



Using spot pattern recognition to examine population biology, evolutionary ecology, sociality, and movements of giraffes: a 70-year retrospective

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Abstract

Individual-based studies where animals are monitored through space and time enable explorations of ecology, demography, evolutionary biology, movements, and behavior. Here, we review 70 years of research on an endangered African herbivore, the giraffe, based on individual spot pattern recognition, and profile an example of a long-term photographic mark–recapture study of Masai giraffes in Tanzania. We illustrate how individual-based data can be used to examine the fitness consequences (variation in survival and reproduction) of extrinsic environmental factors or intrinsic traits in an evolutionary ecology framework. These data also allow the study of social structure, space use, life histories, and health. The giraffe offers an excellent opportunity to study dynamics of an ungulate species with a highly fission–fusion social system using spot pattern recognition.

Keywords *Giraffa camelopardalis* · Photographic capture–mark–recapture · Demography · Social network analysis · Long-term ecological research · Individual recognition

Introduction

The ability to recognize individuals through space and time is extremely valuable in studies of wildlife populations, enabling detailed explorations of ecology (Durant et al. 2004), demography (Lee et al. 2016a), evolutionary biology (Ozgul et al. 2010), and behavior (Goodall 1986). Individual-based studies also inform conservation biology

by identifying factors critical to population recovery and by evaluating management or conservation strategies (Coltman et al. 2003; Lee 2018). For many species, natural characteristics have been discovered that are stable through time within individuals, yet variable among individuals, providing reliable markers for identifications (e.g., Foster 1966; Karanth 1995). Natural marks are superior to artificial marks in many ways (Walker et al. 2012), primarily because natural marks enable identification without the dangerous and invasive act of physically capturing and affixing an identifier to animals (Cuthill 1991; Daly et al. 1992; Mowat et al. 1994), and because natural marks cannot be lost so the resultant data are not biased by tag loss (McDonald et al. 2003).

Using marks that do not affect the behavior or survival of the study animals and do not violate any of the critical fundamental assumptions of capture–mark–recapture statistics creates ideal conditions for longitudinal socio-ecological studies of demography, evolutionary ecology, and behavior. Examples of such studies are profiled in this Special Issue (Karczmarski et al. 2022a, b). Cost-effective methods such as photographic mark–recapture that enable large sample sizes and produce precise population parameters and behavioral measurements are extremely useful for facilitating a deeper understanding of processes that drive

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population dynamics (Nichols 1992; Yoccoz et al. 2001; Williams et al. 2002; Peters 2010; Contasti et al. 2013; Lee 2018) and sociality (Whitehead 2008; Croft et al. 2011). Here, we present a review of research on population biology, social structure, movements, and evolutionary ecology of a uniquely marked mammal—the giraffe (*Giraffa camelopardalis*)—using individual identification in free-ranging populations. We profile the Masai Giraffe (*G. c. tippelskirchi*¹) Project in northern Tanzania, a long-term study collecting photographic mark–recapture data from active encounter surveys,² as a model study design for examining many ecological and social questions. We also describe all studies to date that used individual identification of wild giraffes to better understand the life history, health, and habitat requirements of this endangered megaherbivore (Table S1).

Giraffes are endemic African ruminant ungulates, and one of only a few extant terrestrial megaherbivore species, defined as animals reaching more than 1000 kg in mass (Owen-Smith 1988). Giraffes are individually identifiable from their unique and unchanging coat patterns (Foster 1966). Scientists have used the giraffe's unique spot patterns to recognize individuals since the 1950s, but the advancement of two technologies—digital photography and pattern-recognition software—has facilitated analyses of unprecedented large sample sizes and greatly advanced scientific knowledge of the species' demography, movements, sociality, and their interactions (Fig. 1; Table S1).

Giraffes serve as an informative window into savanna ecosystem processes because the species interacts with and responds to many of the factors that have been hypothesized to drive population dynamics and sociality in other ungulate species such as seasonal and spatial changes in vegetation, predators, and poaching (Strauss et al. 2015; Lee et al. 2016b; Muller 2018). Although the vast majority of the world's ungulate species live in the tropics and sub-tropics, most studies of ungulates have taken place in the temperate zone, often in single populations with little or no predation (Gaillard et al. 2000), and few studies have investigated the demography of large tropical herbivores (Owen-Smith and Marshall 2010). Giraffes provide a tropical or subtropical, asynchronously breeding case study with

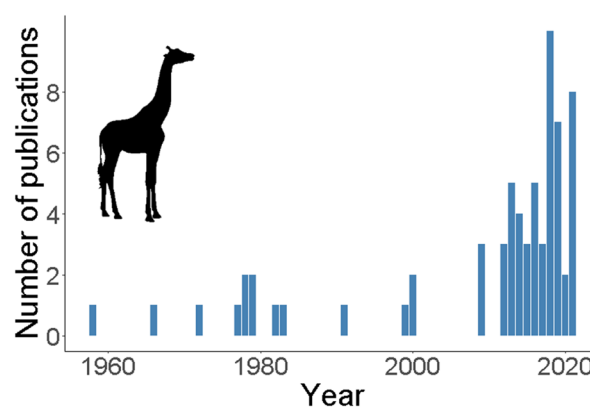


Fig. 1 Number of publications about giraffes (*Giraffa camelopardalis*) by year that used spot patterns to identify individuals, from 1958 to 2021

which to test findings from temperate ungulate ecology studies (Lee et al. 2016a, 2017). Furthermore, given the giraffe's fission–fusion social system, which is typical of many ungulate species (Whitehead and Dufault 1999), and its tendency to range widely in temporally and spatially heterogeneous environments (Knüsel et al. 2019), studies of giraffes can improve our general understanding of environmental and anthropogenic influences on grouping behavior and social structure as related to the costs and benefits of sociality.

Study species

Giraffes are long-lived (approximately 25–28 years; Dagg and Foster 1976; Dagg 2014) and slow breeding. Females in the wild become sexually mature at a mean of 4.8 years of age (Bercovitch and Berry 2009) and mean gestation period is 14.7 months (del Castillo et al. 2005), thus they bear their first offspring at ~6 years of age, with a mean subsequent interbirth interval of 20 months (Lee and Strauss 2016). Females reproduce throughout the year, with estrous cycling approximately every 15 days, and can become pregnant while still nursing their previous offspring (Dagg and Foster 1976; Bercovitch et al. 2006; Dagg 2014; Lee et al. 2017). Female giraffes in estrous are dispersed over space and time, so reproductive adult males adopt a strategy of roaming among female groups to seek mating opportunities, with periodic hormone-induced rutting behavior that appears to occur approximately every 2 weeks (Seeber et al. 2013), a temporal scale that would overlap with local cycling females (Pratt and Anderson 1985; Bercovitch et al. 2006).

The giraffe's primary natural predators are African lions (*Panthera leo*), leopards (*Panthera pardus*), and spotted hyenas (*Crocuta crocuta*) (Dagg and Foster 1976; Dagg 2014). Predation is an important limiting factor for juvenile survival (Strauss et al. 2015; Lee et al. 2016a; Muller 2018) but only

¹ The IUCN SSC Giraffe and Okapi Specialist Group (GOSG) currently recognizes a single species, *Giraffa camelopardalis*, and nine subspecies. Genetic analyses have indicated three (Petzold and Hasnanin 2020; Petzold et al. 2020), four (Fennessey et al. 2016; Coimbra et al. 2021), and six (Brown et al. 2007) species of giraffes and the GOSG suggests that a taxonomic reassessment might be in order. To avoid confusion, here we continue to use the currently recognized subspecies as presented on the IUCN Red List: <https://www.iucnredlist.org/species/9194/136266699#taxonomy>.

² Active encounter surveys actively seek individuals as opposed to passively collecting data from box traps, camera traps, acoustic sensors, etc.

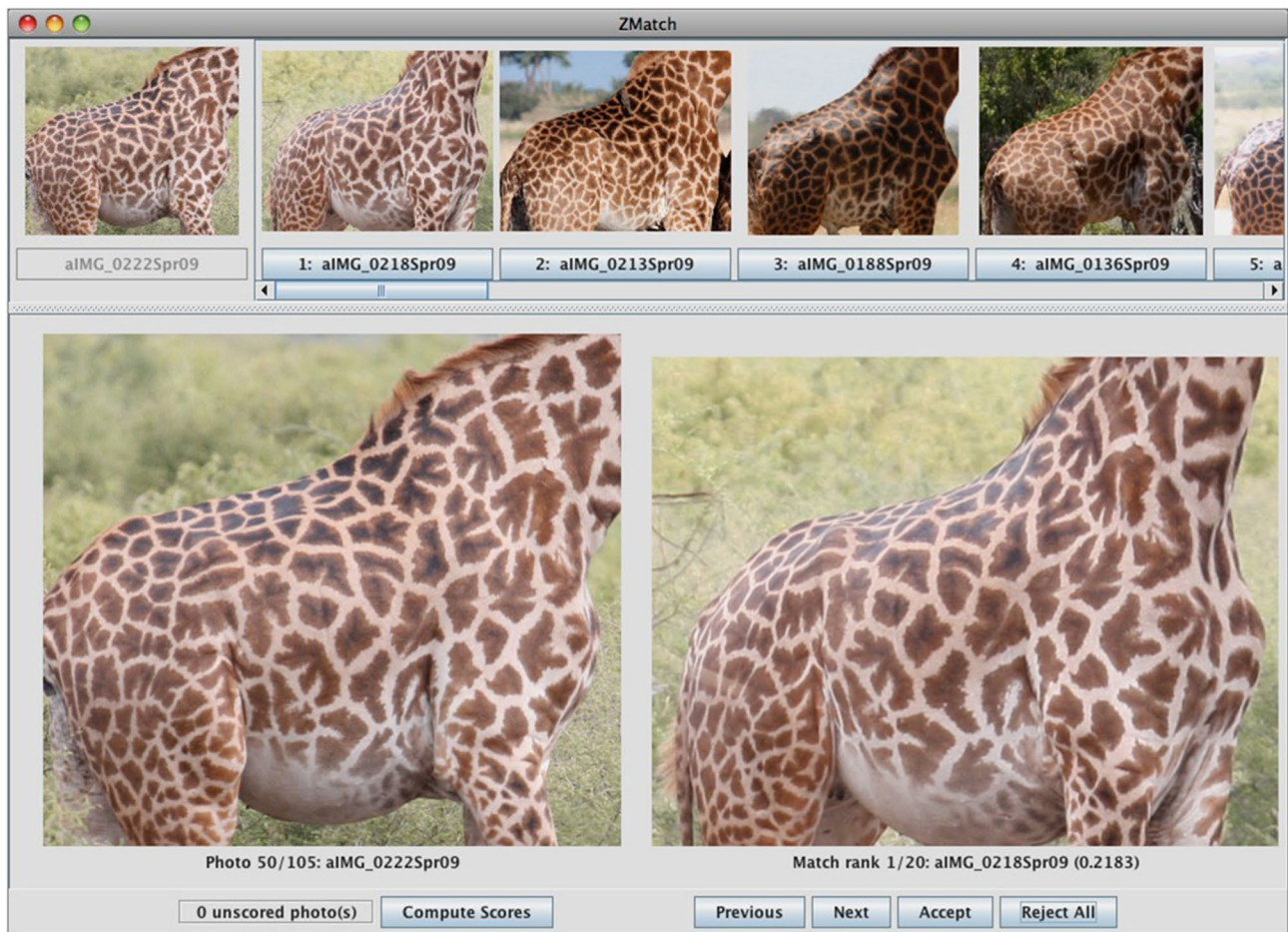


Fig. 2 Screenshot of Masai giraffe (*Giraffa camelopardalis tippelskirchi*) images collected in the Tarangire Ecosystem, Tanzania, from the WildID pattern-matching program

a minor source of adult giraffe mortality (Schaller 1972; Strauss and Packer 2013). However, adult giraffes in many regions of Africa are poached by humans for meat and products such as hide, bones, and tail hairs (Muller et al. 2018a).

The social structure of giraffes is described as a fission–fusion process wherein group composition and size changes frequently over the course of a day but is structured due to non-random aggregate social associations between adult females that likely reflect kinship (Bercovitch and Berry 2012; Carter et al. 2013a, b).

Pattern identification methods

The technique of studying wild giraffes by recognizing individuals from their unique and unchanging spot patterns was pioneered in the 1960s by Bristol Foster (Foster 1966). In early studies, researchers identified animals by eye in the field, using either photographs (Foster 1966; Foster and Dagg 1972; Leuthold and Leuthold 1978; Pellew 1983; Young and Isbell 1991; Le Pendu and Ciofolo 1999;

Bercovitch and Berry 2009) or hand-drawings of spot patterns (Pratt and Anderson 1979, 1982; van der Jeugd and Prins 2000). Shorrocks and Croft (2009) moved a step beyond matching patterns by eye in the field by creating a ‘neck code’ according to the angle that the neck spots made with the mane of reticulated giraffes (*G. c. reticulata*), and then using the neck code to search a spreadsheet. Shortly thereafter, matching of patterns in photographs was fully automated by Bolger et al. (2012), who developed an open-source application implemented in Java that matches patterns from digital images, called WildID (http://software.dartmouth.edu/Macintosh/Academic/Wild-ID_1.0.0.zip) (Fig. 2). A test of the program showed it matched large datasets of giraffe images with low error rates—the first use of pattern-matching computer software for giraffes. WildID has subsequently been used in applied research to analyze social networks of large numbers of individual Angolan giraffes (*G. c. angolensis*) in Namibia (Carter et al. 2013a, b), to study demography of Masai giraffes in Tanzania (Serengeti Ecosystem: Strauss et al. 2015 and Tarangire Ecosystem:

Lee et al. 2016a, b; Lee et al. 2017), and to quantify individual movements and population structure of Rothschild's giraffes (*G. c. rothschildi*) in Uganda (Brown et al. 2019; Brown and Bolger 2020).

Photographic identification of uniquely marked animals of all kinds is now a well-developed field with many computer vision applications available to identify pelage patterns (Kelly 2001; Foster et al. 2007), whisker spots (Pennycuik and Rudnai 1970; Anderson et al. 2010; Osterrieder et al. 2015), or other features (Whitehead 1990; Arzoumanian et al. 2005). The use of pattern-matching software programs like WildID and HotSpotter (Crall et al. 2013) has become the norm for giraffe field studies. Each software has its own strengths and weaknesses relative to other programs, and we recommend that every project conduct their own testing and verification of image matching software programs to determine error rates and workflow efficiency (Kelly 2001; Bolger et al. 2012; Morrison et al. 2016a; Matthé et al. 2017).

Most photo-ID procedures require multiple image processing steps before computer vision applications can be applied to identify and match images of individuals. Wild Nature Institute and Microsoft AI for Earth developed an automated procedure to efficiently crop photos to the giraffe torso (Buehler et al. 2019), an area of interest for individual identification and matching. This automated procedure removed a time-consuming step in the workflow when > 1000 giraffe photographs are obtained on each survey DE Lee, pers observation.

To quantify how pattern recognition has contributed to the study of giraffes, we informally searched the literature for published research articles that used spot pattern recognition to monitor individuals, and grouped the articles into four broad categories: demography and populations; sociality and behavior; large-scale movements; and other. The 67 publications, their focus of research, sample size of individually recognized individuals, study duration, subspecies, and locations of the study areas are presented in Table S1. This sample represents the overwhelming majority of available publications and offers insights into the types of questions that can be answered using spot pattern-recognition techniques. The study of giraffes using individual identification has surged in recent years, as evidenced in Fig. 1, likely due to the ease of finding giraffes in the field, the tractability of matching giraffe patterns using digital photography and freely available software, and the increased attention on conservation of giraffes as their populations decline.

Individual-based studies of wildlife populations can reveal links among the environment, sociality, and demography, but require long-term, large-scale data collection that includes contrasting environmental and social conditions (Clutton-Brock and Sheldon 2010). Below we profile an example of a long-term photographic mark–recapture study of giraffes—the Masai Giraffe Project—initiated by

the authors, including field collection techniques and data analysis methodologies. We then discuss some of the main giraffe-focused research questions from the literature and synthesize findings from key studies in the four broad categories (Table S1), to demonstrate the myriad investigations based on individual identification that have substantially enhanced our understanding of social–ecological influences on demography and behavior. Finally, we present an example of using research results to guide giraffe conservation efforts (Table 1) and we highlight the benefits and challenges of collecting individual identification data versus other approaches such as count data.

Masai Giraffe Project: case study

Masai giraffes are the most numerous of the giraffe subspecies, but the global Masai giraffe population declined ~50% over the past several decades, leading to the subspecies being classified as endangered (Bolger et al. 2019). The Masai Giraffe Project was initiated in 2011 primarily as a population biology study to quantify how survival, reproduction, and movements of giraffes varied in response to natural and human-caused factors, to help recover the subspecies, and to test ecological theories developed from ungulate studies in temperate latitudes, in a tropical ungulate subspecies. The project is a landscape-scale photographic capture–mark–recapture study of a giraffe metapopulation in a human-dominated landscape to generate estimates of population size, sex and age structure, reproduction, age-specific survival rates, and movement rates among the connected subpopulations (Lee et al. 2016a; Lee and Bolger 2017; Bond et al. 2021a; Lavista Ferres et al. 2021). The design of the study also enabled us to examine the evolutionary implications of intrinsic traits or extrinsic environmental factors by estimating the consequences of variation in that trait or factor on survival or reproduction, the components of fitness (e.g., land management and reproductive rate: Lee et al. 2016a; seasonality and calf survival: Lee et al. 2017; spot pattern and calf survival: Lee et al. 2018; sociability and adult female survival: Bond et al. 2021b). Our design additionally allowed us to investigate the social structure and sociability of our study animal (Bond et al. 2019; Bond et al. 2021a, b, c, d; Lavista Ferres et al. 2021), and to evaluate management actions (e.g., community conservation: Lee 2018; Lee and Bond 2018 and translocations: Lee et al. 2020).

Study area

The Masai Giraffe Project study area is in the Tarangire Ecosystem of northern Tanzania, a system that supports a high density of giraffes and is representative of the current diversity of threats and conservation opportunities across the

Table 1 General threats to giraffes; studies that focused on effects of the threats; study results; and recommendations

Threat	Focused studies	Results	Recommendations
ICUN RedList*			
Habitat loss/ecological changes	Strauss et al. (2015) Knüsel et al. (2019) Lee et al. (2017), Lavista Ferres et al. (2021)	Giraffes may limit their own food supply by targeting favored forage species in the central Serengeti Adult females in the Tarangire system living near towns have larger home-range sizes as they must travel greater distances to avoid humans Movements documented among subpopulations (management units and socially defined super-communities) through agricultural areas and across tarmac roads	Conduct experiments to determine if preferred forage plants can be managed at scale Land-use planning to limit urban and agricultural expansion into remaining giraffe habitats Land-use planning to maintain connectivity between key subpopulations by conserving habitat, and reducing traffic speeds at giraffe crossings
Illegal hunting (poaching)	Strauss et al. (2015) Lee et al. (2016a), Lee (2018) Bond et al. (2021b)	Poaching likely reduced the population in western and northern Serengeti compared with 30 yr prior Lower adult female survival outside areas with anti-poaching activities in the Tarangire system, but establishment of a community wildlife management area improved adult survival Lower adult female survival closer to towns, but no effect of cattle herder compounds	Expand anti-poaching efforts and increase access to legal economic opportunities Support and expand community conservation areas and effective anti-poaching activities Land-use planning to limit urban and agricultural expansion into remaining giraffe habitats
Published literature			
Natural predation	Lee et al. (2016a) Lee et al. (2016b) Muller (2018)	Lower calf survival inside protected areas with higher predator densities in the Tarangire system, but no adverse effects on population growth rates Higher calf survival in the presence of migratory herds of wildebeests and zebras Only 20% of an enclosed population of 77 individuals with lion predation in Kenya was juveniles, while 63% of an enclosed population of 89 individuals without lion predation was juveniles	Natural predation does not adversely influence population growth rates in large, unfenced populations with sufficient alternative prey, but likely results in a lower proportion of juveniles in small, enclosed populations
Human disturbance	Bond et al. (2019), Bond et al. (2021a,d)	Proximity to cattle herder compounds resulted in weaker and more exclusive relationships among adult females, but calves were more likely to be sighted near these compounds, possibly due to lower predator densities there	Encourage cattle herders to avoid disrupting giraffe groups (e.g., have scheduled daylight hours for wildlife-only at water sources and no dogs at water sources), but otherwise low-impact human settlements appear to be compatible with giraffe persistence
Disease	Bond et al. (2016)	No mortality effects of Giraffe Skin Disease in the Tarangire Ecosystem	No veterinary interventions needed

*From Muller et al. (2018a)

range of the species. Giraffe habitat outside the ecosystem's two national parks has been conserved by traditional pastoralists, or degraded by agriculture, charcoal making, and other human activities (Newmark 2008; Msoffe et al. 2011; Morrison et al. 2016b). Giraffe habitat throughout Africa has become similarly fragmented, thus the Tarangire Ecosystem is representative of much of the remaining landscape for these megaherbivores. The Masai Giraffe Project provides data on how giraffe demography and social behavior vary across realistic gradients of human land-use, poaching, natural predation, and vegetation.

The study area size of ~4,500 km² is large enough to encompass multiple home ranges of giraffes (Knüsel et al. 2019), yet small enough to survey relatively quickly (approximately 15 days per sampling occasion) to meet assumptions of closed populations within occasions for robust design described by Pollock (1982). We conducted a pilot study in 2011 to estimate recapture probabilities and population sizes to ensure sufficient sample sizes and estimator precision.

Sampling

We collect giraffe photographic data systematically according to a strict sampling protocol to ensure equal sampling effort across time and space. We sample near the end of every precipitation season (short rains, long rains, dry) by driving the same network of fixed route road transects. We survey according to a robust design sampling framework (Pollock 1982) with three sampling occasions per year, where each sampling occasion is composed of two replicate sampling events during each of which we survey all transects in the study area (3 occasions per year × 2 events per occasion = 6 independent, complete survey events per year). The robust design of > 1 replicated survey event during each sampling occasion improves precision of demographic parameters and allows for more complex analyses (Pollock 1982; Kendall et al. 1995; Kendall and Bjorkland 2001). Our surveys are frequent enough to capture important temporal variation such as seasonal changes, but the sampling occasions are separated by sufficient periods of time for demographic or other ecological processes to generate detectable variation in our estimates. Figure 3 shows the road transects throughout the Masai Giraffe Project study area. Road density throughout the study area is high relative to giraffe home-range size, with coverage of road transects ranging from 0.21 to 0.87 km/km² within a sample of 152 individual giraffe home ranges (data from D.E. Lee and M.L. Bond). Comparison of land cover, tree cover, elevation, human population density, and distance to human infrastructures was similar between our survey transects and randomly placed transects, indicating our transects were representative of the entire study area (data from D.E. Lee and M.L. Bond). Our study design resulted in 80% of all adult females in the

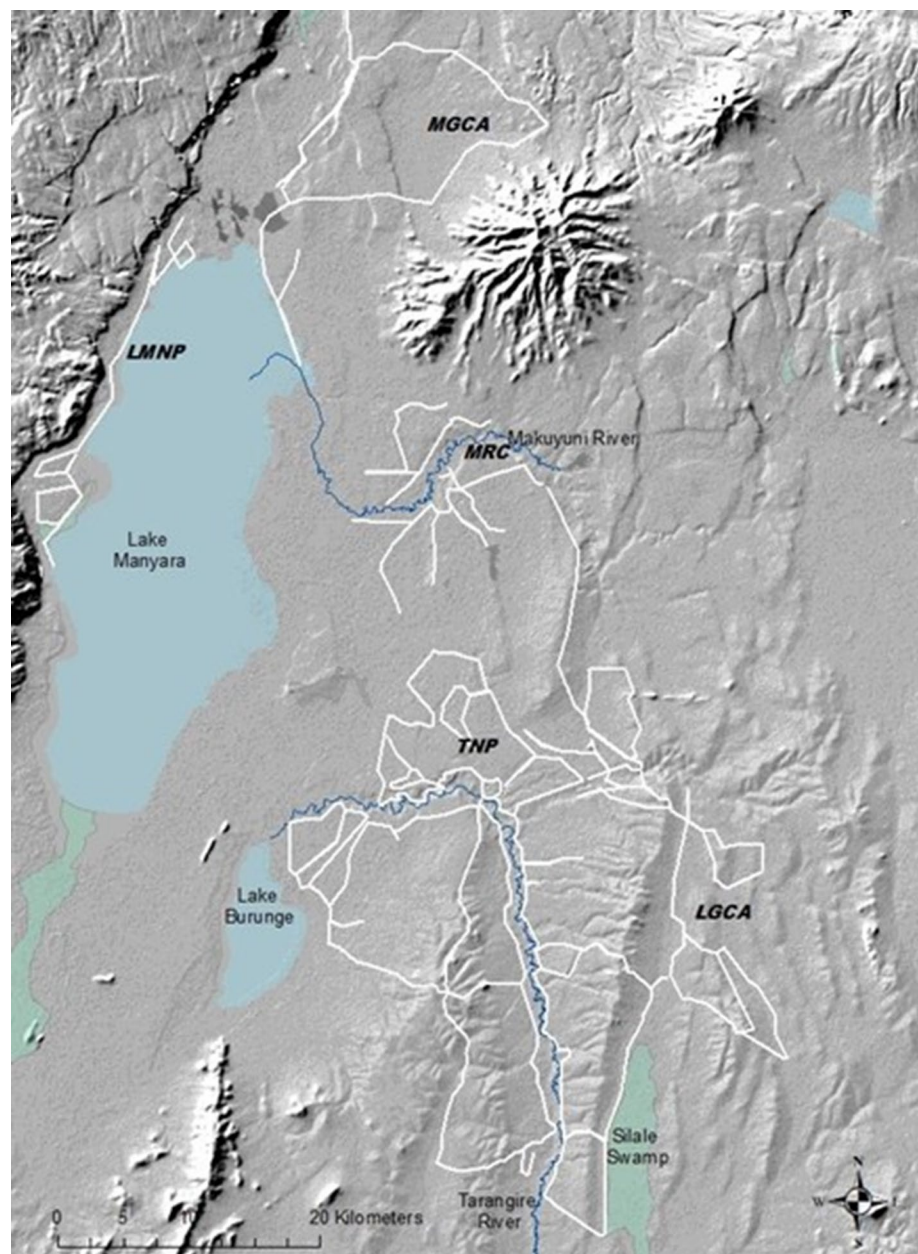
population being identified by the end of the first full year of the study (2012; excluding the pilot survey in 2011) and nearly 100% had been identified by the end of the third full year of the study (Bond et al. 2021c). Survey teams maintain a driving speed between 15 and 20 km/h on all transects, and all teams include trained observers and a driver. We sample each road segment only 1 time in a given survey event and systematically shift the order and direction in which we sample sites and road transects to reduce sampling biases.

During photographic capture–mark–recapture sampling events, when we encounter any giraffe, we “mark” newly observed individuals or “recapture” previously observed animals by slowly approaching and photographing the giraffe's right side. We attempt to photograph every giraffe encountered for individual identification from within a distance of approximately 100 m ($x = 90 \pm 39$ m) at an angle that is as close to perpendicular (90°) as possible. We record sex (male, female), age class, and GPS location of the group (defining a group is one of the key challenges in giraffe research; see “Challenges”). We categorize individuals into four age classes: newborn calf (0–3 months old), older calf (4–11 months old), subadult (1–3 years old), or adult (> 3 years) using a suite of physical characteristics. Giraffe studies have varied in how the authors define age classes (see “Challenges”). Sex, age class, and location are powerful gradients for stratifying and grouping individuals for analyses to ensure that assumptions are not violated regarding equal detectability and survival within groups.

For every image, we record the distance from the camera to the target animal using a laser rangefinder (Bushnell Arc 1000; Overland Park, Kansas) to calculate individual giraffe body sizes with photogrammetry (for details see Lee et al. 2016a). We quantify sampling effort during every survey and note any changes of observers and equipment to account for any associated variation in detection probabilities. Occasionally, to answer a particular question of interest, we have collected additional targeted ancillary data such as disease status (e.g., quantifying mortality effects of Giraffe Skin Disease; Bond et al. 2016).

We followed general study design guidance for capture–mark–recapture in Yoccoz et al. (2001), Amstrup et al. (2006), and Lindberg (2012). Our mean capture (0.34) and recapture (0.42) rates per survey event for adult females suggests that each year we detect every individual in the entire population on average 2.5 times. Other longitudinal giraffe demographic studies that employed robust design in field data collection, computer-aided image processing with WildID, and capture–mark–recapture statistical analyses methods include Masai giraffes in Serengeti National Park, Tanzania (Strauss et al. 2015) and Rothschild's giraffes in Murchison Falls National Park, Uganda (Brown et al. 2019; Brown and Bolger 2020). These studies all employed active photographic encounter surveys, but camera trapping arrays

Fig. 3 Road transects in the Masai Giraffe Project in the Tarangire Ecosystem of northern Tanzania. White lines are tracks surveyed for giraffe groups, blue lines are rivers, blue polygons are alkaline lakes, green polygons are swamps, and grey polygons are towns. TNP= Tarangire National Park, LMNP= Lake Manyara National Park, MRC= Manyara Ranch Conservancy, LGCA= Lolikisale Game Controlled Area, MGCA= Mtowambu Game Controlled Area. The entire study area is unfenced



are also a useful option in many circumstances (O'Connell et al. 2011; Burton et al. 2015; O'Connor et al. 2017; Efford and Boulanger 2019).

Research questions

Demography and population dynamics

Based upon individual pattern-recognition techniques, in the 1970s and early 1980s giraffe demographic rates were estimated from simple return rates of relatively small numbers of known animals (Foster and Dagg 1972; Dagg and

Foster 1976; Leuthold and Leuthold 1978; Pellew 1983). However, capture–mark–recapture modeling accounts for imperfect detection (Lebreton et al. 1992; Burnham and Anderson 2002; Amstrup et al. 2006; Borchers and Fewster 2016; Cooch and White 2019), and demographic research on giraffe populations using these statistical modeling methodologies has further advanced our knowledge of factors affecting giraffe population ecology (Lee and Strauss 2016). In the first publication that used capture–mark–recapture models of individually recognized giraffes, Surau et al. (2012) showed a high population growth rate of a population of West African giraffes (*G. c. peralta*) following a period of severe poaching. Strauss et al. (2015) subsequently

documented a declining population growth rate of Masai giraffes in Serengeti National Park, which might be attributed to poaching and limited food resources, and Brown and Bolger (2020) found no seasonal survival patterns in adult/subadult Rothschild's giraffes.

Adult females are generally the most reproductively important segment of polygynous vertebrate populations (Caswell 2002), and variation in adult female survival seems to drive variation in population growth rates for giraffes at regional and range-wide scales (Lee et al. 2016a). Predation and disease are often important sources of mortality in terrestrial vertebrate populations (Hill et al. 2019; Daszak et al. 2000). In the Masai Giraffe Project study area, adult female survival rates were typically higher in protected areas even though predator densities were highest there, and lower in areas with fewer wildlife protections where poaching by humans was prevalent (Lee et al. 2016a). Adult female giraffe survival rates were unaffected by Giraffe Skin Disease, expressed by lesions on the back of the forelegs (Bond et al. 2016), but other diseases can certainly cause considerable mortality (e.g., rinderpest: Barrett and Rossiter 1999). Proximity to settlements of cattle herders altered the structure of adult female giraffe social communities, resulting in weaker and more exclusive relationships (Bond et al. 2021d), yet females with calves tended to congregate closer to these settlements (Bond et al. 2019), probably because the herders actively kill or drive away predators (Kissui 2008) to the benefit of giraffe calves. Survival of adult female giraffes was not adversely affected by living close to these herder settlements but was negatively correlated with proximity to more densely populated towns, which are inhabited by poachers and surrounded by agricultural fields (Bond et al. 2021b). The most important factor determining adult female survival in the Tarangire Ecosystem—even more important than proximity to humans—was a female's gregariousness, or the number of other adult females in her groups, with higher survival rates for females with mean larger group size (Bond et al. 2021b). Because of these factors, targeted efforts to improve survival of adult females by reducing poaching, land-use planning to conserve savanna habitat, and preventing disruption to their social relationships would help sustain giraffe populations in the long term. Community-based natural resource management such as Wildlife Management Areas in Tanzania are a good example of local targeted conservation efforts that have successfully increased giraffe survival rates in the Masai Giraffe Project area (Lee 2018).

In addition to adult female survival, juvenile survival can vary due to many factors and can be an important driver of population dynamics of ungulates (Gaillard et al. 2000). Juvenile giraffes are the age class most susceptible to predation by lions (Strauss and Packer 2013). Muller (2018) compared population structure of Rothschild's giraffes in two small (<90 individuals) enclosed populations, one

with lion predation and one without, and found few juveniles in the population with a high density of lions. In the larger, unfenced Masai Giraffe Project study area, there is substantial seasonal variation in ungulate density and biomass as migratory herds of thousands of eastern white-bearded wildebeests (*Connochaetes taurinus albojubatus*) and plains zebras (*Equus quagga*) move between seasonal ranges (Morrison et al. 2016b). Giraffe neonatal and calf survival probabilities were higher when the migratory herds were present, suggesting that the alternative prey attracted predation away from giraffes (Lee et al. 2016b). In this ecosystem, certain spot pattern traits were associated with variation in calf survival, possibly due to camouflage effects (Lee et al. 2018). Overall, calf survival probabilities were lower in protected areas where predator densities are highest (Lee et al. 2016a; Bond et al. 2021a); nonetheless, the protected areas of Tarangire National Park and Manyara Ranch support source populations that are the engines of giraffe metapopulation growth in the region (Lee and Bolger 2017). This indicates that demographic rates typically seen in long-lived species—high adult female survival with lower and more variable juvenile survival (Gaillard et al. 2000)—are regulated by natural levels of predation on giraffes and other prey in the Tarangire Ecosystem, as opposed to the unnatural constraints to such processes seen in small, enclosed populations (Muller 2018).

Variation in timing of reproduction and subsequent juvenile survival can play an important role in population dynamics of temperate and boreal ungulates (Bunnell 1982; Clutton-Brock et al. 1982). Tropical ungulates often give birth year-round, but survival effects of birth season for tropical ungulate species are largely unknown. In the Masai Giraffe Project study area, juvenile survival according to season of birth was significant, with calves born during the dry season experiencing the highest survival probability (Lee et al. 2017). Phenological match may impart a survival advantage to offspring born during the dry season from: (1) greater accumulated maternal energy reserves in mothers who conceive in the long rainy season, (2) high-protein browse in the late dry—early short rains supplementing maternal and calf resources, (3) reduced predation due to decreased stalking cover, or (4) some combination of these (Lee et al. 2017). Hart et al. (2021) also found that season of birth affected juvenile giraffe survival in the sub-tropics, as Angolan giraffe calves born earlier in the year (before or during the wet season) were more likely to survive than those born later in the year.

These studies provided robust estimates of the various components of demographic processes, some possible ecological and anthropogenic factors driving those processes, and potential selective forces. The differing demographic rates documented in contrasting systems (e.g., small, enclosed populations versus large metapopulations in

unfenced landscapes) underscores the value of such studies for conservation and management purposes.

Sociality and behavior

Individuals living and interacting together leads to complex relationships and social structure of populations (Alexander 1974; Krause and Ruxton 2002; Clutton-Brock 2016), and as a social mammal, giraffes are no exception. Hinde (1976) suggested a framework for the description of social organization based on interactions between pairs of known individuals, called dyads, whereby social relationships result from repeated interactions between dyads. The content, quality, and temporal pattern of individual interactions describe the relationship of the dyad, and the content, quality, and temporal pattern of relationships among dyads in a population define the social structure (Hinde 1976; Whitehead 2008).

A network is a representation of social structure, and formal social network analysis provides a means to describe and understand social complexity and its fitness consequences by measuring relationships (Whitehead 2008). The strength of social network analysis is that it elucidates how individual processes influence group-level properties by accounting for every individual's social environment (Farine and Whitehead 2015). Long-term demographic studies of individually identified animals recognized by their unique markings have provided data that also yielded insights into the social structures of mammal populations in a diverse range of taxa, including African elephants (*Loxodonta africana*; Wittemyer et al. 2005), felids (Packer et al. 1990; Durant et al. 2004), cetaceans (Lusseau et al. 2006; Parsons et al. 2009; Cantor et al. 2012; Augusto et al. 2017; Tavares et al. 2017), and giraffes (Table S1).

Researchers have long used the unique markings of giraffes to identify individuals and describe their social relationships, especially grouping dynamics. Early studies reported continual turnover in group composition and lack of close ties between individuals (Foster and Dagg 1972; Leuthold 1979; van der Jeugd and Prins 2000; Le Pendu et al. 2000). In contrast, Pratt and Anderson (1985) were the first to suggest a relatively stable structure of female Masai giraffe groups composed of a few mothers with calves, usually of a similar age, that remained together. However, all eight identified members of one female 'group' monitored over 10 months by Pratt and Anderson (1985) were together during only one-third of the sightings. Our current understanding of giraffe sociality is that group composition is highly fluid throughout the course of the day, but aggregate non-random associations between adult females, and linking of female groups by roaming adult males, result in a structured, multilevel society. Many individual-based studies have focused on factors influencing giraffe group composition and size, including age proximity (Bercovitch and Berry 2013)

and ecological conditions (Bercovitch and Berry 2009; Muller et al. 2018c; Wolf et al. 2018b; Bond et al. 2019). Not surprisingly, relatedness also drives association strength. Among Thornicroft's giraffes (*G. c. thornicrofti*) closer relatives were more likely to be found together in groups compared to non-relatives, and mother-offspring dyads had the strongest associations (Bercovitch and Berry 2012). Carter et al. (2013a, b) showed preferred and avoided relationships among females, but not among males, in a large population of Angolan giraffes; females in 'preferred' relationships were more related to each other than expected from random associations; female (but not male) relationships were stable over time; and young females (compared with older females) increased their number of associations as they aged. Studies of reticulated (VanderWaal et al. 2014), Masai (Lavista Ferres et al. 2021), and Rothschild's giraffes (Muller et al. 2022) also confirmed association patterns were influenced by age and sex class. Other studies examined how giraffe social affiliations were influenced by activity (Muller et al. 2018b), humans (Bond et al. 2021b, d), humans and lions (Muller et al. 2019), season (Prehn et al. 2019), a male's color (Castles et al. 2019), and presence of calves in female groups (Saito et al. 2020), as well as how associations influence male rutting (Seeber et al. 2013), grouping (Bercovitch and Berry 2014), and sparring behaviors (Granweiler et al. 2021). A recent review of giraffe social behavior suggested that giraffes display many features of a complex cooperative social system (Muller and Harris 2021).

As with other social mammals, giraffe societies consist of multiple scales of social organization. VanderWaal et al. (2014) identified three hierarchical levels of clusters in a population of 170 identified individuals monitored over 6 months. Females exhibited the strongest social associations within a core group (cliques) and maintained moderate associations with other members of their subcommunity, but had low association rates between their two identified, spatially separated communities. Subsequent research on social structure of a larger metapopulation (2680 identified individuals) in the Masai Giraffe Project over a longer time frame (> 5 years) revealed higher levels of organizationally distinct sets of social connections beyond those described by VanderWaal et al. (2014). Adult female Masai giraffes in the Tarangire Ecosystem formed multiple modular yet spatially overlapping social communities (Bond et al. 2021d), with each community comprised of approximately 60–90 females that showed stable membership over time (Bond et al. 2021a, c, d). These social communities had different demographic rates (Bond et al. 2021a) and proximity to settlements of cattle herders resulted in weaker relationship strengths among social community members, and more exclusive relationships with fewer others (Bond et al. 2021d). Lavista Ferres et al. (2021) detected distinct mixed-sex social communities of similar population size (800–900

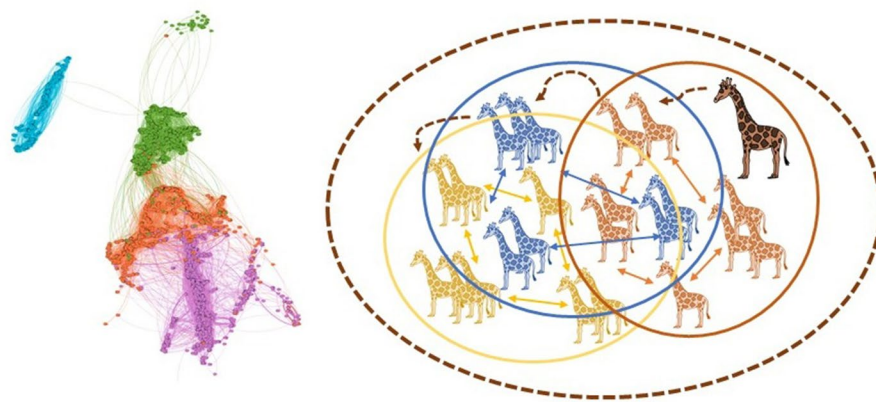


Fig. 4 Schematic of the multi-level social structure in a Masai giraffe metapopulation in the Tarangire Ecosystem, Tanzania. Left graphic depicts all observations (points) and connections (edges) from 2011 to 2016, with color reflecting super-community membership. To the right: yellow, blue, and red giraffes represent hypothetical adult females in groups that merge and split (arrows), with stronger and long-term associations among similarly colored animals. These association patterns form adult female communities which overlap in space (yellow, blue, and red circles represent intersecting community

home ranges) but are socially discrete and stable over time. Adult males (large brown giraffe) visit multiple female communities seeking mating opportunities (dotted brown arrows), thereby linking the discrete female communities into a larger, mixed-sex, stable super-community (brown oval). Thus, giraffes reside in a complex society with dynamic groups embedded into stable communities within stable super-communities, all of which are driven by the variation in social connections among individuals

individuals) in the Tarangire Ecosystem, which the authors termed ‘super-communities’ to differentiate this apex level of social organization from the intermediate-level female-only communities that were embedded within the super-communities (see Fig. 4). Similar to the female communities, these super-communities were also stable over time, as evidenced by dynamic network clustering. Overall, based on identified individuals repeatedly recorded over time, we can summarize giraffe social structure as core units of temporally dynamic group formations based upon fission–fusion processes that are mediated by kinship, sex, and age proximity as well as seasonal and environmental factors, with individuals coalescing into ‘cliques’ that are embedded in successively larger, nested, upper levels of ‘subcommunities’ and ‘communities’, to the apex level of ‘super-communities’ in a metapopulation—all driven by the variation in social connections among individuals.

Translocations are sometimes used as a tool to re-introduce giraffes into areas where they have been extirpated or to establish populations in new areas (Muller et al. 2020). However, the importance of social relationships among adult females to their survival and the key role adult females play in maintaining population growth means capturing and moving females could have long-term adverse consequences on the founding population. As such the purpose and need for translocations should be carefully considered (Lee et al. 2020; Muller et al. 2020).

Future studies of the population dynamics and social structure would benefit from knowing the relatedness of individuals, which could be assessed by genetic variation

known to exist in giraffes (Brown et al. 2007; Coimbra et al. 2021).

Large-scale movements

Space use by animals, and their movements across landscapes or among social groups, are behaviors that are strongly influenced by socio-ecological factors. For example, the amount of space used by an individual is dependent upon the distribution and abundance of critical resources including food and mates (Börger et al. 2008; Powell and Mitchell 2012). Movements among social groups or subpopulations are mediated by life history requirements such as natal dispersal (Clobert et al. 2001) or mating strategy (Leuthold 1979; Pratt and Anderson 1985). Investigating factors that drive space use and movements is important for understanding key components of population dynamics and the processes that drive decision-making behaviors of animals and provides important information for land managers to ensure that sufficient amounts of habitat are being conserved to sustain populations.

Due to high costs and substantial risks, capturing and affixing a transmitter on an animal as sizable as a giraffe to acquire information on its movements is not possible for large samples. However, if enough resights for known individuals are obtained through capture–mark–recapture, it is possible to generate estimates of home-range size and large-scale movements of giraffes across landscapes and among subpopulations, and to quantify factors that influence these behaviors. We distinguish large-scale movements across

landscapes from small-scale progressions of groups (e.g., Innis 1958; Berry and Bercovitch 2015).

Several studies of giraffes have taken advantage of detections of individuals recognized by their unique spot patterns to quantify movements (Table S1). Home range estimates of giraffes across Africa that were calculated from capture–mark–recapture methods were collated and presented in Knüsel et al. (2019) and home-range sizes were found to be correlated with rainfall at the continent-wide scale. At the ecosystem scale of the Masai Giraffe Project, female giraffe home-range sizes were larger for individuals living near towns, suggesting a need to range farther to meet life history requirements due to conflicts with humans. Lee and Bolger (2017) showed variation in movements among spatially defined subpopulations in the Masai Giraffe Project that contributed to source–sink population dynamics. The study also revealed that giraffes occasionally traversed across human-dominated areas to reach other subpopulations. In further research on this metapopulation, Lavista Ferres et al. (2021) calculated movements among socially defined subpopulations (super-communities) rather than across management unit boundaries. Most (70%) giraffes remained within their same super-community, and those that visited a different super-community (usually adult males) often returned to their original super-community. Both Lee and Bolger (2017) and Lavista Ferres et al. (2021) demonstrated that one population—Lake Manyara National Park—was essentially isolated. In the Masai Giraffe Project study area, Bond et al. (2021c) quantified natal dispersal across space and among social communities, mostly by young male giraffes. In Uganda, Brown and Bolger (2020) discovered that transition probabilities among different sectors of Murchison Falls National Park differed by season, especially for males. These studies provide important information on space and resource requirements for different populations of giraffes.

Other avenues of research using spot pattern recognition

Some studies have used individual identification of giraffes in novel ways (Table S1). For example, in a longitudinal study of Thornicroft's giraffes in Zambia, Bercovitch and Berry (2015) found no evidence for repeatability of birthing locations of adult females. Strauss and Packer (2013) used claw marks present on identification photographs to estimate patterns of lion predation on Masai giraffes. Strauss (2014) also used photographs of the same calves over time to estimate umbilical cord stump retention, which assists in age estimation.

Individual identification has aided in the assessment of giraffe health. van der Jeugd and Prins (2000) assessed changes in body condition of individual Masai giraffes in

Lake Manyara National Park, Tanzania over the course of a year, and Muneza et al. (2017) quantified the spatial patterns and abundance of Giraffe Skin Disease in Masai giraffes in Ruaha National Park, Tanzania. Finally, Wolf et al. (2018a, c) examined factors influencing levels of steroids and androgens in male South African giraffes.

Using research results for management and conservation of giraffes

It is well established that understanding population biology and social behavior of a species can support conservation efforts (Sutherland 1998; Morris and Doak 2002). Table 1 presents a potential means of using key results from various studies about giraffe demography, sociality, movements, health, and other topics to guide and aid wildlife managers and conservation biologists (*sensu* Sutherland et al. 2004). The Table presents two threats highlighted in Muller et al. (2018a) but excludes the threat of civil unrest as no studies have focused on this. We also presented several other potential threats that have been identified in the published literature. We only included examples of studies that had relevance for conservation actions that could be implemented by managers, such as human settlements, anthropogenic habitat loss, vegetation manipulation, lion densities, poaching, or disease, rather than those studies that examined processes that cannot be managed, such as season or general habitat type. This is a brief example of how research can be used in the decision-making process for where and how to focus conservation efforts with the most positive impact on giraffe populations.

Benefits and challenges of individual recognition studies

Benefits

Non-invasive capture–mark–recapture using natural marks allows scientists to pursue their inquiries without the need for expensive, dangerous, and invasive physical captures, and advances in freely available automated procedures in photograph cropping and pattern-matching enable ever-larger sample sizes. Individual identification also provides more precise demographic parameter estimates, which is critical for effective population monitoring and management. For example, as long ago as the 1960s, Foster (1966) demonstrated that wildlife counts can be inaccurate for estimating population size of giraffes, which was confirmed by Lee and Bond (2016) for aerial counts. Thus, with a bit of extra effort, simple counts can be replaced by a systematic, longitudinal photographic capture–mark–recapture framework to generate more precise estimates of population size, age

and sex structure, reproduction, survival, and movements. In contrast, other less-intensive methods such as aerial surveys can cover much larger areas than a ground-based photographic identification study, so calibrating correction factors can help improve the accuracy of broader-scale count methods (Lee and Bond 2016).

Challenges

Giraffes are a good species with which to test hypotheses on factors that influence ecology and behavior of ungulates in both tropical and temperate regions, but at the same time, there are ways in which they are different. For example, many other ungulates form clearly demarcated groups that are usually obvious to the researcher. Giraffes may also form similar discrete groups but among giraffe researchers, a group is notoriously difficult to define. Foster (1966, p. 143) stated “as giraffe can often maintain visual contact over wide distances (1 km or more) it is sometimes difficult to decide what constitutes a herd.” This quandary remains true to this day. It is possible giraffes might communicate using infrasonic vocalizations (Baotic et al. 2015) similar to elephants (Garstang 2004), so future research might examine communication among giraffes to more accurately quantify group membership at any given time.

Age classes are also notoriously difficult for giraffe researchers to define. Studies have used different age classes, from three to six (e.g., three: Foster and Dagg 1972, Muller 2018; four: Leuthold and Leuthold 1978, Suraud et al. 2012; six: Pellew 1983, Strauss et al. 2015), making comparisons among studies challenging. Advances in the use of photogrammetry (e.g., Lee et al. 2016a) and age-height curves (Strauss et al. 2015) could help to more accurately age giraffes and determine a consistent age class system for research.

During study design, trade-offs always must be made between sampling more individuals less frequently or monitoring fewer individuals more intensively. Giraffes have highly dynamic group formations and vast home ranges, and many areas have relatively sparse road networks, making it challenging to collect sufficient data from enough individuals to accurately estimate parameters for demography, sociality, and other subjects of interest that reflect true population processes. For demographic research, pilot studies should be conducted so that the precision of estimates can be quantified and to confirm that sample sizes are sufficient. For studies of sociality, intensively following a few individuals for relatively short periods of time can improve the accuracy of metrics of social associations compared with sparser data from many individuals collected over longer time scales when social structure could change. The downside is that data from

small numbers of individuals may not be reflective of processes occurring at the scale of the population. Fortunately, even relatively low numbers of observations can still capture the strongest edges in a social network and thus represent real network structure (Davis et al. 2018). Overall, sampling larger numbers of individuals helps ensure that results are not biased by a few individuals and are indicative of broader population-level patterns, but the trade-off is sparser data.

Conclusions

Long-term, longitudinal studies of individually marked animals provide the best data to answer key questions in ecology and evolution. Giraffes have unique qualities that render them particularly amenable to individual recognition, such as conspicuous size, a typically tolerant nature towards humans, and pelage patterns that offer one of the best built-in marks in the animal kingdom. Fortunately, the basic elements of a photographic mark–recapture study are not very expensive, and a long-term large-scale study of giraffes, such as the Masai Giraffe Project, can be initiated with just the ‘three Cs’: a camera, a car, and a computer. On the other hand, giraffes are long-lived and slow breeding, thus some questions about giraffe demography and life history variation will require long time frames to answer. Long-term studies necessarily involve the collection of data by many individuals and so maintaining consistency and quality requires regular attention and adherence to standardized written protocols. Longitudinal studies of a long-lived species require extra commitment but the pay-offs in terms of scientific advancement are well worth the effort.

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Declarations

Conflict of interest All the authors declare that they have no conflict of interest.

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