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ORIGINAL ARTICLE

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Integrating video and genetic data to estimate annual age-structured apparent survival of American black bears

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Abstract

Camera or genetic data are increasingly used to estimate wildlife abundance and density. We integrated video camera data with genetic data over 7 years to estimate annual age-structured apparent survival of American black bears (*Ursus americanus*). We identified 70 individuals through meticulous scrutiny of 7531 video captures, cross-referenced with 721 genetic captures from hair samples concurrently collected from stations in view of cameras. We used the Cormack–Jolly–Seber model in Program Mark to estimate annual age-structured apparent survival for yearling males, yearling females, 2+ year-old males, and 2+ year-old females. We manually calculated cub survival. We compared parameter estimates based on combined video and genetic data with those based on only genetic data. Combining video and genetic data provided a means to test video-based identification accuracy, which was highest for females (97%–100%). Annual apparent survival was highest for yearling females ($\varphi = 0.92$, $SE = 0.07$), followed by 2+ year-old females ($\varphi = 0.88$, $SE = 0.05$), 2+ year-old males ($\varphi = 0.84$, $SE = 0.06$), and yearling males ($\varphi = 0.80$, $SE = 0.14$). Annual cub survival ($\varphi = 0.86$, $SE = 0.07$) was likely biased because we could not account for mortality that occurred in-den through early spring. Annual apparent survival and recapture probabilities derived from only genetic data were lower than those derived from combined video and genetic data. Our finding that noninvasive data can be used to estimate annual age-structured apparent survival of a species with relatively indistinct traits is broadly relevant to wildlife research and conservation.

KEYWORDS

age-structured population dynamics, genetic sampling, noninvasive, *Ursus americanus*, video capture-recapture

1 | INTRODUCTION

Understanding wildlife demography is important for effective wildlife conservation. Increasingly, researchers interested in modeling demography of wildlife populations use noninvasive camera or hair traps to monitor individuals (Burton et al., 2015; Laufenberg et al., 2018; O'Connell et al., 2010). These cost-effective methods (Trapp & Flaherty, 2017) reduce risk to research animals by minimizing or eliminating the need for physical capture of animals (Foster & Harmsen, 2012). Thus, researcher effects on animal behavior are minimized, which can affect the probability of recapture (Otis et al., 1978).

Regarding camera data, two common approaches used to study wildlife demography are Capture-resight (C-r) and Capture-Mark-resight (C-M-r). For C-r studies, animals are captured and recaptured by cameras, wherein individuals are identified based on natural markings. For example, spots on snow leopards (*Uncia uncia*; Jackson et al., 2006), ocelots (*Leopardus pardalis*; Trolle & Kéry, 2003), and cheetahs (*Aclonyx jubatus*; Marnewick et al., 2008), stripes on tigers (*Panthera tigris Linnaeus*; Karanth et al., 2006), and rosettes on jaguars (*Panthera onca*; Silver et al., 2004) have been used to identify individuals and estimate population abundance and density. Although most C-r studies of terrestrial mammals have focused on felid species that have obvious natural markings (Trolle & Kéry, 2003), meticulous scrutiny of C-r data has also been used to identify species with relatively indistinct traits. For example, Sarmento et al. (2009) used C-r data to identify individual red foxes (*Vulpes vulpes*) and to estimate abundance, and Rich et al. (2014) used C-r data to identify individual pumas (*Puma concolor)* and to estimate density.

Individuals that have minimally distinct traits have also been monitored using Capture-Mark-resight methods. For C-M-r methods, animals are initially captured and artificially marked for identification (e.g., collar flagging) and thereafter recaptured using camera traps. Researchers have used C-M-r methods to estimate density and abundance of mesopredator and large carnivore populations, including fishers (*Martes pennanti*; Jordan et al., 2011), Florida panthers (*Puma concolor coryi*; Sollmann et al., 2013), American black bears (*Ursus americanus*; Martorello et al., 2001), and grizzly bears (*Ursus arctos horribili*; Mace et al., 1994).

No study to date has used camera data, without initial physical capture and artificial marking, to estimate annual apparent survival of a large carnivore that has relatively indistinct markings. Estimating demographic parameters requires accurate identification of individuals, which is nearly impossible using still photo data when individuals do not have distinct natural or artificial markings (Mace et al., 1994). However, continuous video data are significantly more effective than still photo data for identifying individuals (Higashide et al., 2013; Parsons et al., 2015; Reyes et al., 2017).

Continuous video data provide seamless viewing of captured individuals throughout specified time durations. For example, a 1-min video delivers up to 1800 frames per capture event, compared with only one frame per capture event provided by still photos. Importantly, an identifying trait that is not visible in the first frame of a video may be visible in the middle of the video (Figure 1). This vast increase in additional information leads to a greater capacity to identify unique characteristics (Reyes et al., 2017). These include distinct traits and behaviors, temporary traits, individual gender (Ramsey et al., 2019), and physical conditions affecting individual mobility that aid in individual identification (Reyes et al., 2017). Thus, using continuous video data to estimate demographic parameters of animals that have relatively indistinct characteristics may be possible.

Regarding hair snare data, genetic-based individual identifications have been successfully used to estimate population abundance and density (Harrison, 2013; Hooker et al., 2015; Stricker et al., 2012). Detection rates associated with hair snares can be relatively low because some hair samples do not generate genetic samples that can be reliably genotyped and some individuals may be trap shy (Boulanger et al., 2008). Gurney et al. (2020) installed trail cameras at hair stations and found that 32% of black bears that visited hair stations did not enter stations and were not genetically detected. Moreover, genetic data do not provide information about individual age, which is critical to fully evaluate population structure. Pairing genetic data from hair stations with continuous video data collected from video cameras aimed at hair stations should maximize the probability of individual detection (i.e., individuals that visit but do not enter a hair station can still be captured via video) and may also provide information about individual age. For example, black bear cubs captured via video are easily recognized as being <1 year old. If those individuals can be tracked through time as they transition into subsequent age classes, then age information can be included in their encounter histories. Thus, combined information from genetic and camera data should increase accuracy of abundance and density estimates and may provide a means to estimate vital rates (e.g., yearling female survival, adult female survival, etc.).

One objective of our study was to determine whether we could evaluate age-structured annual apparent survival of American black bears using noninvasive video and genetic data. Other studies of bear survival have used capture-mark-recapture data (Brongo et al., 2005; Reynolds-Hogland et al., 2007), known fate data from radio collars (Hebblewhite et al., 2003; Hellgren & Vaughan, 1989; Kasworm & Thier, 1994; Koehler & Pierce, 2005; Obbard & Howe, 2008),

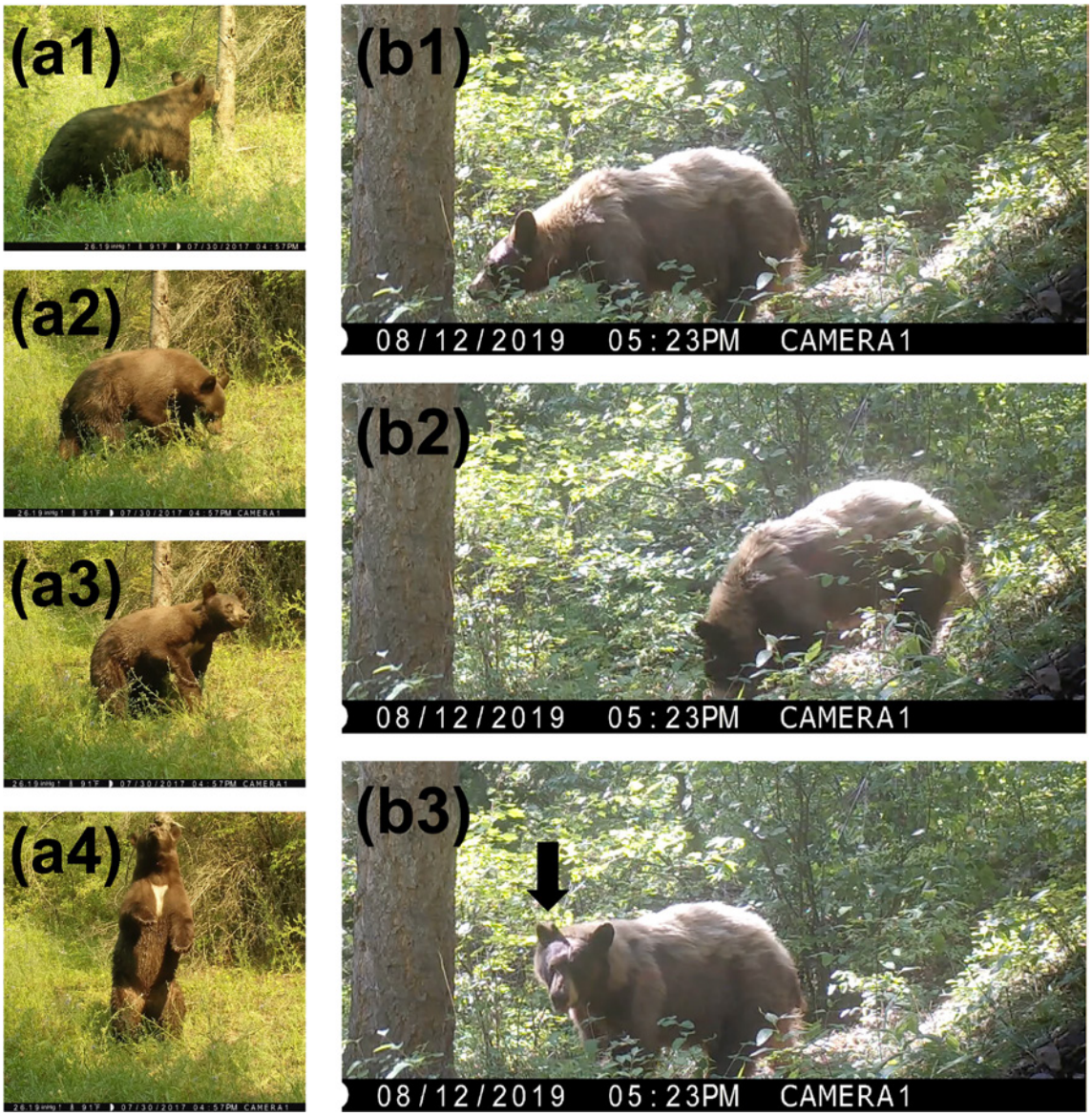

FIGURE 1 Frames of 1-min videos of American black bears (*Ursus americanus*) taken on MPG Ranch in western Montana during 2013–2019 that demonstrate the identifying traits that are not visible in the first frame may be visible in subsequent frames. (a1) the first frame of a 1-min video of a bear taken at 4:57 p.m. on July 30, 2017, (a2–a3) the second and third frames of the same video, (a4) the fourth frame of the same video showing Bear F7's unique chest blaze. (b1) the first frame of a 1-min video of a bear taken at 5:23 p.m. on August 12, 2019, (b2) the second frame of the same video, (b3) the third frame of the same video showing Bear F10's unique split in her right ear [Color figure can be viewed at wileyonlinelibrary.com]

or both (Lee & Vaughan, 2005), all of which required physical capture of bears. Boulanger et al. (2004) and Pederson et al. (2012) used data from hair snares and the Pradel model (Pradel, 1996) to estimate annual apparent survival of grizzly bears and black bears, respectively. However, age could not be determined by genetic data so neither study estimated age-specific apparent survival. Previous studies have also used hair from snares to estimate bear abundance or density (Gardner et al., 2010; Graves et al., 2011; Stetz et al., 2018). Our research is the first to use noninvasive data to estimate age-structured apparent survival of American black bears.

Our study builds on previous work by Ramsey et al. (2019) who evaluated the efficacy of using continuous video data to identify black bears in western Montana. Ramsey et al. (2019) compared identifications of black bears determined from careful scrutiny of 3228 continuous videos with those from genetic analyses using bear hair concurrently collected at 33 hair stations equipped with video cameras. They identified individual bears with ~82% accuracy when video data alone were evaluated. The estimated identification accuracy rate was ~98% when both video and genetic data were evaluated

together. They were also able to categorize bears into age classes. In this article, we (1) evaluate whether combined video and genetic data can be used to estimate annual age-structured apparent survival of American black bears, a large carnivore that can be difficult to distinguish visually, (2) compare estimates of annual apparent survival and recapture probability derived from combined video and genetic data with those derived from only genetic data, and (3) provide recommendations for scaling our approach for larger study sites.

2 | METHODS

2.1 | Study area

Our study was conducted on MPG Ranch (46°42′26″N, 114°00′16″W), a 6191-ha conservation property located in the Northern Sapphire Mountains in western Montana, USA (Figure 2). Elevations range from the summit of Mount Baldy (1833 m) to the river floodplain (966 m). Tree species dominating the eastern and northern

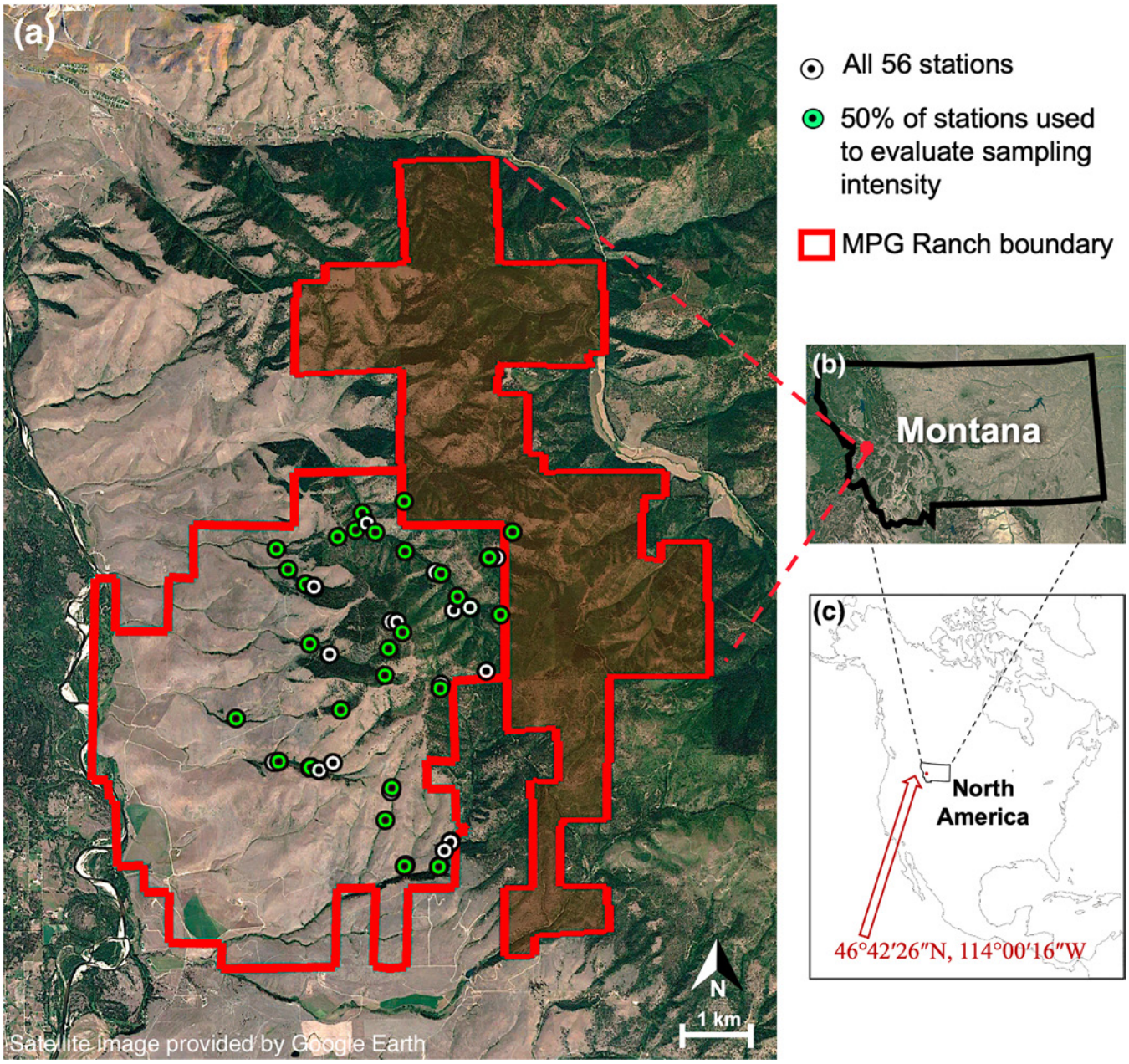

FIGURE 2 MPG Ranch (a), a 6191-ha conservation property in the Northern Sapphire Mountains in western Montana (b), North America (c). The unshaded and shaded portions of MPG Ranch were purchased in 2009 and 2016, respectively. The 56 video camera stations are represented by all circles. The 28 stations that were selected to evaluate sampling intensity are represented by the green circles. Some circles represent >1 station. Satellite image provided by Google Earth [Color figure can be viewed at wileyonlinelibrary.com]

portions of the study site include Douglas fir (*Pseudotsuga menziesii*), subalpine fir (*Abies lasiocarpa*), Ponderosa pine (*Pinus ponderosa*), and quaking aspen (*Populus tremuloides*). The western and southern portions of the study site consist primarily of open, grass-covered slopes with narrow deciduous woody draws that lead to bottomland riparian cover in the Bitterroot River floodplain (Durham et al., 2017). Other large mammals on MPG Ranch include elk (*Cervus canadensis*), mountain lions (*Puma concolor*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*Odocoileus virginianus*). Elk and deer hunting occurs on MPG Ranch, but black bear hunting is prohibited on the Ranch and on ~4000 ha of adjoining private lands. Black bear hunting is permitted on some adjoining public lands as well as on nearby lands held in block management by The Nature Conservancy.

2.2 | Video camera data

The video camera systems we used were Stealth Cam model STC-DVIRHD, Stealth Cam model STC-G42NG (Grand Prairie, TX), Browning model 8FHD-P (Morgan, UT), Reconyx XR6 UltraFire (Grand Prairie, TX), and Bushnell model 1197678 (Overland Park, KS). During 2010–2012, we placed video cameras throughout the study site to learn which areas were frequented by black bears. We used these observations to adjust the location of 56 video camera stations in 2013 to maximize detection of black bears. A station was a unique feature, such as a rub tree, rub post, water source, or wildlife trail. The original intent of the camera study was to capture bear behaviors. Thus, camera stations were not placed in a grid pattern across the landscape, which is typical for most studies using noninvasive data to estimate species occupancy, abundance, and density (e.g., Gerber et al., 2011; Kendall et al., 2016; Laufenberg et al., 2018). For the study herein described, we opportunistically used video and genetic data to estimate annual apparent survival by sex and age class.

We placed 107 video cameras at the 56 camera stations. We placed cameras 0.3–1.0 m off the ground to view distinguishing black bear characteristics such as blazes, genitals, and facial and body features. Cameras recorded for 1-min intervals at up to 30 frames a second, with a 1–30 s delay (depending on weather and season). Cameras were operational 24 h per day. To maximize detection and individual identification, we often placed multiple video cameras at different angles at single stations (Karanth, 1995; Karanth & Nichols, 1998; Rich et al., 2014; Silver et al., 2004). In instances when multiple cameras detected an individual bear at a single station during a capture event, we used all video data to identify the individual, but only one video was counted as a capture event.

When estimating demographic parameters by using C-r data, ensuring equal trap effort among years is important. For our study, trap effort was a function of consistency in the number and placement of camera stations across years and camera functionality at each station throughout the study period. Of the 56 camera stations, 23 were initially installed during summer 2013 and, thus, were active from the date of installation through December 31, 2019. The remaining 33 camera stations were active from January 1, 2013 to December 31, 2019. We calculated trap effort per year as the sum of all days that each of the 56 camera stations were "on." During each camera check in the field, we recorded the camera's dates of first trigger, last trigger, and the date of the camera check. If the date of the last trigger of a camera coincided with the date of the camera check, we considered that camera to be "on" during the entire period between the dates of the first and last triggers. If the date of the last trigger of a camera did not coincide with the date of the camera check, we considered that camera to be "off" during the period between the date of its last trigger and the date of the camera check. When video camera stations had more than one camera, we summed only nonredundant "on" days among video cameras for that station, by trap year.

2.3 | Genetic data

In 2013, we installed 36 hair collection systems on the study site to obtain genetic-based individual and sex identifications. The hair collection systems included 12 hair corrals, 16 rub trees, and eight rub posts (Ramsey et al., 2019; Sawaya et al., 2012). We distributed the hair collection systems over 3840 ha to maximize the number of individuals sampled. All hair collection systems were placed at video camera stations in view of multiple video cameras. The 12 hair corrals were removed in late 2014 because they were unproductive, but the 16 rub trees and eight rub posts remained in place throughout 2019. Also, three additional rub trees and six additional rub posts were installed during years 2014–2016. We used a nonfood scent lure at hair corrals and rub posts, but not at rub trees because we did not want to affect bear behavior at trees for unrelated research objectives focused on bear behavior.

We defined a hair sample as all the hairs found on one barb at the moment of hair collection. We partitioned each rub feature into 12 sections and documented in which section of the rub feature each hair sample was collected. We collected bear hair samples, rebaited rub posts and hair corrals with scent lure, and checked all video cameras at hair collection stations every 2–3 weeks

during summers 2013–2014 and replaced camera batteries 4–5 times annually. During 2015–2019, we collected hair every 2–3 weeks and replaced camera batteries every 6 weeks during the bear active season (March–November, annually). We flame-sterilized hair-trap barbs between collections to limit cross-contamination of samples. We dried hair samples in paper envelopes and stored them with silica desiccant to minimize DNA degradation. When more than one bear visited the same rub object between camera checks, they may have rubbed the same barbs or different barbs. If they rubbed the same barbs, either enough time passed between the rubs and we only collected hair from one bear or we collected hair from the two bears from the same barb. If the latter happened, we had a mixed sample of two bears, which would not successfully genotype.

All hair samples from hair collection stations were cleaned of debris, and hairs with visible follicles were placed in tubes for DNA extraction. Individual identity analysis was performed on purified extracts at the USDA National Genomics Center using a panel of nine microsatellite loci (Paetkau & Strobeck, 1994, 1998) and one sex identification locus (Carmichael et al., 2005). Detailed methods of genetic analyses are provided in Ramsey et al. (2019).

2.4 | Identifying individual bears

We used genetic-based individual and sex identifications to inform video capture-based individual and sex identifications, by using cross reference methods described by Ramsey et al. (2019). Generally, we separated videos of black bears from other wildlife video footage and chronologically sorted videos. For each video capture of a bear rubbing a rub feature (e.g., rub tree or rub post), we documented in which of the 12 sections of the rub feature the bear rubbed. Before genetic data were evaluated, one researcher carefully scrutinized all video data and assigned an individual identification to each video capture using a combination of distinguishing bear characteristics, including permanent traits, temporary traits, and individual behaviors. Temporary traits were used only selectively, and always in conjunction with other more permanent features.

We used multiple characteristics to add certainty to each identification. Permanent individual traits for bears included blazes, profile snout shape, ear notches, eyebrow color, bare spots and scars, relative ear size, temporalis and masseter size, snout and head shape, snout mustaches, snout color, snout scars and lines, female or male genitals, and shoulder humps (Figure 3). Temporary traits included coat color in sunlight, coat-shedding patterns during a given period, coat shedding across periods, wet coats, burr presence, nipple visibility, general weight gain, and uneven weight gain. Individual behaviors included gait type, back floating, and so forth. Importantly, individual identification was aided by frequent and regular video captures of individuals (e.g., Bear F2 was captured 904 times during 2013–2019; Table 1). The more often we captured an individual bear, the easier it became to identify the bear, and regular captures of individuals allowed us to track gradual changes and temporary marks, which helped us minimize misidentification error associated with camera data due to changes in natural marks (Yoshizaki et al., 2009).

Some individuals were video-captured only a few times and were never genetically captured (Bears F3, F10, M18, M19, M25, M27; Table 1), so we could not use genetic data to cross-reference identifications for those individuals. All but two of those bears had distinct traits, which we used to identify them. For example, Bear F3 was a mature female with a distinct tail, Bear F10 was a mature female with a cinnamon-colored coat and a distinct floppy ear tear in her right ear (Figure 1b), Bear M19 had a distinct chest blaze and white lips, and Bear M25 had a distinct blaze. Two bears (Bears M18 and M27) were identified based on the process of elimination (Supporting Information S1). Although unlikely, it was possible that we misidentified these two bears, which could have affected parameter estimates.

We identified video-captured cubs during their first year and we tracked cubs that remained on the study area through time. Cubs that were video-captured were always with their mothers, so we used traits of mothers to help identify cubs. Some cubs had unique traits, which we also used for cub identification. Cubs that were recaptured the following year as yearlings were almost always video-captured with their mothers at least once before family break-up, which helped us identify individual yearlings. The two exceptions were yearlings Bear F15 and Bear M20, offspring of Bear F6 (Table 1). Bear F15 had a distinct blaze and Bear M20 had a frost-bitten right ear and a very light-colored coat, making both bears easy to identify in 2018 without their mother. As cubs transitioned into yearlings, they experienced shifts in coat and morphological appearance. We documented the shifted traits for individual yearlings during video captures of yearlings with their mothers. Subsequently, we used the shifted individual traits of yearlings to help identify yearlings throughout their second year and as they transitioned into 2+ year-old bears. We also used the date stamp on each video to help determine individual identities, as some yearlings captured in spring can almost double in size by fall. Five bears were first captured as yearlings (Bears M6, M18, M26, M27, M32; Table 1). All five bears were male and none had been previously

FIGURE 3 Identifying traits of black bears, including: (a) mustache-like hair above lip, (b) ear notch, (c1) female genitals, (c2) male genitals, (d1) light coat color, (d2) brown coat color, (e1) eyebrow coloration, (e2) no eyebrow coloration, (f1–f9) examples of different chest blazes, (g) coloration around the eyes, (h1) left frost-bitten ear, (h2) right frost-bitten ear, and (i) scar on muzzle [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Capture events for the 49 American black bears (*Ursus americanus*) that were included in modeling annual apparent survival at MPG Ranch in western Montana [Color table can be viewed at wileyonlinelibrary.com].

Bear ID	Age class	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019
F1	2+	4	12	46	60	70	66	31			
M1	2+	4	6	22	19	38	9	32	8	20	12
F2	2+	5	6	118	130	101	145	127	112	156	133
M2	2+	10	9	55	45	38	52	58	9	31	12
F3	2+		4	5	11						
M3	2+		2	19	8	16	1	14			
F4	2+		1	34	12	37	17	44	42	72	63
F5	2+		1	3	7	3	5				
F6	2+		1	21	55	74	86	134	131	121	73
M4	2+			6	11	9					
M5	2+			17	54	73	64	100	41	12	
F7	Y			5	32	31	17	35	34	44	20
F8	Y			5	5			13	12		
M6	2+			2	31	68			1	22	10
M7	2+				7						
F9	C				14	15	1	9	16	2	15
M8	C				15	7[a]					
F10	2+				2			3			1
M11	C					104	65	40			
M12	C					69	53	100	14		
F11	C					69	80[a]	83	95	91	54
M13	C						18	29	13		
F12	C						18	19	6	6	1
M14	2+						18	42	24	36	34
M15	2+						37	108	38	87	16
F14	C							21	59[a]	16	7
M16	C							27	5		
M17	2+								6		
M18	Y							8	2	7	
M19	2+							7	2	15	9
M20	C								127	3	
F15	C								119	45[a]	87
M21	2+								37	153	
M22	C								116	115[a]	69
F17	C								43	23[a]	56
M23	C								36	34[a]	47
M24	2+									7	
F18	C									40	67
M25	2+									4	
M26	Y									2[a]	37
M27	Y									4	
M28	2+									9	

(Continues)

TABLE 1 (Continued)

Bear ID	Age class	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019
M30	2+									3	1
M32	Y										22[a]
M35	2+										21
M36	2+										9
M37	2+										4
M38	2+										8
F23	2+										7

Note: Our preliminary study occurred during 2010–2012. Our demographic study occurred during 2013–2019. Age class, age class at first capture; Yellow shading, cub video-captures; Orange shading, yearling video-captures with mother; Red shading, yearling video-captures without mother; Green shading, video-captures of 2+ year-olds where genetic data were concurrently collected; Gray shading, video-captures of 2+ year-olds without genetic capture.
[a]Video-capture of cubs or yearlings where genetic data were concurrently collected.

captured as a cub with their mother. We assumed that they immigrated into our study site.

All video captures of cubs were collected at camera stations, except one. Bear U1 was not video-captured at a station, but was filmed by a researchers over a period of 5 h with its mother (Bear F2) during May 4–6, 2014. We feel confident that Bear U1 was the cub of Bear F2, because Bear F2 was easily identifiable owing to her unique coat pattern.

After individuals were identified using video data, genetic analyses based on hair samples were used to cross-reference and inform individual identifications that were based on video captures. We were able to match bears captured via video to their hair samples for many capture events because there was only one bear observed via video and one hair sample collected during a sampling period. When 2+ bears left hair during a sampling period, we matched many bears observed via videos to their hair samples based on which section of the rub feature each bear rubbed and in which section of the rub feature hairs were collected. If two bears rubbed in the same section of a rub feature, the general result was a mixed genetic sample, which did not successfully genotype. We documented sex for individual bears when genetic-based sex identifications were available, and/or when genitals or engorged nipples were visible on video captures.

After identifying individual bears in each video capture event, cross-referenced with genetic data, we summed the total number of capture events for each identified bear, by year (Table 1). The temporal resolution of the capture events was 24 h (Mace et al., 1994), which we considered to be one calendar day. Therefore, if we had multiple capture events of individual i at camera station x during calendar day y, individual i was documented as being captured only one time at camera station x on calendar day y. We censored the first capture event of each animal to minimize bias due to possible transiency (Morrison et al., 2011).

To estimate annual age-structured apparent survival, we also needed to know bear age or age class at first capture. Based on video data, we could determine age at first capture when bears were cubs ($n = 37$) or yearlings ($n = 7$). In addition, one female (Bear F1) captured during our preliminary study (during 2010–2012) had cubs in 2010, so we could determine that she was an adult (≥5 years old; Kasworm & Thier, 1994) in 2013. Also, one male (Bear M1) captured during our preliminary study was first captured as a 2+ year-old in 2010, so he was an adult in 2013. The remaining 24 bears in our study were first captured as either subadults or adults. We could not determine specific age for every bear, but we could visually determine whether bears were cubs, yearlings, or 2+ year-olds using video data. Therefore, we conservatively grouped bears at first capture into those three age classes.

2.5 | Estimating individual identification accuracy

To estimate how accurately we identified individuals using video data alone, we compared identifications of individuals based on only video data with genetic-based identifications using bear hair concurrently collected at hair stations equipped with video cameras (Ramsey et al., 2019). Our identification accuracy assessment was a blind test because we first identified bears via video before genetic data were analyzed (i.e., the original video-based identifications were uninformed by genetic data). A genetic identification-video identification set (hereafter named genetic-video set) was defined as one genetic identification and all blind video identifications from the same station within a sampling period. Because some bears left multiple (i.e., redundant) hair samples at the

same time and location, we included only one successfully genotyped hair sample per video capture event to prevent inflation of the identification accuracy estimate. If the video-based identification correctly matched the genetic-based identification, the genetic-video set was considered accurate. If the video-based identification did not correctly match the genetic-based identification, the genetic-video set was considered inaccurate. If the video-based identification was documented as "Unidentified," then the genetic-video set was considered inaccurate.

2.6 | Estimating yearling and 2+ year-old annual apparent survival

We created encounter histories for each identified bear based on a 1-year time interval, by collapsing total capture events per bear, per year (Table 1) into single data points ("1" if bear *i* was captured, or "0" if bear *i* was not captured, during calendar year *x*) for each bear and year from 2013 to 2019. We did not include capture data collected during our preliminary study during 2010–2012 because many video stations used during 2010–2012 were moved in 2013. To estimate annual apparent survival, we included only capture data collected from stations that remained in place and were active throughout 2013–2019.

Although we obtained encounter histories for 70 bears during 2010–2019, our sample size for modeling apparent survival was reduced. We removed five bears due to possible transiency (bears with <3 capture events). We also removed five individuals for whom we did not know gender. Two of these five bears were cubs at first capture and both died during year 1. Thus, removing their encounter histories from analyses would have resulted in a positively biased estimate of cub survival. Therefore, we manually calculated cub survival (see below) and we modeled apparent survival for only the following age-sex classes: yearling males, yearling females, 2+ year-old males, and 2+ year-old females. Bears that were first captured as cubs during 2013–2019 and recaptured as yearlings and/or 2+ year-olds ($n = 15$) were retained for modeling apparent survival, but their first year captures were censored. For example, Bear F9 (Table 1) was first captured as a cub in 2013 and was recaptured as a yearling in 2014. Thus, Bear F9's encounter history was included in modeling apparent survival, but she was considered a yearling at first capture in 2014 (not a cub at first capture in 2013). Bears that were captured only as cubs during the study period (i.e., cubs that were never recaptured as yearlings or as 2+ year-olds; $n = 11$) were not included in models of apparent survival. Nine of these 11 censored cubs were only captured during the last year of our study, so removing their encounter histories did not affect sample size for estimating survival of yearlings or 2+ year-olds.

We used the Cormack–Jolly–Seber model (CJS; Lebreton et al., 1992) in Program Mark (White & Burnham, 1999) to estimate annual apparent survival (the probability that an animal is alive and remains on the study area and hence is available for recapture; φ) and recapture probability (p). We used the CJS model because it had the least number of estimable parameters (only φ and p), from which we could build age-structuring without including nuisance parameters. To further reduce the number of parameters, we held p constant. Our data set for modeling apparent survival was limited to 49 encounter histories, so minimizing total number of parameters was necessary. We modeled annual apparent survival as a function of age structure for four age-sex classes: yearling males, yearling females, 2+ year-old males, and 2+ year-old females. For the age-structured model, we partitioned φ of bears that were yearlings at first capture into two groups: (1) φ during the first 1-year interval when yearlings were between 1 and 2 years old and (2) φ during all other 1-year intervals, after yearlings had transitioned to 2+ year-olds. Apparent survival of bears categorized as 2+ year-olds at first capture was modeled the same as yearlings that had transitioned to 2+ year-old bears. We also modeled time-dependent φ and constant φ. We considered the intercept-only model (φ {.} p {.}) to be the null model.

Apparent survival was bounded between 0 and 1, so we used the logit link to develop models of φ. We evaluated goodness-of-fit of the saturated model using a bootstrap approach with 1000 simulations (Franklin et al., 2004). The saturated model was defined as the model for which the number of parameters equaled the number of data points or data structures (Cooch & White, 2002). For our data, the saturated model was φ {age structure * time} p {age structure * time}. We estimated the overdispersion parameter (c) and, in the case of overdispersion, we adjusted c-hat accordingly. We used Akaike's (1973) information criterion adjusted for sample size ($QAIC_c$) to rank models in terms of their ability to explain the data. Models with ΔAIC values <2.0 were considered to have substantial support (Burnham & Anderson, 2002). We evaluated Akaike weights for each model to gauge the relative importance of factors affecting survival (Burnham & Anderson, 1998). We calculated parameter estimates based on all models with ΔAIC value <2.0, and we used model averaging to calculate parameter estimates by including weighted averages of parameter estimates from all models that had a ΔAIC value <2.0.

2.7 | Estimating annual apparent survival based on only genetic data

We performed a second φ analysis to compare parameter estimates based on combined video and genetic data with parameters based on only genetic data. We created encounter histories for each genetically identified bear based on a 1-year time interval, by collapsing total genetic captures per bear, per year into single data points for each bear and year from 2013 to 2019. We used the CJS model to estimate φ and p. Genetic data provided information on sex, but not age. Thus, we modeled φ as a function of sex. We also modeled time-dependent φ and constant φ. We considered the intercept-only model (φ {.} p {.}) to be the null model. We evaluated goodness-of-fit of the saturated model, which for this analysis was φ {sex * time} p {sex * time}.

It is important to use the appropriate saturated model for evaluating goodness-of-fit because results of the goodness-of-fit evaluation can affect overall model ranking via adjustments to c to account for overdispersion. To directly compare results of modeling φ using only genetic data with results of modeling φ using combined video and genetic data, therefore, we repeated the latter φ analysis and used the saturated model φ {sex * time} p {sex * time} for evaluating goodness-of-fit.

2.8 | Cub survival

We manually estimated annual cub survival following Mace and Waller (1998), where $S_c = 1 - \{(\text{cub deaths})/(\text{total \# of cubs born})\}$. We estimated annual cub survival for each time step (e.g., 2013–2014, 2014–2015, etc.), and mean annual cub survival over the study duration. We calculated the 95% confidence interval of mean annual cub survival as $\overline{x} \pm t\left(\frac{\sigma}{\sqrt{n}}\right)$.

2.9 | Correlation between trap effort and captures, annual apparent survival

To evaluate whether annual trap effort (i.e., number of trap days) correlated with annual number of video capture events and with annual number of individual bears captured, we used Pearson's correlation coefficient. To evaluate whether annual trap effort correlated with annual survival rate, we used survival estimates calculated from the highest-ranked fully time-varying model of apparent survival (φ {t} p {.}), transformed annual survival estimates into their logits, and used Pearson's correlation coefficient. We used Program R version 3.1.2 (R Core Team, 2016) for all correlation analyses.

2.10 | Estimating apparent survival using data from 50% of stations

Our study site was relatively small (61 km^2) and our stations were located in only part of our study site, so our effective sampling intensity was relatively high (~2.5 stations/km^2). For our study, many individuals were captured multiple times at multiple stations annually. Thus, our sampling intensity may have been excessive for estimating demographic parameters. We performed a third φ analysis to determine if substantial data would be lost by reducing our sampling intensity by 50%. For the third φ analysis, we selected 28 of the 56 stations and repeated φ analyses using the same methods we used to model φ using combined video and genetic data from all 56 stations. To select the 28 stations, we grouped the 56 stations into 28 areas that were ≥200 m apart from all other groups. We then selected the station from each group that was placed in the best location for detecting bears.

3 | RESULTS

We documented 7531 capture events of 70 individual black bears between 2013 and 2019. During 524 capture events (7%), the individual bear was not identifiable because the bear was obstructed by darkness, the bear was too far from the video camera, or the bear was otherwise not in view.

Total trap effort throughout the entire study duration was 116,228 camera trap days (Table 2). Annual trap effort was lowest in 2013 because cameras at some stations were installed in the middle of 2013. Thereafter, the number of stations remained unchanged, but trap effort increased over time due to our improved ability to keep cameras active throughout the year (i.e., ensuring batteries were functioning, replacing broken cameras, etc.). We collected 783 black bear hair samples and successfully extracted DNA from 721 (Table 3). Of those samples, we successfully genotyped 323 (45%), from which we identified 35 unique individual bears (22M, 13F).

The amount of time that was required to set up camera and hair stations was ~175 h. We spent an additional ~255 h (~32 days) visiting stations to switch out SD cards and to collect hair samples, annually. Analyzing video data and cross-referencing video captures with genetic captures required ~400 h (~50 days), annually.

3.1 | Identification accuracy

Although we collected 318 hair samples that were successfully genotyped (Table 3), 133 of those hair samples were redundant so we removed them from analyses to ensure our estimate of identification accuracy was not

TABLE 2 Number of video camera stations, camera trap days, video capture events, and unique American black bears (*Ursus americanus*) captured on MPG Ranch in western Montana each year, 2013–2019.

Year	Sampling period	# Camera stations	# Camera trap days	# Video capture events	# Unique individuals captured
2013	August 15–December 31	56	12,229	620	20
2014	January 1–December 31	56	14,403	868	18
2015	January 1–December 31	56	15,564	804	18
2016	January 1–December 31	56	17,073	1166	24
2017	January 1–December 31	56	18,139	1274	29
2018	January 1–December 31	56	19,015	1302	31
2019	January 1–December 31	56	19,805	1532	42
Total			116,228	7566	

TABLE 3 Number of hair samples of American black bears (*Ursus americanus*) collected at MPG Ranch, number of samples for which DNA was extracted and successfully genotyped, and number of unique individuals identified by sex, 2013–2019.

Year	# Hair samples	# Samples DNA extracted	# Successful black bear genotypes	# Individual bears	# Males	# Females	# Gender unknown
2013	149	98	39	10	6	4	0
2014	90	79	37	12	7	5	0
2015	35	35	17	4	2	2	0
2016	103	103	53	15	8	7	0
2017	82	82	50	12	7	5	0
2018	127	127	50	12	7	5	0
2019	197	197	72	15	8	7	0
Total	783	721	318	35[a]	22[a]	13[a]	0
# Bears identified using video and genetic data				70	42	23	5

Note: For comparison, the number of individuals that were identified using combined video and genetic data during the same time period are presented at the bottom.
[a]Some individuals were genetically identified multiple years, but each individual was counted only once for the "Total" throughout the study period.

inflated. For three genetic-video sets, the view of the bear was inadequate to identify the bear (the bear was obscured by darkness, etc.), so the bear was documented as "Unidentified." Our sample size for estimating identification accuracy was 185 successfully genotyped hair samples matched with 185 video capture events. We accurately matched the video identification with the genetic identification 168 times (91%; Table 4). Our accuracy rate was lowest for 2+ year-old males (86%). For 11 of the 14 capture events where a 2+ year-old male was misidentified, the genetically identified 2+ year-old male was incorrectly video-identified as a different 2+ year-old male. For the remaining three capture events, the genetically-identified 2+ year-old male was video-documented as "Unidentified." Our accuracy rate for identifying 2+ year-old females was 97%. For the two cases where a 2+ year-old female was misidentified, the genetically identified 2+ year-old female was incorrectly video-identified as a different 2+ year-old female. Our accuracy rate was 92% for identifying yearling males and 100% for identifying yearling females.

We accurately identified yearling bears across time (Table S1). Many individuals that were first genetically-captured as yearlings were recaptured multiple times as yearlings and/or as 2+ year-olds. In all cases where a bear was genetically captured as a yearling and subsequently recaptured as either a yearling or a 2+ year-old, our video-based identifications correctly matched the genetic-based identifications.

3.2 | Age-structured annual apparent survival based on combined video and genetic data

Our sample size for modeling φ was 49 bears (12 yearling males at first capture, 9 yearling females at first capture, 20 2+ year-old males at first capture, 8 2+ year-old

females at first capture). Two yearlings (1M, 1F) were captured for the first time in 2019 (the last year of our study), so we could not determine if they survived one time step (i.e., to year 2020). Thus, our effective sample size for modeling φ of yearlings was 19 (11M, 8F). Five 2+ year-old bears (4M, 1F) were first captured in 2019, so we could not determine if they survived one time step. Yearlings transitioned into 2+ year-old bears throughout our 7-year study, increasing the sample size of 2+ year-old bears. Yearlings born in 2018 transitioned into the 2+ year-old age class in 2019 (if they survived), so for those 2+ year-old bears we could not determine if they survived to year 2020. Thus, our effective sample size for modeling φ of 2+ year-olds was 35 (22 M, 13F).

TABLE 4 Estimated identification accuracy of individual American black bears (*Ursus americanus*) based on a blind test where video-based identities were paired with genetic-based identities from bear hair samples at rub features in view of video camera stations on MPG Ranch on western Montana, 2013–2019.

Age-sex group	# Genetic-video sets	# Accurate	# Inaccurate	% Accuracy
Yearling males	13	12	1	92
Yearling females	6	6	0	100
2+ year-old males	101	87	14	86
2+ year-old females	64	62	2	97
Female cubs	1	1	0	100
Total	185	168	17	91

Two models had $\Delta QAIC_c$ <2.00 (Table 5a). The top-ranked model was the null model and the second-ranked model ($\Delta QAIC_c = 1.17$) included the effect of age structure on φ. The AIC_c weight for the top-ranked model was 0.63, compared to 0.36 for the second-ranked model. The estimated value of c-hat was 1.38, within the range for global model fit (Anderson et al., 1994), so we adjusted for overdispersion.

Based on model averaging (i.e., weighted parameter estimates from models with ΔAIC_c values <2.00),

TABLE 5 (a) Model rankings for annual apparent survival (φ) of American black bears (*Ursus americanus*) on MPG Ranch in western Montana, 2013–2019 based on combined video and genetic data and (b) estimates of annual apparent survival (φ) based on the two top-ranked models and based on model averaging from the two top-ranked models, with *SE*s and 95% confidence intervals.

(a) Model	ΔQAICc	ω	Model likelihood	k	Deviance
φ (.) p (.) Null	0.00	0.63	1.00	2	67.15
φ (age structured) p (.)	1.17	0.36	0.56	5	61.88
φ (t) p (.)	8.86	0.01	0.01	7	65.09
φ (age structure * time) p (age structure * time)	134.55	0.00	0.00	48	40.64

(b) Model	Parameter	Estimate	*SE*	LCI	UCI
Top ranked model	φ All bears	0.87	0.04	0.77	0.93
	p All bears	0.87	0.04	0.75	0.94
2nd ranked model	φ Yearling males	0.68	0.18	0.29	0.92
	φ Yearling females	1.00	0.00	0.99	1.00
	φ 2+ year-old males	0.80	0.07	0.63	0.90
	φ 2+ year-old females	0.93	0.04	0.78	0.98
	p All bears	0.89	0.04	0.78	0.95
Model averaged	φ Yearling males	0.80	0.14	0.40	0.96
	φ Yearling females	0.92	0.07	0.64	0.99
	φ 2+ year-old males	0.84	0.06	0.68	0.93
	φ 2+ year-old females	0.88	0.05	0.75	0.95
	p All bears	0.88	0.05	0.76	0.94

Note: ΔQAICc, difference between model QAICc and lowest QAICc; ω, QAICc model weight; k, number of estimable parameters; Deviance, measure of model fit.

Abbreviations: LCI, lower confidence interval; UCI, upper confidence interval.

estimated φ was 0.80 for yearling males (95% CI: 0.40, 0.96; Table 5b), 0.92 for yearling females (95% CI: 0.64, 0.99), 0.84 for 2+ year-old males (95% CI: 0.68, 0.93), and 0.88 for 2+ year-old females (95% CI: 0.75, 0.95). Recapture probability was 0.88 (95% CI: 0.76, 0.94).

3.3 | Annual apparent survival based on only genetic data

Our sample size for modeling φ using only genetic data was 34. Two models had $\Delta QAIC_c$ <2.00 (Table S2). The top-ranked model was the null model and the second-ranked model included the effect of sex on φ. The AIC_c weight for the top-ranked model was 0.49, compared to 0.39 for the second-ranked model. The estimated value of c-hat was 1.30, so we adjusted for overdispersion.

When combined video and genetic data were used to estimate φ, only the model with the effect of sex on φ had $\Delta QAIC_c$ <2.0 (Table S2). The AIC_c weight for the top-ranked model was 0.77, compared to 0.23 for the null model. The estimated value of c-hat was 1.23, so we adjusted for overdispersion.

Based on modeling that included only genetic data, estimated φ was 0.69 for males (95% CI: 0.50, 0.84; Table S3), estimated φ was 0.85 for females (95% CI: 0.64, 0.95), and p was 0.73 (95% CI: 0.54, 0.87). Based on modeling that included combined video and genetic data, estimated φ for males was 0.78 (95% CI: 0.63, 0.88; Table S3), estimated φ for females was 0.94 (95% CI: 0.81, 0.98) and p was 0.89 (95% CI: 0.78, 0.95).

3.4 | Cub survival

During 2013–2019, we captured 31 cubs. Of those, 20 (8M, 9F, 3U) were captured before the last year of our study, so 20 cubs was the effective sample size for calculating cub survival. Based on manual calculations, annual cub survival was 0.86 (95% CI: 0.72, 0.99).

3.5 | Correlation between trap effort and captures, apparent survival

Annual trap effort was significantly and positively correlated with the annual number of video captures ($r = 0.97$, $p = 0.0003$) and with the annual number of individual bears captured ($r = 0.84$, $p = 0.017$). Annual trap effort was not correlated with the annual logit of survival rate ($r = -0.50$, $p = 0.31$).

3.6 | Estimating annual apparent survival using data from 50% of stations

When we used combined video and genetic data from only 50% of the stations ($n = 28$) to estimate φ and p, our sample size of bears ($n = 49$) was the same as that used to estimate φ and p based on data from all 56 stations. Using data from 50% of the video stations, c-hat was 1.48, within range for global model fit (Anderson et al., 1994). Model rankings based on analyses using data from 50% of stations were exactly the same as that using data from 100% of the stations. Parameter estimates and *SE*s were almost identical between the two analyses.

4 | DISCUSSION

We demonstrated that noninvasive video data cross-referenced with genetic data, without physical capture and artificial marking of individuals, can be used to estimate age-structured annual apparent survival of black bears. While it is true that black bears have relatively indistinct natural markings compared to species like tigers and ocelots, we nonetheless found that most individual bears in our population had unique traits like distinct mustache-like hair above lips, snout colors or profiles, chest blazes, ear shapes, eyebrow colors, behaviors, and gaits (Figure 3, for additional examples of unique bear traits see Ramsey et al., 2019), which when viewed via video and carefully scrutinized, could be used to help identify individuals.

4.1 | Individual identification accuracy

We assessed our ability to accurately video-identify individuals by comparing blind video-based identifications with genetic-based identifications of bears that left hair in view of video cameras. Our identification accuracy for female bears (97%–100%) was higher than that for male bears (86%–92%). A misidentification during a sampling period can affect the encounter histories for both bears involved in the misidentification, when both bears are not captured multiple times (and accurately identified at least once) during the sampling period. Misidentifications that affect encounter histories can ultimately scale up to affect estimates of φ. Importantly, all misidentifications of 2+ year-old males in our study occurred because we inaccurately identified a 2+ year-old male as a different 2+ year-old male, or because the view of the bear (e.g., bear obscured by darkness, etc.) hindered our ability

to video-identify the 2+ year-old male. Thus, error stemming from the misidentification of 2+ year-old males may have affected encounter histories and φ estimates of 2+ year-old males. Alternatively, our estimates of female φ were relatively unaffected by misidentification error.

An additional source of error occurred when a video capture provided a poor view of the bear (e.g., bear obscured by darkness, bear in the far distance, etc.), which happened during 524 of 7531 video captures (7%). For each of those 524 video captures, the bear was documented as "Unidentified." During those 524 video capture events, it was the view of the bear and not bear recognizability that hindered our ability to identify individuals. If a bear documented as "Unidentified" during a sampling period was not captured again (and accurately identified) during the same sampling period, then our encounter histories would have been incomplete, which could have affected estimates of φ.

We accurately identified yearling bears, even as they transitioned into 2+ year old bears (Table S1). Identifying yearlings was aided by traits of yearlings' mothers, as 20 of the 22 bears that were first captured as cubs and recaptured as yearlings were captured with their mothers during both years. The two bears that were first captured as cubs with their mother and recaptured as yearlings without their mother (Bears F15 and M20) were siblings and both had unique traits that we used to identify them. As bears transitioned from cubs into yearlings, they experienced shifts in their coats and other morphological features. We used those shifted yearling traits to help identify individuals while they were yearlings and as they transitioned into older age classes.

4.2 | Annual apparent survival

A limitation of our study was that we estimated annual apparent survival, which was confounded with permanent emigration. Most male black bear offspring disperse when they are 1–3 years old (Costello, 2010; Schwartz & Franzmann, 1992) so true survival of male yearlings and male 2+ year-olds on our study site may be higher than what we report. Female black bears rarely emigrate (Elowe & Dodge, 1989; Immell et al., 2014; Powell et al., 1997; Rogers, 1987a; Schwartz & Franzmann, 1992) and this appeared to be the case for our study population. All females that were captured as yearlings were recaptured as 2+ year-old bears (Table 1) and most were recaptured multiple times annually as they aged through time. Thus, our estimates of female survival were likely not confounded by emigration.

Our models of φ assumed that the fate of each animal with respect to capture and survival probability was independent of the fate of any other animal. This assumption was likely not met for bears when they were cubs and when they were yearlings prior to family break-up as those bears were generally with their mothers. Thus, cubs and yearlings before family break-up were more likely to be captured only when their mothers were also captured.

Based on model averaging, yearling females had the highest estimated annual apparent survival, followed by 2+ year-old females, 2+ year-old males, and yearling males. All yearling females in our study transitioned into the next age class. Estimated φ for 2+ year old males (0.84) and females (0.88) were similar to that reported for adult black bears in Alberta (Hebblewhite et al., 2003), adult females in Washington (Koehler & Pierce, 2005), and subadults in Alaska (Schwartz & Franzmann, 1991), but higher than that reported for adult black bears in northwest Montana (Kasworm & Thier, 1994). Bear harvest occurred in the northwest Montana bear population (Kasworm & Thier, 1994) and in some areas adjacent to our study site, but it was prohibited within MPG Ranch during our study, which may help explain why φ for our study population was higher than that reported by Kasworm and Thier (1994).

The relatively high estimates of φ we found for bears on our study site are reasonable for bear populations that are establishing and growing. At the beginning of our demographic study in 2013, we captured 20 bears. By 2019, the number of bears we captured had doubled to 42 (Table 2; Figure 4). This growth may be explained by bear response to changes in bear harvest and land management on our study site. Prior to 2009, bear harvest had occurred for decades on our study site. In 2009, our study site was purchased and immediately transitioned into a conservation property. Beginning in 2009, bear harvest was prohibited and conservation goals for our study site included minimizing human disturbance in forested areas that provided habitat for bears and other wildlife. Beginning in 2011, sturdy gates were installed on perimeter roads and a security officer patrolled our study site to prevent motorized access and hunting.

The availability of bear foods may have increased during our study period, which may also help explain the relatively high estimates of bear φ that we found. Timber harvest occurred across much of our study area between 2000 and 2007, which opened the canopy and allowed for understory species to establish and grow. We did not test if bear foods on our study site increased through time, but many plants that bears consume (e.g., hawthorn, chokecherry, serviceberry, arrowleaf balsamroot, sweet

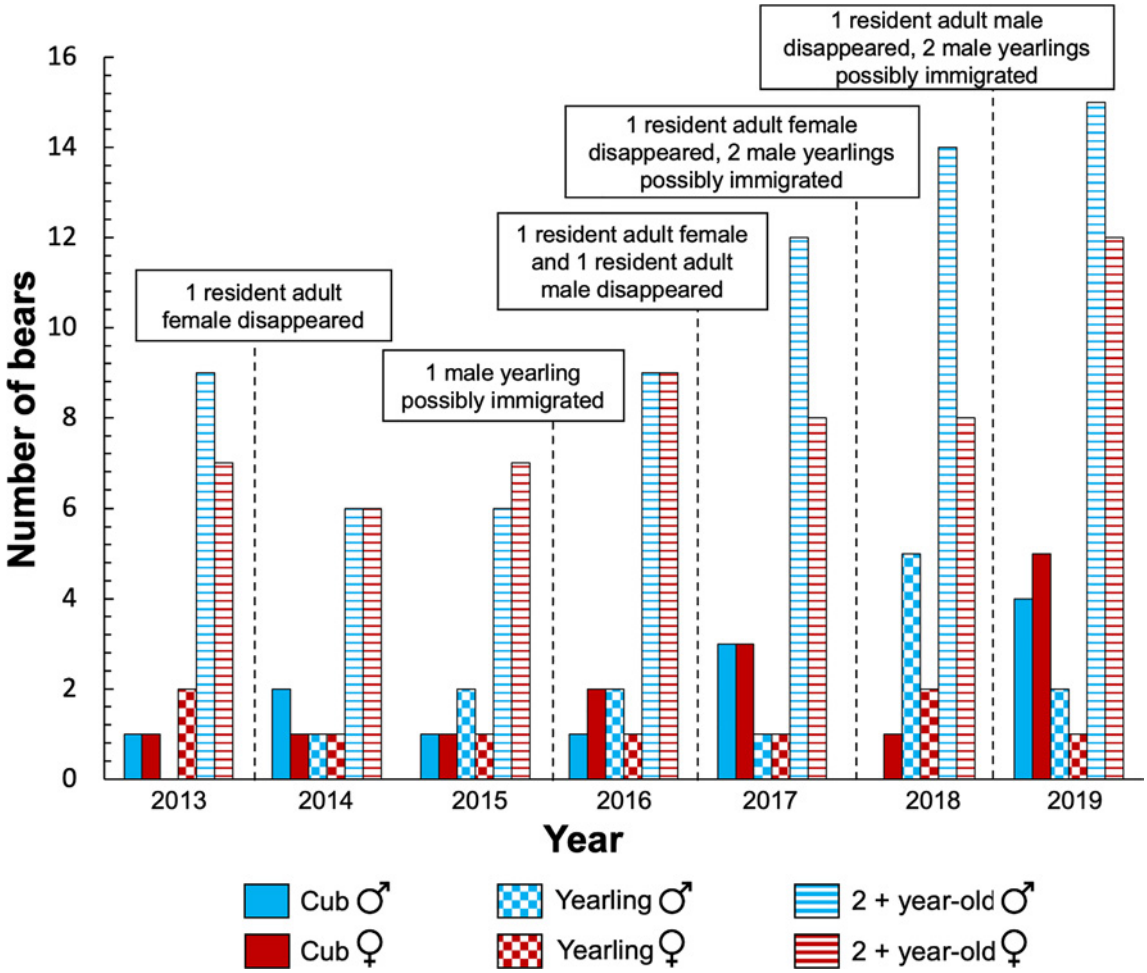

FIGURE 4 Annual number of American black bear (*Ursus americanus*) cubs, yearlings, and 2+ year-olds by sex captured by noninvasive video cameras, cross-referenced with genetic data on MPG Ranch, 2013–2019. Only individuals for which we knew both gender and age class were included (i.e., bears with unknown sex were not included in Figure 4) [Color figure can be viewed at wileyonlinelibrary.com]

cicely, cow parsnip, horsetail, currant, strawberry, thimbleberry, clover, etc.) were abundant on our study site by the end of our study (Durham et al., 2017).

Although we could determine specific age for many bears, we could not determine whether some 2+ year-old bears were subadults or adults. We conservatively grouped all noncub and non-yearling bears at first capture into one age class, 2+ year-old bears. Thus, φ estimates for 2+ year-old bears in our study included both subadult φ and adult φ. Given survival of subadult black bears can be lower than that of adult black bears (Jonkel & Cowan, 1971; McLaughlin, 1998), adults in our study site may have experienced higher φ than what we reported for 2+ year-old bears. It may be possible to estimate adult (5+ years) female apparent survival using noninvasive camera and genetic data by tracking females that were first captured as cubs or yearlings and assigning an adult age class beginning the sixth year after first capture (for bears first captured as cubs) or the fifth year after first capture (for bears first captured as yearlings). We attempted to do this with our data, but our sample size of adult females was too small.

We found that annual cub survival was 0.86 (95% CI: 0.72, 0.99), which was the same as estimated cub survival for Montana black bears documented ~50 years ago (Jonkel & Cowan, 1971), but higher than more recent estimates of black bear cub survival in western United States (Hebblewhite et al., 2003; Miller, 1994) and southwestern United States (Costello et al., 2003; Cunningham & Ballard, 2004). Our estimate of cub survival was likely biased high owing to small sample size ($n = 20$) and because we estimated cub survival during the period when cubs were first captured via video cameras (mean Julian date = 21 May) through year 1. Thus, possible cub mortality that occurred in-den through ~mid-May was not incorporated into our estimates. We suspect one reason we did not

detect cub presence immediately post-den emergence was because females with cubs likely avoided areas intensively used by other bears (e.g., ponds and rub trees where we placed camera stations) during the first weeks post-den emergence when cubs were particularly vulnerable.

4.3 | Recapture probability

Estimates of recapture probability (p) from our study were relatively high. The model averaged estimate of p for all bears was 0.88 (0.76, 0.94). The two estimates of p we found from black bear survival studies that used capture-mark-recapture (0.43–0.77, Lee & Vaughan, 2005) or genetic capture (0.26–0.37, Pederson et al., 2012) were relatively low. For these two studies, bears were captured during 2 or 3 months in summer, annually. For our study, hair and video camera stations were active year-round each year, which may help explain why our estimate of p was relatively high.

Harris et al. (2011) showed that sample duration and intensity affected estimates of λ for bear populations. Likewise, sample duration and intensity should also affect estimates of p and, ultimately, estimates of apparent survival when apparent survival is estimated using capture-recapture data. That is, studies with relatively long within-year sampling durations (e.g., traps or stations are active year-round) should be more likely to capture and recapture individuals compared to studies with relatively short within-year durations (e.g., traps or stations are active 3 months each summer). In our study, we captured five males and three females during late spring/summer in some years, but during only early spring or fall in other years. Had our within-year sampling duration included only three summer months annually, we would have missed those eight individuals during years when they were captured during only early spring or during only fall, which could have resulted in biased estimates of p and φ. Consequently, we recommend that wildlife research using capture-mark-recapture or capture-resight methods to estimate survival should strive to maximize within-year sampling durations.

Our regular visits to stations to switch out camera batteries and SD cards and to collect bear hair may have altered movements by bears on our study site, which may have affected encounter histories and estimates of p and φ. Previous studies have shown that human recreation altered spatio-temporal patterns of habitat use by wildlife (Dertain et al., 2021; Doherty et al., 2021; Naha et al., 2021), including bears (Coleman et al., 2013; Naves et al., 2001). Compared to demographic studies that use capture-collar data and require daily trap checks, the degree of landscape impact by our study design was minimal. We visited stations once ~ every 3 weeks and we minimized human impact by driving slowly, not vocalizing, and hiking quietly. Nonetheless, our station visits may have temporarily or permanently pushed bears away from stations. If the latter occurred, then our encounter histories would have been incomplete and estimated φ could have been biased.

4.4 | Sex ratio

The sex ratio of our sample was skewed toward males. We captured 70 individuals via video, of which the gender could be determined for 65. Forty-one of the 65 individuals (63%) were males and 24 (37%) were females. Similarly, 22 of the 35 (63%) bears that were genetically identified from hair were males and 13 (37%) were females. The male-biased sex ratio of bear captures was not likely due to males using rub features more than females because 22 of 42 (52%) documented males and 13 of 23 (57%) documented females rubbed and left hair. Although the sex ratio of black bear cubs is often approximately 1:1 (Garrison et al., 2007; Jonkel & Cowan, 1971; Miller, 1994), the sex ratio of black bears >1 year old that are captured for research is often male-biased. For example, Hellgren and Vaughan (1989) captured 71 males and 30 females in Virginia and North Carolina, Kasworm and Thier (1994) captured 217 males and 102 females in Montana, Koehler and Pierce (2005) captured 31 males and 11 females in Washington, and Sargeant and Ruff (2001) captured 229 males and 105 females in Alberta. The male-biased sex ratio of captured black bears may be explained by differences in space use between genders (Jonkel & Cowan, 1971). Yearling and subadult males travel beyond their natal ranges (Costello, 2010) and adult males roam widely to find and mate with receptive females (Costello et al., 2009; Rogers, 1987b; Sandell, 1989). Comparatively, adult females have relatively small home ranges (Koehler & Pierce, 2003; Powell et al., 1997). Thus, the number of males available for capture in our study was likely larger than the number of females that were available for capture.

4.5 | Multiple data sources

We found using multiple data sources increased the probability of detecting individuals. Had we used only genetic data from hair samples, we would have captured 35 individuals during 2013–2019. By combining video and genetic data, we captured 70 unique individuals during the same time period. Many of the individuals that we captured via video but not via hair snares were cubs with their mothers, which provided data necessary for

estimating cub survival. Importantly, 12 of the 49 (24%) bears that comprised our sample size for modeling apparent survival were captured only via video during the last year of their encounter history. For example, Bear M2 was captured via genetics and video each year 2013–2017, but he was captured only via video during 2018 and 2019 (Table 1). Bear M2 was easily identifiable on video because he had an ear tear, a limp, a pronounced concave snout, and he was the largest bear on the study site. Given this scenario occurred for ~25% of the bears in our study, it was not surprising that our estimates of p and φ were much lower when we used only genetic data from bear hair to model φ (Table S3). Estimated p from analyses based on only genetic data was 0.72, whereas estimated p from analyses based on combined video and genetic data was 0.89. For all bears, estimated φ from analyses based on only genetic data was 0.77, while estimated φ from analyses based on combined video and genetic data was 0.87. Parameter estimates from analyses based on only genetic data were also more variable (*SE* ranged from 0.06 to 0.09; Table S3) than estimates from analyses based on combined video and genetic data (*SE* ranged from 0.04 to 0.07). Previous work similarly showed that genetic tagging from hair samples underestimated animal presence (Fisher & Bradbury, 2014; Long et al., 2007). To address this issue, Boulanger, Kendall, et al. (2008) used multiple genetic data sources, which improved population estimation for grizzly bears. Similarly, our findings suggest that wildlife demography research that use hair sampling could benefit from adding video cameras at hair snare stations.

With video cameras placed at hair stations, we were also able to determine individual age class (cubs, yearlings, 2+ year-olds) and gender, which yielded insights into the dynamic distribution of age-sex classes through time (Figure 4) that could not be ascertained using genetic data alone. For example, we observed only one cub in 2018, whereas we observed nine cubs in 2019. Of the six cubs born in 2017, three males and two females transitioned into yearlings in 2018. Of the five male yearlings captured in 2018, two had not been captured previously as cubs, indicating they may have immigrated into the study site. During our study, three resident adult females (Bears F1, F3, F8; Table 1) and two resident adult males (Bears M3, M5; Table 1) disappeared. A bear was defined as a resident if it was consistently captured for at least 4 years, or if a female had been captured with cubs at heel (e.g., Bear F3). For these five resident bears, we determined that they were adults based on their capture histories. The one exception was Bear F3, who we first captured during our preliminary work in 2010; she had one cub in 2010 and two cubs in 2012. Sargeant and Ruff (2001) suggested that the removal of adult male black bears may result in changes in social pressure or competition for resources, possibly opening up higher quality habitat and/or mating opportunities to less dominant bears. Thus, the disappearance of the resident adult male in our study in 2017 may help explain why two yearling males suddenly showed up on our study site in 2018. These insights underscore the value of knowing both individual sex *and* age or age class, which can be used to help tease apart multiple factors affecting population structure over time. Moreover, such data can be used to estimate age-structured apparent survival, which is important because reliable estimates of vital rates allow for informed demographic modeling and projection analyses. Such analyses are critical to defining conservation actions and evaluating population response, which is increasingly important within the context of climate change.

Studies that use only camera data to estimate wildlife demography may also benefit from adding hair stations in view of cameras. For our study, genetic data provided a way for us to estimate accuracy of video-based identifications, which helped us to partition error and to understand reliability of parameter estimates. Based on our identification accuracy assessment, we found that 17 of 182 (9%) video-based identifications benefitted from genetic information. Genetic data also provided information on mother-offspring relatedness, which was useful for confirming offspring identities as they aged through time.

4.6 | Scaling up

To estimate bear demography, we opportunistically used video and genetic data from stations that were initially placed on our study site to capture bear behaviors. Our goal was to maximize bear detection, so we placed stations in areas that were most frequented by bears. To identify areas of high bear use, we a priori scouted our study site. Areas with high bear use were not systematically arranged across our study site, so we did not place our camera and hair stations in a systematic grid pattern.

We did not test if detection or φ probabilities using our irregular placement of stations was higher than that using a systematic grid arrangement of stations. It is possible that stations arranged in a grid pattern may not detect bears in specific hot spot areas of bear use. For example, a water source that multiple bears frequent may not be included as a station using a systematic grid pattern, which could result in biased parameter estimates. However, stations placed in a grid pattern that are baited with food or food scents (Kendall et al., 2016; Laufenberg et al., 2018) should attract bears that use nearby areas (including hot spots of bears use), assuming the spacing of the grid is appropriate for the species of study.

TABLE 6 Study designs using noninvasive data to estimate wildlife demography

	HR size (km^2)	Grid pattern	Grid size (km)	# Grids	Area sampled (km^2)	# Stations	# Cameras	Sampling intensity (# stations/km^2)
(a) Mean HR size = 36 km^2	36	8 × 8	3.0 × 3.0	64	576	64	128	0.11
(b) This study: 56 stations		NA	NA	NA	20	56	107	2.50
(c) This study: 28 stations		NA	NA	NA	20	28	52	1.25
(d) Pederson et al. (2012)		4 × 4	4 × 4	16	16	16		1.00
(e) Mean HR size = 45 km^2	45	7 × 7	3.5 × 3.5	49	600	49	98	0.08

Note: (a) Study design using a grid pattern for station placement when the home range size of the study animal is 36 km^2, (b) study herein, using all 56 stations, (c) study herein, using 50% of the stations, (d) study design by Pederson et al. (2012) who used a grid pattern for hair station placement, and (e) study design using a grid pattern for station placement when the mean home range size of the study animal is 45 km^2.
Abbreviation: HR, home range.

Otis et al. (1978) provided guidelines for determining trap (i.e., station) spacing for wildlife demography studies that use data collected from traps placed in grid patterns. In their paper on estimating animal abundance, Otis et al. (1978) recommended that the spacing of traps should be determined by the mean home range size of the study population. They recommended that four traps should be used per the mean home range area. Thus, the grid size should be ~25% of the mean home range area. For a study population with a mean home range size equal to 36 km^2, therefore, the grid size should be 3 km × 3 km (Table 6a). Assuming the total study area is ~600 km^2, 64 stations should be placed throughout the study area, for a sampling intensity equal to 0.11 stations/km^2 (Table 6a).

Our sampling intensity was much higher than that recommended by Otis et al. (1978). When we used data from all 56 stations to model φ, our sampling intensity was ~2.5 stations/km^2 (Table 6b). We found that ~2.5 stations/km^2 was excessive for estimating black bear demography, as no critical information was lost when we reduced the number of stations by 50%. Our sampling intensity using combined video and genetic data from 50% of the stations was 1.25 stations/km^2 (Table 6c), which was similar to that used by Pederson et al. (2012) who used hair DNA to estimate black bear demography (Table 6d). We do not suggest that other researchers necessarily replicate our high sampling intensity to estimate bear demography. Rather, we suggest that study designs that include hair stations may benefit by adding video cameras at hair stations to increase detection rates (e.g., bears that visit hair stations but do not leave hair can still be detected via video) and to provide information on individual age class.

Adding video cameras at hair stations can be practical. Consider the following hypothetical example. Assume a researcher collected hair and video data for a black bear population in northwestern Montana. Given the mean home range size for adult female black bears in northwestern Montana is 45 km^2 (Thier, 1990), the researcher arranged hair stations in a grid pattern according to Otis et al. (1978) across a 600 km^2 study area. In this hypothetical example, the total number of hair stations would be 49 (Table 6e). If the researcher installed two cameras at each station (Karanth, 1995; Karanth & Nichols, 1998; Rich et al., 2014; Silver et al., 2004), the total number of video cameras would be 98 (Table 6e), which is well below the number of cameras considered unrealistic for research programs that use camera data to model species occupancy (n = 400 cameras; Gálvez et al., 2016). For our hypothetical example, the amount of added time needed to switch out camera SD cards and to replace batteries is negligible because field crews can quickly maintain cameras at the same time that hair stations are visited. Assuming the number of video captures that are collected by 98 cameras is similar to that collected by the 107 cameras in our study, the amount of added time needed to analyze video data and cross-reference video data with genetic data is ~400 h, annually. Thus, one research team member would need to spend ~50 days annually to carefully scrutinize video data. Considering the fact that 32% of black bears that visited hair stations in Michigan did not leave hair (Gurney et al., 2020), the added time and expense to incorporate video cameras at hair stations may be worthwhile.

There may be a limit to the number of bears that can be accurately identified using hand-coded video data that are cross-referenced with genetic data. We did not reach that limit with our sample size of 70 bears. For future studies, automated facial recognition algorithms and similarity comparison networks may aid in animal re-identification (Schneider et al., 2020). For example, Clapham et al. (2020) recently developed the application BearID, which they used to identify 132 individual brown bears (*Ursus arctos*)

with 84% accuracy. As facial recognition software continues to improve, wildlife researchers should be able to use video data to estimate vital rates without the need for meticulous scrutiny of videos.

The method we present may not be viable for large study sites (e.g., 45,000 km^2) with very large sample sizes of individuals (e.g., 5000+), particularly if individuals have similar coat colors and few traits such as chest blazes, eyebrow coloration, mustache coloration, ear tears, coat patterns, shed patterns, and so forth. On our study site, bear coat color varied (54% brown, 20% black, 13% dark brown, 9% cinnamon, and 4% blonde), which helped us identify individuals. Also, we were able to distinguish unique traits for the vast majority of bears on our study site.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

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