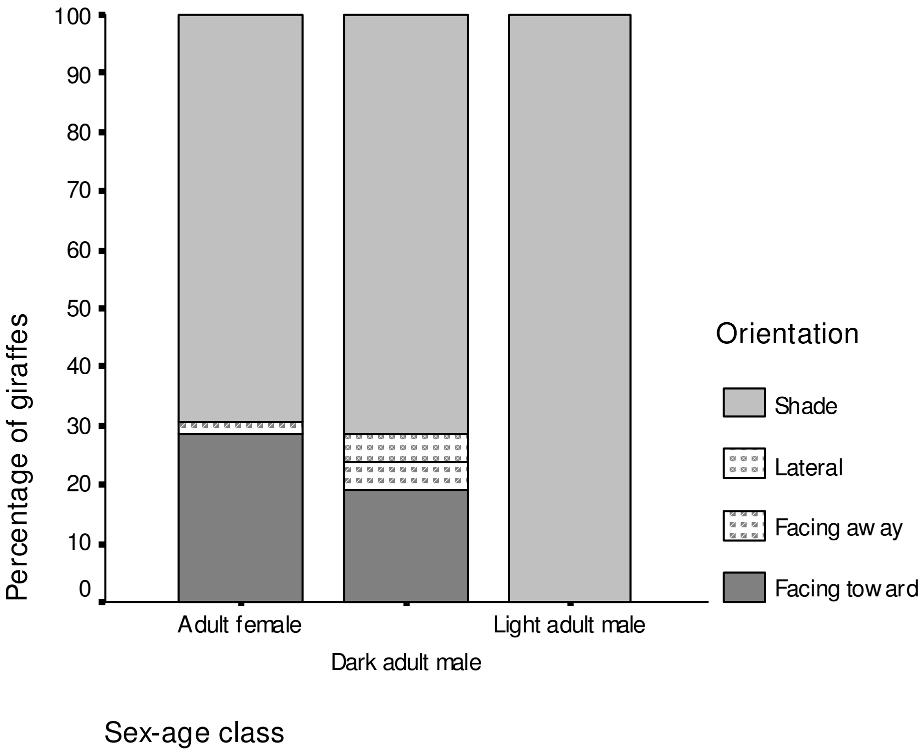


Figure 7.15. Thermoregulatory behaviour of giraffe standing resting or ruminating in the warmer months (March to April, October to December).

Figure 7.16. Thermoregulatory behaviour of giraffe standing resting or ruminating in the cooler, dry months (May to September).

7.4.2.3 Changes in individual coat colouration

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 pale males and of four dark males faded noticeably between one wet season and the end of the following dry season (Table 7.3, Figure 7.17). In four cases, the male also experienced a noticeable loss of condition during the same period; in all other cases there was no clear positive or negative change in condition. Three of the pale males that lost pigmentation in 2005 (M183, M202, M219) had also been observed to gain pigmentation between the end of the previous dry season (2004) and the 2004-2005 wet season. Thus, this seasonal darkening possibly represented a recovery from a similar loss of pigmentation during the preceding dry season.

Table 7.3. Observed losses in male patch pigmentation from the wet season to the following dry season. Males that also lost condition are highlighted in bold type.

Male ID	Age-colour class	Wet – dry season colour cat. change	Wet season sighting (Mar-Jul)	Dry season sighting (Aug-
M111	Pale adult	2 – 1	08/06/04	02/10/04
M128	**Sub-adult**	**2 – 1**	**23/06/04**	**16/10/04**
M131	Sub-adult	2 – 1	25/05/05	06/08/05
M183	Pale adult	2 – 1	14/05/05	26/10/05
M189	**Pale adult**	**2 – 1**	**22/07/04**	**29/11/04**
M198	Pale adult	2 – 1	22/03/05	16/10/05
M202	Pale adult	2 – 1	13/05/05	26/10/05
M219	**Sub-adult**	**2 – 1**	**29/04/05**	**30/11/05**
M269	Sub-adult	2 – 1	07/07/05	26/09/05
M95	Pale adult	2 – 2 (paler)	28/05/04	06/09/04
M82	Dark adult	3 – 3 (paler)	24/05/04	01/09/04
M243	Dark adult	3 – 3 (paler)	13/03/05	14/10/05
M56	**Dark adult**	**4 – 3**	**26/06/05**	**14/10/05 & 22/11/05**
M88	Dark adult	4 – 3	25/05/04	09/09/05

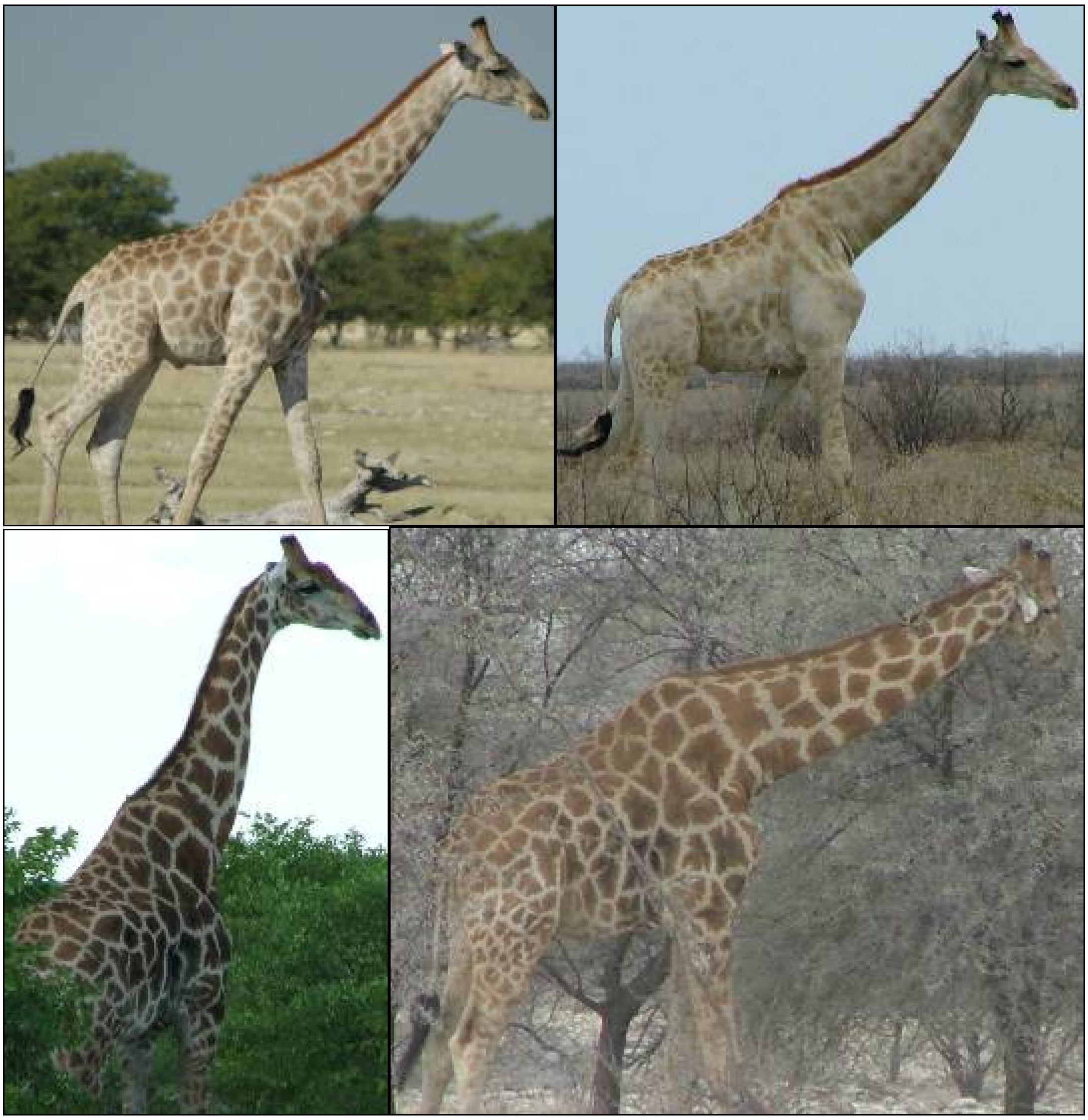


Figure 7.17. Examples of dry-season pigmentation loss in male giraffe. Top: M202 in May (left) and October (right); bottom: M243 in March (left) and October (right).

By comparison, only four females lost pigmentation to an extent that warranted a reclassification of patch colour category. These changes all occurred from the dry to the wet season, instead of from the wet to the dry season. Two adult females changed from category three to two, and two from category two to one. Notably, two of these females lost pigmentation when lactating following the birth of a calf.

7.5 Discussion

7.5.1 Biogeographical variation in patch cover and colouration

Here, I tested the hypothesis that biogeographical variation in giraffe coat colouration results from an adaptation to minimise heat and water stress, and as such can be explained by geographical variation in environmental selection pressures. Solar heat gain is important in determining water consumption and survival in stressful conditions (Finch & Western 1977). The results suggested that bright sunshine does indeed act as a limiting factor in the evolution of giraffe coat markings.

Results indicated that variation in climate across Africa can better explain biogeographical variation in giraffe coat colouration in females than in males. As predicted, in females potentially costly dark coats appear to be selected against in more stressful environments. Specifically, patch cover was found to be greatest in areas of lower rainfall, but was strongly affected by sunshine; patch cover was reduced in areas of high insolarity relative to areas of lower insolarity. Bright sunshine also appears to select for paler patches, especially in females. The relationship between patch cover and climatological factors was greater in more harsh environments; where insolarity was highest and females palest (*G. c. angolensis*), patch cover was greater in females living in cooler, drier areas.

Male giraffe across Africa tend to darken with age (see also Chapter 6), and as a result, mature males were generally darker than mature females, even in areas of high insolarity. Indeed, the degree of dichromatism varied in relation to the predicted level of environmental stress; it was most prominent in areas where predicted heat stress was high, due to the stronger limiting effect of high insolarity on female coat colouration.

These results were partially replicated by the phylogenetically controlled analysis using CAIC. The lack of significant results from the CAIC analysis could possibly be explained firstly by the loss of detail that resulted from pooling the population data into subspecies means, and secondly from the reduction in degrees of freedom that resulted from using contrasts rather than raw data points. However, the results were also partially replicated at lower taxonomic levels, lending further weight to the findings. Perhaps not surprisingly, at the subspecies level, the results remained clearer for the subspecies living in the most stressful environment (in terms of insolarity; *G. c. angolensis*) than a subspecies living in a less stressful environment (*G. c. tippelskirchi*).

These results are consistent with a greater importance in females of natural selection for adaptations to reduce environmental heat stress, due to the energetic costs of gestation and lactation (Pellew 1984b) and the risks of heat stress to embryo development (e.g. Hansen *et al.* 2001; Garcia-Ispierto *et al.* 2006). The widespread maintenance of dark colouration in males can be explained by sexual selection of a costly signal of genetic or phenotypic quality or competitive status (e.g. Zahavi 1975; Moller *et al.* 1998, see also Chapter 6; West & Packer 2002). The reliability of dark coat colouration as an honest signal of status could be greatest where insolarity is high: where insolarity is low, a dark coat might not be as honest an indicator of male quality, as the lower cost of signalling (bearing a dark coat) could leave the system open to cheating by poor quality males (e.g. Zahavi 1975; Kodric-Brown & Brown 1984).

7.5.2 Changes in coat colouration: is pigmentation costly to produce?

Where animals are polygynous and dimorphic, males often face greater costs of growth, metabolism and direct competition than females (Clutton-Brock *et al.* 1982b). They may also be less well adapted than females at securing nutritional resources (Clutton-Brock et al. 1982b). As a result, they are likely to suffer from higher mortality and survival costs than females, particularly in times of environmental stress (Clutton-Brock *et al.* 1982b; Owen-Smith 1993). Indeed, mortality records from Etosha NP (Birgit Kötting & Wilferd Versfeld, unpublished data) and the South-African Lowveld (Hall-Martin & Basson 1975) suggest that the end of the dry season can be a difficult time for male giraffe in particular. Increased mortality at the end of the dry season could be attributable to nutritional stress, as this is generally a nutritionally limiting period for giraffe (Hall-Martin & Basson

1975; Parker & Bernard 2005). If pigmentation is also affected by nutritional state, then a lower tolerance of nutritional stress could explain the greater occurrence of dry-season pigmentation loss in males than in females. This is further supported by the observation that of the four females that also suffered pigmentation loss, two (possibly all) had recently given birth and may have been experiencing nutritional stress due to the additional energetic demands of lactation (Pellew 1984b).

Furthermore, McGraw (2003; 2007) has proposed a biochemical mechanism, through the medium of nutrient acquisition, by which the condition-dependence and honesty of melanin-based signals of status could be maintained. He posited that trace minerals such as Ca, Zn, Fe and Cu are rare in the environment but also critical to the synthesis of melanin. If high concentrations are ingested, such minerals can also be toxic, but if bound to melanin granules and then sequestered in dead tissue such as hair, these minerals could help signal that the animal has good dietary access to limited resources and can also deal with the cost of potentially toxic high mineral concentrations. All of the above-mentioned micro-minerals are vital for the formation of intermediate products that lead to melanin synthesis. Furthermore, the critical rate-limiting steps of melanin biosynthesis involve the copper-requiring enzyme tyrosinase, the activity of which is likely regulated by copper availability (McGraw 2003). Thus, dietary mineral deficiencies could lead to loss of pigmentation.

In an encounter with a competitor, before deciding whether to retreat or escalate, a male should assess his opponent's probable ability to fight using visual criteria (Parker & Rubenstein 1981; Maynard-Smith 1982, see also Chapter 6). Fighting ability will be determined largely by a male's resource holding power (Maynard-Smith & Parker 1976) or 'fitness budget' (Parker 1974), which will be dependent on factors such as genotypic quality, age, body size, strength, social status, and also current body condition (Clutton-Brock *et al.* 1982a; Maynard-Smith 1982; Forchhammer & Boomsma 1998). Furthermore, according to traditional models of sexual selection, any character selected as an honest signal of quality should reflect ecological stresses specific to the species and environment (Zahavi 1975), and most of the variability in the trait should correlate with environmental effects such as nutritional status (the remaining variability being due to heritable variation, Kodric-Brown & Brown 1984).

Therefore, a moderately labile, partially condition-dependent status signal (e.g. Ligon et al. 1990; Hill et al. 1999; McGraw et al. 2002; Cotton et al. 2004) that weakens with declining body condition could be a very reliable signal of male quality and competitive ability, both in competitor assessment (e.g. Parker & Rubenstein 1981; Clutton-Brock *et al.* 1982d) and female mate choice (e.g. Andersson 1982; Andersson 1994). Female preference for males in good condition, with a strong signal of quality (i.e. dark colouration), would operate through selection for indirect genetic benefits for offspring (e.g. a good immune system, Hamilton & Zuk 1982; Kirkpatrick & Ryan 1991), or for direct benefits (e.g. males that are most likely to be able to successfully defend and inseminate her, Trivers 1972).

7.5.3 Behavioural thermoregulation

Many ungulates have behavioural thermoregulatory strategies, particularly body orientation, as one of their adaptations to help reduce the environmental heat load in hot, dry environments (e.g. Maloney 2005). This has also been observed in giraffe (Kuntzsch & Nel 1990). Here I attempted to test whether differences in coat colouration, and thus expected solar heat load, affected male behavioural thermoregulatory strategies.

Light adult males appeared to optimise their behavioural thermoregulatory strategy in relation to the season, seeking shade in the warmer months, and exposing themselves to the sun in the winter months. The latter observation corroborates the finding of Kuntzsch and Nel (1990) that at lower ambient temperatures giraffe position themselves so as to absorb heat over the largest possible body surface. Dark males also optimised their exposure to sun to an extent, but were more likely to be found resting away from shade during the summer months, possibly due to limitations imposed by the following of females during this time.

Through matching female movements and habitat use more closely than light males (see chapters 3 and 5), dark males may be forced to adopt a sub-optimal thermoregulatory strategy. Indeed, pale males selected only wooded habitats with abundant shade to rest and ruminate, whereas dark males were seen resting in a similar range of habitats to females. As a result, dark males may not be optimising their exposure to the sun for the best thermoregulatory effect, as would be expected with a dark coat. Rather, their exposure to the sun and use of shade appear to be constrained by their mating strategy.

However, darker-than-normal females were only seen to rest in the shade, whereas paler-than-normal females often rested in direct sunlight. Since movements and habitat selection of pale and dark females should not differ (whereas those of pale and dark males do, see Chapter 3), this further substantiates the hypothesis that there is a thermoregulatory cost to exposure to sunlight for giraffe with darker coats.

The observed differences in behaviour between dark and pale males in the cooler months may actually highlight a limited advantage of dark coat colouration at the coolest times of day and year. Dark males may not need to orient their body laterally to the sun on cold mornings because their dark colouration enables them to acquire body heat from solar radiation quicker than the lighter coats of pale males and females (e.g. Ohmart & Lasiewski 1971; Finch et al. 1980). However, this advantage is likely to be limited, relative to the costs of dark colouration in heat and sunshine, as the greatest costs related to heat loss should occur overnight (when there is no sunlight and thus no direct effect of coat colour on heat transfer) and during just a few hours on winter mornings. Conversely, dark colouration could be potentially costly (in terms of increasing solar heat gain) for a large proportion of each day, and throughout the year. Furthermore, large, dark males, with their greater body mass, should have higher thermal inertia (i.e. function as a more effective heat sink (Louw & Seely 1982)), thus better retaining their body heat during the winter nights, and having a reduced need for heat gain on winter mornings than smaller males and females. Therefore, if there was a true thermoregulatory benefit to dark colouration, one might expect smaller males, females and juveniles to be darker than larger males.

It has been proposed that patches could help regulate heat balance by acting as "thermal windows through which giraffes dissipate heat" (Skinner & Smithers 1990; Mitchell & Skinner 2005), or by aiding in the absorption of radiant heat on cold but sunny days (Mitchell & Skinner 2003). This would be possible due to the arrangement of subcutaneous anastomotic blood vessels beneath patches (Mitchell & Skinner 2005). Nonetheless, even accepting that patches may function as thermal windows, differences in coat colouration will affect heat gain considerably more than heat loss. It is highly plausible that on hot and sunny days, large, dark patches may exacerbate rather than enhance thermostatic control, and this effect will be greater the darker the patches.

8 GENERAL CONCLUSIONS AND DISCUSSION

In this thesis, I set out to describe in more detail the evolutionary ecology of a large ungulate, the giraffe, living in a semi-arid environment with limited and highly variable resource availability. In particular, I sought to test the hypothesis that spatially restricted foods and artificially provisioned water might predictably concentrate females (spatially and temporally) and thus increase the potential for dominant males to monopolise females for mating. I also sought to explain biogeographic variation in giraffe coat colouration, and to test the hypothesis that dark coat colouration is costly, and as such, functions as a reliable signal of status in males. I shall now summarise the key findings of the thesis, discuss whether they support these hypotheses, and highlight possible areas for further work.

8.1 Main results and conclusions of the thesis

First of all, I established that in Etosha NP, male and female giraffe differ in their choice of food plants and habitat, and also in their feeding strategy (Chapter 3). As predicted, females appeared to maximise their food intake year-round, while males minimised their time spent foraging during the wet season, when food was more plentiful (Section 3.4.3.1, see also Pellew 1984a; Pellew 1984b; Ginnett & Demment 1997), in accordance with Schoener's theory of feeding strategies (Schoener 1971). Females were more selective in their choice of food, responding more noticeably than males to the production of flowers, fruit and new leaves (Section 3.4.3.3).

As observed elsewhere (e.g. Oates 1972), females tended to avoid feeding on *Colophospermum mopane* (3.4.3.4), and as a result, were less likely to be found in habitats containing mopane than males (3.4.3.5). Females browsed most on mopane when it was nutritionally most profitable (3.4.3.2; high protein, low tannin levels), and mothers of calves appeared to limit their intake of *C. mopane* until their calves had begun to feed regularly on solid foods themselves (after six months). This provides further support for the proposal by Caister *et al.* (2003) that nursing females may avoid feeding on mopane to limit their tannin intake.

I also discussed the possibility, raised elsewhere (Young & Isbell 1991; Ginnett & Demment 1999), that females may be avoiding closed habitats such as mopane veld in order to reduce predation risk for their offspring. Habitat use also differed between males that were in bachelor groups and those that were alone, with habitat preferences of solitary males more closely resembling those of females throughout the year (3.4.3.5). This result supports the hypothesis that solitary males leave their preferred habitats (including those avoided by females) to search for potential mates.

I found that group size was largest overall in the wet season (3.4.3.6). This could either be a result of spatially-restricted preferred foods causing females to aggregate in the wet season, limitations on maximum female group sizes in the dry season, when food is scarce, or due to females forming larger social groups as a means of predator defence during the peak calving season (Jarman 1974; Gosling 1986). Female aggregations formed in different habitats in different seasons as a result of large numbers of females browsing on preferred, ephemeral food sources. As predicted, the highest densities of female giraffe overall were to be found in one of the most spatially limited habitat types (mixed broadleaf woodland). More specifically, large groups and high densities of females were found to occur in mixed broadleaf woodland throughout the year, but particularly during the wet season (October to December and March to May), and also in *A. nebrownii* thickets between June and September, during the *A. nebrownii* flowering season (3.4.3.6). Females aggregated in an open habitat (*A. nebrownii* shrub savannah) in the cooler, drier season, and in more wooded habitats, with more shade, in the warmer, wetter months. Certain taller, more closed habitats appeared to be used for shade during times of year when they were not producing new vegetative growth (3.4.3.5).

Despite the apparent water independence of giraffe to the west of Etosha NP (Fennessy 2004), giraffe in Etosha used water sources regularly. Unlike most giraffe populations previously studied (Berry 1978; Leuthold & Leuthold 1978b; Ginnett & Demment 1999; Le Pendu & Ciofolo 1999; Fennessy 2004), the Etosha population resides in an area devoid of natural water courses and the associated riverine habitat. Instead, water is only available at a limited number of point water sources. As expected, use of perennial waterholes was lowest in the months that heavy rain occurred, and increased steadily throughout the dry season (3.4.4.1). During the driest months in terms of water availability (July to September), this resulted in female giraffe being found more predictably at waterholes than elsewhere in the park (3.4.4.2), and during the same period large groups of females were common in open plains surrounding waterholes (3.4.3.6). However, female groups did not tend to be larger at perennial waterholes than elsewhere in the study area (Section 3.4.4.3). The apparent concentrating effect, in terms of female groups size, of one specific waterhole (Ombika) could be attributed to its location within another spatially limited resource (mixed broadleaf woodland). These results support the hypothesis that limited resources, both food and water, cause females to aggregate predictably in the study area, with food having a greater concentrating effect in the wet season, and water in the dry season.

As expected, based on other studies in southern Africa (Berry 1973; Hall-Martin *et al.* 1975), while breeding occurred throughout the year, a peak in births was found to occur between March and June, corresponding with a peak in conceptions between December and March, coinciding with the peak rainy season (Chapter 4). This closely resembles the conception peak previously found in the South African Lowveld (Hall-Martin *et al.* 1975), and suggests that this slight breeding seasonality may be reflected in wild giraffe populations throughout southern Africa. I considered two possible explanations for the observed breeding seasonality, one related to selection for minimising costs of lactation, and one relating to a physiological constraint on conception (see also Hall-Martin *et al.* 1975).

As predicted by traditional models of mating systems and space use (Trivers 1972; Clutton-Brock 1989; summarised in Schwab 2000), adult males were found to range over larger areas than females, but home ranges of dark males were also highly variable in size (5.4.1.2). Female movements tended to be concentrated near perennial waterholes and preferred food sources (5.4.2.1). In line with expectations, males were found to associate more with females when in these areas of high female usage than when outside these areas. However, more mature males generally associated less with females than younger males, rather than more (5.4.2.2).

Some males were only sighted within the study area during a short period in each year, suggesting seasonal movement in and out of the study area (5.4.3.1). These ‘seasonal visitors’ used smaller ranges than more resident males, but the extent of their movements once they left the study area were unknown. Males with smaller home ranges tended to be found in larger groups, spent more time in areas of high female usage, and were more likely to be seen with females, than males with larger home ranges (5.4.1.2, 5.4.2.2). I concluded from these observations that adult males in the study area employ a diversity of ranging strategies that may relate to male competitive ability, with dominant males probably using a mating strategy involving area-restricted search behaviour (Ims 1990) and possibly temporary localised defence of females (e.g. van der Jeugd & Prins 2000) in areas of high and predictable female usage.

Due to seasonal variation in female aggregation (Chapter 3), and in the proportion of females that are receptive (Chapter 4), it was predicted that mature males might vary their mating strategy seasonally. Indeed, mature, dark males, but not pale adult males, were found to associate more with females during the wet, higher-conception-rate season than during the rest of the year (5.4.3.2). Further evidence was presented to suggest that mating strategies differed among mature males. A proportion of dark males appeared to avoid female concentration areas, possibly because of the risk of high encounter rates and costly conflicts with other dark males. Younger, pale males, on the other hand, appeared to be tolerated, and commonly used these areas (5.4.3.3).

In accordance with predictions, waterholes were shown to locally increase encounter rates between males and females, and consequently to increase the frequency of mating and agonistic interactions throughout the year (6.4.2.2, 6.4.2.3). Mating interactions (urine-testing attempts) were more likely to occur at waterholes during the dry than the wet season, due to the greater predictability of occurrence of females (6.4.2.4). Waterholes appear to provide pale males with an increased opportunity to urine-test females, due to increased intruder pressure and a reduced ability of dark males to exclude subordinates from this activity (6.4.4.2). However, pale males were tolerated by dark males in this respect, as dark males always succeeded in securing mating rights to females in accordance with the ‘priority of access’ model (6.4.4.3, Altmann 1962; Cowlishaw & Dunbar 1991). Male intra-sexual competition was generally greater during the wet season, with a greater relative involvement in urine-testing attempts and in displacements, and a greater intolerance of one another, by dark males during this time (6.4.3.1-6.4.3.3).

I validated my categorisation of dark and pale adult males as separate social classes by demonstrating a difference in participation in agonistic interactions (6.4.1.2). Further, I found evidence for pelage colour relating to height and thus age, especially up to full maturity, but with a less clear fit among fully-grown males (6.4.1.1; refer also to necking fights, 6.4.1.3). I also tested the relationship between coat colour and social status; the results confirmed an association between colour and the outcomes of both displacements between males (6.4.1.3) and courtship interactions (urine-testing attempts, 6.4.1.5). These results support the hypothesis that male coat colour functions as a signal of status, and suggest a role in both competitor assessment and female mate choice (e.g. Parker 1974; Zahavi 1975; Andersson 1982; Smith 1982).

I highlighted two possible regulatory costs associated with the production and maintenance of dark coat colouration, which would aid in maintaining the ‘honesty’ of coat colouration as a signal of quality or status (Zahavi 1975): a nutritional cost (7.4.2.3, McGraw 2003), and a thermoregulatory cost (e.g. West & Packer 2002). The latter, when combined with geographical variation in environmental conditions, helps explain existing biogeographical variation in giraffe coat colouration (Section 7.4.1). As hypothesised, a key determinant of environmental heat stress, bright sunshine (e.g. Finch & Western 1977), appears to be a limiting factor in the evolution of coat colouration, although this effect is stronger in females than in males. As a result, sexual dichromatism tends to be most significant where insolarity is greatest. I concluded that natural selection is responsible for biogeographic variation in female coat colouration, and that the maintenance of dark coat colouration in mature males can be explained by sexual selection for an honest (costly) signal of quality or status (e.g. Zahavi 1975; Moller *et al.* 1998). This is the first study that explores the function of a purely visual secondary sexual trait in the giraffe (as opposed to one also involved in combat, such as body size or horn dimorphism (Simmons & Scheepers 1996)).

Thermoregulatory behaviour of dark males was predicted to differ from that of pale males and females due to the hypothesised thermoregulatory costs of a dark coat. However, behavioural data did not provide clear evidence for a heat load cost of dark colouration in males, as the thermoregulatory behaviour of dark males appeared to be constrained instead by their matching of female movements and habitat preferences (7.4.2.2). Pale males, on the other hand, which may have been less constrained by their reproductive strategy, did optimise their thermoregulatory behaviour in relation to the season: they tended to seek shade in the summer, and rest in the open with the body oriented perpendicular to the sun on winter mornings (e.g. Kuntzsch & Nel 1990; Maloney 2005). Nonetheless, darker females appeared to have a greater preference for shade than very pale females. This observation, combined with the low proportion of females of dark colouration relative to males, provides some support for the hypothesis.

I assessed probable reproductive skew in the study population by reviewing relative participation of pale and dark males in mating interactions. I also compared apparent mating success (copulations and multiple consortships) with male association with females and potential for monopolisation of females based on a simplified priority of access model (e.g. Altmann 1962; Hirotani 1994; Fisher & Lara 1999). Based on this, I proposed a surrogate measure of probable male mating success based on two socio-behavioural measures: the proportion of time a male spends with females, and the proportion of that time that a male is in a position to monopolise mating opportunities (i.e. the only or dominant male in the group; 6.4.4.3). This suggested that pale males and younger dark males contribute little to reproduction, and that variance in reproductive success among dark males may be high, with a small number of dominant males possibly monopolising a large proportion of mating opportunities.

8.2 Insights into the giraffe mating system in Etosha NP

This study should add considerably to the current understanding of giraffe mating systems. I have attempted to clarify some aspects of giraffe behavioural ecology that have already been raised elsewhere, and considered them within the context of traditional socio-ecological models and theories. For example, I have related variation among males in their appearance, movements and behaviour to probable differentials in individual competitive ability and mating strategies.

8.2.1 Male coat colouration as an honest signal of status

I have also discussed aspects of giraffe evolutionary ecology that have not before been considered, namely the evolution of a purely ornamental signal of status (in contrast with traits that serve in combat, such as neck musculature and horns). Male coat colouration appears to be sexually selected through both male contest competition (e.g. Pryke & Andersson 2003) and female mate choice (e.g. Petrie *et al.* 1991).

Escalated contests among male giraffe are clearly risky and potentially fatal (Dagg & Foster 1982), and competitor assessment apparently involves relatively accurate role assessment (i.e. near-perfect information, Smith & Parker 1976; Parker & Rubenstein 1981) since the initiator of a displacement is rarely challenged, and consequently escalated contests are extremely rare. Male coat colour may be one of the key traits used as an indicator of status and probable competitive ability, as darker males were more likely to displace lighter males than vice versa (6.4.1.3). Among fully mature males, it may in fact be a more reliable indicator of potential competitive ability than height or other indicators of age (e.g. horn development), since in all of the three observed necking fights, the winner was darker but had the least developed horns and skull ossifications, and in one case the winner was also the shorter of the two adversaries (6.4.1.3). As demonstrated in Chapter 7, the honesty of the trait could be maintained by the thermoregulatory ‘handicap’ of bearing a dark coat in a high insolarity environment, a cost that is greater for males with darker coat colouration, but which may be better tolerated by high quality than low quality males (e.g. Zahavi

1975; Andersson 1982; Smith 1991). This point may only be fully resolved through experimentation or collection of detailed physiological field data.

In attempts by males to urine-test females, females were more likely to reject (not urinate for) pale males than dark males, and most likely to reject very pale adult males (6.4.1.5). Some evidence was found for male coat colour being affected by nutritional stress (7.4.2.3 and 7.5.2), suggesting that coat colour might be dependent not only on age and social status, but also on male condition. Indicator models of mate choice argue that a signalling trait is condition-dependent and honestly indicates male viability because producing a signal of a given strength should be more costly for weak than for strong males (Andersson 1982; David *et al.* 1998; Westneat & Birkhead 1998; Gonzalez *et al.* 1999; McGraw & Hill 2000b). Thus, females could be using male coat colour as a cue in mate choice, rejecting males of both low status and poor condition in favour of males that are more likely to confer direct benefits to the females (e.g. high male fecundity) or genetic fitness benefits to their offspring (‘good genes’, e.g. parasite resistance (Kirkpatrick & Ryan 1991; Smith 1991; Folstad & Karter 1992; Petrie 1994; Neff & Pitcher 2005)).

In other ungulate species in which purely ornamental signals (i.e.not weaponry) have been studied, the traits considered have been relatively inconspicuous, or small compared to total surface colouration (e.g. black cheek patches in pronghorn, *Antilocapra americana* (Min 1997); neck patches in puku, *Kobus vardoni* (Rosser 1990)). The significance of sexual dimorphism in patch colouration in the giraffe is that the dichromatic trait applies to a large proportion of the body surface, so potential thermoregulatory costs become an important consideration. This idea relating sexual selection for an honest signal of status to the thermoregulatory cost of dark colouration has previously been treated in lions (*Panthera leo*) by West & Packer (2002), who not only found evidence for darker manes influencing both female choice and male-male competition, but also found that males with darker manes suffered higher surface temperatures, higher rates of abnormal sperm, and lower food intake during hot months. This proposed explanation for coat dichromatism may also be applicable to a number of other sexually dimorphic ungulate species. For example, both the sable antelope (*Hippotragus niger*) and the blackbuck (*Antilope cervicapra*) are polygynous, also live in sub-tropical to semi-arid environments, and whereas juveniles and females have tan coats, males develop striking black pelage colouration (Skinner & Smithers 1990; Nowak 1995).

8.2.2 Limited resources and the potential for mate monopolisation

I also tested the hypothesis that a highly limited resource, such as water, can increase the potential for male monopolisation of mates in the giraffe, through the predictable concentration of females (see also Ritter & Bednekoff 1995). The results supported this hypothesis as I found that while perennial waterholes appeared to increase the detectability of females for all males (e.g. Ims 1990), and increased access to females for urine-testing for pale males, they also appeared to reduce the probability of subordinate (pale) males gaining mating opportunities (6.4.3.1, 6.4.4.2, 6.4.4.3). This resulted from increased encounter rates at waterholes, and consequently an increased likelihood of a dark male ‘stealing’ a potential mating opportunity from a pale male (Altmann 1962; Ims 1988a).

Thus, a small number of waterholes appear to favour a relatively small number of dark males with a higher competitive ability (or resource holding power), as by focussing their search effort on waterholes, these males can rely on a lower search time to find a ‘takeable resource (i.e. a receptive female not defended by an individual of higher RHP, (Parker 1974)), than males of lower RHP. These results highlight the relative importance of direct male conflict and priority of access (e.g. Altmann 1962), compared to scramble competition (e.g. Schwagmeyer 1988) and female mate choice (e.g. Kirkpatrick & Ryan 1991), in determining male reproductive success in the giraffe when females are predictably concentrated.

Similar conclusions were reached by Fisher and Lara (1999) in their study of the bridled nailtail wallaby, which has a comparable mating system to the giraffe. They also concluded that priority of access (in this case determined by proximity to receptive females when in a group of at least two males) explained the greatest amount of variation in male reproductive success, and that smaller, subordinate males, unable to displace larger males, might be able to increase their mating success by searching more widely for uncontested females (Fisher & Lara 1999). This reinforces the suggestion made here that male giraffe with large home ranges and low contact with females are of low competitive ability, and are adopting a mating strategy that makes the 'best of a bad job' by relying on increased mobility to encounter uncontested females (e.g. Trivers 1972; Dunbar 1982; Smith 1982; Isaac 2005). Unfortunately, the lack of genetic data in this study of giraffes precluded a comparison between home range, priority of access, predicted potential mating success and actual reproductive success.

8.2.3 Resource defence versus mate-searching

It has been suggested that where more stable groups of giraffe occur in high cover areas, resource defence polygyny might occur (van der Jeugd & Prins 2000). Territoriality can be expected where females (or the resources that concentrate them) are predictable and economically defendable (Emlen & Oring 1977; Gosling 1986; Clutton-Brock 1989). Females were found to occur predictably at very high densities in one specific habitat type (mixed broadleaf woodland) during the wet season, and in the dry season the vast majority of females were found feeding on *Acacia nebrownii* (Chapter 3). Therefore, it was suspected that males in the study area might exhibit territoriality at times when females were most predictably concentrated, as a means of increasing encounter rates with potentially receptive females (e.g. Carranza *et al.* 1996).

However, no clear evidence for territoriality (sensu Owen-Smith 1977) was found (male home ranges tended to be large, overlapping considerably, especially in areas of high female usage, and large numbers of pale adult males appeared to be tolerated in *A. nebrownii* habitat; Chapter 5). In the light of these observations, it is proposed that attempting to increase reproductive success by defending a seasonal territory in *A. nebrownii* habitats would be an uneconomical mating strategy, even during the flowering season. This is because the start and duration of *A. nebrownii* flowering is highly variable across relatively short distances. Therefore, although the flowering season may last three months, individual patches may only be in flower for a couple of weeks. Consequently, although *A. nebrownii* shrub savannah may constitute a relatively widespread, homogenous habitat, flowering within it is patchy and relatively unpredictable, such that groups of females are never in the same place for very long. As a result, males that attempted to defend territories in *A. nebrownii* shrub savannah might spend a long time defending a patch that might not come into flower for many weeks.

Thus, actively searching for receptive females by roaming across large areas of *A. nebrownii* habitat is likely to be a more economical strategy than resource defence (e.g. Gosling 1986; Clutton-Brock 1989). Furthermore, *A. nebrownii* may not be an ideal habitat for males, as males tend to prefer to feed on taller, more biomass-heavy species than females, and they prefer habitats with shade-trees for resting. Thus, it may be too costly for males to remain in *A. nebrownii* habitat long enough to establish and defend a territory. Relatively few dark males spent the majority of their time in *A. nebrownii* shrub savannah during the dry season, whereas many dark males spent the majority of their time in mixed-woodland in the wet season.

During the wet season, females were located more predictably within a highly spatially restricted habitat. Throughout the peak rainy season (a period of about five months), mixed broadleaf woodland consistently produced high quality food (a number of species producing first leaves, then flowers, then pods). As a result, relatively large numbers of females were constantly present within an area of just a few kilometres diameter throughout the wet season. Any male that could defend a territory in this area would have predictable long-term access to a large number of females, so resource defence would seem more likely to arise under such conditions (Gosling 1986). However, although some dark males (possibly subordinates) appeared to avoid this area during the wet season, again no clear evidence for defence of exclusive territories was observed: home ranges overlapped considerably, and a number of pale and dark males were typically using the area at the same time, especially during months when seasonal visitors (with small home ranges) were present (the opposite would have been expected if these seasonal visitors were territorial).

It is possible that mixed broadleaf woodland is un-defendable, in terms of excluding all potential competitors, because intruder pressure is high, and visibility, and thus the probability of detecting intruders, is very low (Gosling 1986; Ims 1988a). Giraffe rely heavily on vision to detect competitors over long distances, but would be unable to see intruders in a woodland habitat until they were very close. Of the three violent fights, two took place in broadleaf woodland. In one case, the males appeared to detect one another at about 200 m, but only because both moved onto a road at the same time (see Appendix 2). On the other occasion, the males encountered each other in dense bush, and did not seem to be aware of one another until they were within 30 m of each other. This does not, however, rule out the possibility that resource defence might occur in areas where giraffe occur in much higher densities (e.g. parts of central and eastern Africa, Pratt & Anderson 1982; Nje 1983; Pellew 1983b; van der Jeugd & Prins 2000).

8.3 Limitations of this study and areas for future work

Questions that arise from the observed relationship between coat colouration and status are how exactly is this relationship maintained, and is it strongly coupled to body condition? It would be interesting to investigate whether this relationship could be maintained by testosterone through its effect on pigmentation, as testosterone levels often relate to both social status and colouration (Rohwer & Rohwer 1978; Setchell & Dixson 2001b; Setchell & Dixson 2002). Testosterone assays of a small number of male giraffe by Hall-Martin *et al.* (1975) revealed a significant relationship between testosterone levels and age but not season, and testosterone levels were not compared to any morphological or social variables.

For logistical reasons (e.g. difficulties in accurately measuring height and age), it was not possible to ascertain exactly which factors (e.g. height, age, developmental factors) determined individual competitive ability (e.g. Appleby 1982; Barrette & Vandal 1986; Ligon *et al.* 1990; Fisher & Lara 1999). However, male coat colouration categories and maturity classes were found to be relatively good predictors of dominance and potential mating success, especially when combined with socio-behavioural indicators. It remains to be seen if the mate-searching ability, competitive ability, attractiveness to females, and reproductive success of individual males are all positively and significantly correlated, which would be expected if all were related to male quality (Ims 1988a; Neff & Pitcher 2005). It also remains to be determined if the observed short-term differences in mating strategy and potential access to mating opportunities actually reflect lifetime differences in reproductive success (e.g. Clutton-Brock *et al.* 1982a; McElligott & Hayden 2000).

It would also be interesting to explore whether these individual differences involve a spatial reference for dominance, whereby one male may be dominant to another in one location, but subordinate to the same male elsewhere (e.g. Owen-Smith 1977; Gosling 1986; Ims 1988a). If such a spatial reference for dominance does exists, and if it holds even in the absence of females (i.e. not female defence), then this could be considered as evidence for a form of resource defence or territoriality (Owen-Smith 1977; Gosling 1986). Unfortunately, this study lacks sufficient qualitative data on directional agonistic interactions and male reproductive success to answer these questions, partly due to the logistical limitations of observing sufficient agonistic interactions and copulations in a highly mobile, large, low-cover population (e.g. Thirgood *et al.* 1999), and partly due to the lack of genetic paternity data.

Because of the scale of giraffe home ranges, a more extensive use of GPS collars may also be a necessity in order to fully understand giraffe movements. For example, GPS satellite tracking could be used to ascertain where seasonal visitors to the study area move to during the remainder of the year, and to examine the relative costs, in terms of daily and seasonal movements, of the different ranging strategies. However, identification of these inter-individual differences in movement patterns could not have been possible if this study had relied on GPS collars alone, as they would have had to be fitted to a large number of individuals to obtain a fair representation of the whole continuum of home range sizes and ranging strategies. Perhaps with the advance of technology, and possibly through the use of mobile phone-based tracking (e.g. Sundell *et al.* 2006), GPS collaring will in time become more affordable and more reliable (collars often do not last more than a few months (e.g. Fennessy 2004)). Then, by carrying out a preliminary study to establish males of interest (e.g. wide-ranging residents and seasonal visitors, fully mature and younger adult males), it might be possible to provide a more complete picture of individual variation in movements and mating strategies.

As pointed out by Clutton-*Brock et al.* (1986), it may only be possible to achieve a reliable description of mating systems if recognisable individuals are studied for a substantial proportion of their lifetime. Thus, a longer-term behavioural study (e.g. McElligott & Hayden 2000; McElligott *et al.* 2002; Setchell *et al.* 2005), with a successful genetic component, is likely to be necessary before the above questions can be satisfactorily answered. This need for longer-term studies of giraffe has already been highlighted (Fennessy 2004), and as giraffe populations become increasingly isolated and conservation-dependent, such studies are likely to become ever more crucial for generating informed management of giraffe habitats and populations.

APPENDIX 1.

Scientific and common names of tree and large woody shrub species present in the study area.

Scientific name	Common names
Acacia hebeclada	Candle pod Acacia, Candle thorn
Acacia kirkii	Floodplain Acacia, Seyal
Acacia luederitzii	Kalahari Acacia, False umbrella thorn
Acacia mellifera detinens	Black-thorn Acacia, Hook thorn
Acacia nebrownii	Water Acacia, Water thorn
Acacia reficiens	Red thorn
Acacia tortilis heteracantha	Umbrella thorn, Curly-pod Acacia
Albizia anthelmintica	Worm-cure Albizia
Boscia foetida	Smelly shepherd's bush, Stinky shepherd's tree
Catophractes alexandri	Trumpet thorn, Rattle-pod
Colophospermum mopane	Mopane
Combretum apiculatum	Red bushwillow, Kudu bush
Combretum hereroense	Russet bushwillow, Mouse-eared combretum
Combretum imberbe	Leadwood
Dichrostachys cinerea	Sickle bush, Chinese lantern tree
Gymnosporia senegalensis	Red spike thorn, Confetti spike thorn
Moringa ovalifolia	Moringa, Phantom tree
Rhigozum brevispinosum	Western rhigozum, Short-thorn pomegranate
Terminalia prunoides	Purple-pod Terminalia, Lowveld cluster-leaf
Ziziphus mucronata	Buffalo thorn, Wait-a-bit tree

APPENDIX 2.

Descriptions of intense necking fights observed between males

Date: 08/04/05

Start of observation: 16:45

Location: G6 (near Ombika waterhole)

Participants: M90 and M248

M90 encountered M248 in dense bush --> short but very intense bout of necking - only a few blows, all delivered by M90.

M248 walked away, and M90 continued in direction of two females that he was originally pursuing --> re-joined females.

M90 later smelled the rump of one of two females (younger). M248 stood and watched at c. 200m away.

Date: 23/05/05

Start of observation: 07:12

Location: G279 (south of Leeubron dry waterhole)

Participants: M83 and M262

M262 already with females.

M83 approaches from GPIT51 - doesn't stop when he sees M262.

M83 assumes erect posture.

M262 also assumes erect posture, and walks towards M83.

Both males assume parallel walk for c. 10 seconds, then engage in intense necking for c. 20 s, with the smaller bull (M262) delivering the most blows, M83 resisting. They stop delivering blows but continue pushing against each other for c. 18s, then M262 breaks off and walks away, with M83 following - M83 in erect posture, M262 not.

M83 then joins the females, while M262 watches from c. 100 m --> successful takeover of female group.

M83 later displaces M262 further from the female group by walking towards him, and then herds the female group away from M262.

APPENDIX 2 (cont.)

Date: 17/10/05

Start of observation: 16:50

Location: G461 (near Ombika waterhole)

Participants: M97 and M295

17:01: M97 with a group of two pale males and four females.

17:29: Another group approaches: M295 with three females. This group crosses the road, moving in the direction of the waterhole, about 200m to the north of M97's group.

M97 'coughs' four times, while standing in erect posture, looking towards M295.

17:50: M97 starts walking, in erect posture, towards the other group, which is heading towards the waterhole.

M97 walks straight towards M295 → M295 also assumes erect posture and walks towards M97.

The two males begin parallel-walking, then engage in a short period of intense necking, followed by circling, with M295 walking behind M97

Both stand still about 50m apart for four minutes, before M295 walks away and rejoins his group.

M295 re-joins his females at the waterhole, and tries to urine-test one of the females but she walks off.

M97 re-joins the remainder of his group (some have joined the females that were with M295), east of the tar road

Outcome not very clear, but M295 stayed in erect posture for longer, and was able to return to his females plus some of M97's group.

APPENDIX 3.

Descriptions of observed attempted and successful copulations

Date: 07/05/04

Location: G12 (near Ombika waterhole)

Participants: M90 and F78

Note: these two giraffe had been observed in an early courtship interaction between 16:40 and 17:15 the previous day.

08:27	M90 sniffs rump of F78; F has tail held out; M standing close behind F in erect posture
08:29	Laufschlag; Following of F by M; F's tail held out again
08:34	Laufschlag
08:36	M standing behind F standing
08:39	M nosing F: driving her on, testing for receptivity. No comp. from other Males. M following F closely around bush with ritualised nosing, kicking and standing close. M throwing head back occasionally – intention movement for mounting?
09:09	More standing close, less nosing
09:15	F moving fwd less in response to kicks; M has erection periodically
09:20	*1st attempted mounting, followed by more circling*
09:35	*2nd attempted mounting*
09:40	*3rd attempted mounting*
	Just before mounting F braced her legs and M bent his
09:55	*4th attempted mounting*
10:01	*5th attempted mounting*
10:01	*6th attempted mounting*
10:04	Almost attempted mounting
10:09	Both ran across road, M in pursuit of F
10:12	*7th mounting: not clearly visible because of trees, but assumed successful copulation*
10:15	Both browsing close together
10:26	F walks away, M follows at a distance of c.100 m – mate guarding?
	U18 runs to join F78 (calf)
11:10	M still guarding F

APPENDIX 3 (cont.)

Date: 29/11/04

Location: G120

Participants: M86 and F222

M86 following F222 very closely, nosing rump frequently and standing in erect posture behind her.

16:26	Laufschlag repeatedly. F continues to browse. Some courtship circling
16:33	F now standing still – no longer browsing
16:37	F walking again; M following closely
16:38	*1st attempted mounting, followed by more circling, laufschlag, nosing etc*
16:46	*2nd attempted mounting*
16:51	*3rd attempted mounting*
17:04	F walking quickly; M following
17:08	*4th attempted mounting*
17:12	*5th attempted mounting*
17:15	Assumed that last mounting achieved successful intromission, as M begins to browse on *A. tortilis* – no longer following F
17:16	F walks away from M and resumes browsing; M walks away from F and continues browsing
17:26	Still browsing – uninterrupted during last 10 minutes; now c.20 m apart
18:16	Still browsing; c.60 m apart

N.B. M86 was killed by lions 11 months later, aged 8-9 years.

Date: 04/07/05

Location: G344 (W-Drive)

Participants: M267 and F140 (young female, probably only just sexually mature)

11:17	Quite advanced stage of consortship. F140 not browsing; just circling trees in response to close following by M267. M contacting F's rump with upper forelegs and head; slight laufschlag; repeated nosing of F's rump; M occasionally putting his head on F's back or against her flanks.
11:36	F stops moving. M's penis partly unsheathed then re-sheathed. M then leaning against F's rump
11:38	F resumes walking. F has slightly distended vulva.
11:40	F stands still again
11:42	Penis unsheathed fully then re-sheathed again
11:43	Both resume courtship circling, quite fast, female even running for a short distance
11:50	F stops. M pushes slightly from behind and F only takes a couple of steps in response
11:53	Penis unsheathed again
11:54	Both resume courtship circling
12:00	F stops again, tail to one side. M unsheathes and then re-sheathes penis. M gives F small kicks with knee
12:05	Both resume courtship circling. F runs for a short distance, then browses briefly
12:10	Both stop circling. Then as at 12:03, twice.
12:16	Both resume courtship circling. F runs again for a short distance.

APPENDIX 3 (cont.)

12:19	*1st attempted mounting*. F moves forward
12:21	Both resume courtship circling
12:23	M noses F’s rump
12:25	Both stop circling
12:29	Both resume courtship circling. M noses F regularly, as at 11:17
12:46	Stop circling
12:47	Resume circling
12:50	Stop circling. Laufschlag. Resume circling
12:54	Stop circling
12:57:	Resume circling
13:04	F browsing
13:06	Resume circling
13:18	Stop circling. M has partly unsheathed penis, then it is re-sheathed
13:23	M leans against F’s rump. Penis unsheathed fully, then r-sheathed
13:25	Resume circling
13:33	Stop circling. Laufschlag twice. Penis unsheathed. M makes small jumping movements behind F. F still moving forward a few steps in response each time.
13:38	Two other females approach. M smells F202; she urinates; he tests urine with flehmen. M then returns to F140.
13:44	*2nd attempted mounting*
	M continuing to stand immediately behind F, giving small kicks with knee and making small jumping movements (intention movements)
13:49	Resume courtship circling
13:59	Stop circling
14:02	Resume circling. Both walk away from road into the bush
14:20	Both stop circling
14:21	Resume circling / weaving and nosing
14:24	Stop circling (details of behaviour cannot now be observed because they are now in thick mopane bush)
14:27	M making intention movements again
14:28	F walks off. They then resume circling, but stop 30 seconds later. M making intention movements again
14:30	F walks off again, then stops 20 seconds later, then walks 30 seconds later. M rubs head on her flank. Both walking briskly
14:36	Stop circling in shade of Acacia tree
14:40	F attempting to browse, but M keeps pushing her from behind
14:44	Stop circling. Both circle the tree once, then stop again.
	For the next half hour, there is intermittent, brief circling, interspersed with M standing behind F, M nudging F, and F walking a few steps round to her right or left.
15:18	Both resume courtship circling. F walks towards other two females. M follows, with his nose to her rump. They walk deeper into mopane bush
15:22	Stop circling
15:29	Both resume courtship circling. F walks towards other two females again. M again follows, with his nose to her rump. They walk deeper into mopane bush
15:33	Stop circling
15:35	Resume circling and nosing
Stopped observation at 15:39 – becoming more and more difficult to observe as the two giraffe move deeper into Mopane bushveld, where it is impossible to follow	

APPENDIX 4. Pelage characteristic values (non-juvenile giraffe only) for each of the sites sampled for the analysis of photographs.

			Males				Females			
Country	**Location**	**Subspecies**	**N(a)**	**a) Mean patch cover**	**N(b)**	**b) % giraffe in dark categories**	**N (a)**	**a) Mean patch cover**	**N(b)**	**b) % giraffe in dark categories**
Niger	Koure region	*G. c. peralta*	5	0.56	7	0.86	1	0.51	2	0.50
Uganda	Murchison Falls NP	*G. c. rothschildi*	0	-	6	0.67	0	-	1	-
Kenya	Aberdare	*G. c. reticulata*	5	0.71	11	0.36	3	0.64	3	0.67
	Lake Nakuru NP	*G. c. tippelskirchi*	0	-	3	0.67	2	0.67	6	0.33
	Meru NP	*G. c. reticulata*	2	0.75	2	0.00	0	-	0	-
	Nairobi NP	*G. c. tippelskirchi*	6	0.56	12	0.92	8	0.60	12	0.67
	Samburu GR	*G. c. reticulata*	35	0.74	47	0.68	18	0.76	21	0.29
	Tsavo East & West NP	*G. c. tippelskirchi*	9	0.61	13	0.77	6	0.61	12	0.83
Kenya / Tanzania	Masai Mara GR / Serengeti NP	*G. c. tippelskirchi*	43	0.57	62	0.68	33	0.58	41	0.73
Tanzania	Arusha NP	*G. c. tippelskirchi*	4	0.63	5	0.80	5	0.59	13	0.92
	Lake Manyara NP	*G. c. tippelskirchi*	4	0.53	9	0.89	0	-	0	-
	Selous GR	*G. c. tippelskirchi*	1	0.57	1	-	1	0.57	1	-
	Tarangire NP	*G. c. tippelskirchi*	0	-	2	1.00	0	-	0	-
Zambia	Mosi-Oa-Tunya NP	*G. c. angolensis*	2	0.47	2	1.00	0	-	0	-
	South Luangwa NP	*G. c. thornicrofti*	1	0.58	3	1.00	2	0.60	2	1.00
Namibia	Etosha NP	*G. c. angolensis*	47	0.64	63	0.46	15	0.60	25	0.04
	Kunene region	*G. c. angolensis*	8	0.58	15	0.20	2	0.61	6	0.00
Botswana	Chobe NP	*G. c. angolensis*	3	0.59	8	0.50	3	0.56	5	0.00
	Okavango Delta	*G. c. angolensis*	6	0.60	8	0.38	7	0.57	11	0.09
Zimbabwe	Hwange NP	*G. c. angolensis*	13	0.59	19	0.53	8	0.59	8	0.25
South Africa	Kruger NP	*G. c. giraffa*	25	0.64	36	0.50	11	0.61	20	0.40

APPENDIX 5.

Weather stations (Meteorological-Office 1972) selected for the collection of climatological data for use in the population-level photographic analysis of biogeographical variation in patch cover and coat colouration.

Country	Location sampled	Weather station
Niger	Koure region	Niamey
Uganda	Murchison Falls NP	Masindi Arua
Kenya	Aberdare NP	Nakuru Nanyuki
	Lake Nakuru NP	Nakuru
	Meru NP	Nanyuki Garissa
	Nairobi NP	Nairobi
	Samburu NR	Nanyuki Wajir
	Tsavo East & West NP	Voi
Kenya / Tanzania	Masai Mara GR / Serengeti NP	Magadi, Kenya Musoma, Tanzania
Tanzania	Arusha NP	Arusha
	Lake Manyara NP	Mbulu Arusha
	Selous GR	Morogoro
	Tarangire NP	Arusha Kondoa Mbulu
Zambia	Mosi-Oa-Tunya	Livingstone
	South Luangwa	Chipata Petauke
Namibia	Etosha NP	Tsumeb Outjo Ondangwa
	Kunene region	Outjo Ondangwa
Botswana	Chobe NP	Kasane Maun
	Okavango Delta	Maun
Zimbabwe	Hwange NP	Dete
South Africa	Kruger NP	Lyndenburg Pafuri, Mozambique

APPENDIX 6. Climatological values used in the analysis of photographs. Mean values for sites from which photos of giraffe were obtained. For each location, data were taken from the nearest one to three climatological stations (Meteorological-Office 1972). Mean yearly precipitation was derived primarily from the UNEP-WCMC World Database on Protected Areas. Sites classed as 'high-insolarity' are those with mean total yearly hours of bright sunshine above the median (2917); these are highlighted in bold type.

Country	**Location**	**Subspecies**	**Mean yearly max. temp. (°C)**	**Mean yearly min. temp. (°C)**	**Relative humidity at 14:30 (%)**	**Mean yearly precipitation (mm)**	**Mean yearly hrs bright sunshine**
Niger	Koure region	*G. c. peralta*	36.1	21.8	33.0	550	**3184**
Uganda	Murchison Falls NP	*G. c. rothschildi*	28.5	16.9	55.0	1085	-
Kenya	Aberdare	*G. c. reticulata*	24.9	8.9	48.5	834	2378
	Lake Nakuru NP	*G. c. tippelskirchi*	26.1	9.2	45.0	965	2584
	Meru NP	*G. c. reticulata*	29.0	15.6	48.5	534	2172
	Nairobi NP	*G. c. tippelskirchi*	25.4	13.1	49.0	762	2503
	Samburu GR	*G. c. reticulata*	28.6	15.3	50.0	350	2172
	Tsavo East & West NP	*G. c. tippelskirchi*	30.6	19.4	46.0	531	**2987**
Kenya / Tanzania	Masai Mara GR / Serengeti NP	*G. c. tippelskirchi*	31.3	20.5	47.0	1118	2901
Tanzania	Arusha NP	*G. c. tippelskirchi*	25.3	13.5	57.0	1072	2526
	Lake Manyara NP	*G. c. tippelskirchi*	24.4	13.1	58.0	650	-
	Selous GR	*G. c. tippelskirchi*	30.1	18.6	55.0	1000	1845
	Tarangire NP	*G. c. tippelskirchi*	24.0	13.0	58.3	750	-
Zambia	Mosi-Oa-Tunya NP	*G. c. angolensis*	29.5	14.6	35.0	650	**3061**
	South Luangwa NP	*G. c. thornicrofti*	27.9	16.4	46.5	832	2669
Namibia	Etosha NP	*G. c. angolensis*	30.1	13.8	28.7	400	**3387**
	Kunene region	*G. c. angolensis*	30.4	13.6	28.5	325	**3458**
Botswana	Chobe NP	*G. c. angolensis*	30.3	14.8	33.0	600	**3399**
	Okavango Delta (Moremi NP)	*G. c. angolensis*	30.3	14.4	33.0	476	**3399**
Zimbabwe	Hwange NP	*G. c. angolensis*	28.6	12.6	37.0	653	**3210**
South Africa	Kruger NP	*G. c. giraffa*	27.8	13.2	40.5	563	**2934**

APPENDIX 7

Weather stations (Meteorological-Office 1972) selected for the collection of climatological data for use in the subspecies-level phylogenetically controlled analysis of biogeographical variation in patch cover and coat colouration.

Subspecies	Country	Locality
G. c. angolensis	Namibia	Gobabis Tsumeb Outjo Ondangwa Nkarapamwe
	Angola	N'Giva Mupa Dirico
	Botswana	Maun Kasane Ghanzi
	Zambia	Livingstone Sesheke
	Zimbabwe	Dett/Dete
G. c. giraffa	South Africa	Lydenburg
	Mozambique	Pafuri
	Swaziland	Mbabane
	Zimbabwe	Bulawayo Beitbridge
G. c. thornicrofti	Zambia	Chipata Petauke
G. c. reticulata	Kenya	Nakuru Nanyuki Garissa Wajir Marsabit Moyale
	Ethiopia	Nagele
	Somalia	Bardera Belet Uen
G. c. rothschildi	Uganda	Masindi Arua Kitgum Gulu Mbale
	Kenya	Kitale Eldoret Lodwar

Subspecies	Country	Locality
G. c. peralta	Niger	Niamey Maradi Tahoua
	Mali	Menaka Gao
	Nigeria	Kano Sokoto Maiduguri Bauchi Katsina
	Cameroon	Maroua Garoua
	Chad	Bousso Bokoro N'Djamena Pala Mongo Sarh Moundou Am Timan
	CAR	Birao N'Dele
G. c. tippelskirchi	Kenya	Magadi Nairobi Voi Makindu
	Tanzania	Musoma Arusha Mbulu Morogoro Kondoa Dodoma Mwanza Biharamulo Kigoma Tabora Moshi Same Amani

APPENDIX 8.
Molecular methodology

DNA extraction

Once returned to Newcastle, the faecal pellets preserved in silica gel beads were stored at 4°C, and those preserved in ethanol were kept at room temperature. The outer surface of the giraffe faecal pellets was carefully scraped off using a clean scalpel onto foil, and 100-200 mg was placed in a labelled 2 ml tube. Between one and eight pellets were used for each extraction, depending on the size of the pellets. Any remaining pellets were returned to storage in case a second extraction was required.

DNA was isolated from the faecal material using a commercially available extraction kit (QIAgen’s QIAamp DNA stool mini-kits), which includes a PCR inhibitor removal step, and which has found reasonable success in a number of recent studies (Garnier *et al.* 2001; Frantz *et al.* 2003; Hedmark *et al.* 2004). The recommended protocol (see Appendix 9) was followed with some minor alterations. Since the faecal material was dry, it was covered in 1.6 µl ASL buffer, vortexed for one minute, and then left for at least 90 minutes before proceeding with the extraction (Morin *et al.* 2001). Before application of elution (AE) buffer to the column, the filter was left to air-dry for five minutes to allow any residual alcohol-based wash (AW2 buffer) to evaporate. Following Nsubuga *et al.* (2004), once the elution buffer had been applied, the spin columns were incubated for 20 minutes at room temperature. An elution volume of 150 µl was chosen to increase DNA concentration (e.g. Garnier et al. 2001; Bellemain & Taberlet 2004). The following centrifugation was also increased from one minute to two. The resulting DNA solution was initially stored at 4°C, and later at -20°C. Between six and twelve extractions were processed at one time. It was not possible to include a negative control including no faecal material with each set of extractions (e.g. Bellemain & Taberlet 2004) due to limited resources.

Each DNA extract was first pre-screened to test amplification performance using one microsatellite (11HDZ550) that gave strong amplification products (Bellemain &

Taberlet 2004; Hedmark *et al.* 2004). A negative control was included with each PCR run to monitor reagents for contamination (Taberlet *et al.* 1999). PCR products were separated on a 2% agarose gel stained with ethydium bromide, and viewed with a 50 bp size marker under UV light. Only those extracts that produced a clear band at approximately 200 kb were assumed to contain DNA of sufficient quality for further analyses. DNA extracts that did not produce a band and were not colourless were cleaned by re-extraction with the QIAgen kit, and then re-screened.

PCR amplification

Huebinger et al. (2002) characterised sixteen microsatellite markers for giraffe. One primer that amplifies lengths of DNA longer than 300 bp was immediately excluded for use in this study as most faecal DNA is degraded into short fragments, and shorter fragments more reliably amplify than those longer than 300 bp (Frantzen *et al.* 1998; Taberlet *et al.* 1999). The remainder were all tested using five DNA samples, and annealing temperatures were optimised. Of the sixteen, twelve dinucleotide-repeat loci were selected; three were subsequently found to be monomorphic in the sample population.

All PCR preparation was carried out in a lab free from giraffe DNA or PCR products, using PCR-dedicated pipettes (Taberlet *et al.* 1999; Constable *et al.* 2001). The forward primers were fluorescently labelled with either 5'FAM or 5'HEX. Individual PCR reactions were performed using 96-well plates and a 15 µl reaction volume comprising 1.5 mM MgCl2, 0.1 mM of each dNTP, 0.13 µmol of each primer, 100 µg/ml bovine serum albumine (BSA), 0.5U BioTaqTM polymerase and 1.5 µl of the template DNA solution. Reactions were performed on a MJ Research PTC-100 thermocycler with the following conditions: an initial denaturation at 95°C for 12 minutes, then 10 cycles of denaturation at 94°C (15 seconds), locus-specific annealing temperature (15 s) and extension at 72°C (15 s), then 30-35 cycles of 89°C (15 s), locus-specific annealing temperature (15 s) and extension at 72°C (15 s). A final extension period of 30 minutes at 72°C was used to avoid incomplete 3' adenine nucleotide addition (Erill *et al.* 2005). Most PCR reactions were carried out with negative controls to monitor for contamination of PCR reagents.

Forty-eight DNA samples that did not amplify well were cleaned and concentrated with Zymo Research's DNA Clean & ConcentratorTM-5, using 80 µl of the original DNA solution, and eluting in 8 µl of water. Then 1 µl of the concentrated DNA solution was amplified using GE Healthcare's GenomiphiTM DNA Amplification Kit (for protocols, see Appendix), before repeating PCR amplification and fragment analysis for all loci.

Microsatellite profiling

After PCR amplification, 0.5-2 µl of PCR product were added to 13-14.5 µl of a 60:1 mixture of Hi-Di™ formamide (Applied Biosystems) and size standard (GeneScan® - 500 [ROX]). For the genetic profiling, loci were combined into sets of two to four in the same well, such that there was no overlap in fragment length, and adjacent loci (in terms of fragment size) were labelled with different colours. The fluorescent products were separated by capillary electrophoresis on an ABI Prism® 3100 genetic analyzer (Applied Biosystems) and fragment lengths analysed using GeneScan® Analysis Software v1.1 (Applied Biosystems). The length of each allele was considered to be represented by the highest peak(s) on the electroferogram. The actual fragment peak was often preceded by a couple of smaller stutter bands that are consistent with dinucleotide-repeat loci. Any samples that could not be unambiguously assigned to a homozygote or heterozygote genotype were re-amplified and re-typed once, or twice if necessary. If the same genotype was obtained twice, then it was accepted as the correct genotype. Resources were insufficient for a complete multiple-tubes approach (e.g. Taberlet *et al.* 1996; Frantz *et al.* 2003; Hedmark *et al.* 2004). To establish the basic genotyping error rate, a randomly selected subset of 32 DNA samples were re-genotyped, by carrying out a second independent PCR amplification and fragment analysis.

Parentage assignment

Paternity assignment was attempted using the software package CERVUS (Marshall *et al.* 1998), which uses a likelihood-based approach to assign paternity. The identity of the mother was not known in most cases, although in some cases there were a small number of suspected possible mothers, so for these, attempts were also made to first ascribe maternal relationships using CERVUS, prior to assigning paternity.

APPENDIX 9.

DNA extraction protocol, taken from QIAamp DNA Stool Mini Kit Handbook (08/2001)

Protocol for Isolation of DNA from Stool for Human DNA Analysis

Lysis conditions in this protocol are optimized to increase the ratio of human DNA to non-human DNA. Non-human DNA is not excluded by this procedure.

Important notes before starting

- Ensure that Buffers AW1 and AW2 have been prepared according to the instructions on the labels.
- Mix all buffers before use.
- If a precipitate has formed in Buffer ASL or AL, dissolve by incubating at 70°C.
- Prepare a 70°C water bath for use in step 11.
- All centrifugation steps should be carried out at room temperature (15–25°C) at 20,000 x *g* (~14,000 rpm). Increase the centrifugation time proportionately if your centrifuge cannot provide 20,000 x *g* (e.g., instead of centrifuging for 5 min at 20,000 x *g*, centrifuge for 10 min at 10,000 x *g*).
- The 2 ml tubes used in step 4 should be wide enough to accommodate an InhibitEX tablet (e.g., Eppendorf Safe-Lock, cat. no. 0030120.094 or Sarstedt Safe-Seal, cat. no. 72.695).
- To increase robustness of downstream PCR assays of DNA eluates from stool samples, we strongly recommend adding BSA to PCR mixtures to a final concentration of 0.1 µg/µl (e.g., Serva cat. no. 11920 or New England Biolabs® BSA, cat. no. BSA-007). To increase PCR specificity, we recommend the use of QIAGEN HotStarTaq DNA Polymerase (see ordering information on page 38).

1. Weigh 180–220 mg stool in a 2 ml microcentrifuge tube (not provided) and place tube on ice.

   If the sample is liquid, pipet 200 µl into the microcentrifuge tube. Cut the end of the pipet tip to make pipetting easier. If the sample is frozen, use a scalpel or spatula to scrape bits of stool into a 2 ml microcentrifuge tube on ice.
2. Add 1.6 ml Buffer ASL to each stool sample. Vortex continuously for 1 min or until the stool sample is thoroughly homogenized.

Note: It is important to vortex the samples thoroughly. This helps ensure maximum DNA concentration in the final eluate.

3. Centrifuge sample at full speed for 1 min to pellet stool particles.
4. Pipet 1.4 ml of the supernatant into a new 2 ml microcentrifuge tube (not provided) and discard the pellet.

   Transferring small quantities of pellet material will not affect the procedure.
5. Add 1 InhibitEX tablet to each sample and vortex immediately and continuously for 1 min or until the tablet is completely suspended. Incubate suspension for 1 min at room temperature to allow inhibitors to adsorb to the InhibitEX matrix.
6. Centrifuge sample at full speed for 3 min to pellet stool particles and inhibitors bound to InhibitEX.

   Note: When processing more than 12 samples, for this step and step 7 we recommend processing batches of no more than 12 samples each. This is because the pellets formed after centrifugation will break up quickly if the supernatant is not removed immediately.
7. Immediately after the centrifuge stops, pipet all of the supernatant into a new 1.5 ml microcentrifuge tube (not provided) and discard the pellet. Centrifuge the sample at full speed for 3 min.

   Transferring small quantities of pellet material from step 6 will not affect the procedure.
8. Pipet 25 µl Proteinase K into a new 2 ml microcentrifuge tube (not provided).
9. Pipet 600 µl supernatant from step 7 to the 2 ml microcentrifuge tube containing Proteinase K.
10. Add 600 µl Buffer AL and vortex for 15 s.

    Note: Do not add Proteinase K directly to Buffer AL. It is essential that the sample and Buffer AL are thoroughly mixed to form a homogeneous solution.
11. Incubate at 70°C for 10 min.

    Optional: Centrifuge briefly to remove drops from the inside of the tube lid.
12. Add 600 µl of ethanol (96–100%) to the lysate, and mix by vortexing.

    Optional: Centrifuge briefly to remove drops from the inside of the tube lid.
13. Label the lid of the QIAamp spin columns provided in a 2 ml collection tube. Carefully apply 600 µl lysate from step 12 to the QIAamp spin column without moistening the rim. Close the cap and centrifuge at full speed for 1 min. Place the

QIAamp spin column in a new 2 ml collection tube, and discard the tube containing the filtrate.

Close each spin column in order to avoid aerosol formation during centrifugation. If the lysate has not completely passed through the column after centrifugation, centrifuge again until the QIAamp spin column is empty.

14. Carefully open the QIAamp spin column, apply a second aliquot of 600 µl lysate and centrifuge at full speed for 1 min. Place the QIAamp spin column in a new 2 ml ollection tube, and discard the tube containing the filtrate.

    Close each spin column in order to avoid aerosol formation during centrifugation. If the lysate has not completely passed through the column after centrifugation, centrifuge again until the QIAamp spin column is empty.
15. Repeat step 14 to load the third aliquot of the lysate onto the spin column.
16. Carefully open the QIAamp spin column and add 500 µl Buffer AW1. Centrifuge at full speed for 1 min. Place the QIAamp spin column in a new 2 ml collection tube, and discard the collection tube containing the filtrate.
17. Carefully open the QIAamp spin column and add 500 µl Buffer AW2. Centrifuge at full speed for 3 min. Discard the collection tube containing the filtrate.

    Note: Residual Buffer AW2 in the eluate may cause problems in downstream applications. Some centrifuge rotors may vibrate upon deceleration, resulting in the flow-through, which contains Buffer AW2, contacting the QIAamp spin column. Removing the QIAamp spin column and collection tube from the rotor may also cause flow-through to come into contact with the QIAamp spin column. In these cases, the optional step below should be performed.

    Optional: Place the QIAamp spin column in a new 2 ml collection tube (not provided). Centrifuge at full speed for 1 min. Discard the collection tube containing the filtrate.
18. Transfer the QIAamp spin column into a new, labelled 1.5 ml microcentrifuge tube (not provided) and pipet 200 µl Buffer AE directly onto the QIAamp membrane. Incubate for 1 min at room temperature, then centrifuge at full speed for 1 min to elute DNA.

    Note: When using eluates in PCR, for maximum PCR robustness we highly recommend adding BSA to a final concentration of 0.1 µg/µl to the PCR mixture. For maximum PCR specificity we recommend using QIAGEN HotStarTaq DNA

Polymerase (see ordering information on page 38). For best results in downstream PCR, use the minimum amount of eluate possible in PCR; the volume of eluate used as template should not exceed 10% of the final volume of the PCR mixture. Also, note that high amounts of template DNA may inhibit the PCR. DNA yield is typically 15–60 µg but, depending on the individual stool sample and the way it was stored, may range from 5 to 100 µg. DNA concentration is typically 75–300 ng/µl. For long-term storage, keeping the eluate at –20°C is recommended.

APPENDIX 10.

DNA purification and amplification protocols

DNA Clean & ConcentratorTM-5 Protocol

(Zymo Research)

Before starting: Add 24ml of 100% ethanol to the Wash Buffer Concentrate to make final Wash Buffer.

1. Add 2 volumes of DNA Binding Buffer to each volume of DNA sample.
2. Load sample into a Zymo-Spin Column and place into a 2ml collection tube
3. Centrifuge at full speed (≥10,000g) for 5-10 seconds*. Discard the flow-through.
4. Add 200µl of Wash Buffer to the column. Spin at top speed for 5-10 seconds*. Add another 200µl of Wash Buffer. Spin at top speed for 30 seconds**.
5. Add 6-8µl of water directly to the column matrix. Place column into a 1.5ml tube. Spin briefly to elute the DNA*. To increase the DNA recovery, you can add another 6-8µl of water to the column and spin briefly to elute the DNA.

   Note: Elution efficiency is related to the pH. Optimal range is pH7.0 to pH8.5 for buffered solution. When water is used, make sure that the water pH is above 6.0. Waiting for one minute after adding water before centrifuging can improve DNA recovery rate for larger sizes of DNA (>6Kb).

* Columns were actually spun for 30 seconds.

** Columns were actually spun for 60 seconds.

GenomiphiTM DNA Amplification Kit Short Protocol

(GE Healthcare)

1. Mix 1µl of template DNA with 9µl of sample buffer. Heat to 95°C for 3 minutes to denature the sample. Cool to 4°C on ice.
2. For each amplification reaction, prepare the GenomiPhi Kit reaction premix by combining 9µl of reaction buffer with 1µl of enzyme mix on ice. Add this to the cooled sample. When performing multiple reactions, it is most convenient to

prepare a master mix (9µl of reaction buffer and 1µl of enzyme mix for each template), and use 10µl for each denatured sample.

3. Incubate the sample at 30°C for 16-18 hours.
4. Heat the sample at 65°C for 10 minutes to heat-inactivate the enzyme. Cool to 4°C.

The DNA can now be used in experiments or stored (4°C or -20°C)

APPENDIX 11.

Molecular results

DNA extraction success

A total of 164 faecal samples were collected from 149 different giraffe, all but 32 of which were known individuals. In all, 241 DNA extractions were carried out, with an average of 1.6 extractions per individual. Of these, 108 samples were cleaned by re-processing with the QIAgen DNA extraction kit, 73 of which then produced amplifiable DNA. Subsequently, 46 DNA samples were concentrated using the Zymo DNA Clean & ConcentratorTM-5, then amplified using the GenomiphiTM DNA Amplification Kit (of these, 29 had already been cleaned).

In total, 147 (61%) 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 different individuals.

Factors affecting extraction and amplification success

Both storage medium and length of storage had effects on DNA extraction success (binary logistic regression, $X^2 = 18.8$, df = 2, $P < 0.001$). DNA extracted from faeces stored in ethanol were more likely to produce bands on a gel (71%) than those stored in silica gel beads (49%; $X^2 = 9.844$, df = 1, $P < 0.05$). But of samples stored in ethanol, those that had been stored for longer were less likely to produce bands ($X^2 = 15.2$, df = 1, $P < 0.001$), whereas this was not the case for samples stored in silica gel ($X^2 = 0.6$, df = 1, $P = 0.438$). Samples stored in silica gel, and those that had been stored in ethanol for longer, tended to produce a darker supernatant and as a result a darker DNA eluate. Of those samples that produced a dark supernatant, samples that were cleaned by processing a second time with the Qiagen kits were significantly more likely to produce a band on the gel ($X^2 = 7.761$, df = 1, $P < 0.01$).

There was a slight, but not significant, effect of storage medium on the success of microsatellite genotyping (Mann-Whitney U = 766, N=88, P = 0.078) before concentrating samples. However, time in storage had a significant effect on the number of loci successfully typed for samples stored in silica gel ($F_{39,1} = 7.0$, P <

0.05), but not those stored in ethanol ($F_{47,1} = 0.489$, $P = 0.488$), as no samples were stored in ethanol longer than 8.5 months before extraction, whereas for silica gel the maximum was 13 months. Because of the effect of age, DNA samples that were later concentrated and amplified could then be scored for more loci if the faeces had been stored in ethanol than if they had been stored in silica gel ($U = 282$, $N=61$, $P < 0.01$). Of all samples genotyped, 88% of those stored for 8.5 months or less could be successfully typed for at least seven loci, whereas only 46% of the older silica gel samples could be typed at seven or eight loci.

Summary genotype statistics and parentage assignment

Two of the 16 available markers (Huebinger *et al.* 2002) were not used because one had previously been found to be monomorphic in the Etosha NP population (11HDZ480, Rick Brenneman, personal communication), and the other amplifies microsatellite products over 300 bp (11HDZ334), 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 (11HDZ102, 11HDZ447, 11HDZ567), and three markers were difficult to amplify or score reliably (11HDZ073, 11HDZ626, 11HDZ748).

The mean number of alleles for the eight remaining markers was 3.1. The average observed heterozygosity was 0.277, and the average expected heterozygosity was 0.335. Null alleles were suspected in three markers (11HDZ561, 11HDZ582, 11HDZ665). In two of these (582 and 665), stuttering may also have resulted in scoring errors. Based on the re-scoring of random selection of 32 samples at seven loci, the genotyping error rate was estimated at 2%.

In the first instance, attempts were made to ascribe paternity at the 80% confidence level to 35 juvenile and young sub-adult giraffe using the programme CERVUS (Marshall 2001). The mother was known and typed for only 5 of these offspring. All sampled giraffe that were assumed to have reached sexual maturity (>4 years of age) were included as candidate parents. The number of candidate fathers was estimated to be the 161 known adult males who had been seen within the study area plus the 9 unknowns sampled (170). With 38 adult males typed, the proportion of candidate fathers sampled was just 22%. Similarly, the number of candidate mothers was estimated to be the 151 known adult females plus 11 unknowns sampled (162). Thus 34% (55) of candidate mothers were typed. For the 128 individuals included in the analysis, 93% of loci were typed.

Unfortunately, the informativeness of the markers used was not sufficient for a successful assignment of paternity (mean PIC = 0.292 (range = 0.084-0.466), overall total exclusionary power (first parent) = 0.429, total exclusionary power (second parent) = 0.76). Consequently, no paternities could be assigned unless the parameters were further relaxed (e.g. half the assumed candidate parents, and thus twice the proportion of candidate parents sampled); then only one paternity could be assigned at the 80% confidence level (specifically, to M90, the seasonal visitor seen in both a necking fight and a successful copulation, as described above). The paternity assignment could not be enhanced by first carrying out an assignment of maternity, as maternities could similarly not be assigned with any confidence.

The problem of lack of genetic variability was further compounded by the low proportion of candidate parents sampled (less than 30% of putative fathers and less than 40% of putative mothers), and the lack of a known, genotyped mother for the majority of calves. It is often difficult to assign giraffe calves to the correct mothers with certainty (Dagg 1968), as females often leave their calves alone or with other females for periods of up to four days (Foster & Dagg 1972), for example while they go to drink (personal observation).

APPENDIX 12. Primer details for the eight microsatellites used

Annealing temperatures were optimised; these differ slightly from those in Huebinger *et al.* (2002). Polymorphism data refer to genotypic variation found in this study.

Locus	Primer sequence (5' to 3')	Annealing temp. (°C)	Fragment size (bp)	No. of alleles	Percentage genotyped	H_O	H_E
11HDZ443	F: CAT AAA ATT AAA AGG CAC TTG TTC C R: ATG GGG GTC ACA AAG AGT CTG	52	129-135	4	96.9	0.492	0.540
11HDZ550	F: GGA CAG TGG ACT AGG AGA AAA GG R: GCC TGG GAT TCC TGG TAA AC	52	165-177	4	92.2	0.169	0.180
11HDZ561	F: CAA CAA AGA CAA ACT GGA TAG C R: TCT AAC ATC TGA GCC ACC G		181-185	3	60.2	0.260	0.353
11HDZ562	F: AAA GAG TTA GAT GCA ACT GAG TGA C R: TCA GCA TCC TAT ATT TTC ACA CC	50	133-137	3	96.1	0.341	0.396
11HDZ582	F: TTC CTA AGT TAC CCT CTC TGC C R: TTA GCA CCA CCC CTC TCA AC	48	121-123	2	97.7	0.200	0.264
11HDZ665	F: GCC CCT TGC CTA GCT TAA C R: CCG ACT GTA GAA ATG AAG CG	54	202-210	5	84.4	0.167	0.361
11HDZ835	F: CCC ACA CTG CAA CTA AAC CTG R: AAG AAA CTC AAA AGC CTG CAA G	54	201-203	2	95.3	0.492	0.501
11HDZ1004	F: CTC ATG TCT CTT GCA CTG GC R: GTA ATG GCA TAT TTC ACT CTT TTT C	52	142-158	2	93.8	0.092	0.088

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