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CHAPTER 1

INTRODUCTION

You know you are truly alive when you're living among lions.
—KAREN BLIXEN

In some ways the lion needs no introduction as our relationship with the species extends back for millennia. Our ancestors drew paintings of archaic lions on the walls of their caves, ancient civilizations portrayed lions as sphinxes (human-headed lions); griffins (half-lions, half-eagles); servants of the goddesses Ishtar and Parvati; and the vanquished foes of exalted Assyrian kings. Many of us grew up with the lion as a character in children's literature (the Cowardly Lion from the *Wizard of Oz*, Aslan from *The Lion, the Witch and the Wardrobe*, Simba from *The Lion King*), and we often describe someone we admire as being brave as a lion, as having a leonine grace, as being lionhearted. But none of these portrayals tell us much about what it's really like to be a lion. What it's like to belong to an extended family of multiple mothers, aunts, cousins, and grandmothers, as well as fathers and uncles and sometimes even dad's best friend. What it's like to raise cubs in a world where the next big meal may not arrive in time. What it's like to be surrounded by neighboring lions who would be perfectly happy to cripple you or kill your young. But most importantly, this long history doesn't prepare us for the very real possibility that the lion may not survive in a world that is increasingly filled with humans.

The reality of the beast is far more engaging than the historical myths and the literary characterizations. Despite an ancient feline ancestry of habitual distrust toward others of their own kind, lions tackle most challenges as a group: they hunt together, raise cubs together, and defend a joint territory. Female pridemates are a sisterhood not only in terms of their genetic relationships but also in the idealized sense of a nonhierarchical feminism; males are comrades in arms to an almost gladiatorial extent.[1] But are any of these behaviors truly cooperative, or do slackers parasitize the generosity of the rest? And if any of these behaviors is truly cooperative, what is its basis? Close genetic kinship? Some cold calculating form of scorekeeping? Or the warm comfort of mutual dependency? And, if all this cooperation is such a good idea, why haven't tigers and leopards followed a similar path in their own evolution?

But not all aspects of lion behavior are admirable; lions also have their dark side. Family life involves prolonged periods of parental care—mostly by the mothers, but fathers matter, too—and the very fact of extended care provides incentives for outsiders

1 The Cowardly Lion needed a companion more than he needed a medal; Aslan could never have ruled Narnia alone; Scar would never have contrived to kill Mufasa.

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to try to eliminate any obstacles so as to speed up their own chances for reproduction. How do families protect themselves against this constant threat of disruption and infanticide? And how do the potential consequences of infanticide extend to seemingly distant aspects of lion life, including the choices females make when seeking new mates or even to the defining characteristic of the mature male, the conspicuousness of his mane?

As impressed as we may be with the lions' strength and size, they face the fundamental challenge of trying to capture an animal that doesn't want to be eaten, and some prey species are more difficult to catch than others. How do the lions overcome these challenges? Is it always better to hunt together or should they sometimes revert to the ways of their solitary ancestors? What happens when the herds are out of reach for months at a stretch? Beyond the daily drama of catching their next meal, the back-and-forth between predator and prey plays out over a longer time scale in ways that may determine the number of lions that can live in a particular area. Hence, we might ask how many wildebeest does it take to feed a lion? Conversely, do too many lions ever threaten the future of their own food supply? Lions can be terrible, horrible, awful animals when it comes to their interactions with smaller carnivores. What happens to these species in a landscape filled with lions?

If we take a wide-angle view of the lion across the broad landscape of twenty-first-century Africa, we cannot ignore the dark clouds on the horizon. Successful lion conservation is in doubt even in many of the best-protected parks in Africa, and solutions are urgently needed. Geneticists have long warned about the consequences of close inbreeding, and many of the smaller parks and reserves host lion populations that are unlikely to remain viable in the long term. But how does this actually manifest itself in a species as robust and resilient as the lion, and is there any practical way to address the problem? Human populations have grown to such an extent that lion habitat now directly abuts livestock pastures and agricultural fields across much of their remaining range. What happens when lions leave the confines of a national park and come face-to-face with livestock herders? Is there any way to promote human-lion coexistence? Even worse is when lions become man-eaters—yes, man-eating lions still exist even in the twenty-first century. What leads to this sort of behavior? Can we predict when and where people will be most at risk? And at what point should we just give up on coexistence and erect physical barriers to protect people from lions and vice versa?

These are just a few of the questions that we addressed during our intensive studies of the Serengeti and Ngorongoro Crater lions. In the following pages, the initial chapters will focus on various aspects of lion behavior before broadening out to include ecological issues and then expanding to cover lion conservation. But in first introducing the lions, I want to provide a picture of how we were able to keep track of everyone on a day-to-day basis. Though I will often describe lions in general terms such as "males," "females," or "cubs," we recognized every animal as an *individual*. Some lions had telltale markings like conspicuous scars or broken tails, and almost every adult had a diverse collection of ear notches acquired from squabbles with its companions at kills. But most lions are difficult to distinguish as they lack the conspicuous black stripes or rosettes of a tiger or a leopard. We therefore relied on Pennycuick and Rudnai's (1970) method of identifying individuals by the pattern of their whisker spots.

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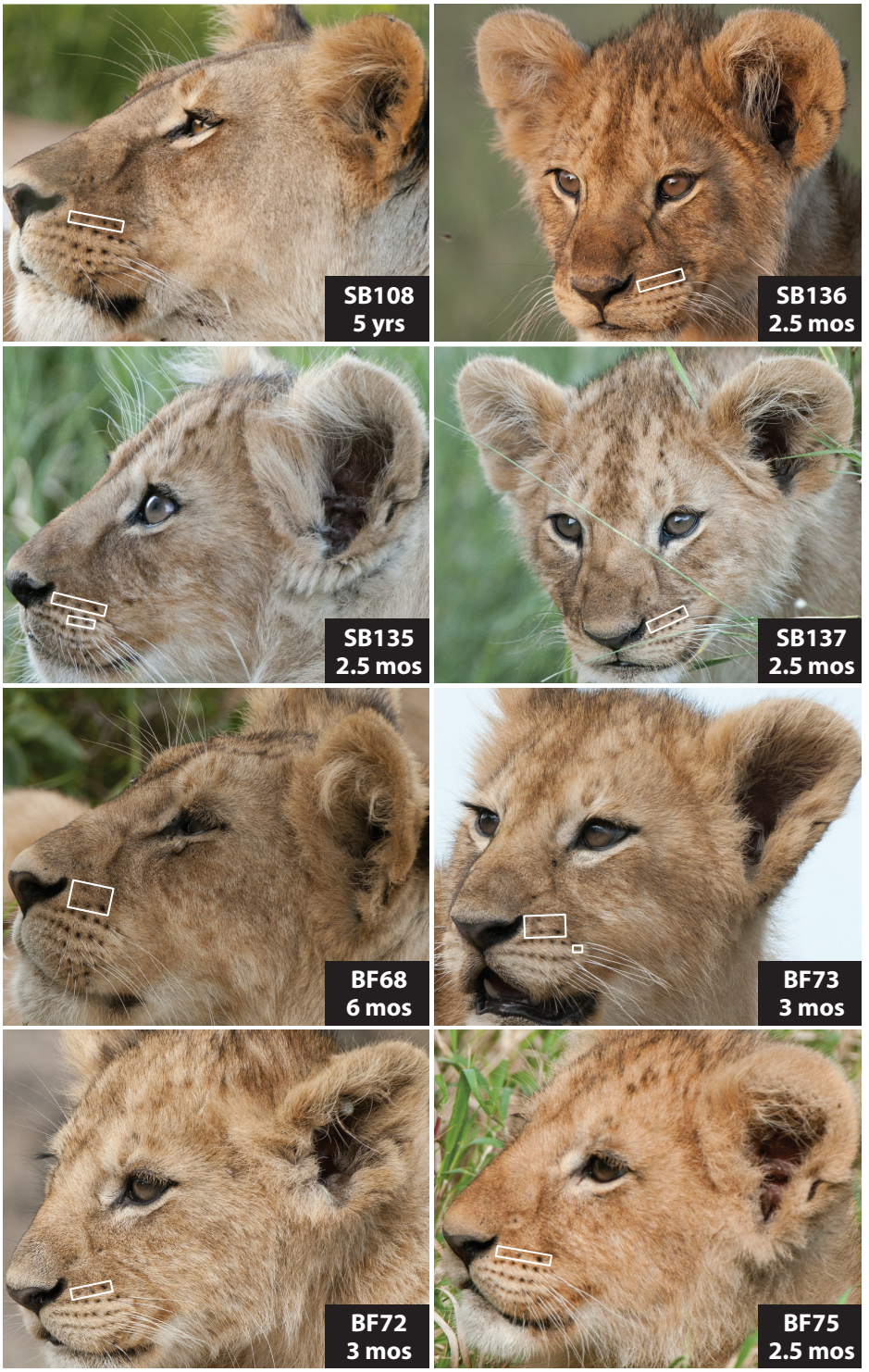

FIGURE 1.1. Identification photos for eight Serengeti lions in the Simba (SB) and Barafu (BF) prides. Large boxes indicate the primary whisker spots used to recognize each individual; small boxes highlight the "between-row spots" of SB135 and BF73. SB108 is the mother of littermates SB135–137; BF72 and BF73 are also littermates.

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The well-defined rows of vibrissae on either side of each lion's face almost always include a few extra dots above the top row (figure 1.1), and these can be easily noted on an ID card. Whisker spots are distinct even in the smallest cubs and though these may become obscured by scars or age, the steady accumulation of additional markings keeps each animal unique throughout its entire life.

The daily monitoring required an inordinate amount of patience. The initial pulse of excitement at finding a group of lions was soon tempered by the fact that they have usually melted for the day and were unlikely to rise again until the cool cover of darkness (see figure 1.16a). But we needed to know who was there, who was mating with whom, who had just had babies, what species of prey they had obtained. Often, we found only two or three adults in a group, and the chores were fairly simple, but a bigger group with a large pile of cubs could be exhausting. Grant Hopcraft's description of one particular sighting provides a sense of the challenge:

> **4-Dec-1999 09:00.** I identified each one of a group of 17 lions from the Masai Kopje (MK) pride as they meandered toward a nearby kopje [rocky outcrop]. The four adult females were easy. Each marking helped to tell them apart—a notched ear, scarred nose, or distinctive dilated pupil with a brown dot in the iris. The 13 cubs were the hardest to identify, yowling behind their mothers or ambushing their unsuspecting sisters, and only differentiated from each other by a subtle whisker spot pattern. I spent nearly two hours, sometimes feeling like a rock climber clinging to an identification by my fingertips. An extra spot between the ordered rows of whisker spots is like a Christmas present as it distinguishes one cub from the next. The trick is to start with the easy ones and whittle down to the final few. Deductive logic, note taking, and a series of sketches helps keep track of each one before they disappear into a gully or kopje; any leftovers are listed as "unknowns" that at least provide an idea of the number of individuals in the group that day.

Though often tedious and laborious, these observations were the bread and butter of the long-term lion project, and, with 56,640 separate sightings like Grant's encounter with the MK pride, we were able to assemble mosaic portraits of 5,309 known individuals in 111 prides.

To assure an accurate accounting of so many individuals over the fifty years of the long-term study, we gave each animal a unique name. Schaller had mostly used numbers (Female-49, Male-107) except for a few distinctive individuals (Brownmane, Blackmane, One-eye). Bertram also used numbers (S-79, M-22), whereas the Bygotts preferred Swahili words: Mbili (two), Miwani (eyeglasses), and Mwindaji (hunter), in one pride; Shida (trouble), Shika (hold), and Safi (clean), in another. Anne Pusey and I kept the names of animals that had been christened by our predecessors but then christened each new cub with a code beginning with the two-letter abbreviation of its natal pride (SM for the Sametu Pride; LL for Loliondo) either followed by the letters of the alphabet or by numbers. Hence, SB108 in figure 1.1 was the 108th cub born to the Simba (SB) pride and BF68 was the 68th cub in the Barafu (BF) pride after we joined the project. We weren't averse to giving them longer names, but each name could only be used once, and so many cubs die before reaching maturity that there aren't enough names to go around. On the other hand, the relatively small number of older

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animals that immigrated into the study areas from elsewhere were far more likely to survive, so these received names that ranged from the sublime (Dorian and Gray) to the ridiculous (Twirp-1 and Twirp-2), but generally with a common theme indicating who had first been seen with whom.

A LION PRIMER

Before taking a deep dive into specific research topics, I first want to give a sense of the lions' food supply in the Serengeti and Ngorongoro, introduce more lion-monitoring methodology, provide a few basics about the lion's day (and night), and briefly describe their overall life course.

All Ecology Is Local

The Serengeti National Park is located two degrees south of the equator, just west of the Ngorongoro Crater highlands and east of Lake Victoria, and the Serengeti study area lies in the approximate center of the park (figure 1.2). Rain clouds moving off the Indian Ocean only surmount the Crater highlands for a few months each year, as the mountains produce a "rain shadow" that limits total rainfall over the open plains of the Ngorongoro Conservation Area (NCA) and the southern Serengeti, whereas Lake Victoria generates its own weather in the far west of the park (Sinclair and Norton-Griffiths 1979), thus, the Serengeti experiences a pronounced rainfall gradient from north to south and from east to west (figure 1.3). The seasonal rainfall patterns drive the annual migration of wildebeest, zebra, and Thomson's gazelle as they seek out the nutritious grasses on the volcanic soils of the eastern plains each wet season then retreat to the north and west each dry season (figure 1.4). Rainfall is heavier in the woodlands portion of the lion study area, allowing grazing species, such as Cape buffalo, hartebeest, and warthog, to remain throughout the year, and the woody vegetation also supports resident browsers, such as impala and giraffe. In contrast, the 250-km^2 floor of the Ngorongoro Crater is an island of open grasslands interspersed with swamps and marshes. The Crater receives substantially more rainfall than the Serengeti (figure 1.3), and as the floods recede each dry season, the emerging vegetation remains green at the margins, providing a continuous supply of forage (Estes and Small 1981). Thus, the larger herbivores reside on the Crater floor all year round, except for a proportion of wildebeest that move to the Serengeti plains each wet season and about a third of the Cape buffalo that move up to the Crater rim each dry season (figure 1.5).

The Crater lions subsist almost entirely on three species: wildebeest, zebra, and buffalo, with wildebeest being the most common prey throughout the year (figure 1.6a); zebra and buffalo are both taken somewhat more often in the dry season compared to their seasonal availability, possibly reflecting lower body condition in the driest months. During the wet season, the lions on the Serengeti plains are regularly able to "feast" on the migratory wildebeest, zebra, and Thomson's gazelle, but they are forced to subsist on a broader range of prey during the "famine" of the dry season (figure 1.6b). The lions in the woodlands study area mostly take wildebeest, zebra, and

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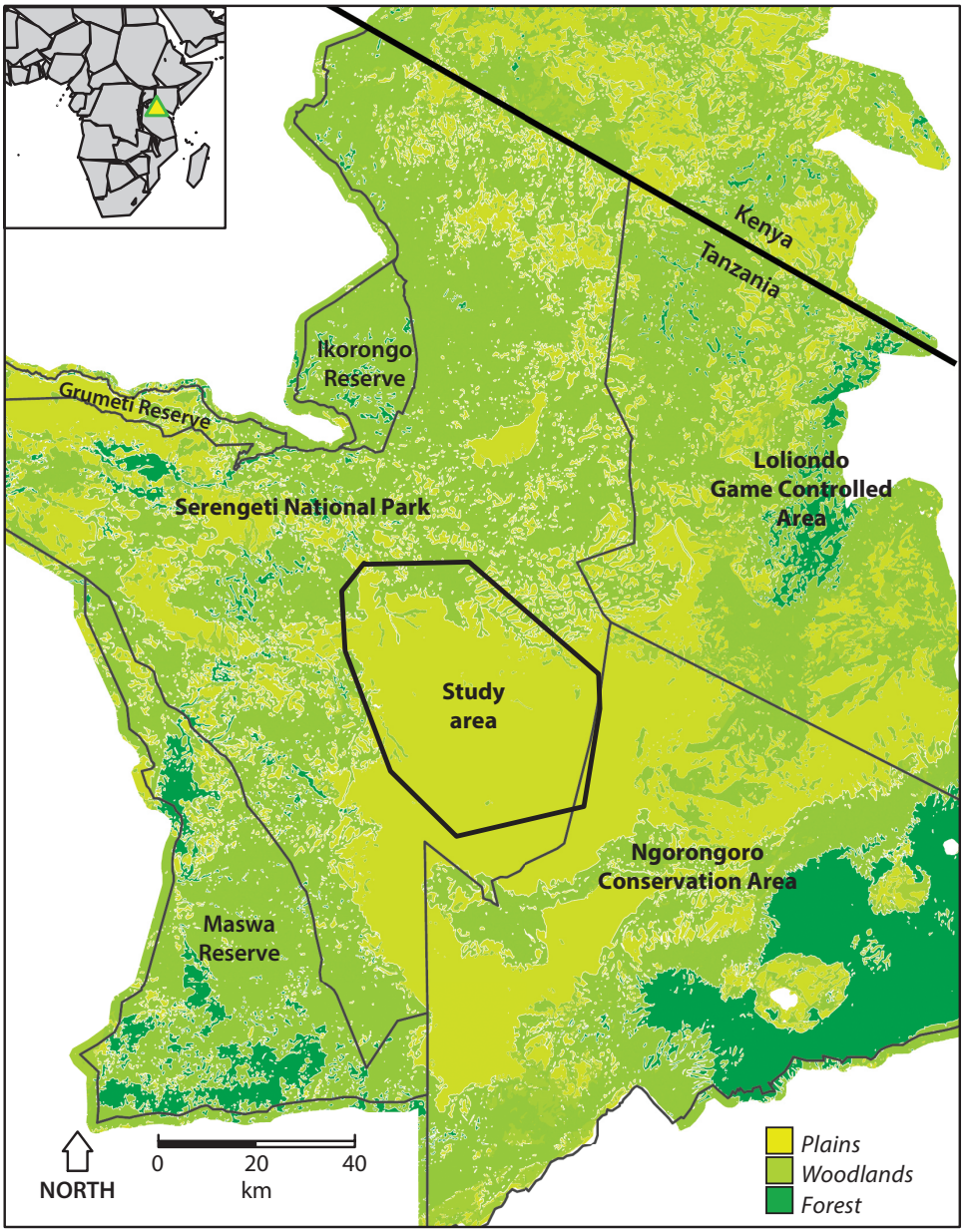

FIGURE 1.2. Map of the greater Serengeti ecosystem. Dark green indicates forest, light green woodlands, and yellow open grasslands. The long-term Serengeti study area covers about 2,000 km^2 and extends from the central woodlands to cover much of the open plains. The Ngorongoro Crater is located inside the Ngorongoro Conservation Area.

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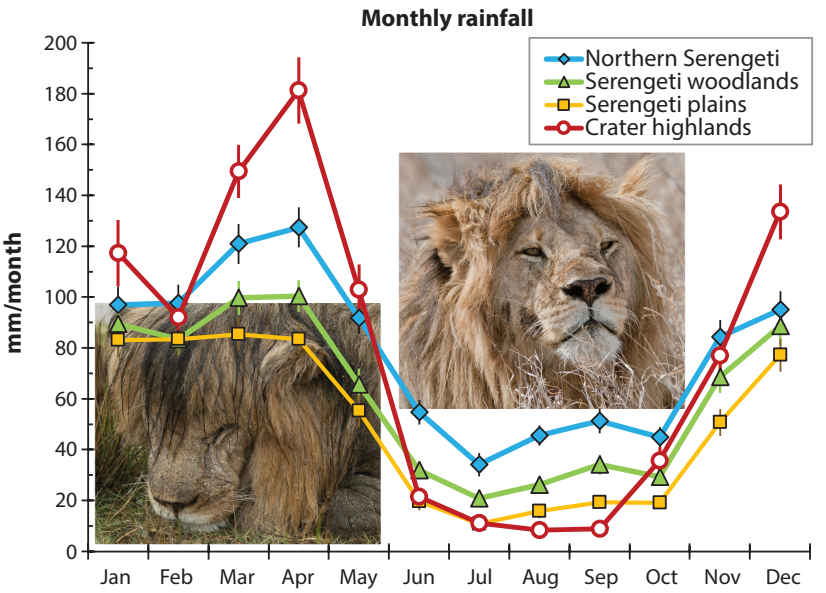

FIGURE 1.3. Monthly rainfall in the greater Serengeti ecosystem. Data from the Serengeti were collected between 1966 and 2000 from three to eighteen rain gauges in each part of the park; data from the Crater highlands were collected from a single gauge between 1963 and 2014; see Sinclair et al. (2013) for details. Vertical bars are standard errors.

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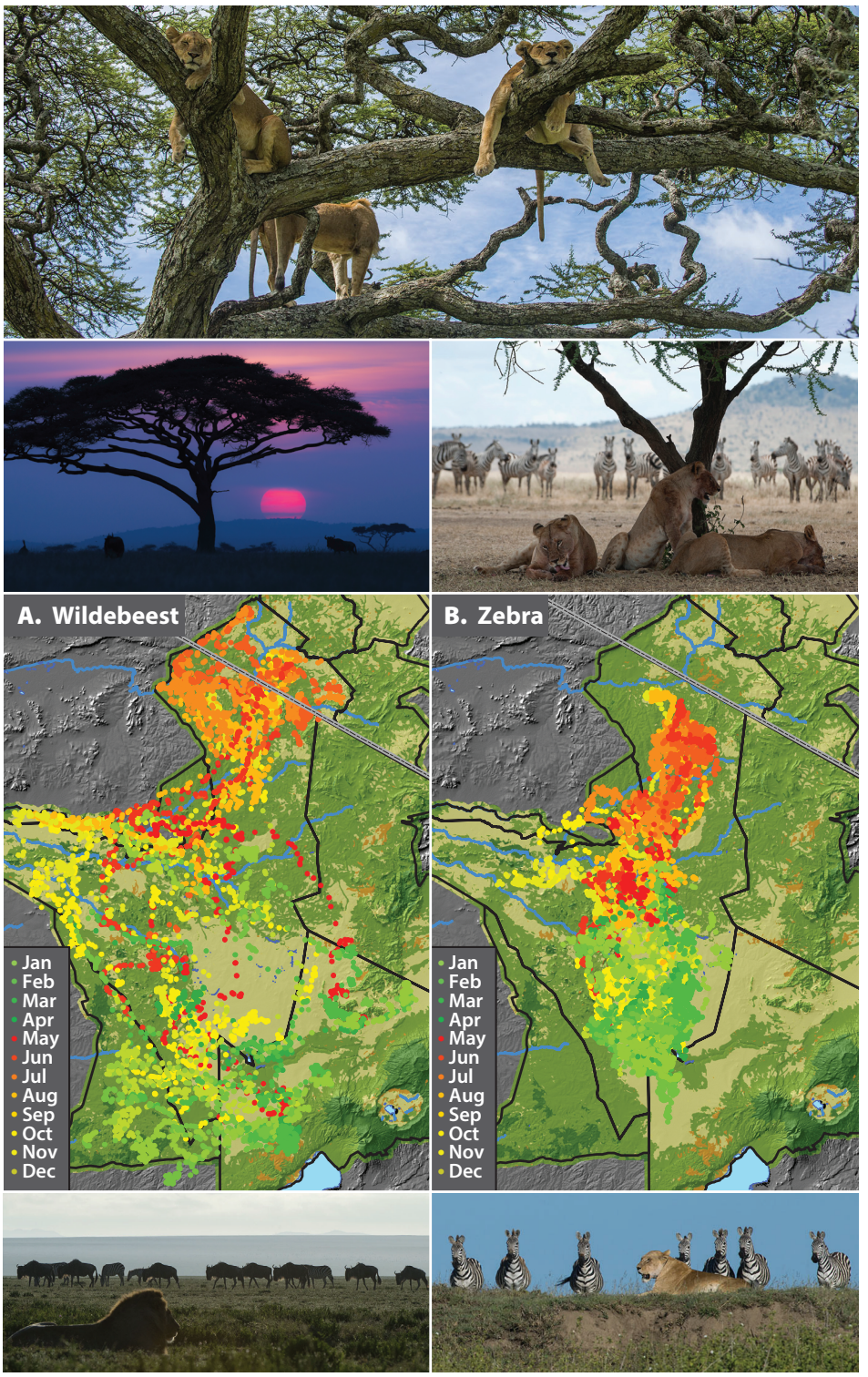

FIGURE 1.4. Daily movements of **A.** three GPS-collared wildebeest and **B.** three collared zebra. Data from Boone et al. (2006) and Hopcraft et al. (2014).

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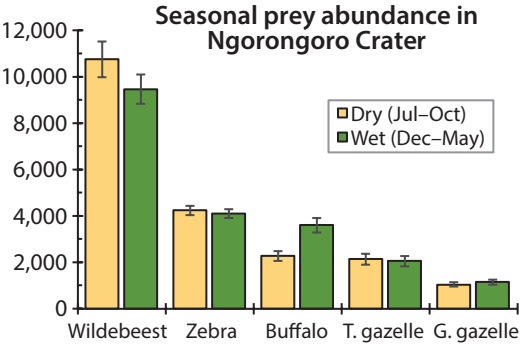

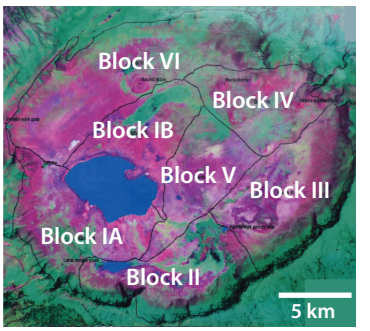



FIGURE 1.5. Seasonal prey counts in Ngorongoro Crater 1969–2012. Data were restricted to the thirty-three years when animals were counted in both the wet and dry seasons of the same year. All ground counts were conducted by MWEKA wildlife college; see Estes et al. (2006) for details. **Inset:** infrared satellite photo outlining the blocks surveyed during the ground surveys.

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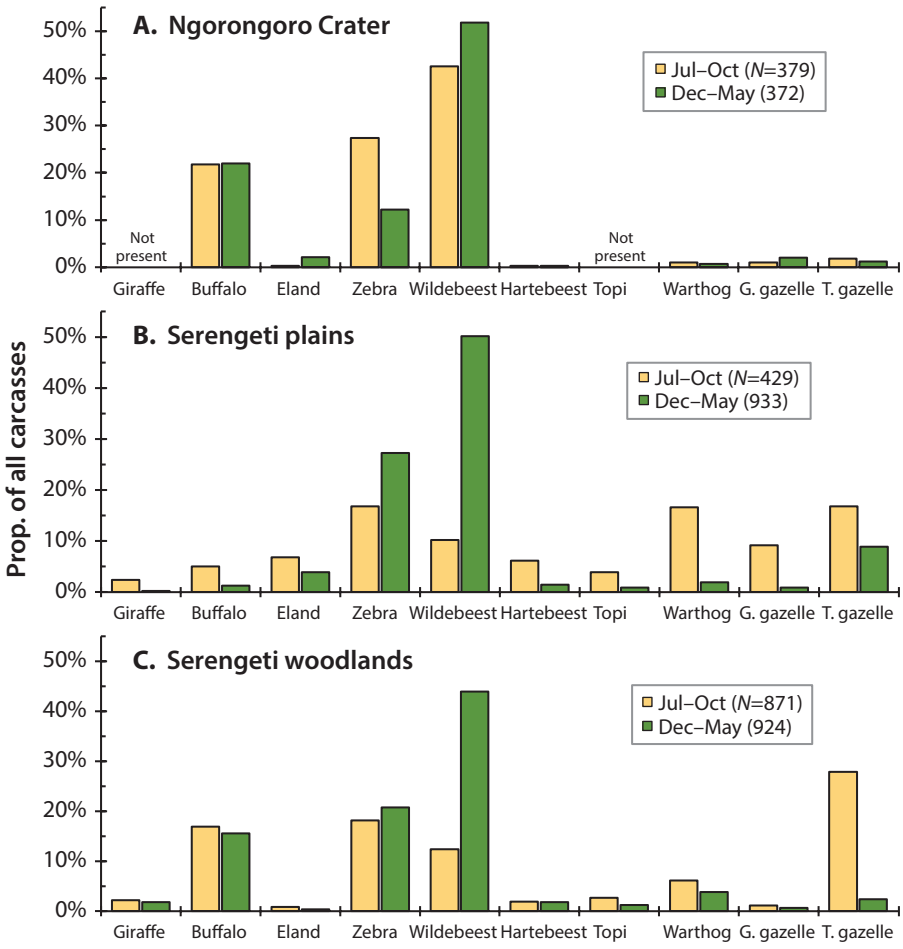

FIGURE 1.6. Species composition of the prey consumed by the lions in each habitat. Data are divided between the driest and wettest months of the year. Sample sizes are given in brackets and include all carcasses, regardless of whether they were scavenged or killed by the feeding lions. Data from the Ngorongoro Crater are from 1974 to 2015 and the two Serengeti study areas are from 1966 to 2015.

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buffalo in the wet season, whereas wildebeest are replaced by Thomson's gazelle in the dry season (figure 1.6c). Thus, the plains lions endure the greatest seasonal variation, while the woodlands lions' diet is more similar to the Crater lions' in the wet season and less harsh than the plains lions' during the dry season.

Tabulating the number of prey animals in the lions' diet ignores important differences in food intake, as larger individual prey animals provide far larger meals.[2] A freshly caught male buffalo, for example, provides over 400 kg of edible biomass—enough food to sustain a large pride for several days—compared to only 10 kg from a female gazelle (see appendix). The Crater lions thus subsist almost entirely on buffalo, wildebeest, and zebra meat all year round (figure 1.7a). In contrast, lions on the Serengeti plains largely consume wildebeest, zebra, and eland during the wet season, and a more diverse diet during the dry season (figure 1.7b), whereas the woodlands lions rely heavily on buffalo, wildebeest, and zebra with the occasional giraffe during the wet season versus a continued high intake of buffalo in the dry season along with the three major migratory species and eland (figure 1.7c).

Tracking the Lions

The vast majority of the Serengeti and Ngorongoro lions live in stable pride territories that persist for decades. Figure 1.8 shows the movements of a GPS-collared female, K82, over a two-year period.[3] K82 belonged to a pride that occupied a small stretch of the Ngare Nanyuki River at the northern edge of the Serengeti plains, and she generally centered her activities along the course of the riverbed in both the wettest and driest months of the year, returning repeatedly to the confluences of two small tributaries. As will be discussed in chapter 9, river confluences are the most important "real estate" within a lion pride's territory, as they provide a relatively consistent supply of food and water as well as greater vegetative cover.

Despite their overall stability, pride territories in the Serengeti generally shift to the south and east each wet season as the lions respond to the seasonal migration out to the open grasslands: whereas prides in the largely nonmigratory Crater only move 1 to 2 km (and in no consistent direction) between seasons, the prides in the Serengeti woodlands shift 2 to 5 km to the southeast versus 5-to-10-km shifts by the prides on the Serengeti plains (figure 1.9). The influence of the Serengeti migration is even more apparent in the case of nomadic males. After leaving their natal prides, most

2 We almost exclusively monitored the lions during the daytime, so we undoubtedly underestimated the number of smaller prey animals captured during the hours of darkness. We did occasionally see the lions feed on animals as small as hares (2 kg) or spring hares (3 kg), but these were rare even during nighttime observations. The lion's diet throughout Africa is dominated by species weighing 200 kg or more (Hayward and Kerley 2005), thus the contribution of these smaller species to the lions' overall food intake is insignificant.

3 Beginning in 1984, we attached VHF radio collars to one or two females per Serengeti study pride. Each transmitter had a range of 2 to 5 km on the ground (depending on topography) and 5 to 20 km from the air. We fixed a directional antenna to the roof of each research vehicle and drove to the location of the signal during day-to-day monitoring. We also located every collared animal once each month from a light aircraft. Whereas we typically only tracked the VHF collars during daylight hours and usually obtained only a single data point per day, GPS collars transmitted multiple locations per day without our having to track the animals ourselves; however, our modest research budget only permitted the use of a limited number of GPS collars each year.

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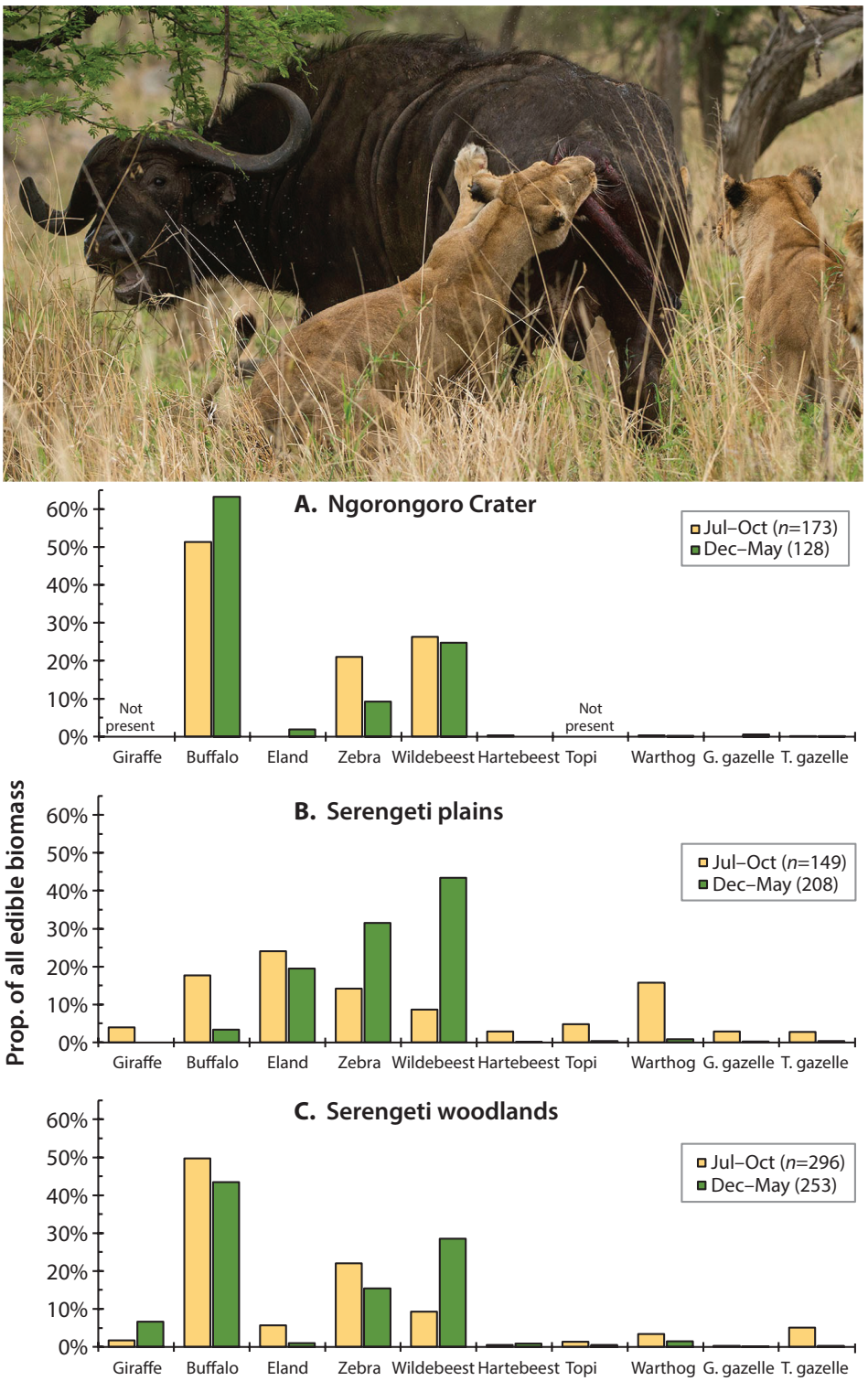

FIGURE 1.7. Edible biomass of all carcasses known to have been killed by lions in each habitat. Biomass from each carcass is taken from the age-sex data in appendix; sample periods as in figure 1.6.

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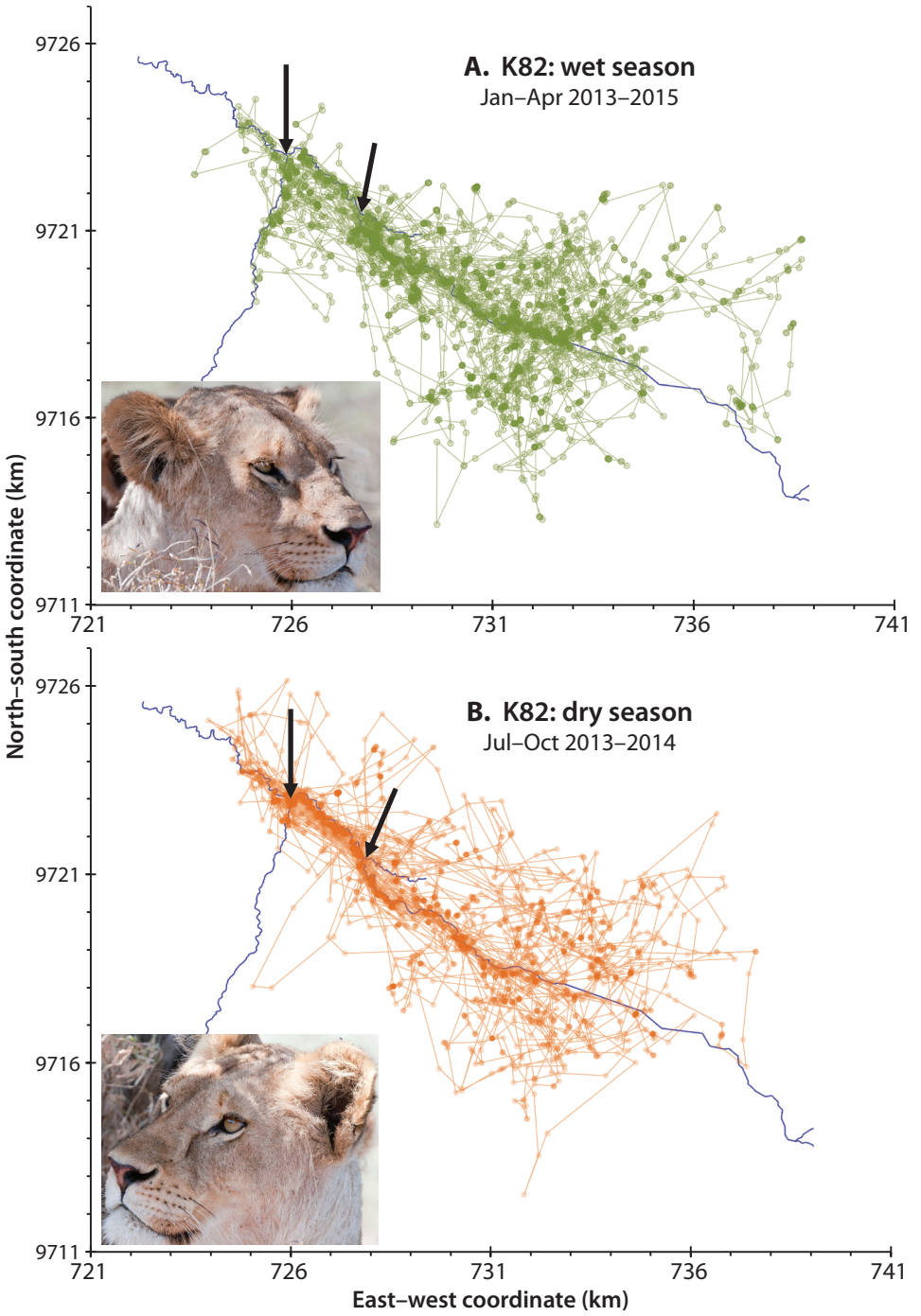

FIGURE 1.8. Seasonal ranging patterns of a GPS-collared Serengeti female named K82. Dots indicate hourly locations from 19:00 to 07:00 and at noon each day. Arrows highlight confluences along the Ngare Nanyuki River. Note that each map includes the same number of sightings ($n = 3{,}588$). Insets: ID photos of K82.

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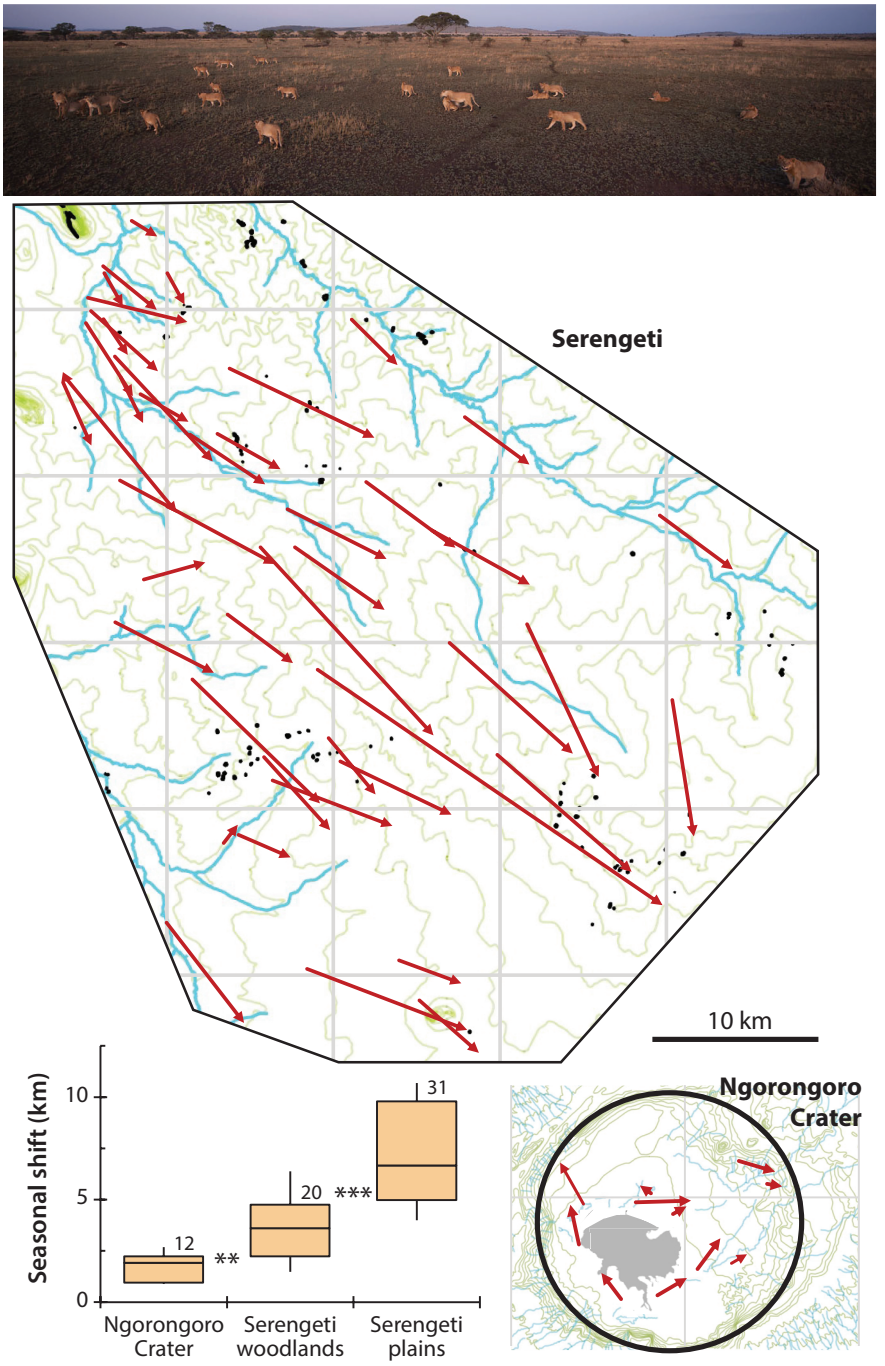

FIGURE 1.9. Seasonal shifts in midpoints of home ranges. In the wet season, all fifty-one Serengeti prides shifted eastwards and forty-nine of fifty-one shifted southward; Crater prides moved into more open areas, but otherwise showed no consistent directional change. Shifts by Crater prides were significantly smaller than in woodlands prides, which in turn moved shorter distances than plains prides. Box plots indicate medians, quartiles, and 10th and 90th percentiles. n = number of prides. Data include all prides observed at least ten times each season (median = 371 dry-season and 240 wet-season sightings/pride); prides were not all contemporaneous.

In this and all subsequent figures: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

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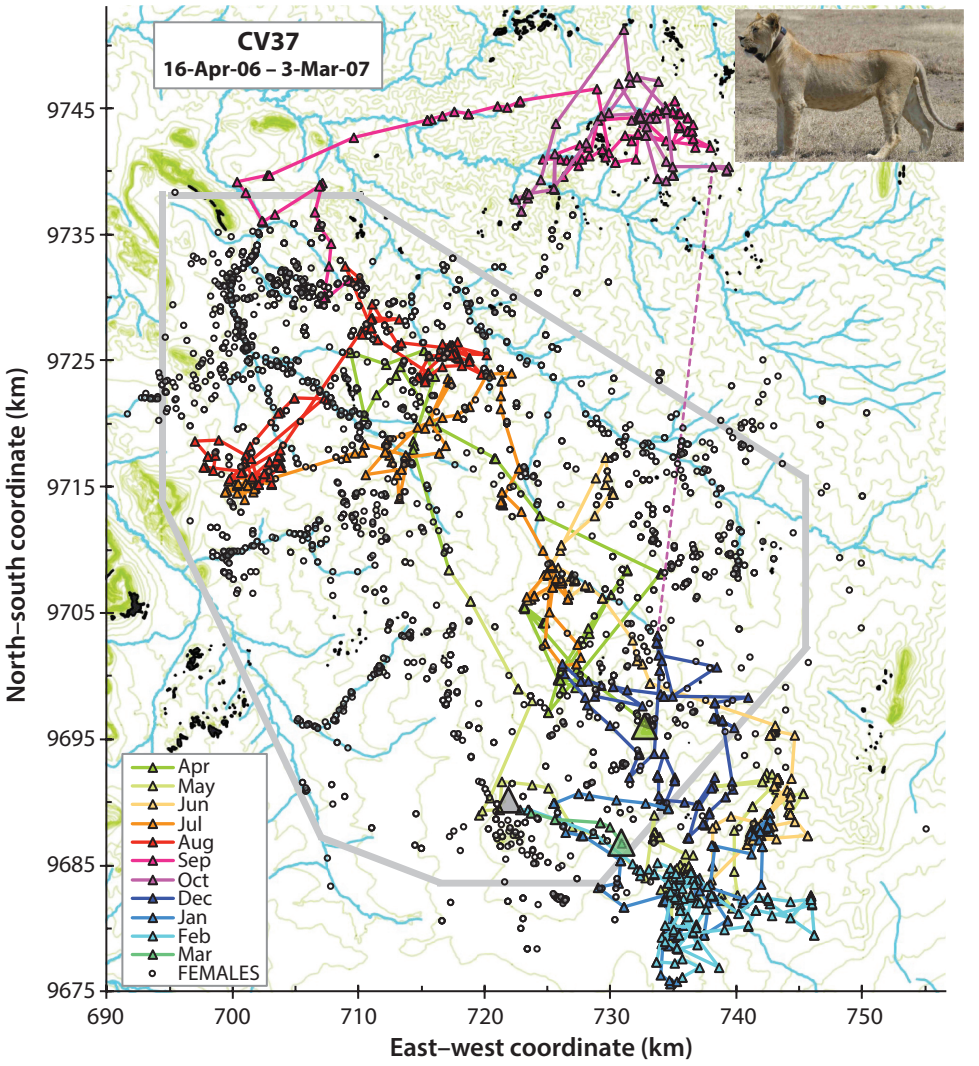

FIGURE 1.10. Movements of a two-year-old GPS-collared nomadic male in the Serengeti. Colored lines connect locations of CV37, who was born in March 2004; solid lines indicate approximately six-hour intervals; dotted line indicates a fifty-six-day gap between October 16 and December 12. Large green triangle marks site where CV37 was collared, the collar was removed at the large turquoise triangle, and the large gray triangle marks his last-ever sighting on March 9. CV37 was alone when collared, but accompanied by his littermate, CV36, at almost every sighting from June 2006 onward. Black circles indicate concurrent sightings of every VHF-collared female in the Serengeti study prides.

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subadult males move across large areas, as seen in figure 1.10, where the two-year-old male, CV37, traveled around a substantial swath of the Serengeti, remaining in the open plains during two successive wet seasons and moving deep into the central woodlands in the intervening dry season (figure 1.10). Because year-round residency is impossible on the short-grass plains to the south and east of our long-term study area, this featureless landscape provides a seasonal refuge among the migratory herds of wildebeest, zebra, and gazelle, thus allowing young nomads like CV37 a short-term reprieve before following the migration into the densely occupied woodlands during the dry season.

Fueling the Beast

Feeding lions engorge themselves to such an extent that their bellies often become obviously distended; conversely, their bellies become deeply concave if they have not fed in several days (figure 1.11). Bertram (1975b) developed a "belly scale" that ranges from 1.0 for maximum distension to 4.0 for hungry lions with protuberant ribs. We subdivided these scores in 0.25 increments and assessed their belly sizes whenever we saw their standing profiles. Female lions generally keep their belly size at around 2.50–2.85, and recent food intake has a strong effect on the lions' subsequent feeding and ranging behavior: thinner lions are more likely to have fed by the next day, whereas the belly sizes of "fuller" lions typically shrink (figure 1.12a), and these patterns are still apparent four days later (figure 1.12b). Although females are similarly successful in maintaining consistent short-term food intakes in all three habitats, the lions on the Serengeti plains travel considerably further to do so: plains females move an average of about 4 km overnight when they are very thin versus 2 km when they are "full," whereas Crater and woodlands females only move about 1 km per day regardless of belly size (figure 1.12c). After four days, plains females have typically shifted 5 km when thin versus 3 km when full, whereas Crater and woodlands females have only moved about 2 km (figure 1.12d).

At monthly time scales, food intake rates are virtually constant throughout the year in the Crater and the Serengeti woodlands, whereas the lions on the Serengeti plains enjoy the feast of abundant migratory prey during the wet season and suffer from the famine of prey scarcity in the dry season (figure 1.13a). The seasonal variation in food intake rates profoundly influences female reproductive rates on the Serengeti plains. Although lions give birth every month of the year in the Ngorongoro Crater and Serengeti woodlands, females in the plains show a striking birth peak in March and April and rarely give birth during the heart of the dry season (figure 1.13b). This peak occurs about two to three months after the plains females attain their largest average belly sizes, and the trough in reproduction follows a few months later (figure 1.13c). Gestation in lions is about 3.5 months, so fertility of the plains females is presumably triggered by the return of the migration in November or December (when their average belly size first reaches ~2.5 before peaking at ~2.4 in March–May) whereas their nutritional plane falls too low (~2.85) to maintain reproduction during the hardest months of the dry season.

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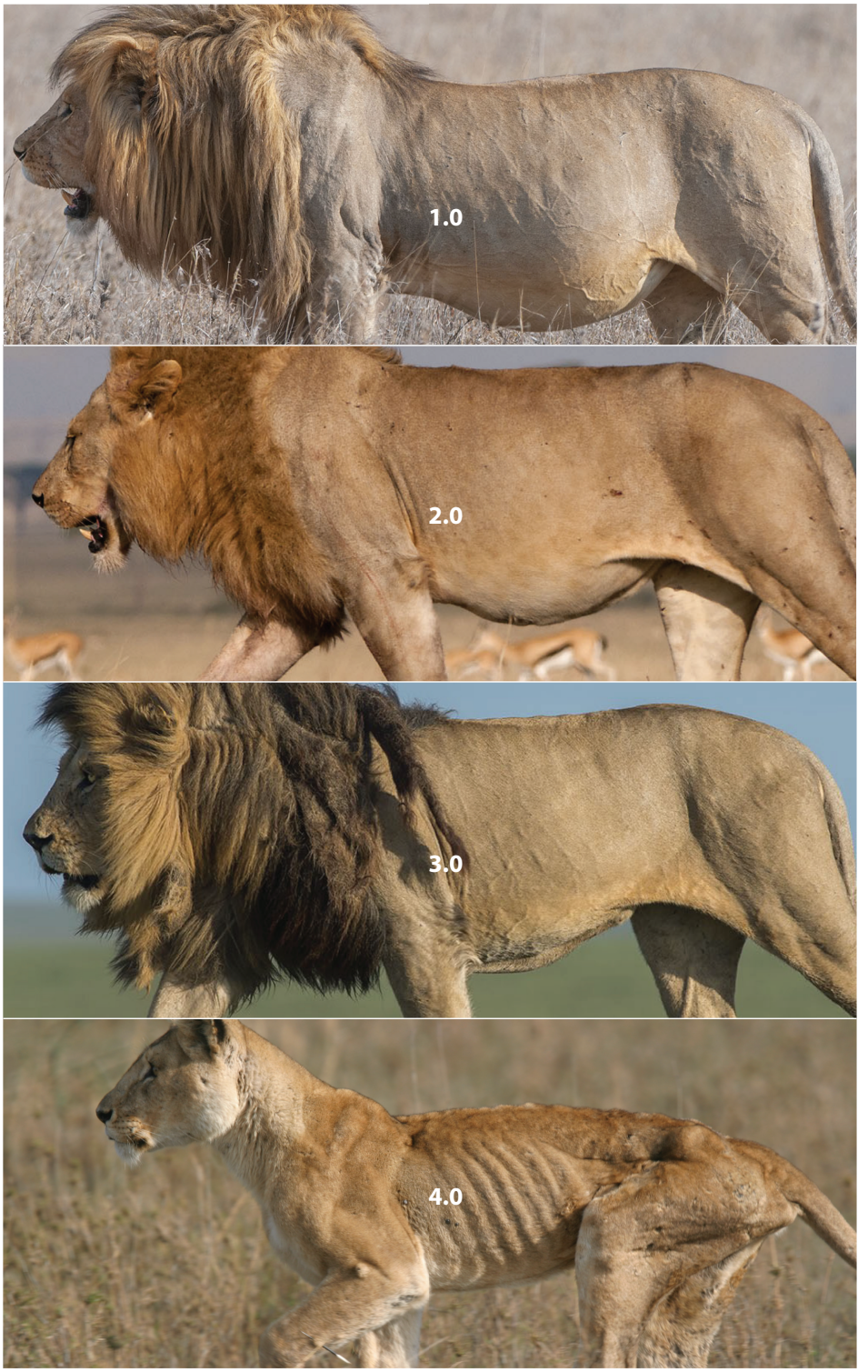

FIGURE 1.11. Profiles of lions with varying degrees of abdominal distension, labeled with the respective values of the "belly scale." Bottom photo by Ingela Jansson.

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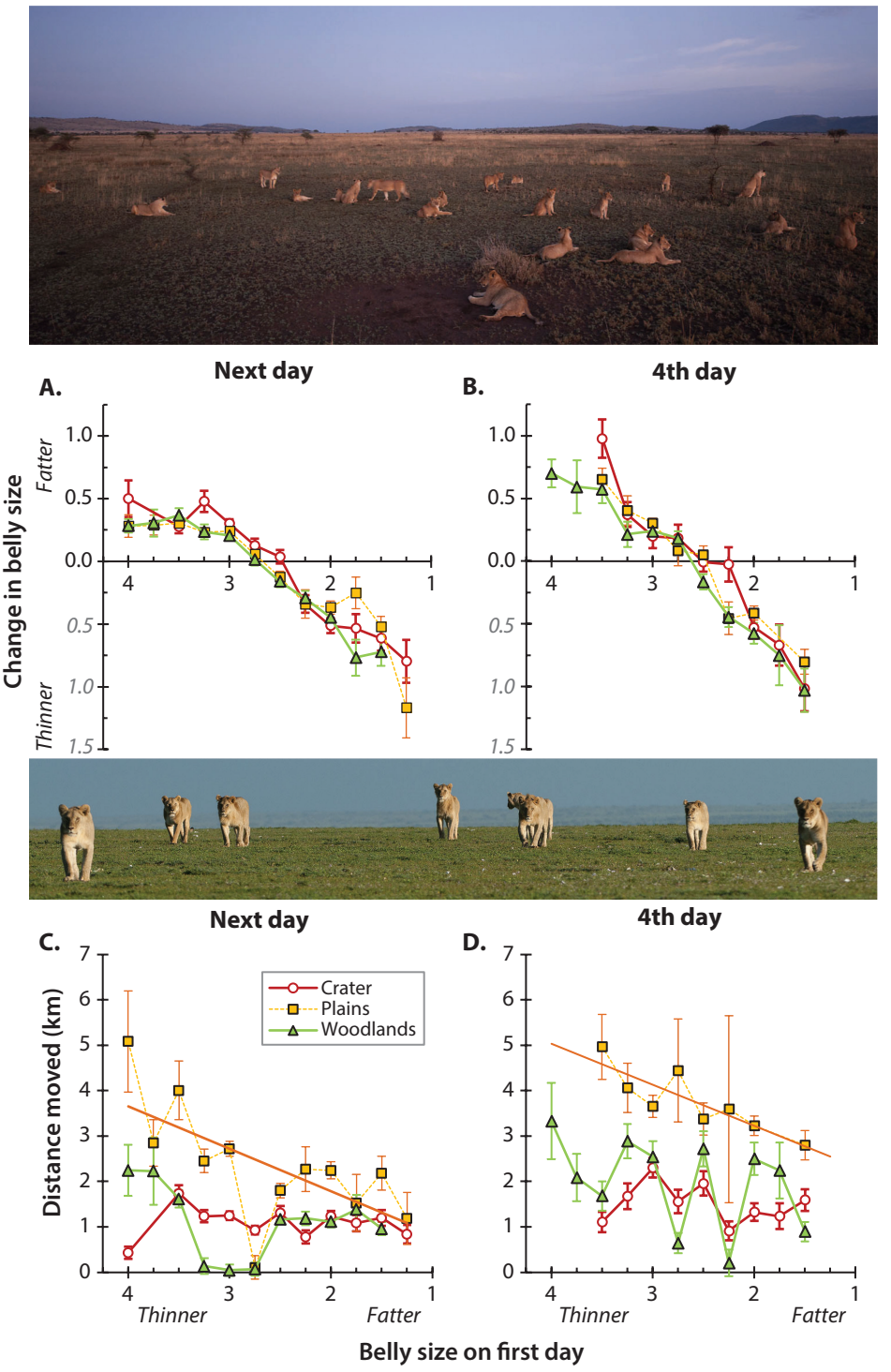

FIGURE 1.12. Changes in female belly sizes over (**A**) one- and (**B**) four-day time spans. "Full" females are thinner the next day whereas thin females tend to have eaten by the next day. Straight-line distances between locations at (**C**) one- and (**D**) four-day time spans. Plains females traveled farthest, especially when they were thinnest. Each point is based on at least six observations.

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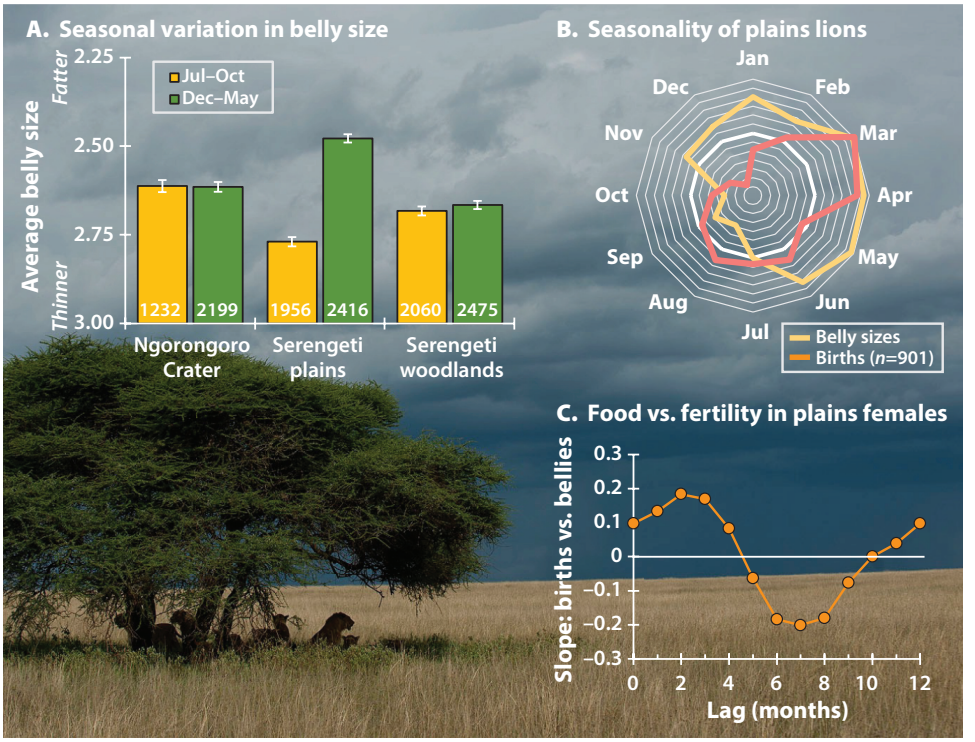



FIGURE 1.13. Seasonal differences in food intake and movement patterns of adult females in each habitat. **A.** Average belly sizes. **B.** Food intake rates versus birth rates in the plains prides. Food intake is highest from November through June; births mostly occur in March and April. White polygon indicates values if births were evenly distributed across the year; belly sizes have been rescaled to show the same range as births. **C.** Slopes of regressions between belly size and birth rate in the plains lions. The largest belly sizes were strongly correlated with birth rates two to three months later (i.e., the height of the rainy season) and negatively correlated with birth rates six to eight months later (i.e., the following dry season).

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Across all three habitats, individual females that maintain higher belly sizes produce more milk (figure 1.14a),[4] enjoy higher cub survival (figure 1.14b), and shorter interbirth intervals for mothers whose prior cubs reached their second birthdays (figure 1.14c). Brian Bertram (1975b) found that chest circumference was closely related to overall bodyweight (excluding current stomach contents) (figure 1.15a), so we used chest girth as our standard for body size,[5] as lions are too difficult to weigh under most circumstances. Our belly size measures suggest that females do not translate better nutrition into more body mass: females that maintained larger belly sizes over the course of a year were no larger the following year than were poorly fed females (figure 1.15b). In contrast, well-fed males had significantly larger chest measurements the following year (figure 1.15b). Taken together, these data suggest that females translate more food into greater fertility, more frequent litters, and better cub survival, whereas males translate more food into more bulk.

A Day in the Life

Lions have the reputation of being profoundly lazy, but most people encounter lions during the day, and lions are primarily active at night, as illustrated by the movements of K82, the female that wore a GPS collar for two years (figure 1.16a). K82 traveled consistently farther each hour through the night than during the daytime, although her movements were highly sporadic: on a quarter of all days, she moved less than 30 m on average even during the most active hours of the night and less than 5 m during each hour of daylight. During the 1980s, we followed lions for ninety-six consecutive hours just before or after the day of the full moon (Packer et al. 1990), and most prey captures occurred during the hours of darkness; the few daytime kills were mostly juveniles (e.g., calves, fawns, foals, etc.) (figure 1.16b). Similarly, lions scavenged more carcasses during the night (figure 1.16c), stealing daytime carcasses mostly from diurnal species like cheetahs and vultures. Lions have far better night vision than their prey, but this advantage is reduced during nights of the full moon with a concomitant loss in hunting success (Van Orsdol 1984; Funston et al. 2001). Figure 1.17a shows that lions were thinnest in the days closest to the full moon—and this apparently forced them to forage more during the daytime, with a greater incidence of daytime kills and scavenging in the days closest to the full moon (figure 1.17b). Given that our extended nocturnal observations were made so close to the full moon, the number of *daytime* feeding events illustrated in figure 1.16b and figure 1.16c was no doubt higher than would have been observed during other times of the lunar cycle.

4 We immobilized eleven lactating females and injected them with 1 cc of oxytocin while they were apart from their cubs then extracted the milk by hand from a single anterior mammary gland (Pusey and Packer 1994a).

5 From Bertram's data, $y = 5.6554e^{0.0287x}$ where y = weight in kg and x = chest girth in cm, but I will report chest girths rather than bodyweights throughout the remainder of the book.

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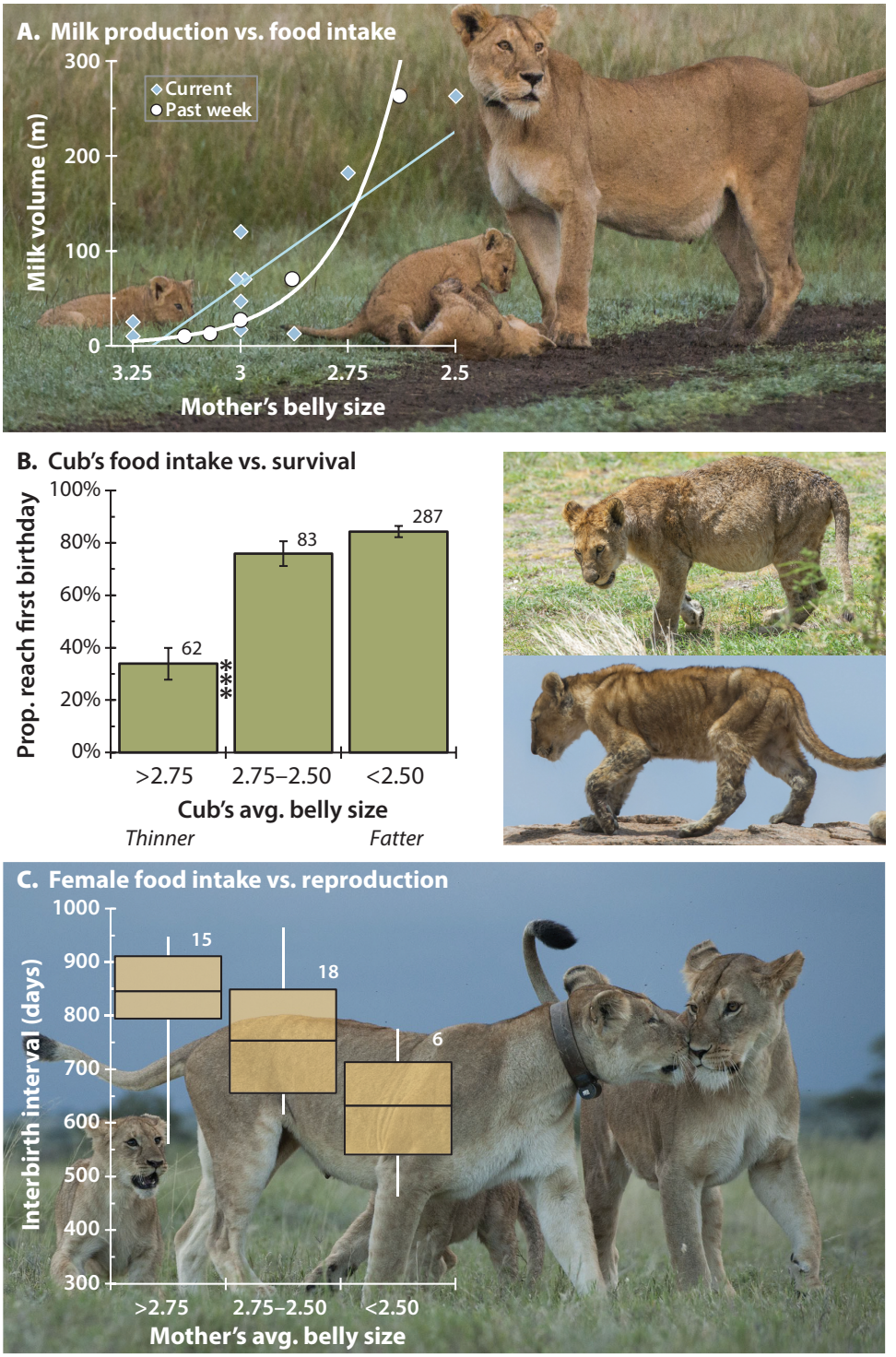

FIGURE 1.14. **A.** Milk production as a function of the mother's current and average belly size over the past week; $n = 11$ and 5 lactating females, respectively. Data replotted from Pusey and Packer (1994a). **B.** Cub survival versus average belly size prior to first birthday. Data restricted to cubs whose belly sizes were measured at least three times. The difference between cubs with average belly sizes that were thinner than 2.75 were significantly less likely to survive than those that maintained more moderate belly sizes ($p < 0.0001$). n = number of cubs. **C.** The interval between the birth of a female's surviving cubs and her next birth declined significantly with increasing food intake; Spearman rank test across all intervals: $t = 2.28$, rs = 0.351, $p = 0.028$, two-tailed. n = number of females.

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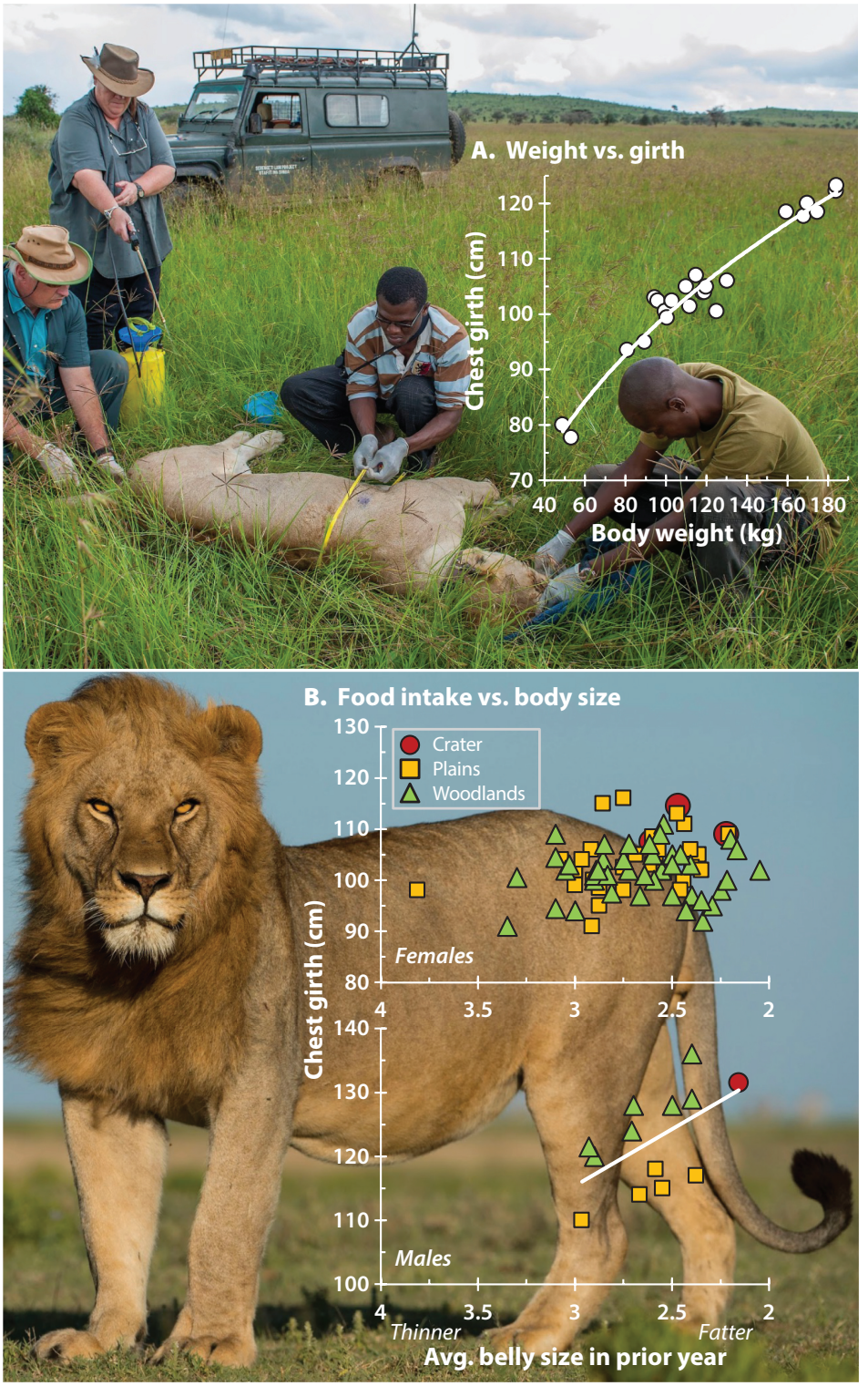

FIGURE 1.15. Body-size measurements. **A.** The relationship between chest girth (y) and body weight (x) is $y = 21.853x^{0.3296}$. Data are replotted from Bertram (1975b). **B.** Chest girths versus average belly sizes of females (top) and males (bottom). Data are restricted to individuals with at least five belly size measurements in the twelve months prior to immobilization. The relationship is significant for males ($p < 0.05$, including all data) and highly significant after controlling for habitat ($p < 0.0001$).

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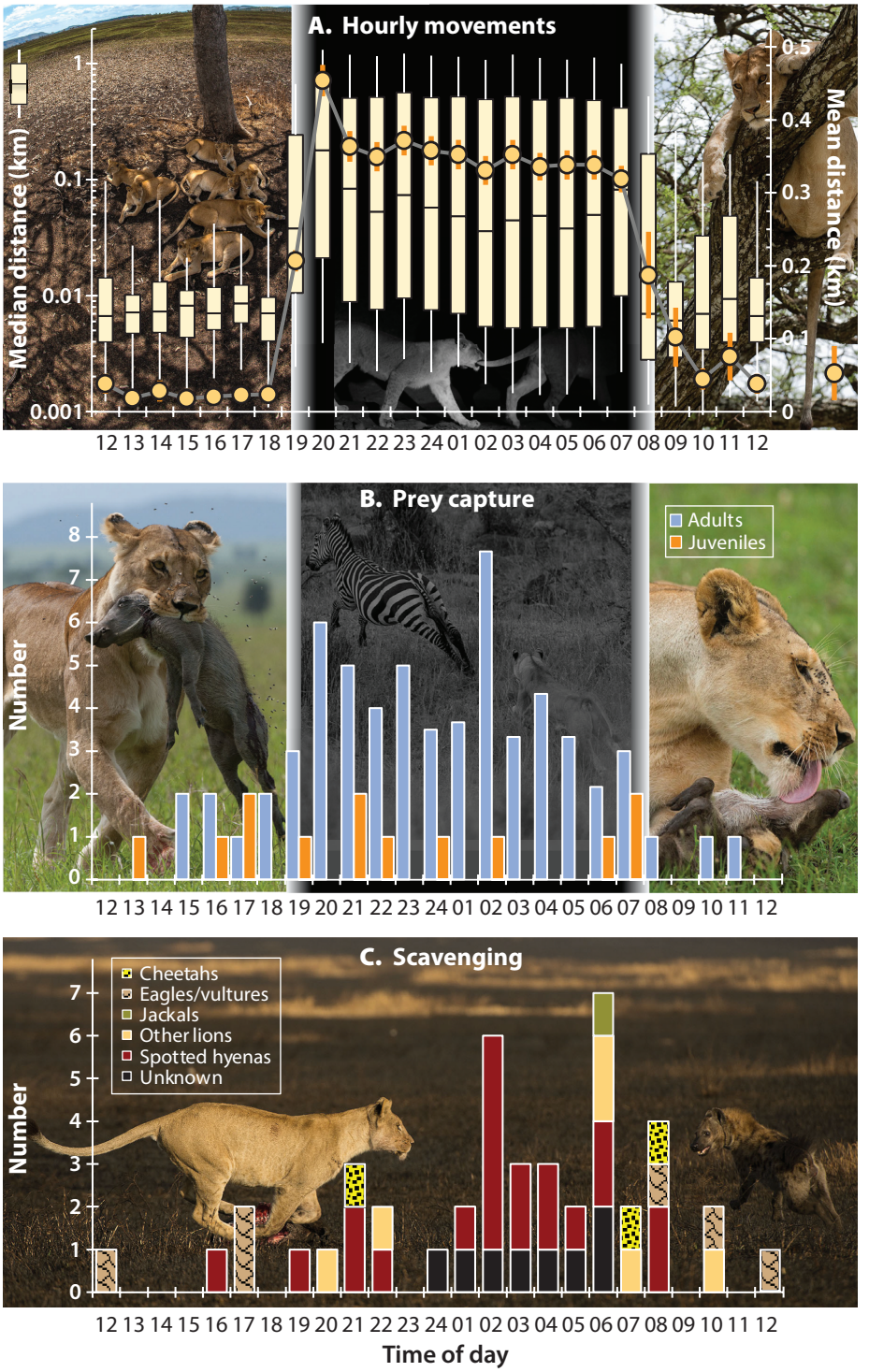

FIGURE 1.16. Daily activity patterns. **A.** Hourly distances moved by a GPS-collared female in the Serengeti plains study area in 2013–2014. Measurements are straight-line distances between successive GPS coordinates. **B.** Number of prey animals captured by female lions each hour. Data are taken from 194 complete days of observation in the first 4 days preceding and the first 4 days following the full moon each month in 1984–1987. Adult prey were mostly captured at night ($p < 0.001$); juveniles were more likely to be caught in the day than were adults ($p < 0.02$). **C.** Time of day that lions scavenged from other species during the 194 days of twenty-four-hour observation. Note: over the course of the year, sunrise and sunset in the Serengeti vary between 06:18–06:49 and 18:30–19:01 respectively.

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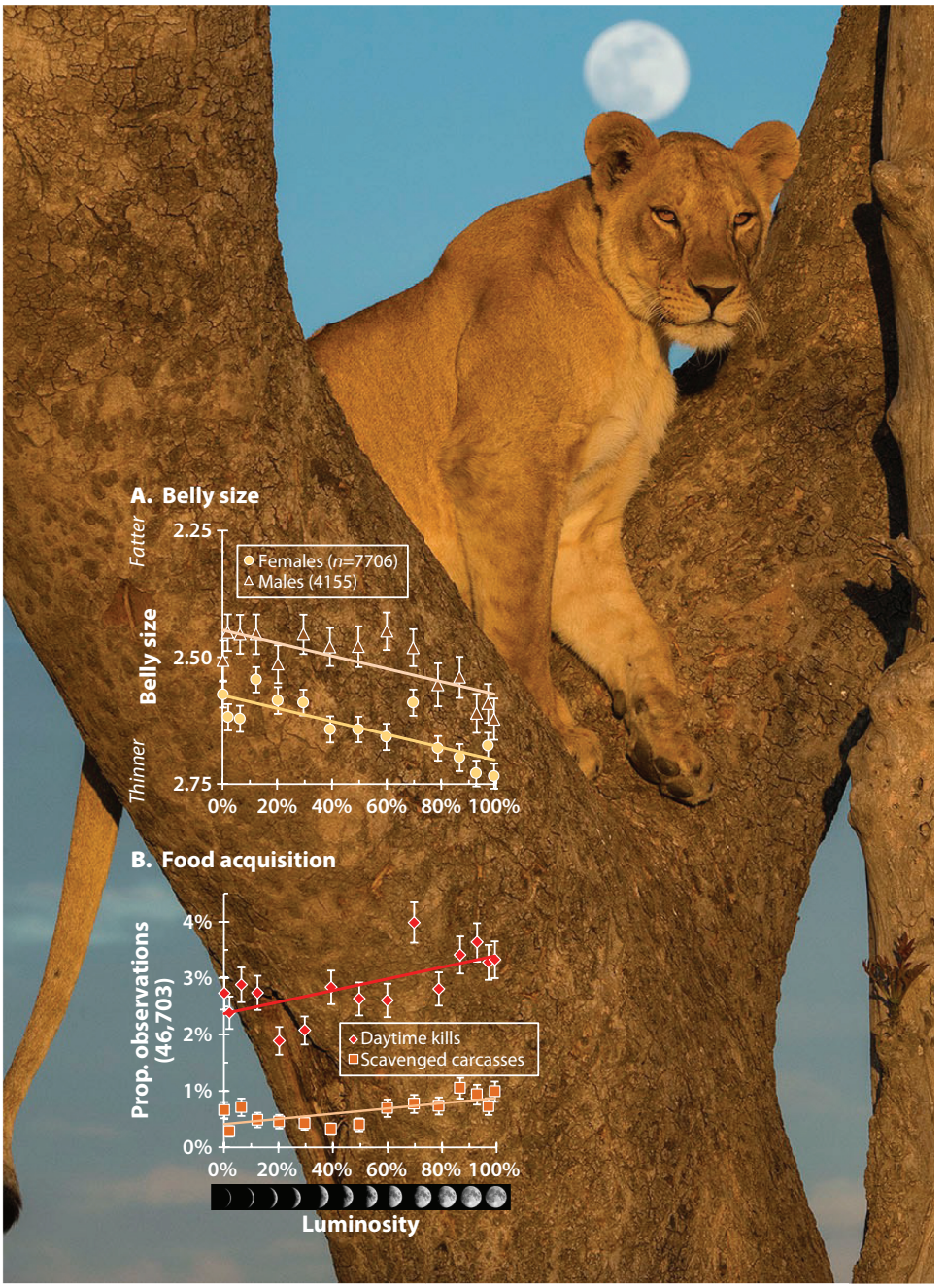

FIGURE 1.17. Relationships between moon phase and food intake. **A.** Effect of moon phase on belly size. **B.** The number of daytime kills and scavenged carcasses across the lunar cycle. Redrawn from Packer, Swanson, et al. (2011).

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A Pride Is Not a Pack—the Fission-Fusion Nature of Lion Society

Lions are social, but they are mostly found in "subgroups," and pride composition is only obvious after repeated observations (Schaller 1972). For example, figure 1.18a illustrates the daily locations and associations of an adult female, Glossie, over a ten-day period. Glossie was a member of the Gol Pride, which at the time consisted of six adult females and a "coalition" of seven adult males. On the first day, Glossie was found with three of her five pridemates, and the group had moved 3 km by the following morning. On the third day, Glossie was alone with three of the resident males, one of which "guarded" her as if she were coming into estrus. She had reunited with her three initial companions by the fourth day, and the quartet was joined by a fifth female on the fifth day. Over the course of the ten days of observation, Glossie was eventually seen with every member of her pride, but they were never found in the same place at the same time. Thus, subgroups generally vary in size and composition from one day to the next, with each individual spending time alone and entire prides rarely being all together.

We defined two lions as being together in the same subgroup whenever they were found within 200 m of each other, but pridemates can spread out over considerable distances. We usually radio collared only one female per pride but sometimes collared multiple pridemates (either two females or one female and one male) and could thereby measure the extent of their spatial separation. When separate, collared females were typically located ≈2 km apart and even spent about 10 percent of their time >5–6 km apart, depending on season and habitat (figure 1.18b) while females in neighboring prides typically remain 5–9 km apart (figure 1.18b).

Keeping in Touch

Given that the lions' fission-fusion social system often involves being separated from their companions, how do the pridemates communicate when they're so far apart? Lions rely on long-range vocalizations, "roars," to keep track of distant pridemates and members of neighboring prides (Schaller 1972). The lion's roar (figure 1.19a) carries up to ≈8 km,[6] and these vocalizations are individually distinctive: as shown in chapter 8, lions distinguish between the roars of friends and foes, and they can accurately count the number of unseen roaring individuals—an essential skill in a group-territorial species. Suffice it to say here that lions are far more likely to roar in response to distant roars when they are separated from most of their companions (figure 1.18c) and that lions mostly roar at night (figure 1.19b), when they are most active. Thus, roaring plays an important role in maintaining social cohesion despite being physically separated for varying periods of time—and it is noteworthy that pridemates spend the great majority of their time less than 6 km apart and, hence, well within earshot of each other, whereas neighbors generally remain close to the limits of the audible range of their rivals (figure 1.18b). Note, too, that while single-sexed groups of males most often roar in the hours before dawn, when sound is likely to carry farthest (see Larom et al.

6 Schaller reported hearing roars from 3 to 4 km but suggested that they might be audible at 8 km, a distance we were able to confirm by sitting a known distance apart in two separate vehicles.

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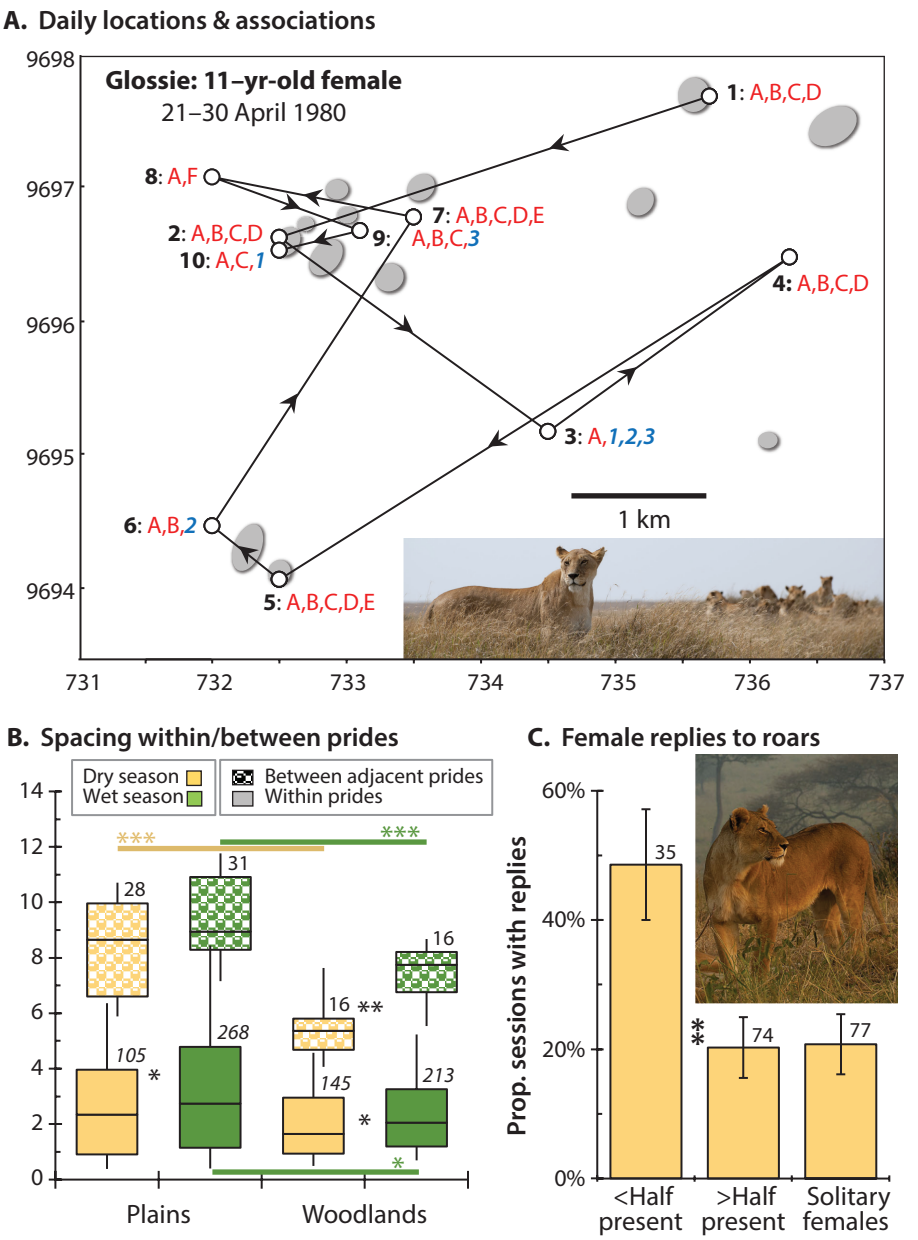

FIGURE 1.18. Fission-fusion grouping patterns and long-distance communication. **A.** Locations and group compositions of an adult female over ten consecutive days. Red letters refer to individual females (Glossie is represented as "A"); blue numbers refer to individual males. Gray ovals represent rocky outcrops. Modified from Packer (1986). **B.** Spatial separation of radio-collared pridemates and neighboring prides. Within-pride data are restricted to collared females that were observed at separate locations (more than 200 m apart) on the same day; *n* = number of paired sightings. Between-pride data are the average distance (in kilometers) between a collared female in each focal pride and her four closest neighbors; distances are from pairwise observations made on the same days (including interpride encounters where prides were less than 200 m apart); *n* = number of prides (overall, the four seasonal/habitat comparisons involved a total of more than eleven thousand pairwise measurements). Female pridemates in separate subgroups were spaced farther apart during the wet season in both habitats, and plains subgroups were more widely spaced than woodlands subgroups during the wet season. Females in adjacent woodlands prides were farther apart during the wet season than in the dry season; and plains prides were farther apart than woodlands prides in both seasons. **C.** Females in small subgroups roared significantly more often in response to the roars of distant lions than were groupings containing the majority of female pridemates ($p = 0.0035$); small subgroups also responded more often than did solitary females (who have no companions) ($p = 0.0013$). Sample sizes indicate the total number of roar sequences that were separated by gaps of at least thirty minutes; "replies" were defined as responses within fifteen minutes of the distant roars.

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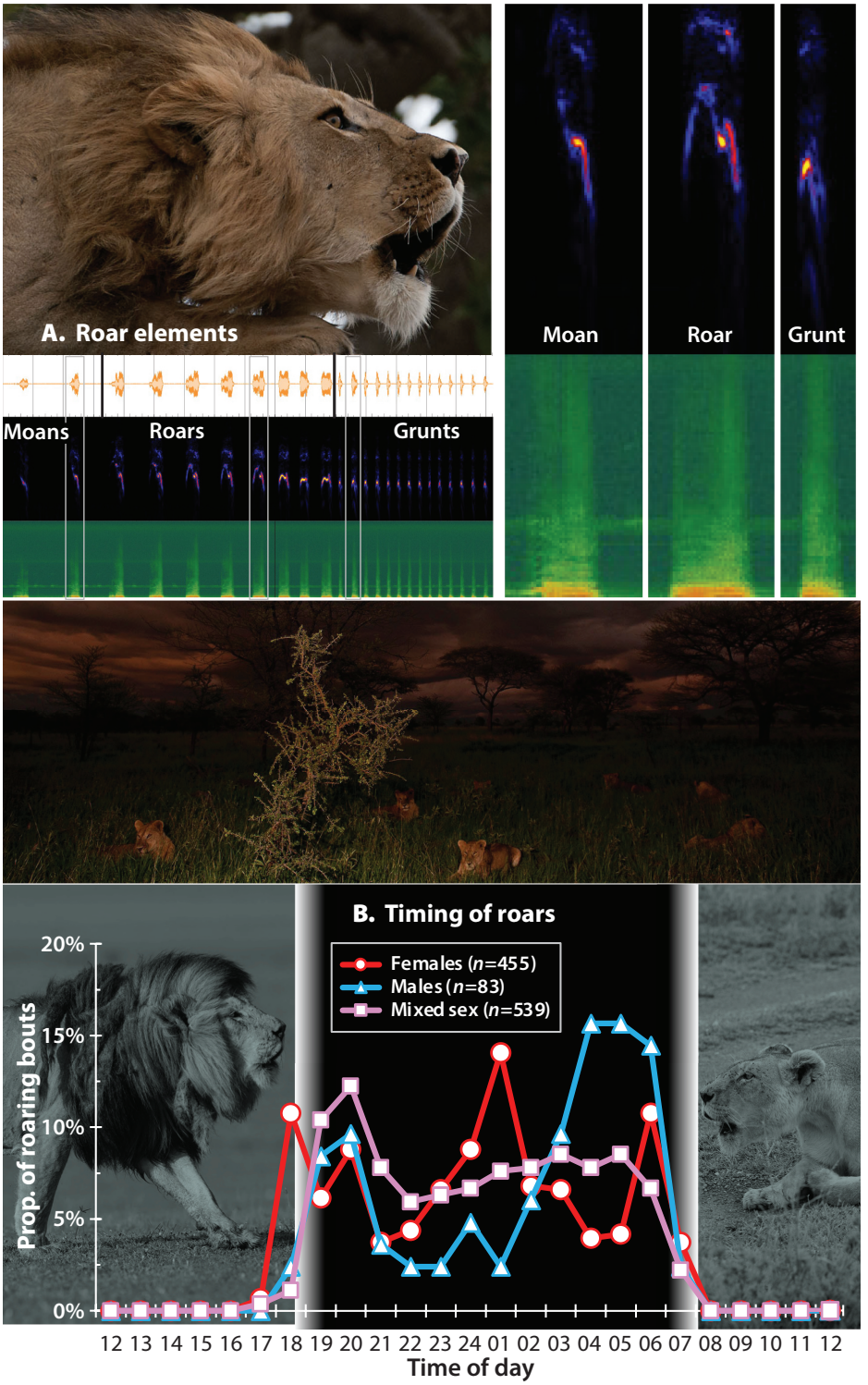

FIGURE 1.19. The lion's roar. **A.** Waveform and melodic range spectrogram of the complete roar sequence of an adult male. *Bottom left*: The sequence involves an initial pair of moans followed by a series of eight distinct roars and a sequence of fourteen staccato grunts. The vertical lines are spaced at three-second intervals. The three highlighted elements are presented in more detail on the right. **B.** Timing of roaring bouts by single-sexed and mixed-sexed groups. All data were collected during the first four days preceding and the first four days following the full moon. Each roaring "bout" consists of a connected series of roars followed by a sequence of grunts.

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1997, Wijers et al. 2021), female groups also show peaks at dusk and midnight, whereas mixed-sex groups roar most in the first hours after dusk (figure 1.19b).

A Life in Full

An animal's body size, its age at maturation, its lifespan—these fundamental features of the lion's natural history are summarized in figure 1.20. As is typical for mammals, female lions are smaller and live longer than males: females reach full body size between their second and third birthday, whereas males reach full size about a year or two later (figure 1.20a). Mortality is much higher in males than females at all ages, resulting in an average life expectancy of approximately 4.5 years for females versus about 2.5 years for males (figure 1.20b), and the oldest-known-aged female in our study reached 19.75 years versus 17.59 years for the oldest male. For most purposes, we classify females as "adult" once they reach their second birthday: since the typical interbirth interval is about 730 days (figure 1.14c), two-year-old females are capable of capturing their own prey, and they fully participate in territorial defense (chapter 8). However, successful reproduction is highest in mothers between the ages of 3 to 14 years (figure 1.20c), so I will sometimes consider only the reproductive performance of older females. We generally classified males as adults after their fourth birthdays, allowing for the extra time required to reach full body size as well as to complete mane development. DNA fingerprinting confirmed that resident males are the fathers of all the cubs conceived during their tenure (chapter 2), and the age structure of resident coalitions indicates that male reproductive rates are highest between the ages of four to fourteen years (figure 1.20c). Note that because so few males gain residence, per capita reproduction is higher for *pride* males than for females. Only a few individuals survive to advanced ages, so age-specific measures exaggerate the apparent contribution of older individuals, thus figure 1.20d shows the proportion of surviving cubs produced by adults of each age. At any one time, most cubs in the population have mothers that are three to eleven years old and fathers that are four to nine years old.

Both sexes show clear signs of physiological aging (senescence) (figures 1.20 and 1.21). Cub survival follows an inverted U–shaped relationship with maternal age (figure 1.21a), presumably because of the lack of experience in very young mothers and reduced physical capabilities at advanced maternal age (chapter 4). Litter size also declines to a single cub in the final years before the female lions' equivalent of "menopause" (figure 1.21b). Because males must protect their prides from incursions by rival coalitions (chapter 3), cub survival declines linearly with paternal age as the fathers' physical prowess fades to the point that they can no longer maintain pride residence (figure 1.21a).

KEY POINTS

1. Though lions lack conspicuous coat patterns, their "whisker spots" persist until they are sufficiently tattered and scarred to become more readily recognizable. This made it possible to track thousands of lions in the Serengeti and Ngorongoro Crater throughout their entire lifespans over a dozen generations.

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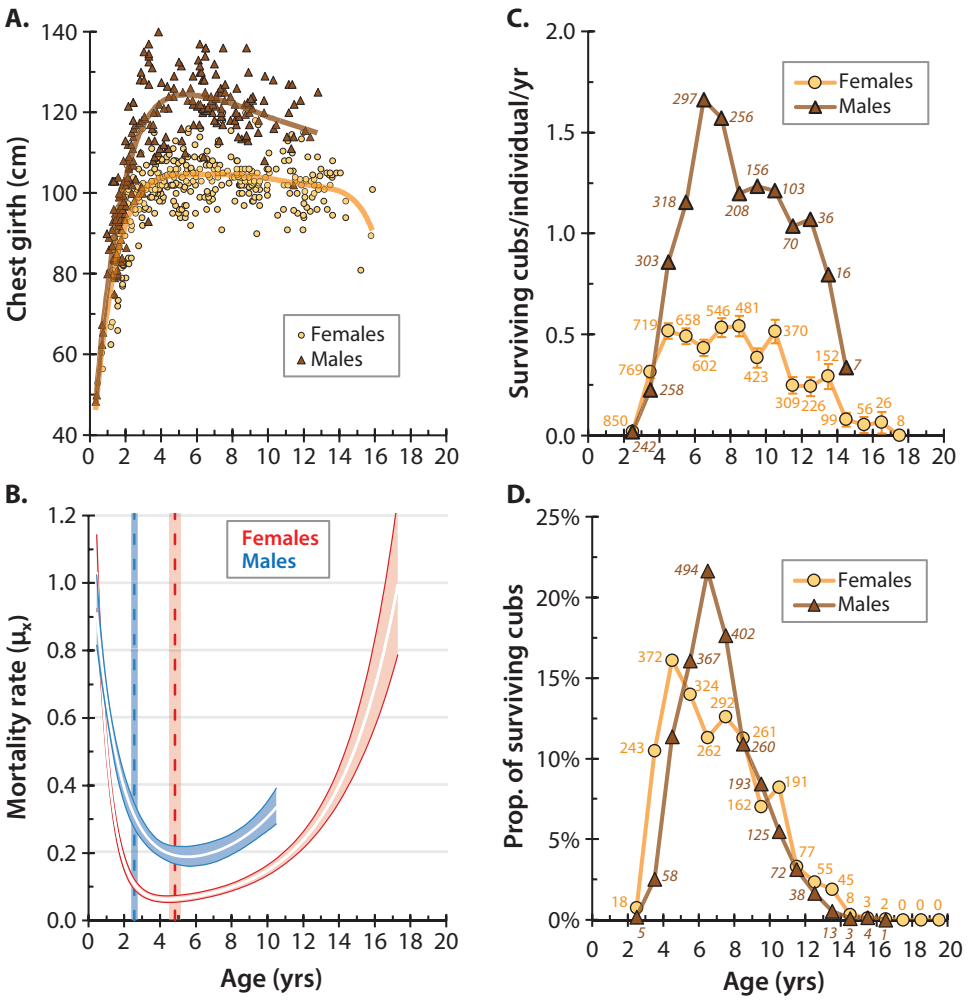

FIGURE 1.20. Age-specific rates of growth, mortality, and reproduction. **A.** Chest girth versus age. Data include occasional re-sampling of the same individuals. **B.** Age-specific mortality of males and females. The male curve treats disappearance of potential dispersers as right-censored; all other records are considered deaths. Polygons represent 95 percent credible intervals of age-specific mortality; curves extend to the age where 95 percent of each sex are assumed to have died. Vertical dashed lines give the mean life expectancy of cubs when first seen (typically three months of age); widths indicate 95 percent confidence intervals. Redrawn from Barthold et al. (2016). **C.** Age-specific production of surviving cubs. Cubs with multiple "candidate" mothers or fathers are partitioned as described in chapter 4; error bars cannot be estimated for males. *n* = number of males/females at each age. **D.** Proportion of surviving cubs with parents of each age. *n* = cubs born to mothers/fathers of each age.

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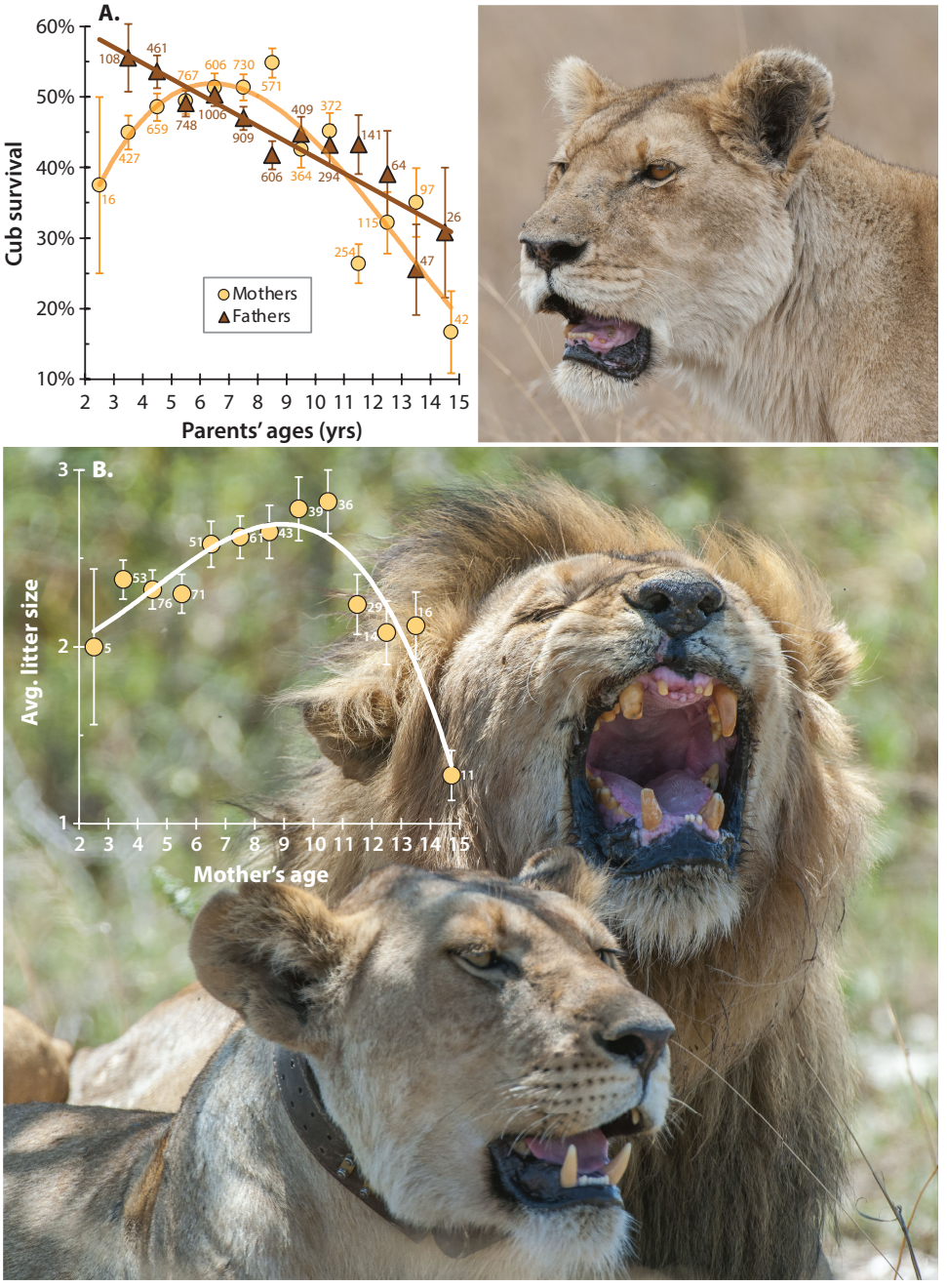

FIGURE 1.21. Age-specific reproductive performance. **A.** First-year cub survival versus parental age at birth. Mean parental age was calculated for cubs with multiple "candidate" mothers/fathers. The rise and fall with maternal age are both highly significant ($p < 0.0001$, $n = 5020$ cubs); the decline with paternal age is also significant ($p < 0.0001$, $n = 4819$ cubs). **B.** Age-specific litter size of females. Litter size data are restricted to cubs with known maternity; redrawn from Packer et al. (1998).

(continued...)

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