RESEARCH ARTICLE

Sparring dynamics and individual laterality in male South African giraffes

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Abstract

Sparring by male giraffes has been commonly reported since its first description in 1958 and is believed to play a role in establishing male dominance hierarchies. However, despite being often documented, quantitative investigations of sparring behaviour are currently lacking. Here, we investigate the factors affecting the frequency, duration and intensity of sparring bouts in a population of giraffes *Giraffa camelopardalis giraffa* living on a private fenced reserve in Limpopo, South Africa. We show that sparring bouts were most frequently observed in young adults, and between males that were more evenly matched in size. Sparring bouts between males of similar body size were also characterised by being of high intensity and of short duration. Taken together, these results support the suggestion that sparring functions principally to provide maturing males a means of testing their competitive ability without escalating to full-scale fights. Additionally, mature bulls intervened on young adults possibly to disable any winner effect achieved by the latter, with the most dominant bull being responsible for the majority of interventions. For the first time, we also show that individuals displayed strong laterality when engaged in sparring: individuals consistently preferred delivering blows from either their left or right side, and these preferences dictated the orientation of sparring bouts (whether head-to-head or head-to-tail). Lastly, we show that sparring displayed a seasonal peak which coincided with the onset of the wet season and possibly reflected the increased aggregation of males at this time. A more nuanced understanding of how social and environmental factors shape interactions among individuals, such as sparring, will improve our understanding and management of this charismatic animal.

KEYWORDS
animal contests, assessment, fighting, laterality, play, social behaviour

1 | INTRODUCTION

Competition between individuals over access to mates and resources shapes the morphology, physiology and behaviour of all organisms. Some of the most striking examples of the evolutionary consequences of competition are seen in polygynous species where the most competitive males, through the ornaments they possess or the armaments they use in direct contests, are able to monopolise access to a large number of females (Andersson, 1994; Emlen & Oring, 1977; Shuster & Wade, 2003). To understand intrasexual

competition, researchers have therefore often turned to conspicuous displays of fighting behaviour between males, and these provide some of the classic models for animal contests (Clutton-Brock et al., 1982; Leboeuf, 1974). Yet, in many species males also engage in interactions that closely resemble the motor patterns of fighting but that lack much of the intensity or risk of fully escalated fights, and where there is no apparent winner or loser from the interaction: such behaviours have often been termed "sparring", or in some cases, play-fighting (Barrette & Vandal, 1990; Evans & Harris, 2008; Geist, 1974; Green & Patek, 2015).

Distinctions between sparring and fighting have been best studied in ungulates, where the role of body size, antler size and rank on sparring dynamics has been used to try and determine its function. One common observation from this work is for sparring to take place most frequently among young males, prompting the suggestion that sparring serves as a form of training for skills that will be later used in fights (Fagen, 1981; Rothstein & Griswold, 1991; Thompson, 1996). Further supporting this argument, the same collection of studies noticed that individuals who spar together are often matched in age or size, perhaps allowing for males of comparable strength and skill to assess each other without incurring the costs of fighting. In interactions among caribou (*Rangider tarandus caribou*) for example, small-antlered males initiated approximately 50% of sparring bouts but ended 90% of them, presumably abandoning contests after assessing their relative inferiority (Barrette & Vandal, 1990). However, while training and assessment may well provide general explanations for the occurrence of sparring behaviour, there remain few studies that have explored sparring quantitatively. Even among ungulates, where polygyny is widespread, species differ widely in their grouping patterns and social structure and so we should not necessarily expect sparring to serve a similar function in all contexts or to consistently play an important role in male social dynamics.

In this study, we investigated sparring dynamics among males in a population of South African giraffes, *Giraffa camelopardalis giraffa*, living on a private reserve in the northeast of South Africa. Male giraffes follow a strict dominance hierarchy that is defined by age and size (Horová et al., 2015; Wolf, Bennett, et al., 2018), and

while young adult males are often observed in bachelor herds or in mixed herds (Bercovitch & Berry, 2015; Seeber et al., 2013), mature bulls adopt a roaming lifestyle in search of receptive females and are therefore often observed alone or in close proximity to female groups (Bercovitch et al., 2006). It has been suggested that one of the ways in which hierarchies among males are established and maintained is through encounters involving fighting and sparring behaviours (Coe, 1967; Leuthold, 1979; Pratt & Anderson, 1985). In both contexts, bulls position themselves side by side and proceed to deliver blows to one another by swinging their necks and striking with their heads and ossicones, albeit at different levels of intensity. The earliest accounts of sparring in giraffes laid out the patterns of the behaviour and described how sparring is typically preceded by necking and rubbing, with partners adopting either a head-to-head or a head-to-tail position before delivering blows (Figure 1). Subsequently, Leuthold (1979) observed that sparring was mostly conducted by subadults and young adults, a pattern that was later confirmed by Pratt and Anderson's (1982, 1985) detailed records of giraffe behaviour in Northern Tanzania. Since then, a large number of field studies have testified to the ubiquity of sparring behaviour across giraffe populations (Brand, 2007; Le Pendu et al., 2000). Based on the accumulated knowledge to date and observations of other ungulates, sparring in giraffes has been suggested to have two main functions: (1) as practice for young adults and subadult bulls to gain the skills needed for fighting (Bercovitch & Berry, 2015; Pratt & Anderson, 1985) and (2) to establish and maintain social cohesion in the dominance hierarchy of male bulls, without incurring the high costs of fighting (Coe, 1967; Leuthold, 1979; Pratt & Anderson, 1982).

Yet, despite numerous reports of sparring in giraffes, the causes and consequences of variation in sparring remain little known. To our knowledge, beyond broad descriptions of the occurrence of sparring among individuals, no studies have provided quantitative information on the effects of different social or environmental factors on the frequency of sparring bouts, or considered the factors that cause sparring bouts to differ in duration or intensity. In this study, we investigated three main aspects of sparring dynamics.
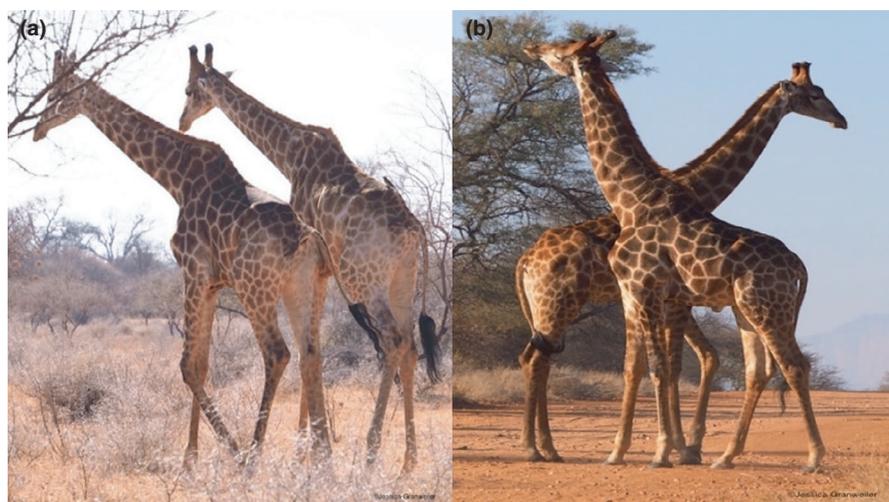

FIGURE 1 Sparring orientation. Giraffe bulls pictured sparring in either (a) a head-to-head position or (b) a head-to-tail position

First, we examined the distribution of sparring across males and tested whether the frequency, duration and intensity of sparring bouts varied according to the size and age class of the individuals involved. In line with the suggestion that sparring acts as training for future fights and provides males a means of assessing their competitiveness, we predicted that young adult males would be seen to spar most frequently and that males would be more likely to spar with peers with whom they were more evenly matched in size. Second, we examined the broader social and seasonal context in which sparring occurred. Giraffes give birth year round (Dagg & Foster, 1976; Ogutu et al., 2014), though in some populations patterns of calf production indicate an increase in conception rates around the onset of the wet season (Brand, 2007; Hart et al., 2021). Giraffe social structure is also known to vary with changes in seasonality (Bercovitch & Berry, 2010; Bond et al., 2020; Wolf, Ngonga Ngomo, et al., 2018), but how this affects behaviours such as sparring has been little explored. If sparring is to have some role in structuring male–male competition, we might therefore expect increases in sparring frequency in the wet season when females are most receptive and aggregate in larger groups.

Lastly, following patterns that emerged during field observations, we also examined whether male giraffes displayed a consistent preference to spar from one side or another. Lateralisation of complex motor skills (e.g. fighting, playing or tool use) is widespread in the animal kingdom (Ströckens et al., 2013) and in the context of agonistic animal contests both right and left side biases have been demonstrated (Convict cichlids *Amatitlania nigrofasciata*: Arnott et al., 2011; Fallow deer *Dama dama*: Jennings, 2012; Przewalski horse *Equus przewalskii*: Austin & Rogers, 2014; Australian cuttlefish *Sepia apama*: Schnell et al., 2019). A preference for using one side or other has been linked to individual perception and is thought to facilitate conspecific assessment during contests, such as in the lateral display of male fallow deer (Jennings, 2012). Giraffes might derive similar benefit by lateralising sparring behaviour, while at a proximate level, individual lateralisation may also allow individuals to repeatedly use the stronger side of their body, from which they can deliver blows more efficiently. We examined whether male giraffes display lateralisation in sparring and tested whether this affected the posture (head-to-head or head-to-tail, Figure 1) and intensity of the interaction.

2 | METHODS

2.1 | Study area & population

The study was conducted at the Mogalakwena River Reserve (MRR) in the north of the Limpopo Province, South Africa, between November 2016 and May 2017. MRR is a fenced reserve of 14 km², and the vegetation is arid sweet bushveld, comprising a combination of shrubland and woodland, interspersed with a few open savannah areas. Yearly population counts were conducted since the introduction of six giraffes in 2003. Weekly observations of the population

since 2012 provided information on the birth date and mother of individuals born after 2012, but population founders and individuals born prior to this date were of unknown age. The precise relatedness structure of the population is unknown. However, as the population has grown from the recruitment of a smaller founder stock, it can be assumed that some individuals are close relatives, with the current population coming from the few introduced individuals in 2003 and no subsequent mixing has occurred. The giraffe population in May 2017 included seven juveniles (<1 year old: four males and three females), seven subadults (1.5–4 years: two males and five females) and 17 adults (>4 years: nine males and eight females; categorised as per Van Der Jeugd and Prins (2000)) generating a population density of 2.13 giraffes/km². Males were further classified according to Pratt and Anderson (1985) based on the following physical traits: body size, neck girth, the appearance and thickness of ossicones, secondary growths on the skull and frontal bones, and body colour. These traits are closely related to age (Berry & Bercovitch, 2012; Castles et al., 2019; Pratt & Anderson, 1985). Class A bulls ($n = 5$) were defined as mature adult males that were of large body size and possessed thick necks, large, scarred ossicones, prominent secondary growths on their skull and a darker coat colour. Class B bulls ($n = 4$) were young adults of intermediate body size, with bold tops to their ossicones and small secondary growths on their skulls. Class C bulls ($n = 2$) were the youngest and smallest males, representing subadults with thin necks, an absence of secondary growths and ossicones topped by fur (Figure S1). We also ranked males according to their relative body size for some analyses. Specifically, bulls were ranked according their relative height at the shoulder (1 = highest ranking, 11 = lowest ranking). Shoulder height has been shown to be closely correlated with overall mass across a range of African herbivores, including giraffe (Cumming & Cumming, 2003), and allows for straightforward comparison of individuals when they are sparring or otherwise in close proximity (e.g. feeding from the same tree). Juveniles were not considered as they were still immature and took part in juvenile play rather than sparring. A1 was considered the most dominant male in the population on the basis of both behavioural and morphological information: being larger and darker than other males, as well as most frequently showing mate guarding and displacement behaviours. Whether this translated into a higher share of paternity was not known. All individuals could be recognised by their unique coat pattern.

2.2 | Data collection

Field observations were conducted on foot between 6:00 and 12:00, and all giraffes were habituated to human presence and approachable to a distance of 10–30 m. The reserve was walked daily along routes where giraffe groups were frequently sited, and when a group was found that contained at least two non-juvenile males it was followed. A group was defined as two or more individuals that were feeding or moving in the same general direction within 500 m distance of each other (Leuthold, 1979; VanderWaal et al., 2014). On

average, groups were followed for 3.7 ± 0.9 h (±SD), during which all occurrences of sparring bouts were recorded (as per "all occurrence sampling," Altmann, 1974).

The dynamics of each sparring event were recorded vocally on an iPhone. We recorded the start and end of the sparring bout, the identity and relative position of the sparring partners, and the total number of blows delivered by each bull. A sparring bout started whenever the first blow was delivered and ended when the dyad stopped exchanging blows and walked away from each other. Sparring bouts were defined as any reciprocal exchange of blows between two males. If only one male delivered blows, but the other bull did not reciprocate, this was deemed as an unsuccessful attempt to initiate sparring and was not considered. A blow was defined as a full swing of the neck and head regardless of whether the blow made contact with the sparring partner.

Typically, other group members remained in the vicinity for the duration of the sparring bout and the dyad would usually re-join the group at the end of a bout. The size and composition of the group immediately prior to each sparring bout were recorded. The position adopted by the dyad was noted as either head-to-head or head-to-tail (Figure 1), and the relative position of each sparring partner was recorded as being on the left or right side. For example, in Figure 1a, the male in the foreground is noted as "right-sided," whereas the male in the background is noted as "left-sided." By contrast, in Figure 1b, both males are noted as "right-sided" as both stand with their partner on their respective right side. Lastly, we recorded any intervention behaviour, defined as a third-party trying to position himself in-between two sparring partners, resulting in a premature ending of the encounter.

A total of 118 sparring bouts were recorded, which covered 63 observation sessions and a total of 226.04 observation hours on 11 male giraffes. When followed, the mean hours of observation per male per day was 3.43 ± 0.06 h. All classes of individual were observed for a similar length of time when present in the group (class A, 3.45 ± 0.09 h; class B, 3.40 ± 0.10 h; class C: 3.47 ± 0.15 h). Thus, the opportunity to observe sparring bouts was uniform across the classes. Sparring bouts were observed in both mixed-sex herds and all-male herds, and in no cases were females observed sparring.

2.3 | Data analysis and statistics

We investigated the social and environmental factors associated with the frequency, duration and the intensity of sparring bouts. Frequency refers to the total number of sparring bouts observed at the level of the individual, the dyad or the group (aggregated observations of all individuals in a group on any given day). Duration refers to the total length of each bout, and intensity refers to the total number of blows delivered per bout.

Three analyses examined the frequency of sparring bouts. First, we tested whether class B bulls—those a priori predicted to engage in sparring most often—differed in their sparring frequency compared with class A and class C bulls, using a Wilcoxon signed-rank test (two-sided, α = .05), where the number of sparring bouts that

each individual was involved in, corrected for the total observation time for each male, was aggregated across the study period. Second, we tested whether the number of sparring bouts between males was related to the rank size difference between them. To do so, we employed a permutation test (Manly, 2007), which allowed us to control for the fact that a higher frequency of sparring among closely ranked individuals can be expected on the basis of chance alone, because there is a greater possible combination of closely ranked dyads (i.e. rank difference of 1 or 2) than distantly ranked dyads (i.e. rank difference of 10). We took the observed mean difference in size rank between sparring individuals across all bouts (2.71 units) and compared this value to the distribution of mean differences in size rank generated under the null hypothesis that sparring was unrelated to contrasts in size. To generate our null distribution, we fixed the initiator of each sparring bout and randomised the recipient to be any other male present at the time (on the given day). We fixed the initiator, because we anticipated that different individuals might be more or less willing or motivated to initiate sparring. Our procedure therefore provides a more conservative test of assortativity (the strength of association between phenotypically similar or dissimilar individuals) than a randomisation procedure in which both members of the dyad are picked at random. The randomised distribution was generated from 10,000 permutations of the data, and significance was calculated as the proportion of randomised values that were equal to or larger than the empirical mean (subsequent permutation tests also used the same number of iterations and test of significance). Third, we investigated the frequency of sparring bouts at the level of the group (*n* = 63 observation days), modelled using a generalised linear model (GLM) with negative binomial error. As covariates we considered the month of the year (November–May), the presence of the most dominant male, and the presence of any females, and a continuous variable noting the number of males in the group. An offset term for the [log] hours of observation per day was included so that the model estimated the hourly rate of sparring bouts on any given day.

To investigate variation in the duration and intensity of sparring encounters, we fitted generalised linear mixed effects models (GLMM). The duration and intensity of sparring encounters were only recorded from December 2016, so these analyses focussed on a reduced subset of 95 sparring bouts observed on 28 separate days. For both responses, a negative binomial distribution was specified. As fixed effects, the absolute rank size difference between individuals (1–10), and the total number of males at the group were included as continuous variables. The presence of the most dominant male and the presence of any females were included as categorical variables. Each model also specified a random effect of dyad to control for the non-independence of repeated sparring interactions between the same individuals. For the intensity model, the duration of the sparring encounter was included as a [log] offset term such that the model estimates the number of blows per minute.

Intervention behaviour was unevenly distributed across individuals with the dominant male A1 performing most of it. Using a permutation test, we examined whether the observed high engagement of the dominant male in interventions was significantly different

than what would be expected if interventions were spread equally among males. We randomly distributed the interventions between all males that were ever recorded doing them (*n* = 5) and used the resulting should be permuted distributions to obtain the probability of the observed number of the dominant male interventions under the null assumption of equal intervention conduct.

Lastly, we quantified individual laterality in sparring—the propensity for individuals to repeatedly use one side of their body when engaging in sparring bouts. Using a permutation test, we tested whether individual preferences were significantly more consistent than could be expected by chance. For each individual, we calculated the absolute difference between its proportion of spars to the right and the expected proportion under no side preference, .5 (we could just as well have chosen sparring to the left instead). We then averaged this value among the sparring males (*n* = 10 males) and examined the probability of obtaining this observed deviation from a proportion of .5, or larger, by chance. For this, we randomly assigned a sparring side to each individual in every sparring event and re-calculated the average deviation from 0.5 (the resampled deviation).

Statistical analyses were performed in R 4.0.2 (R Core Team, 2020). Generalised linear models were fitted in the *glmmTMB* package (Brooks et al., 2017). In all models, continuous variables were centred around the mean, and inspection of the scaled model residuals indicated that assumptions of independence and normality of errors were met (Hartig, 2020). Summary statistics report the mean ± 1 standard error of the mean unless noted, and in-text model estimates are provided on the log-link scale.

3 | RESULTS

3.1 | The frequency of sparring bouts

The number of sparring bouts that male giraffes were engaged in varied widely across individuals (Figure 2). On average, males were observed in 21.45 ± 4.32 sparring bouts (median: 18, range: 0–40). This reflected an average sparring frequency of 0.20 ± 0.03 (median: 0.20, range: 0.00–0.36) events per observation hour. Across classes, Class B bulls sparred more frequently than category A and C bulls together (Wilcoxon signed-rank test, *W* = 24, *p* = .01). All males were involved in sparring except the most dominant male (A1), who was never seen sparring. After controlling for the number of males present, neither the presence of the dominant male (GLM estimate = −0.245 ± 0.249, *p* = .33) nor the presence of females (GLM estimate = 0.627 ± 0.397, *p* = .11) affected the frequency of sparring at the group-level.

Sparring was also more likely to take place between individuals that were more evenly matched in size (Figure 3). Permutation tests revealed that this effect exceeded that which could be expected by chance alone (Figure 3b, test statistic (empirical mean rank difference) = 2.71, *p* < .001). By comparing the observed incidence of sparring in each rank-contrast class to the expected incidence if sparring occurred at random, it is apparent that the increased incidence of sparring between size-matched individuals was driven principally by
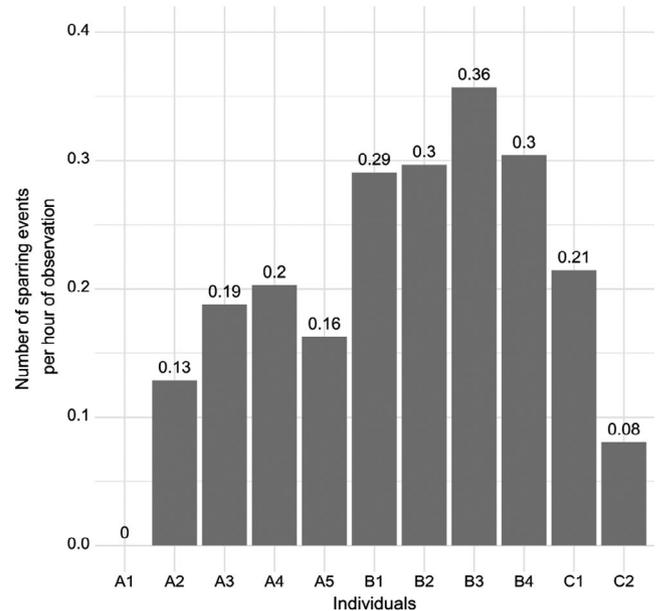

FIGURE 2 The rate of sparring bouts across individuals. Bars display the total number of sparring bouts undertaken per individual giraffe, corrected for observation time. Class A, B and C (see Section 2) correspond, respectively, to adult mature bulls, young adult bulls and subadult bulls. Individuals are ordered in descending body size (A1 being the tallest and most dominant individual). A Wilcoxon signed-rank test indicated that Class B males engaged in significantly higher levels of sparring bouts than Class A and C

individuals that differed in rank by three positions or less (74.5% of all sparring bouts).

Sparring activity peaked in December and occurred at a significantly higher frequency in this month than in all other months (Table S1: all pairwise contrasts *p* < .011). Visualisation of rainfall data and the normalised vegetation index for the Limpopo region across the 7 months of our study shows that this December increase coincided with the commencement of the rainy season (Figure 4) and the greening of the vegetation (Figure S2).

3.2 | The duration and intensity of sparring bouts

Sparring bouts lasted 12.15 ± 1.35 min on average (median: 7, range: 1–61) and had a mean intensity of 5.98 ± 0.36 blows/minute (median = 5.20, range = 0.80–16.33). There was a trend of increased duration with increasing class (class A mean = 18.40 ± 4.53 mins, median = 13, range = 1–61; class B mean = 11.42 ± 1.63 mins, median = 7, range = 1–61; class C mean = 6.20 ± 1.28 mins, median = 5.25, range = 1–29) and an associated decrease in intensity (class A mean = 3.45 ± 0.40 blows/min, median = 3.33, range = 0.8–9.33; class B mean = 6.44 ± 0.43 blows/min, median = 5.87, range 1.0–15.5; class C mean = 8.12 ± 1.38, median = 7.25, range 1.5–16.3), but both trends could not be examined statistically due to small sample size per class. When all bouts were considered, there was a negative correlation between the duration and the intensity of a sparring bout (*r* = −.252, df = 93, *p* = .014).
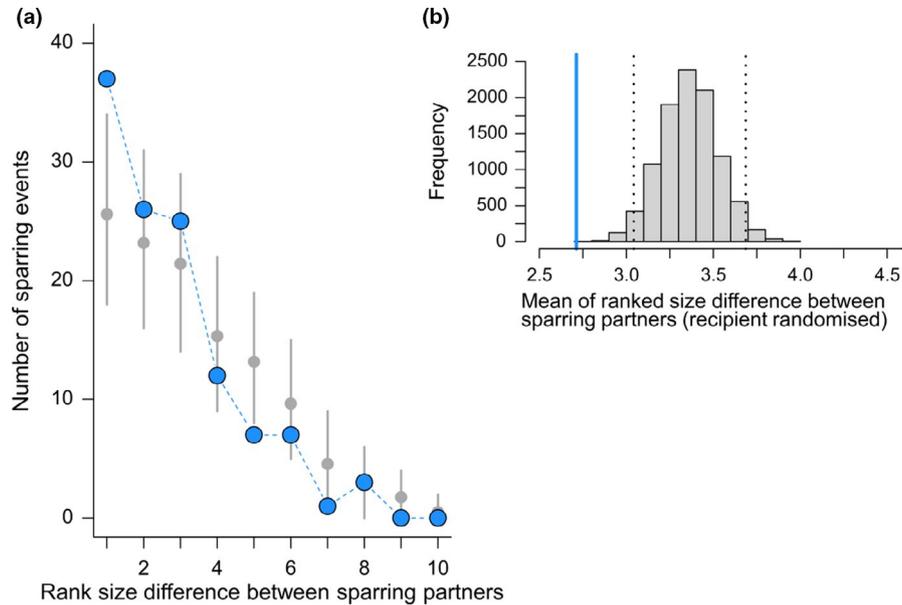
FIGURE 3 Size-assorted sparring bouts. (a) The frequency of sparring bouts in relation to the ranked size difference between sparring partners. Large points display the observed number of sparring bouts between ranked size classes. Small points display the expected number of sparring bouts between each ranked differences under the assumption that males in the population spar with one another at random (mean ± 95%CI); where the recipient of each sparring bout is randomised among other males present in the group (permutation test in main text, and (b)). (b) The distribution of mean rank differences between sparring partners under the assumptions of the permutation test. The observed mean of rank size differences (solid line) falls outside the lower 95% confidence interval (dotted line) of the randomised distribution (n = 10,000 permutations), illustrating that closely size-matched individuals are more likely to spar with one another than expected by chance.
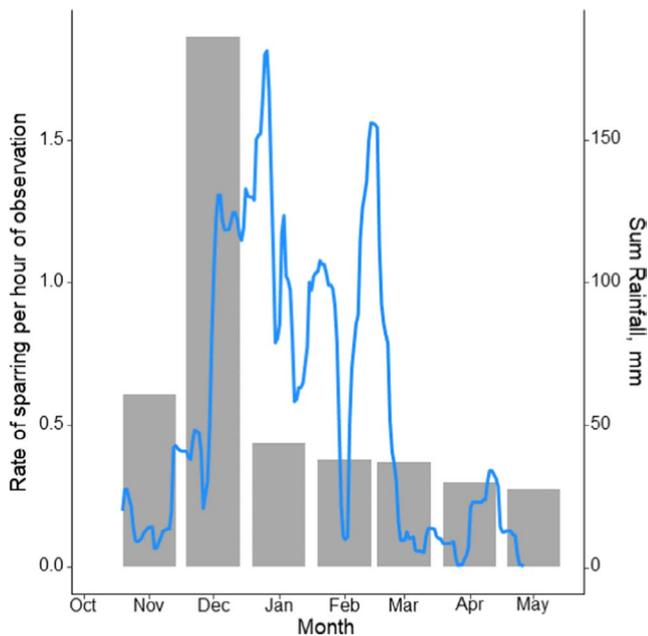

FIGURE 4 Seasonal variation in sparring bouts. Bars indicate the rate of observed sparring per month. The blue line indicates the seasonal pattern of daily rainfall (mm), plotted as a seven day moving average

The rank size difference between the two partners significantly affected both the duration (GLMM estimate = 0.156 ± 0.076, p = .041) and the intensity (GLMM estimate = −0.122 ± 0.041,

p = .003) of the sparring encounter. Greater mismatches in body size led to bouts that were longer, but of lower intensity. Refitting the models but by replacing the rank size difference term with a term for the dyad class (e.g. "BC" for sparring between a class B and class C bulls) showed differences in duration and intensity of sparring bouts across bulls classes (Supplementary material). The composition of groups did not significantly affect the duration or the intensity of sparring bouts (Tables S2 and S6).

3.3 | Intervention behaviour

Across the 118 sparring bouts observed, 27 interventions were recorded (22.9% of bouts). The dominant male, A1, was responsible for most interventions (44.4%), and the remaining intervention behaviours were spread among the next five largest males (A2 to B1 in Figure 1). When considering only those males seen to intervene at least once (n = 5), male A1 performed significantly more intervention behaviours than would be expected by chance (permutation test, test statistic = 0.44, p = .015).

3.4 | Laterality and sparring dynamics

Male giraffes universally favoured one side or another when delivering blows (Figure 5, permutation test, test statistic = .47, p < .001). Of the 10 males, six were "right-sided" and four were "left-sided."

In practice, when two males preferred the same side, a sparring bout took place in a head-to-tail orientation; otherwise, when two males preferred different sides, the sparring proceeded in a head-to-head orientation (Figure 1). The sparring orientation affected the intensity of an encounter, with bouts being of higher intensity when individuals were positioned in a head-to-tail orientation (GLMM estimate = 0.415 ± 0.144, p = .004).

4 | DISCUSSION

Our study provides new information on the dynamics of sparring in male giraffes. At the individual level, sparring was most often observed between young adults, and between individuals that were evenly matched in size. The size difference between two partners also affected the duration and the intensity of the sparring encounter, with shorter and more intense bouts between closely size-matched individuals. More generally, a negative correlation existed between the duration and the intensity of encounters that was suggestive of a possible a trade-off between these two axes of sparring. The most dominant bull (A1) was never seen sparring and was responsible for most of the third-party interventions. We also revealed, for the first time, that giraffes display strong individual lateralisation in their sparring bouts, which dictated the orientation in which a bout took place.

Alongside our results, various studies have converged on the finding that sparring occurs most frequently in subadult and young adult giraffes (Brand, 2007; Le Pendu et al., 2000; Leuthold, 1979). We also found that sparring occurred more frequently between individuals of similar size rank and that sparring bouts between individuals of closer rank were more intense. Similar results have been seen in pronghorn antelope *Antilocapra americana* (Miller & Byers,

1998), where the authors suggested that sparring with individuals of the same sex, age and skill will maximise the benefits of training and facilitate the formation of male hierarchies. We could not separate rank effects from age effects per se in our study (Appleby, 1983), but as individuals were ranked on the basis of body size, and body size is closely associated with age, it is highly probable that sparring bouts were assorted by age. Indeed, young male giraffes in other populations have been shown to prefer to associate with males of similar age and body size (Le Pendu et al., 2000; Leuthold, 1979; Pratt & Anderson, 1982, 1985; VanderWaal et al., 2014), which are likely to have similar social and ecological needs (Bercovitch & Berry, 2015). Taken together, these results provide support for sparring serving as a form of mutual assessment in male giraffes. Individuals may train key motor skills with peers (Bercovitch & Berry, 2015; Coe, 1967) and gain information about their competitive rank (Leuthold, 1979; Pratt & Anderson, 1982, 1985), without needing to escalate into more costly fighting behaviours.

Similar interpretations about the function of sparring behaviour have been suggested across ungulates, though it is worth noting that direct evidence for a role of sparring as training for future fights is currently absent. As noted by Smith (1976), the key test of this "fighting skills hypothesis" would be to show that high levels of sparring behaviour (or other forms of imitation fighting) during development are associated with increased fighting ability in adulthood and thus increased reproductive success. Acquiring such information from ungulates in either a field or a captive setting is extremely challenging and is presumably why no such studies have been performed. In giraffes, this task is made all the more difficult by the rarity of fighting behaviour among mature adults. Nevertheless, the fact that sparring uses behavioural patterns that are almost identical to fighting behaviour and that individuals spar most frequently with their closest ranked peers, from whom they are anticipated to gain the most information from an
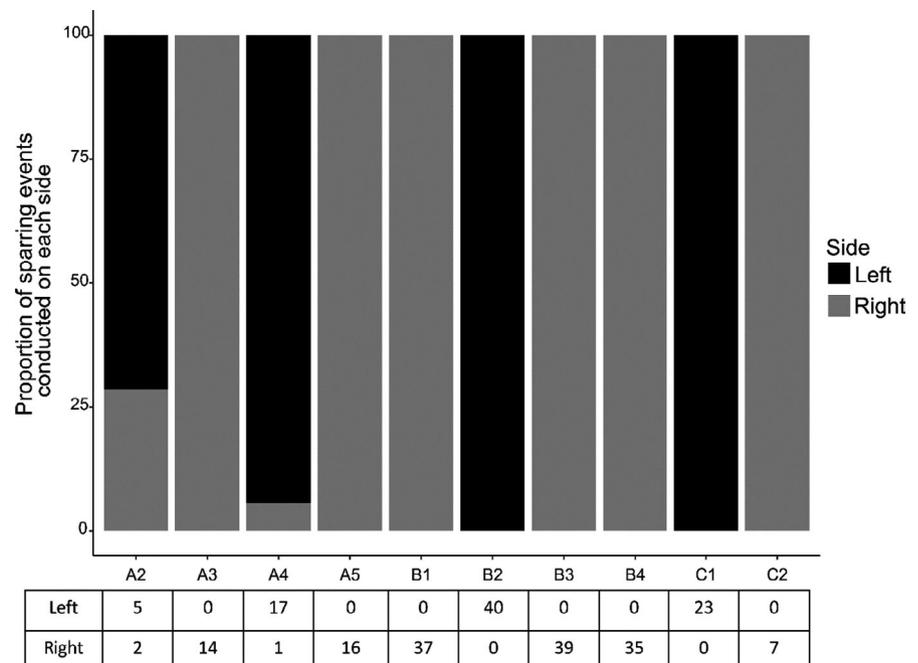

FIGURE 5 Individual lateralisation in sparring bouts, represented as the proportion of sparring bouts executed on either side by each individual. Note that individual A1 was excluded as he was never observed sparring. Class A, B and C (see Section 2) correspond, respectively, to adult mature bulls, young adult bulls and subadult bulls. Individuals are ordered in descending body size

	A2	A3	A4	A5	B1	B2	B3	B4	C1	C2
Left	5	0	17	0	0	40	0	0	23	0
Right	2	14	1	16	37	0	39	35	0	7

encounter, are probably indicative of the role of sparring as practise for fighting. It is also possible that the relative benefits of sparring change as individuals develop and face different social and physical needs and that this is reflected in the manner in which they spar (see further discussion of "class" effects in the supplementary material).

The negative correlation that we found between the duration and the intensity of sparring bouts may have several explanations. One possibility is that high intensity bouts are energetically demanding and are therefore curtailed earlier, because the individuals exhaust themselves quickly. Such physiological costs in animal contests are ubiquitous (Briffa & Sneddon, 2007), but in the context of sparring, the precise physiological costs have not been measured. Alternatively, being a highly ritualised behaviour (Coe, 1967), the negative correlation might reflect a behavioural mechanism that prevents higher intensity sparring bouts from developing into fights by ending such bouts earlier. Like Pratt and Anderson (Pratt & Anderson, 1985), in no instance did we see sparring bouts develop into a fight.

Sometimes sparring bouts between giraffes ended when another male intervened. In ungulates, intervention behaviour has mostly been described in the context of fighting. In fallow deer fights for example (Jennings et al., 2009, 2011, 2017), intervention behaviour was shown to be a way for higher-ranking males to stop any "winner effect" that could be gained by lower ranking males in fights with one another (dominance assurance) and to maintain uncertainty in the dominance relations between the two original opponents. The intervener was also likely to initiate a fight with one of the original contestants following the intervention (Jennings et al., 2009). Although, our study investigated intervention in sparring, and not fighting, there were clear parallels between our findings and those described in fallow deer. Intervention was performed mostly by class A bulls and targeted towards bouts involving class B bulls, and it was commonly observed that the intervener would try to spar with one of the original sparring partners after intervening. Fully mature class A bulls may therefore intervene in sparring bouts among class B bulls to stop the latter from establishing their place in the dominance hierarchy. In line with this argument, it was the most dominant male in our population—the individual that is likely to be most threatened by any winner effects—who instigated most of the observed interventions. Other possible reasons for third-party intervention have been proposed, mostly in primates, and typically involve either coalitionary support or putative group benefits of intervention, such as by stabilising group structure (Beisner & McCowan, 2013; Flack et al., 2006; Kulik et al., 2012). The relevance of such mechanisms in giraffes are currently unclear but are perhaps less likely than in primates where other forms of relationally complex behaviour have been well described (e.g. high rates of aggression, symmetry in grooming: Lukas & Clutton-Brock, 2018).

A seasonal peak in sparring was observed in December, which matches the first rainfall and the green-up of the vegetation. The onset of the wet season has been previously linked to an increase group size in some populations (Prehn et al., 2019; Seeber et al., 2013; Wolf, Ngonga Ngomo, et al., 2018), and an increase in conception in others (Brand, 2007; Hart et al., 2021). The fact that we saw increases in sparring in young adults in December might therefore have reflected heightened competition among males at this time driven by female receptivity. We did not find any effect of female presence on sparring rates. However, our population was small and likely contained some genetic structure, potentially reducing any importance of females in driving sparring behaviour. An effect of females on sparring dynamics might be apparent in larger, unbounded populations.

4.1 | Individual laterality

Motor lateralisation, or the preference to use one limb or side of the body, was initially thought to be unique to humans but has since been found to be common across the animal kingdom (Ströckens et al., 2013). Lateralisation is thought to provide various neural benefits, from increasing multi-tasking capacity to improving recognition abilities in visually orientated tasks (Dadda & Bisazza, 2006; Güntürkün et al., 2000). Our observations demonstrated strong lateralisation of sparring, with 60% of individuals solely using their right side when sparring, and 40% heavily favouring their left side. The few deviations from the preferred side were observed when mature males (A2 and A4) sparred with the youngest subadult male (C2) such that the large disparity in body size might have contributed to the discrepancies. A previous study by Svoke (2017) examined lateralisation in splay posture in male giraffes and showed a moderate tendency of individuals to place their left leg first when splaying to drink, though the three captive individuals in this study varied greatly in their degree of lateralisation.

Where suggested to be adaptive, lateralisation often also displays biases at the population level. Specifically, many vertebrates favour their left visual field to guide social recognition behaviours and to mediate defensive and aggressive behaviours (Ströckens et al., 2013). Such a right-sided bias in sparring was not apparent in our population, but whether present in giraffes in general warrants further study. Either way, individual laterality is presumably acquired early in a giraffe's life as in our population the youngest individual (C2, 1.5 years old) demonstrated clear laterality from his first sparring encounters. In juvenile giraffes, both sexes take part in sparring-like play behaviour, with awkward and disorganised necking, but only males continue to ritualised sparring into subadult and adulthood. By extension, individual lateralisation may already be revealed during juvenile play and thereafter be favoured by males throughout their life, first when sparring, and later when fighting as mature bulls.

Innis (1958) was the first to describe the two sparring partners to be placed either in a head-to-head or head-to-tail position (Figure 1). Coe (1967) suggested that the two positions differed in intensity and context, with the head-to-tail orientation having a greater intensity and a sexual connotation. Our data did support a greater intensity in the head-to-tail orientation, but the position adopted by a sparring pair was completely dictated by the lateral preferences of the interacting males. By extension, we suggest that there is no obvious sexual connotation of the head-to-tail position (Coe, 1967) and that the increased intensity is more likely a consequence of the nature of the position. Thus, the intrinsic side preferences of the sparring partners affect both the sparring posture and its intensity.

The social structure of giraffes has received growing attention in recent years and has been shown to be more complex than initially thought, with various environmental and social factors shaping grouping dynamics (Bond et al., 2020; Carter, Brand, et al., 2013; Carter, Seddon, et al., 2013; Muller et al., 2018; Prehn et al., 2019; VanderWaal et al., 2014; Wolf, Ngonga Ngomo, et al., 2018). Our results add to this research effort and highlight important trends and social preferences that shape sparring dynamics. While our findings originate from a limited number of sparring males in a moderately size fenced reserve, a large number of the world's giraffes are maintained in similar conditions. The generality of our conclusions in larger unbounded populations therefore remains unknown, but given that sparring appears to play an important role in mediating male social dynamics, any similarities or differences are likely to prove useful for ongoing management. Future research should focus on comparisons of sparring behaviour across populations with different social and environmental conditions and explore the consequences of sparring on subsequent fighting behaviour.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

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