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A test of motion-sensitive cameras to index ungulate densities: group size matters

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Abstract

The use of species detection rates gathered from motion-sensitive cameras as relative abundance indices (RAIs) could be a cost-effective tool to monitor wildlife populations; however, validations based on comparisons with reference methods are necessary. We considered 3 ungulates, wild boar (*Sus scrofa*), roe deer (*Capreolus capreolus*), and fallow deer (*Dama dama*), and compared 2 different RAIs with independent indices of density obtained through feces counts across 3 summers (2019–2021) in a protected area of central Italy. We estimated the number of detections per day (RAI_{events}), and the number of individuals per day ($RAI_{individuals}$) from remote camera videos. Both indices were correlated with density estimates, yet only $RAI_{individuals}$ correctly ranked interspecific densities. Values of RAI_{events} for the most abundant and gregarious ungulate (i.e., wild boar) were biased low and were lower than those of fallow deer. The uncertainty of RAIs was acceptable for the 2 most abundant study species (CVs ≤ 25%) but was greater for roe deer. At the intra-specific level, density estimates and RAIs showed comparable but slight inter-annual variation. Our results support the use of RAIs derived from motion-sensitive cameras as a promising and cost-effective tool to monitor ungulate populations, and researchers should incorporate group size into monitoring. We advocate the necessity of field tests based on comparison with locally reliable reference methods to validate the use of motion-sensitive cameras.

KEYWORDS
capture rate, group size, motion-sensitive cameras, population density, population monitoring, relative abundance indices, ungulates

Monitoring wildlife populations is necessary to evaluate the success of management actions aiming to favor their persistence, or to mitigate negative impacts on habitat, on species of conservation concern, and on human activities (Acevedo et al. 2010, Franzetti et al. 2012, Engeman et al. 2013, Ferretti et al. 2016, Massei et al. 2018). Changes in population density should be reliably estimated in a timely manner to adaptively tune management actions to population dynamics (Williams et al. 2002, Moeller et al. 2018); however, efficiently estimating abundance or density can be difficult for some species and in certain ecological conditions (e.g., areas with steep, rocky terrain or dense vegetative cover, nocturnal or cryptic species).

Under a range of circumstances, indices of relative abundance are often used by wildlife managers to estimate population trends (Rovero and Marshall 2009, Kinnaird and O'Brian 2012, Palmer et al. 2018, Peris et al. 2019); however, the relationship between relative abundance indices and traditional population density estimates should be assessed (Williams et al. 2002), and ideally the former should increase linearly with the latter, not showing any trend leading to saturation at high density values (ENETWILD Consortium et al. 2018). Estimates of absolute abundance from motion-sensitive cameras are possible in the case of individuals recognizable through natural marks or human-placed tags (e.g., through capture-mark-recapture models; Karanth 1995, Forsyth et al. 2019, Macaulay et al. 2019). When animals are not individually recognizable, estimates based on distance sampling (Pal et al. 2021) or other models have been developed such as the random encounter model (Rowcliffe et al. 2008), random encounter and staying time model (Nakashima et al. 2018), association model (Campos-Candela et al. 2018), and time-to-event model (Moeller et al. 2018). These models require a variety of assumptions and random placement of cameras to achieve independence of sampling locations with respect to animal movements (Rogan et al. 2017, Santini et al. 2022). An alternative use of remote cameras has been to estimate relative abundance indices (RAIs), usually expressed as the ratio of the number of detections of a given species over the sampling effort, in terms of days of camera surveys (O'Brien et al. 2003, Rovero and Marshall 2009, Lijun et al. 2019). Results differ across studies and, although RAIs have been widely used, researchers have questioned their reliability as a method to evaluate relative abundance of wild populations and recommended field tests comparing reference methods to RAIs (O'Brien et al. 2003, Sollmann et al. 2013, Massei et al. 2018, Lijun et al. 2019).

Most uses of RAIs are based on the raw count of detections per day through pictures (O'Brien et al. 2003, Rovero and Marshall 2009, Sollmann et al. 2013, Tanwar et al. 2021). This approach is labor-saving in respect to intensive procedures based on counting individuals in videos, and it may be appropriate for solitary species. For gregarious species, such as most ungulates in temperate ecosystems, ignoring group size may lead to underestimating indices, generating potential biases when RAIs are compared across species. In these cases, indices based on the count of individuals within detection events would be recommended, although field tests are scarce (Palmer et al. 2018).

We conducted a field test of RAIs based on motion-sensitive cameras on 3 species of wild ungulates: the native wild boar (*Sus scrofa*), the introduced fallow deer (*Dama dama*), and the native European roe deer (*Capreolus capreolus*). We worked in a Mediterranean protected area where long-term population monitoring of these species has been implemented through indices based on feces counts (Fattorini et al. 2011, Fattorini and Ferretti 2020, Ferretti and Fattorini 2021), which would serve as a reference method to camera surveys. Over 3 years, we used motion-sensitive cameras to estimate 2 RAI indices: the first was based on the count of events per day, and the second was based on the count of individuals per day. Our objectives were to test the correlation between RAIs and independent indices of ungulate densities and compare relevant uncertainty, calculate interspecific ratios of density estimates and relative abundance to assess whether the differences in RAIs among species were consistent with interspecific differences in densities, and examine inter-annual variations in density indices and RAIs to evaluate their consistency.

STUDY AREA

We conducted our study in Maremma Regional Park (central Italy, ~90 km^2; Figure 1; 42.626371°N, 11.099303°E; 0–417 m) in summers 2019, 2020, and 2021. The local climate is Mediterranean with hot summers and rainfall occurring especially in autumn. Mean daily temperature ranges from 9°C (Jan) to 24°C (Aug) and monthly rainfall ranges from 9.3 mm (Jul) to 81.8 mm (Nov; average values for 2014–2018: data from https://sir.toscana.it; Ferretti et al. 2021).

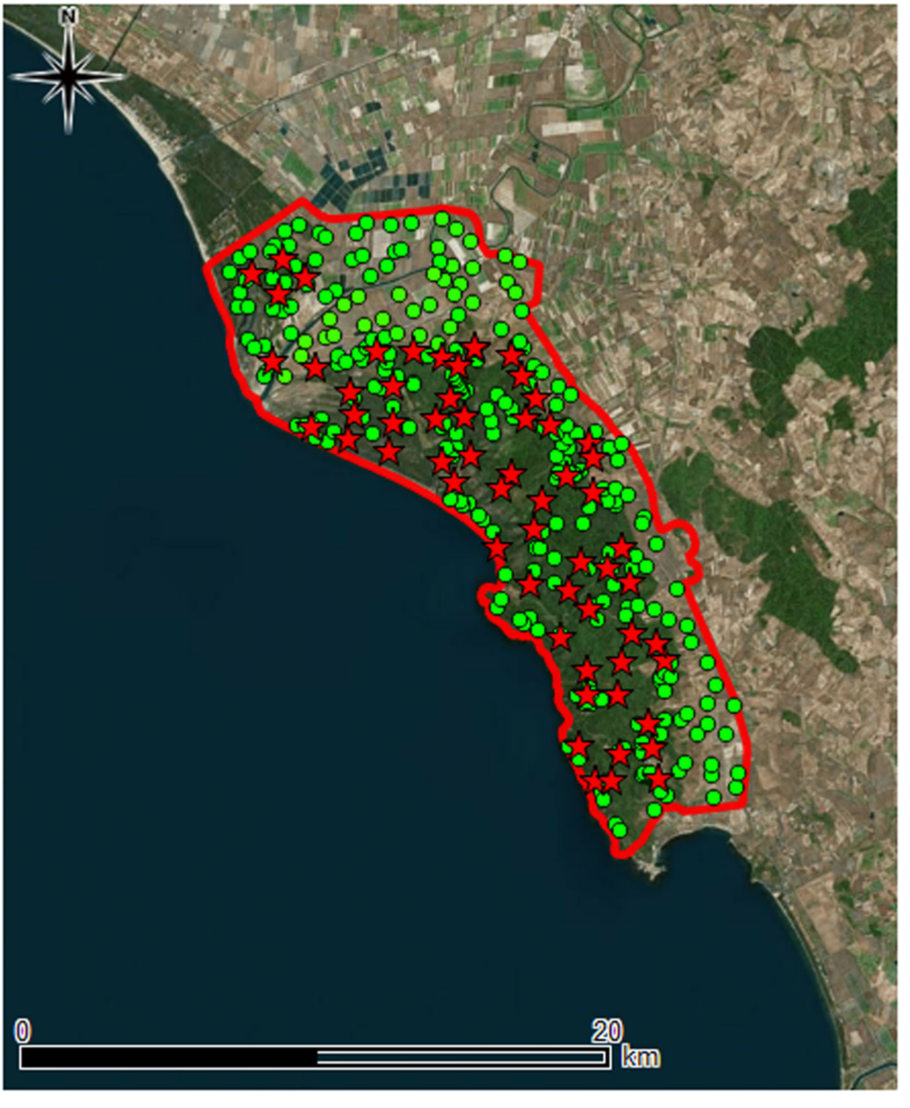

FIGURE 1 Locations of sampling plots of ungulate pellet group counts (green circles) and camera sites (red stars) in Maremma Regional Park (red line), Italy, 2019–2021.

Vegetation includes Mediterranean sclerophyllic scrubwood (58%), with 3 main forest types: oak (*Quercus* spp.), dominated by holm oak (*Q. ilex*) with a height >7 m; scrub, dominated by holm oak and strawberry tree (*Arbutus unedo*), with a height <7 m; and garrigue, including bushes with a height <2 m, with holm oak, rosemary (*Rosmarinus officinalis*), juniper (*Juniperus* spp.), and rockrose (*Cistus* spp.; Mencagli and Stefanini 2008). Other cover types included pine (*Pinus* spp.; 10%, especially domestic pine [*P. pinea*]), ecotones with abandoned olive groves and pastures partially recolonized by scrub (15%), set-aside grassland (4%), and cultivated fields (12%, especially cereals and sunflower). Further details on cover type composition are reported in Sforzi et al. (2012) and Melini et al. (2019).

Large wild mammals include wolves (*Canis lupus*), fallow deer, wild boar, and European roe deer. Medium-sized mammals occurring in the area are crested porcupine (*Hystrix cristata*), coypu (*Myocastor coypus*), European brown hare (*Lepus europaeus*), red fox (*Vulpes vulpes*), European badger (*Meles meles*), European wildcat (*Felis silvestris*), stone marten (*Martes foina*), and pine marten (*Martes martes*), with various species of smaller mammals. Livestock (cattle, horses, and sheep) are present in some portions of the area. Population control of wild boar and fallow deer is conducted under the responsibility of the Maremma Regional Park Agency through culling (both species) and trapping with removal (wild boar) conducted by Park wardens and, in the case of trapping, authorized personnel, to limit the negative impacts of these ungulates on habitats, species with conservation relevance, and agriculture. As a result of culling, wild boar and fallow deer densities decreased by 40–60% over the last decade (Fattorini and Ferretti 2020, Ferretti and Fattorini 2021). Culling might influence movements of wild ungulates (Cromsigt et al. 2013), but local information is not available; however, previous studies suggested no significant impact on fallow deer distribution in our study area (Pecorella et al. 2016). We conducted feces counts and camera surveys during the same season across the same area, thus ruling out potential effects of culling on our comparisons.

METHODS

Feces counts

We estimated indices of ungulate densities in summer through pellet group (deer species) and feces (wild boar) counts, a method that has been consistently used to estimate ungulate densities in wooded areas with limited visibility of animals (Bailey and Putman 1982, Mayle 1996, Borkowski 2004, Campbell et al. 2004, Marcon et al. 2019). This method has been used in our study area for 2 decades and the sampling design has been described by Fattorini et al. (2011), Ferretti et al. (2016), and Fattorini and Ferretti (2020). We placed 271 circular plots (5-m radius; Figure 1) within the study area using stratified sampling that exploited tessellation stratified sampling (TSS; Barabesi and Franceschi 2011, Barabesi et al. 2012). First, we stratified the area according to main land cover features, and local differences in deer densities detected through preliminary surveys, which led us to identify 13 homogeneous strata (2 strata with scrub, 3 strata with pine and marshland, 2 strata with abandoned olive groves and ecotones, 6 strata with cultivated fields). We allocated plots proportionally to strata size. In the largest strata (scrub north and south, and a pine stratum) we adopted a 2-phase strategy. We partitioned these strata into spatial units delineated by natural or artificial bounds (e.g., lanes, streams, cultivation bounds) and selected a sample of spatial units within each stratum proportionally to strata size (4–9 units per stratum). Finally, in the second phase, in each selected unit, we placed plots using TSS: we divided the units into patches of equal size and randomly placed a plot within each patch (7 plots per patch). In the other strata, we used a one-phase TSS strategy (Fattorini et al. 2011). We assigned geographic coordinates to the center of each plot using QGIS 2.18 (QGIS Development Team 2016) and located plots in the field with a portable global positioning system unit.

We used the fecal accumulation rate technique to avoid potential issues related to the estimate of the decay rates of pellet groups, which vary between habitat characteristics (Mayle et al. 1999, Campbell et al. 2004, Minder 2006). We visited each sampling plot twice: we cleared all pellet groups and feces from sampling plots in mid-June to early July and then 35–40 days later (a suitable temporal interval according to the local decay rate of ungulate feces; Massei et al. 1998, Minder 2006) we revisited each plot to count all deer pellet groups and wild boar feces accumulated in plots. Wild boar feces can be identified by their shape and size. We distinguished fallow deer pellets from roe deer pellets according to shape and size: the former defecates cylindrical pellets, usually with a pointed end and slightly concave at the other, whereas the latter makes small, elongated pellets, usually rounded at both ends (Mayle et al. 1999). The same 2 observers (FF, NF) performed all pellet group counts in this study.

For wild boar, we used a defecation rate of 6.7 feces/individual/day, estimated in an ecologically similar site to our study area, 40 km away, that included a known number of individuals (Fattorini and Ferretti 2020). For fallow deer, we used a defecation rate of 25 pellet groups/individual/day suggested by a study conducted on a known number of individuals within a large enclosure, in our same study area (Massei and Genov 1998). For roe deer, as local information on the defecation rate was lacking, we used the recommended value of 20 pellet groups/individual/day estimated in an enclosed area in the United Kingdom (Mitchell et al. 1985, Ratcliffe and Mayle 1992, Mayle et al. 1999). Although these density estimates could not be tested against true densities, estimated deer densities were consistent with spotlight counts in a roughly 1,000-ha portion of our study area (Fattorini et al. 2011), whereas wild boar densities indexed by feces counts showed a strong and significant correlation with independent indices based on harvest rates (Ferretti et al. 2016). We considered densities estimated through feces or pellet group counts as indices of population abundance and called them feces counts. Methodological details and theoretical justifications were given in Fattorini et al. (2011) and Fattorini and Ferretti (2020), where an unbiased estimator of feces abundance and a conservative estimator of its standard error was provided.

Camera surveys

This study is part of a larger project on behavioral and ecological relationships within the mammalian community; therefore, camera surveys were primarily designed to evaluate spatio-temporal patterns and interactions of medium-sized and large wild mammals (Ferretti et al. 2021, Rossa et al. 2021). We defined locations within a sampling grid (cell size = 1 km × 1 km) superimposed to the non-agricultural part of our study area, with an extension of about 60 km^2, through the QGIS software (Figure 1). In summer 2019, we defined 57 locations. In July 2019, we put 19 motion-sensitive cameras on site, along animal trails or forest roads. We subsequently rotated cameras to other locations monthly, to monitor all 57 locations for ≥1 month in July–September (i.e., a period consistent with post-birth density estimates conducted through fecal counts. In summer 2020–2021, we increased the number to 60 locations, which we monitored continuously and kept fixed in all study years (i.e., we did not move them during field seasons). For comparison, we considered data collected in July to mid-August for cameras working ≥5 days (2019: $n = 50$; 2020: $n = 51$; 2021: $n = 52$) and with a maximum of 31 days with actual sampling per location.

We attempted to put cameras at a height of 30–100 cm above the ground, and 86.4% of 177 deployments (considering the 3-year period) were <100 cm above the ground. Considering constraints related to the nature of the terrain, presence of dense scrub, and to reach a compromise between visibility and reducing risk of theft, 11.9% of deployments had to occur at a height of 101–150 cm and 1.7% of deployments at a height ≥150 cm. We used various models of motion-sensitive cameras for this work (Owlzer Guard Z2, Shenzhen, China; Comitel Guard and Comitel Guard Micro 2; Comitel, Cesena, FC, Italy; Ir-Plus HD and Ir-Plus 110°, Ziboni Technology srl, Costa Volpino, BG, Italy), which were triggered by passive infrared sensor (PIR) and had a trigger time of ≤1 second. To account for potential influence of different camera models on analyses of spatial and temporal patterns of our study species, we included this variable as a random effect in mixed models (see below). Cameras were furnished with external batteries (6 or 12 Volt) and 16–32 gigabyte memory cards. We replaced memory cards every 15–30 days and we also replaced batteries if needed. We set cameras to record videos of 30 seconds with no lag between subsequent videos. We set cameras to work 24 hours/day with medium PIR sensitivity. We determined the sampling effort at each location by the number of days elapsed between installation and checkout of the camera. When the batteries ran out or the memory card became full before the check period, we determined the time of the last exposure from the downloaded videos and considered it to be the last operational date (Rowcliffe et al. 2008).

We recorded all times and dates of each check for each camera location to minimize the data loss and possible problems with the correct times recorded by cameras. From each video, we obtained the following information: date, solar time, species, number of individuals, and camera location. Operators who watched the videos and recognized the species first passed an identification test on 100 videos (≥95% correct identifications).

When the same camera took >1 video of the same species within 30 minutes, we counted them as 1 event (Tobler et al. 2008, Lucherini et al. 2009, Torretta et al. 2016, de Satgé et al. 2017). For each event, we assessed the group size as the number of different individuals detected in the event. For each year, species, and each *i*th location, we estimated 2 indices of relative abundance. First, we calculated the ratio of the number of events over the number of operational days of the camera (was denoted as $RAI_{events\text{-}i}$). Second, we calculated the ratio of the sum of the number of individuals over the number of operational days of the camera ($RAI_{individuals\text{-}i}$). Then, for each species and year, we estimated RAI_{events} and $RAI_{individuals}$ as the mean value across different locations. We estimated standard errors and relative standard errors (i.e., coefficients of variation) from 10,000 bootstrap samples through bootstrap resampling. For each species, we also estimated mean group size each year by the ratio of the cumulative number of individuals over the number of events (i.e., the average number of individuals per event). Also in this case, we estimated standard errors from 10,000 bootstrap samples through bootstrap resampling.

Statistical analyses

We initially computed estimates of ungulate densities and camera-based relative abundance indices ($RAI_{individuals}$ and RAI_{events}) of each species, as described above. Subsequently, we evaluated the correlations among estimates obtained through the 3 different methods and calculated relevant correlation coefficients (i.e., RAI_{events} vs. feces counts; $RAI_{individuals}$ vs. feces counts; RAI_{events} vs. $RAI_{individuals}$, using 9 yearly estimates). The camera sampling season was slightly different between 2019 (when cameras were rotated across locations in Jul–Sep) and 2020–2021 (when camera locations were fixed in Jul–mid-Aug). Thus, we calculated a second series of correlations among methods by removing data collected in 2019 to ensure that results were unaffected by differences in camera sampling. We performed feces counts over the whole area of Maremma Regional Park, including the agricultural land, but we did not place cameras on agricultural land. To check whether results were affected by differences in spatial coverage of sampling, we calculated additional correlations between camera indices and densities estimated over the non-agricultural part of Maremma Regional Park (i.e., removing sampling strata relevant to cultivated fields).

To test whether the relationship between camera-based indices and density estimates was better explained by a linear or a logarithmic function (with the latter indicating a possible saturation at the highest densities; ENETWILD Consortium et al. 2018), we used different linear models to relate $RAI_{individuals}$ and RAI_{events} to density estimates. First, we fitted linear models predicting RAIs as linear functions of density estimates. Then, we fitted models predicting RAIs as linear functions of the log density estimates. For each index, we compared the 2 models through Akaike's Information Criterion corrected for small samples (AIC_c) and selected the model with the lowest AIC_c value. Then, for each year we calculated interspecific ratios of densities and interspecific ratios of camera indices by dividing the density of species *a* by the density of species *b* (i.e., wild boar/fallow deer; wild boar/roe deer; fallow deer/roe deer), to evaluate whether density ratios among species were consistent across methods.

Eventually, for each species we assessed inter-annual variation of densities and indices of relative abundance. We estimated inter-annual differences in densities through generalized linear mixed models with negative binomial errors. As response variable, we considered the number of pellet groups (for deer species) or feces (for wild boar) accumulated in each sampling plot during the temporal interval between plot clearance and counts, which we defined as accumulation time. We used the log accumulation time as an offset variable to standardize local pellet group or feces densities according to potential differences in accumulation time. We entered year (factor; reference level: 2019) as a predictor, and plot identity as a random intercept to account for repeated observations in the same sampling plots in different years. We also estimated inter-annual differences in camera-based indices through generalized linear mixed models with negative binomial errors. We fitted the number of events in each camera site (for RAI_{event}) or the cumulative number of individuals across all the events in each camera site (for $RAI_{individuals}$) as the response variable. For each camera site, we defined the number of days with the camera working as sampling effort. We used an offset (log sampling effort) to account for potential differences in sampling effort across camera sites. We used year (factor; reference level: 2019) as a predictor. We used camera location identity as a random intercept to account for repeated observations in the same sites in different years. Additionally, we also used the camera type (i.e., brand and model) as a random intercept to account for the potential effects of camera devices on species detection. We estimated coefficients of predictor variables and relevant 95% confidence intervals. We conducted statistical analyses through the RStudio software. We estimated model parameters using the R package glmmTMB (Brooks et al. 2017), and validated models through visual inspection of residuals through the DHARMa package (Hartig 2021).

RESULTS

Indices of ungulate densities

Results of feces counts ranged from 10.5–11.7 individuals/100 ha for the wild boar (relative standard error [RSE] = 15–20%), from 7.7–8.7 individuals/100 ha for fallow deer (RSE = 12–15%), and from 3.0–3.7 individuals/100 ha for roe deer (RSE = 20–23%; Figures 2 and 3).

With cameras, we collected 923 wild boar detections, 1,170 fallow deer detections, and 207 roe deer detections, over 3,432 sampling days (Table 1). Ungulate detection rates expressed as number of events per day (RAI_{events}) ranged from 0.25–0.37 for wild boar (RSE = 17–22%), 0.30–0.41 for fallow deer (RSE = 16–20%), and 0.05–0.07 for roe deer (RSE = 22–34%; Figures 2 and 3).

Ungulate detection rates expressed as number of individuals per day (i.e., $RAI_{individuals}$) ranged from 0.78–0.84 for wild boar (RSE = 21–25%), 0.50–0.61 for fallow deer (RSE = 18–21%), and 0.05–0.09 for roe deer (RSE = 24–39%; Figures 2 and 3). Group size, in terms of number of individuals per event, was 2.2–3.0 for wild boar, 1.5–1.6 for fallow deer, and 1.1–1.2 for roe deer (Figure 4).

Relationships between RAIs and feces counts

Both camera indices were correlated with results of feces counts (Table 2). The 2 camera indices were also correlated ($r = 0.85$, $P = 0.004$). Correlations between camera indices and feces counts were supported also when we removed feces counts conducted in the agricultural area from analyses and when we restricted the analyses to 2020–2021 (Table 2).

For $RAI_{individuals}$, the relationship between detection rate and feces counts was better explained by a linear model than by a logarithmic model (Tables 3 and 4; Figure 5). Conversely, a logarithmic function explained the relationship between RAI_{events} and feces counts better than a linear one (Tables 3 and 4; Figure 5).

Interspecific differences in density indices

Indices of wild boar densities were 1.3–1.4 times greater than those of fallow deer, depending on the year, consistent with the ratio observed for $RAI_{individuals}$ (1.3–1.6; Figure 6). Conversely, wild boar relative abundance from RAI_{events} was 0.7–1.0 times that of fallow deer. Indices of wild boar and fallow deer densities were 3.2–3.7 and 2.4–2.7 times greater than those of roe deer, respectively (Figure 6). Conversely, relative abundances of wild boar and fallow deer estimated through camera indices were 4.2–8.5 times (RAI_{events}) and 5.4–14.8 times ($RAI_{individuals}$) greater than those of roe deer (Figure 6).

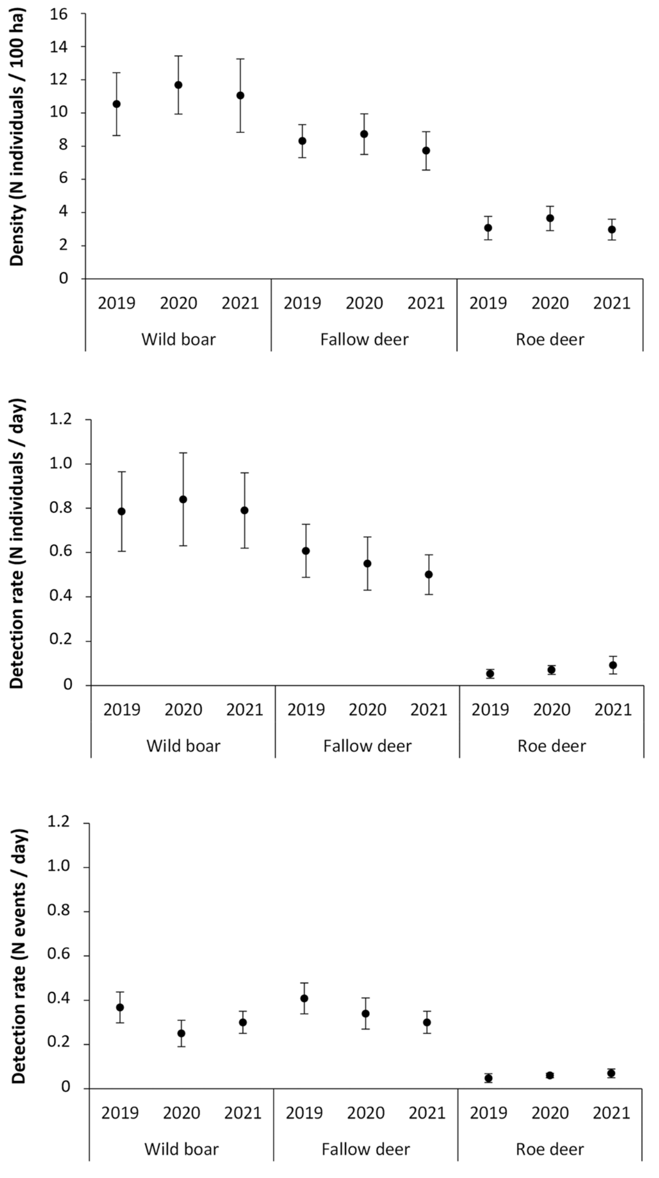

FIGURE 2 Estimates of density indices of wild boar, fallow deer, and roe deer in summer in Maremma Regional Park, Italy, 2019–2021. The top frame reports density estimates (dots) and standard errors (bars) using feces counts in sampling plots (n = 271/year). The middle frame reports relative abundance index estimated through camera surveys (n = 50–52 cameras/year) as number of individuals per day ($RAI_{individuals}$). The bottom frame reports relative abundance index estimated through camera surveys as number of events per day (RAI_{events}).

Inter-annual variations

For wild boar, the data provided no evidence for inter-annual variation in the number of feces accumulated per plot or detection rates (Table 5). For fallow deer, there was no evidence of inter-annual variation in the number of feces accumulated per plot, but density estimates were 12% lower in 2021 than in 2020 (Table 5; Figure 2). There was not a decrease in detection rates between 2020 and 2021 (Table 5). Similarly, for roe deer there was no support for inter-annual variation in the number of feces accumulated per plot or detection rates (Table 5).

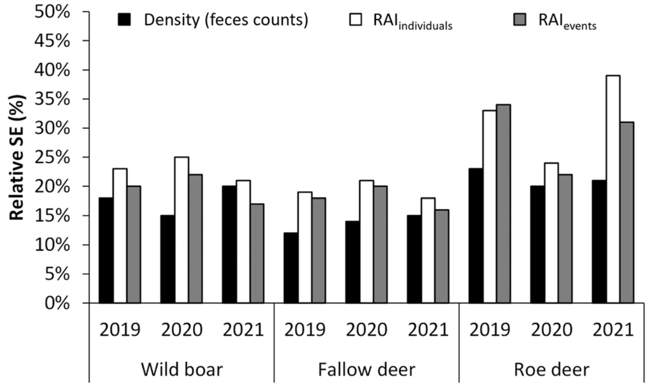

FIGURE 3 Uncertainty of density estimates and relative abundance indices of wild boar, fallow deer, and roe deer in summer in Maremma Regional Park, Italy, 2019–2021, expressed as relative standard error (%). We obtained density estimates through feces counts and relative abundance indices through camera trapping as number of individuals per day ($RAI_{individuals}$) and number of events per day (RAI_{events}).

TABLE 1 Sampling effort (total number of camera locations deployed and operational camera days) and sample size (number of detections) for remote cameras used to estimate indices of relative abundance of wild boar, fallow deer, and roe deer in Maremma Regional Park, Italy, in summers 2019–2021.

			Detections (*n*)		
Year	**Camera locations (*n*)**	**Sampling effort**	**Wild boar**	**Fallow deer**	**Roe deer**
2019	57	1,160	384	441	64
2020	60	1,072	217	376	65
2021	60	1,200	322	353	78

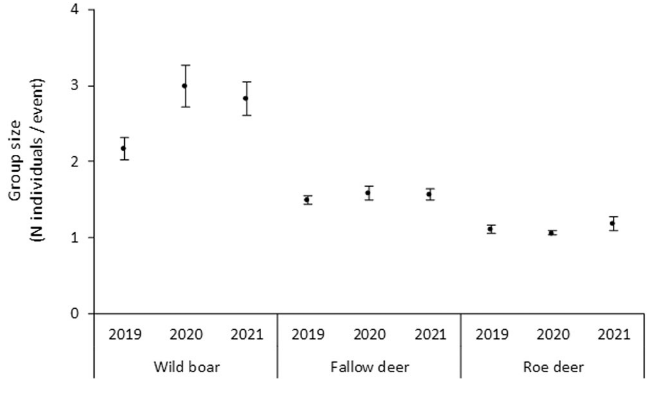

FIGURE 4 Mean group size (dots) and standard errors (bars) of wild boar, fallow deer, and roe deer estimated through camera surveys in summer in Maremma Regional Park, Italy, 2019–2021.

TABLE 2 Correlations between density estimates of wild boar, fallow deer, and roe deer obtained through feces counts in sampling plots and relative abundance indices estimated from data collected through motion-sensitive cameras in the Maremma Regional Park, Italy, in summers 2019–2021 ($RAI_{individuals}$: number of individuals per day; RAI_{events}: number of events per day).

Dataset	Correlations	*r*	*P*
Full dataset	Density vs. $RAI_{individuals}$	0.99	<0.001
	Density vs. RAI_{events}	0.82	0.007
Without cultivated fields	Density vs. $RAI_{individuals}$	0.97	<0.001
	Density vs. RAI_{events}	0.87	0.002
Without 2019	Density vs. $RAI_{individuals}$	1.00	<0.001
	Density vs. RAI_{events}	0.83	0.042
Without cultivated fields and 2019	Density vs. $RAI_{individuals}$	0.95	0.003
	Density vs. RAI_{events}	0.86	0.030

TABLE 3 Comparison between linear and logarithmic models relating ungulate density estimated through feces counts to relative abundance indices obtained from motion-sensitive cameras in the Maremma Regional Park, Italy, in summers 2019–2021 ($RAI_{individuals}$: number of individuals per day; RAI_{events}: number of events per day). We ranked models using Akaike's Information Criterion corrected for small samples (AIC_c) and present number of parameters (*K*) and difference in AIC_c from the top model (ΔAIC_c).

Response variable	Model formula	logLikelihood	*K*	AIC_c	ΔAIC_c	Weight	R^2
$RAI_{individuals}$	$RAI_{individuals}$ ~ density	17.782	3	−24.8	0.00	0.981	0.99
	$RAI_{individuals}$ ~ $\log_{10}$(density)	13.854	3	−16.9	7.86	0.019	0.97
RAI_{events}	RAI_{events} ~ $\log_{10}$(density)	12.044	3	−13.3	0.00	0.841	0.77
	RAI_{events} ~ density	10.375	3	−10.0	3.35	0.159	0.67

TABLE 4 Relationships between ungulate density estimates and relative abundance indices estimated through motion-sensitive cameras in the Maremma Regional Park, Italy, in summers 2019–2021, assessed by general linear models ($RAI_{individuals}$: number of individuals per day; RAI_{events}: number of events per day).

Response variable	Model formula	Predictor	ß	SE	95% CI	
					Lower	Upper
$RAI_{individuals}$	$RAI_{individuals}$ ~ density	Intercept	−0.223	0.032	−0.298	−0.148
		Density	0.093	0.004	0.084	0.102
RAI_{events}	RAI_{events} ~ $\log_{10}$(density)	Intercept	−0.180	0.089	−0.390	0.030
		$\log_{10}$(density)	0.509	0.104	0.263	0.755

DISCUSSION

Motion-sensitive cameras have been increasingly used in ecological research to estimate spatio-temporal patterns and interspecific interactions (Rovero and Zimmermann 2016). Although they represent promising tools in population-level studies, their use for monitoring abundance indices still requires further tests (Sollmann et al. 2013,

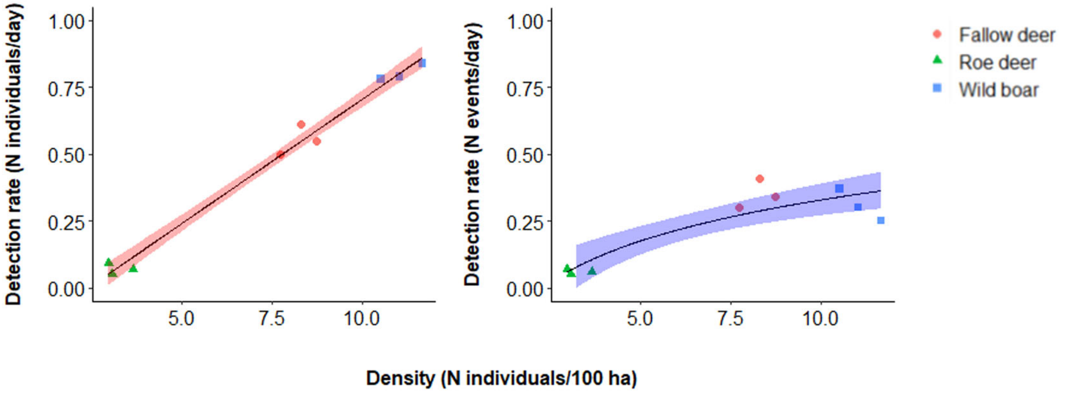

FIGURE 5 Supported relationships between indices of relative abundance of fallow deer, roe deer, and wild boar estimated through camera surveys (detection rates, $n = 50–52$ cameras/year) and feces counts (density) in summer 2019–2021 in Maremma Regional Park, Italy. Detection rates refer to number of individuals per day (left: $RAI_{individuals}$), with individuals defined as the cumulative number of individuals across all detections; and number of events per day (right: RAI_{events}), with events defined as the number of detections of the focal species at a temporal distance of ≥30 minutes. Lines represent the supported fitted relationships between detection rates and density estimates (left: linear relationship; right: logarithmic curve). Shaded areas represent 0.95 confidence intervals of relationships estimated through linear models.

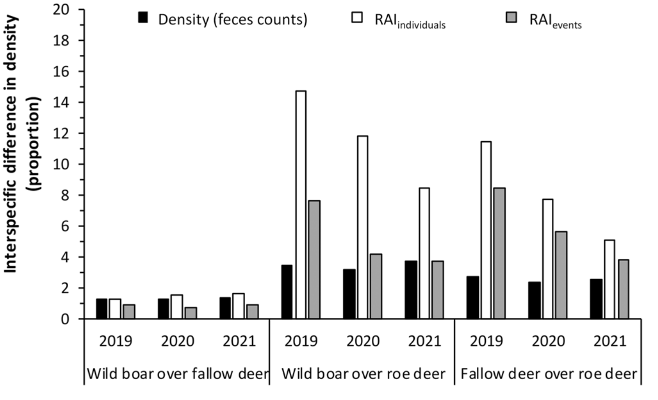

FIGURE 6 Interspecific ratios of density indices derived from feces counts and camera surveys ($RAI_{individuals}$: number of individuals per day; RAI_{events}: number of events per day) for ungulates in summer in Maremma Regional Park, Italy, 2019–2021.

Massei et al. 2018, Lijun et al. 2019, Santini et al. 2022). Camera-based indices for 3 ungulate species revealed a general positive correlation with estimates of ungulate densities, coefficient of variation values ≤25% for the 2 most abundant species (Forsyth et al. 2022), and intra-specific stability across 3 years, which was consistent with estimated variation in population densities. But the performance of estimates was not consistent between camera indices.

Although our correlations were based on a limited sample size, they suggested that the relationship between indices and population density based on fecal counts was stronger for indices based on the count of individuals across the events, which increased linearly with density estimates, than it was for indices based on the raw count of

TABLE 5 Inter-annual differences in density estimates (i.e., number of feces accumulated per plot) and detection rates ($RAI_{individuals}$: number of individuals per day; RAI_{events}: number of events per day) of wild boar, fallow deer, and roe deer in the Maremma Regional Park, Italy, in summers 2019–2021, assessed through generalized linear mixed models with negative binomial errors.

Species	Indicator	Predictor	ß	SE	95% CI Lower	95% CI Upper
Wild boar	Density	Intercept	−5.991	0.211	−6.404	−5.579
		Year [2020]	0.097	0.186	−0.268	0.462
		Year [2021]	−0.008	0.191	−0.382	0.366
	$RAI_{individuals}$	Intercept	−0.974	0.247	−1.458	−0.490
		Year [2020]	−0.085	0.231	−0.537	0.367
		Year [2021]	0.082	0.238	−0.384	0.548
	RAI_{events}	Intercept	−1.643	0.284	−2.200	−1.087
		Year [2020]	−0.325	0.247	−0.809	0.160
		Year [2021]	−0.008	0.227	−0.453	0.438
Fallow deer	Density	Intercept	−5.185	0.167	−5.512	−4.858
		Year [2020]	0.042	0.112	−0.176	0.261
		Year [2021]	−0.084	0.115	−0.310	0.142
	$RAI_{individuals}$	Intercept	−1.132	0.402	−1.920	−0.343
		Year [2020]	−0.215	0.323	−0.847	0.417
		Year [2021]	−0.257	0.312	−0.869	0.355
	RAI_{events}	Intercept	−1.518	0.334	−2.173	−0.863
		Year [2020]	−0.224	0.255	−0.723	0.275
		Year [2021]	−0.272	0.248	−0.758	0.215
Roe deer	Density	Intercept	−6.750	0.315	−7.367	−6.133
		Year [2020]	0.176	0.201	−0.218	0.570
		Year [2021]	−0.047	0.213	−0.465	0.371
	$RAI_{individuals}$	Intercept	−3.594	0.347	−4.274	−2.914
		Year [2020]	0.445	0.369	−0.278	1.168
		Year [2021]	0.534	0.370	−0.191	1.258
	RAI_{events}	Intercept	−3.689	0.337	−4.349	−3.030
		Year [2020]	0.495	0.357	−0.204	1.194
		Year [2021]	0.566	0.357	−0.135	1.266

events. Thus, $RAI_{individuals}$ efficiently detected the ranking of densities across study species over a 3-year period. Conversely, indices based on the count of events (detections) increased nonlinearly with population density. Despite their correlation with density estimates, RAI_{events} did not track the inter-specific ranking of densities. Wild boar density estimates were 1.27–1.43 greater than those of fallow deer, depending on the year; however, while this ratio was consistent with that observed for $RAI_{individuals}$ (1.29–1.58), wild boar RAI_{events} were 0.74–1.0 times those of fallow deer. The raw count of events per day does not consider the number of individuals detected, which is expected to underestimate the relative abundance of the most gregarious species (i.e., wild boar). We observed similar issues for inter-annual comparisons of wild boar densities and RAIs. Although density and RAI estimates showed only a mild variation across years, RAI_{events} showed an opposite trend in respect to both density estimates and $RAI_{individuals}$ which were consistent with inter-annual variation of wild boar group size. Our results indicate that ignoring group size would have led to an incorrect ranking of inter-specific densities, and an opposite estimate of intraspecific variations of wild boar densities.

Indices based on the count of individuals in groups performed better than indices based on the raw count of events (i.e., the most commonly used RAI indices). The divergence between camera indices increased from the most solitary species (roe deer) to the most gregarious one (wild boar), with $RAI_{individuals}$ being 1.1–1.2 larger than RAI_{events} for the former and 2.1–3.4 larger for the latter. These results support findings obtained on non-gregarious mammals, for which RAI estimates based on the count of events correlated with density estimates (Rovero and Marshall 2009, for forest-dwelling ungulates).

Although results were encouraging for the 2 most abundant ungulate species in our study area, wild boar and fallow deer, findings were less satisfactory for roe deer. While estimates of roe deer densities were 2.4–3.7 times smaller than those of fallow deer and wild boar, their RAI estimates were 3.7–14.8 times smaller than those of the other 2 ungulates. Movements and ranging patterns are expected to influence detectability, thus affecting detection rates (Rowcliffe et al. 2008, Nakashima et al. 2018, Rogan et al. 2019, Santini et al. 2022). Roe deer have smaller home ranges than fallow deer and wild boar; mean local seasonal home range size is roughly 40 ha for roe deer (Börger et al. 2006) and 100–350 ha for wild boar in our study area (Massei et al. 1997) and 125–380 ha for fallow deer in an ecologically similar Mediterranean coastal area (Ciuti et al. 2003). Additionally, in our study site, roe deer reached lower densities than the other 2 ungulates (Ferretti and Fattorini 2021, this study) and showed a median group size of 1 individual in summer, with a maximum 3 individuals per group (Fattorini and Ferretti 2019). Lower mobility and densities, together with smaller group size, would be expected to reduce detectability (Sollmann et al. 2011), which may explain our roe deer results.

Uncertainty of RAI estimates were generally higher than that obtained through feces counts and was consistently lower for fallow deer and wild boar than for roe deer. Coefficients of variation were 12–23% for feces counts, whereas they were 18–25% (wild boar and fallow deer) and 24–39% (roe deer) for $RAI_{individuals}$. For wild boar and fallow deer, uncertainty was below the 25% threshold commonly considered useful for management and research (Skalski et al 2005, Forsyth et al. 2022) and consistent with (or better than) results obtained through other methods to estimate densities of deer (Forsyth et al. 2022) and wild boar (capture-mark-recapture: 11–20%, Franzetti et al. 2012; distance sampling: 10–60%, Franzetti et al. 2012, Focardi et al. 2020; cameras without individual recognition: 20–30%, Massei et al. 2018; cameras with individual recognition: 11–37%, Peris et al. 2019). Thus, our estimates achieved using $RAI_{individuals}$ reached adequate levels of precision to monitoring population of wild boar and fallow deer.

More efforts and longer-term studies encompassing a greater variability in values of population density are necessary to test the potential for camera-based indices to track population changes across years at the intra-specific level. Only slight inter-annual differences in ungulate densities occurred during our study period, which prevented testing the sensitivity of RAIs to variations in population densities, but the inter-annual stability of $RAI_{individuals}$ was generally consistent with that observed for estimates of population densities. The low density and the small number of detections, and the ensuing increase in uncertainty of estimates, did not allow a proper evaluation for roe deer, but results for wild boar and fallow deer were promising. Despite minimal differences between study years (feces counts: 5–11%; $RAI_{individuals}$: 7–9%), wild boar feces counts and $RAI_{individuals}$ had the same inter-annual variation. For fallow deer, $RAI_{individuals}$ had a steady decrease across years (9% in 2020 and 15% in 2021), whereas feces counts were substantially comparable between 2019 and 2020, decreasing by 12% in 2021, albeit with overlapping confidence intervals.

MANAGEMENT IMPLICATIONS

Our results highlight the necessity of field tests based on comparison with locally reliable reference methods to validate the use of indices derived from motion-sensitive camera data. Indices of relative abundance derived from cameras are a promising alternative to other indices to monitor ungulate populations. We recommend that such indices should be based on the count of individuals, particularly for gregarious species. Thus, videos with an adequate length (e.g., 30 sec, or even shorter if there is no lag between consecutive videos) would be better suited than pictures to adequately assess the minimum number of individuals within a group, although videos would require a greater effort to analyze than pictures. Therefore, RAI estimates should be adjusted by group size to reliably track population trends of wild ungulates for management.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ETHICS STATEMENT

This study adhered to regulations of Italy and was conducted within the framework of a research agreement between the University of Siena–Department of Life Sciences–and the Maremma Regional Park Agency (resolution n. 12, 15 March 2019, Maremma Regional Park Agency Board of Directors).

DATA AVAILABILITY STATEMENT

The data analyzed during the current study have been collected under an agreement between the Maremma Regional Park Agency and the Institution of the corresponding author (Department of Life Sciences, University of Siena) and are available from the corresponding author on reasonable request and upon permission of the above mentioned parties.

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