Forage selection by Masai giraffes (*Giraffa camelopardalis tippelskirchi*) at multiple spatial scales

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Management of rangelands requires knowledge of forage species that are preferred or avoided by wildlife and livestock. A recent expansion of woody vegetation into previously open grasslands in African savanna ecosystems negatively impacts many mammalian grazers. Nevertheless, the ecological role of bush encroacher plant species as food may present a benefit for browsing species. We quantified diet selection by Masai giraffes (*Giraffa camelopardalis tippelskirchi*) through foraging observations and vegetation sampling in the Tarangire Ecosystem of Tanzania, which includes large areas of a native shrub that livestock managers have classified as an encroacher species (*Dichrostachys cinerea*). We compared woody plant species used by giraffes for foraging with availability at two different spatial scales during the wet and dry seasons. Giraffes selected some woody plants such as *Vachellia* species while significantly avoiding others, both at the local and landscape scales. Giraffes preferred foraging on *D. cinerea* at both spatial scales and in both the wet and dry seasons. Management that has focused on benefiting grazing livestock by removal of encroaching species (e.g., *D. cinerea*) may have unintended consequences for wildlife, especially for browsing species like giraffes that feed extensively on the expanding bush species.

Key words: browser, rangeland ecology, resource selection, savanna landscapes, Tanzania, woody vegetation

Understanding resource selection by animals has been a cornerstone of basic ecology and rangeland management for decades (Pellew 1983; Mahenya et al. 2016). Resource selection studies provide empirical evidence about feeding ecology and habitat suitability, which can inform species conservation (Pellew 1984a, 1984b; Arthur et al. 1996; Manly et al. 2002; Bryson-Morrison et al. 2017). Recent and rapid transformation of habitat by humans has led to increased concerns about proper management of rangelands (Belayneh and Tessema 2017; Birhane et al. 2017; Devine et al. 2017). In African savannas, this transformation is sometimes expressed as an expansion of woody vegetation into open grass-dominated lands, which holds the potential to alter ecosystem processes (Hudak and Wessman 1998; Van de Vijver et al. 1999; Ludwig 2001; Roques et al. 2001; Ludwig et al. 2008; Devine et al. 2017). Savannas support the highest densities of wild mammalian

herbivores of any biome (Grady and Hoffmann 2012; Shorrocks and Bates 2015), so understanding how herbivores select food resources is critical for maintaining ecosystem function and for conserving endangered species such as the Masai giraffe (*Giraffa camelopardalis tippelskirchi*).

The Masai giraffe is an endangered megaherbivore inhabiting savanna ecosystems of East Africa (Bolger et al. 2019). Abundance of Masai giraffes has declined 49–51% during the last three decades (Bolger et al. 2019), primarily because of habitat loss and degradation associated with human activities such as deforestation, livestock grazing, bush fires, and illegal hunting (Zarovali et al. 2007; Belayneh and Tessema 2017; Bolger et al. 2019). Forage species most commonly used by giraffes in East African savannas include *Vachellia* spp., *Commiphora* spp., and *Combretum* spp. (Pellew 1983, 1984b; Mahenya et al. 2016); however, encroaching woody

plants may serve as alternative forage for browsing giraffes. *Dichrostachys cinerea* is a native shrub that can form clonal mats in areas heavily impacted by domestic livestock grazing (Tjelele et al. 2014), and some land managers believe that a reduction of *D. cinerea* is needed to maintain grazing resources for wildlife and livestock (Njagi 2019). Studies have examined the response of grazing mammalian species to this shift from grass-dominated to woody-dominated vegetation dynamics (Dalle et al. 2006; Smit and Prins 2015), but little is known about how this shift might affect browsing species such as giraffes. We aimed to quantify forage selection by Masai giraffes in a human-influenced landscape with areas dominated by the encroaching woody species, *D. cinerea*.

Resource selection is defined as the ratio of proportional use over availability for a given plant species or taxa (Johnson 1980; Manly et al. 2002; Dumont et al. 2007). In theory, animals should select forage of the highest quality in order to meet their nutritional requirements (Pellew 1984a; Shipley 2007). Selection of forage resources occurs at different spatial scales, ranging from an entire geographic area (landscape) exploited by a species to the selection of forage within foraging patches (Johnson 1980; Johnson et al. 2002; Boyce 2006). Different spatial scales affect the proportions of available forage resources and, consequently, resource selection (Bissonetie et al. 1997). Thus, inferences made during resource selection studies and associated management decisions must account for the spatial scale of selection being considered (Johnson 1980; Wiens 1981; Orians and Wittenberger 1991; Manly et al. 2002). Using only one spatial scale of resource assessment, especially in heterogeneous landscapes, is potentially biased (Arthur et al. 1996) and may misinform rangeland management decisions (Wiens 1981; Kotliar and Wiens 2013).

We examined diet and forage selection at local and landscape scales by Masai giraffes in the Tarangire Ecosystem of northern Tanzania. We gave particular attention to the use of *D. cinerea* by giraffes because we were interested in determining if this bush species, which often is classified as an encroaching species, is an important forage species for giraffes. We posed six research questions: (i) What woody plant species do giraffes eat in the Tarangire Ecosystem? (ii) Is the use of forage species random or selective? (iii) If selective, which species are preferred or avoided? (iv) To what extent is *D. cinerea* an important component in giraffe diets? (v) Does forage selection of giraffes differ between the wet and the dry season? (vi) Does forage selection of giraffes differ between landscape and foraging patch spatial scales?

Giraffes live in a fission/fusion system, with herd sizes averaging four to six individuals but ranging upwards of 60 individuals (Bond et al. 2019). Giraffe herds can be single sex or mixed groups comprised of individuals feeding on an array of forage plants (Bercovitch and Berry 2013; Bond et al. 2019). We predicted that giraffes would be selective in their foraging, as demonstrated in previous studies in other ecosystems (e.g., Transvaal, South Africa: Sauer et al. 1977; Sahel, Niger: Caister et al. 2003; South Africa: Parker et al. 2003) and that foraging selection would change according to spatial scale (Bissonetie et al. 1997) and season (Sauer et al. 1977; Berry and Bercovitch

2016). We also predicted that giraffes would avoid browsing on *D. cinerea*, a shrub that is believed to be unpalatable to large mammalian herbivores. Lastly, we predicted that local-scale forage selection would be less visible than the selection at the landscape scale because, while foraging, giraffes would have already chosen to be in locations with their preferred food sources (Bissonetie et al. 1997; Anderson et al. 2005).

MATERIALS AND METHODS

Study area.—We conducted our study in the Tarangire Ecosystem, northern Tanzania (Fig. 1; between 35°80′, −3°80′ to 36°20′, −4.20′). The Tarangire Ecosystem receives a mean rainfall of 529 mm (Peterson 1978), distributed in two periods called short rains (October–January) and long rains (February–May) separated by a dry (June–September) season (Galanti et al. 2006). Its undulating plateaus are composed mainly of dark-red sandy clay loam, waterlogged areas, and floodplains of black cotton soils, with elevation varying between 900 and 1,200 m above sea level (Kahurananga and Silkiluwasha 1997; Galanti et al. 2006). Our study area in the Tarangire Ecosystem included a national park (Tarangire National Park) and rangelands outside the park (Manyara Ranch and Randilen Wildlife Management Area), where suitable giraffe habitat exists. The study area was predominantly savanna, comprised of open grasslands, woodlands, riverine forests, and shrublands, and falls in the semiarid zone, based on rangeland classification by Pratt et al. (1966). The study area represents one of the largest remaining refugia during the dry season for migratory ungulates in the country (Stoner et al. 2007; Bolger et al. 2008) as well as an important giraffe metapopulation (Lee and Bolger 2017). During the wet season, as food resources become abundant, wild herbivores were distributed widely across this human-influenced landscape (Newmark et al. 1994; Galanti et al. 2006; Msoffe et al. 2011).

Behavioral observations.—Foraging observations were collected during 15 days per month in March and April 2019 (wet season observations), and August and September 2019 (dry season observations). Each day, we drove in a car along the road network of our study area during daylight hours at a speed of 5–20 km/h, searching for giraffes. At an opportunistic encounter of a giraffe herd, we started 2-h observation records. During each 2-h observation period, we obtained foraging observations using instantaneous scan sampling (Martin and Bateson 1993). We conducted 5-min scans at 10-min intervals, using binoculars (10 × 50), with one observer and one data recorder. Foraging events were recorded from the left to the right-hand side of the group in a first seen–first recorded style within 5 min (Martin and Bateson 1993). In every scan, we identified and recorded each plant species eaten by each foraging giraffe within the group to assess general diet composition. Giraffes were followed as closely as possible without disturbing them, at a distance of 60–200 m. We considered a herd as the sampling unit, so we summarized individual foraging data during an observation period into proportional use by the entire herd (Fig. 1). The problem of group fusion was avoided by maintaining the original number of individuals that
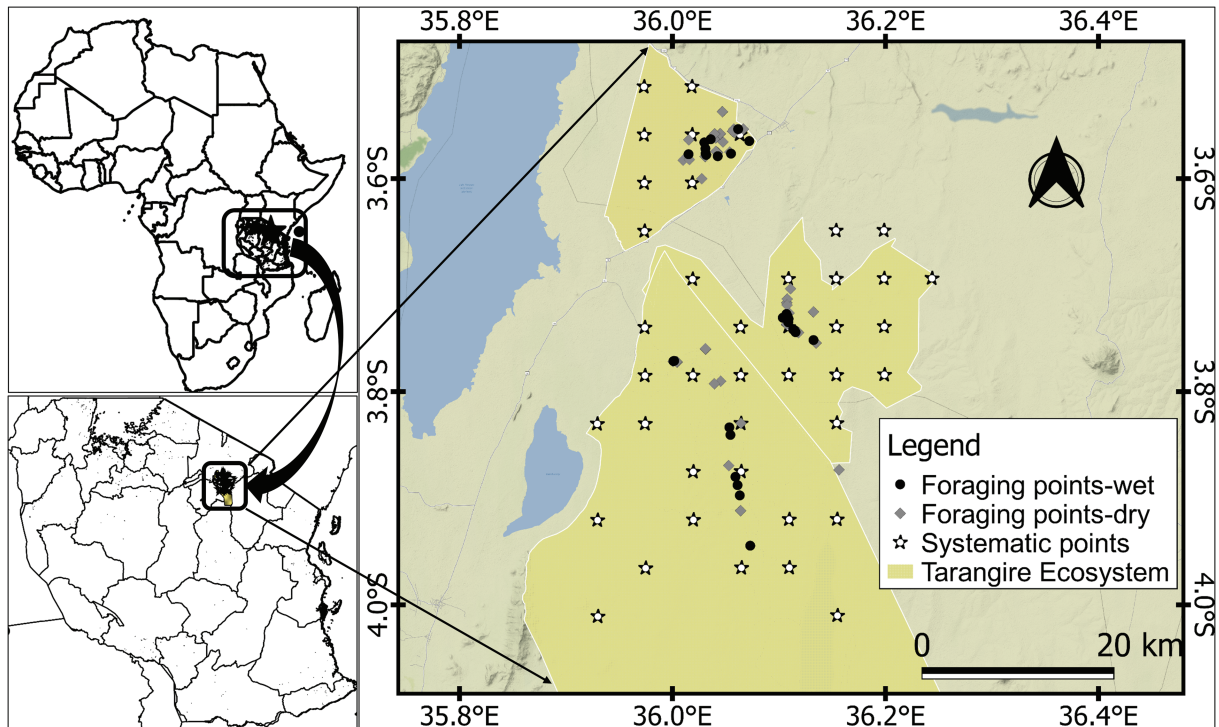
Fig. 1.—Map showing systematic vegetation point transects (black and white stars), where landscape-scale vegetation sampling was conducted, and the locations of Masai giraffe foraging observations, where local-scale vegetation sampling was conducted during the dry (gray squares) and the wet season (black filled circles) in the Tarangire Ecosystem, in 2019.

our scans had started with. In the case of group fission, we tried as much as possible to continue observing the same individuals and treating scattered individuals as a group. We ended observations when some members of the group were no longer within our vicinity. Observations of giraffes followed ASM guidelines (Sikes et al. 2016), and all work was permitted by the Tanzania Commission for Science and Technology (COSTECH) and the Tanzania Wildlife Research Institute (TAWIRI).

Forage availability.—We assessed availability of forage plant species at local (within foraging patches) and landscape (entire study area) scales. Woody plants were identified directly in the field by a botanist while unidentified woody plant specimens were pressed in a plant press, assigned a collection number (symbol), and recorded in a field notebook for further identification. At both scales, our assessment was aimed at capturing proportions of available species considering both used and nonused forage resources (Bissonetie et al. 1997). We collected data on available woody plants in March and April 2019 (wet season observations) and in August and September 2019 (dry season observations).

The local scale was intended to assess forage availability at a fine-scale of selection within areas where giraffes were observed foraging (Johnson 1980; Manly et al. 2002; Boyce 2006). To quantify the availability of woody plant species at local scale, we sampled vegetation plots along giraffe routes at patches where giraffes had been observed foraging, immediately after the foraging herd had moved on. In each foraging patch, we laid three circular plots of 10 m in diameter, 5 m away from each other. Within each circular plot (Banda et al. 2008; Chytry et al. 2013), we identified all woody species and determined the percent cover for each forage species.

To quantify forage availability at the landscape scale, we conducted systematic vegetation sampling within the area where giraffes had been seen regularly for the last 6 years (Lee and Bond 2016; Lee et al. 2016; Lee and Bolger 2017). We established 44 points systematically across the landscape using QGIS 2.18.12; all points were 5 km apart. At each point, we established four "strip transects" of 40 × 10 m to the North, East, South, and West (Lindgren and Sullivan 2001). Within each strip transect, we recorded the woody vegetation following the same three-circular-plot methodology as used for the local vegetation assessment.

Data analyses.—To understand which plants were selected by giraffes, we listed all woody plant species giraffes were observed to consume. Our selection analysis applied a chi-square test in combination with Bonferroni confidence intervals (*CIs*; Neu et al. 1974) for both local and landscape scales. To determine whether foraging was selective or random and if giraffe forage selection differed with regard to spatial scale and season, we included in our analysis those forage species with >5 forage observations (Manly et al. 2002). We used a chi-square test to compare observed foraging observations against the expected foraging observations (calculated based on proportions of forage availability).

To determine patterns of selection of forage at both spatial scales and across the seasons, we used Manly's selection ratio ($\hat{W}$) and Bonferroni *CIs* (Neu et al. 1974; Manly et al. 2002). Manly's selection ratios for each forage species were calculated based on proportions of the forage resource used versus its availability (Manly et al. 2002). To obtain proportions of forage used, P_o, for each foraged woody plant species, we

calculated the number of foraging observations in each consumed species divided by the total number of foraging observations for all consumed species across all giraffe herds. We computed local-scale proportional availability (local P_a) of all woody plant species for the foraging route taken by each herd using each species' average percent cover across the three circular plots. We obtained landscape-scale available proportions (landscape P_a) for each woody plant species by taking the average proportion of occurrence of all woody plant species from the systematic vegetation sampling. We determined preference or avoidance as $\hat{W}$ being greater or less than 1, respectively. Significance of selection for a given species was based on the CI of each $\hat{W}$: if the CI was >1, this was categorized as preferred, and if the CI was <1 the species was categorized as avoided, while no selection occurred if the CI of $\hat{W}$ included 1 (Manly et al. 2002). We used the generic name, *Vachellia*, in place of the former genus *Acacia* for Africa and Asia as agreed by the Nomenclature Session of the Seventeenth International Botanical Congress (IBC) in 2003 (Maslin 2008).

RESULTS

Diet composition and forage selection

The instantaneous scan sampling produced 3,728 foraging observations during 1,250 scans of 105 giraffe herds. In our vegetation sampling at the landscape scale (*n* = 44) and the local scale (*n* = 105), we identified 118 woody plant species. Giraffes consumed 38 of the 118 woody plant species that we identified, with 29 consumed in the wet and 33 in the dry season (Supplementary Data SD1 and SD2). The most-consumed plant species in both the wet and dry season were *Vachellia tortilis* (25%), *D. cinerea* (23%), *V. mellifera* (17%), *V. drepanolobium* (9%), *Balanites aegyptiaca* (7%), *V. kirkii* (4%), *Dalbergia melanoxylon* (4%), *Maerua triphylla* (2%), and *Ziziphus mucronata* (1%).

Giraffes foraged nonrandomly at both the local (x^2 = 1,068, d.f. = 30, P < 0.001) and landscape scales (x^2 = 1,670, d.f. = 29, P < 0.001). Giraffes preferred *V. tortilis*, *V. mellifera*, and *V. drepanolobium* consistently through the year (Fig. 2; Supplementary Data SD3 and SD4). In contrast to what we had predicted, giraffes exhibited a high and year-round preference for the native shrub *D. cinerea* at both local and landscape scales (Fig. 2; Supplementary Data SD3, SD4 and SD5). Giraffes also avoided some woody species such as *Kigelia africana*, *Commiphora schimperii*, *Commiphora africana*, *Adansonia digitata*, and *Euphorbia candelabrum* (Fig. 2; see Supplementary Data SD3 and SD4).

Local scale.—Giraffes were selective in foraging at the local spatial scale (x^2 = 1,068, d.f. = 30, P < 0.001), which was visible in both dry (x^2 = 709, d.f. = 28, P < 0.001) and wet seasons (x^2 = 501, d.f. = 21, P = 0.001). Giraffes demonstrated a strong preference toward *D. cinerea*, *V. tortilis*, *V. drepanolobium*, and *V. kirkii* at the local scale during the wet season, whereas during the dry season, *D. cinerea*, *V. mellifera*, *Strychnos potatorum*, and *Combretum zeyheri* were selected more frequently than their proportional availability (Fig. 2; Supplementary Data
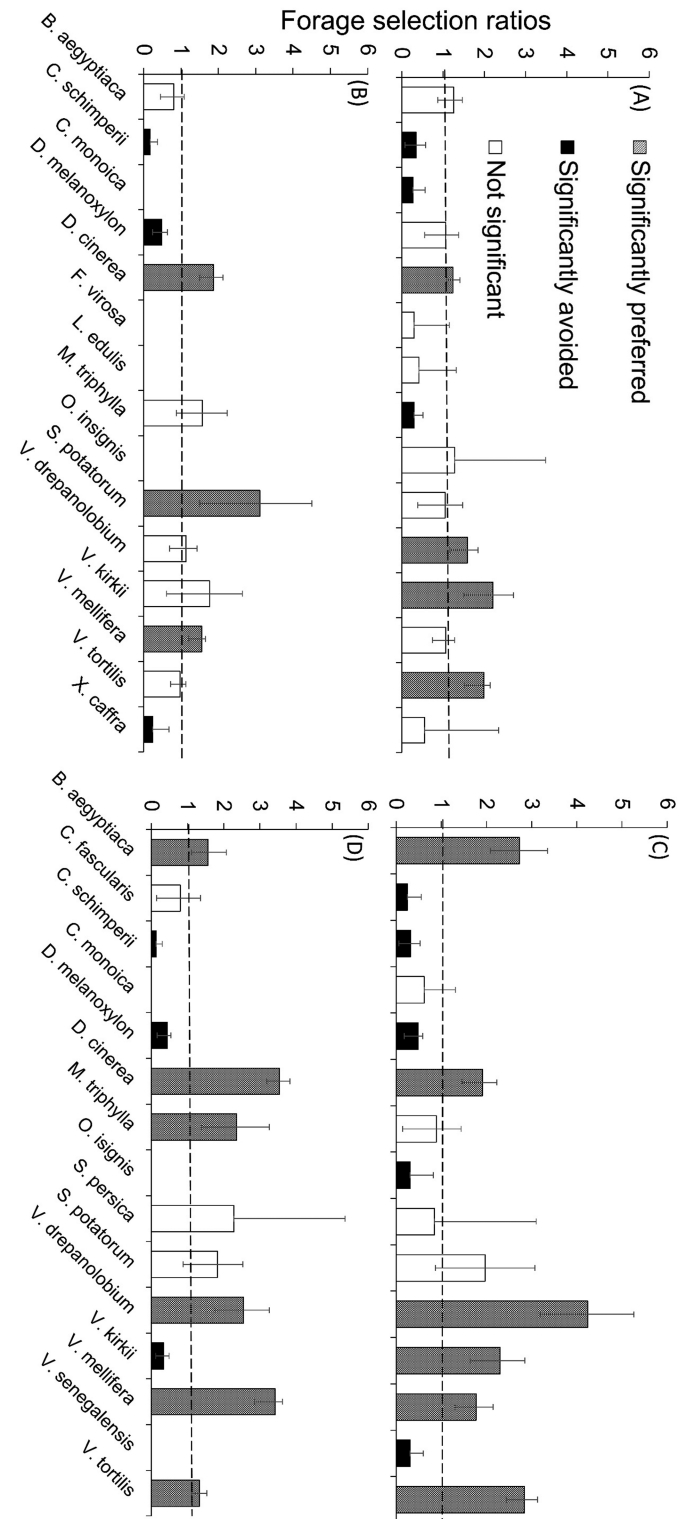
Fig. 2.—Local- (A and B) and landscape-scale (C and D) forage selection ratios and direction of forage selection indicated by confidence intervals ($\hat{W} \pm CIs$) for the 15 most frequently selected forage species by Masai giraffes during both the wet (A and C) and dry season (B and D) in the Tarangire Ecosystem, in 2019. Shaded bars = significantly preferred, black bars = significantly avoided, and open bars = not preferred/avoided. The black dotted line (x-axis) indicates the threshold for forage selectivity. The selection coefficient is significant if the CI for $\hat{W}$ does not contain the value 1.

SD3). Giraffes used *B. aegyptiaca*, *Carrisa spinorum*, *Scolopia zeyheri*, and *Z. mucronata* in proportion with their availability, but avoided *A. digitata*, *Capparis fascularis*, *Cordia monoica*, *C. schimperii*, *E. candelabrum*, *K. africana*, *Lanchocarpus eriocalyx*, *V. nilotica*, and *V. senegal* in both the wet and dry seasons at the local scale (Fig. 2; Supplementary Data SD3).

Landscape scale.—Giraffes also foraged selectively at the landscape scale ($x^2 = 1,670$, d.f. = 29, $P < 0.001$), during both the dry ($x^2 = 1,495$, d.f. = 29, $P < 0.0001$) and wet ($x^2 = 856$, d.f. = 29, $P < 0.0001$) seasons. At the landscape scale, *B. aegyptiaca*, *D. cinerea*, *V. drepanolobium*, *V. mellifera*, and *V. tortilis* were the most strongly favored forage species throughout the year. During the wet season, *B. aegyptiaca*, *D. cinerea*, *V. drepanolobium*, *V. mellifera*, *V. tortilis*, and *V. kirkii* were preferred, whereas in the dry season, giraffe preferred foraging on *B. aegyptiaca*, *D. cinerea*, *Ficus natalensis*, *M. triphylla*, *V. drepanolobium*, *V. mellifera*, and *V. tortilis* relative to availability on the landscape (see Fig. 2 and Supplementary Data SD4).

DISCUSSION

The diet of Masai giraffes in the Tarangire Ecosystem consisted of a variety of woody plant species and confirmed previous studies in other regions (Pellew 1984b; Parker and Bernard 2005; Dagg 2014; Berry and Bercovitch 2016) that giraffes will forage on many plant species but concentrate on a narrow range of forage options, most notably *Vachellia* species. For example, in the Serengeti National Park, five forage species accounted for about 70% of the giraffe's diet (Pellew 1984b). Parker and Bernard (2005) assessed the giraffe diet in the Eastern Cape Province of South Africa, where 46 forage species were consumed, but *Vachellia karroo* and *Rhus longispina* comprised 60% of the total diet. In a recent study by Mahenya et al. (2016) in Arusha National Park in Tanzania, the giraffes' diet was 90% composed of *V. xanthophloea*. Similarly, in our study in Tarangire Ecosystem, *D. cinerea* and *Vachellia* species contributed about 65% of the overall giraffe diet. Selection for *D. cinerea* and *Vachellia* species was likely due to the high nutritional value and digestibility of these woody plant species (Sauer 1983; Pellew 1984a). Giraffes also demonstrated strong avoidance of some woody species such as *K. africana* and *A. digitata*, likely because of their poor digestibility (Woodward and Coppock 1995; Proll et al. 2018).

We detected seasonal differences in forage selection by Masai giraffes for particular plant species at both the local and landscape scale, probably because of a decrease in forage plant availability during the dry season compared to the wet season (Beyer and Haufler 1994; Whittingham et al. 2005; Boyce 2006). Masai giraffes appear to demonstrate seasonal forage use toward a few species to guarantee sufficient amount and nutrient content of food (Sauer et al. 1977; Sauer 1983; Pellew 1984b; Parker et al. 2003). Most deciduous woody plants such as *C. zeyheri*, *D. cinerea*, *V. kirkii*, *V. mellifera*, and *V. tortilis* contributed strongly to giraffe diet during the wet season, but some became less important in the dry season, in agreement with similar studies (Sauer 1983; Pellew 1984b).

Giraffe foraging preferences in the Tarangire Ecosystem switched to semideciduous plants during the dry season, most notably *Combretum* species, which retain their leaves and protein content as the dry season progresses (Sauer 1983). Our results are in line with those of Sauer (1983) that the selection of *Vachellia* species often declines in the dry season because of a decrease in protein and water content, while *Combretum* species lose their proteins more slowly, making them a suitable forage source for longer into the dry season. This result likely explains why giraffe groups in the Tarangire Ecosystem were larger in stands of *Combretum* during the dry compared with the long rainy season (Bond et al. 2019).

Our results did not support our prediction that local-scale forage selectivity would be expressed less strongly than at the landscape scale. However, giraffe forage preferences were sensitive to spatial scale changes (Bissonetie et al. 1997; Anderson et al. 2005). For example, *Combretum zheyeri* was preferred on a local scale during the dry season but became less important when the resource availability scale enlarged to the landscape level. The shift of forage preference as spatial scale increases is presumably associated with aggregates of habitat units within a heterogeneous landscape, which in turn affects estimates of resource availability (Li and Reynolds 1993; Bissonetie et al. 1997), and consequently, resource selection decisions. Nevertheless, giraffes at the landscape scale exhibited similar foraging selection patterns, with only two more forage species preferred at least once across the season, compared to the local scale. The detected slight differences in forage selection patterns may be attributed to giraffes' relatively limited seasonal migrations in savanna landscapes (Pellew 1984b), making only a portion of forage options accessible to giraffes. The multispatial scaled analyses for forage-procuring strategies that were used in this study provide a reliable means of comparing use versus available estimates at local and landscape scales of selection (Bissonetie et al. 1997; Mysterud et al. 1999; Anderson et al. 2005; Fortin et al. 2005; Boyce 2006; Kotliar and Wiens 2013), which eventually leads to judicious management decisions (Andren 1994; Johnson et al. 2002).

Our observed high and year-round preference for the native shrub *D. cinerea* at both local and landscape scales might be linked to *D. cinerea*'s high nutritional quality (Pellew 1984b; Mlambo et al. 2004; Smith et al. 2005; Dagg 2014; Tjelele et al. 2014) despite the belief that this plant is unpalatable. Further, *D. cinerea*'s gradual loss of leaves followed by quick recovery upon the onset of the wet season (Sauer 1983) might ensure that giraffes receive a constant supply of this food resource throughout the year. Hence, despite the negative attitudes of livestock managers toward *D. cinerea* in a rangeland ecosystem, this plant species might be contributing significantly to the quality and quantity of food for the full suite of savanna browsers (Reyes et al. 2010; Liu et al. 2015).

Conservation implications.—Giraffes in the Tarangire Ecosystem selected a broad array of woody plant species from which some were preferred, while others were avoided. Forage selection in giraffes was influenced primarily by spatial and temporal changes in the quantities and, presumably, qualities of forage species at both local and landscape scales. Giraffes also

showed a strong preference for the native shrub *D. cinerea* at both local and landscape scales. *Dichrostachys cinerea* is a fast-growing nutritive shrub, well adapted in the study area, palatable to giraffes, and resistant to strong browsing pressure, providing giraffe with a constant supply of this food resource throughout the year. The removal of this species for the purpose of maintaining grazing lawns for livestock might negatively impact browsing wildlife. Therefore, management that is focused on benefiting grazing livestock by removal of encroaching woody plant species may have unintended consequences to browsing species such as giraffes that feed extensively on these food resources.

ACKNOWLEDGMENTS

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Woody plant species consumed by Masai giraffes (*Giraffa camelopardalis tippelskirchi*) in the Tarangire Ecosystem of Tanzania in 2019, and their relative proportions in the diet (P_o) over the entire year and split up into the dry and wet season based on direct foraging observations (*n* = 3,728) during scan sampling.

Supplementary Data SD2.—Woody plant species encountered in vegetation sampling in 2019 in Tarangire Ecosystem, Tanzania.

Supplementary Data SD3.—Masai giraffe (*Giraffa camelopardalis tippelskirchi*) local-scale forage selection ratios ($\hat{W}$), and their Bonferroni confidence intervals (*CIs* $\hat{W}$), and *P*-values for seasonal selection differences for 38 woody plant species in the Tarangire Ecosystem, 2019.

Supplementary Data SD4.—Masai giraffe (*Giraffa camelopardalis tippelskirchi*) landscape-scale forage selection ratios ($\hat{W}$), their Bonferroni confidence intervals (*CIs* $\hat{W}$), and seasonal selection differences for 38 woody plant species in the Tarangire Ecosystem, 2019.

Supplementary Data SD5.—Masai giraffe feeding on *Dichrostachys cinerea* in Tarangire National Park in 2019.

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