

A computer-assisted system for photographic mark–recapture analysis

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Summary

1. Photographic mark–recapture is a cost-effective, non-invasive way to study populations. However, to efficiently apply photographic mark–recapture to large populations, computer software is needed for image manipulation and pattern matching.
2. We created an open-source application for the storage, pattern extraction and pattern matching of digital images for the purposes of mark–recapture analysis. The resulting software package is a stand-alone, multiplatform application implemented in Java. Our program employs the Scale Invariant Feature Transform (SIFT) operator that extracts distinctive features invariant to image scale and rotation.
3. We applied this system to a population of Masai giraffe (*Giraffa camelopardalis tippelskirchi*) in the Tarangire Ecosystem in northern Tanzania. Over 1200 images were acquired in the field during three primary sampling periods between September 2008 and December 2009. The pattern information in these images was extracted and matched resulting in capture histories for over 600 unique individuals.
4. Estimated error rates of the matching system were low based on a subset of test images that were independently matched by eye.
5. Encounter histories were subsequently analysed with open population models to estimate apparent survival rates and population size.
6. This new open-access tool allowed photographic mark–recapture to be applied successfully to this relatively large population.

Key-words: *Giraffa camelopardalis*, giraffe, noninvasive methods, photographic mark–recapture, Scale Invariant Feature Transform, survival, Tanzania, Tarangire

Introduction

Perhaps, the most important tool of animal population biology is the ability to recognize and follow individual animals over space and time. Recognizing individuals allows researchers to estimate vital rates, to quantify fitness and life-history trade-offs and enumerate social behaviour. Traditionally, this recognition has been accomplished by capturing animals and placing visible and unique marks on them. A rich array of analytical methods, known as mark–recapture modelling, has been developed to analyse data from marked populations (summarized by Williams, Nichols & Conroy 2002). Capture-based marking and telemetry are clearly

important methods that provide unique insights and cannot be fully replaced with less invasive methods. However, the possible animal welfare consequences (McMahon, van den Hoff & Burton 2005) as well as the difficulty and cost for researchers have been a continuing prod to develop noninvasive techniques for individual recognition. One such method, photographic mark–recapture (PMR), has gained popularity in recent years because of advances in digital photography and image-processing software. The abundance of species with variable natural marking patterns makes this an attractive method for many researchers. PMR has three required conditions:

1. Individuals can be photographed either while free ranging, after being captured, or with remotely triggered cameras.
2. Individuals bear patterns on some region of their coat or skin that are sufficiently variable to discriminate among individuals.

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3. An individual's pattern is stable over the duration of the study period and can be unambiguously photographed under differing conditions.

Many early applications of PMR employed hard copy catalogues of photographs against which new photographs were visually compared to determine whether the new images were resightings of previously 'marked' individuals or individuals new to the study. PMR has been employed particularly in the studies of relatively small populations of marine mammals and mammalian terrestrial predators (e.g. Karanth & Nichols 1998; Forcada & Aguilar 2000; Langtimm 2004; Silver *et al.* 2004). However, image matching 'by eye' is less feasible for larger populations. Large catalogues are unwieldy and as the number of images increases so does the probability of visual pattern-matching errors (Katonas & Beard 1990; Gamble, Ravela & McGarigal 2008).

For larger populations, there have been a number of attempts to use computers to semi-automate the matching process. Early systems used database software to store and categorize observer-derived categorical pattern descriptors (Mizroch & Harkness 2003). More recently, image analysis algorithms have been used to extract, store and compare pattern information from digital images (Table 1; see Sherley *et al.* 2010 for a fully automated ID system). Most of these systems include the following three components: a database of previously acquired images, a pattern extraction method to extract a reduced amount of pattern information from each image and a pattern-matching algorithm that compares the pattern information from each new image to that of the images in the database and returns a score indicating the relative closeness of the match. Researchers then visually inspect a small number of the highest ranked matching images to confirm positive matches and reject false-positives. Sightings of individuals can then be compiled into encounter histories and analysed using mark-recapture modelling software (Pradel & Lebreton 1993; Hines 1994; White & Burnham 1999).

Photographic mark-recapture will only be useful in studying population dynamics if it provides capture histories that can be analysed using mark-recapture modelling in a cost-effective manner. There are mark-recapture analytical methods for most study designs, but many are data hungry and often researchers cannot take full advantage of them because of the cost and difficulty in gaining sufficient sample sizes. For suitable species, PMR allows for larger sample sizes compared with conventional methods. An important further labour savings of computer-assisted photo matching is that it greatly reduces the total number of 'match' or 'no-match' decisions that have to be made by a human observer. In a catalogue of 2551 images, Morrison *et al.* (2011) estimated that computer matching led to a 38-fold labour savings relative to a completely manual matching process. In a mark-recapture context, this labour savings from computer-assisted systems allows for a greater number of images to be processed with a given level of effort, which can translate into higher recapture rates. An increase in recapture rate improves the power of demographic estimates and allows a greater number of parameters to be estimated, such as movement or transition probabilities in multi-

state models (Pollock *et al.* 1990; Williams, Nichols & Conroy 2002).

One possible limitation of computer-assisted photo identification systems is that they may generate misidentification errors (Table 1) that can severely bias mark-recapture demographic estimates (Lukacs & Burnham 2005; Yoshizaki *et al.* 2009). False-negative errors (failing to match two images of the same individual) can be common (Morrison *et al.* 2011) and positively bias abundance estimates and negatively bias survival estimates. Therefore, estimating misidentification error is an important step in evaluating the efficacy of photo identification software (Hastings, Hiby & Small 2008).

A basic impediment to the wider use of computer-assisted PMR has been the lack of a widely available software tool to accomplish this. There is one commercial product (Hiby & Lovell 1990) and several individual investigators have written their own code (Arzoumanian, Holmberg & Norman 2005; Van Tienhoven *et al.* 2007; Gamble, Ravela & McGarigal 2008; Sherley *et al.* 2010). Here, we describe the development of a flexible, open-source software application that can be used for pattern extraction and image matching of wild animal populations. We apply the software to images of Masai giraffe (*Giraffa camelopardalis tippelskirchi*) from the Tarangire Ecosystem of northern Tanzania. We estimate misidentification error rates and analyse the resulting capture histories using mark-recapture models to estimate abundance and adult survival.

Materials and methods

SOFTWARE

Our pattern extraction and matching program employs the Scale Invariant Feature Transform operator (SIFT; Lowe 2004). SIFT was designed to find and extract distinctive image features invariant to image scale, rotation, viewpoint, local distortion and illumination (Lowe 2004). The scale and orientation invariance are particularly useful because they allow reduced preprocessing of images (e.g. no need to put them all at the same scale) and accept a greater range of images (e.g. tolerates images taken at $>$ or $<$ 90° from the pattern). We adapted a Java implementation of SIFT (<http://fly.mpi-cbg.de/~saalfeld/Projects/javasift.html>).

Given a pair of images our image-matching code proceeds in four steps:

1. SIFT features are extracted for each image. The major stages of the operator are as follows: (i) Scale-space extrema detection: The grey-scale transformed image is searched over all scales and image locations using a difference-of-Gaussian function to identify potential interest points. The image is sequentially down-sampled using Gaussian smoothing, then images at adjacent scales are differenced to find areas that change greatly with a small change in scale; (ii) Keypoint localization: at each candidate location, at the appropriate scale, Taylor expansions are used to interpolate the subpixel location of the actual extremum; (iii) Orientation assignment: one or more dominant orientations (angles relative to image axes) are assigned to each keypoint location based on the gradient in pixel intensity around the keypoint; and (iv) Keypoint description: To provide more information for the matching process, additional local image gradients are measured at the selected scale in four regions immediately surround-

Table 1. Summary of computer-assisted photographic identification studies where false rejection rate (FRR) and false acceptance rate (FAR) have been estimated. We list only the minimum FRR and FAR values for each study, as well the sample sizes (parentheses)

| Species | Pattern type | FRR (sample size) | FAR (sample size) | Image comparison methods | References |
|---------------------------------------------------------------------|----------------------|----------------------|------------------------------|--------------------------------------------------------------------------------------------|----------------------------------------|
| African elephant (<i>Loxodonta africana</i>) | Ear edge | 0.150 (200) | – | Inspect 10 highest ranking candidate images | Ardovini <i>et al.</i> (2008) |
| African penguin (<i>Spheniscus demersus</i>) | Ventral spots | 0.080 (797) | <0.001 (73 600) | Fully automated matching; threshold 0.01% false accept rate | Sherley <i>et al.</i> (2010) |
| Bottlenose dolphin (<i>Tursiops truncatus</i>) | Dorsal fin edge | 0.250 (NR) | – | Inspect 30 highest ranking candidate images | Gope <i>et al.</i> (2005) |
| Cheetah (<i>Acinonyx jubatus</i>) | Lateral spots | 0.064 (72) | – | Inspect all excellent and medium quality images with 'similarity coefficients' ≥ 0.45 | Kelly (2001) |
| Common wall lizard (<i>Podarcis muralis</i>) | Ventral scales | 0.020 (50) | – | Inspect 5 highest ranking candidate images | Sacchi <i>et al.</i> (2010) |
| Giraffe (<i>Giraffa camelopardis</i>) | Reticulated polygons | 0.007 (300) | 0.000 (516) | Inspect top-ranked candidate image | This study |
| Grey whale (<i>Eschrichtius robustus</i>) | Fluke edge | 0.250 (NR) | – | Inspect 23 highest ranking candidate images | Gope <i>et al.</i> (2005) |
| Harbour seal (<i>Phoca vitulina</i>) | Ventral spots | 0.042 (1020) | – | Inspect top 0.3% of ordered list of good/excellent quality images | Hastings, Hiby & Small (2008) |
| Humpback whale (<i>Megaptera novaeangliae</i>) | Fluke patches | 0.174 (42) | – | Inspect 3 highest ranking candidate images | Ranguelova, Huiskes and Pauwels (2004) |
| Marbled salamander (<i>Ambystoma opacum</i>) | Dorsal spots | 0.05 (101) | – | Inspect 10 highest ranking candidate images | Gamble, Ravela & McGarigal 2008 |
| Plains zebra (<i>Equus burchelli</i>) | Lateral stripes | 0.202 (NR) | – | Inspect top-ranked candidate image | Foster, Krijger and Bangay (2006) |
| Spotted ragged-tooth shark (<i>Carcharias taurus</i>) | Spots | 0.193 (NR) | – | Inspect 10 highest ranking candidate images; Repeated 100 times | Van Tienhoven <i>et al.</i> (2007) |
| Sea-lion (<i>Eumetopias jubatus</i>) | Flipper edge | 0.250 (NR) | – | Inspect 28 highest ranking candidate images | Gope <i>et al.</i> (2005) |
| Whale shark (<i>Rhincodon typus</i>) | Lateral spots | 0.080 (27) | – | Inspect moderate or high confidence match categories | Arzoumanian, Holmberg & Norman (2005) |
| White-bearded wildebeest (<i>Connochaetes taurinus</i>) | Shoulder stripes | 0.070 (50) | – | Inspect 50 highest ranking candidate images; Images inter-annual | Speed, Meekan and Bradshaw (2007) |
| | | 0.076 (198) | <0.001 (4925) | Inspect 10 highest ranking candidate images | Morrison <i>et al.</i> (2011) |

ing each keypoint to generate a keypoint *descriptor*. The term *SIFT feature* refers to a keypoint location together with its scale, orientation and descriptor.

2. Candidate matched pairs of SIFT features are identified from the two images. This matching relies on a brute-force comparison of all features from image 1 against all features of image 2. For each feature in image 1, the program locates the feature in image 2 that minimizes the Euclidean distance between the feature descriptors. During this step, the features' orientations have no effect on matching, and their relative scales are allowed wide latitude.

3. A modified version of the RANSAC algorithm (Fischler & Bolles 1981) is employed to find a geometrically self-consistent subset of the candidate matches from step 2. At each iteration step, the algorithm randomly chooses three of the candidate matches between image 1 and 2 and determines whether they are geometrically consistent. A triple of candidate matches forms a triangle in image 1 and, presumably, a corresponding triangle in image 2. This pair of triangles is geometrically self-consistent if they are approximately similar – meaning that they contain the same three angles and their edge lengths have the same proportions. In addition, while some degree of rotation or rescaling between the two triangles is tolerated, the candidate matches may be deemed inconsistent if the orientation and scale information from step 1 differs between the triangles. When a triple satisfies all the consistency criteria, the algorithm adds the triple to its pool of geometrically self-consistent matches. This process is repeated with a large number of randomly selected triples of candidate matches. The pool of consistent matches collected during this iterative process is then used as the basis for an affine transform between the two images.

4. The goodness-of-fit of the match between image 1 and 2 is assessed. After experimenting with six different metrics that were found to have nearly equivalent discriminatory power, we settled on a

metric that we call 'triangles' that simply measures the proportion of random triples considered in step 3 that satisfy the consistency criteria.

Figure 1 illustrates the matching SIFT features between two pairs of images.

USING THE SOFTWARE

The pattern extraction and matching process works on a set of digital images contained in a directory (folder). To ensure faster processing and more accurate matching, the images should be cropped to include just the area of interest – the region of the animal with the distinctive patterns. For giraffes, we used the right side of the body and lower neck and cropped out most of the neck, head, legs and background (Fig. 1).

After pattern extraction and matching are complete, the matching interface presents each focal image in turn (Fig. 2). In addition to the focal image, the top twenty ranked potential matches are presented as thumbnails. Any of these can be compared side-by-side with the focal image by double-clicking on the desired thumbnail. When a match is found, it is recorded with the press of a button or a no-match result can be recorded.

In our preliminary work with giraffe images, we realized the method very reliably ranked matching images as number one. Thus, we used the system by visually inspecting only the top-matching image. If this appeared not to be a match, we concluded that there were no matching images in the database.

The software, source code and documentation are available for download by following the Wild-ID link at <http://www.dartmouth.edu/~envs/faculty/bolger.html>. It is a Java, cross-platform application that runs on recent versions of Windows, Mac OS and Linux.



Fig. 1. Visualization of the match between images. Each vertical pair of images is a match identified by Wild-ID. The white points on each show the locations of matching Scale Invariant Feature Transform (SIFT) features identified by the program. Red lines connect these putative matches. The green lines indicate where the features on the lower image 'should' have been located based on the affine transform applied to the upper image. Large green lines indicate nonlinearities in the mapping between the two images not captured by affine transform. High-scoring matches have a high density of red lines and short green lines. The pair of images on the left have few matching features, presumably because the lower image is out of focus, yet this was still sufficient for this match to score highest. The pair on the right is a more typical, high scoring, matching pair.

Wild-ID user interface

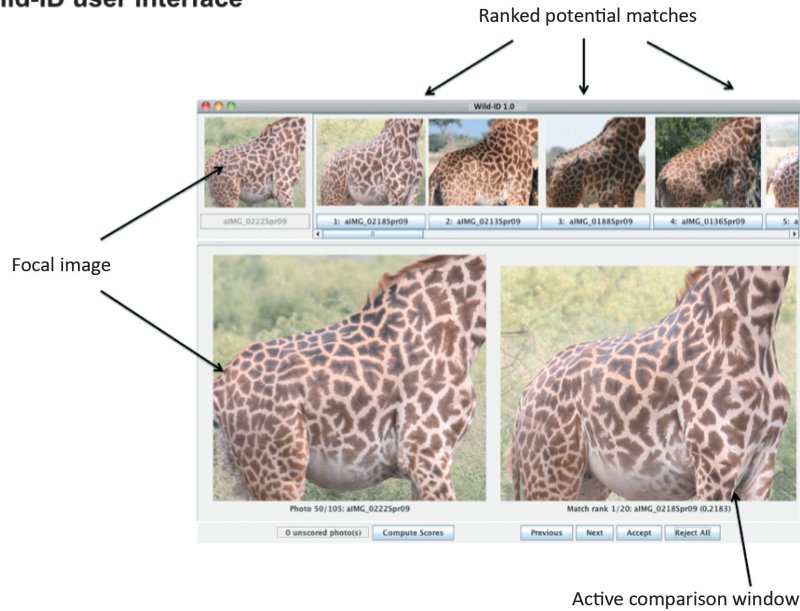


Fig. 2. The user interface of Wild-ID.

STUDY AREA

The Tarangire–Manyara Ecosystem (TME) is in the eastern branch of the Great Rift Valley in northern Tanzania and encompasses roughly 20 000 km² (Fig. 3) defined by the migratory ranges of wildebeest and zebra (Kahurananga & Silkiluwasha 1997; Foley & Faust 2010). TME is a savanna-woodland ecosystem that supports one of the most diverse communities of migratory ungulates in the world (Bolger *et al.* 2008). This area includes a variety of human land-uses, including two national parks (Tarangire (TNP) and Lake Manyara), a private wildlife conservancy that permits livestock grazing and limited tourism (Manyara Ranch) and a number of Game Controlled Areas (Mto wa Mbu, Simanjiro Plains, and Lolkisale) that permit wildlife harvesting (subsistence and trophy hunting), agricultural cultivation and permanent settlement (Nelson *et al.* 2010). Since the 1940s, human population and agricultural development have increased fourfold to sixfold throughout the TME (Gamassa 1995), causing substantial habitat loss and reducing connectivity (Tarangire Conservation Project (TCP) 1998, Newmark 2008). As a consequence, a number of migratory wildlife populations appear to be declining rapidly (Tanzania Wildlife Research Institute (TAWIRI) 2001).

IMAGE ACQUISITION

From prior aerial survey data and our own reconnaissance, we knew that the giraffes were concentrated in the north end of TNP and in Manyara Ranch, so we focused our efforts there. The two areas are separated by a major paved road and several kilometres of agricultural land that surrounds the southern areas of the ranch, but migratory wildebeest and zebra move seasonally between them. Images were taken with a Canon ES 40D and a Canon 100–400 mm f/4.5–5.6L zoom lens with electronic image stabilization. Giraffes were spotted by driving the extensive network of dirt roads in the study areas (Fig. 3). Visibility in these open savanna areas is excellent. When individual giraffe or herds were spotted, we drove slowly to

within suitable range (20–50 m) to take high-resolution images. Giraffes were generally very tolerant of vehicles and we had little trouble positioning the vehicle without causing the animals to flee. Thus, we were able to obtain high-quality images (i.e. good lighting and focus,

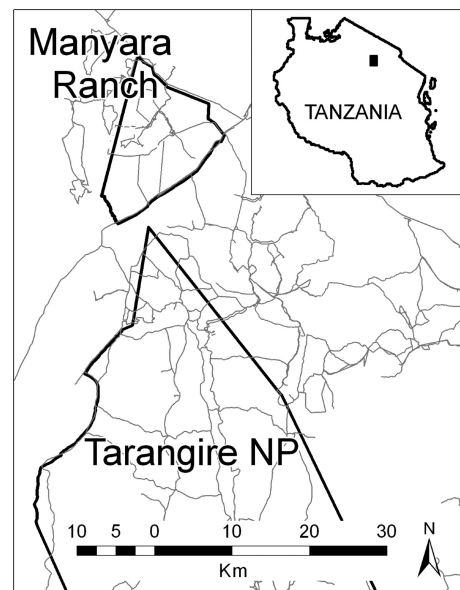


Fig. 3. Map of the study area within the Tarangire Ecosystem in n. Tanzania. Dark lines represent reserve boundaries and grey lines indicate the road network used to find and photograph giraffe. For scale, female giraffe homeranges are 96 km², approximated by the circle with a diameter of 11 km. Homerange size is the average of published estimates (references in Supporting Information): Foster & Dagg (1972), Langman (1973), Moore-Berger (1974), Berry (1978), Leuthold & Leuthold (1978), Pellew (1984), duToit (1990), Pendu & Ciofolo (1999), Jeugd & Prins (2000) and Fenessey (2009).

close to perpendicular). Images were taken of the right side of each individual in the herd from as close to perpendicular as possible. The sex and age (calf, juvenile, adult based on relative size) of each individual was recorded as was herd size and stage/sex composition. Images were acquired over three primary sampling occasions: (1) 20 August to 26 October 2008, (2) 10 January to 17 March 2009 and (3) 17 to 20 December 2009.

ESTIMATING MISIDENTIFICATION ERROR

To evaluate the performance of the image-matching system, we estimated the false rejection rate (FRR: the probability of failing to match two images of the same individual) and false acceptance rate (FAR: the probability of matching two images of different individuals). These metrics are similar to false-negative and false-positive error and are often used in biometric performance assessments (Jain 2007). To estimate FRR and FAR, we created test sets of known matching images. Giraffes were photographed in small herds (c. 1–15 individuals), and we attempted to photograph every individual in the herd. As a consequence, we often unknowingly photographed an individual twice or more in the same bout. This made it easy to find known matches by visually inspecting the set of images from a single herd and finding matching images. The small number of images from each herd enabled us to compare each pair of images side-by-side. As demonstrated in the Results section, when compared in this way matches are detected and false matches are avoided virtually without error.

We then assembled a test set of these 'known' matches choosing some that had challenging differences including differences in angle, lighting and intervening image noise such as vegetation or a tail. We thus assembled a test set of 100 images comprised of pairs of photographs of 50 unique individuals. We felt that this test set provided pairs of images that were as challenging for matching as pairs collected over a longer period of time (e.g. between sampling occasions).

We estimated FRR from two sources: error because of the limitations of the image-matching algorithm and observer error. Given that our threshold for visual inspection was one (only the top-ranked match was inspected), if true matching images were not the highest ranked image, we would commit an algorithm-generated false rejection error. Because of the possibility for declining performance as the number of nonmatching images in the image database increases (Gamble, Ravela & McGarigal 2008), we embedded our test set in databases of increasing numbers of nonmatching images (100, 328, 680 and 1103 images) to see whether FRR was affected by database size. The latter database (1103 images) was the full image database for the study.

Even if the identification system reliably ranks true matches as the highest rank, false rejections and false acceptances are possible if observers fail to either recognize true matches or discriminate against nonmatches. To estimate these observer errors conservatively, we used inexperienced assistants. Six assistants were individually instructed in the use of the program for several minutes and then, without supervision, allowed to make the designation of match or no-match. For this test, we combined our 100 image test set with 86 images from another part of Tanzania that we were sure would not contain matches to the test set. Thus, each observer had 50 opportunities to make false rejection errors and 86 opportunities to make a false acceptance (because photographs are considered sequentially, images with a match are matched only once, that is, a–b but not b–a). FAR and FRR were calculated as the number of incorrectly matched photographs over the total number of match

evaluations (of top-ranked true nonmatching (86) and true matching images, respectively (50)).

POPULATION PARAMETER ESTIMATION

We analysed the capture histories that resulted from the PMR data to estimate population parameters using the robust design model in program MARK (White & Burnham 1999). The robust design model is a combination of the Cormack–Jolly–Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965) and closed capture models (Kendall & Nichols 1995; Kendall, Pollock & Brownie 1995; Kendall, Nichols & Hines 1997). Instead of just one capture event between survival intervals, as in CJS, multiple 'secondary' capture events are clustered together in time in 'primary' sampling occasions. Within a primary occasion, closed population models are used to estimate abundance, and open population models are used between primary occasions to estimate survival, temporary emigration and immigration of marked animals back to the surveyed area.

For each primary capture occasion, we estimated the probability of capture (p_{ij}) and recapture (c_{ij}) (where j indexes the number of secondary capture events within the i th primary occasion). For the intervals between primary occasions, we estimated the probability of survival (S_i), the probability of emigration from the surveyed area (γ_i') and the probability of staying away from the surveyed area given that the animal has left the surveyed area (γ_i'').

Population size (N_i), the total number of animals in the population just before primary occasion i , is a derived parameter computed by dividing the number of marked and unmarked animals in the population just before occasion i by p_i^* . The quantity $p_i^* =$ probability that an animal is captured in at least one of the j sampling events in occasion i given that the animal is located in the sampled area during occasion i (i.e. not a temporary emigrant).

We used only the captures from Tarangire National Park and areas immediately adjacent to its boundaries for this analysis. Because we devoted more effort to TNP than Manyara Ranch, the recapture probabilities and sample size were higher there. We used PMR data to create encounter histories for the three primary capture occasions. The first primary occasion contained three secondary events: (1.1) 20–26 August 2008; (1.2) 4–26 September 2008; (1.3) 18–26 October 2008. The second primary occasion contained two secondary events: (2.1) 10–17 January 2009; (2.2) 5–17 March 2009. The third primary occasion contained two secondary events (3.1) 17–20 December 2009; (3.2) a placeholder event to permit robust design analysis where no capture surveys were actually performed, so all individuals have a zero coding for this event in their capture histories and recapture probability is fixed at zero in this event (W. Kendall *pers comm.*). The time interval between primary occasion 1 and 2 was ≈ 5 months and between primary occasions 2 and 3 was ≈ 10 months, so estimates were computed for a 5-month time span and we later transformed them to annual rates. Although secondary sampling occasions lasted 1 to 3 weeks, all captures during a given event were pooled into a single event (Hargrove & Borland 1994; Pradel *et al.* 1997a,b). We defined groups by sex (male and female).

For logistical reasons, our first two primary sampling occasions were 67 and 66 days. Thus, it is unlikely that the within primary period closure assumption was strictly met. O'Brien, Robert & Tiandry (2005) report that survival bias can be a problem if $> 50\%$ of mortality occurs during the sampling period. Survival in giraffe does not appear to be highly seasonal, so it is very unlikely that this much mortality could occur in any two-month interval. For movement, bias is only an issue if movement is nonrandom (Kendall 1999). Our modelling results did not lend strong support to nonrandom

(Markov) movement (Supporting Information, Table S1). Thus, it appears unlikely that deviations from the closure assumption caused bias in our parameter estimates; however, they could affect the standard errors of the estimates.

Our model set (Supporting Information, Table S1) included models of survival, emigration and recapture with sex and time structure as simple effects [e.g. $S(\text{sex})$ & $S(t)$], additive effects [$S(\text{sex} + t)$] and multiplicative effects [$S(\text{sex} \times t)$]. We included age-like encounter class structure (denoted by $e2$) in survival to control for transients (Pradel *et al.* 1997a,b; see Results). Emigration was modelled with random ($\gamma'' = \gamma'$), Markovian ($\gamma'' \neq \gamma'$) and zero emigration ($\gamma'' = \gamma' = 0$) models (see Kendall, Nichols & Hines 1997). To keep the number of parameters manageable, we assumed capture and recapture rates were equal ($p = c$). With a noninvasive technique such as PMR, there is no reason to expect capture and recapture probabilities to differ within an occasion. Capture and recapture probabilities were modelled as constant, sex- and time-dependent (c and p estimated separately for each sampling event) and with additive ($\text{sex} + t$) and multiplicative ($\text{sex} \times t$) structure. We also modelled capture and recapture as varying among primary occasions, but constant within an occasion [$p(\text{occ})$].

Goodness-of-fit tests have not been developed for the robust design, so we assessed goodness-of-fit (GOF) by treating the data as if they were recaptures only data (Nichols & Pollock 1990). We performed GOF tests with programs U-CARE (Choquet *et al.* 2005) and MARK. We ranked competing models in our model set according to quasi-AICc values (Burnham & Anderson 2002). We constructed a set of alternative *a priori* models beginning with a highly parameterized general model $\{S(\text{sex} \times e2) \gamma''(\text{sex} \times t) \gamma'(\text{sex}) p = c(\text{sex} \times t)\}$ that we systematically constrained into the most parsimonious form (Lebreton *et al.* 1992). First, we ranked competing models of p while holding γ and S in their general form. After identifying the most parsimonious model of p , we ranked competing models of immigration (γ'' and γ'), and finally survival (S) holding constant previously constrained parameters in their most parsimonious form (Lebreton *et al.* 1992). Models with $\Delta\text{qAICc} < 2$ are nearly equivalent in explaining the data and indicate some model selection uncertainty.

Results

FAR AND FRR

The true match ranked highest in every trial regardless of the size of the database. With databases of 105, 328, 680 and 1103 images the known match always ranked highest. Thus, failure to reliably rank true matches as number one is not a significant source of error in our protocol.

Observer errors were also rare. Cumulatively, the six assistants committed two false rejections ($\text{FRR} = 2/300 = 0.67\%$) and no false acceptances ($\text{FAR} = 0/516 = 0.00\%$). These rates were by far the lowest among the 15 published PMR studies employing digital pattern matching we found that contained error estimates (Table 1).

POPULATION PARAMETER ESTIMATES

We collected 1026 suitable images from TNP and Manyara Ranch. After processing with Wild-ID these reconciled to 568 unique individuals (335 females, 232 males and one individual

Table 2. Model average estimates of apparent local survival (S), temporary emigration (γ' , γ'') and recapture (p) probabilities as well as population size (N) with standard errors (SE) of adult male and female giraffe in the Tarangire ecosystem 2008–2009. Time interval for S and γ is 5 months

| | Male | SE | Female | SE |
|--------------|-------|-------|--------|-------|
| S_1 | 0.764 | 0.518 | 0.961 | 0.105 |
| S_2 | 0.761 | 0.447 | 0.949 | 0.120 |
| γ''_1 | 0.233 | 0.888 | 0.206 | 0.244 |
| γ''_2 | 0.169 | 0.999 | 0.145 | 0.278 |
| γ'_2 | 0.457 | 0.503 | 0.435 | 0.515 |
| $p_{1:1}$ | 0.048 | 0.023 | 0.047 | 0.021 |
| $p_{1:2}$ | 0.096 | 0.036 | 0.043 | 0.019 |
| $p_{1:3}$ | 0.096 | 0.036 | 0.140 | 0.045 |
| $p_{2:1}$ | 0.196 | 0.051 | 0.142 | 0.038 |
| $p_{2:2}$ | 0.196 | 0.051 | 0.230 | 0.055 |
| $p_{3:1}$ | 0.298 | 0.065 | 0.298 | 0.065 |
| N_1 | 188.2 | 45.7 | 257.7 | 64.2 |
| N_2 | 198.4 | 49.5 | 271.1 | 68.3 |
| N_3 | 191.3 | 46.1 | 266.8 | 66.0 |

of unknown sex). Proportionately, the individuals were 0.71 adults, 0.20 juveniles and 0.09 calves. For mark-recapture analysis, we used the encounter histories of adults and juveniles from TNP, which included 375 individuals (200 females, 175 males; 286 adults, 89 juveniles).

We used program U-CARE to test the GOF of model $\{S(t) p(t)\}$, which included time effects, but not sex or encounter class effects. Program U-CARE global GOF test indicated a significant transient effect (N statistic = 2.05, $P = 0.04$). Transient effects result from differential probability of survival between newly captured individuals and those that have been resighted at least once after capture. Transient effects can be controlled for with age-like encounter class model structure ($e2$ in model notation; Pradel *et al.* 1997a,b). Median \hat{c} and Bootstrap GOF tests in MARK indicated minor over-dispersion in model $\{S(\text{sex} + t) p(\text{sex} + t)\}$ ($\hat{c} = 1.221\text{--}1.659$), likely due to the transient effects detected by U-CARE. To account for this heterogeneity in recapture probabilities, we applied a variance inflation factor ($\hat{c} = 1.659$) during model selection (Burnham & Anderson 2002).

The top-ranked model in our set was constant sex-specific survival, constant random emigration and fully time-dependent capture according to sex (model #1 in Supporting Information Table S1) and was 1.7 times more likely than the second-ranked model to be the best model in our set. We computed model averaged parameter estimates to account for model selection uncertainty (Table 2; Burnham & Anderson 2002). Apparent survival and temporary emigration estimates are for a 5-month time interval. Annual (12 month) female apparent survival = $0.961^{2.42} = 0.908$. Annual male apparent survival $0.764^{2.42} = 0.521$. Population size was estimated for primary occasion 2 (January–March 2009) to be 193 (± 47) and 265 (± 66) for the TNP male and female populations (adults + juveniles), respectively.

MOVEMENT

Over the 15 months of the study, we documented only three individuals moving between Manyara Ranch and TNP. One adult female moved from TNP to Manyara Ranch, two adult males from Manyara Ranch to TNP.

Discussion

Computer-assisted photographic mark–recapture proved to be a very useful tool in estimating demographic parameters of the TME giraffe population. The SIFT algorithm performed excellently for matching giraffe images. Measured error rates were very low and unlikely to cause significant bias across the entire range of possible parameter space (Yoshizaki *et al.* 2009; Morrison *et al.* 2011). Relative to other studies conducted with computer-assisted image-matching systems, the error rates we achieved, FRR and FAR, were comparatively quite low (Table 1). These rates were realized with inexperienced users, so we anticipate lower error rates with experienced observers. Recapture rates and standard errors were reasonable despite the relatively low sampling effort in this preliminary study: our second primary sampling occasion involved only 5 days of sampling at TNP and the third occasion only 2 days.

These analyses indicate that our sampling protocols and methodology yield data that pass goodness-of-fit tests and can be used to estimate demographic parameters and perform model selection for giraffe populations in the Tarangire ecosystem. We discuss the parameter values we obtained in the context of the Tarangire–Manyara Ecosystem in the Supporting Information.

The PMR method provides an enormous savings over conventional mark–recapture techniques in addition to avoiding possible animal welfare consequences. Morrison *et al.* (2011) estimated the cost of darting and marking a wildebeest in TME at \$250 and that PMR provided a 50-fold savings over conventional mark–recapture. Owing to their large size, long neck and associated respiratory and circulatory adaptations, giraffes pose additional risks to immobilization (Bush, Grobler & Raat 2002) and thus costs of conventional marking would be significantly higher. Costs of aerial surveys would be more comparable with PMR but would only estimate total population size with higher SE's and unknown sources of bias. Estimates of age- and sex-specific mortality are not possible from aerial survey data. Our estimates of population size and survival establish baselines from which we plan to continue to monitor the population, seek more precise and accurate estimates and monitor for temporal trends.

The high matching accuracy obtained with the Wild-ID software may not hold for other types of coat patterns. Morrison *et al.* (2011) applied the system to patterns in wildebeest using a search criteria that involved comparing the top 20 highest scoring candidate matches (as opposed to the top scoring photograph in this study) and achieved a FRR of 0.058. However, Morrison *et al.* (2011) also show that these methods do

not need to be error free to adequately estimate population parameters. While these results are highly encouraging for use on giraffes and wildebeest, use of PMR with other animals will require pilot work to estimate error rates to determine feasibility. We stress that the use of computer-assisted identification requires careful consideration of the potential sources of error (i.e. FRR and FAR) and how these errors violate assumptions of the parameter estimation models used (Morrison *et al.* 2011).

The increasing availability of noninvasive methods that allow cost-effective means of high-resolution demographic data raises the potential for basing choices of model organisms on the availability of a noninvasive method for that species. The giraffe may be such a candidate. Giraffes are strong interactors with Acacia, one of the woody dominants of African savannas that help shape ecosystem structure and function (Furstenberg & van Hoven 1994; Miller 1994; Bond & Loffell 2001). Thus, demographic studies of giraffe populations, enabled by the Wild-ID software, may be a useful window into savanna ecosystem dynamics.

Acknowledgements

This work was supported by the National Science Foundation grant 0754773 to DTB and HF. Support is also acknowledged from the Neukom Institute for Computational Science at Dartmouth College, Marion and Jasper Whiting Foundation, the Nelson A. Rockefeller Centre at Dartmouth College. We thank the Commission for Science and Technology and the Tanzania Wildlife Research Institute for permission to conduct research in Tanzania, and the Tanzania National Parks for permission to work in Tarangire National Park and Robert Molle for his assistance in the field.

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Received 16 February 2012; accepted 3 April 2012
Handling Editor: Robert Freckleton

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Additional details of the model selection process and discussion of the results for the Tarangire National Park giraffe population.

Table S1. Model selection results for apparent survival (S), temporary emigration (γ'' & γ'), and capture recapture (p) probabilities of giraffe in Tarangire National Park, Tanzania 2008–2009.

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