Tracking a better way to count wildlife: testing the Formozov-Malyshev-Pereleshin (FMP)

formula in the Kalahari

by

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Abstract

The science of conservation biology is about conserving species. To do so often requires information about population sizes. Great efforts have been devoted to counting animals, the diverse means by which are invariably taxa and environment-limited. Faced with a biodiversity crisis, conservationists have a pressing need for methods that are robust but also practical and cost-effective. Comprehensiveness, that is the ability to capture many species simultaneously, is also advantageous. Animals, defined by their mobility, are often hard to see, mammals in particular. They do however leave tracks which in some environments are conspicuous and ubiquitous whereas the animals themselves are not. It is self-evident that more animals leave more tracks, but there are a host of other factors difficult to diagnose and suspected to confound this simple relationship. As a result, the mainstream demotes tracks to indices of relative abundance instead of attempting inference on population sizes. Almost 90 years ago Russian biologists derived a parsimonious model explaining transect counts of animal tracks in relation to population density and movement rates. The Formozov-Malyshev-Pereleshin (FMP) formula is both contentious for its simplicity, and little-known to the English scientific literature. The goal of this thesis was to examine the FMP formula as a means of expanding the use of tracking in conservation science. The setting for my studies was the sandy semi-arid Kalahari, with optimal year-round tracking conditions, host to a diverse mammalian wildlife community, and wherein I collaborated with expert local !Xo hunters to obtain accurate track counts and animal movement data. I first subjected the FMP formula to tests using simulations with both virtual and empirical data. By way of various simulated controls and manipulations of density, day range, and travel path tortuosity, I verified that the FMP estimator is theoretically robust. In so doing, I also highlighted the counter-intuitive necessity to enumerate all track interceptions with the sample

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transect regardless of double-counting individual animals. Secondly, I tested whether allometrically-estimated day range could adequately substitute empirical day range, in order to make FMP application more efficient for abundance assessments of complete wildlife communities. I found that obtaining locality-specific day ranges for a subset of species improved density estimates among the larger multi-species community derived from general allometric relationships. Thirdly, I made empirical comparisons of FMP-based population estimates to those using independent methods, namely distance sampling and aerial counts. I found little evidence that such conventional methods of standard practice exceeded FMP estimates in accuracy or precision, while the track-based estimates were clearly superior in terms of species comprehensiveness, distribution mapping, and cost-effectiveness. Whereas tracks are typically downplayed in relevance as nebulous indices and increasingly supplanted by high technology solutions for wildlife observations, I conclude that my research into the FMP formula warrants a reconsideration of tracking and future allocation of limited conservation resources. This is perhaps no more relevant than in the Kalahari environment where a dearth of reliable data and absence of local community involvement in conservation monitoring and practice ultimately imperils wild landscapes, while also contributing to the decline in advanced tracking skills and thus future possibility.

Preface

Chapter 2 of this thesis has been published as Keeping D, Pelletier R. 2014. Animal density and track counts: understanding the nature of observations based on animal movements. *PloS one* 9(5): p.e96598. The article was published under the terms of the Creative Commons Attribution License. Co-author R Pelletier developed the simulation environment and ran the computer simulations generating outputs that were then analyzed by myself.

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Dedication

For the trackers of the Kalahari,

and for the Kalahari itself,

may you endure the future more than just in memory and imaginations.

Acknowledgements

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1 Introduction

Throughout human evolutionary history, tracking arguably played a significant role in shaping our cognitive abilities (Liebenberg 1990, Hewes 1994, Shaw-Williams 2014, Stuart-Fox 2015, Lombard & Gärdenfors 2017); more so, perhaps, than most people realize. Mentally linking a track to the earlier presence of a track-maker is a seemingly simple yet profound leap and a plausible early step in the multi-staged evolution of causal cognition (Lombard & Gärdenfors 2017). Following an animal's tracks entirely by vision is a trait believed to be especially human; to the best of our knowledge other animals are incapable of it. Even our closest extant relatives - the other great apes - appear to be unaware of their own footprints. In the hollow mask illusion, our brains convert photographs of concave faces - like the hollow side of a mask or impression of a face in snow - into convex projections of faces. It is often argued (e.g. Eagleman 2015) that because our brains are conditioned to seeing human faces as convex, this top-down conditioning overrides the bottom-up data collected by our eyes. Interestingly, the same illusion sometimes happens with photographs of tracks (Plate 1-1): our brain seems conditioned to notice them.
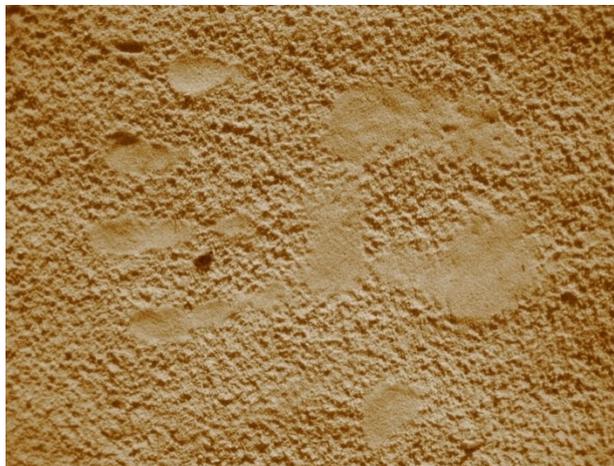
**Plate 1-1   Human hand print: appears as a depression in the sand
or protruding outwards?**

How important tracking was to our ancestral past is evident in the earliest art. Tracks were painted and etched into stone often alongside depictions of animals that predominate the subject matter of prehistoric rock art on all six habitable continents (Layton 1991, Van Der Ryst

et al. 2004, Carden 2009, Devlet et al. 2015). In their authoritative decipherment of meaning behind southern Africa's exquisite rock art, Lewis-Williams & Challis (2011) wrote, "Their art was not a record of daily events, heroic deeds or the natural world around them. . . So much infinite care went into the creation of this great variety of images that we cannot avoid concluding that they were immensely important to their makers and far from simple." Inexplicable tracks have fascinated humanity across time and cultures (Mayor & Sarjeant 2001), and some prehistoric paintings reveal the tracker-artists' ability to interpret physical characteristics of extinct creatures from their fossilized prints alone: "Bushman artists anticipated modern reconstructions of bipedal dinosaurs and produced depictions that are more realistic than many paleontological reconstructions that endured until quite recently" (Ellenberger et al. 2005).

Liebenberg (2013) posed a paradox of human evolution: the human brain had completely developed by the time we were Pleistocene hunter-gatherers yet this same neural hardware also gave us the scientific revolution. Among modern Kalahari hunters engaged in advanced tracking pursuits he observed the essential hallmarks of science at work. Earlier observers (e.g. Blurton-Jones & Konner 1976, Heinz 1978) were likewise struck by Kalahari hunters' care to distinguish between hypotheses, data and interpretation, discriminate their own observations and hearsay, willingness to change their minds as new evidence comes to light and often through critical discussion not dissimilar to the peer-review process, and curiosity about the natural world far exceeding that necessary for practical survival leading to knowledge purely for knowledge's sake. Liebenberg (1990, 2013) emphasized their hypothetico-deductive reasoning characterizing what he defined as 'speculative tracking'. This differs from 'systematic tracking' whereby hunters do not deviate in their pursuit of quarry from the immediate empirical evidence provided by tracks and sign. The systematic approach is time-consuming and therefore successful only under certain favorable environmental conditions. By contrast, speculative tracking involves going beyond available evidence to conjecture about an animal's behavior and direction of movement. Trackers don't waste time systematically following tracks, but take short cuts, looking for sign only where they expect to find it, to confirm or refute their expectations. Through this iterative process their hypothetical reconstructions are either reinforced, or if proved incorrect by new spoor evidence, their working hypotheses must be modified. While more difficult than systematic tracking, speculative tracking may be the only means of pursuit in difficult terrain where tracks are often invisible. It was realizations such as these that led

Liebenberg (1990, 2013) to convincingly argue that the practice of interpreting animal tracks co-evolved with human cognitive abilities that marked the origin of scientific thought. Notably, the latest evaluation of mitochondrial DNA (Chan et al. 2019) locates this sandy tracking environment in present day Botswana as the evolutionary crucible of modern humankind.

Given the important role tracking might have played in our evolution as intellectual creatures as a prerequisite to the eventual emergence of scientific institutions, it is ironic how minor a role tracking plays in modern science. Some reasons for this are obvious. Animal tracks are not apparent in many environments and therefore most people are exposed to them at only brief junctures throughout their contemporary lives. This deviates greatly from the experience of our hunting and gathering ancestors. Modern scientists might notice their dogs' tracks in a mud puddle or perhaps at the beach once in a while; minor events that in any case have no survival value and therefore little impact on their lives. Credentialed academics may have difficulty conceding Liebenberg's (1990) profound thesis simply because they cannot relate. Spending the majority of time living on artificial surfaces of concrete, linoleum, tile, hardwood, asphalt and manicured turf, people are oblivious how pervasive tracks were and how taken for granted awareness of tracks was to our African ancestors inhabiting semi-arid savannas. Modern schoolchildren are far better at identifying corporate logos or virtual taxonomies like Pokémon characters than they are in naming common wildlife (Balmford et al. 2002), let alone have any awareness of tracks.

At each step along the trajectory of technological evolution since humanity's departure from hunting-gathering to agriculture, industrialization through to the Digital Age, tracking became less important and less relevant to people. Today, few scientific applications consider tracking in any detail, with notable exceptions such as the field of ichnology (Lockley 1999), forensics and some military operations (Scott-Donelan 1998, Carss 2000, Stapleton 2015). Considering the overwhelming importance tracking held for our understanding of wildlife over the greater part of human history, one would expect it to play prominent in the modern field of wildlife science. Indeed it has, but the development of methods by which tracks can be quantified seems comparatively handicapped. With time, tracking application seems to be diminishing and increasingly supplanted by technology such as camera traps. Our lost tracking awareness might only be part of the reason.

This thesis focuses on the application of tracking to conservation biology, specifically, inferences about population abundance from animal tracks. There is an urgent practical need for methods to estimate wildlife abundance and/or determine its trend. For example, data on population size or trend is directly relevant to 3 of 5 IUCN red list criteria used to decide the conservation status of species and subsequent direction for intervention. Science and the limits of our empirically knowable universe are demarcated by human powers of observation, and technologies invented to extend those powers. The inherent observational limitations mean conservationists often struggle with basic and deceptively simple questions. Providing an answer to the question: "How many animals are there in this population?" seems simple enough but in practice it is not.

Many wildlife species are difficult to see, but their tracks can be conspicuous and ubiquitous in some environments. It is therefore tempting to make use of them. Wildlife scientists have long done so, especially for the study of rare, elusive, and cryptic species. Tracks are often the first evidence that an animal is present at all. They have placed animals thousands of kilometres outside of their known range, for example cougars (*Puma concolor*) in eastern North America (Cumberland & Dempsey 1994). The last fragments of Sumatran rhinos (*Dicerorhinus sumatrensis*) are known from their tracks (Flynn & Abdullah 1984) and have frequently eluded attempts to camera trap them (e.g. Kawanishi, Sunquist & Sahak 2003). In the extreme example, a scattered record of sasquatch tracks (*Anthropoidipes ameriborealis*) appears across western North America (Meldrum 2007) not easily dismissed as false positives (e.g. Bodley 1988), before a type specimen has been secured.

A read through the anecdotes in McDonald's (2004) survey of biologists' pioneering attempts to census sparse, rare and elusive species is enough to impress the latent value that tracks have, at least in verifying presence. Under the subtitle 'Failure Due to Lack of Proper Methodology', the story related by Doug Crowe is particularly telling:

"Doug Crowe indicated that his biggest failure was in an attempt to institute a census of aardvark (*Orycteropus afer*) in a region of Botswana, Africa. In his words, 'It was a disaster. I'm not even sure they are rare. They feed on termites . . . and the sign of them tearing into termite mounds is everywhere. However, they are active only at night. At

least that is what the books say. After a number of sleepless nights, we gave up the search. To date, I have yet to see a damned live aardvark!' (pg 34, McDonald 2004)

Indeed, a summary of encounter rates in Table 4-4 of this thesis illustrates the quantitative sampling disparity between spotlighting aardvarks (442 km/encounter) and observing their <24hrs old tracks (3.9 km/encounter) in Botswana's Kalahari ecosystem. Doug Crowe's frustration highlights a common theme plaguing the application of tracks in wildlife science; it is also a primary motivation for this thesis: a standard method to estimate the abundance of wildlife directly from counts of their tracks has been elusive. I sought a method not only applicable to rare species, but generalized for all terrestrial track-makers, abundant or rare. After all, everything that walks leaves footprints that are identifiable under the right substrate conditions such as sand, snow, dust or mud.

If tracks are possibly the most effective way to detect mammals, then why is there no common procedure available for estimating abundance from tracks? The simple answer is that it is not at all intuitively straightforward to infer the number of animals within a defined area from their tracks because of the inherent time element: tracks indicate the presence of an animal in the past i.e. the animal was certainly here, but now it is somewhere else. Scientists have struggled translating track observations into spatial density, a fact clearly reflected in authoritative reviews on estimating abundance (e.g. Krebs 1989, Schwarz & Seber 1999, Sinclair et al. 2006) wherein track data is infrequently mentioned.

The difficulty of estimating abundance from tracks is reflected in the scattered ways it has been approached. Widespread and various attempts appeared in the literature during the latter half of the 20th century. Some of the earliest were for over-abundant deer populations in the eastern US and in Poland. Tyson (1952, 1959) derived a formula to estimate deer density from track counts (see Appendix in Fritzen et al. 1995) that attracted considerable attention and refinements (e.g. Mitchell 1986, Fritzen et al. 1995). The method, based on the maximum straight-line distance over which deer ranged during nocturnal activity periods, lacked generality beyond a restrictive set of assumptions about deer behavior. Mandujano & Gallina (1995) lamented its inapplicability to other ecosystems and the elusiveness of a reliable deer track-to-density conversion factor.

Various techniques have been developed focussing on a single axis of animal movement and the probability such tracks intersect a network of parallel transects. Hayashi et al. (1979) proposed an approach that was constrained by the need to measure all intersecting trail lengths or the unrealistic assumption that trails are straight lines of known constant length that are randomly distributed. Becker (1991) and Becker, Spindler & Osborne (1998) developed techniques that require fresh tracks to be identified (after obliterating snowfall) from a slow-moving airplane or helicopter and then followed continuously to map the animals' coverage between sampling units. This method gained attention from statisticians (Fattorini & Marchesselli 2002) and has had repeated successful demonstrations with wolverines (*Gulo gulo*) (Golden et al. 2007) and lynx (*Lynx canadensis*) (Becker 1991), wolves (*Canis lupus*) (Becker, Spindler & Osborne 1998, Patterson et al. 2004) and cougars (Van Sickle & Lindsey 1991), but practical application is limited to low density species in snowy environments with sparse canopy cover. Enari & Sakamaki (2011) used radio-telemetry to estimate x-axis movement distances of Japanese macaques (*Macaca fuscata*) and developed a network of ground transects instead of aerial.

In several parts of the world there have been seemingly independent implementations of a 'drive census' involving a sweep of personnel driving animals over transects to register their tracks and count them (e.g. Overton 1971, Odendaal, Cameron & Priday 1980, Bobek, Perzanowski & Zieliňski 1986). However, drives are labour intensive, applicable in relatively small areas only, and cause disruption to populations that may be unacceptable. Other invasive methods have been proposed, for example based on measuring the relative decrease in track activity following the removal of a known number of animals (Sarrazin & Bider 1973) or capture and marking (toe-clipping) so subsequent tracks are distinguishable from unmarked individuals (Skalski 1991), neither of which are usually acceptable beyond populations of abundant small mammals.

Attempts to estimate population size through the identification of individual animals from their tracks are also prevalent. This was the basis of India's tiger (*Panthera tigris*) census for 30 years (Karanth et al. 2003), and Russia's for 50 years (Hayward et al. 2002). Even simple track measurements have been successfully utilized to census very small populations (<10 individuals) like Pyrenean brown bears (*Ursus arctos*) (Taberlet et al. 1997). However, there is a trend toward increasing sophistication of measurements and reliability in distinguishing individual animals

with the assistance of digital photography coupled with discriminating algorithms (e.g. Jewell, Alibhai & Law 2001, Alibhai, Jewell and Law 2008, Li et al, 2018). Initially constrained by the necessity of taking measurements from multiple tracks of every individual animal, the technique can now be extended beyond the initial database to classify free-ranging animals of unknown identity (Jewell et al. 2016). There have long been calls for applying individual track recognition to a mark-recapture framework (e.g. Smallwood & Fitzhugh 1995, Sharma, Jhala & Sawarkar 2005), but few demonstrations exist (O'Neil & Swanson 2010). The general approach to individual identity is fairly exclusive to small populations exhibiting tracks of large enough size to be distinguishable by expert observers or from which to obtain measurements with enough variation i.e. large carnivores, elephants, rhinos and tapirs. Attempts to differentiate smaller species such as pine marten (*Martes martes*) (Zalweski 1999) have proven less reliable, but there has been success using finely detailed papillae patterns of fisher (*Pekania pennanti*) and raccoon (*Procyon lotor*) prints on track plates (Herzog et al. 2007, Ellison & Swanson 2016).

Another stream proposes calibrating track counts to independent estimates of density by way of double-sampling (Eberhardt & Simmons 1987). Following Stander's (1998) seminal work with large carnivores, efforts have combined several species into single predictive models (Funston et al. 2010, Winterbach et al. 2016). Many have cautioned about comparing track indices between species (e.g. Beauvais & Buskirk 1999, Engemann 2005) and others have recently argued that the regression-based calibrations are statistically flawed (Gopalaswamy et al. 2015). As emphases on detectability have increased in the wildlife literature, the validity of calibrations applied to changing situations and conditions is increasingly called into question (e.g. Hayward et al. 2015). The main practical issue with double-sampling is that multiple paired independent estimates of density using rigorous methods (like mark-recapture, distance sampling, and occupancy approaches) are required, and these are expensive to obtain. The greater the frequency it is believed calibrations must be re-estimated for changing conditions that might affect detectability, the more the practical cost-savings of tracking are diminished.

A simple generalized method for estimating abundance directly from track counts with widespread applicability to diverse terrestrial species has evaded wildlife scientists. A common theme is the recognition that animal movement, sometimes framed as 'activity' (e.g. Allen &

Engeman 2015) is key to linking tracks to animal abundance. However, formalizing them together in a mathematical expression has been elusive.

Ironically, the theoretical breakthrough occurred almost 90 years ago (Formozov 1932) but remained largely confined to the Russian language. Casual references appeared from time to time in the English scientific literature (e.g. Dzięciołowski 1976, Högmander & Penttinen 1996, Zalewski 1999, Goszczyński 1999), but apparently attracted little attention. Now known as the Formozov-Malyshev-Pereleshin (or FMP) formula, it expresses a theoretically derived probability of two lines intersecting in a known space (see Stephens et al. 2006 for derivation). Thus, in essence the detection process of animal movements intersecting transects is modelled as a geometry problem. This theoretical development parsimoniously distilled the complication of estimating animal density from track counts down to a third variable: animal day range. Being the first to draw attention to the formula for English-speaking scientists, Stephens et al. (2006) wrote ". . . a formulation of equivalent simplicity and elegance does not appear to have been used outside the former Soviet Union".

It is my thesis that this long-hidden formula has unrecognized potential to transform and improve the use of tracking in modern conservation science. Stephens et al. (2006) discussed a variety of reasons that the FMP formula may be contentious and therefore not applied to its potential. Foremost among them is concerns over its theoretical basis and doubts regarding the potential for bias to be introduced by the spatial patterns of animal movements. Although "the FMP formula treats the probability of intersections between each transect section and movement section as independent" (Stephens et al. 2006), an intermediate step in its derivation describes the probability of the complete animal movement path intercepting the total transect length. This leaves it somewhat equivocal whether the number of track intersections in the final formula reflects the number of individual animals intersecting the transect, or the total number of intersections including multiple intersections by the same individuals. Another concern is potential for errors arising from misidentification of tracks. Stephens et al. (2006) also conclude that "independent validation of density estimates is essential if we are to have real confidence in the track-based approach." After bringing the FMP formula to the English-speaking scientific community in 2006, Stephens believed it would have attracted greater attention and more widespread application (pers comm). These concerns form the launching point for my thesis

research. In this thesis I attempted to directly address or control these issues, to see if understanding could be advanced and confidence increased regarding the FMP formula to yield more general application outside of Russia.

I used both simulation and field studies to test the FMP formula. For the field component I sought the optimal environment and collaborators. The tracking abilities of San Bushmen are legendary (Van der Post 1958, Thomas 1959, Biesele & Barclay 2001), with reason. The Kalahari Mega Sand Sea (McKee 1979) creates a surface underfoot much the same consistency as beach sand. To grow up in such an environment observing tracks virtually every day for a lifetime encourages an awareness of and ability to read tracks that is taken for granted by those who possess this skill but can appear astonishing to the uninitiated. This was apparent when Kalahari trackers were brought to France in 2013 to interpret 17,000-year-old Pleistocene human footprints in caves. They not only pointed out additional human tracks unrecorded by archeologists, but generated novel interpretations previously not possible due to the "insufficient knowledge of academically trained scientists in dealing with tracks" (Pastoors et al. 2015). While the hitherto archeological literature offered explanations including ritual dancing and claims of the only known Pleistocene print of a shod foot, trackers provided more plausible narratives and moreover pointed out specific features recognizable even to untrained observers supporting the validity of the trackers' interpretations (Pastoors et al. 2015). When Bushmen track-reading abilities have been tested to western scientific standards they have proven remarkably accurate and reliable even in distinguishing individual animals from their tracks and reconstructing complex past events (Stander et al. 1997).

I collaborated with southern !Xo speaking Bushmen, the last group known to practice what might be considered the epitome of advanced tracking skills - persistence hunting (Liebenberg 2006). I was interested in more rudimentary applications of their tracking skills however, essentially their capacity to correctly and reliably detect and identify tracks. It is perhaps worth noting that much of the anthropological work with Bushmen served to dispel Western notions about indigenous hunter-gatherers' preoccupation with supernatural explanations for phenomena and superstition-dominated daily lives (e.g. Heinz 1971, Blurton-Jones & Konner 1976). The truth is Kalahari hunters are especially empirically and critically-minded. During the serious business of tracking, "Non-real things are just not allowed to skew

the tracking process" (Lewis-Williams & Challis 2011). Afters years spent tracking with !Xo hunters both old and young, I can corroborate this observation.

In broadest terms, the question I set out to answer in this thesis is: Is the FMP formula useful? That is, does the number of track intersections along transects and day ranges of the animals that made those tracks predict the spatial density of those animals? I ask not only that, but if it is possible in a practical sense to apply the FMP formula to produce useful estimates of wildlife population densities. I discuss how improved understanding of the FMP formula would bring clarity to debates in the methods literature surrounding indices and their utility, as well as bring simple relief from the obsession over explicitly measuring detectability. Finally, and with much less attention devoted than the former problems, I briefly venture into the normative implications of this new knowledge in the context of reconciling western scientific techniques of conservation monitoring with local practices, particularly in the Kalahari. A substantial discourse exists, in North America especially, about integrating traditional ecological knowledge (TEK) and western scientific systems of wildlife conservation (e.g. Polfus et al. 2014, Ramos 2018). I choose not to emphasize a dichotomous view of knowledges and instead suggest that tracking is an exceptional opportunity to unify the advantages of traditional skills with modern quantitative methods.

In Chapter 2, I addressed the specific question: Is the FMP estimator robust against potential biases arising from differing shapes or patterns of animal movement paths? To obtain an answer I employed computer simulations using both virtual and empirical animal movement data that allowed me to control variables while manipulating tortuosity of animal travel paths and measuring its subsequent impact on track counts. To address concerns about non-random animal movements introducing estimator bias, I also made an empirical comparison of FMP estimates against distance sampling estimates under ideal conditions with two species exhibiting measurable differences in their travel paths.

In Chapter 3, I examined whether allometric day range can substitute for empirical day range to estimate wildlife densities using the FMP formula. Allometrically-estimated day range presents on opportunity to enhance the practical application of the FMP formula, especially rapid assessment of wildlife communities, because empirical estimates of day range are often unavailable and require extra effort to obtain. I drew on empirical track counts of 36 Kalahari

wildlife species and compared resultant allometrically-derived density estimates to those from a subset of species for which day range was known empirically. I also compared the allometrically-derived densities to available independent estimates of density in the same region using alternative methods.

In Chapter 4, I asked: Can trackers count free-ranging wildlife as effectively and efficiently as conventional aerial survey and distance sampling? To answer this, I ground-truthed Botswana's aerial survey and in addition to tracking conducted simultaneous line transects (distance sampling) to make a controlled three-methods comparison. In this comparison I addressed not only correspondence of estimates and their precision, but also practical matters such as comparative effort and costs. I enlarge the discussion to livelihood concerns in rural Africa and how an inclusive citizen science led by indigenous trackers would enhance the multi-faceted and inextricably human field of conservation.

2   Animal density and track counts: Understanding the nature of observations based on animal movements

2.1   Introduction

Estimating animal numbers is often a basic requirement for determining the status of species. However, this task is deceptively simple and no single best approach exists; techniques that work well in some situations are useless in others (Caughley & Sinclair 1994). Many terrestrial mammals are nocturnal, cryptic in appearance, and generally adept at avoiding being seen, which limits well-developed methods of direct observation, including distance sampling (Duckworth 1998, Chiarello 2000, Lopes & Ferrari 2000, Jachmann 2001). These challenges leave indirect observation, for example via animal tracks or remote photography, as often the only realistic option.

In many parts of the world, conservationists rely on animal track surveys as an indispensable tool. Animal track surveys are used in a range of efforts, such as large-scale biodiversity monitoring in northern Europe (Lindén et al. 1996, Danilov et al. 1996), North America (ABMI 2012), and Australia (Southgate & Moseby 2008), habitat and land use impact assessments (Soutiere 1979, Raine 1983, Kurki et al. 1998, Forsey & Baggs 2001, Crookes 2002, Fritz et al. 2003, Norris et al. 2008), planning sustainable harvest of ungulates and furbearers (Dzięciolowski 1976, Reid et al. 1987, Ballard et al. 1995, Beier & Cunningham 1996, Engeman et al. 2002, Engeman & Evangilista 2006, Linnell et al. 2007), managing invasive species (Allen et al. 1996, Edwards et al. 2000, Engeman et al. 2001, Southgate et al. 2007), and monitoring endangered populations such as black rhino *Diceros bicornis* (Alibhai & Jewell 1992), tigers *Panthera tigris* (Hayward et al. 2002, Karanth et al. 2003), Florida panther *Puma concolor* (Johnson et al. 2010), wolverine *Gulo gulo* (Edelmann & Copeland 1999, Halfpenny et al. 1995), and polar bears *Ursus maritimus* (Wong et al. 2010). Where substrates are suitable, practitioners continue to use track surveys because they are simple, practical, inexpensive, and readily produce detections for all terrestrial animals including those otherwise difficult to detect. Ironically, science may have origins in tracking. Liebenberg (1990) notes that a fully modern human brain evolved when all humans were hunter-gatherers and argues that efficient tracking techniques necessary for successful acquisition of prey still practiced by contemporary hunter-

gatherers were the origin of creative hypothetico-deductive thought processes now made explicit by modern science.

In spite of this widespread reliance on tracks and historical perspective, theoretical developments to advance our understanding of the relationship between tracks and their makers' true population density have generally been sidelined in favour of direct sightings or technologically advanced approaches to wildlife science. While there have been some creative approaches to estimating density from track counts (Becker 1991, Sarrazin & Bider 1973), such counts are most often relegated to simple indices of relative abundance [e.g. Thompson et al. 1989, Smallwood & Fitzhugh 1995, Carrillo et al. 2000, Silveira et al. 2003, Blaum et al. 2008). Sometimes, these indices are calibrated to true density through double sampling (Servin et al. 1987, Stander 1998, Funston 2001, Houser et al. 2009, Funston et al. 2010). In both cases, the relationship between the index and the population density is assumed to be linear, monotonic, and stable. It is this failure to account for changing detection probabilities that has prompted criticisms on the use of such indices (Anderson 2001, Jennelle et al. 2002), despite urgent practical reasons for conservationists defending their use (Engeman 2003, Carbone et al. 2002). Wildlife management and conservation practitioners around the world would benefit from a better understanding of the mechanistic basis linking indirect observations, such as track counts, to animal abundance.

The Formozov-Malyshev-Pereleshin (FMP) formula is an analytical method for converting track counts to population density. This formula was first developed over 80 years ago to estimate game numbers in the snowy regions of Russia. The formula's conceptual basis and derivation is described in Stephens et al. (2006). In short, it is derived from the probabilistic intersection of lines of specified lengths within a defined area and therefore describes the relationship of both transect length and animal day range (lines) to track counts (intersections) and animal density. The formula has the following form:

$$D = \frac{\pi}{2} \frac{x}{S\hat{M}}$$

where x is the total number of track crossings over one 24-hour period, S is the total transect length, and $\hat{M}$ is the mean daily travel distance for all animals in the study area.

Since its recent introduction to the English scientific literature (Stephens et al. 2006), the FMP formula has prompted a closer look at ideal gas models and the development of a parallel approach to estimate density using camera trapping rates (Rowcliffe et al. 2008). However, despite widespread applicability, the FMP formula still remains underappreciated and is rarely applied outside of Russia. Previous work has addressed the formula's theoretical basis (Stephens et al. 2006), but perhaps the simplicity of the derived relationship leaves lingering doubts regarding the spatial element of animal movement influencing detectability and encounter rates. Concerns over the non-randomness of animal movements seem to persist (see Rowcliffe et al 2013), although these concerns have been addressed to some extent in recent reviews of ideal gas models (Hutchinson & Waser 2007, Gurarie & Ovaskainen 2013). Most work has been based on simulations and there have been few field tests to address doubts regarding the non-random movements of real animals, their non-random dispersions, and their frequently non-independent movements (but see Rowcliffe et al. 2008).

In this paper, we separate animal movements into their day range and tortuosity components to examine the FMP formula. We use three levels that progressively decrease randomness and increase the realism of movements and space use (Table 2-1). If the FMP formula is fundamentally valid, specific shapes of animal movement paths should be irrelevant, i.e., a population of animals displaying linear movements and another population of equivalent density and day ranges but displaying convoluted movements would show no difference in their mean number of track crossings and would therefore be estimated with equal accuracy. We constructed these scenarios using virtual animal populations simulated to exhibit the desired parameters over the range of extremes expected to be encountered in real systems. We then examined two species that showed qualitative and quantifiable differences in the spatial patterns of their daily movements. Using accurate tracings of their actual daily travel paths, we simulated their populations with a random dispersion and tested how accurately the FMP formula could estimate their numbers. This same technique has also been employed previously with three species of deer and wild boar (Stephens et al. 2006, 2006b). Finally, there is an expressed need to compare FMP estimates of real populations with independent density estimates (Stephens et al. 2006). We make this comparison using two sympatric antelope populations since these animals are readily visible and amenable to distance sampling with line transects. Although we use examples from a specific context by necessity, our goal is broad and these explorations reveal a

more general understanding of how animal movement parameters influence their detection. While some findings are not strictly novel, our purpose is to make these findings relevant and advance the field of tracking to benefit conservation.

Table 2-1   Differentiation of animal movements and dispersion with progressively increasing realism over three levels of testing

Level of testing	Animal spatial characteristics	
	movement	dispersion
Simulation (virtual animals)	random	random
Simulation (empirical movements)	non-random	random
Real population comparison	non-random	non-random

2.2   Methods

2.2.1   Study area

Data collection occurred in the KD1 Wildlife Management Area directly north of and adjacent to the Kgalagadi Transfrontier Park in southwestern Botswana. The Government of Botswana via the Ministry of Environment, Wildlife and Tourism and Department of Wildlife and National Parks granted approvals and permits (numbers EWT 8/36/4 XII (35), WP/RES/15/2/2 XXII (87)) to conduct the study within this publically owned, partially protected area. Since the field sampling techniques were non-invasive, ethics approval was not required. An area within 30 km of the unfenced park boundary was selected on the basis of its habitat uniformity and its high densities of the target antelope species. Human impacts in this area are minimal since the nearest settlement is a subsistence-pastoral community 70 km away. The country is relatively open semiarid savanna overlying a consistent sandy substrate. The plant community coincides with the *Schmidtia kalahariensis* type (Skarpe 1986); the dominant species are *Acacia luederitzii, Acacia erioloba, Grewia flava*, and *S. kalahariensis*. Visibility is good in the open savanna and tracking conditions are excellent. We collaborated with local tracking experts and horsemen from the adjacent remote area settlement of Zutshwa to conduct the field study.

2.2.2 Track counts

A single 10 km transect was created to bisect the unbounded study area. Track crossings were counted along this transect over six consecutive 24-hour periods by observers on specialised seats mounted to the front of a vehicle travelling at 6–8 km h^{-1}. One expert local tracker and DK conducted all of the observations. No effort was made to eliminate subsequent crossings of the same individual animal. Surveys began at approximately the same time each morning (08:00 h) and progressed at a similar rate, while concurrently a heavy steel beam was dragged behind the vehicle, which effectively obliterated tracks. This technique ensured a precise 24-hour period for track accumulation.

2.2.3 Diel animal movement

We selected two ungulate species thought to exhibit general differences in both spatial dispersion and the pattern of their travel paths: gemsbok *Oryx gazella gazella* and steenbok *Raphicerus campestris*. We wanted accurate measures of these species' daily travel distances and spatial tracings of their daily travel paths at high resolution.

We followed the tracks of individual animals to retrace the path that they walked. GPS data-loggers (Columbus V-900, Victory Technology, Fujian, China) programmed to take fixes at 1 s intervals captured fine-ruler tracings of each animal's movement. Steenbok were tracked on foot and gemsbok were traced from horseback. Different ecologies dictated different approaches to obtaining diel tracings.

Steenbok pairs defend small territories (0.6 km^2; (Skinner & Chimimba 2005)), which precludes forward-tracing their movements within a diel period because the presence of trackers invariably influences those movements. Instead, we opportunistically used rainfall events that reset the track record. When rainfall ended during the day, we sighted steenbok 24 h later. This was possible because steenbok are abundant and easy to see. From sighting, we back-tracked the animal to the point where the tracks became marked by raindrops.

For gemsbok, we spotted animals in the mid-morning. The next day, early in the morning, the animal was forward-tracked from the point of sighting. The tracing was terminated when the animal was re-sighted or when the animal obviously fled the approaching horsemen. In

some instances, tracings were completed after 24 h had elapsed. Excess distance was subtracted from the travel record according to the fraction of the 24-hour period that had elapsed.

We used a simple metric of tortuosity, calculated as a ratio of the total daily travel distance divided by the distance between the start and finish locations, to quantify differences in spatial patterns of steenbok and gemsbok travel paths.

2.2.4 Line transects

Since both steenbok and gemsbok are abundant enough to be readily visible, we used distance sampling with line transects to independently estimate density. We sampled along three parallel, equally spaced 10 km transects, each separated by 3 km. The centre transect was the same as that used for the track counts. Transects were created simply by driving a vehicle off-road and were sampled several times during daylight hours at a speed of 20–30 km h^{-1}. Animals were spotted by the driver and by two observers positioned on the tracker seats. When animals were spotted, their group size was determined and the vehicle was stopped when the line of sight to the animal(s) was at an angle perpendicular to the transect. The distance between the animal(s) and the transect was determined with a laser rangefinder. Occasionally, when animals fled before the vehicle could reach the perpendicular location, a tracker would walk to the place where the animal(s) was standing so that an accurate reading could be obtained with the rangefinder. Densities with 95% bootstrap confidence intervals (CIs) were estimated using conventional distance sampling (Buckland et al. 2001) with Distance 6 software (Thomas et al. 2010). We selected detection probability functions and adjustments based on Akaike Information Criterion and graphical best fits to the sighting data.

2.2.5 Simulations

We simulated virtual animal populations exhibiting incremental levels of travel path tortuosity (t), across combinations of density (D) and day range (M) expected to approximate the range in variation of most terrestrial species for which tracking is applicable.

We began with a conceptual area of 2500 km^2 (50 × 50 km^2). For each scenario of animal D, M, and t, one straight-line transect 10 km in length was imported into the area with a random starting location and orientation. Then, using an appropriate density, "animals" were

randomly imported as points from which they moved in random directions to the specified M and t, as described below. This process was repeated 1200 times, resulting in a 12000 km survey effort for each permutation of D, M, and t. We simulated t by beginning with a population exhibiting straight-line movements, then incrementally increased the number of "turns" the animals made by breaking the movement paths at random distances and assigning a random turn angle at each vertex. This approach simulates an uncorrelated or pure random walk. Incremental tortuosity was denoted by $t = 0$ (straight lines), $t = 1$ (single turn), $t = 2$ (two turns) . . . 10, 20, 30, 40, 50. Within each level, the tortuosity of individual "animal" paths varied widely because the turn angles were random (between 0 and 2π); however, the average tortuosity for the population increased in proportion with the total number of turns. The levels of movement length were $M = 0.3$, 3, 10, 30 km and the levels of density were $D = 0.0004$ (one animal), 0.0002, 0.004, 0.002 0.04, 0.02, 0.4, 2, and 4 km^{-2}. Intersections between both every "animal" travel path and between each path segment and the transect were summed for each transect.

To increase the spatial realism of the simulation, virtual populations were unbounded by the conceptual area. Animals were dispersed randomly at a specified density within the area, but equally throughout a larger buffer area. The animals were then permitted to move without regard to boundaries. Transect intersections included animals originating inside and outside the conceptual area. For each scenario, an equal number of animals were just as likely to move from inside the area to outside the area and vice versa. Structuring the simulation in this way avoided edge effects and most closely approximated reality when applying a track transect survey to an unenclosed population.

In addition to virtual populations, we simulated populations of both antelope species using their real travel paths. Empirical paths were pulled randomly with replacement from the available data set and imported into the conceptual survey and buffer area with random starting points and orientations until the desired number of animals was reached for a range of densities from 0.02–4 km^{-2}. A 10 km transect was then imported with a random starting point and orientation, over which the transect intersections were enumerated. This process was repeated 500 times. Notably, the locations and orientations of both the travel paths and transects were randomized over each iteration. The same consideration for movement in and out of the study area was also applied.

2.2.6   FMP calculations

We used nonparametric bootstrapping (Efron & Tibshirani 1993) to calculate the uncertainty in the FMP density estimates. For real populations, both daily replicate transects and available movement paths were resampled with replacement at original sample sizes to produce bootstrap replicates of x/S and $\hat{M}$, from which one estimate of D was calculated using the FMP formula. This process was repeated 5000 times to generate the distribution of D for each species, from which the mean and bias corrected and accelerated 95% CIs were calculated. We used a similar approach for the simulated populations, whereby bootstrap replicates of x/S were generated by resampling from the entire data set of iterations in proportion to the appropriate survey effort (i.e., 100 km survey effort generated by resampling 10 random transect iterations, 250 km from 25 transects, etc.). The calculations for virtual populations differed only in that M was a single value and therefore did not contribute to uncertainty in the resulting density estimates.

2.3   Results

2.3.1   Simulated animal movements

The fundamental linear relationships defined by the FMP formula were verified by the simulation results. For example, a doubling of D results in a doubling of x/S, which corroborates previous findings (Stephens et al. 2006b). Similarly, it was clear that for a constant value of D, a doubling in M results in a doubling of x/S.

When D and M were held constant, the mean number of intersections per transect did not change over levels of t, from straight-line movements to highly tortuous random walks. A subset of outputs from several combinations reveals this consistency (left panels in Fig. 2-1). Because the mean encounter rates did not change, the FMP formula estimated densities accurately regardless of the shape taken by the travel paths. At the maximum number of transect replicates (1200), the mean estimates from all scenario combinations deviated by a maximum of 2% from the true simulated densities.

Although tortuosity had no effect on the mean encounter rates and the subsequent accuracy of the FMP estimation, detectability was affected. Detection probabilities, reflected by

the number of individual animals that intersected transects, declined with increasing tortuosity (right panels in Fig. 2-1). Simulated animal movement paths originating from the same point (Fig. 2-2) help to visualise the declining detectability that resulted in the pattern in Fig. 2-1 (right panels). With increasing tortuosity, the average displacement covered by the paths decreased, so that paths at t = 8 covered just over half of the Euclidean distance as t = 0. Transects that sampled populations exhibiting the most tortuous paths (t = 50) counted fewer than 30% of the individual animals that were counted when those populations exhibited straight-line movements (t = 0). The results indicated that detectability is determined by both day range and tortuosity. This effect could only be established via simulations because in a majority of situations it is impractical and impossible to determine with certainty if tracks belong to the same or different individual animals.

A further consequence of the interaction of day range and tortuosity is uncertainty in the resulting density estimates. The sample variance increased when the travel paths became shorter and more convoluted. The effect is apparent over a broad range of expected daily movements for terrestrial species (Fig. 2-3). Species with smaller bodies are more likely to occupy the low end of day range (0.3 km); examples include tortoises, some weasels, mongooses, primates, and likely many rodents (Keswick 2012, Wrangham et al. 1993, Carbone et al. 2005). At the other extreme, spotted *Crocuta crocuta* and brown hyaenas *Hyaena brunnea* in the Kalahari have been recorded moving on average 26.5 and 31.1 km per night, respectively (Mills 1990). However, the majority of terrestrial species for which track counts are applicable are likely to have daily ranges somewhere in between these values (see Wrangham et al. 1993, Carbone et al. 2005). When the survey effort reached 250 km (1 km sampled for every 10 km^{-2}), the 95% CIs ranged at the extremes from 54–154% of the true density (panel d of Fig. 2-3) to 97–102% of the true density (panel c of Fig. 2-3). However, these results likely overestimate the precision that can be achieved in real populations because the virtual animals in the simulations were dispersed randomly, the group size was therefore one animal, and $\hat{M}$ did not vary. Therefore, the outputs in Fig. 2-3 primarily illustrate the general effect of day range and tortuosity on precision.
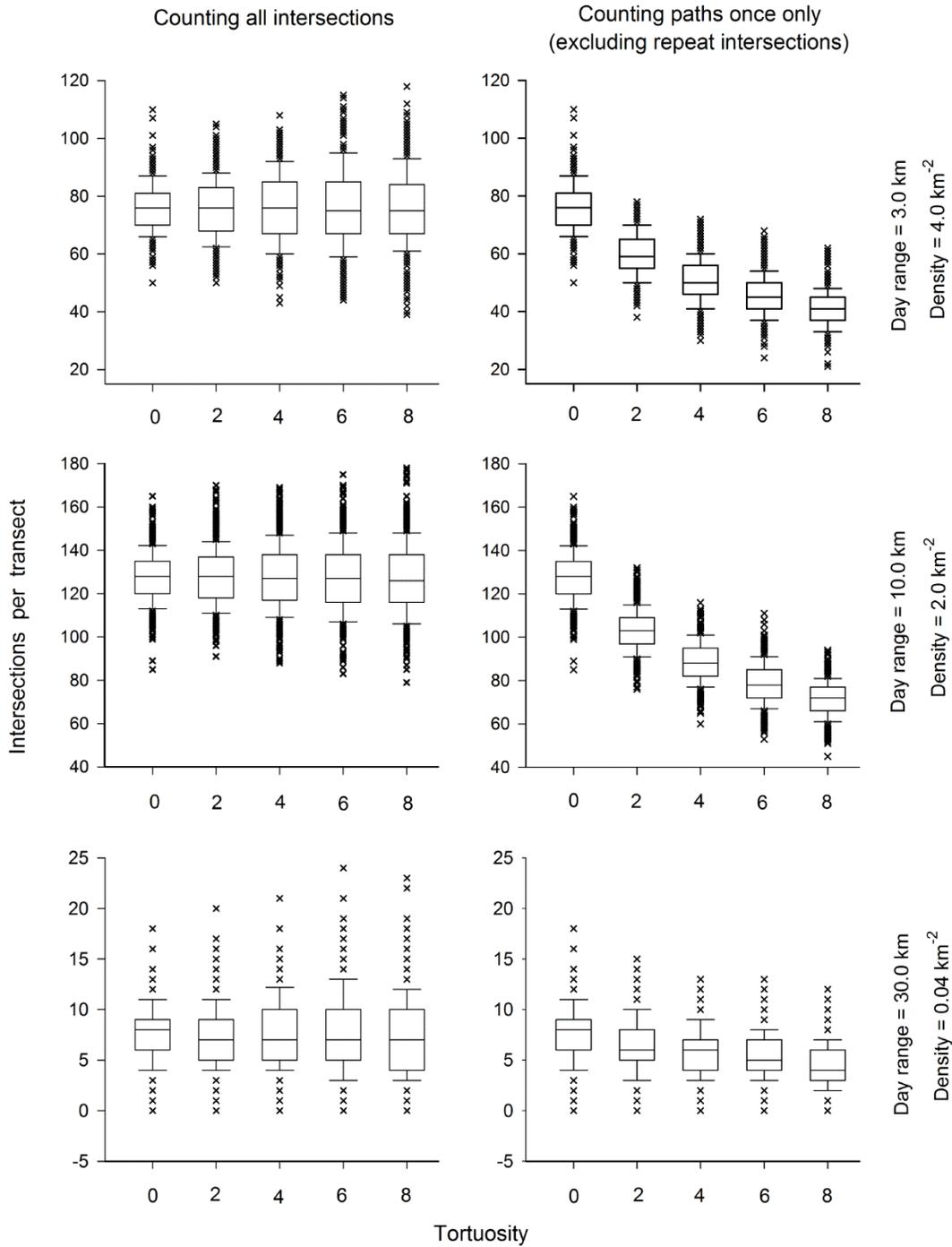
Figure 2-1   Sample output from three combinations of simulated daily travel paths and densities. Box plots with outliers are shown; each data point represents the numbers of intersections per transect (500 iterations) across five arbitrary levels of path tortuosity.
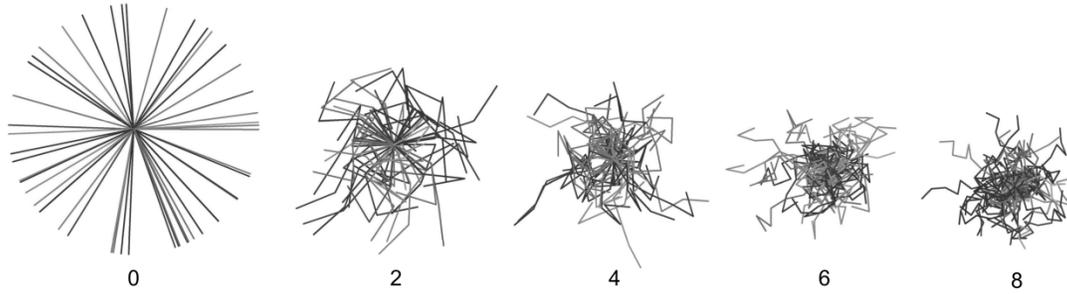
Figure 2-2   Displacement of simulated animal travel paths over levels of tortuosity. Fifty travel paths of equal length originate from a common centroid for each level of tortuosity (numerals indicate the number of random turn angles).
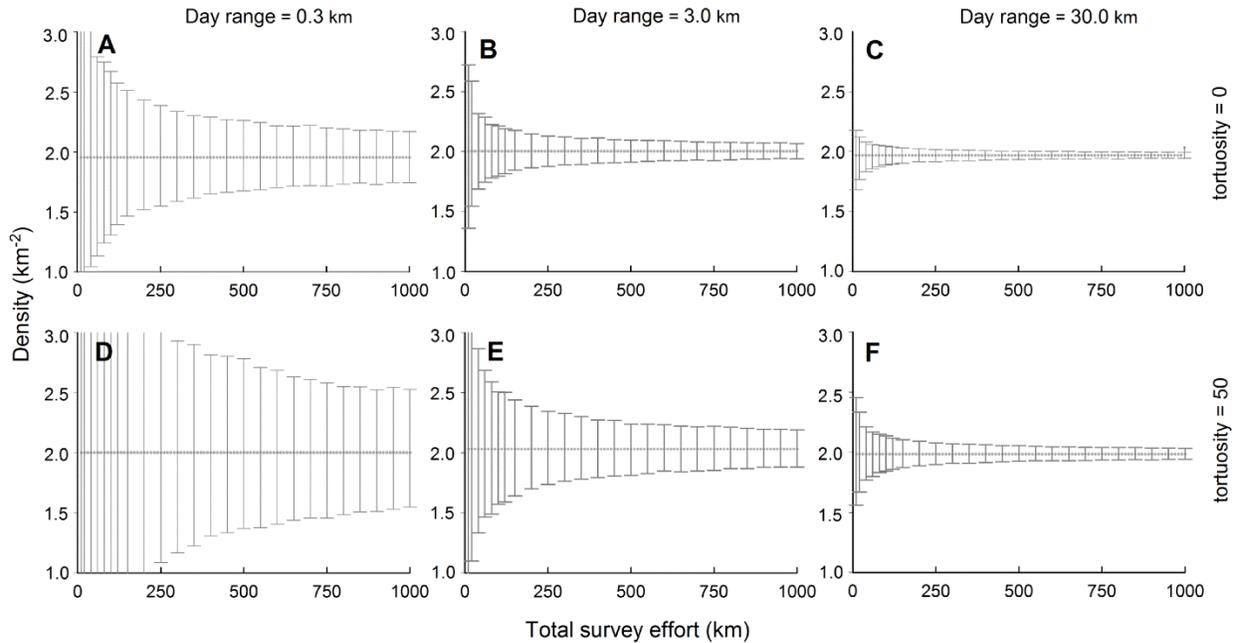
Figure 2-3   Effect of daily travel distance (column panels) and path tortuosity (row panels) on FMP estimate precision. Mean densities and 95% CIs are shown from applying the FMP formula to 10 km transects sampling virtual populations at 2 km^{-2}. Dotted lines indicate the accuracy of mean density estimates at 1200 replicates, which vary within 2% of the true density. Note that both day range and tortuosity influenced achievable precision.

2.3.2 Simulation using empirical travel paths

We traced 17 gemsbok and six steenbok diel travel paths. Despite body sizes that differ by over an order of magnitude, the two species' daily movement distances did not differ considerably; gemsbok travelled 5.65 (coefficient of variation 0.42) km on average and steenbok travelled 4.20 (0.34) km on average. However, the patterns of their travel paths were markedly different. Gemsbok had more linear movements, covering larger areas in the landscape. This aspect was reflected in a tortuosity metric of 4.22 (0.62). Steenbok, confined to relatively small territories, displayed much more tortuous movement patterns, with a tortuosity metric of 10.86 (0.31).

When empirical movements were dispersed randomly in the simulation space, gemsbok had higher detectability than steenbok by virtue of the differences in the shapes of their travel paths and resultant space use (Fig. 2-4). Considering day ranges that differed by only 34.5%, at equivalent densities, 3.3 times more individual gemsbok were detected than steenbok per transect on average. However, if a gemsbok was detected, it was likely to intersect a transect 2.2 times on average. In contrast, if a steenbok was detected, it was likely to intersect a transect 5.4 times on average.

Over the range of simulated densities, when transects were replicated 500 times, the FMP formula returned mean estimates within 5% of their true value, which is further evidence that the estimator is unbiased by the specific shapes of animal movement paths. For example, when the population density was 2 km^{-2}, the number of gemsbok was estimated to be 1.97 km^{-2} and the number of steenbok was estimated to be 2.03 km^{-2} (Fig. 2-5). The accuracy of these mean estimates approached the true densities once the cumulative survey effort reached about 250 km or a sample penetration (Stander 1998) of 1 km of transect per 10 km^2 of survey area. At this effort, CIs around point estimates were 73% of the mean density for gemsbok and 54% of the mean density for steenbok. This precision was poorer than that of deer from Stephens et al. (2006) due to less precise estimates of $\hat{M}$ arising from smaller sample sizes. The effect of variation in $\hat{M}$ on the precision of the density estimates is illustrated by comparing with virtual populations where the day range was constant (see the spread of 95% CIs in Fig. 2-3 versus Fig. 5).
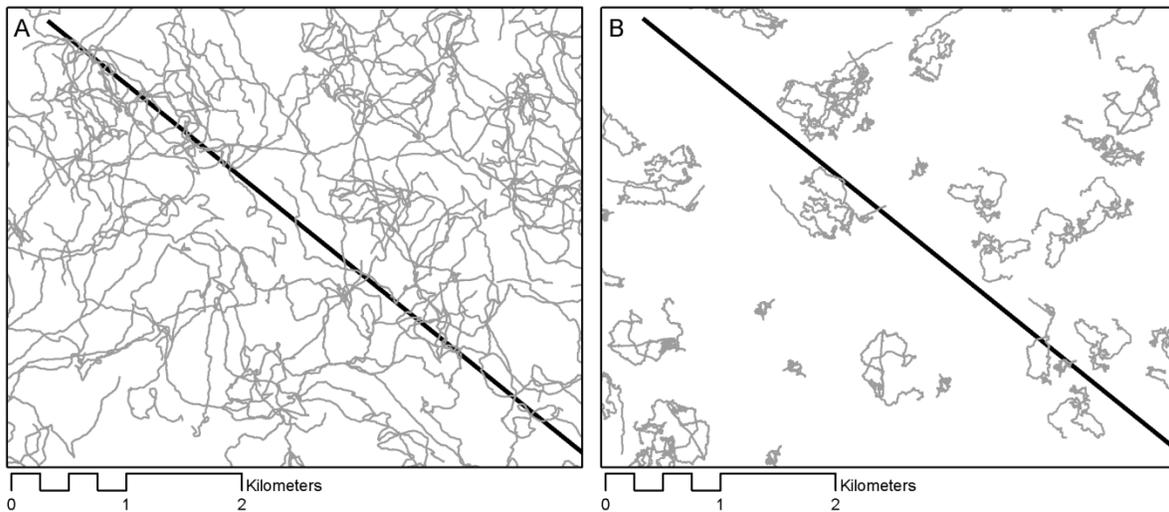
Figure 2-4 **Empirical daily movements dispersed randomly in simulation space.** Image capture (1:50 000) shows a single iteration of simulation runs at 2 km^{-2} density for (A) gemsbok and (B) steenbok. Approximately half of the randomly oriented transect (black) appears diagonally, underlying travel paths (grey). Note that both gemsbok and steenbok have similar daily travel distances but display different tortuosity in their movements, resulting in different spatial use.
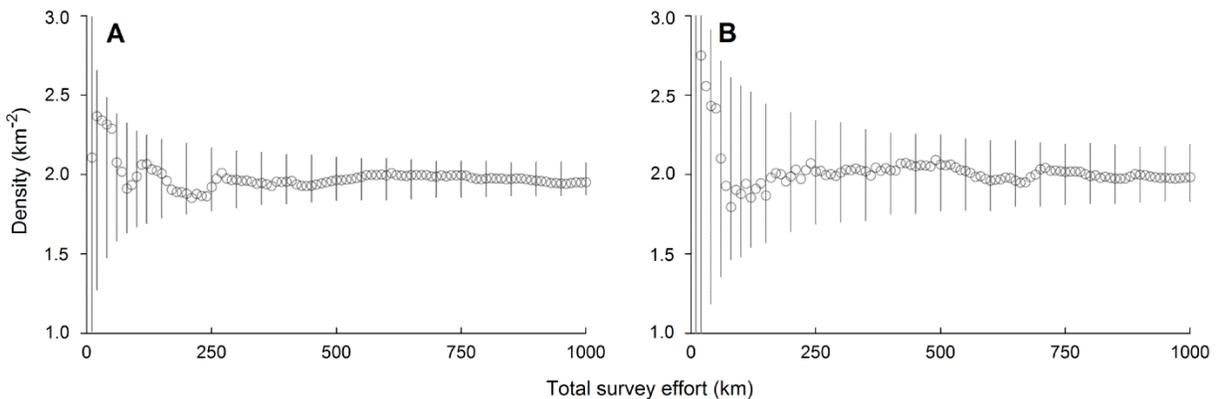
Figure 2-5 **Estimates from simulated densities (2 km^{-2}) using empirical movements of (A) gemsbok and (B) steenbok.** FMP point estimates of density from a random cumulative increase in survey effort (10 km transects) are displayed along with 95% CIs.

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2.3.3 Real population comparison

Both antelope species had similar encounter rates along the track transect: gemsbok with 8.59 intersections km^{-1} 24 h^{-1} on average and steenbok with 9.58 intersections km^{-1} 24 h^{-1}. Combining these data with their respective day ranges in the FMP formula returned density estimates for gemsbok (2.39 km^{-2}; 95% CI: 1.57–3.23 km^{-2}), and steenbok (3.33 km^{-2}; CI: 2.71–4.17 km^{-2}). Line transects (394 km) revealed 74 gemsbok observations (270 individuals) and 66 steenbok observations (72 individuals). Conventional distance sampling analyses and bootstrap CIs produced estimates for gemsbok (2.57 km^{-2}; CI: 1.43–4.62 km^{-2}), and steenbok (3.7 km^{-2}; CI: 2.47–5.55 km^{-2}). Despite small sample sizes and unknown true densities, the two independent approaches returned density estimates that were closely matched (Fig. 2-6). Assuming that the distance-based estimates are accurate, this limited comparison is suggestive that the FMP estimator was also accurate and robust to non-independent animal movement patterns and non-random dispersion.
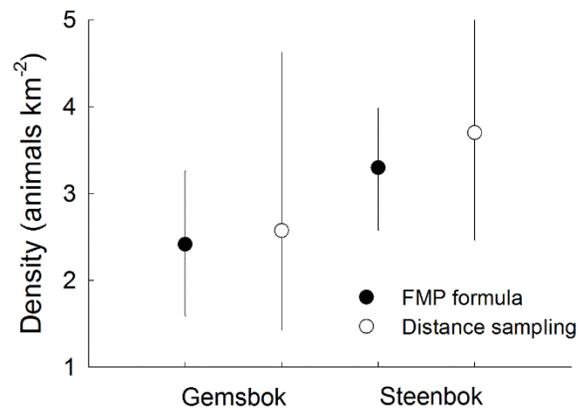
Figure 2-6   Density estimates of two empirical populations using the FMP formula and Distance sampling. Displayed with 95% bootstrap CIs.

Track-based estimates were more precise than distance-based estimates (Fig. 2-6). Transects were only 10 km in length, so direct observations of animals per transect were limited and several line transects had zero counts for each target species. As a result, it was necessary to sample two additional line transects in parallel to the centre transect to obtain a minimum

number of sightings for estimating detection functions. In contrast, track counts captured close to 100 observations per transect. There was higher variance in the numbers of observations on different line transects (CVs of 0.96 and 0.84) compared with track transects (CVs of 0.42 and 0.11) for gemsbok and steenbok, respectively, which was reflected in the wider CIs shown by the distance-based estimates compared with the FMP estimates.

2.4   Discussion

When it is suggested that counts of animal tracks can be used to estimate population density a remarkably immediate and consistent question from both biologists and laymen is "but how do you avoid over-counting the same individual animals?" This issue seems intuitively problematic. Repeated counting of individual animals' tracks along a transect or between spatial replicates during a survey is frequently viewed as a problem. Some efforts have attempted to reduce the rate of re-counting individual animals by using arbitrary exclusion distances between sets of tracks (McBride et al. 2008, Squires et al. 2004) or by separating transects sufficiently in space so that the probability of a single animal being recorded on more than one line is minimized (Smallwood & Fitzhugh 1995, Edwards et al. 2000, Wilson & Delahay 2001, Stanley & Royle 2005). Reliably distinguishing individuals based on their tracks is much more difficult and perhaps possible among a few species such as large cats (Stander et al. 1997, Smallwood & Fitzhugh 1993, Riordan 1998, Sharma et al. 2005), rhinos (Jewell et al. 2001), tapirs (Lizcano & Cavelier 2000), and potentially elephants (Jachmann 1984). However, exceptional trackers or detailed measurements and sophisticated analyses are required. In contrast, counting every track intersection is repeatable and simpler than attempting to separate individual animals, but rarely implemented because such counts are considered to be difficult to interpret (Mahon et al. 1998). At the least, track surveyors typically make some effort to eliminate obvious re-crossings that are visually connected (Stephens et al. 2006, O'Donoghue et al. 1997). Decisions must be made at the outset of every program whether to discount re-crossings of same individual animals, simply record presence over some spatial dimension, or enumerate each and every track. The literature reflects little agreement on an optimal approach.

If density estimates are sought, the FMP formula suggests that re-counting the same individual animals is not a problem and that it is in fact desirable to count the same individuals if they re-cross transects within the same 24-hour period, as many times as they do. Geometry

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dictates a balance between the number of intersections and the length of line segments, regardless of the shapes of the lines. The inference is simply that individuals with more tortuous movements are detected less but, when encountered, those individuals are generally counted a larger number of times by virtue of the convoluted pattern of their movement. Detectability is influenced by tortuosity; the total number of intersections is not. The FMP formula describes the relationship between counts and true density if correct track counting rules are applied. A strict definition of detectability includes the probability that tracks are observed after they intersect a transect. We expect this probability to approach 1 in the Kalahari, where tracks are easily visible and can be verified by more than one expert observer. However, surveyors in different parts of the world surely have wide variation in tracking skill level (see Stander et al. 1997, Evans et al. 2009) and tracker proficiency should be addressed more often (Wharton 2006). Nonetheless, our consideration of detectability here has been limited to the more fundamental probability of intersection between animals and transects. This detection probability remains an imprecise concept, determined by the interaction of day range and path tortuosity. Among two populations with equal movement rates, we have shown that those with more tortuous movements have lower detectability. Likewise, if two animals have equally tortuous movements, the animal with a longer day range will have higher probability of being detected. The interaction of these two travel path parameters can perhaps be conceptualised as the displacement that animals cover during their daily patterns of movement, i.e., those individuals that cover larger distances in Euclidean terms have greater detectability.

2.4.1 Implications for occupancy

Track surveys have often been applied to model the fraction of sampling units in a landscape where a target species is present (occupancy) in order to monitor distributional changes (Squires et al. 2004), but also as a surrogate for abundance to monitor trends in population sizes (Kendall et al. 1992, Zielinski & Stauffer 1996, Hines et al. 2010). Animals have high detection probabilities by their tracks because such indirect observations are time integrated and reflect animal presence over an area typically much greater than the space within which animals can be observed directly at a particular moment. For example, 95% of gemsbok and steenbok sightings along line transects in the present study occurred within 355 and 120 m, respectively. Track counts certainly captured animals that had travelled from, or to, a substantial

distance beyond which direct sightings are possible. This factor contributed greatly to track observations in the 8–10 km^{-1} range, while some line transects failed to detect either species.

Minimizing the imperfect detection of species (false absences) has become a key concern of occupancy studies (MacKenzie & Royle 2005, Vojta 2005, MacKenzie 2005). Although the FMP formula is unaffected by the vagaries of specific spatial patterns of animal movements, applications utilising presence-absence data from indirect sign are vulnerable to biases emerging from changing animal detectability. For example, when empirical movement paths were imported randomly to a density of 0.04 km^{-2} (100 animals within the study area), a survey effort of 100 km (10 transects) had a >99.9% probability of detecting gemsbok presence, but an 86% probability of detecting steenbok presence in the area. When 500 transects were applied to these populations in a single survey, 51% of individual transects detected gemsbok, while the presence of steenbok was recorded on only 18.2% of transects. Differences in detectability between these two species due to tortuosity can be seen in Fig. 2-4. The tortuosity of animal movement paths may fluctuate widely within species and individuals for any number of reasons that are difficult to predict (Roshier 2008). Since detection probabilities of animals by their tracks are not constant, even over short periods (day to day), an appropriate occupancy design would require repeated sampling and assume no unmodelled heterogeneity in detection to make reliable inferences (see MacKenzie et al. 2002). The key concern is whether these heterogeneous detection probabilities can be captured adequately by a combination of environmental covariates and conditions specific to track accumulation period (MacKenzie et al. 2002), or by extending the interval for track accumulation over several days (Stanley & Royle 2005).

It is often reiterated that occupancy studies are advantageous because presence-absence data are often easier and less expensive to collect than count data (e.g. Vojta 2005, MacKenzie & Nichols 2004, Gu & Swihart 2004, Nielsen et al. 2005, O'Connell et al. 2006). However, this suggestion is doubtful in the case of animal track surveys. Since all animal tracks have to be observed during a survey, we suggest that little additional effort is required to count every track intersection, from which presence-absence data are easily extracted later, if desired. Hayward et al. (2002) reported that despite increased variance caused by counting repeat track intersections along transects, this index had more power to detect declines in Amur tigers *Panthera tigris altaica* than did presence-absence data. Presence-absence studies frequently report low power

and capability to detect only large trends (Kendall et al. 1992, Beier & Cunningham 1996, Clevenger & Purroy 1996, Strayer 1999), require intensive sampling protocols with a large number of replicates and repeated sampling over short periods (MacKenzie et al. 2002, MacKenzie & Royle 2005), and necessitate restrictive assumptions regarding independence of sampling units (Royle & Nichols 2003, Stanley & Royle 2005). In contrast, the FMP estimator embraces count data while dispensing with concern over individual animals being detected in more than one sampling unit and negating the explicit requirement to estimate detectability. In many cases, the FMP formula may provide a more parsimonious approach than modelling occupancy as a surrogate for indexing abundance and monitoring population trends from animal tracks.

2.4.1 Implications of indexing

FMP theory clarifies the implicit assumption of all efforts that use track counts as indices of relative abundance with which to monitor change: average daily travel distances remain constant. This fact of course applies equally to the indexing of camera trap rates to density (Carbone et al. 2001, Rovero & Marshall 2009). Practitioners need to appraise the extent to which this assumption is true for populations separated in time or space. If day range is density dependent, the assumed monotonic linear relationship between track counts and true density will not hold. For example, it is possible that a drop in density with declining food availability may be coupled to a disproportionate increase in day range as animals expand their home ranges or disperse (Ward & Krebs 1985, Norbury et al. 1998). Changes may occur over relatively short periods. For example, in applying the FMP formula to estimate deer densities, Stephens et al. (2006) subdivided movement data due to differences in day range between early and late winter. Irrespective of whether track counts or camera trap rates are used as relative indices or converted to density using the FMP formula and other random encounter models, there are obvious implications for the frequency with which day range needs to be reassessed when monitoring populations.

Calibrating track indices to independent estimates of true density, then applying those linear models to estimate density in other areas, is a growing practice applied to large carnivores in southern Africa (Funston 2001, Houser et al. 2009, Funston et al. 2010, Gusset & Burgener 2005, Balme et al. 2009, Boast & Houser 2012). It is assumed during data collection that

individual animals can be differentiated and counted once only during a survey, which may be closely approximated with the help of extremely skilled trackers (Stander et al. 1997). Stander (1998) first mentioned "range utilisation," "habitat use," and "behaviour of species" influencing the slope of the linear relationship between track counts and true density. If individual animals are recorded only once during a survey (and subsequent re-crossings are ignored), then the present results confirm that the shapes of those individual travel paths will become important in the index–density relationship. Stander's (1998) comments are valid since stable animal path tortuosity must be assumed, including the assumption that movement parameters of the populations used to generate the linear calibration model do not differ from the populations to which the calibration model is applied. Furthermore, when multiple species are combined into a single linear model (Funston et al. 2010), this assumption must be extended to: all species used to generate the model and to which it is applied have equal day ranges and movement path tortuosities.

Large carnivores in particular pose a challenge to FMP application because their low densities require large survey efforts, and the logistical practicalities of large survey efforts often dictate convenience sampling by vehicle along pre-existing linear features. Some species such as brown hyaenas are quintessential trail users and most large carnivores habitually use linear features for ease of travel. Indeed, many indexing and occupancy approaches are based on such behaviour (Allen et al. 1996, Kendall et al. 1992, Hines et al. 2010, Thorn et al. 2011). Recent studies (Rowcliffe et al. 2008, Wearn et al. 2013) have highlighted the importance of random placement of camera traps with respect to naturally non-random animal movements to avoid biased inferences – a warning that applies equally to track transects and the FMP formula. Even though predators disproportionately utilise roads and trails throughout a landscape, randomly located sampling points or transects with respect to these linear features will return unbiased estimates at the landscape scale (Rowcliffe et al. 2013). In contrast, applying the FMP formula to large carnivore-specific surveys whereby transects are situated non-randomly along convenience features (Funston 2001, Houser et al. 2009, Funston et al. 2010, Gusset & Burgener 2005, Balme et al. 2009, Boast & Houser 2012) would presumably result in biased density estimates. In a practical sense, it would be useful to know whether these bias errors are generally larger or smaller than the bias errors resulting from collapsing differential day ranges of multiple species into a single index calibration model (Funston et al. 2010), fluctuations in both day range and

tortuosity in the animals to which the calibration model is applied, and the error involved in isolating individuals by their tracks. Sampling along roads and trails is always more practical, especially when large survey efforts are required, but practitioners should strive for random transects with respect to animal movements for unbiased inferences when applying the FMP method.

2.5   Conclusions

Our attempts to disprove the FMP formula through both virtual and empirical tests revealed no flaw in the simple equation. It appears that the number of animal crossings along lines depends simply on the density of those animals and how far they walk; the shape of specific movement paths is irrelevant. While spatial elements of animal movements have no fundamental bearing on accuracy, biases may arise from the placement of transects with respect to the distribution of animals and principles of good survey design, such as appropriate stratification, apply to any method used to survey biological populations. We also stress that the sampling intensity and total survey effort required to achieve desirable levels of accuracy and precision in density estimates will depend on dispersion, day range, and movement patterns, in addition to density and group size (Stephens et al. 2006, 2006b). In particular, populations with lower density, clumped dispersion, larger group sizes, shorter daily movement distances, and greater tortuosity will require larger survey efforts to achieve the desired accuracy and precision. The main practical limitation to the FMP approach is obtaining accurate estimates of day range. While our capacity to obtain and share animal movement data continues to grow with advances in GPS technology, our ability to estimate day range accurately from these data remains presently limited (Rowcliffe et al. 2012). However, even coarse estimates of day range can be profitably applied to the FMP formula for many species whose abundances are impossible to estimate by other means (Keeping 2014).

Bearing the above in mind, the FMP formula should be applicable to any terrestrial species with readily observable tracks if three assumptions are met: (1) animal movements are random with respect to transects, that is, naturally non-random animal movements are not influenced by the presence of a transect, (2) all animals that intersect transects are detected and identified correctly, and (3) all intersections are enumerated regardless of individuals. Several track-based research and monitoring programs use methods that already accommodate these

assumptions, including long-term data sets in the northern hemisphere (Lindén et al. 1996), and many more could easily be made amenable. Russian biologists have understood and have been using the FMP formula for decades. It is fortunate that this formula has become available to English speakers because conservation practitioners around the world can benefit from understanding and utilizing the FMP formula.

3 Rapid assessment of wildlife abundance: estimating animal density with track counts using body mass-day range scaling rules

3.1 Introduction

Estimating abundance is often necessary for animal conservation. Given the urgency of the biodiversity crisis and unprecedented threats facing most ecosystems, methods that can capture the largest number of species in the most efficient way possible are advantageous (Western 1992, Silveira et al. 2003). Since the majority of population estimates of threatened species are based on direct visual counts, there are clearly gaps in our ability to accurately and quickly estimate population size (Katzner et al. 2011). Limited resources, especially in tropical countries (Sheil 2001), dictate the need for practical and efficient means of assessing animal populations.

Indirect observations are a powerful way to detect terrestrial mammals, and are for many species the only practical mode of detecting them (Wilson & Delahay 2001). Both track counts and more recently camera trap rates have been utilized as indices of abundance, and extended to predict density by calibration through double sampling (e.g. Stander 1998, Carbone et al. 2001, Houser et al. 2009, Rovero & Marshall 2009, Funston et al. 2010). The use of population indices has frequently been criticized for assuming unchanging detection probabilities (e.g. Anderson 2001), so much attention in wildlife population assessment has moved in the direction of estimating detectability (e.g. Pollock et al. 2002, MacKenzie et al. 2005). But despite advancements, direct observation techniques such as distance sampling have intrinsic limitations for species with low detectability (Lopes & Ferrari 2000), which includes many, perhaps most, mammal species. They also involve several analytical assumptions often difficult to meet in mammals (Duckworth 1998).

In contrast to rigorous approaches based on direct observations, the conversion of indirect observations to true density has seen surprisingly little theoretical attention. An exception is the Formozov-Malyshev-Pereleshin (FMP) formula, developed and employed by Russian biologists for decades to convert track counts to true density (Stephens et al. 2006). The FMP formula links animal density to the number of track intersections per linear sample distance via the average daily distances that animals travel (day range). Uncommonly reported in the literature, and

effort-consuming to acquire, empirical day range estimates are the main practical constraint to application of the formula. However, there is a consistent allometric relationship between body mass and day range (Garland 1983), less well known than that scaling body mass and home range size (McNab 1963). Carbone et al. (2005) used 200 species of mammals to estimate body mass - day range scaling rules specific to taxonomic groupings. In this paper, I extend these relationships to the FMP formula to evaluate its potential as a tool for rapidly estimating animal density across the range of terrestrial species identifiable by their tracks.

This investigation has equal relevance to parallel developments in density estimation using two-dimensional ideal gas models with camera trapping (Rowcliffe et al. 2008). I consider tracking because it is pertinent and practical in the environment within which the present study was conducted. The two methods share desirable attributes such as equivalent effectiveness over day and night and the ability to detect secretive species. Although camera trapping has more widespread applicability in all habitats, where soil substrate is suitable for tracking, cameras become mostly redundant. Not only can their expense be limiting, especially for remote areas with low-density populations, but track transects accumulate observations more efficiently (Silveira et al. 2003), because they extend the field of detection over greater dimensions than camera point locations.

3.2   Materials and methods

3.2.1   Study area and track transects

I examined an area of southwestern Botswana that encompasses most of the Kgalagadi Transfrontier Park (Botswana side) and surrounding Wildlife Management Areas, together comprising a contiguous ecological unit under minimal human influence (Fig. 3-1). It is generally open semi-arid savanna, and remarkably uniform, with scarcely any relief and only ephemeral surface water after good rains. Vegetation structure is homogeneous overall, with plant composition varying along subtle gradients of sand texture described by Skarpe (1986); dominant species include trees *Acacia erioloba, A. luderitzii, Boscia albitrunca* and *Terminalia sericea*, shrubs *Grewia flava* and *A. mellifera*, and grasses *Schmidtia kalahariensis* and *Stipagrostis uniplumis*. The most distinctive landscape features are clay-bottomed depressions known as pans, which have elevated mineral levels that attract antelope and other wildlife (Parris

& Child 1973). The northern part of the study area overlaps a region known as the Kalahari Schwelle (Parris 1976), recognized for its concentration of major pans (> 500 m diameter) that are important to large semi-migratory antelope (Williamson et al. 1988, Verlinden 1998).
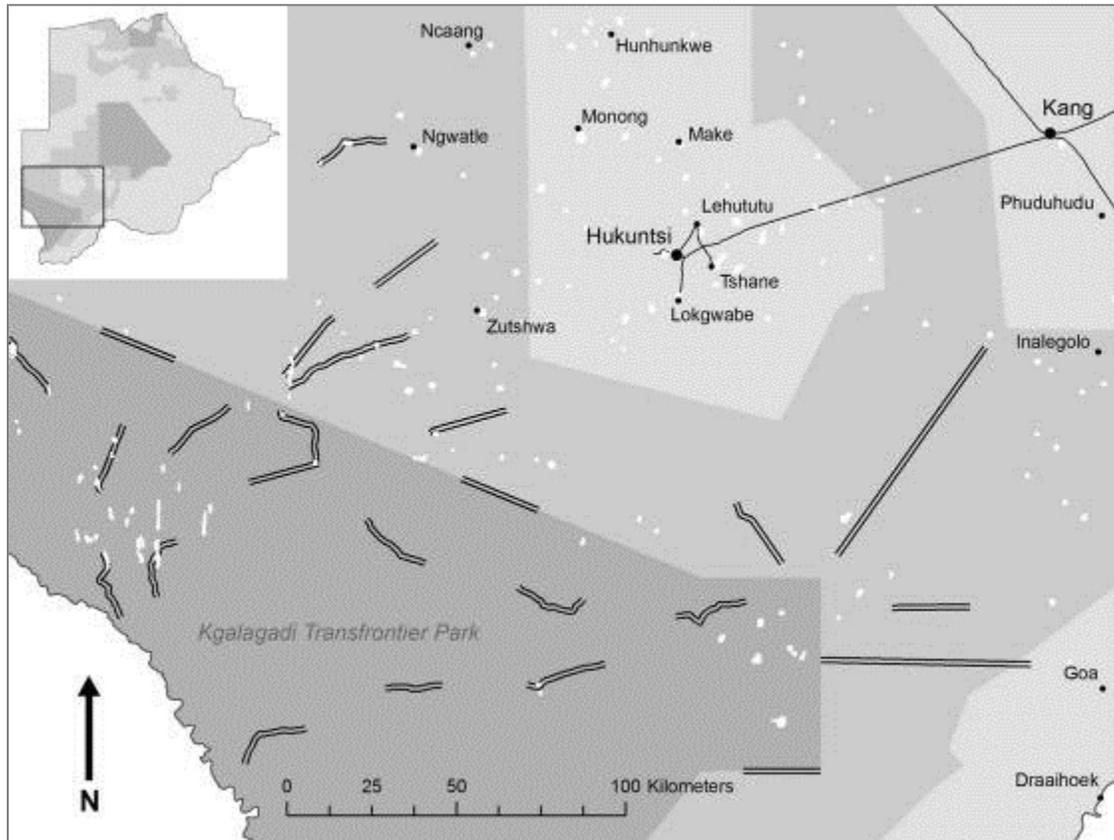
Figure 3-1   Map of study area depicting the 24 track transects, ═══ ; in relation to the Kgalagadi Transfrontier Park, ▮ ; wildlife management areas, ▮ ; and communal grazing areas, ▮ . Pans >500 m in diameter, (white); small towns,●; villages, • ; and improved roads, ─── ; are also shown. The location of the study area in Botswana is shown in the inset at top left.

This area is bisected by a low-density network of 4x4 trails and firebreaks. Firebreaks are 15 m swaths of cleared vegetation forming straight linear features. With respect to subtle habitat gradients, they are randomly oriented and thus expected to sample habitat in proportion to its occurrence. In contrast, 4x4 trails are slightly meandering paths with greater coverage of the study area but more likely to sample major pans than at random. Together, the different features provide favourable coverage of the study area. To address several research questions I established track transects along these convenient features both randomly within land use types

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and systematically covering the continuous distance between human settlements and the park boundary. Transects were sub-sampled from this available pool for the present analysis. I standardized transect length at 20 km mainly to maximize daily coverage and minimize the number of transects with zero counts for low density species. Total survey effort has an overwhelming influence on estimate accuracy (Stephens et al. 2006), so transect length is a somewhat arbitrary practical consideration. Since surveys were comprehensive for species > 0.2 kg, the level of attention required to scrutinize track beds constrained the upper limit of daily coverage to about 20 km.

Transects were sampled during the typically wetter season between October 15th and April 15th, with no temporal replication. Where transects abutted one another, the 20 km lengths were combined for analysis into a single transect to reduce spatial autocorrelation in the data structure. This resulted in 24 spatially separated transects with total sample coverage 634 km. I previously found that human settlements impacted wildlife distribution and abundance up to about 20 km, so transects within this distance of point disturbances were excluded. I therefore suggest the sample coverage represents an area of "undisturbed" native wildlife community that persists in the southern Kalahari ecosystem. Within the area examined there are no fences or other barriers to impede wildlife movement.

I pre-cleared transects of old tracks by dragging a heavy steel beam behind a vehicle, so that fresh tracks accumulated over the following 24-h period before sampling. This precisely controlled the capture of tracks over one diel period of animal movement necessary for density estimation. Dragging did not fundamentally alter the transect but caused light disturbance that erased tracks in the space between the vehicle tyres, or at least made it simple to distinguish tracks that were fresh from those disrupted by the drag. Surveys began early morning and were conducted by two observers on specialized seats mounted to the front of the vehicle - one an expert local tracker, and myself, also a competent tracker. Progressing at a rate between six and eight kph, all track intersections with the transect were recorded as species and numbers with GPS locations. No assumptions were made about track intersections belonging to same individual animals. Only rarely did the lead tracker fail to count re-crossings, mostly in instances where individual tracks became highly tortuous yet remained visually connected over short

distances. Although this is expected to bias estimates, because of the low rate of occurrence, the extent of that bias should be very small.

Although transects overlapped two different types of linear features, the width of the track bed was the same - roughly equal the width of a 4x4 vehicle. However, these linear features potentially influence animal movements differently. Firebreaks are more substantial disturbances that create a microhabitat of open ground and improved line-of-sight. Some species could potentially be attracted to these artificial habitats, which would predictably inflate their counts through higher rates of re-crossings by individual animals. Any discernible increase in encounter rates on firebreaks is likely to result from this factor, and unlikely to result from either avoidance or low utilization of pans along 4x4 trails because such habitats are infrequent point locations in the landscape and small in scale compared transect length. Conversely, neither features are expected to repel species or prevent their crossing, because naturally occurring areas of open sand are frequent in the Kalahari. For each species, I examined the raw data graphically and used a single factor ANOVA to objectively distinguish any bias in track counts between those transects overlapping trails and those overlapping firebreaks.

3.2.2   Daily travel distances (day range)

I predicted day range for all species using allometric relationships described in Carbone et al. (2005). These relationships were modelled using a wide range of species from different biomes (data is available in appendix to online edition of Carbone et al. 2005). Previously, taxonomic grouping (and its correlate feeding type) was found to influence body mass - day range scaling. I therefore fitted a separate least squares linear regression to the $\log_e$ transformed data for each of three orders (Artiodactyla, Carnivora, Rodentia) applicable to the present study species (see Table 3-1 for parameter estimates). These order-specific scaling rules were then most appropriately applied to the Kalahari species (Table 3-2). To predict daily travel distances, body masses were taken from Kingdon (1997), and where ranges were reported I used the mean value between sexes of the median value for each sex. This is justified because the data used to create the scaling rules were produced in the same way. I assume no substantial day range differences between sexes or age categories in sampled populations as most species cannot be reliably sexed and aged by their tracks, but any deviation is presumably negligible in comparison

to error associated with the scaling relationships. Group size influences day range (Carbone et al. 2005, Stephens et al. 2006), but is often difficult to determine from track counts, so was ignored.

Table 3-1   Taxonomic groups with respective exponents and intercepts scaling body mass to day range

Taxonomic group	Scaling exponent	SE	Intercept	SE	n
Artiodactyla	0.26	0.11	-0.11	0.52	22
Carnivora	0.421	0.09	0.147	0.24	39
Rodentia	0.405	0.14	-0.556	0.40	16

Empirical estimates of day range were available for a subset of 12 mammal species, either from the immediate study area or comparable region and habitat. These came from several published and unpublished sources (Table 3-2), and were typically obtained by radio-tracking and following habituated animals. Wildebeest day range was estimated from GPS-collared animals as sums of Euclidean distances between six fixes per 24-h period. These are obviously minimum estimates; true wildebeest day range may be underestimated by a potentially large distance. I acquired more accurate empirical day range estimates for three species (gemsbok, steenbok, aardvark) through following the animals' tracks over a 24-h period with handheld GPS data-loggers programmed to take fixes at 1-s intervals.

Table 3-2   Species grouped by size-feeding type and arranged by alphabetical common name along with data used for density calculations

Latin binomial	Common name	Track count (mean intersections km^{-1} 24 h^{-1})	CV (%)	Mass (kg)	Mass - day range scaling rule	Empirical day range (km 24 h^{-1}) ± SE (n)	Source day range estimate
Taurotragus oryx	eland	1.243	40	561	Artiodactyla		
Oryx gazella	gemsbok	5.055	25	206	Artiodactyla	5.9 ± 0.58 (17)	D. Keeping (unpubl. data)
Alcephalus buselaphus	hartebeest	3.220	30	161	Artiodactyla		
Tragelaphus strepsiceros	kudu	0.143	24	210	Artiodactyla		
Antidorcus marsupialis	springbok	1.821	66	38	Artiodactyla		
Connochaetes taurinus	wildebeest	0·565	58	214	Artiodactyla	4.3 ± 0.41 (7)	M. Selebatso (unpubl. data)
Sylvicapra grimmia	duiker	0.526	21	17.5	Artiodactyla		
Xerus inauris	ground squirrel	0.137	27	0.8	Rodentia		
Lepus capensis & L. saxatilis	Cape & scrub hare	5.170	13	2.63	Rodentia		
Hystrix africaeaustralis	porcupine	0.416	24	17	Rodentia		
Pedetes capensis	springhare	1.574	22	3.5	Rodentia		
Raphicerus campestris	steenbok	6.490	13	11.5	Artiodactyla	4.5 ± 0.45 (6)	D. Keeping (unpubl. data)
Parahyaena brunnea	brown hyaena	0.450	10	47.5	Carnivora	31.1 ± 2.1 (42)	Mills (1990)
Acinonyx jubatus	cheetah	0.049	41	50	Carnivora	9.0 ± 0.79 (24)	M. G. L. Mills (unpubl. data)
Panthera pardus	leopard	0.060	42	55	Carnivora	9.7 ± 0.9 (31)	Stander (1998)
Panthera leo	lion	0.060	40	178.5	Carnivora	19.4 ± 1.4 (16)	Stander (1998)
Crocuta crocuta	spotted hyaena	0.018	39	65	Carnivora	26.5 ± 1.7 (140)	Mills (1990)
Felis silvestris	African wild cat	0.413	17	4.75	Carnivora		
Canis mesomelas	black-backed jackal	3.154	10	10	Carnivora		
Felis nigripes	black footed cat	0.012	33	1.5	Carnivora		
Vulpes chama	Cape fox	0.502	15	3	Carnivora		
Caracal caracal	caracal	0.174	24	13	Carnivora		
Mellivora capensis	honey badger	0.178	24	11.5	Carnivora	10.8 ± 0.8 (144)	Begg *et al*. (2005)
Galerella sanguinea	slender mongoose	0.016	50	0.575	Carnivora		
Genetta genetta	small spotted genet	0.170	24	1.78	Carnivora		
Ictonyx striatus	striped polecat	0.569	17	1.05	Carnivora		
Suricata suricatta	suricate	0.119	47	0.795	Carnivora		
Cynictis penicillata	yellow mongoose	0.381	22	0.62	Carnivora	3.2 ± 0.43 (7)	Cavallini (1993)
Orycteropus afer	aardvark	0.246	13	61	Carnivora	8.6 ± 1.54 (4)	D. Keeping (unpubl. data)
Proteles cristatus	aardwolf	0.161	20	10	Carnivora		
Otocyon megalotis	bat-eared fox	2.144	14	4.15	Carnivora		
Manis temminckii	ground pangolin	0.017	53	12.5	Carnivora	3.8 ± 1.53	Skinner & Chimimba (2005)
Ardeotis kori	kori bustard	0.605	19	7.5	Carnivora		
Struthio camelus	ostrich	0.814	24	70.4	Artiodactyla		
Sagittarius serpentarius	secretary bird	0.027	48	3.8	Carnivora		
Geochelone pardalis & Psammobates oculifer	leopard & Kalahari tent tortoise	0.079	30	0.325	Rodentia	0.435 ± 0.01 (6)	Hailey & Coulson (1996)

CV, standard error as the percentage of the mean; SE, standard error.
[a]mammals - Kingdon 1997; birds - Hockey et al. 2005; reptiles - Keswick 2012.

3.2.3 Density estimation with the FMP formula

Theoretical derivation of the FMP formula is described in Stephens et al. (2006). The derived formula has the form

$$D = \frac{\pi}{2} \frac{x}{S\hat{M}}$$

where x is the total number of track intersections, S the total sample length of all transects, and $\hat{M}$ is the mean travel distance for all individuals of that species in the study area.

Both variance in track counts between spatially-separated transects and variance in estimates of day range contribute to uncertainty in density estimates. I used non-parametric bootstrapping (Efron & Tibshirani 1993) and took the following steps to estimate uncertainty in density estimates for each species:

(1) For the appropriate taxonomic group, resampled the raw data with replacement. Then fitted a least squares regression line to the $\log_e$ transformed bootstrap data to obtain new parameter estimates for slope and intercept, and applied the best estimate of body mass to the equation to produce a single estimate of day range ($\hat{M}$).

(2) Resampled 16 or 24 transects with replacement (depending on whether firebreaks were excluded or included, respectively) to generate a bootstrap replicate of x/S.

(3) Combined estimates of $\hat{M}$ and x/S in the FMP formula to produce one estimate of density.

(4) Repeated steps 1-3 5000 times to obtain the distribution of D, then calculated its mean and bias corrected and accelerated (BCA) 95% confidence intervals.

For select species with empirical day range estimates available, only step 1 differed. Where mean day range and its standard error were reported in the literature, I generated a normal distribution of simulated values based on reported sample sizes, then resampled these with replacement to produce a bootstrap estimate of $\hat{M}$. For those species with raw data available, day range replicates were simply resampled with replacement to produce the bootstrap estimate of $\hat{M}$. Steps 2-4 then followed identically.

3.2.4 Comparison with independent density estimates

Independent estimates from the area are limited in their reliability but, nonetheless, provide the best opportunity to assess the performance of the track-based method. Botswana's wildlife department conducted an aerial strip transect survey (DWNP 2013) several months after the last track counts were conducted, which provides a comparison for large herbivores. Wallgren et al. (2009) offers the only estimates for smaller species using line transect distance sampling from vehicle conducted both during the day and at night with spotlights. Sampling occurred on many of the same trails used for track counts, but several years prior. For large carnivores, Funston et al. (2001) produced a simple linear regression of track counts on true density for lions, and extrapolated this to other large predators. All estimation methods likely have systematic biases and are not strict benchmarks but rather provide a broad basis of comparison across species to evaluate the track-based approach.

3.3 Results

During sampling, and based on casual observations at night, it was obvious certain species were attracted to firebreaks and especially so to firebreaks recently cleared of vegetation. Four species (hare, porcupine, springhare, and steenbok) had substantially greater encounter rates on firebreaks compared to trails ($P < 0.1$). On several firebreaks counts were hyper-inflated, this upper variability depicted in box-and-whisker diagrams (Fig. 3-2). The results suggest that these small animals were disproportionately active on firebreaks compared to surrounding habitat, so I dispensed with their firebreak counts from further analyses (i.e. only transects on trails were considered) to avoid upwardly biased density estimates. All four species have presumably small home ranges (Kingdon 1997) and appear widely and evenly distributed throughout the study region. Their increased activity on firebreaks was therefore unlikely to deduct activity from transects elsewhere, so the removal of firebreaks from their calculations was justified. Kori bustard and ostrich showed slightly greater activity on firebreaks, while there was no discernible differences in track counts among all other species depending on the type of linear feature upon which transects were located. Firebreaks appeared to be just as adequate as 4x4 trails for sampling the majority of species.
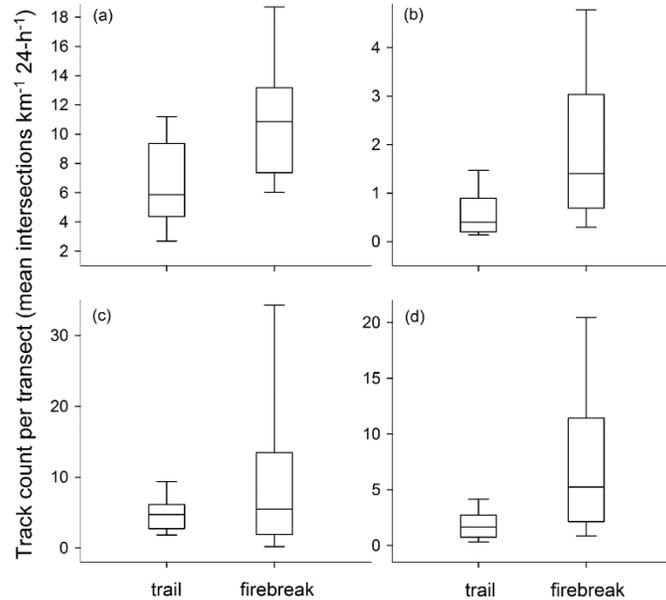
Figure 3-2   Track counts per transect separated into those overlapping trails (n = 16) and those overlapping firebreaks (n = 8) for (a) steenbok, (b) porcupine, (c) hare and (d) springhare.

All 12 mammal species for which empirical day range estimates were available (see Table 3-2), showed movements on average 140% (CV 93%) longer than those predicted by their respective body mass - day range scaling rule. This pattern occurred across taxonomic groups (although no comparisons were available for Rodentia). The semi-arid Kalahari has nutrient-deficient sandy soils and lower productivity compared to other environments from which data were compiled to develop the body mass - day range scaling rules. As animal day range is driven by energetic requirements and food distribution, it is perhaps unsurprising that the subset of Kalahari herbivores, carnivores, and insectivores, consistently showed greater day ranges than predicted. Begg et al (2005) noted larger home ranges and daily movements of Kalahari honey badgers compared to conspecifics in other environments, and their home ranges were greater than that predicted using scaling rules for other mustelids.

As a result of under-predicted allometric day ranges, their application in the FMP formula generally overestimated species densities in the Kalahari. Point estimates of densities showed a positive difference with independent estimates (Wilcoxon matched pairs test, $n = 22$ species, $z = 2.29$, $P = 0.022$). Empirical data were inadequate to adjust each taxonomic scaling model.

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However, given the consistently greater empirical day ranges among all species, I used the slope of the least squares regression equation defining the linear relationship between density estimated using empirical day range, and density estimated using allometric day range (slope = 0.393, y-intercept = 0.039, r^2 = 0.94, $F_{1,10}$ = 168, $P < 0.001$) (Fig. 3-3) as a correction factor to achieve best estimates of density (Table 3-3). Removing the two largest values due to leverage had minor effect on the equation (slope = 0.34, y-intercept = 0.012, r^2 = 0.70, $F_{1,8}$ = 19, P = 0.003). After correction, positive differences between paired estimates disappeared and instead were balanced around zero (n = 22, z = 0.261, P = 0.794) (Fig. 3-4). Carnivores showed the most improvement whereby estimates of 9 out of 11 species moved closer to their independent estimates after correction; only lion and spotted hyaena did not improve, possibly because of low sample sizes. Overall, there was good correspondence between corrected and independent density estimates (Fig. 3-5).
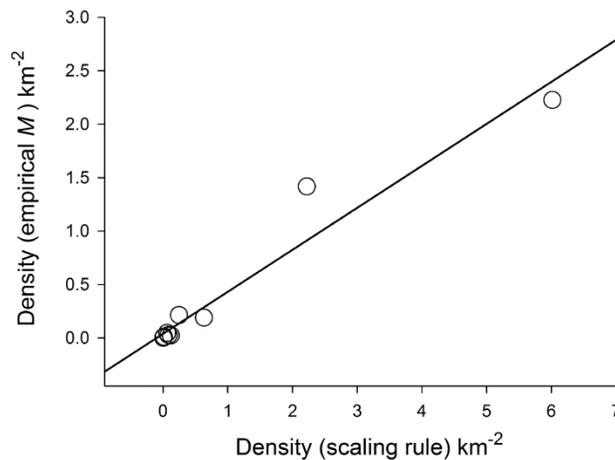
Figure 3-3   Least-squares regression line showing the relationship between densities estimated using empirical day range and densities estimated using predicted day range from scaling rules for 12 species of Kalahari mammals.

Table 3-3   Correction-adjusted Formozov-Malyshev-Pereleshin density estimates with 95% confidence limits for Kalahari wildlife species (>0.2kg) over a contiguous protected and partially protected conservation area in south-western Botswana

Species	Density (100 km^{-2})	LCL	UCL
eland	33.0	5.2	159.2
gemsbok	141.7	65.1	206.0
hartebeest	87.6	18.8	297.5
kudu	3.9	0.8	13.1
springbok	55.3	2.9	172.5
wildebeest	21.4	2.0	47.3
duiker	17.2	5.4	33.6
ground squirrel	6.5	1.8	9.7
hare *spp.*	170.6	115.5	206.5
porcupine	7.3	3.0	11.9
springhare	46.3	22.4	63.1
steenbok	222.6	151.4	282.9
brown hyaena	2.3	1.6	2.8
cheetah	0.9	0.1	1.5
leopard	1.0	0.1	1.7
lion	0.6	0.2	3.4
spotted hyaena	0.1	0.0	0.2
African wild cat	9.6	5.0	12.9
black footed cat	0.4	0.1	0.7
Cape fox	14.2	8.8	18.2
caracal	2.6	1.1	4.1
honey badger	2.7	1.2	3.8
jackal	53.0	32.4	70.6
slender mongoose	0.9	0.1	1.7
small spotted genet	6.0	2.2	8.4
striped polecat	25.3	13.1	32.2
suricate	5.8	0.5	10.8
yellow mongoose	18.9	7.8	27.8
aardvark	4.6	2.6	6.4
aardwolf	2.7	1.2	3.9
bat-eared fox	52.5	29.5	67.8
ground pangolin	0.6	0.0	2.6
kori bustard	10.5	4.8	14.9
ostrich	22.9	4.1	68.6
secretary bird	0.7	0.1	1.4
tortoise *spp.*	30.0	10.1	54.2

Corrected estimates are substituted with estimates derived directly using empirical day ranges for those species applicable. LCL, lower confidence limit; UCL, upper confidence limit.
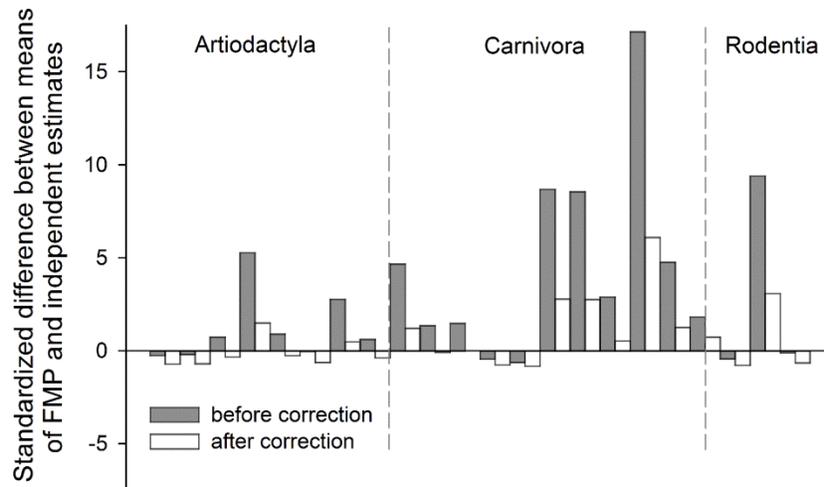
Figure 3-4　Change in differences between Formozov-Malyshev-Pereleshin (FMP) estimates and independent estimates before and after correction for all 22 species available. FMP estimates were divided by their respective independent estimates to obtain standardized values, and the differences displayed with independent estimates set to zero. Species are segregated into taxonomic groups based on scaling rule applied. Note the overall improvement to density estimates across taxonomic groups after correction (i.e. more balanced around zero).
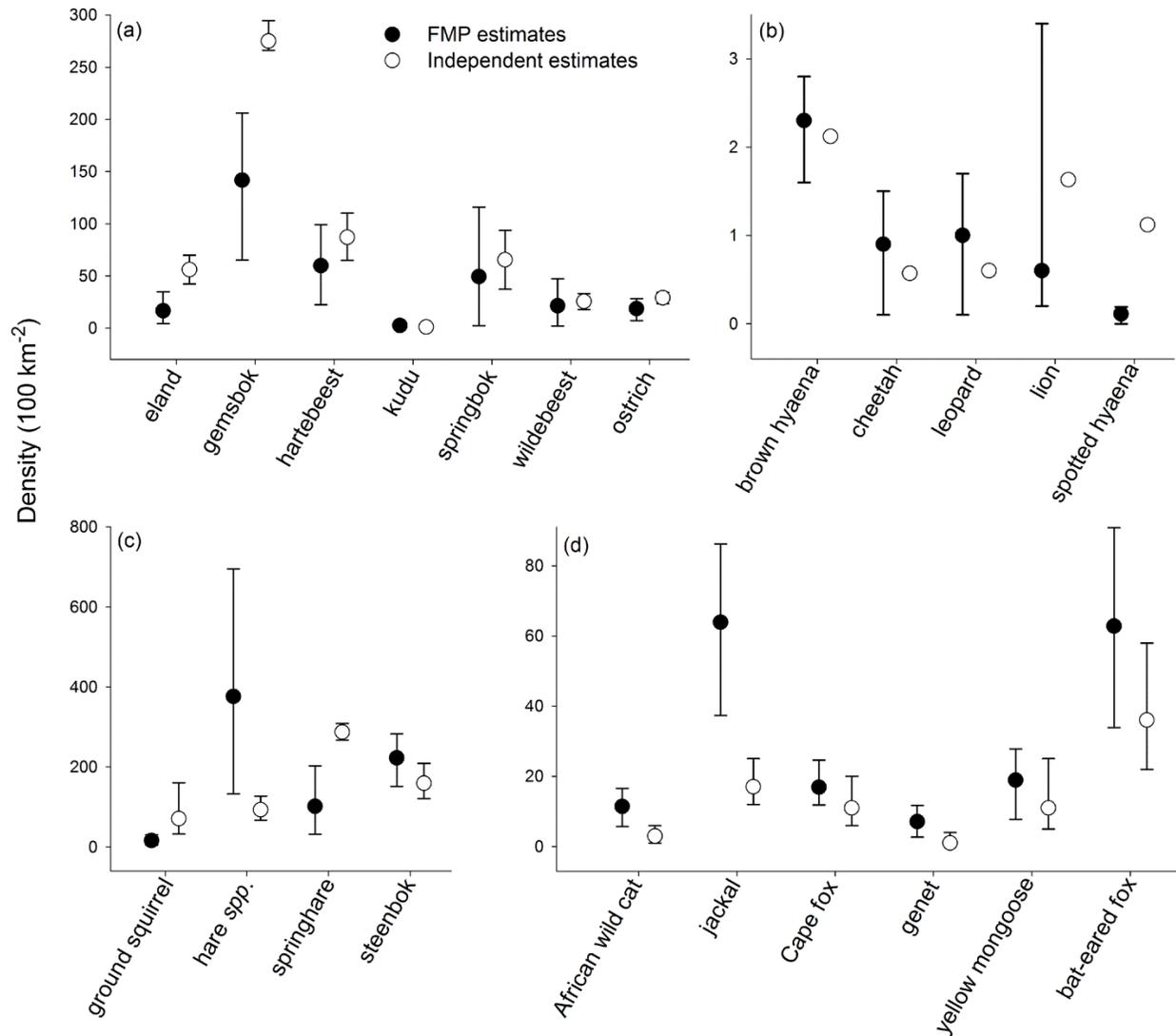
Figure 3-5 **Comparison of correction-adjusted Formozov-Malyshev-Pereleshin (FMP) density estimates to independent estimates with 95% confidence intervals for (a) large herbivores, (b) large carnivores, (c) small herbivores and (d) small carnivores. Independent estimates are from aerial strip transect survey (a), spoor index - true density calibrations (b) and line transect distance sampling by ground vehicle (c) and (d).**

3.4 Discussion

Using day ranges predicted from scaling rules is a coarse approach to the FMP formula. These are model averages of animals from different ecosystems; the actual movement of animals in the study area will determine the accuracy of density estimates. At the very least, however, the approach provides estimates of species abundances relative to one another, which track counts do

not. While the inappropriateness of comparing track indices between species has often been suggested (e.g. Beauvais & Buskirk 1999, Engeman 2005), here it is demonstrated that differential movement rates confound interspecies comparisons using raw track indices. Relative species rankings based on indices changed after conversion to density (Fig. 3-6). Clearly, animals with relatively short daily movements can have higher densities than their track counts suggest (e.g. tortoises), and vice versa (e.g. brown hyaena). Substituting allometric day range in the FMP formula does make density estimation, however rough, possible for animals that are otherwise impossible to estimate using other multi-species survey methods like aerial survey and line transect distance sampling. In the Kalahari this included 11 mammalian carnivores, three insectivores and two herbivores.

Among a subset of Kalahari species, empirical day ranges were consistently greater than those predicted allometrically. Rowcliffe et al. (2012) warn how using infrequent telemetry fixes to estimate day range potentially returns severe underestimates. We obtained very accurate day range estimates for three species by retracing their movements using frequent fix rates (1-s). However, it seems unlikely there was any systematic bias in the accuracy of empirical day range estimates for Kalahari species compared to those data from which the scaling relationships were derived. For example, the local day range estimate for wildebeest was based on infrequent fixes (once every 4-h), but this estimate was still 20% greater than that predicted allometrically. The consistency suggests that rather than any systematic bias, rates of animal movement in the semi-arid Kalahari environment are generally high. This justified the use of a correction factor which improved estimates for most species lacking empirical data. Agreement with independent density estimates reflects some measure of accuracy, accepting that both estimates are of unknown quality. The agreement between density estimates across a large number of species suggests this approach is worth further investigation in other environments. This example warns how application of general scaling rules to the FMP formula can overestimate density of species in ecosystems with low productivity, or conversely, underestimate density in high productivity environments. Therefore, if accuracy of density estimates is important, it seems prudent to understand location-specific day range among a subset of species to either support or correct the scaling rule based predictions.
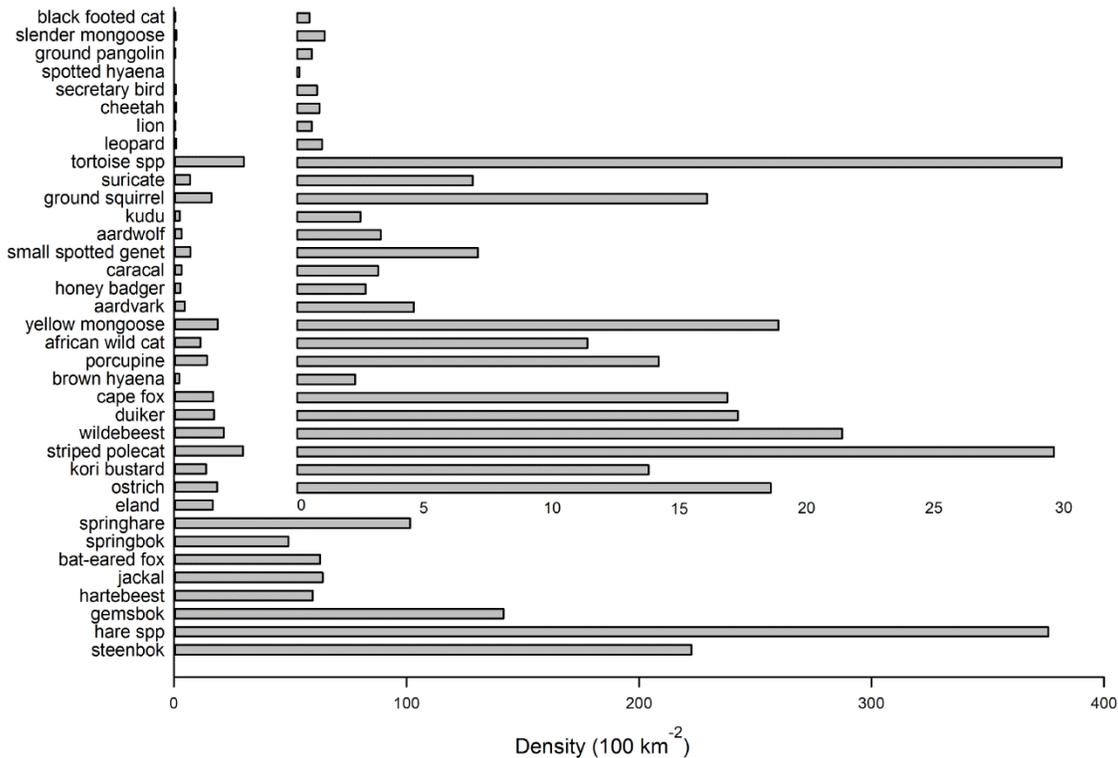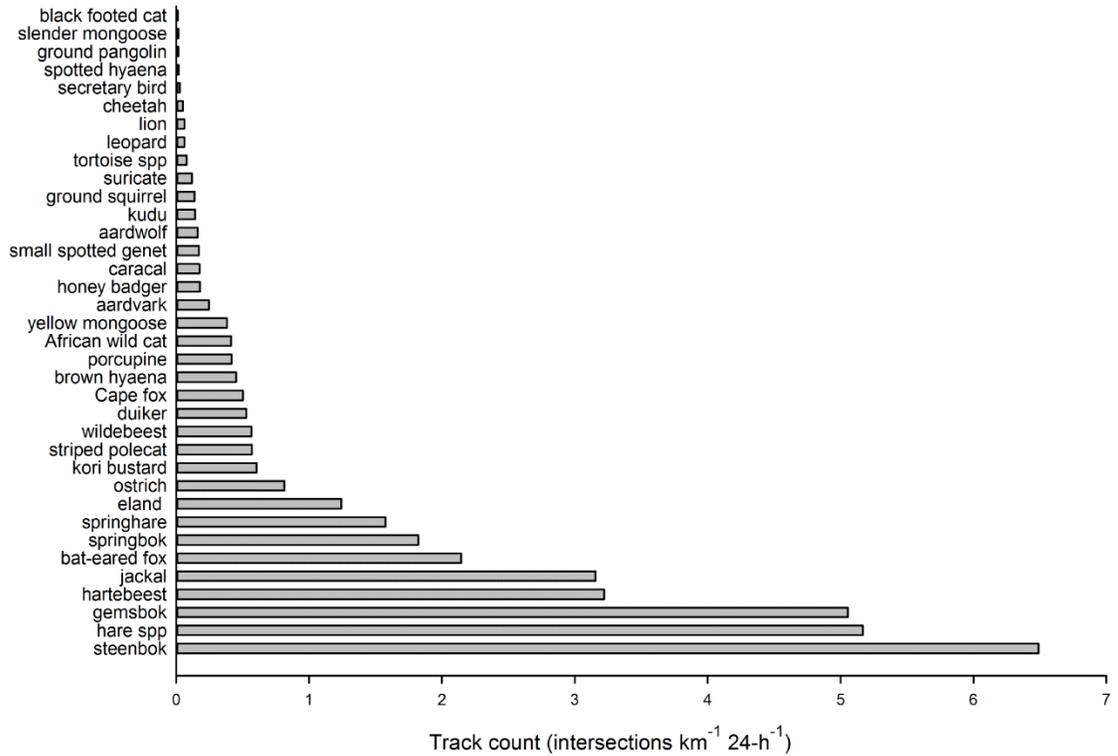
Figure 3-6 **Species ranking based on track counts, with the same rank order after conversion to density. To better illustrate differences among low-density species, the inset in the density panel shows an expanded axis with the eight most numerous species and eland omitted.**

Location-specific data on day range is the primary constraint to estimating density with track counts, as these are typically expensive and time-consuming to obtain. Encouragingly, modest sample sizes in the present study returned useful day range estimates for several species. Further, data from both published and unpublished sources was available for several more species even in this under-researched area of the Kalahari. Published day range estimates are relatively scarce compared to reporting on home range size, however, those same studies may be a hidden repository of data that can be inferred from sequential GPS telemetry locations. Technological advances combined with databases like Movebank (www.movebank.org), where wildlife tracking data is archived and shared, facilitate growing possibilities for FMP application, as it applies equally to recent parallel developments using camera traps (Rowcliffe & Carbone 2008, Rowcliffe et al. 2008). Utilizing such existing data requires sensitivity to potentially large differences in movement rates between habitat types and geographic regions within a species' range, and to the potential severity by which day range estimates can be underestimated using infrequent telemetry fixes (see Rowcliffe et al. 2012). Estimation of day range at a fine spatial scale (Rowcliffe et al. 2012) is presumably important to the accuracy of FMP estimates when each and every track intersection is enumerated (i.e. those belonging to same individuals over short distances), so research into a widely applicable method to obtain unbiased day range estimates from intermittent fixes would increase possibilities for accurate density estimation.

Day ranges are vulnerable to change with time, which is a further limitation to the method. Movement rates often vary intra-annually in environments where primary productivity is seasonal. Major discrete fluctuations in movement such as migration, mating, and juvenile dispersal may or may not be temporally predictable, so a cautious approach is to measure day range within a specific time of year, and limit track surveys to that same period. Even then, inter-annual changes in food availability can affect day range markedly, for example in the case of predator-prey cycles (Ward & Krebs 1985). Quantity of precipitation varies widely both temporally and spatially in semi-arid environments like the Kalahari, in turn affecting large herbivore movements in response to forage conditions (Verlinden 1998), while the timing of precipitation events can trigger surges in animal activity (e.g. Bider 1968). Ambient temperature was shown to cause substantial fluctuations in the daily movements of marten *Martes martes* (Zalewski et al. 2004), and even moonlight (Penteriani et al. 2013) can have considerable influence on day range. Density estimates can improve from increased understanding of the

spatial and temporal factors influencing daily movements (see Stephens et al. 2006), and environmental variables measured in the field at the time of tracking could be incorporated into predictive models of day range. Density-dependent movements add further uncertainty, and implicate the frequency with which day range should be reassessed (Stephens et al. 2006). If density is monitored through time, day range either needs to be reassessed, or assumed not to have changed. These considerations notwithstanding, the allometric approach to extrapolating day ranges, however coarse, appears to have potential for comprehensive snap-shot assessments of wildlife communities in remote areas where other methods are unfeasible.

Day range considerations are essential, but animal movement with respect to transects and how tracks are counted also influence estimate accuracy. Density estimates based on direct observation such as aerial survey and ground line transects are vulnerable to distortion by species-specific visibility biases due to appearances and behaviours, while track counts are much less so. Missed tracks may have slightly greater incidence for smaller, lighter foot-loading species, but this is probably negligible as tracks of all species in the present study were readily visible and could be interpreted by more than one observer. Springhare may be an exceptional example that bound over transects without leaving tracks, possibly explaining the disparity between their estimates (Fig. 3-5). However, an equally plausible explanation for this species along with hare is large changes in populations between the years intervening samples. Rodents have short generation times in addition to known cyclic dynamics of some populations and non-cyclic outbreaks of others. It is speculative discussion to tease out the factors influencing differences observed between the track-based and independent estimates. Considering all that could be driving the comparative estimates apart, when interpreted as a whole over taxonomic groups and species in Fig. 3-5, there was remarkable congruency.

The general accordance between track-based and independent estimates is encouraging evidence that animals are exhibiting unbiased movements with respect to transects, a lingering concern over application of the FMP formula. Density estimates will be most accurate if transects do not influence animal movements, and secondly, if all track intersections are counted regardless of the number of times individual animals may re-intersect a transect. The latter is simple enough to achieve, however, it is interdependent with the former which is often unmet in practice. FMP surveys that utilize linear features for sampling should be interpreted cautiously

because unbiased estimates can be assumed only with transect placement that is random and independent of naturally non-random animal movements. In the Kalahari environment I found firebreaks unsuitable for sampling certain small herbivores that are attracted disproportionately to these artificially open microhabitats. Carnivores are a more ubiquitous concern because many habitually travel along linear features to minimize energetic costs, even so subtle as tyre spoor from a single vehicle passing. Such behaviour could introduce either negative or positive bias to estimates. For example, some carnivores tend to walk long distances along the transect but they are counted once regardless of the distance they travel, unless they exit and re-enter the transect. This altered behaviour may negatively bias estimates because if these animals simply take advantage of linear features when they happen to be encountered, then one would expect uninfluenced movements that are naturally more tortuous to result in more intersections on average in the absence of the linear feature. Alternatively, animals that tend to travel along the features but consistently make exploratory meanders from side to side would predictably generate positive bias to estimates, and jackal may be an example (Fig. 3-5). The extent and direction in which FMP estimates are biased by carnivore movement behavior is not as clear as it is for camera trapping whereby snap shots of movement at point locations along linear features clearly tend to positively bias density estimates for those carnivores that utilize them (Wearn et al. 2013). Perhaps an answer can similarly be reached by comparing estimates from transects overlapping linear features to those randomly situated, or through quantifying fine-scale predator movements in relation to linear features (*sensu* Whittington et al. 2004).

Another difficulty is posed by animals that enter the transect and exit the same direction. Strict interpretation of the FMP formula would include animals that cross a one-dimensional transect centre line only, and exclude those that enter the two-dimensional track bed but fail to cross the centre. This is especially germane on 4x4 trails because some predators do occasionally intersect the first tyre spoor and travel along it before exiting in the same direction. Notably, transects are exceedingly narrow (4x4 vehicle width) relative to the two-dimensional space over which animals range daily, so this only concerns animals influenced by the tyre spoor to parallel, but not cross, the 1-dimensional centre line just centimetres away. Excluding these animals would obviously negatively bias estimates as their daily movements brought them at least to touching the line, if not crossing it. Therefore, I suggest strict adherence to the formula can be relaxed to accommodate these exceptions. Options exist for incorporating the two-dimensionality

of transects with modified ideal gas models (*sensu* Rowcliffe et al. 2008), but this would not resolve the problem of the transect influencing movement behaviour. Such models would be equally affected by violation of the transect-movement independence assumption and in both situations animals are recorded exactly the same - once regardless of the distance they travel along the transect. I suggest that the one-dimensional FMP formula is advantageous in practical simplicity. There seems to be no easy solution to the convenience sampling dilemma, and the interpretation of estimates for animals that habitually travel along transect features are best treated with caution.

The Kalahari semi-arid savanna is open country, but despite good visibility, low animal densities and insufficient observations make direct counting a limited multi-species approach. Aerial surveys efficiently cover ground but are conducted irregularly due to expense and restricted to large-bodied, mostly gregarious, grazing antelopes (Jachmann 2002). Road counts using distance sampling increase those observations to include some of the more common smaller and nocturnal species. Camera trapping could potentially capture everything, but there is a constrained range of animal body size for which camera position and trigger sensitivity can be optimally set. The vastness and remoteness of the area, high initial and maintenance costs, risk of theft or vandalism and harsh conditions contributing to camera failure rates seem prohibitive.

Tracking supersedes the limitations of other methods, and southern Africa in particular is poised to benefit from increased understanding of the FMP formula. With ideal substrate conditions year-round, and latent force of skilled local trackers, there is hardly a better opportunity anywhere to implement track-based wildlife counts and begin compiling a library of species' day ranges through putting trackers on animal trails to trace their movements.

4 Can trackers count free-ranging wildlife as effectively and efficiently as conventional aerial survey and distance sampling? Implications for citizen science in the Kalahari, Botswana

4.1 Introduction

Efficient methods of estimating wildlife numbers in-situ are of fundamental importance to modern conservation, yet a limited number of approaches dominate the toolkit available to practitioners. Furthermore, wildlife managers in developing countries are influenced by prevailing literature on field methods despite local conditions favoring alternative approaches. This paper poses the question: Can Kalahari trackers collect equivalent information as the aerial survey and ground line transects (distance sampling) routinely conducted by Botswana's wildlife authority, and can they do it as efficiently? We sought an answer by comparing simultaneous counts made by air, ground line transects and tracks, their achievable precision, and evaluate efficiency in terms of encounter rates and survey costs. The question and answer are important, in developing countries especially, where both conservation and poverty alleviation are fundamental policy agendas (Agrawal & Redford 2006), local involvement in conservation has become imperative (Hulme & Murphy 2001), and simple cost-effective means of biodiversity monitoring are sorely needed (Danielson et al. 2005). A brief overview of the three methods provides context and relevance to our specific comparison.

For counting large-bodied animals throughout Africa, Australia and North America, strip transects using fixed-wing aircraft continue to be the standard go-to. Several reasons contribute to this including: a) aircraft are the most efficient means of sampling large areas randomly and systematically regardless of topography and surface conditions that might otherwise constrain ground surveys, b) analysis and interpretation of bounded strip transects does not require equivocal assumptions nor modelling - the math is "simple, elegant and absolutely solid" (Caughley & Sinclair 1994, pg 198), and c) long-term datasets using standardized methods entrench their inertia and foster a reluctance to abandon them for alternatives (Pople et al. 1998). Extensive evaluations of aerial counts throughout the latter 20th century led to the conclusion that undercounting bias is often severe, is unavoidable, and difficult to measure (Caughley 1974, Pollock & Kendall 1987). But at least such bias is predictably in the conservative direction, and strict standardization to stabilize it allows counts to be interpreted relative to one another as

trends (Caughley & Sinclair 1994). Others disagree (e.g. Schlossberg et al. 2016, Jachmann 2002). As wildlife managers are ultimately constrained by budgets, schedules and practicality, aerial surveys continue to be a primary, and often the only, data source available for wildlife population numbers and trends, especially over remote land masses.

The line transect method, or distance sampling, was developed to address the practical impossibility of counting all animals within bounded strips due to visibility biases. The essential theory identifies the probabilistic relationship of decreasing detectability as distance from observer to object increases. Detectability is measured from sighting distances and used to estimate a sightability curve, from which effective strip width is defined, thus compensating for animals unseen. The 'theoretical excitement' (Caughley & Sinclair 1994), provision of free user-friendly software with continuing refinements (Thomas et al. 2010) and elaborate guidance on the topic (Buckland et al. 2001) has supported widespread popularity of distance sampling among field practitioners. DISTANCE software has been downloaded by over 30,000 users in 110 countries (Thomas et al. 2010), and applied to animals, plants and other objects in terrestrial and marine environments around the globe. The accuracy of a distance estimate rests on proper selection of the sightability curve. Despite early warnings from the field about assumptions unlikely to hold for some species of mobile animals (Burnham et al. 1980), and other practitioners noting the difficulty of gaining a minimum number of observations with which to estimate robust detection functions (e.g. Duckworth 1998, Jachmann 2001), distance sampling is recommended as a best alternative to aerial strip counts for counting low densities of mammals in savanna environments (Ogatu et al. 2006, Waltert et al. 2008, Msoffe et al. 2010).

Scientists have long recognised the advantage animal tracks pose over direct sightings in detecting wildlife, but have struggled to make inferences on absolute abundance from track data. Instead, tracks are typically considered indices of *relative* abundance and criticized for the fluctuating, unknown and unmeasured detection probabilities that link the index to true abundance (e.g. Anderson 2001, Hayward et al. 2015). There is a notable literature on estimating abundance via identification of individual footprints (e.g. Jachmann 2001, Sharma et al. 2005, Li et al. 2018), an approach limited to few megaherbivores and carnivores with small populations. Another stream uses regression to calibrate track indices to true abundance (e.g. Stander 1998, Bobek et al. 2014, Winterbach et al. 2016), although this approach presupposes several

independent estimates of density. Advances in occupancy modelling have also opened up new possibilities to estimating absolute abundance from track data (Thorn et al. 2011). Interest in tracks has revolved mainly around carnivores given their propensity to avoid detection by other means, while much less attention has been devoted to other taxa. A general and parsimonious relationship linking track indices to population density long employed to enumerate ungulates in the snowy regions of Russia has appeared only rarely in the English language scientific literature (Stephens et al. 2006). The Formozov-Malyshev-Pereleshin (FMP) formula makes it possible to derive estimates of absolute animal numbers from their tracks without the necessity of individual recognition, prior calibration with known densities, or circuitous occupancy modelling. Simulations have verified the FMP an unbiased estimator of population density (Stephens et al. 2006, Keeping & Pelleter 2014, Jousimo & Ovaskainen 2016), but limited empirical validations have been either confounded by time and space (Keeping 2014) or considered few species (Keeping & Pelletier 2014).

In Botswana, as most jurisdictions, the need for reliable knowledge for conservation decision-making eclipses research capacity. Over the past 30 years, Botswana has implemented a remarkable, yet increasingly cost-prohibitive, countrywide aerial survey program. Surveys now occur with less frequency and focus on limited portions of the country, even as pressure on wildlife habitat is increasing. Recognizing limitations, wildlife managers have begun inconsistently conducting line transects on the ground as a compliment to aerial counts. It is unclear just how much this effort adds to the information already gained by the aerial survey. Botswana's challenges and opportunities are not unique. Pivotal resource decisions are frequently made with limited or inadequate data, or no data at all (Sutherland et al. 2004, Cook et al. 2009). Budget-constrained trade-offs are made between wildlife survey methods, and difficult allocation decisions are required. The relative value of data gained through different survey methods in relation to their cost-effectiveness informs these trade-offs. Considering 80% of Botswana's land surface is covered with sand and there is a latent force of erstwhile hunter-gatherers with legendary tracking skills, there seems a good opportunity to develop citizen science based wildlife monitoring, but this potential remains unexplored. An examination of how such an alternative measures up to status quo would be useful. We attempt that in this paper.

4.2 Materials and methods

4.2.1 Study area

We surveyed Kgalagadi District 2 (KD2), a Wildlife Management Area (WMA) occupying 6 425 km^2 in southwestern Botswana bound by Kgalagadi Transfrontier Park (KTP) to the south, KD1 and KD12 WMAs to the west and east respectively, and KD3 communal grazing lands to the north (Fig. 4-1). Boundaries are unfenced and wildlife ranges freely throughout a larger contiguous landscape. This area is near the geographic center of the Mega Kalahari sand sea, one of the most extensive surface deposits of unconsolidated sand in the world (McKee 1979). Climate is semiarid. Scattered trees, shrubs and grasses overlay the sand creating an open savanna (Plate 4-1). Sayre et al. (2013) classify this as the "Kalahari Camel Thorn Woodland & Savanna" ecosystem.

4.2.2 Transects

Since 1986 Botswana's Department of Wildlife and National Parks (DWNP) standardized their aerial wildlife surveys countrywide. The transect grid bisects the country following systematically spaced parallel lines of longitude, stratified to vary in sampling intensity by region. In the Kalahari, transects are separated by approximately 10.2 km. Thirteen such lines bisect KD2, averaging 48.8 km in length and totaling 648.4 km. These run roughly perpendicular to the KTP boundary and areas of increasing disturbance towards the north of KD2 (see Fig. 4-1). Transects are therefore favorably oriented to minimize variance between them.

The same transects flown by aerial survey were sampled for the ground surveys. Surveys occurred within a 9-day period (Oct 25th - Nov 2nd, 2015) to limit error accumulation from animal movements. To minimize bias due to surveyor disturbance, the majority of same-transect surveys were separated by at least one day. Of 39 possible temporally overlapping surveys, only 7 instances arose when two surveys occurred on the same transect during the same day; of those 7, there were only 3 exceptions when the aerial survey occurred simultaneously with a ground survey over short sections of transect. We do not expect these minor instances to cause any discernible bias between surveys.
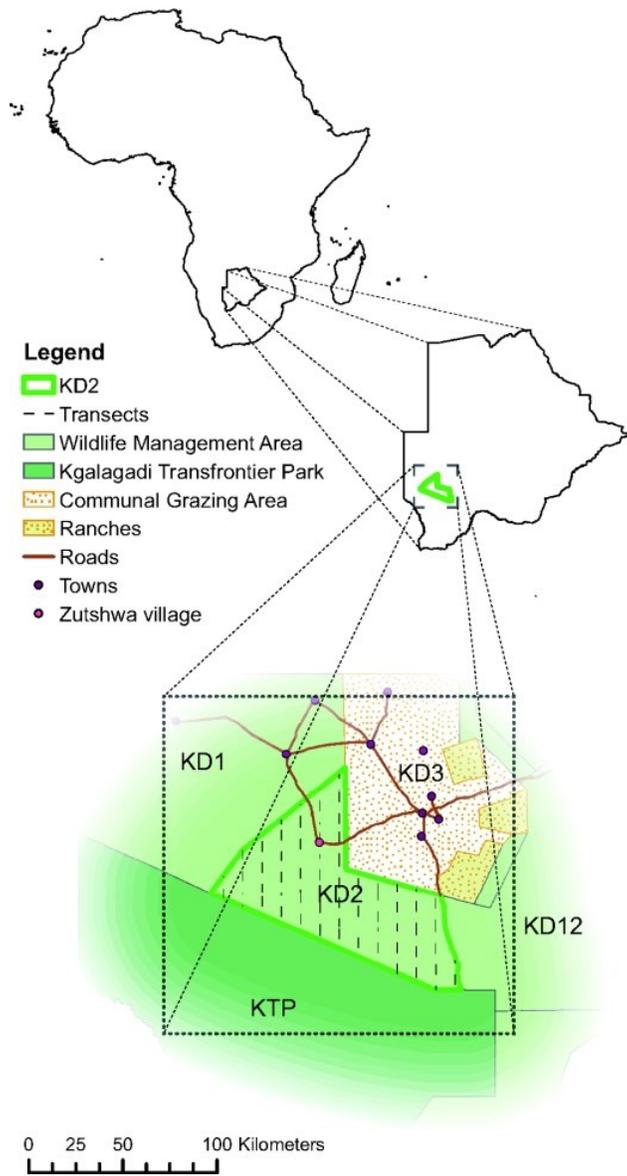
Figure 4-1   Map showing the systematically-spaced transects sampled across 'KD2' Wildlife Management Area, and a geographic perspective of the KD2 study area.

Plate 4-1   Semiarid savanna vegetation structure throughout KD2 study area showing typical visibility along a transect flown by aerial survey, and driven for distance sampling and track counts.

4.2.3   Field surveys

4.2.3.1   Aerial counts

Aerial survey followed standardized DWNP procedures. Cessna 206 aircraft were fitted with navigational GPS and radar altimeter for height control at 91.5 m (300 ft). Aircraft were flown at 167 km h^{-1} (90 knots) while a data recorder seated in the front next to the pilot recorded sightings made by a pair of single observers seated behind in the next row. Multiple wildlife species were surveyed simultaneously including all antelopes and ostrich plus any other species incidentally observed. Markers attached to the lift struts delineated 150 m sampling strips calibrated for each observer looking out either side of the aircraft following Norton-Griffiths (1978). Altimeter readings were recorded consistently during the survey to calculate mean height above ground for each transect. Corrected total strip widths ranged between 299-347 m. Sampling intensity in KD2 was 3.64% by area.

4.2.3.2   Ground surveys

An essential aspect of both ground surveys was local expert observers. Most of the trackers involved in the field surveys reside in the remote village of Zutshwa. Trackers spent pre-

1997 years hunting with subsistence game permits on their traditional territories in KD2, whereby tracking was a fundamental aspect of their livelihoods.

Ground transects were traversed with 4x4 passenger vehicles modified for long-range and equipped for remote survival. Data was collected by five teams, each with a driver, data recorder, and 2 trackers seated over the front of each vehicle. The trackers' positions afforded them a wide view of the ground and elevated eye levels compared to those seated inside the cab.

Ground crews endeavored to keep their travel path deviations within 30 m either side of the transect center line while navigating with GPS. Post-survey, we used ArcGIS to quantify spatial discrepancies by creating vertices every 11 m along the slightly meandering ground transects and measuring the nearest distances between those vertices and the flight paths.

4.2.3.2.1 Line transect distance sampling

We used conventional line transect distance sampling to collect direct sightings. Surveys commenced as early and continued as late as daylight permitted, although midday (11:00 - 16:00) was generally reserved for resting when heat and glare were intense. We surveyed at speeds 15-25 km h^{-1}. Animals were spotted by all passengers but most often by trackers. When sighted, observers stopped at the position where line of sight to the animal(s) formed a perpendicular angle with the transect and recorded object distance using a laser rangefinder. Species and group size where noted along with GPS location. When animals fled before observers reached the perpendicular position, range measurements were made to a shrub or tree marking their previous location. When animal(s) were observed by trackers only, they would walk to and interpret the place where the animal(s) was standing prior to disturbance so that an accurate distance measurement could be obtained.

4.2.3.2.2 Track counts

After completing line transects, the same teams conducted track surveys. For logistical ease, transects where tracked in the reverse direction back to each crew's first line transect starting point. Tyre tracks visible from the first pass outlined a consistent sampling frame whereby animal tracks that intruded the space between the tyres or on the tyre tracks were recorded (Plate 4-2). In practice this relatively narrow space approximates a theoretical 1-

dimensional transect because it is only a minute fraction (1 or 2 step lengths) of large mammal day ranges (Keeping 2014).

Plate 4-2   View of sandy tracking substrate partially obscured by old and new grasses, with tracker pointing the way along a transect. Tyre marks are visible from the previous pass, outlining the sampling frame for track interceptions.

Aerial surveys are limited mostly to large herbivores, so that was our focus. Although dwarf antelopes weighing less than 20 kg such as steenbok (*Raphicerus campestris*) and duiker (*Sylvicapra grimmia*) are directly observed from the air and ground, for expediency trackers restricted their search image to large tracks, including large carnivores, so that the survey could proceed at speeds greater than the meticulous 6 - 8 km h^{-1} required to enumerate smaller species accurately (Keeping 2014). Of the target larger wildlife species, trackers estimated the age of tracks, and only those created within the past 24 h were recorded. All track interceptions with the transect were counted and noted with GPS locations, regardless of whether trackers believed them to be the same individuals or not. Large herds were enumerated using handheld mechanical tally counters. Many of the trackers were illiterate. Irrespective of individual's linguistic or arithmetic ability, these simple devices removed distraction involved in mentally keeping a running count or verbalizing it, freeing the user's attention entirely onto tracks.

4.2.4   Theory - conceptualizing comparisons between direct sightings and indirect detections

Estimating the density of objects from indirect observations is not as intuitive as direct sightings. With direct sightings one strives to locate animals within space: sightings are made from a speeding aircraft before animals have time to flee outside of strip widths, or pinpointed from line transects before moving in response to observers. Density estimation follows rather straightforwardly, whether that be extrapolation of counts within fixed sample strips or applying sightability curves to estimate effective sample space.

Contrasting a 'snapshot' model of animals as stationary objects pinpointed in two-dimensional space, indirect observations of tracks depend on the movement of animals to leave countable evidence of occurrence along what is theoretically a one-dimensional transect. The problem then is anchoring those animals to a two-dimensional area. Borrowing from ideal gas theory in physics, the FMP formula is a random encounter model derived from the probabilistic intersection (track encounter) of lines of known length (transect and animal movement path) within an area. For a concise description of the main steps involved in its derivation, see Stephens et al. (2006). Thus, to estimate density one must obtain a measure of population day range of the species surveyed, corresponding to tracks made within that diel period of movement. The key assumption is random animal movements in relation to transects.

Figure 4-2 illustrates relative areas over which objects are detected between transect methods. In this hypothetical example, aerial survey detected zero gemsbok, line transect detected one, and track survey detected 7 intersections by all 3 gemsbok. Clearly, most species exhibit daily movements that greatly exceed both aerial survey strip widths and the limits of view along line transects, resulting in higher encounter rates and a greater fraction of the study area is effectively sampled by track survey. Differences in encounter rates are further magnified by the fact that a) individual animals can make multiple track interceptions, and b) animals that are within visible range during direct sightings can still be missed by observers. In contrast, without interference from weather the probability that day-old tracks are detected by Kalahari trackers approaches one. Notably, counting multiple track interceptions of the same individual animals does not introduce bias, but is actually necessary for obtaining an accurate density estimate (Keeping & Pelletier 2014).
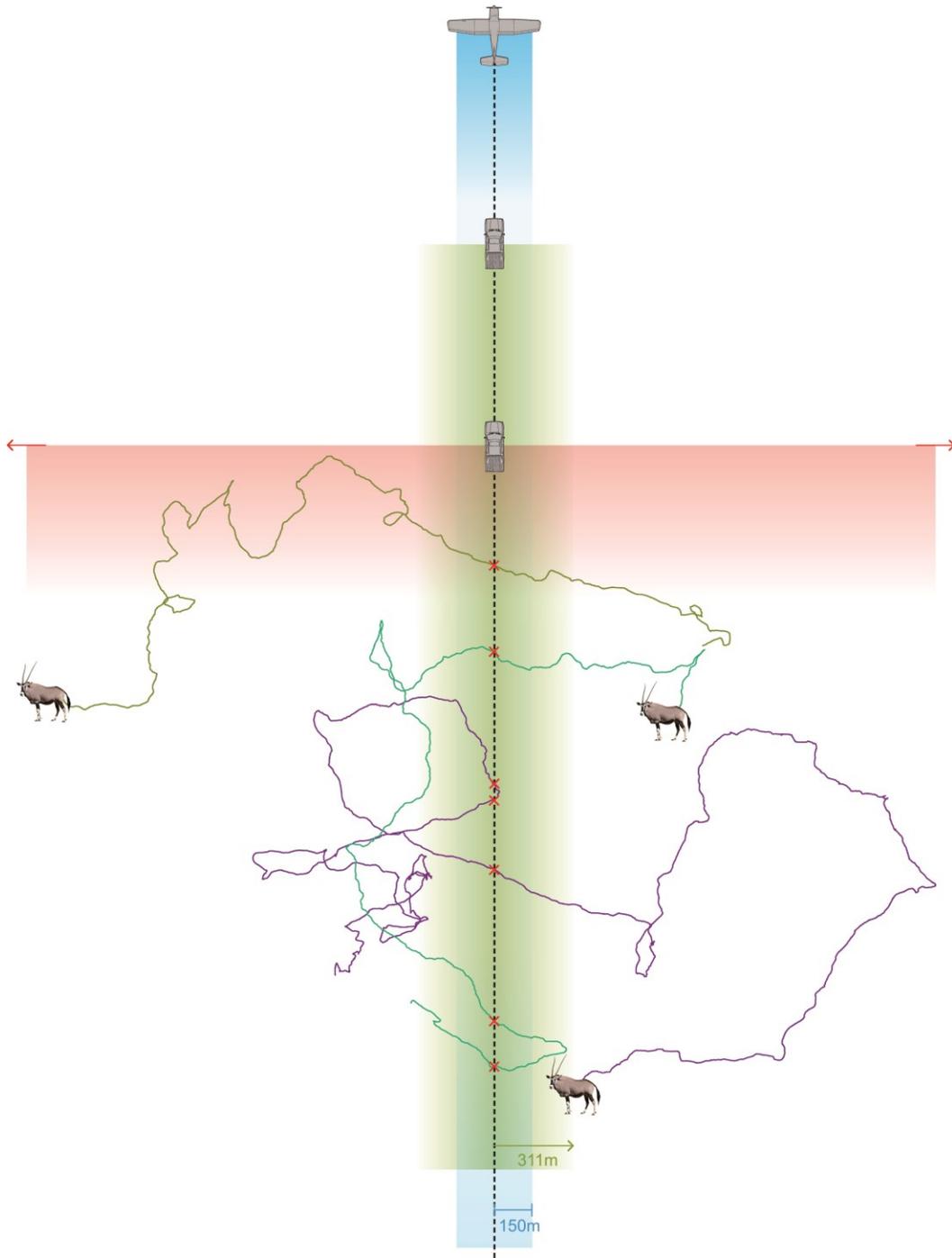
Figure 4-2 **Relative areas over which objects are detected by aerial survey (300 m strip width), followed by line transects (unbounded strip width, although in the present study 95% of observations occurred within 311 m from observers), followed by track survey (undefined strip, related to 24 h animal movements), in scale relation to three gemsbok (*Oryx gazella*) and their movements 24 h prior to surveying.** Gemsbok movements were empirically traced by tracking from horseback (Keeping & Pelletier 2014). Track interceptions are denoted by red x.

4.2.5 Population density estimation

For each of three methods, analyses of density were completed blindly by different co-authors.

Aerial survey data were analyzed with the program BASIS (Wint 2007) using Jolly's method II (ratio method) for unequal-sized sample units (Jolly 1969). The ratio method estimates density within the study area by extrapolating the ratio of animals counted to the area sampled.

Ground line transect data were analysed with DISTANCE 6.2 Software Package (Thomas et al. 2010). DISTANCE software analyses data at the level of observation (individuals or groups of animals), those observations used to fit a detection function to compensate for animals not observed. Buckland et al. (2001) recommended 60 - 80 observations as the minimum requirement for estimating robust detection functions, and an absolute minimum of 40. For species that did not reach this threshold, we pooled data from previous surveys in the region during 2002, 2004 (Wallgren et al. 2009) and 2007-2010 (DWNP, unpublished data) and settled for a minimum of 30 observations when necessary. Uniform, half-normal and hazard-rate key functions were fitted to the observed distances and their fit evaluated based on visual judgment and Akaike´s Information Criteria. Data were truncated to improve fit, where appropriate discarding 5-15% of observations. Density estimates using the subset of observations from the KD2 survey were then based on these key fitted functions.

Track counts were converted to density by applying the FMP formula and non-parametric bootstrapping (Efron & Tibshirani 1993) to estimate precision. The FMP model links track indices (track interceptions km^{-1} $24h^{-1}$) to true spatial density via the 24hr travel distances of the animals that made the tracks. We estimated species-specific day ranges allometrically and applied the correction factor for Kalahari species following methods outlined in Keeping (2014). Briefly, a database of day range (km) - body mass (kg) pairs for 22 species of Artiodactyla (Carbone et al., 2004) was resampled with replacement (n=22), and a least-squares linear regression fitted to the log_e transformed data. We then predicted day ranges from this model applying the best estimate of average body mass for each Kalahari species. For track indices, transects were weighted by their length and resampled according to the proportional fraction that each transect comprised the total survey distance. The bootstrap mean track index was combined

with day range into the FMP formula to create a single estimate of density. This process was repeated 5 000 times to generate the dispersion of densities for each species, from which the mean and bias-corrected and accelerated 95% CIs were calculated. Exceptions were gemsbok (*Oryx gazella*) for which local empirical day range estimates were attained though trailing their daily movement paths (Keeping & Pelletier 2014), wildebeest (*Connochaetes taurinus*) for which GPS collar data was available (M. Selebatso, unpublished data), and large carnivores whereby day range estimates were made through following habituated animals and GPS collars (Mills 1990; Mills & Mills 2017; Stander 1998). A more sophisticated estimate of day range was attempted for cheetah (*Acinonyx jubatus*), outlined in Appendix A.

4.2.6   Encounter rates and survey costs

4.2.6.1   Encounter rates

For a comprehensive comparison of encounter rates we included all species for which prior data from the study region was available. We define encounter rate as expected number of objects detected per unit effort, the definition encompassing the mean distance (km) sampled per line transect observation (groups of any size), and per individual animal (for aerial survey and line transects), and per track interception. To calculate these statistics we pooled data from past surveys over a combined area including KTP and adjacent WMAs in both wet and dry seasons between years 2001-15. Spotlighting surveys provided line transect data for rare and nocturnal species (Wallgren et al. 2009). For species detected during both day and night surveys, we reported encounter rates for whichever sampling period that encounters were most numerous. Calculations were made from 42 614 km of aerial coverage; 11 242 km of ground line transects during the day and 2 652 km of spotlighting at night; and 2 233 km of track surveys for large herbivores and carnivores and 1 602 km for remaining smaller species.

4.2.6.2   Survey costs

Inclusive in our cost estimates were the rental costs of the airplane and pilot, rental cost of suitable 4x4 vehicles, fuel, compensation for non-tracker personnel including trained aerial observers, drivers and data scribes, food and accommodation (where appropriate) and tracker compensation. While drivers and data scribes for the ground surveys were volunteers, we applied a low pay rate estimated from DWNP field officers as hypothetical non-volunteer personnel to

make the comparison fairer. Excluded from the costing was standard non-consumable field equipment common to all surveys such as handheld GPS units. From the total costs of completing each survey of KD2 we calculated the cost km^{-1} sample effort. We then used these unit costs and the encounter rates to estimate the costs of accumulating species-specific observations.

4.2.7   Density-distribution maps

We generated species-specific maps in identical format to those routinely presented in Botswana's aerial survey reporting. These aerial survey maps have been the benchmark for inference about wildlife distributions in the Kalahari over the past 30 years (e.g. Verlinden 1998), therefore, they are the standard to which alternative surveys can be compared. Resolution is dictated by transect spacing, ensuring that both transect length is maximized within each grid cell and coverage of the study region is complete. Thus, the study area was divided into grid cell squares averaging 112.4 km^2, each bisected through the centre by a transect segment averaging 11.1 km. Observations along each segment were used to calculate point estimates of density within each grid cell. We quantified correspondence in density-distribution maps between methods using Pearson's correlation coefficients, suitable for zero-clustered data (Huson 2007).

4.3   Results and Discussion

4.3.1   Similarity among KD2 population estimates

Using 94 125 points of measurement between ground transects and flight paths, deviations between the two lines averaged 23 m (SD 31 m). As this is well within strip widths, we are confident that all three methods sampled the same populations on a per transect basis, and frequently the same individual animals.

The true number of wildlife in KD2 is unknown so the accuracy of estimates cannot be determined. Caughley & Sinclair (1994, pg 241) warned: "Most estimates of population size require that the manager makes a leap of faith. There is seldom any certainty that the population fits the assumptions of the model, nor whether the estimate is wildly inaccurate, nor whether the confidence limits have much to do with reality." Nevertheless, undercounting bias is expected from aerial survey, and simultaneous ground counts are often employed to estimate that bias (e.g.

Jachmann 2002). As Distance sampling is widely regarded as more reliable than uncorrected strip counts, this provides a useful anchoring point for comparisons.

Raw counts of six large grazers were highly correlated among all methods (Tables 4-1 and 4-2). Slight reduction in population estimate correlation between tracks and direct sightings compared to raw counts (Table 4-2) hint that there was some error in the track-based density conversion, namely error in day range estimation. Despite this, no method appeared to return markedly different population estimates than another, and 95% confidence intervals showed large overlap between all three methods among large grazers (Fig. 4-3). Wilcoxon matched pairs tests showed non-significant results for contrasts between air-distance ($P = 0.92$), air-tracks ($P = 0.46$) and distance-tracks ($P = 0.46$), suggesting no systematic discrepancy in population estimation between the three different methods over the six grazers.

Table 4-1   Raw observations by three survey methods along 13 transects (648.4 km) covering KD2 Wildlife Management Area

Species	Air Individuals counted	Ground Individuals (observations) counted	Tracks Track sets counted
eland	995	1 774 (37)	9 884
gemsbok	584	333 (113)	4 613
hartebeest	133	250 (73)	1 932
ostrich	61	21 (12)	259
springbok	104	131 (21)	1 259
wildebeest	170	111 (11)	735
kudu	25	13 (6)	612
duiker	12	12 (12)	-
steenbok	48	267 (243)	-
brown hyaena	1	2 (2)	139
cheetah	1	3 (2)	42
leopard	0	0	47
lion	3	2 (1)	45
spotted hyaena	0	2 (2)	15
wild dog	0	0	2
	2 137	2 921	19 584

Table 4-2 Cross-species correlations between methods for raw counts and population estimates for 6 large grazers

	Aerial versus Distance	Distance versus Tracks	Aerial versus Tracks
	r (P)	r (P)	r (P)
Raw counts	0.916 (0.010)	0.960 (0.002)	0.982 (<0.001)
Population estimates	0.965 (0.002)	0.790 (0.062)	0.831 (0.040)

The similarity among estimates runs contrary to an extensive literature in which aerial surveys of conspicuous savanna ungulates typically return around 60% the numbers of ground counts (see summary in East 1998, pg 91-92). In our surveys aerial estimates averaged 93% of line transect estimates, excluding wildebeest for which the aerial count was greater by a factor of 4. These results lend support to Botswana's multi-species counts of large grazers by fixed-wing aircraft in the southern Kalahari. Environmental specificity is an important caveat, and we add that our surveys were conducted during the late dry season before substantial leaf flush. Ground-truthing might reveal quite different discrepancies for the same species after leaf flush and in other areas of Botswana.

Contrasting grazers, a systematic pattern of undercounting bias from the air was apparent for browsers (Fig. 4-3). For kudu, duiker and steenbok, the aerial survey returned 60, 29 and 5% of line transect estimates respectively. Even greater disparity occurred between air and tracks, the aerial count returning 35% of the track-based kudu estimate. We suggest this is a true reflection of aerial undercounting bias, as it is hinted in the raw counts: the air-track ratios for raw counts of large antelopes were neatly in the 1:10 range or higher, with the exception of kudu for which that ratio was 1:25 (Table 4-1). We believe kudu track counts were accurate because their tracks are easily distinguished from similar-sized grazing antelopes even by non-expert observers. The diminutive steenbok appear most severely underestimated by aerial survey in the southern Kalahari. They are sand-colored, shade-loving, and usually do not move in response to aircraft. If counts typically return 5% of the true number of steenbok inhabiting this relatively open-country environment with good visibility, then undercounting discrepancies might be greater over the rest of the country.
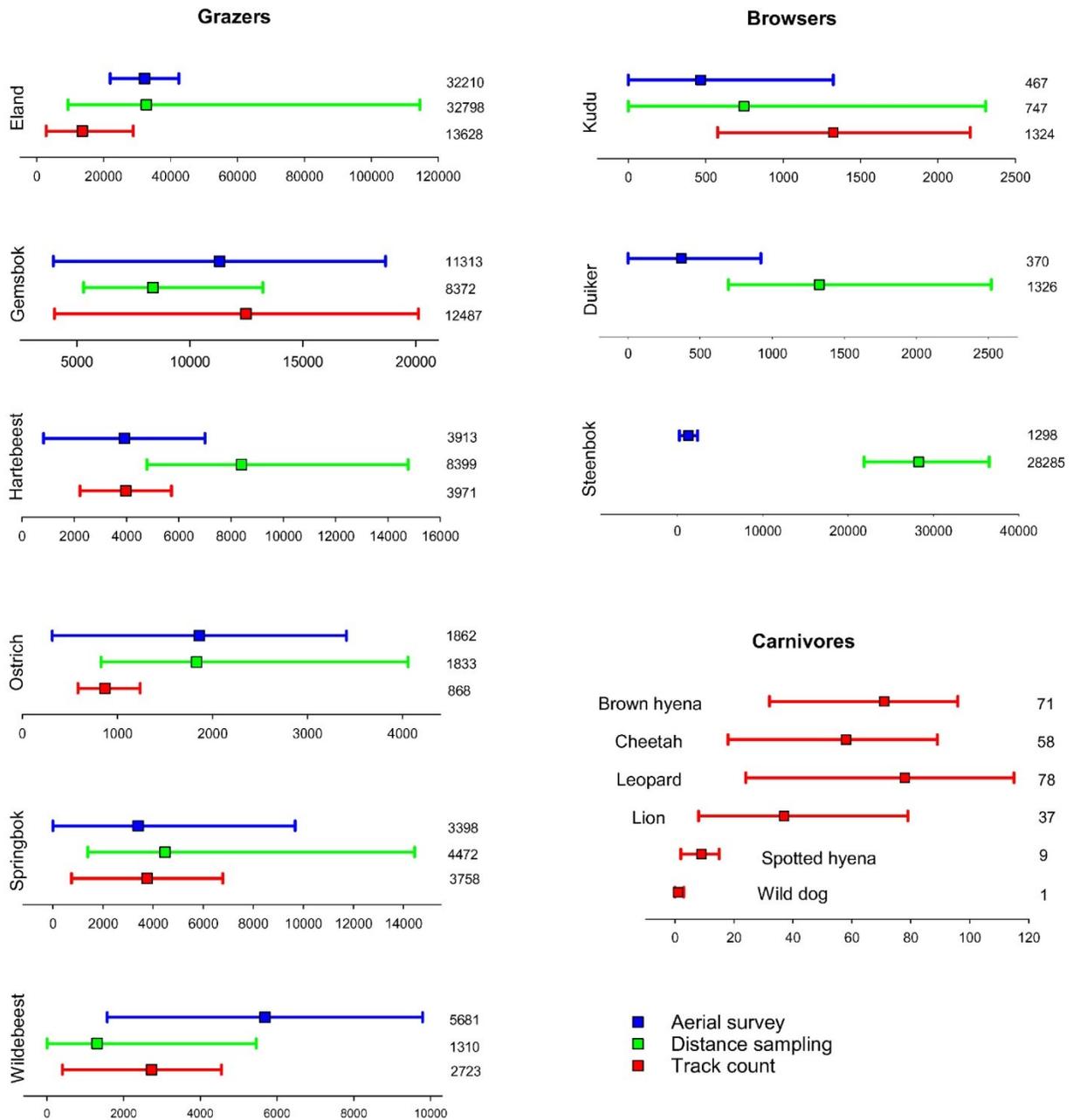
Figure 4-3   Population estimates (number of animals) with 95% confidence intervals from aerial survey, distance sampling (ground line transects) and track survey in KD2 (6425 km^2). Note different x-axes scales for each species.

Comparative density estimate percent Coefficients of Variation (CVs) also showed close similarity between methods (Table 4-3), averages for 7 large antelopes being 46.0%, 50.1% and 38.4% for air, distance and tracks respectively. CV percentages exceeded thresholds of 20-15% typically considered suitable for monitoring trends, but this is unsurprising considering sampling intensity was a low 3-4% by air. In Kruger National Park, where game densities are higher, aerial survey CVs for most species of large grazers fell below the 20% target at relatively high sampling intensity (15%), while thereafter increasing intensity to 22 and 28% gave only marginal gains in precision (Kruger et al. 2008). Even at the highest sampling intensity some species, such as wildebeest, still failed to reach target precision. Encounter rate variance, a function of both variation in density among sampling units and sampling intensity, accounts entirely for the precision of aerial estimates, typically 70-80% of the precision in distance sampling (Fewster et al. 2009), and in this study roughly 72% of the precision in track-based estimates (the remaining 28% portion comprised of day range variance). Thus, with equal levels of transect sampling, more precise estimates of day ranges might marginally improve precision of track-based population estimates compared to direct sightings.

Table 4-3   Comparative density estimates, 95% confidence intervals and percent coefficients of variation between 3 survey methods for 9 antelope species in KD2 (6425 km^2)

Species	Aerial survey			Distance sampling			Track count		
	D	95% CI	CV(%)	D	(95% CI)	CV(%)	D	(95% CI)	CV(%)
eland	5.01	3.41 - 6.60	14.7	5.10	1.46 - 17.83	68.5	2.12	0.44 - 4.49	55.0
gemsbok	1.76	0.62 - 2.90	30.0	1.30	0.82 - 2.06	22.4	1.94	0.62 - 3.13	33.5
hartebeest	0.61	0.13 - 1.09	36.4	1.31	0.74 - 2.30	28.3	0.62	0.34 - 0.89	25.2
ostrich	0.29	0.05 - 0.53	38.4	0.29	0.13 - 0.63	41.3	0.14	0.09 - 0.19	27.4
springbok	0.53	0 - 1.51	84.1	0.65	0.20 - 2.10	58.8	0.58	0.11 - 1.05	45.8
wildebeest	0.88	0.24 - 1.51	33.4	0.20	0 - 0.85	74.9	0.24	0.07 - 0.41	39.9
kudu	0.07	0 - 0.20	84.8	0.12	0 - 0.36	56.7	0.21	0.09 - 0.34	41.9
duiker	0.06	0 - 0.15	68.9	0.21	0.11 - 0.39	30.8	-	-	-
steenbok	0.20	0.04 - 0.36	37.4	4.40	3.41 - 5.69	12.1	-	-	-

4.3.2 Survey efficiency - encounter rates and costs

Buckland et al. (2001) recommend collecting 60-80 line transect observations, and no less than 40, to estimate reliable detection functions and resulting density estimates using DISTANCE software. By comparison, simulations have shown that FMP estimates experience small gains in accuracy and precision when sampling penetration exceeds 1 km/10 km^2 (Stephens et al. 2006, Keeping & Pelletier 2014) - which was very close to that of the KD2 survey (648.4 km/6 425 km^2). The KD2 surveys are therefore convenient for comparing which species can be profitably tackled by each method.

The difference between what is directly seen from an overhead or ground-level perspective, and what is detected by tracks after one diel period of animal movement in the Kalahari is remarkable (Fig. 4-4). Consistent for all species, track encounters accumulate over minute sample distances compared to direct sightings (Table 4-4). Similar discrepancies between line transect and track encounter rates have been noted before (Silveira et al. 2003, Fragoso et al. 2016). Despite open country with good visibility we had difficulty obtaining prerequisite minimum observations for common antelopes by ground line transects. Our study is not the first to comment on this shortcoming; the problem is pronounced in heavily forested environments (e.g. Barnes 2001, Rovero & Marshall 2004), but also tropical deciduous woodlands (e.g. Jathanna et al. 2003, Waltert et al. 2008) and more open savannas and grasslands (e.g. Harris 1996, Ogutu et al. 2006, Nimmo et al. 2015). The recommended minimum 40 observations was achievable for only 1/3 of antelopes during the KD2 survey (see Table 4-1); the other species required supplements from previous surveys. We failed to assemble more than 32 observations for duiker after pooling several survey efforts exceeding 11 000 km over a much greater area. Kudu detection rates were only slightly better. It would take roughly 12 000 km and 15 000 km of surveying to obtain 40 observations for kudu and duiker respectively (see Table 4-4). For this reason, with the exception of steenbok, ground line transects in the Kalahari add little to the aerial survey results.

In Table 4-4 we present 'inverse' encounter rates so that total sampling effort and cost can be quickly estimated for particular species when applying rules of thumb for recommended minimum observations. While it is often claimed that line transects are applicable to smaller, uncommon animals, a study of Table 4-4 shows that from an effort and cost perspective line

transects are not practicable for many species in the Kalahari environment. For example, 442 km of spotlighting at a cost of $3 171 USD is the expected sampling effort required to see an aardvark (*Orycteropus afer*). Attempting an aardvark density estimate by distance sampling with a minimum 40 observations would thus require 17 608 km of transect at a cost of $126 840 USD. By contrast, it takes an average of 3.9 km of surveying tracks for $28 USD to intercept an aardvark from the previous night. In the Kalahari the application of aerial strip counts is limited to large-bodied grazing ungulates. Unbounded line transects on the ground capture more smaller species, especially with night-lighting (Wallgren et al. 2009), but like aerial surveys the diversity of species that can be assessed with realistic levels of sampling effort is modest. Indirect, time-integrated observations of animal tracks overcomes the detection problem. Conservationists' interest in tracks revolves largely around carnivores because they elude detection by other means and are often conservation priorities. Our results suggest that track surveys have a more encompassing application than currently considered, whereby different groups of savanna mammals thought better counted by separate methods could be assessed simultaneously by tracks in the Kalahari at less cost than direct sightings methods. Extremely high encounter rates make it practical to assess the comprehensive mammalian community above threshold body size (Keeping 2014).
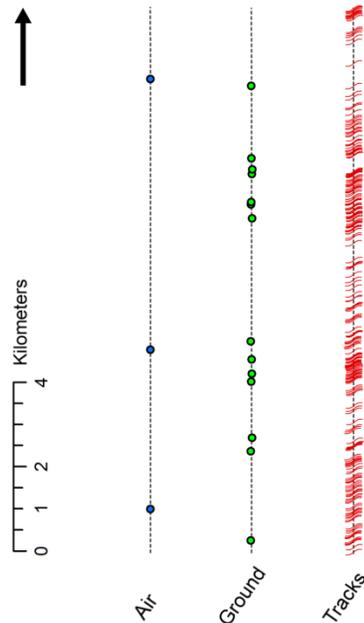
Figure 4-4   Locations of encounters (combined antelope species) by aerial survey, ground line transects and tracks (≤ 24 hr^{-1}) along Transect 1 (12.7 km) in KD2.

Table 4-4   Comparative encounter rates and cost estimates (USD) per observation (groups of any size), individual animal and individual track set collected by aerial survey, ground line transects, and track survey for 35 species on conservation lands within Kgalagadi District, Botswana

Latin binomial	Common name	Aerial Survey		Line Transect		Track Survey	
		Km per (observation) and individual encountered	Cost per (observation) and individual encountered	Km per (observation) and individual encountered	Cost per (observation) and individual encountered	Km per individual track set 24 h^{-1} encountered	Cost per individual track set 24 h^{-1} encountered
Taurotragus oryx	eland	(108) 9.3	$(1 320) 114	(131) 4.5	$(940) 32	0.2	$1.43
Oryx gazella	gemsbok	(12) 2.9	$(147) 35	(11) 2.2	$(79) 16	0.2	$1.43
Alcephalus buselaphus	hartebeest	(35) 6.4	$(428) 78	(21) 3.7	$(151) 27	0.3	$2.15
Struthio camelus	ostrich	(38) 17	$(465) 208	(33) 12	$(237) 86	1.6	$11
Antidorcus marsupialis	springbok	(273) 19	$(3 339) 232	(35) 2.3	$(251) 17	0.3	$2.15
Connochaetes taurinus	wildebeest	(294) 27	$(3 596) 330	(194) 39	$(1 392) 280	1.4	$10
Tragelaphus strepsiceros	kudu	(439) 132	$(5 369) 1 614	(304) 100	$(2 181) 717	2.6	$19
Sylvicapra grimmia	duiker	(168) 143	$(2 055) 1 749	(379) 331 *	$(2 719) 2 375	1.6	$11
Raphicerus campestris	steenbok	(22) 18	$(269) 220	(5.1) 4.1	$(37) 29	0.1	$0.72
Phacochoerus africanus	warthog	(1 291) 804	$(15 790) 9 833	(1 874) 1 405	$(13 445) 10 080	43	$309
Proteles cristatus	aardwolf	?	?	(884) 884 *	$(6 342) 6 342	6.1	$44
Parahyaena brunnea	brown hyaena	(14 204) 14 204	$(173 721) 173 721	(221) 221 *	$(1 586) 1 586	2.7	$19
Crocuta crocuta	spotted hyaena	(21 307) 8 523	$(260 594) 104 240	(663) 126 *	$(4 757) 904	44	$316
Felis silvestris	African wild cat	?	?	(83) 74 *	$(596) 531	2.9	$21
Felis nigripes	black footed cat	?	?	?	?	55	$395
Caracal caracal	caracal	?	?	(884) 884 *	$(6 342) 6 342	7.9	$57
Acinonyx jubatus	cheetah	(6 088) 2 507	$(74 459) 30 662	(2 248) 937	$(16 129) 6 723	22	$158
Panthera pardus	leopard	?	?	(331) 331 *	$(2 375) 2 375	21	$151
Panthera leo	lion	(2 029) 1 121	$(24 816) 13 710	(884) 241 *	$(6 342) 1 729	20	$143
Lycaon pictus	African wild dog	?	?	?	?	165	$1 184
Otocyon megalotis	bat-eared fox	(3 874) 1 639	$(47 381) 20 046	(43) 21 *	$(309) 151	0.4	$2.87
Canis mesomelas	black-backed jackal	(384) 292	$(4 969) 3 571	(40) 35 *	$(287) 251	0.3	$2.15
Vulpes chama	Cape fox	?	?	(58) 52 *	$(416) 373	2.2	$16
Orycteropus afer	aardvark	?	?	(442) 442 *	$(3 171) 3 171	3.9	$28
Smutsia temminckii	ground pangolin	?	?	?	?	93	$667
Xerus inauris	ground squirrel	?	?	(67) 25	$(481) 179	5.0	$36
Lepus capensis & L. saxatilis	Cape & scrub hare	?	?	(38) 37 *	$(273) 265	0.2	$1.43
Hystrix africaeaustralis	porcupine	?	?	(295) 265 *	$(2 117) 1 901	0.9	$6.46
Pedetes capensis	springhare	?	?	(2.4) 1.6 *	$(17) 11	0.3	$2.15
Mellivora capensis	honey badger	?	?	(1 249) 1 124	$(8 962) 8 065	6.3	$45
Ictonyx striatus	striped polecat	?	?	(2 652) 2 652 *	$(19 027) 19 027	2.0	$14
Galerella sanguinea	slender mongoose	?	?	(336) 259	$(2 411) 1 858	55	$395
Genetta genetta	small spotted genet	?	?	(115) 115 *	$(825) 825	5.3	$38
Suricata suricatta	suricate	?	?	(160) 21	$(1 148) 151	12	$86
Cynictis penicillata	yellow mongoose	?	?	(187) 146	$(1 342) 1 048	2.7	$19

?, no data; *, line transect conducted at night by spotlighting

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4.3.3 Spatial density-distributions

Bearing in mind some animal movement between days that surveys occurred, overall there were remarkable correspondences in density-distribution patterns among different surveys, for all species (Fig. 4-5). There were moderate but mostly positive correlations between grid cell densities among methods (Table 4-5), although correlation strength was dampened by the fact that tracks had many more detections for which corresponding direct sighting grid cells had zero. Springbok, being both highly visible and having the most clumped dispersion of any species, showed the strongest correlations.

All species were consistently detected by their tracks in a greater number of grid cells than by direct observations (Fig. 4-5). The number of grid cells with detections were at least 50% greater in the case of gemsbok, but on average 3.3 times more grid cells by tracks than aerial survey, and 4 times more by tracks than line transects. At the most extreme, kudu were detected in 6.8 times more cells by tracks than by air and 8.5 times more cells by tracks than by line transect. These differences in presence detection are unsurprising as direct sightings are constrained to relatively narrow strip widths and limits of view while tracks capture animals moving over larger areas (Fig. 4-2).

In the absence of other data over vast areas of the Kalahari, map outputs from Botswana's aerial survey are increasingly relied upon to inform land use change discussions, namely relinquishing marginal portions of WMAs for livestock expansion. The contrasts in Figure 4-5 show that vacant cells in Botswana's aerial survey maps are often false absences -an unsurprising artifact of low sampling intensity (3-4% by air). While counting animals is the primary objective, less equivocal distribution maps would be an additional benefit of implementing track-based surveys.
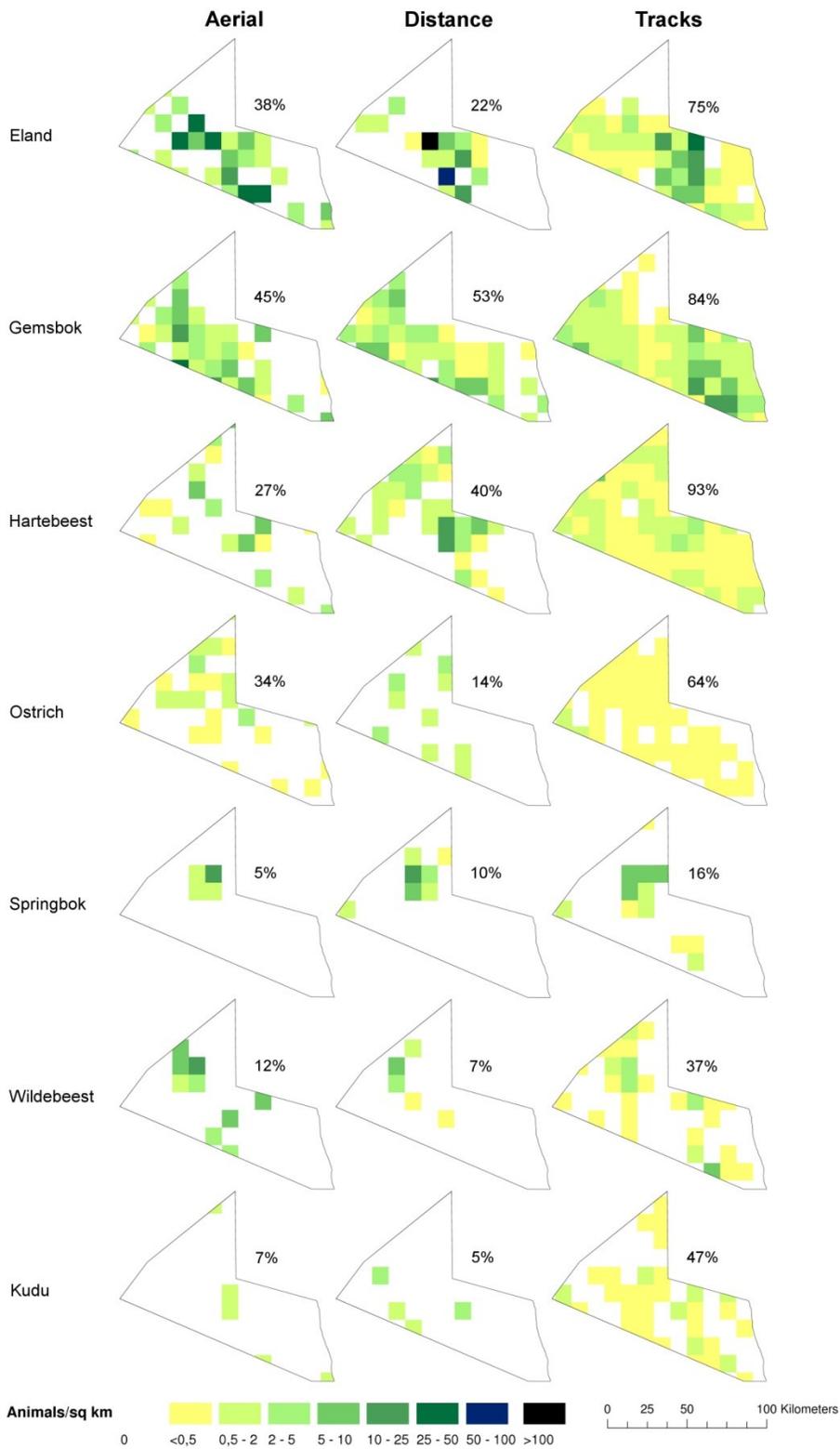
Figure 4-5   Population density-distribution maps over KD2's 6425 km² area for 7 large herbivores surveyed by aerial strip counts, ground distance sampling and tracks. Each map is labelled with percentage of cells occupied (N = 73) .

Table 4-5   Within-species correlations in density estimates between methods by map grid cell (N = 73)

Species	Aerial versus Distance r (P)	Distance versus Tracks r (P)	Aerial versus Tracks r (P)
eland	0.728 (<0.001)	0.190 (0.142)	0.211 (0.102)
gemsbok	0.450 (<0.001)	0.089 (0.494)	0.124 (0.339)
hartebeest	0.624 (<0.001)	0.360 (0.004)	0.401 (0.001)
ostrich	-0.232 (0.072)	0.017 (0.899)	0.026 (0.844)
springbok	0.998 (<0.001)	0.934 (<0.001)	0.934 (<0.001)
wildebeest	0.240 (0.062)	0.106 (0.416)	0.612 (<0.001)
kudu	-0.032 (0.804)	0.080 (0.540)	-0.062 (0.633)

4.3.4   Implications for citizen science

Identifying nearly 20,000 tracks of similar-sized antelopes over few days is a remarkable feat. To our knowledge this is the first time a community in Botswana has not only participated in, but successfully led a wildlife count within their WMA. The distribution of remote communities in WMAs throughout western Botswana is favourable for implementing a rigorous citizen science at a large spatial scale comparable to its aerial survey. This citizen science presents several advantages over conventional methods:

Firstly, resources severely constrain the capacity of Botswana's wildlife authority to survey all wildlife areas of the country at regular intervals. Whereas countrywide aerial surveys were being conducted annually in both wet and dry seasons during the 1990's, they now occur with up to three years intervening, in the dry season only, and are increasingly restricted to portions of the country. Similarly, ground line transects happen haphazardly. To survey KD2 by airplane cost \$7 927 USD or \$12.23 km^{-1}, while the costs of both ground surveys were equivalent, each \$4 652 or \$7.17 km^{-1} (Table 4-6). Despite substantial difference in time commitment required to survey KD2 (1.5 days by air; 15 team-days for each ground survey), the aerial survey was more expensive due to the aircraft, pilot, fuel, and accommodation for the crew. Thus, for equivalent levels of investment KD2 could be surveyed more frequently by ground than by air. Zutshwa trackers are also expert horsemen, and their horseback tracking skills have been utilized in previous research (Keeping & Pelletier, 2014). Horses remove the

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need for 4x4 vehicles which are by far the most expensive components of both ground surveys (Table 4-6). Similarly, CyberTracker software (Liebenberg et al. 2016) loaded onto inexpensive re-purposed smartphones remove the need for non-tracker field personnel time, as trackers can gather their own observations and upload data directly into a national database via cellular networks now present in remote communities. Assuming trackers on horseback would sample 25 km/day, or half the daily distance by vehicle and thus taking twice the number of team-days required to survey KD2, the total cost of a horseback track survey would be $1 400 USD - a threefold drop compared to using vehicles (Table 4-6). Camels offer further advantages over horses in terms of forage, water independence, and lion safety. Availability of funding and adequate resources are highlighted as the most likely limitations to implementing citizen science and community-based monitoring (Chandler et al. 2016). Visitors accompanying Kalahari trackers on animal-back surveys is a creative possibility for funding citizen science, an option impracticable with conventional surveys conducted by wildlife authorities.

Table 4-6 Costs (USD) of surveying KD2 WMA (648.4 km of transect) by air, ground line transects, track survey using motor vehicles, and trackers without vehicles or supervision

	Air	Distance	Tracks	Tracks (citizen science)
survey team-days	1.5	15	15	30
airplane and pilot	$3 371.73	-	-	-
4x4 vehicles	-	$2 400.00	$2 400.00	-
fuel (avgas and diesel)	$1 426.71	$236.85	$236.85	-
accommodation	$1 441.04	-	-	-
subsistence allowance	$246.94	$823.12	$823.12	$823.12
trackers	-	$288.30	$288.30	$576.42
personnel	$1 440.80	$903.90	$903.90	-
survey cost	$7 927.21	$4 652.17	$4 652.17	$1 399.54
cost km^{-1}	$12.23	$7.17	$7.17	$2.16

Secondly, trackers can simultaneously capture a broader picture of biodiversity. Our track survey generated population estimates for the six large carnivores inhabiting the region (Fig. 4-3), the majority of which are conservation priorities. At such low densities these species obviously cannot be surveyed by direct sightings and require an entirely different survey

approach. Furthermore, if we had increased the track survey intensity, so halving the km coverage per day and doubling the total team-days to survey KD2, we could have captured the entire mammalian community at once down to the small viverrids and lagomorphs (Keeping 2014). Track-based detection may be the only practical means for monitoring rare and cryptic species over large areas of the Kalahari. Ground pangolin (*Smutsia temminckii*) is one example that is wholly data-deficient and an urgent global conservation priority (Heinrich et al. 2016) since pangolins have recently taken the unfortunate title as most illegally-trafficked wild mammals in the world (Challender et al. 2014). Tracker data addresses not only wildlife monitoring but also anti-poaching efforts.

Thirdly, long-term conservation will likely require community buy-in and participation. Since 2014 Botswana suspended hunting country-wide. This was motivated by publicised declines of certain antelope species in the Okavango Delta and vicinity (Chase & Landen 2011; Gifford 2013), the causes of which were ambiguous. As a blanket intervention the hunting moratorium is poorly resolved geographically especially as the aerial survey record shows stable or increasing trends in hunted species in the Kalahari over the last 3 decades, with the exception of springbok (DWNP 2015). Enforcing the moratorium requires additional high costs of increased anti-poaching patrols against remote communities that were previously benefitting from subsistence and commercial wildlife utilization. These communities have long expressed dissatisfaction over their lack of involvement in wildlife counts, and skepticism of aerial survey results (Phuthego & Chanda 2004). A step towards some local involvement in wildlife monitoring would likely catalyze knock-on effects beyond the volumes of new field data available to wildlife managers, that ultimately benefits conservation. Without tangible benefits from wildlife through utilization or involvement in local conservation human-wildlife conflicts predictably increase (Mbaiwa 2018), and without livelihood alternatives poorly managed livestock expansion is the default direction in which land use tends to gravitate in the semiarid Kalahari.

4.3.5 Limitations of the track-based approach

Estimating animal numbers from their tracks requires knowledge about their day ranges. Error in day range estimation compared to the true movements of animals within the study area at the time of the survey, and extra-survey field effort required to reduce this error, are valid

criticisms of the approach. We used allometry to approximate population day ranges for most large antelopes in the present study. Fortunately, the accuracy of population estimates relies overwhelmingly on the accuracy of track counts, and less on the accuracy of day range estimates. Although both are proportional to density in the FMP formula, that is a doubling or halving in either track numbers or day range equates to a doubling or halving of density, in reality animal densities typically vary over a much greater scale than do those species' respective day ranges. Among large herbivores in the present study, track counts varied over an order of magnitude (Table 4-1), while true day ranges are unlikely to differ by much greater than a factor of two. Field-estimating day ranges accurately is not greatly limiting in the Kalahari, where trackers can obtain fine ruler tracings of animal movements (i.e. 1 s GPS fix rates) by following animals' tracks (Keeping & Pelletier 2014). Critics may argue that detectability is intrinsically measured in line transect observations and therefore distance sampling is a superior approach. The practitioner must decide if the excessive sampling efforts and costs required to obtain minimal observations with which to estimate detectability is a better allocation of resources than tracing a sample of animal movements to obtain empirical estimates of day range.

Inaccurate counting of large groups by their tracks is another concern. Eland (*Taurotragus oryx*) showed potential for underestimation (Fig. 4-3, Table 4-3). They were concentrated into large herds, some exceeding 1 000 animals. When such sizeable groups intercept a transect, tracks laid down by animals at the front of the herd can be erased by hooves at the rear of the herd, making it impossible to count tracks accurately when masses are moving in long linear shapes especially. The challenge of enumerating large groups of animals by their tracks requires further investigation. To be fair, eland raw counts were strongly correlated with direct sightings, so it is possible that an inappropriate day range caused the discrepancy between population estimates. Also, counting bias of large herds is not exclusive to track surveys; it affects direct sightings substantially (Sharma et al. 2000, Frederick et al. 2003), and it is best practice during aerial surveys to photograph groups numbering 20 or more (Norton-Griffiths 1978, Jachmann 2002).

Finally, track surveys are limited by skilled observers, i.e. those who can correctly identify tracks to species with >95% consistency, and reliably age tracks ≤ 24 h^{-1} old. Few tests of track identification skills among wildlife professionals have shown that even experienced field

observers are often far below this high standard required for scientific monitoring programs (Evans et al. 2009, Zielinski and Schlexer 2009, De Angelo et al. 2010). By contrast, Kalahari trackers have demonstrated near-perfect accuracy, even in identifying individual large carnivores and reconstructing their complex behaviours (Stander et al. 1997). But like spoken language and other aspects of indigenous cultures, tracker skills are in decline. In the Kalahari, the remaining pool of trackers with requisite skills is still large, but without a modern application to replace traditional hunting, talent will inevitably diminish with time.

Box 1. Key advantages and limitations of citizen science-based track survey compared to conventional aerial survey and distance sampling in the Kalahari

Advantages:

- similar population estimates and achievable precision with equal transect effort

- higher encounter rates allow comprehensive species assessed simultaneously

- more complete spatial density-distribution maps, i.e. fewer false absences

- costs <20% of the aerial survey if trackers use animal transportation instead of vehicles

- more frequent and comprehensive surveys = potentially more rapid/effective interventions

- participatory conservation, much needed employment

Limitations:

- reliable estimates of population day ranges at time of survey

- counting error accumulation with large herd sizes

- decline in traditional tracking skill levels (high consistency species identification, reliably aging tracks ≤ 24 h^{-1})

4.4 Conclusion

We have helped Kalahari trackers demonstrate that their data rivals those collected routinely by wildlife authorities using conventional methods. Besides continuing standard surveys in the Kalahari for the purpose of consistency in long-term monitoring, we found little

evidence that direct sightings are superior to tracks in terms of achievable precision, species comprehensiveness, distribution mapping, and costs. Rather, the track survey showed advantages in all these aspects. Given the exceptional opportunities presented in the Kalahari, we urge Botswana to consider track-based wildlife counts led by citizen scientists at a large scale to compliment its aerial survey.

Across Africa and beyond aerial surveys will continue to be invaluable for counting large-bodied wildlife over huge areas, but bounded strip counts will not improve by great measure anymore. Similarly, distance sampling has become indispensable given the ability to measure detectability from sightings data and widespread applicability across taxa and environments, but ongoing refinements will bring only marginal gains. By contrast, track-based density estimation can benefit greatly from increased attention. Line transect development in the 1980's revealed a "rich lode of theoretical gold" that drew excitement and interest away from bounded strip counts, the mathematics of which had been "cracked 50 years previously" (Caughley & Sinclair 1994, pg 204). This fad in wildlife science has since shifted towards its most recent phase: camera-trapping. The explosion of attention devoted to remotely triggered cameras reflects in part the limitations of direct sightings (Rowcliffe 2017). Ironically, advancements in estimating population density from camera captures without the need for individual recognition were influenced by FMP theory (Rowcliffe et al. 2008), thus converging on the solution Russian biologists devised decades earlier for the estimation of density animal tracks. As the detection process between cameras and tracks is similar, both benefit by cross-pollination of theoretical advancements. Camera-trapping obviously has great versatility and widespread applicability in many environments. Climate change is rendering long-term snow tracking programs in boreal regions less viable (Helle et al. 2016), some of which may be ultimately replaced by camera-trapping programs. Although cameras return lower encounter rates than track transects (e.g. Silveira et al. 2003, Lyra-Jorge et al. 2008, Pirie et al. 2016), their popularity extends even to the Kalahari (Van der Weyde et al. 2018). These trends tempt a belief that cameras could ultimately render tracking redundant for conservation monitoring.

More is sacrificed than just data if extraordinary field craft disappears and is replaced by high technology. Exceptional track interpretation skills represent an intangible cultural heritage. Tracking is largely forgotten by industrialized societies, including scientists, even though it may

have been fundamental to the evolution of human intellectual abilities (Liebenberg 2013). The most advanced tracking skills that have survived into modern times are often found in the most remote and marginalized communities (Liebenberg et al. 2016). Retrospectively, decline in traditional tracking skills is attributable to the failure of governments to recognize subsistence livelihoods as a valid human endeavour in the 21st century. However, evidence suggests that uplifting trackers through involvement in conservation could reverse the trend. Over a two-year project where Kalahari trackers conducted field surveys using CyberTracker, Liebenberg (2013) noted their tracking skills improved dramatically to the exceptional level observed ten to twenty years prior when they were hunting on a regular basis. Liebenberg et al. (2016) suggest that "Only by developing tracking into a modern profession, will tracking itself survive into the future."

It is remarkable that destitute trackers from forgotten quarters of the globe possess advanced observation skills that greatly surpass trained wildlife professionals. From a data accuracy perspective, the present field survey was impossible without them. Is tracking replacement with aircraft, laser rangefinders and camera-traps justified? Maybe not on lands where local people have tremendous value to add, are invested in long-term conservation and are without jobs to replace their subsistence livelihoods. As a signatory to the UNESCO *Convention for Safeguarding of the Intangible Cultural Heritage*, Botswana is obliged to address the rapid loss of tracking skills, just as it is equally committed to develop biodiversity monitoring and conservation measures as a signatory to the *Convention on Biological Diversity*. Facilitating a rigorous citizen science whereby biodiversity monitoring is conducted by Kalahari trackers would address both objectives.

5   General Conclusions

I conclude that the results of my investigations have contributed to a defensible paradigm shift in how track data is considered, collected and treated with regards to inference about wildlife abundance. In Chapter 2 I dispelled suspicions about the variable shapes of animal movement paths influencing the accuracy of the FMP estimator, and clarified the need to enumerate all track intersections regardless of individual identity to produce an accurate density estimate. In Chapter 3 I described how multi-species community abundances could be estimated from track surveys using allometric substitutes for empirical day range. In Chapter 4 I challenged the conventional methods by which wildlife are counted in savanna Africa and showed that track counts returned comparable precision, enhanced species comprehensiveness, improved distribution mapping, and substantial cost savings. Empirical tests of density estimator accuracy always have an element of ambiguity because the absolute density of free-ranging populations cannot be known. I have strived to reduce the uncertainty by conducting several comparisons that varied and traded off level of control, species considered, and spatial scale. Notably, the most tightly-controlled empirical comparison (in Chapter 2) which occurred at relatively small scale and with only two species, had among the strongest correspondence between estimates. Furthermore, through these multiple density estimation comparisons in all three chapters resulting in similar counts using independent methods, I have provided some *indirect* inference on the reliability of tracker observations, building confidence in the Kalahari at least. Taken together, this thesis builds support for the use of track surveys to estimate population density rather than being restricted to ambiguous indices of relative abundance.

The field of wildlife abundance estimation has trended towards a condemnation of the use of indices and simultaneous calls for 'robust' methods that explicitly measure detectability instead (Anderson 2001, 2003, Buckland et al. 2001, Pollock et al. 2002, Jennelle et al. 2002, MacKenzie et al. 2006, Hayward & Marlow 2014, Hayward et al. 2015). Within the nebulous category of 'indices', tracks are inevitably binned. At its most basic, "An index of density is some attribute that changes in a predictable manner with density . . . [so] we could be confident that if the index halved or doubled it would reflect roughly a halving or doubling of animal density. Formally, that holds only when the relationship between index and density is a straight line that passes through the point of zero index and zero density" (Caughley & Sinclair 1994). Critics

argue this monotonic direct relationship between index and density is unrealistic and unsupportable because it assumes a constant detection probability.

> *There are 3 classes of variables that affect the probability of detection and therefore the index, in addition to true abundance. . . First are variables related to the observer, or perhaps several observers used during a multi-year survey. These variables include the observer's training and education, experience, interest, hearing ability, eyesight, height, and fatigue level. Each of these variables can affect the probability of detection and therefore have substantial effects on the index. . . Second are variables associated with the environment that have substantial effects on number detected and counted (the index). These include wind speed, temperature, precipitation, time of sunrise, habitat type, season of year and its phenology, vegetation height and density, human disturbance, cloud cover, and a host of others. The third class of variables includes aspects of the species itself that affect its detectability - e.g. coloration, behavior, gender, flock size, calling intensity and rate, and matedness . . .* (Anderson 2001)

How many factors on this list are relevant to track indices in particular? Many variables can affect detection probability, but more important is the extent to which such variables cause errors that are quantitatively meaningful. Detectability by direct sightings can be both low and highly variable in accordance to Anderson's (2001) first two classes of variables. Concerning the detection of tracks, however, the opposite is true - methods typically ensure consistently high detection rates of tracks. Where substrates and observers are good, the probability of detecting tracks on a well-managed transect can be near perfect. The tracks are not hidden but fixed and plain to see. There are no doubtful phantom sounds or fleeting glimpses by single observers but rather a luxury of time for several trackers to scrutinize and verify observations. Direct observation is sensitive to time of day and most mammal activity occurs in low-light conditions during crepuscular and nocturnal periods when visibility is poor. By contrast the time-integrative nature of track capture means animal activity over diel periods can be detected with equal efficiency. Regarding the third class of variables, differences in species characteristics such as size, color, sex, behavior, social structure, etc. are mostly irrelevant because every locomotory terrestrial creature makes tracks, even very small animals including most arthropods, annelids and mollusks (Bider 1968).

The fundamental detection process characterizing direct observation differs from indirect observation of animals through their signs. Direct observation assumes stationary animals within

an area that can be defined, while indirect observation relies on animal movement over an undefined extent. Chapter 2 makes clear that if one is to apply a strict definition of detectability to tracks then it involves two components: the first is the probability that an animal present in the area leaves tracks within the sampling frame (i.e. transect, quadrat, track plate); the second is the probability that those tracks are noticed and correctly recorded by observers. The first probability is difficult to diagnose because of the definition's individual animal focus. As demonstrated in Chapter 2, the detection probability of individual animals by tracks emerges from the interaction of both day range and spatial patterns of movement in relation to the sampling frame. However, two species dispersed at identical density but exhibiting marked differences in path tortuosity (and therefore detectability) can be estimated with equal accuracy if individual identity is ignored during data collection. Explicit measurement of detectability is therefore not necessary to accurately estimate animal density from tracks. Counting all track interceptions regardless of individual identity negates concern about varying spatial patterns of movement, reducing the problem to the all-important variable day range. The "long list of variables associated with the observer, the environment, and characteristics of the species being surveyed" (Anderson 2001) pervasively concerning to direct observations and commonly argued to be afflicting indices in general, and tracks by association, can be rendered negligible by methodological controls coupled with understanding the FMP formula.

Understanding the FMP formula brings into question the relevancy of the detectability concept applied to track surveys, and the validity of criticisms leveled for failing to measure detectability. The FMP model was derived as a geometrical problem of randomly intersecting line segments. More recently, Random Encounter Models (REM), increasingly applied to camera traps (Rowecliffe et al. 2008, Lucas et al. 2015, Nakashima et al. 2018), are derived directly from a two-dimensional interpretation of the three-dimensional ideal gas model long described in physics (Maxwell 1860). Although the FMP and REM have different starting points in their formulation, Rowcliffe et al. (2008) showed how both converge into an identical formula when the camera detection zone is reduced to a one-dimensional line. Fundamentally, the ideal gas model is unconcerned with the probability of contact between individual gas molecules, but rather overall collision rates. Likewise, the FMP and REM do not require probabilities of detection for individual animals, but rather estimation of the total track intersection rates with transects, or total photographic encounter rates, respectively, regardless of individual animal

identity. Thus, the concept of detectability is somewhat mismatched when applied to these animal movement-based models, and the deficiency of explicit estimation of such is an inappropriate criticism for models that do not require it for density estimation.

Once again, the FMP formula:

$$D = \frac{\pi}{2} \frac{x}{S\hat{M}}$$

Without any algebraic manipulation, this form states a linear equation whereby density (D) is predicted by the index of track intersections per 24 hours per kilometres sampled (x/S) with a slope defined by day range ($\pi/2\,\hat{M}$) passing through the origin.

Thus, the FMP model does two important things: first it is a formula by which density can be directly estimated from track counts, and second it is a distilled framework by which track indices can be understood.

As of 2015, researchers still seem unaware of these implications. In Australia's dingo debate Hayward et al. (2015) mentioned the oft-repeated unmeasured variables associated with the "environment, observers, animal movements and animal status . . . habitat type, substrate, season and local weather" all combining to effectively invalidate inferences from track indices. They held that such track indices are unreliable unless they are properly validated for each circumstance. They suggested that the double-sampling calibration work of Funston et al. (2010) is "exactly the kind of research that needs to be done". Double-sampling, synonymous with index-calibration experiment, requires several independent estimates of density using robust methods in those same areas that track indices are collected so that regression equations can be estimated. However, the impracticality of employing robust methods such as mark-recapture and distance sampling in Australia's outback is precisely the reason that researchers used tracks to index abundance in the first place (Nimmo et al. 2015)

Both sides of the dingo debate seemed unaware that if practitioners could adopt the specific track counting rules necessary to fit the FMP framework, then it is established that the index of track counts per kilometre per 24 hours is directly proportional to animal density and day range. Thus, to have confidence in comparing indices over space or time one must simply

have a confident understanding of potential changes to day range of those animals sampled over space or time. The FMP formula demystifies the track index - abundance relationship. Proper methodological controls render the many variables believed to constitute restrictive and unrealistic assumptions in comparing indices either null or largely irrelevant; the uncertainty is instead focussed onto the single variable day range. Day range investigations could be a much more efficient allocation of field effort than struggling with impracticable sample sizes required to meet the assumptions of 'robust' density estimation techniques. The FMP formula renders calls for increased double-sampling efforts (*sensu* Hayward et al. 2015) unnecessary.

Furthermore, the method of Funston et al. (2010) encourages identifying individual animals from their tracks in the field and recording them once only, regardless of how many times they re-intersect a transect. As shown in Chapter 2 this practice complicates interpretation of index-calibration equations by granting importance to animal movement patterns. Stander (1998) found it possible because he worked with large carnivores in a modest sized reserve area where exceptional indigenous trackers knew all the animals present individually. Unfortunately, the trackers Stander (1998) worked with are now deceased, and such top-level skills are diminishing with the aging population of traditional Kalahari hunter-gatherers. Stander's (1998) method of individual differentiation based on tracks is infeasible in large areas where many animals are unknown to trackers and where species are more abundant. For example, it is very unlikely that trackers are able to differentiate individual spotted and brown hyenas from their tracks with any reliability even though this is implied in the methods of Funston et al. (2010) and Winterbach et al. (2016, 2017). It is unfortunate that this track counting approach has been propagated since Stander's (1998) seminal paper, because index-calibration models would be more interpretable if their slopes were simply determined by day range in the FMP framework.

If track counting rules could be adjusted slightly so that all animal intersections are considered regardless of their individual identity, then the slopes of these index-calibration models could be interpreted simply and explicitly in the context of the FMP formula. Hayward et al.'s (2015) concerns about the unreliability of comparing indices between sites are still relevant, however, a more parsimonious understanding offered by FMP could accommodate this by researching variation in day range, which is easier than attempting independent calibrations for every novel situation. Instead of the preoccupation with the many non-isolatable variables

believed to influence detection probability, accuracy could be improved efficiently by explaining error due to variability in day range estimates in each new area. This concern is predictably greater for comparisons between sites at small spatial scales that capture small sample sizes because day range may fluctuate substantially between those few animals sampled. As sample sizes and spatial scales increase, the distribution of day ranges converges and stabilizes as an accurate estimate of the true population day range. Ironically, after stressing the need for track index validation, Hayward et al. (2015) further suggest a 'way forward' to solving the dingo debate that includes camera trapping using Rowecliffe et al.'s (2008) random encounter model - which is precisely analogous to the FMP model. Cameras would bring no advantage unless researchers believe they are better at detecting wildlife than track surveys. Cameras and tracks generate identical concerns about fluctuating day range causing error in estimates or invalidating comparisons of indices between sites or though time.

The proponents and critics of calibrating track indices by double-sampling (e.g. Houser, Somers & Boast 2009, Funston et al. 2010, Gopalaswamy et al. 2015, Hayward et al. 2015, Winterbach et al. 2016, Elliot & Gopalaswamy 2017, Belant et al. 2019) have yet to provide a clear explanation for the slope of such equations. Stander's (1998) suggestion that the "slope of such regressions portrays the ecological characteristics of the relationship between spoor and true density" has not been explicated since. In the context of the FMP formula the coefficient of variation R^2 simply reflects how similar day range was for those populations sampled at each different site. The FMP formula also reveals why the slopes of such calibrations significantly differ between populations sampled on clay vs sandy soils (Funston et al. 2010, Winterbach et al. 2016): higher density carnivore populations inhabiting the richer environments underlain by clay soils simply move less than their equivalents on semi-arid sandy soils, probably due to differences in prey densities. These interpretations are of course complicated if the methodological assumptions of the FMP formula (i.e. transects do not influence animal movements, and all intersections enumerated regardless of individual identity) are not met; which is typically the case with large carnivore track surveys. In Chapter 4 I noted that animal densities and track counts vary more than day ranges among species. This is well understood in allometric scaling of day range. Generally, across sites in similar environments used for double-sampling there is little reason to believe average day range and patterns of movements with respect to linear features used for sampling vary by any substantial degree. It is therefore

unsurprising that index-calibration experiments have returned encouraging R^2 values such as 0.98 for leopards and 0.98 for combined lions and wild dogs (Stander 1998), 0.97 and 0.98 for cheetahs in wet and dry seasons respectively (Houser, Somers & Boast 2009), 0.96 for combined large African cats and hyaenas (Funston et al. 2010), 0.84 for tigers (Jhala et al. 2011) and 0.95 for lowland tapirs (Moriera et al. 2018). Ignoring the underlying detection process (animal movement) while instead attempting to indirectly model heterogeneity in detection probability led Gopalaswamy et al. (2015) to conclude that "the high R^2 estimate in the [Jhala et al. 2011] study is non-reproducible". The consistently strong empirical relationships between track counts and true abundance are not surprising at all and will certainly continue to be reproduced.

Excessive criticism of indices in general, and tracks specifically, surely has unintended negative consequences for conservation in parts of the world. Wildlife authorities in developing countries cannot avoid being influenced by what gets published in leading international journals that they cannot test or refute easily. Thus, Botswana's wildlife department started to implement ground line transects to compliment its aerial surveys despite that effort adding very little to existing knowledge, as I showed in Chapter 4. Meanwhile, destitute trackers residing in remote communities ostensibly empowered to sustainably manage their own wildlife via the Community Based Natural Resource Management (CBNRM) programme sat idle with little if any contribution to conservation decision-making. It is a remarkable fact that there are far more PhDs in the world than there are people who can interpret tracks at the level of the Kalahari's remote community dwellers. Typically, society rewards rare and exceptional talent proportionally, but in the case of expert indigenous trackers this is clearly not so. As I have argued, if trackers continue to sit jobless while all around them wildlife authorities and researchers implement aerial surveys, distance sampling and camera trapping to study their wildlife, then that is in part because of the failure of modern wildlife science to comprehend the information contained in track distributions.

At the time of this writing, Botswana's new leadership has announced the re-instatement of hunting after a 5-year suspension. The government needs data that can inform science-based quota setting in remote community areas of the Kalahari region especially. I have strived in this thesis to show the unrealized possibility at Botswana's fingertips to implement a large-scale track-based wildlife monitoring program that finally and crucially involves local expert

stakeholders. I hope this work can bring some honor to the last vestiges of marginalized humanity that still hold remarkable tracking abilities. Recognition of their gifts provides employment and gives them a stake in decision-making within those wildlife areas where they reside. More broadly, I hope this thesis moves conservation a small step forward by shedding light on the FMP formula as a way to inform urgent conservation efforts around the world through the use of animal tracks.

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Appendix A: An example of fine-tuning density estimates for Kalahari cheetahs with demographically stratified empirical day ranges

Detailed information on daily movements of Kalahari cheetahs is uniquely available from the southern Kgalagadi Transfrontier Park (KTP) from Gus and Margie Mills' recent study. Mills & Mills (2017) subdivide the cheetah population into 7 demographic groups and provide day range estimates for each group. To deduce the relative proportions that each demographic group comprises the total cheetah population, we used the following information about cheetah life history traits (Mills & Mills 2014, Mills & Mills 2017):

- adult sex ratio 1.8 males:1 female

- ratio of males comprising coalitions is 57% while 43% are solitary

- continuous breeding throughout year

- average litter size = 3.4

- 53.6% of cubs survive to emergence from den

- 66% cub survival from emergence to 4 months

- 95.8% cub survival from 4 months to 14 months

- time period cubs in den = 0 - 2 months

- time period small cubs = 2 - 6 months

- time period large cubs = 6 - 19 months

- female sexual maturity/first litter at 3 years

- cubs independent at 18.9 months

- average birth interval 23.4 months

- 62% of adult females with cubs and 38% without at any given time

- day range for "Female with cubs" includes both mother and cubs travelling together, "Female with cubs in den" is mother travelling alone (see Table A.1).

These traits predict the proportions of each demographic group comprising the Kalahari cheetah population (see Table A.1).

The product of mean day range for each demographic group and the proportion that it contributes to the total population was then used to tally a mean population day range estimate of 11.44 km travelled per cheetah per day.

Table A.1. Number of day range samples, mean day ranges with standard deviation for the southern Kalahari cheetah population stratified into 7 demographic groups (from Mills & Mills 2017), the relative proportion of the cheetah population comprised of each demographic group (derived from life history traits), and the proportion of day range from each group contributing to the mean day range for the total population on the Kalahari landscape

Demographic group	Number of days followed	Mean day range (km)	Proportion of total population	Proportion of day range comprising total estimate for population (km)
Coalition males	36	14.8 ± 6.3	0.22	3.33
Single male	17	14.9 ± 6.7	0.17	2.53
Single female	41	10.1 ± 5.4	0.08	0.84
Female with cubs in den	26	11.3 ± 5.9	0.01	0.16
Female with small cubs	28	7.7 ± 3.4	0.08	0.62
Female with large cubs	47	8.6 ± 4.7	0.20	1.76
Sibling groups	24	9.9 ± 3.9	0.22	2.21
(sums)	N = 219		1	11.44 mean day range (total population)

Estimating 95% confidence limits around the population density estimate required a 2-stage bootstrapping procedure for day range. Each iteration depended first on the proportional probability of selecting one of the demographic groups, and then secondly a value was sampled randomly from the day ranges within the selected group. This process was repeated to generate bootstrap replicate means from total sample size (N=219), 5000 times. The track index bootstrapping procedure was consistent with the other species: spoor counts on each transect were resampled in proportion to the length each transect contributed to the total sample distance within KD2.

The key assumption of the resultant density and population size estimates is that the day ranges from Mills & Mills (2017) study population in the southern KTP are representative of the cheetah population over a larger area of the Kalahari. As climate, habitat and primary cheetah prey densities are comparable throughout, this assumption is probably fair. Any local deviations from this overall model of day range for the population are likely numerically minor and therefore not expected to affect the density and population size estimates greatly.

To check the extent that detailed knowledge of cheetah demography improved population estimates, we simulated a 'naive' day range estimate assuming the field practitioner has no knowledge of cheetah demography and samples empirical day ranges from the population at random. We did this by applying a bootstrapping procedure whereby values within each demographic group were resampled at random. The naive mean day range was 11.04 km, which is only 3.5% less than the demographic estimate. Although a single example, it provides some reassurance that empirical day ranges estimated from populations whereby nothing is known about demography, can be usefully applied to approach accurate density estimates from track counts.

Appendix B: Cost for aerial survey of KD2 - all figures in USD

Cost for aerial survey of KD2 - All figures in USD

	No.	Unit	Unit Cost	Total	Notes
Pilot charges					
Pilot (supply of C206 aircraft)	13	hour	240.17	3,035.49	*4 hours in the morning*
Naviagation trip/fee	4	legs	7.69	30.74	*and 2 hours in the*
Parking fee	2	parking	1.44	2.88	*evening; hence two*
Landing fee	5	Landings	2.88	14.41	*nights for KD2*
Accommodation/food/beverages for pilot	2	person/day	144.10	288.21	*hotel*
Phase Sub total				**3,371.73**	
200-litre drums of aviation gasoline	2.86	each	451.53	1,293.28	** fuel requirements below*
Phase Sub total				**1,293.28**	
DWNP personnel					
Subsistence allowance	9	person/day	13.72	246.94	
Hotel Stay (including meals and beverages)	5	person/day	144.10	1,441.04	
Overtime allowances	14	person/day	102.91	1,440.80	*experienced aerial survey observers*
Phase Sub Total				**3,128.78**	
TOTAL				**7,793.79**	

* Fuel requirements

Total transect length (km)	648.4
Airstrip to start transect 1 (km)_AM	110
End last transect to airstrip (km)	55.2
Airstrip to start transect 1 (km)_PM	49.2
End last transect to airstrip (km)	46.5
Airstrip to start transect 1 (km)_AM2	42.1
End last transect to airstrip (km)	96.2
Total distance (km)	**1047.6**
Average speed of the aircraft (kph)	160
Estimated Flying time (h) *Execution*	6.5475
Estimated Flying time (h) *Calibration*	3
Estimated Flying time (h) Total	**9.5475**
Average fuel Consumption (L/h)	60
Total Fuel consumption (L)	**572.85**
Number of drums of fuel required	**2.86425**

Appendix C: Cost for ground survey of KD2 - all figures in USD

Cost for ground survey of KD2 - All figures in USD

	No.	Unit	Unit Cost	Total	Notes
4x4 vehicles	15	days	160.00	2,400.00	*fully-equipped rental*
diesel	341	Litres	0.69	236.85	*1363.8 km driven during survey and to/from staging area, assumes 4km/L fuel consumption*
subsistence allowance	60	person/day	13.72	823.12	*2 trackers and 2 personnel per team*
trackers	30	person/day	9.61	288.30	
personnel	30	person/day	30.13	903.90	*basic salary (lowest scale) for wildlife field officers*
TOTAL				**4,652.17**	