Relationships between male giraffes' colour, age and sociability

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Abstract

In species in which males signal competitive ability through secondary sexual traits, males with different levels of trait expression may adopt different reproductive tactics to maximise their reproductive success. In fission-fusion social systems, the most dominant males often roam widely in search of females in oestrus, and thus exhibit different patterns of sociability from subordinate males that utilise alternative reproductive tactics. Giraffes, *Giraffa camelopardalis*, are rare among mammals in that they are sexually dimorphic in colour, and colour is hypothesised to function as a signal of males' social status by displaying their competitive ability. Here we analyse the coat colour and sociability of 77 wild male giraffes over twelve years at Etosha National Park in Namibia to test two premises underlying this hypothesis. First, we demonstrate that not all males darkened at the same rate or to the same degree, and that colour variation increased with age. This suggests that colour is not solely an age-based trait but could be a secondary sexual trait. We then show a distinct difference in the sociability of both young and pale males compared to darker males. Both younger and paler old males tended to be more gregarious while darker males were more solitary. This is consistent with a system where darker, more dominant males roam looking for females in oestrus. Younger or subordinate males may delay roaming or use an alternative tactic, such as remaining in groups with females to gain copulations when a more dominant male is not present. Our results are consistent with the hypothesis that male giraffe coat colour functions as a signal of social status through competitive ability, but deeper study into movement patterns and the costs and benefits associated with darker colours is required.

Introduction

In most mammal species without pair bonding or paternal care, the reproductive success of males depends on maximising their mating opportunities (Birkhead & Parker, 2009). To be successful, a male must find a female, guard her against competitors and be accepted by her as a suitable mate. This creates a scramble competition mating system in which competition between males is likely to be high (Ims, 1988). In such a system, males' access to females is often based upon aggressive interactions with other males that allow males to mutually assess one another's competitive abilities (Berglund, Bisazza, & Pilastro, 1996). However, aggressive interactions can be risky. Instead, secondary sexual traits can function as honest signals of males' relative competitive ability, allowing males to assess each other visually and thereby reducing the need for aggressive interactions (Santos, Scheck, & Nakagawa, 2011). Such traits may also signal males' quality to females (Weaver, Koch, & Hill, 2017).

Secondary sexual traits may take the form of armaments, used in combat and thus related directly to competitive ability, or ornaments, exaggerated traits and/or colours that may be costly to produce or maintain but have no function in physical combat (Berglund et al., 1996). Ornaments have most commonly been studied in species in which male reproductive success is heavily influenced by female mate choice, a phenomenon well known in birds (Berglund et al., 1996). In mammals, armaments such as increased physical size and horns are more common (Caro, 2013; McPherson & Chenoweth, 2012). However, secondary sexual ornaments do exist in some mammal species, usually in the form of colours. The darkness of male lion manes, *Panthera leo*, correlates positively with dominance and female mate preference (West & Packer, 2002) and the colour intensity of sexual skin patches on male mandrills, *Mandrillus sphinx*, and geladas, *Theropithecus gelada*, increases with social status (Bergman, Ho, & Beehner, 2009; Setchell & Dixson, 2001). In Himalayan tahr, *Hemitragus jemhahicus*, males with lighter-coloured fringed hairs along their back hold more dominant positions (Lovari, Pellizzi, Boesi, & Fusani, 2009).

Honest signals are often explained by the costly signalling hypothesis or the index hypothesis (reviewed by Biernaskie, Grafen & Perry, 2014; Fraser, 2012; Számadó, 2011; Weaver et al. 2017).

The costly signalling hypothesis suggests that only high-quality individuals can present such signals because of the costs they involve, such as the costs of producing or maintaining the signal, including possible costs from aggression from competitors. The index hypothesis does not involve costs, but instead proposes that physiological/developmental mechanisms mean that only high-quality individuals can produce the signal. In either case, where colour has evolved as an honest indicator of male quality or status, for male-male competition or female preference, it must be related to an underlying aspect of a male's current physical condition, genetic quality or potential reproductive success. Brown and black colours in mammals are thought to almost always be due to eumelanin pigments (Ducrest, Keller & Roulin, 2008). Extensive research, mostly on birds and insects, has shown that melanin-based colouration is partly heritable and that other traits, such as aggressiveness, immune functioning and sexual activity levels can vary with colour due to pleiotropic effects (reviewed by Ducrest et al., 2008; Roulin 2016).

Males of differing competitive ability may adopt alternative reproductive tactics to maximise their lifetime reproductive success. The tactics used will depend on social and ecological environments and on the relative ability of competitors (Oliveira, Taborsky, & Brockmann, 2008). Therefore, the tactics that an individual exhibits may change throughout its life depending on its age, current competitive ability and experience, which may affect its dominance status and can also be influenced by environmental conditions (Oliveira et al., 2008). A dominant male may search out, defend and mate with oestrous females unchallenged. One alternative tactic for less dominant males might be to "sneak" copulations when a dominant male is absent, not vigilant, or unable to defend all the oestrous females present. This tactic is used by northern and southern elephant seals, *Mirounga angustirostris* and *M. leonina* (Hoelzel, Le Boeuf, Reiter, & Campagna, 1999; Le Boeuf, 1974), plains zebras, *Equus burchelli*, (Rubenstein, 1986) and red deer, *Cervus elaphus* (Clutton-Brock, Guinness, & Albon, 1982). In musk oxen, *Ovibos maschatus,* less dominant males spend more time with females, thus increasing their chances of monopolising access to a female if she comes into oestrus in the absence of a more dominant male (Forchhammer & Boomsma, 1998). Individuals that are competitively excluded due to their size, physical condition or level of experience may instead increase their lifetime reproductive success by delaying competitive breeding to invest in growth and building condition. For example, in African elephants, *Loxodonta africana*, waterbuck, *Kobus ellipsiprymnus*, and raccoons, *Procyon lotor*, bachelor herds exist in which younger, smaller males may learn from more experienced males and practise fighting to improve their competitive ability later in life (Evans & Harris, 2008; Gehrt, Gergits, & Fritzell, 2008; Wirtz, 1982).

Males' use of different reproductive tactics based on their current competitive ability should lead to predictable differences in males' patterns of sociability, particularly given that an individual's social environment can be an important determinant of fitness (Blumstein, Williams, Lim, Kroeger, & Martin, 2018; Cameron, Setsaas, & Linklater, 2009; Silk et al., 2010). Thus individuals may tailor their association patterns and preferences, and sometimes their group sizes, to their own shifting social and reproductive needs. This may result in individuals having varying patterns of sociability in different contexts (Gero, Bejder, Whitehead, Mann, & Connor, 2005; Muller, Cantor, Cuthill & Harris, 2018), at different ages (Wey & Blumstein, 2010) and when in different physical or reproductive conditions (Goldenberg, De Silva, Rasmussen, Douglas-Hamilton, & Wittemyer, 2014). If competitive ability is signalled through ornamentation, then differently-ornamented males may have measurably different sociability patterns (Oh & Badyaev, 2010).

Species with fission-fusion social systems present an opportunity to investigate how ornamentation relates to males' patterns of sociability, and thus perhaps to mating tactics. In species with fission-fusion social dynamics, there are no fixed groups; temporary groups change in size and composition frequently. The flexibility of fission-fusion systems allows group sizes to change so that individuals can best balance exploitation of available resources (Aureli et al., 2008; Rubenstein & Wrangham, 1986; Smith, Kolowski, Graham, Dawes, & Holekamp, 2008) and predation risk, both of which can vary both spatially and temporally (Kelley, Morrell, Inskip, Krause, & Croft, 2011). Individuals can choose to join or leave groups based on their own shifting nutritional, social and reproductive needs (Goldenberg et al., 2014; Patriquin, Leonard, Broders, & Garroway, 2010). Honest visual signals may be particularly useful in fission-fusion social systems because the flexibility of group compositions means that individuals may not associate regularly and may thus need to judge the competitive ability or social status of new associates as they come into contact (Bergman & Beehner, 2009).

Giraffes, *Giraffa camelopardalis,* exhibit fission-fusion social dynamics (Bercovitch & Berry, 2013; Shorrocks & Croft 2009), and are rare among mammals in that they are sexually dimorphic in colour. The coats of giraffes have patches that are individually unique and retain their shape throughout the animal's life, but the colour of the patches varies among individuals and may change during an individual's lifetime (Dagg, 1968). The colour of males' patches varies to a much greater extent than those of females. Males' patches can range from pale brown to completely black, and darkness tends to increase with age, though the relationship between colour and age is not clear and causes of variation in this relationship are still unknown (Berry & Bercovitch, 2012; Brand, 2007). Giraffe social groups are often widely dispersed, depending on resource availability, and may change in composition as often as hourly (Leuthold, 1979). Females come into oestrus for about four days every two weeks when not pregnant and males travel over large distances in search of females in oestrus (Bercovitch, Bashaw & Del Castillo, 2006). Mating opportunities are determined through a dominance-based polygynous mating system characterised by intense male-male competition (Bercovitch et al., 2006). Males' coat darkness has been positively linked to success in aggressive interactions and female interest (Brand, 2007). Darker males have also been observed to travel over larger distances (Brand, 2007). Giraffes' coats tend to be paler in habitats more exposed to sunlight, towards the end of the dry season when resources are limited, and postpartum in some females (Brand, 2007). Observations and small-scale studies suggest that patch darkness may function as an honest signal of competitive ability of male giraffes (Brand, 2007; Dagg, 2014). However, the social implications of such melanin-based ornamentation, which is uncommon in mammals, have rarely been examined.

In this study we test two predictions stemming from Brand's (2007) hypothesis that male giraffe colour functions as an honest signal of competitive ability. First, if colour expression is an honest signal of competitive ability, we predict that variation in colour should increase with age, with some males never becoming very dark. Second, if dark colour signals social status through competitive ability, darker, more dominant males should use mating tactics that make them more likely to encounter females, such as roaming, more than should paler males. In systems where females are spread throughout the landscape and males do not defend harems, roaming is likely to be the most reproductively successful tactic (Fisher and Lara 1999; Whitehead, 1990; 1994). It is also known that younger male giraffes are frequently found in all-male groups, possibly to reduce their predator risk and/or to gain information about resources (Bercovitch & Berry, 2014). Thus, we predict that darker males should spend more time alone than lighter-coloured males. To test these predictions, we use five metrics of sociability and twelve years of photographs of 77 male giraffes from a large, wild population in the Etosha National Park in Namibia. Specifically, we aimed to (1) determine the relationship between males' age and colour; and (2) investigate how colour and age relate to the association patterns of males. This study population of giraffes provides a valuable opportunity to understand the behaviour of giraffes in a very natural setting, as it is part of a large population of over 3,000 giraffes (Kilian, 2015) that occupy the 22,270 km^2 national park, which is not fenced internally.

Methods

Study population, study site and study periods

Our study subjects were male members of the population of giraffes (*G. c. angolensis*) that inhabit an approximately 1000 km^2 area in the southern-central region of the Etosha National Park, Namibia (19°10' S, 15°54' E). We collected photographs, demographic and grouping data on the giraffes in this population intensively during four study periods spanning twelve years. These studies occurred during May 2004–January 2006, May 2009–April 2010, July–December 2013 and April–November in 2015 and 2016 (Studies 1-4). Individuals were distinguished by their unique patch patterns, which were recorded in a photographic catalogue, allowing us to repeatedly identify individuals across periods. Over this twelve-year period, we identified 1467 individual giraffes, 646 of which were male. A mean of 451 ± 60 (SE) giraffes was identified during each study. Photographs of identified males taken *ad libitum* outside of these periods were also included in our patch darkness analysis.

Data collection

We collected data along four road transects of approximately 65 km each in length. We drove each transect evenly in morning and afternoon sampling periods, varying the direction of travel haphazardly, and did not drive the same transect twice in one day. Data were not collected during the middle of the day (1100-1500) as giraffes rest in the shade during the hottest period and are more difficult to find, identify and observe. A mean of one group flux event (a change in group composition) every three hours has been recorded for this population (Castles, 2018), so this protocol allowed ample opportunity for individuals to change associates between sample periods, increasing the likelihood that association data were independent. When a group of giraffes was encountered along a transect, we recorded the group's location, size and composition. We also recorded the apparent age class of each individual and photographed its left and right sides where possible for identification and patch darkness scoring. Groups were defined as individuals foraging or moving together, as has previously been used to define giraffe groups (Carter, Brand, Carter, Shorrocks, & Goldizen, 2013). Groups were generally self-defining as there was clear spatial differentiation among groups. In the rare cases when groups were not self-defining, we divided individuals into groups in which the outer individuals were within 400 m of each other, as was usually the case. All individuals were assumed to be associating equally with all other group members ("gambit of the group", Whitehead & Dufault, 1999). If an individual was sighted more than once on a transect drive, only the first observation was used. Due to park regulations all observations were made from inside a vehicle, which had to remain on roads. These roads were designed for tourism and thus were not evenly spaced through the habitat, leaving some areas of our giraffes' home ranges unavailable to us. Similar data collection protocols were used in all four studies, ensuring comparability of data (Brand, 2007; Carter, Brand, et al., 2013; Carter, Seddon, Frere, Carter, & Goldizen, 2013). Data collection was approved by the Namibian Ministry of Environment and Tourism and animal ethics approval was granted by the University of Queensland Native/Exotic Wildlife and Marine Animals Animal Ethics Committee (approval nos. SBS/439/14, SBS/093/11/GCF and SIB/124/09/URG).

Patch darkness scoring

At each group sighting during study periods 1, 3 and 4, as well as recording behavioural and demographic data, we also recorded a patch darkness score for each male in the observed groups. Following Brand (2007), scores were based on brown colour saturation or “gross darkness,” as opposed to variation in hue, and were assumed to correspond to incrementally increasing levels of eumelanin pigmentation (Meunier, Figueiredo Pinto, Burri, & Roulin, 2011). Patch darkness was broken into four categories (1–4) based on shades of brown, with half scores representing transitional states between shades (Figure 1). Transitional characteristics included darkening at the centre of patches (Berry & Bercovitch, 2012) or in particular regions of the body. We developed a graduated colour reference chart with descriptors of each category. A score of 1 represented a giraffe that was washed out with patches that were difficult to distinguish from the paler background, a 2 was equivalent to the colour of a standard female or sub-adult male and 4 represented a male whose patches were almost entirely black.

Age calculation

Giraffes were categorised in the field as juvenile, sub-adult or adult based on their height, behaviour and ossicone development. Juveniles, aged between zero and two years, were recognised by their short stature, up to 3.25 m (Dagg & Foster, 1982), and behaviours including following female adults, suckling or being in crèche groups with other young individuals. Sub-adults, aged between two and four years, were independent of their mothers but shorter than adults. Male sub-adults also had fringed hair around the tips of their ossicones, which is worn off in adulthood. Individuals over the age of four years were considered sexually mature and thus adults, though it should be noted that males continue to grow until age eight.

To determine the accuracy of ages assigned in the field, we reviewed the sightings data and photographs. If an individual was assigned the same age at three or more sightings in a period, we assumed it to be correct. If we found inconsistencies or an individual was sighted fewer than three times during one of the studies, we examined the ages of the individual in the other studies and reviewed photographs. We were able to estimate the age of individuals from their height in comparison to other individuals in photographs. If we could not reliably estimate the age of the individual, it was recorded as an individual of unknown age in the group and included in the social network but not in further analysis.

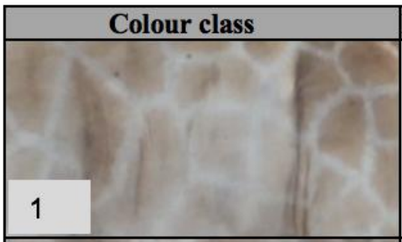
Colour class	Patch descriptors
 1	- Pale brown - Patches on small areas of the body such as upper neck or belly may be becoming indistinguishable from background
 1.5	- Paler than the usual colour of a female or sub-adult male - Patches on the upper neck and hip may be beginning to fade
 2	- Light tan colour - The standard colour of a female or sub-adult male
 2.5	- Richer/darker tan than colour class 2 - Centre of patches beginning to darken to chocolate brown - Presence of chocolate brown patches but not entire body
 3	- Chocolate brown patches covering the entire body - No completely black patches but some with black centres
 3.5	- Completely black patches present but not covering the entire body
 4	- Black patches over the entire body with the possible exception of the upper neck

Figure 1: Patch darkness colour categories and descriptors for male giraffes in the Etosha National Park

To account for errors in age estimation that may arise from variation in height among individuals of the same age, and because we could not estimate the birth month for most individuals, identified giraffes were further classified into multi-year age cohorts based on their age class when first sighted (Table 1). We could not reliably estimate the age cohort of individuals that were first observed as adults after 2005 as they could have been between four and fifteen years old when first seen, so these individuals were included in the network but not in further analysis (40.1% of individuals). This led to a skew in the proportions of different age classes recorded in each study, with the oldest age categories only recorded in the later studies. This was accounted for in analyses.

Table 1: Giraffe age categories used in this research. Individuals were classed as juveniles (J), sub-adults (S), young adults (YA), middle-aged adults (MA), or old adults (OA) based on their age when first sighted. Individuals observed as adults in 2004-2005 could only be aged in 2015-2016 when we knew that they had to be at least fifteen years old. Individuals first observed as adults in all other study-periods were included as "age unknown" in networks and then removed from further analysis.

Age Category	**Age at 2016 (years)**
Juvenile	< 2
Sub-adult	2 - 4
Young adult	5 - 8
Middle-aged adult	9 - 14
Old adult	15+
Adult (age unknown)	4+

Patch darkness scoring from photographs

Patch darkness scores were not recorded in the field for all individuals in all four of the studies and the data in the four periods were collected by different observers. Although all observers were trained to score colour by the previous observers, with photographs as references, we could not completely ensure the reliability of male colour scores given in the field. Instead, we chose to score male patch darkness from photographs. We included 249 photographs taken opportunistically by R. Brand and other visiting researchers outside of the times of the four studies (see acknowledgements), which increased the size and improved the continuity of the dataset. Photographs of identified males from over the 12 years of data collection were collated into the following five periods: 2004-2005 (P1), 2009-2010 (P2), 2011-2012 (P3), 2013-2014 (P4), and 2015-2016 (P5). We limited our colour and age analysis (Aim 1) to aged males that had been photographed in a minimum of two periods. This provided a candidate set of 77 males (mean of 3.0 ± 1.0 SD periods/individual). We only calculated sociability metrics for individuals that had been seen a minimum of 8 times in a period (see below), thus analyses for Aim 2 were limited to a subset of 44 males (N = 44, mean = 1.1 ± 0.7 periods/individual). As no group composition data were collected in P3, because this period was not part of one of our four intensive studies, this period was excluded from the analyses for our second aim.

Field conditions meant that it was impossible to standardise lighting conditions or to include a colour standard in photographs. In addition, variation in cameras and image quality over the 12 years of data collection meant that the use of image analysis software (as in Gerald, Bernstein, Hinkson, & Fosbury, 2001) was not possible. Therefore, we scored patch darkness by eye. Scoring colour consistently has been shown to be possible using photographs (Mizokami, Ikeda, & Shinoda, 2004; Phuangsuwan, Ikeda, & Shinoda, 2014). To improve the accuracy of our scoring we only scored images taken under daylight lighting (no dawn or dusk photographs), and which were not backlit, hazy or blurry.

For each photograph we scored patch darkness using the same colour categories and criteria as in the field. When more than one image was taken at a sighting, we first scored each photograph blindly, then compared all images and scores against each other and the scoring criteria to decide upon the score for that sighting (mean 1.8 ± 1.2 images/sighting). When a giraffe was photographed at more than one sighting in a period, we again blindly scored the photographs then compared all images and scores to each other and the scoring criteria and decided on the score for the period (median 3, IQR 1-6 sightings/period). Using multiple photographs in this way likely increased our accuracy. In the rare cases in which a male appeared to change colour class during a period, we assigned it the lowest recorded category for that period. If an image did not meet the acceptable photograph conditions it was not scored, and if we had no acceptable images in a period for a given individual, that period was removed for that individual from the analysis. All image scoring was conducted by the same observer (MC), under standardised lighting using a MacBook Pro with the screen turned to full brightness. We chose not to crop out the background of photographs as the human brain uses cues from the surrounding environment to adjust colour perception (Mizokami et al., 2004).

Validation of photo colour scoring

While field scores were not used for analysis, to test that we could score photographs as accurately as in the field we took a random subset of 200 sightings of males from P5 in which males had been assigned a colour score in the field and a photograph had been taken. We used only sightings where the photograph was taken in acceptable light conditions and the animal was not obstructed by vegetation or out of focus. Multiple sightings of the same individual were allowed. The colour of the male in each photograph was then scored independently by three trained observers using the same criteria as used in the field. Observer one (M Castles) completed two full, seven-month data collection periods (2015 and 2016), while observers two and three had each spent one month in Etosha National Park collecting field data on this project as research assistants in 2016. The accuracy test was conducted in mid-2017, reducing the likelihood of observers being able to recognise individuals and recall the scores given to them in the field.

To test inter-observer reliability among the three observers, we calculated an intra-class correlation coefficient (ICC) and 95% confidence intervals in the R package *psych* (Revelle, 2017), based on the mean of four scores, those of the three observers and the field score, absolute agreement (exact same score given), and a two-way mixed effects model (Koo & Li, 2016). We then tested the correlation between the photograph scores of MC and the field scores using a Spearman's rank correlation.

Calculation of association data

We generated weighted social networks for each of the four studies from the observed group compositions using the R package *asnipe* (Farine, 2017). We excluded groups for which less than 80% of individuals could be identified (Silk, Jackson, Croft, Colhoun, & Bearhop, 2015). To control for differences in grouping patterns between wet and dry seasons (Brand, 2007), we only included groups observed between April and November in each study, leaving 2428 groups over the four studies. We calculated the strengths of association (edge weighing) between dyads (pairs of individuals) using the half-weight index (HWI, Whitehead, 2008):

$$HWI = \frac{X}{X + Y_{ab} + \frac{1}{2}(Y_a + Y_b)}$$

in which X is the number of times individuals a and b were seen together, Y_{ab} denotes the number of times both individuals were observed in a survey but not together and Y_a and Y_b denote times that a was observed but not b and vice versa. This index controls for biases that may arise when individuals are more likely to be seen apart than together, which is likely to occur when individuals have large home ranges and the population exhibits a high degree of fission-fusion dynamics (Croft, James, & Krause, 2008). HWI scores fall between zero and one, with zero representing a dyad that is never observed together and one a dyad that is always in the same group (Cairns & Schwager, 1987; Whitehead, 2008). We did not filter rare edges or individuals (nodes) with low sighting frequencies. We could not analyse the social network metrics of individuals with low sightings (see below), however these individuals may be important to the structure of the network and the position of others within it (Croft et al., 2008) and thus were included in the calculations of other individuals' metrics.

Calculation of gregariousness and sociability metrics

To quantify males' social behaviour, we calculated two metrics of gregariousness, two social network metrics that describe different aspects of individuals' sociability, and the proportion of individuals' associates (group members) that were males. These metrics were calculated for data collected during each of the four studies.

Gregariousness metrics:

Median group size: We calculated the median group size for each male in each study. To standardise across the studies, we calculated the median group size for all males in each study and subtracted this from each male's median to obtain a difference from the study's median group size.

Proportion of time spent alone: We divided the number of sightings where an individual was alone by its total number of sightings. Again, to standardise we calculated the median time spent alone across all males in each study and subtracted this from males' scores to obtain differences from the median proportion of time alone.

Sociability metrics:

Weighted transitivity: Also known as clustering coefficient, this metric measures the degree to which an individual's associates are also connected to one another. Individuals in highly "cliquish" or tight-knit subgroups have high relative transitivity (see Whitehead, 2008 Table 5.3 for formula). We predicted that darker males would have lower transitivity than other males. Darker, more dominant males are expected to spend more time roaming in order to encounter and assess females, and thus would spend less time with particular males and have lower transitivity. Younger, subordinate male giraffes are often seen in all-male groups (Bercovitch & Berry, 2014), and thus would be expected to have higher transitivity.

Weighted Betweenness: This metric determines how important an individual is as a connector between others in the network by measuring the number of dyads whose geodesic distance (shortest path) passes through the individual (see Whitehead, 2008 page 173 for a description of the calculation). High betweenness scores represent individuals that are important network connectors and thus may be key in the spread of information through a network. We predicted that darker males would have higher betweenness measures as they would encounter, and thus associate with, more individuals than would other males.

Proportion of associates that were males: For each sighting of a male we counted the group size (minus one to account for the individual) and the number of other males in the group. We then summed each of these for each male and divided their total number of male associates by their total number of associates. We then calculated a median proportion of male associates across all males in each study and subtracted this from the score for each male in that study.

Comparison of raw individual metrics from networks that are of different sizes and have different characteristics is not appropriate (Krause, Croft, & James, 2007). Thus, to allow comparison among transitivity and among betweenness scores across the four studies, we used a similar approach to that of Wilson, Krause, Dingemanse, & Krause (2013) and ranked each individual within each study by its metric, then rescaled them to fall between zero and one with one representing the highest ranked individual. To reduce inaccuracy due to sparse data we analysed only males seen more than eight times in a particular study. This threshold was chosen as a trade-off between maximising the number of individuals included in the analyses while still suitably sampling their association patterns. We controlled for differences in sighting frequencies among individuals above the minimum number of sightings by utilising a permutation method that maintains group composition and individual sighting frequency while randomly moving individuals among groups (explained below).

The relationship between colour and age (Aim 1)

To test the relationship between males' age and coat colour we ran a cumulative link mixed model in the R package *Ordinal* (Christensen, 2015). We used colour as an ordered response variable, with age (also ordered) and period as predictors. We also included ID as a random factor. To test the goodness of fit of the model we calculated McFadden's pseudo R^2 (Domencich & McFadden, 1975). This returns a value between zero and one, but values close to one are unlikely and values between 0.2 and 0.4 are considered to represent a suitable model fit (McFadden, 1978). Our model fit value was 0.3.

Homogeneity of variance is not of concern when modelling ordinal data. However, we were interested in differences in the variation in colour among age categories and found clear evidence of increasing variance with age in a preliminary analysis. Therefore, we tested for this formally by treating colour as a numeric variable and running a Levene's Test against age, using the *car* package in R (Fox & Weisberg, 2011). This test assesses whether the variance of a variable is statistically different among groups.

The relationships between sociability and colour (Aim 2)

To test whether and how individuals' median group size related to colour, we ran a linear mixed effects model with individuals' differences from the study's median group size as the response, colour (ordered) as a predictor and ID and study number as random effects in the R package *lme4* (Bates, Bolker, & Walker, 2015). Because age is related to males' gregariousness (Castles, 2018), we controlled for age by also including it as a predictor in the model. Although there is a relationship between age and colour (see Results below), a chi-square test between ordinal variables showed that the correlation was significant but not strong ($R = 0.62$, $X^2 = 35.68$, simulated-$P = 0.008$), so both variables could be included in the model (Dormann et al., 2013). We used the same approach to test the relationships between male colour and (a) difference to median proportion of time alone, and (b) difference to median proportion of male associates. Each variable was modelled with age and colour as ordinal predictors and individual identity and study number as random effects. We combined colour classes 3.5 and 4 in all analyses due to low sample sizes of each class. N = 5 was our minimum sample size; this was recorded from colour classes 1.5, 2.5, 3 and 3.5+, colour class 2 had 24 individuals. To test the fit of each model we compared the log-likelihood of the model with that of a null model, which showed that the included variables significantly improved the predictive performance of all models ($P_{\text{group size}} < 0.01$, $P_{\text{time alone}} = 0.04$, $P_{\text{male associates}} < 0.01$, full results in supplementary material). The sample size did not allow us to include an interaction term between age and colour in any of our five models of the sociability metrics.

To examine the relationships between colour, age and each of the social network metrics (betweenness and transitivity), we ran generalised linear mixed effects models with a beta distribution and logit link in the R package *glmmTMB* (Magnusson et al., 2017). The rescaled- ranked sociability metric was the response variable. As with the gregariousness metrics, because age is related to sociability (Castles, 2018), age was included in the models as a predictor variable along with colour. We included individual identity as a random factor in all models, but study number was not included as it had only minimal influence on the variance of the rescaled ranked data. Network data are non-independent and thus violate this assumption of regression modelling (Croft, Madden, Franks, &

James, 2011). Thus, to calculate appropriate p-values we used a randomisation approach by permuting the network, recalculating the sociability metrics and rerunning the model 1000 times (Farine & Whitehead, 2015). Explanatory variables were considered significant if the observed effect size was larger (further from zero) than 95% of the randomised effect sizes. This approach has the additional benefit of controlling for differences in sighting frequencies among individuals. Again, we used a log-likelihood comparison with a null model to confirm the model fit. Despite similarity between the models the variables significantly improved our betweenness model when compared to a null model ($P < 0.01$) but not our transitivity model ($P = 0.33$, full results in supplementary material).

Results

After the removal of unacceptable photographs, we used 1793 photographs to score the patch darkness of 66 males in 206 male/period combinations for Aim 1 and 41 individuals in 44 male/study combinations for Aim 2. This included males in all age classes from juveniles (< 2 years) to old adults (15+ years). Individuals ranged in patch darkness from 1.5 (paler than an average female) to 4 (almost all patches completely black), with a median darkness score of 2.

Consistency of colour scoring

We calculated an $ICC_{3,k}$ value of 0.94 with a 95% confidence interval of 0.93-0.95, suggesting high inter-observer reliability in scoring colour from photographs (Koo & Li, 2016). The correlation between the photograph scores of the primary observer (MC) and the scores assigned in the field was significant ($R = 0.84$, $N = 200$, $t = 21.595$, D.F. = 199, $P < 0.001$). We concluded that we could reliably score male colour from photographs under these conditions.

The relationship between colour and age (Aim 1)

The hypothesis that colour functions as a signal of competitive ability predicts that not all males should become equally dark as they age. Our data supported that prediction. In general, coats darkened with age and the oldest males were the darkest; however, variation in colour increased with age (Figure 2). Juveniles were only found to have colour classes 1.5 and 2 while old males ranged from classes 2 to 4. The Levene's test showed significant differences in the variance of colour scores among age classes (DF = 4, F = 6.00, P < 0.01). Colour class 2 was the most common for all age classes except old males, for which colour 3 was more common. Twenty individuals (26%) did not change colour between periods at all and one particular individual was recorded as colour 2 as a juvenile, young adult, middle-aged adult and old adult. Colour was linearly and quadratically related to age and period had no significant effect (Table 2).

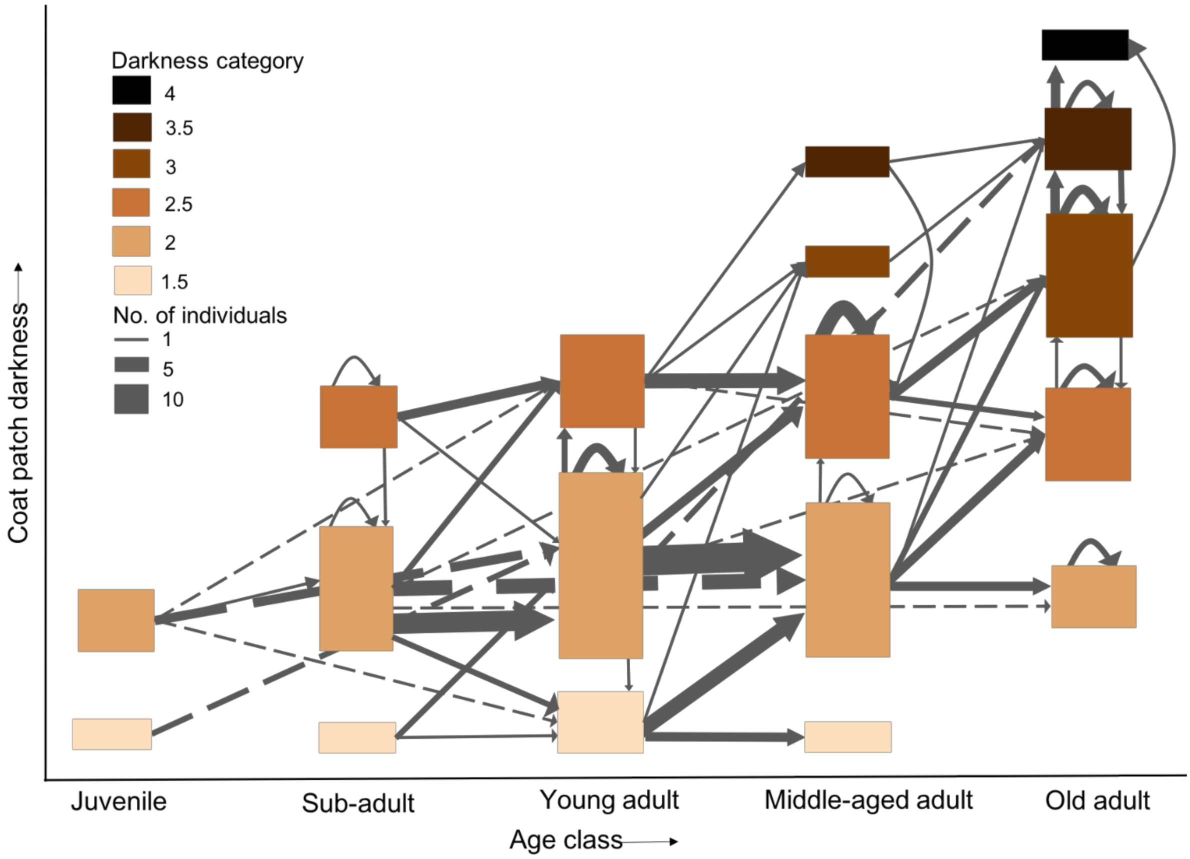


Figure 2: Progression of colour with age for 66 males, each photographed in a median of 3.0 periods, for a total of 206 male-period combinations. Box height denotes the number of individuals observed in each category and line width denotes the number of individuals that followed a given path between age classes. Dashed lines represent paths that skipped an age class, which occurred when individuals were not sighted in consecutive periods or their colour could not be scored. Vertical lines show cases where individuals were in the same age class in consecutive periods and changed colour, and “U-turn” arrows denote individuals that were in the same age class in consecutive periods but did not change colour.

Table 2: Full model output from the cumulative link mixed-effect model of the effect of age and period on colour (Aim 1). As age was included as an ordered variable the model fits one less polynomial function than there are levels. The model includes 206 observations of 66 males. Significant variables are shown in bold.

Parameter	Estimate	SE	Z-value	P-value
Age - linear	**4.44**	**1.07**	**4.15**	**<0.01**
Age - quadratic	**2.37**	**0.63**	**3.74**	**<0.01**
Age - cubic	0.72	0.52	1.39	0.16
Age - quartic	-0.52	0.39	-1.34	0.18
Period 2	1.39	0.86	1.61	0.11
Period 3	2.00	1.07	1.87	0.06
Period 4	0.72	1.00	0.72	0.47
Period 5	1.46	1.11	1.32	0.19

The relationships between sociability, age and colour (Aim 2)

If male giraffes' colour reflects their relative competitive ability, males of different colours might exhibit different mating strategies. Such differences might be reflected in their patterns of sociability. We found partial support for this prediction. Colour class two was the most common ($N_2 = 24/44$ male/study combinations) but males' gregariousness generally decreased with age and darkness. Gregariousness decreased linearly with age but for colour there was a stark contrast between gregariousness metrics of males that were paler versus those that were darker than colour class 2.5 (Figure 3). This result was reflected in significant negative linear relationships between males' differences from the median group size and both colour and age (Table 3) and a quartic relationship between difference to median group size and colour (Table 3). A quartic relationship suggests that there are two points of inflection. We also found that the proportion of time alone (measured as the difference from the study's median) increased linearly with both age and colour, with the effect of colour larger than that of age (Table 3). We found no significant effects of age or colour on rescaled betweenness rank as estimates fell within the spread of possible values from randomised data (Table 4). We also found no effect on rescaled transitivity rank, however the variables did not improve the predictive performance of the model compared to a null model (log-likelihood comparison, P = 0.33, full results in supplementary material). We found no effect of colour or age on the proportion of associates that were males (measured as the difference from the study's median, Table 4).

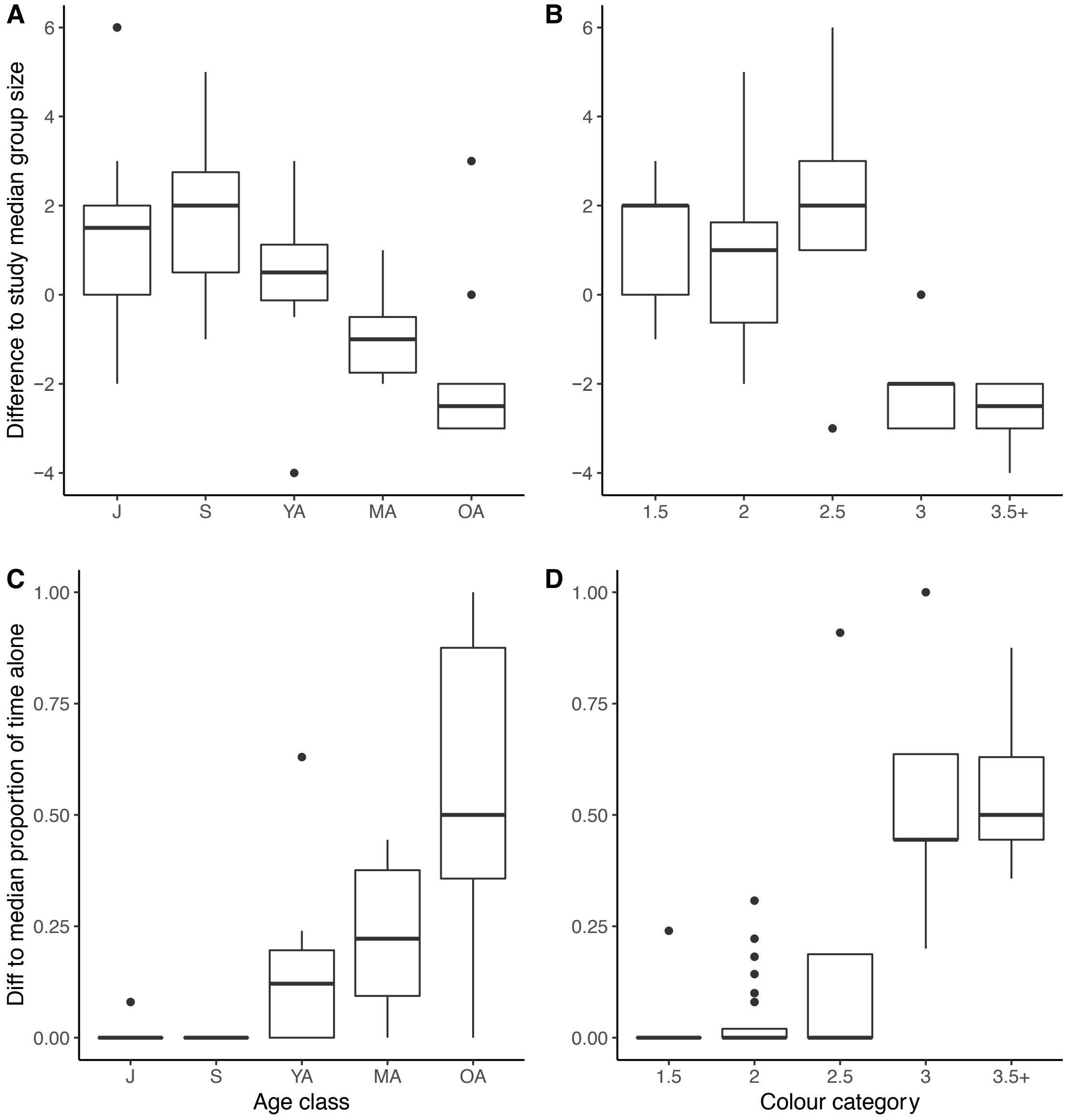


Figure 3: Relationships between males' gregariousness metrics and age and colour (N = 44 observations of 41 males in 4 studies). The top row shows the relationships between median group size (measured as the difference from the median for all individuals in a study) and age (A) and colour (B). The bottom row shows the relationships between the difference to study's median proportion of time alone and age (C) and colour (D). Boxes show the median and interquartile range (IQR) with whiskers to 1.5 times the IQR. Data outside of this range are shown as points.

Table 3: Full model output results for the relationship between gregariousness metrics, male associates and colour. As age and colour were included as ordered variables the model fits one less polynomial function than there are levels for each variable. All models were made on 44 observations in the 4 studies. Significant variables are shown in bold.

Measure of sociability	**Parameter**	**Est.**	**SE**	***df***	**T**	**P**
Difference to median group size	(Intercept)	0.19	0.37	35.00	0.50	0.62
	Age - linear	**-2.08**	**0.84**	**35.00**	**-2.49**	**0.02**
	Age - quadratic	-0.37	0.68	35.00	-0.55	0.59
	Age - cubic	1.22	0.65	35.00	1.87	0.07
	Age - quartic	-0.17	0.65	35.00	-0.25	0.80
	Colour - linear	**-2.17**	**1.03**	**35.00**	**-2.11**	**0.04**
	Colour - quadratic	-1.37	0.78	35.00	-1.77	0.09
	Colour - cubic	-0.30	0.70	35.00	-0.44	0.67
	Colour - quartic	**1.82**	**0.71**	**35.00**	**2.55**	**0.02**
Difference to median proportion of time alone	(Intercept)	0.24	0.04	35.00	6.39	0.00
	Age - linear	**0.22**	**0.09**	**35.00**	**2.58**	**0.01**

	Age - quadratic	0.05	0.07	35.00	0.67	0.51
	Age - cubic	0.01	0.07	35.00	0.12	0.90
	Age - quartic	0.07	0.07	35.00	0.97	0.34
	Colour - linear	**0.31**	**0.11**	**35.00**	**2.95**	**0.01**
	Colour - quadratic	0.02	0.08	35.00	0.24	0.81
	Colour - cubic	-0.07	0.07	35.00	-1.34	0.19
	Colour - quartic	-0.06	0.07	35.00	-0.86	0.39
Difference to median proportion of male associates	(Intercept)	0.01	0.04	2.37	0.25	0.83
	Age - linear	0.14	0.08	12.10	1.86	0.09
	Age - quadratic	0.00	0.06	33.32	0.05	0.96
	Age - cubic	-0.00	0.06	16.77	-0.07	0.95
	Age - quartic	0.02	0.05	32.54	0.38	0.71
	Colour - linear	-0.05	0.09	33.44	-0.52	0.61
	Colour - quadratic	-0.00	0.07	33.41	-0.04	0.97
	Colour - cubic	-0.05	0.05	33.53	-0.99	0.33
	Colour - quartic	-0.09	0.06	33.57	-1.67	0.10

Table 4: Full model output results for the relationship between sociability metrics and colour. As age and colour were included as ordered variables the model fits one less polynomial function than there are levels for each variable. All models were made on 44 observations of 41 males in the 4 studies.

Measure of sociability	Parameter	Est.	SE	Z	P (Randomisation)
Rescaled ranked betweenness	(Intercept)	0.03	0.22	0.114	
	Age - linear	-0.07	0.49	-0.14	0.97
	Age - quadratic	-0.63	0.40	-1.55	0.26
	Age - cubic	-0.61	0.37	-1.62	0.19
	Age - quartic	0.16	0.37	0.45	0.80
	Colour - linear	-0.02	0.68	-0.03	0.98
	Colour - quadratic	0.47	0.47	0.98	0.42
	Colour - cubic	0.20	0.38	0.52	0.41
	Colour - quartic	0.34	0.40	0.85	0.06
Rescaled ranked transitivity	(Intercept)	0.18	0.24	0.73	
	Age - linear	0.29	0.54	0.55	0.50
	Age - quadratic	0.84	0.44	1.92	0.37
	Age - cubic	0.38	0.40	0.96	0.76
	Age - quartic	0.12	0.40	0.31	0.99
	Colour - linear	0.18	0.74	0.24	0.66
	Colour - quadratic	-0.55	0.53	-1.04	0.60
	Colour - cubic	-0.35	0.41	-0.86	0.76
	Colour - quartic	-0.14	0.42	-0.35	0.72

Discussion

The observed variation in the coat patch darkness of male giraffes is hypothesised to function as an honest visual signal of males' competitive ability or social standing (Brand, 2007; Guindre-Parker & Love, 2014; Roulin, 2016). We examined the coat colour and sociability of male giraffes over a 12-year period to examine two predictions pertaining to this hypothesis. Our results showed that the rate at which males darken was not equal among males; not all males reached the darkest colour category in the oldest age group, and some appeared not to darken with age at all (Aim 1). These results differ from the findings of Berry and Bercovitch (2012), who reported that a small sample size of Thornicroft's giraffe in Zambia all had black spots by approximately nine years of age. Further research is required to understand variation in colour patterns across populations in different environments, but it is known that coat colour of giraffes varies with climate (Brand 2007). We also showed that darker males tended to be in smaller groups and to spend more time alone than paler males, but that males of different colours did not differ in two social network metrics or the proportions of their associates that were male (Aim 2). The first of these results is consistent with the hypothesis that colour may be a secondary sexual trait that honestly signals competitive ability and the second is consistent with the hypothesis that darker males are more likely than paler ones to use a roaming strategy to find oestrous females. We discuss these findings below in the broader context of status signalling and mating tactics before considering potential future avenues to further investigate the function of male patch colour and its relationship to the sociability of male giraffes.

Colour and Age

As expected for an honest secondary sexual trait, the coat patch darkness of our giraffes generally increased with age but there was considerable variation among individuals. Below a specific threshold in height, weight, or level of experience, males may be competitively excluded from mating opportunities (Fisher & Lara, 1999), and thus receive minimal benefits from investing in secondary sexual characteristics. Once that threshold is reached and males are competitive, those in good condition may trade off or supplement continued investment in growth with investment in secondary traits (Mysterud, Langvatn, & Stenseth, 2004). These may be costly (Rohwer & Ewald, 1981) but can highlight a male's superior physical condition (Roulin, 2016) or convey additional information about testosterone level or genetic quality that may not be conveyed through other physical features (Gasparini et al., 2009; Meunier et al., 2011; Peters, Astheimer, Boland, & Cockburn, 2000; Setchell, Smith, Wickings, & Knapp, 2008). Thus, hypothesised condition-dependent signalling of quality and/or status suggests that older males with strong trait expression are likely to be the most dominant (Freeman-Gallant et al., 2010). Giraffes' heights increase towards an asymptote at around eight years

(Dagg & Foster, 1976) and males live sixteen years on average (Berry & Bercovitch, 2012); thus, as age increases, height is less likely to be a reliable predictor of age or competitive ability. Brand (2007) concluded that male giraffes' colour is used in competitor assessment and female mate choice, so colour may be more reliable than height for potential competitors and mates to judge competitive ability.

The mechanisms that might link colour and quality in giraffes are unknown. However, the following are a number of possibilities that could be explored. (1) Pleiotropic genes could cause a link between colour and testosterone levels, signalling aggression and sexual activity (Ducrest et al., 2008; Setchell et al., 2008; Roulin, 2016). (2) Some studies have shown that melanic pigments are costly to produce, in terms of energy or dietary components required. Since mammalian hair is replaced regularly, changes in body condition (and energy and nutrients available) could cause colour to be linked to body condition (Roulin, 2016). However, we do not know how quickly giraffes replace their hair and thus how rapidly their colour could change. (3) Darker male giraffes could be more likely to be challenged aggressively by other males, so that there could be a cost to a giraffe being dark if he was not as fit and strong as other dark males. Male red junglefowl, *Gallus gallus*, who had larger combs, a signal of condition and status, and behaved like dominant males, were more likely to be attacked by dominant males than were other males (Parker & Ligon, 2002). This is an example of the honesty of a signal likely being maintained, at least in part, through punishment of cheaters by conspecifics. While we do not know if a dark but not correspondingly fit giraffe would be "punished", the most intense fights occurred only between pairs of dark males in Brand's (2007) study. (4) Colour may also function through the handicap principle (Zahavi 1975) if darker males suffer higher heat stress (Acharya, Gupta, Sehgal, & Singh, 1995; West & Packer, 2002) or are more conspicuous to predators (Stuart-Fox, Moussalli, Marshall, & Owens, 2003). Further research is required to support the hypothesized link between the colour of male giraffes and their body condition, and these possible mechanisms.

Despite this uncertainty about the mechanisms that might link colour and quality in giraffes, our data suggest that giraffes' coat colour functions as a secondary sexual characteristic in the same manner as the mane of the African lion. Lions' mane growth and colour increase with age; however, the length of manes can be influenced by injury, testosterone and nutrition (Smuts, Robinson, & Whyte, 1980; West & Packer, 2002) and colour can vary with ambient temperature and testosterone level (West & Packer, 2002). Indeed, there is so much variation in the mane characteristics of male lions that it is not used as a reliable indicator of age (Miller et al., 2016). The colour and length of lions' manes have been associated with female choice and male-male competition, but darker manes have been associated with higher coat surface temperature and higher rates of abnormal sperm (West & Packer, 2002). As well as its use in competitive assessment and mate choice in giraffes, Brand's (2007) results suggest that darker colour may be associated with higher heat stress in environments with high insolation. Some female giraffes become paler towards the end of the dry season and post-partum, and darker males appear to suffer high mortality in drought years (Brand, 2007; A. Goldizen, personal observations; S. Kotting, personal comm.). It thus appears that giraffes' colour may function in a similar way to the lion's mane. This possible thermoregulatory cost of darker coat colours in giraffe requires further research, but if supported it would suggest that a comparable colour handicap system has evolved as an honest signal of male quality in unrelated species in response to similar environmental conditions. Purely visual secondary sexual traits are rare in wild ungulates. However, the sable antelope, *Hippotragus niger* and the nyala, *Tragelaphus angasii* both display sexual dimorphism in coat colour (Kingdon & Hoffmann, 2013) and inhabit regions that may have high insolarity, so colour could function as a sexually selected signalling trait in a similar manner in those species. Further study into the costs associated with coat colour, in particular coat surface temperature, as well as potential links to testosterone or cortisol levels, dominance and reproductive output would increase our understanding of the function of colour in giraffes and other species in hot environments.

Linking colour and age to social patterns

The sociability patterns of giraffes were consistent with the prediction that males with different levels of trait expression should exhibit different patterns of sociability, as expected if they pursue different breeding tactics. Males using different breeding tactics should exhibit different patterns of sociability

(Oh & Badyaev, 2010). Indeed, we found that darker and older males tended to be in smaller groups and to spend more time alone than younger and paler males. Gregariousness declined evenly with age but there was a clear distinction between the gregariousness of males above and below colour class 2.5. In taxa in which competition exists and quality varies among males, the association patterns of males are driven primarily by the use of tactics that increase mating opportunities through the gaining of access to females in oestrus (Gross, 1996). Thus, the differences in association patterns of male giraffes of different colours are consistent with a system in which dominant, darker individuals roam over large areas looking for females in oestrus and subordinate paler individuals either delay competitive breeding or do not invest heavily in competitive breeding but take opportunistic non-competitive breeding opportunities when available (Whitehead, 1994). This is similar to the "rovers" and "stayers" model described in musk oxen by Forchhammer & Boomsma (1998). Further research with larger sample sizes is needed to better understand the effects on sociability of the complex interaction between age and colour, but we have shown that both variables are important.

The roving strategy, also known as roaming, is common in species in which females are spread out unpredictably throughout the environment (e.g. stray cats, *Felis catus*, Say & Pontier, 2004; bridled nailtail wallabies, *Onychogalea fraenata*, Fisher & Lara, 1999; African elephants, Barnes, 1982; and sperm whales, *Physeter microcephalus,* Whitehead, 1993) and increases encounter rates with females. Males with larger home ranges have higher fertilization success in male bridled nailtail wallabies (Fisher & Lara, 1999). Darker giraffes, which we assumed to be in better physical condition due to demonstrated relationships between melanin levels and condition in other species (Roulin 2016), may be able to cover greater distances than lighter males and thus increase their likelihood of finding receptive females. Further research is required to confirm that darker males roam further or travel more than lighter males. The large home ranges of our giraffes, limited roads and regulations against driving off roads in Etosha prevented us from collecting the data required to test this. Darker giraffes are dominant over paler males and are preferred by females (Brand, 2007), so if more than one male attends a receptive female the darkest male will be able to monopolise the opportunity and is more likely to be accepted quickly by the female. This tactic may increase reproductive output, but roaming, and establishing and maintaining dominance, are likely to be costly. Travelling great distances requires high metabolic expenditure (Parker, Robbins, & Hanley, 1984) and limits time available for foraging (Mysterud et al., 2004). Travelling alone also increases predation risk (Alberts & Altmann, 1995; Lucas, Waser, & Creel, 1994), particularly if darker individuals are more conspicuous (Stuart-Fox et al., 2003). Dominance interactions can also be energetically costly and males risk injury if interactions escalate to a fight.

A possible alternative explanation for these findings could be that darker males choose to spend most of their time alone or in small groups to avoid aggression from other males, or competition with either sex for food, rather than as a result of roaming in search of receptive females. However, we do not believe that this is the case, at least for most dark males. The reduced sociability of a small number of darker males could be explained by 'retirement', either temporary or permanent, from the mating game, rather than by mating strategies. We saw a small number of apparently very old males that were usually alone and who appeared to be "retired" and not to move very far (M. Castles, unpublished observations). In contrast, most of the darker males seemed to range further than these "retired" males, suggesting that their ranging was due to searching for females, rather than avoiding aggression or competition, which should be possible to achieve in a relatively smaller area.

The high gregariousness we observed for young and pale males may be explained by younger or subordinate males delaying competitive breeding to invest in growth and physical condition, which may prove more beneficial over a lifetime. This is the case for young sperm whales, which exclude themselves from mating opportunities by remaining at higher latitudes than breeding females (Best, 1979; Waters & Whitehead, 1990). Males that form bachelor groups may also gain additional benefits of reduced predation risk and opportunities for social learning. This may be an explanation for the bachelor groups of giraffes observed in this population and others (Bercovitch & Berry, 2014; Brand, 2007). Paler, older males that are not competitive may "make the best of a bad situation" by remaining near females to gain access to them when more dominant males are not around (Koprowski, 1993). "Sneaker" males have proven successful in ring-tailed coati, *Nasua nasua*, siring between 9 and 23% of offspring (Hirsch & Maldonado, 2011). In eastern grey squirrels, *Sciurus* *carolinensis*, “satellite” males gained equal numbers of copulations to dominants by mating when dominant males were fighting or pursuing other females (Koprowski, 1993). This tactic is most commonly recorded in species that have synchronised breeding seasons because dominant males are unable to guard all of the females in oestrus. However, this tactic could also work when dominant males cannot guard females because the males are not present, as in our system. Alternatively, subordinate male giraffes may benefit from being familiar to females when they come into oestrus, being more readily accepted as a mate as a result (East, Burke, Wilhelm, Greig, & Hofer, 2003).

In a highly competitive environment, the optimal behaviour of a male will depend on the behaviour and competitive ability of other males (Gross, 1996; Schradin & Lindholm, 2011). The point at which a male shifts reproductive tactics should occur when the maximum fitness benefit of the alternative tactic equals the minimum benefit of the dominant tactic (Gross, 1996). Colour class 3 was only achieved by middle-aged and old adults and was more common in old adults. Middle-aged adults (8-15 years), should have reached or be close to their peak height (Dagg, 2014) and thus be physically competitive. We suggest that middle-aged males in good condition may be able to increase their reproductive success by investing in colour to signal their competitive status and thus improve their chances of efficiently out-competing other males through visual assessment and more easily gain access to mates. If so, once they reach colour class 3, males may gain increased fitness benefits from switching to roaming behaviour in this population.

Despite the clear trends in patterns of gregariousness, we found no effect of age or colour on social network metrics. Carter, Brand et al. (2013) calculated social network metrics for non-juvenile males in this population in 2004-2005 and 2009-2010 based on a minimum of six sightings of each individual. They found that males’ metrics were no different to those expected from random assortment and suggested that because males move between groups regularly their association patterns may be essentially random. This may also be an explanation for our finding. However, as younger and paler males are more gregarious, we may have expected to see some structure to their association patterns. The roaming behaviour of adult males makes them notoriously difficult to sample and while we increased our minimum number of sightings of individuals to eight for inclusion in our analyses, we still may not have had enough statistical power to distinguish an overall pattern. Indeed, our model to test for a relationship between age, colour and transitivity did not explain the variation better than a null model.

We found no effect of age or colour on the proportion of a male's associates that were male. Thus, while males' overall number of associates decreased with increasing darkness, males of all levels of darkness associated with similar ratios of males to females. This is surprising as males that roam should prefer to associate with females when they are associating, thus have a lower proportion of male associates. A possible explanation for this is the apparent importance of aggregations around resources such as vegetation patches and waterholes, which seem to strongly drive grouping patterns in this population (Castles, 2018). Where resources are limited, males may have to associate with both females and males regardless of the potential for competitive or aggressive interactions. Furthermore, we did not include the colour of male associates in our analysis. If we had, we may have found darker males were less likely to tolerate the presence of similarly-coloured competitors. It may be unusual to find two very dark males in a group, but paler males may be tolerated by dark ones (Brand, 2007). This is an avenue for future analysis.

While our results do not directly relate giraffe colour to males' social status or roaming patterns, they support the following two predictions of this hypothesis: (1) if colour is linked to competitive ability, then not all males should increase equally in colour expression with age, and (2) males with different degrees of trait expression exhibit different patterns of sociability, as would be expected if they pursue different mating tactics. Using longitudinal data, we show that not all males reach the peak trait expression by old age and that darker males are more likely to be found alone or in small groups. Our association data show that fission-fusion dynamics allow males to tailor their association patterns depending on their age and colour. These patterns likely reflect variation in reproductive tactics, but further research, including movement data, is required. In this study we focused on colour, but male giraffes also continue to invest in bulk and skull ossification as they age (Simmons & Scheepers, 1996). These features are likely to be advantageous in the "necking" fighting technique used by giraffes but may also be used in visual competitive assessment (Kraaijeveld, Kraaijeveld-Smit, &

Komdeur, 2007). It is common for individuals to display multiple features as complementary signs of their fitness (Vergara & Fargallo, 2011); thus, future studies on the dominance, signalling of competitive ability and life history traits of giraffes should include these features. Environmental conditions may also be important factors influencing colour but we could not reliably test for this because we did not have an even spread of ages and colours in each period. Further research, comparing courtship and mating behaviour among males, is needed to determine the evolutionary fitness benefits that males of different colour gain from using different reproductive tactics in societies with fission-fusion dynamics.

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Supplementary material

S1: Log-likelihood tests for model fit Aim 2 models; the relationships between colour and (A) group size, (B) proportion of time alone, (C) proportion of associates that were male, (D) betweenness and (E) Transitivity.

	Model	**DF**	**Loglik**	**ChiSq**	**P**
A	Difference to median group size ~ ordered(Age) + ordered(Colour) + (1|ID) + (1|Period)	12	-77.95		
	Null model	3	-98.22	40.55	<0.01*
B	Difference to median proportion of time alone ~ ordered(Age) + ordered(Colour) + (1|ID) + (1|Period)	12	1.43		
	Null model	3	-7.46	17.78	0.04*
C	Difference to median proportion of associates that were male ~ ordered(Age) + ordered(Colour) + (1|ID) + (1|Period)	12	10.788		
	Null model	3	21.927	22.277	<0.01*
D	Scaled betweenness rank ~ ordered(Age) + ordered(Colour) + (1|ID)	11	4.59		
	Null model	3	-5.94	21.06	<0.01*
E	Scaled transitivity rank ~ ordered(Age) + ordered(Colour) + (1|ID)	11	6.91		
	Null model	3	2.31	9.181	0.33

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Animal ethics note

The data collection protocols used in this study were assessed and approved by the University of Queensland Native/Exotic Wildlife and Marine Animals Animal Ethics Committee (approval numbers SBS/439/14, SBS/093/11/GCF and SIB/124/09/URG). Data collection was approved by the Namibian Ministry of Environment and Tourism under research permit numbers 2017/2016, 2005/2015, 1082/2013, 1468/2010, 1365/2009, 876/2005 and 760/2004. We followed all regulations when working within Etosha National Park, including a maximum speed limit of 60 km/h (we drove much slower around wildlife ~10 km/h) and remaining in a vehicle and on road when outside of the rest camps.

This is was a purely observational study aiming to record natural behaviour of wild animals. Thus, animals were not housed, translocated, fed, trapped or manipulated in any way. We identified individuals by their unique spot patterns so no individual tagging was required. The national park is a popular tourist attraction so the wildlife are habituated to observation from vehicles. We maintained a respectful distance to not disturb natural behaviour and drove slowly around all wildlife.

Over our four data collection periods spanning twelve years we recorded data on 1484 individuals (575 female, 668 male and 241 individuals of unknown sex). Data on 77 of these males was analysed in this study.