

A comparison of capture-mark-recapture and camera-based mark-resight to estimate abundance of Alpine marmot (*Marmota marmota*)

Authors: Forti, Alessandro, Partel, Piergiovanni, Orsingher, Michel J., Volcan, Gilberto, Dorigatti, Enrico, et al.

Source: Journal of Vertebrate Biology, 71(22023)

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: <https://doi.org/10.25225/jvb.22023>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

A comparison of capture-mark-recapture and camera-based mark-resight to estimate abundance of Alpine marmot (*Marmota marmota*)

Alessandro FORTI^{1*}, Piergiorgio PARTEL¹, Michel J. ORSINGHER¹, Gilberto VOLCAN¹,
Enrico DORIGATTI¹, Luca PEDROTTI^{2,3} and Luca CORLATTI^{2,4}

¹ Ente Parco Naturale Paneveggio-Pale di San Martino, Villa Welsperg, Primiero San Martino di Castrozza (TN), Italy; e-mail: alessandro.forti90@gmail.com, piergiorgio.partel@parcopan.org, veterinario.orsingher@gmail.com, gilberto.volcan@parcopan.org, enrico.dorigatti@parcopan.org

² Stelvio National Park – Ersaf Lombardia, Bormio, SO, Italy; e-mail: luca.pedrotti@stelviopark.it, luca.corlatti@ersaf.lombardia.it

³ Sustainable Development and Protected Area Service, Stelvio National Park Office, Autonomus Province of Trento, Cogolo di Peio, TN, Italy

⁴ Chair of Wildlife Ecology and Management, University of Freiburg, Freiburg, Germany; e-mail: luca.corlatti@wildlife.uni-freiburg.de

► Received 7 April 2022; Accepted 16 June 2022; Published online 19 August 2022

Abstract. Obtaining reliable estimates of population abundance is of utmost importance for wildlife research and management. To this aim, camera-traps are increasingly used, as this method has the advantage of being non-invasive and allows for continuous monitoring. Camera traps can be used to estimate abundance in combination with traditional capture-recapture techniques, as well as with estimators that do not require marked individuals. Here, we investigated the use of camera-based mark-recapture methods applied to an Alpine marmot (*Marmota marmota*) population in the Paneveggio-Pale di San Martino Natural Park (eastern Italian Alps). We compared abundance estimates derived from a traditional capture-mark-recapture (CMR) framework and camera trap mark-resight (CTMR) over three consecutive years. CMR models estimated a population size of $n = 19$ individuals (95% CI = 18–27), $n = 15$ (14–22) and $n = 24$ (22–32) in 2019, 2020 and 2021 respectively. CTMR returned an estimated population size of $n = 24$ (95% CI = 18–30), $n = 20$ (17–24) and $n = 22$ (21–24) for the same years. The difference between the estimate of these two methods was significant only in 2020, with CMR returning a lower estimate than CTMR (95% CI = –9.4–0.6). This difference was not significant for 2019 (95% CI = –10.9–0.9) and 2021 (95% CI = –1.8–5.9). Based on our results, the use of CTMR techniques is promising in the estimation of absolute population size of marmots, and the estimator was slightly more precise than CMR. Further studies are needed to evaluate the effectiveness of CTMR with reduced capture effort.

Key words: Bowden estimator, camera traps, *Marmota*, population size

Obtaining reliable estimates of population abundance is a key issue in wildlife ecology and management (Fryxell et al. 2014). In mountainous

areas this task is particularly challenging, as poor accessibility and visibility tend to reduce detectability, thus limiting the possibility to meet

* Corresponding Author



some basic assumptions underlying different estimation methods (Singh & Milner-Gulland 2011).

Several estimators have been developed to account for imperfect detection probability and obtain absolute population size, either based on marked (e.g. capture-mark-recapture CMR: Otis et al. 1978, mark-resight MR: Schwarz & Seber 1999) or unmarked individuals (e.g. distance sampling DS: Buckland et al. 2001). Capture-recapture methods are commonly used in population ecology (Williams et al. 2002) but the fulfilment of the underlying assumptions could be problematic in some cases, for example due to adverse environmental conditions and animal behaviour, which can generate heterogeneity in capture probabilities, potentially biasing CMR estimators (see Williams et al. 2002 for a review on model assumptions, how to test them and the effects of their violation). In their basic form, closed capture-recapture models have three basic assumptions (Williams et al. 2002, Royle & Converse 2020): 1) the population is closed (both geographically and demographically) over the course of the investigation; 2) marks are not lost, overlooked, or misread; 3) each sample of individuals is a random sample of the population of interest (i.e. all animals are equally likely to be captured in each sample). Additionally, CMR costs may not be sustainable in the long-run or over large scales, and when a species lacks natural markings (e.g. colour pattern), tracing individual encounter history may be challenging. In the attempt to minimize the possible effects on wildlife welfare due to repeated human handling (McMahon et al. 2005), DNA-based CMR techniques can be used (Mowat et al. 2005), but their cost may be significant. To save time and costs related to captures, in recent years researchers have developed alternative estimators that do not rely on physical or genetic capture (McClintock et al. 2013, Rovero & Zimmermann 2016).

Camera trapping (CT) is one of the most widely used passive methods to survey wildlife populations (Rovero & Zimmerman 2016) and it has greatly expanded research frontiers in the study of mammals (Rowcliffe 2017). Several approaches based on camera-trap data were developed for both unmarked (Gilbert et al. 2020, Palencia et al. 2021) and marked animals, either with natural marks such as individually-distinct fur patterns (Jackson et al. 2006, Karanth et al. 2006, Zimmermann et

al. 2013) or with artificial marks (Parsons et al. 2015, Taylor et al. 2021). In recent years, wildlife ecologists have increasingly used mark-recapture methods combined with photographic records, in several taxa such as sharks (Holmberg et al. 2008), vultures (Santangeli et al. 2020), marine mammals (Mackey et al. 2008), rhinos (Hariyadi et al. 2011) and felids (Karanth et al. 2006, Zimmermann et al. 2013).

Mark-resight (MR) methods are slightly different from traditional CMR, in that animals are resighted rather than recaptured after their initial marking (Schwarz & Seber 1999), hence unmarked animals are not marked on subsequent occasions, which does not allow use of the classic CMR estimators for closed populations for multiple occasions (White & Schenk 2001). In their basic form, both methods share the basic assumption that during surveys marks should be correctly recognized (i.e. all marked animals must be correctly identified, counted and recorded) and no marks are lost. Populations must be closed and all animals (both marked and unmarked) must have the same independent probability of being captured/resighted. In addition, standard mark-resight models require knowing the exact number of marked individuals in the population (Neal et al. 1993, McClintock et al. 2009). In recent years, photographic mark-recapture from CT is increasingly used to estimate wildlife population abundance (Karanth et al. 2006, Alonso et al. 2015). Its application requires that individuals exhibit stable marks (natural or artificial) during the study period. If so, CT can be combined with MR (hereafter CTMR) to estimate population size, as sightings of marked and unmarked animals can be collected from image inspection. CTMR is increasingly used for estimating abundance of several species, in particular rare and elusive carnivores. This method is frequently combined with physical capture (Alonso et al. 2015, Doran-Myers et al. 2021) or hair snags (Alldredge et al. 2019). However, further research is needed to fully assess the accuracy and limitations of the method and a comparison of the estimates obtained with other methods is needed (Doran-Myers et al. 2021). All the previous studies agree that mark-resight could be a viable option to assess population size (Rivero et al. 2022).

The Alpine marmot (*Marmota marmota*) is a semifossorial diurnal and highly social rodent of small-medium size (Armitage 2014) inhabiting



high-altitude open areas of the Southern and Central European massifs (Cassola 2016). Alpine marmot represents a key species for Alpine ecosystems because it is a selective feeder (Bassano et al. 1996) and it contributes by modifying the floristic structure and composition of alpine meadows, therefore helping to maintain biodiversity (Semenov et al. 2003). Furthermore, as a prey species of golden eagle (*Aquila chrysaetos*) (Pedrini & Sergio 2001) and red fox (*Vulpes vulpes*) (Borgo et al. 2009), it could reduce the predation pressure on more endangered species such as black grouse (*Lyrurus tetrix*), rock ptarmigan (*Lagopus muta*) (Figueroa et al. 2009) and Alpine mountain hare (*Lepus timidus*). Estimating the abundance of marmot populations is necessary to implement management measures aimed at its conservation, also in view of possible threats like decrease in survival (Tafari et al. 2013, Rézouki et al. 2016), changes in habitat conditions (e.g. for treeline advance (Hansson et al. 2021)) and global warming (Armitage 2013).

Despite Alpine marmot ecology being well investigated, the choice of methods of abundance estimation is challenging. Recently, different methods to estimate marmot population size have been used, including point transect distance sampling (Pelliccioli & Ferrari 2013), capture-mark-recapture, mark-resight, line transect distance sampling, double-observer (Corlatti et al. 2017) and camera trap distance sampling (Corlatti et al. 2020). The main difficulty when estimating marmot population abundance is owing to their semifossorial behaviour. At any given point in time, some animals are inside their burrows while others are outside, hence individuals that are out of the burrows will represent only a proportion of the total population. In turn, this brings issues of temporary unavailability, which may lead to issues of abundance underestimation, when methods that do not account for this bias are used (Corlatti et al. 2017, 2020).

In this study we tested the relative performance of CTMR on a population of Alpine marmot. Specifically, our aim is to compare the marmot population abundance estimates obtained with CTMR with those obtained with CMR. We expect that if the basic assumptions are met, CMR and CTMR should return similar point estimates, although the CTMR estimator should be more precise than CMR, owing to a greater number of resighting events than of physical captures: in fact,

Corlatti et al. (2017) in a similar study on Alpine marmot, highlighted how (visual) MR was more precise than CMR.

The study was carried out in the Paneveggio-Pale di San Martino Natural Park (Trentino, eastern Italian Alps (Fig. 1a)), at about 1,900 m a.s.l. (Fig. 1b). The study area extends over 26 ha, and consists of subalpine meadows. The climate is characterized by harsh winters and mild summers. We defined the borders of the study site by using natural boundaries (i.e. cliffs and wooded areas) in an attempt to include the entire Alpine marmot group home ranges and avoid movements outside and inside the area, to ensure geographic closure. Each year, we followed six marmot groups at the same time and the minimum average family group size (mean \pm SE) was 3 ± 0.4 , 2.2 ± 0.3 and 3.7 ± 0.5 in 2019, 2020 and 2021 respectively.

The study was conducted between May and June of 2019, 2020 and 2021, soon after the marmots emerged from their burrows following hibernation. Each year, marmots were captured using 28 tomahawk live traps (Tomahawk Live Traps, Hazelhurst, WI, USA) distributed near the marmot burrows. Animals were attracted using dandelion flowers (*Tarassacum officinalis*) as bait. Each year, in May, seven consecutive occasions of CMR through live-trapping were conducted, one per day. These secondary occasions were spread over two weeks at most, if environmental (i.e. rainy days with low availability) or anthropogenic constraints (i.e. days with high touristic disturbance) did not allow to conduct seven secondary occasions in a row. We kept a constant catching effort throughout the closed sampling session during the three years of sampling. Each trap was located near a marmot burrow (Fig. 1c) to maximize capture success (cf. Corlatti et al. 2020). After each capture event, traps were re-baited and kept open from sunrise to sunset. To reduce disturbance and avoid injuries to marmots, traps were checked continuously from a vantage point with a spotting scope. Upon capture, all marmots were marked with a Tracer Bayer transponder and two coloured ear-tags. The marmots were handled without using sedatives. For each individual, we build a capture history (1/0) depending on the occurrence of capture-recapture events during each secondary occasion. Captures were always performed with the assistance of a veterinarian and followed the procedures contained in the application form for capture authorisation.

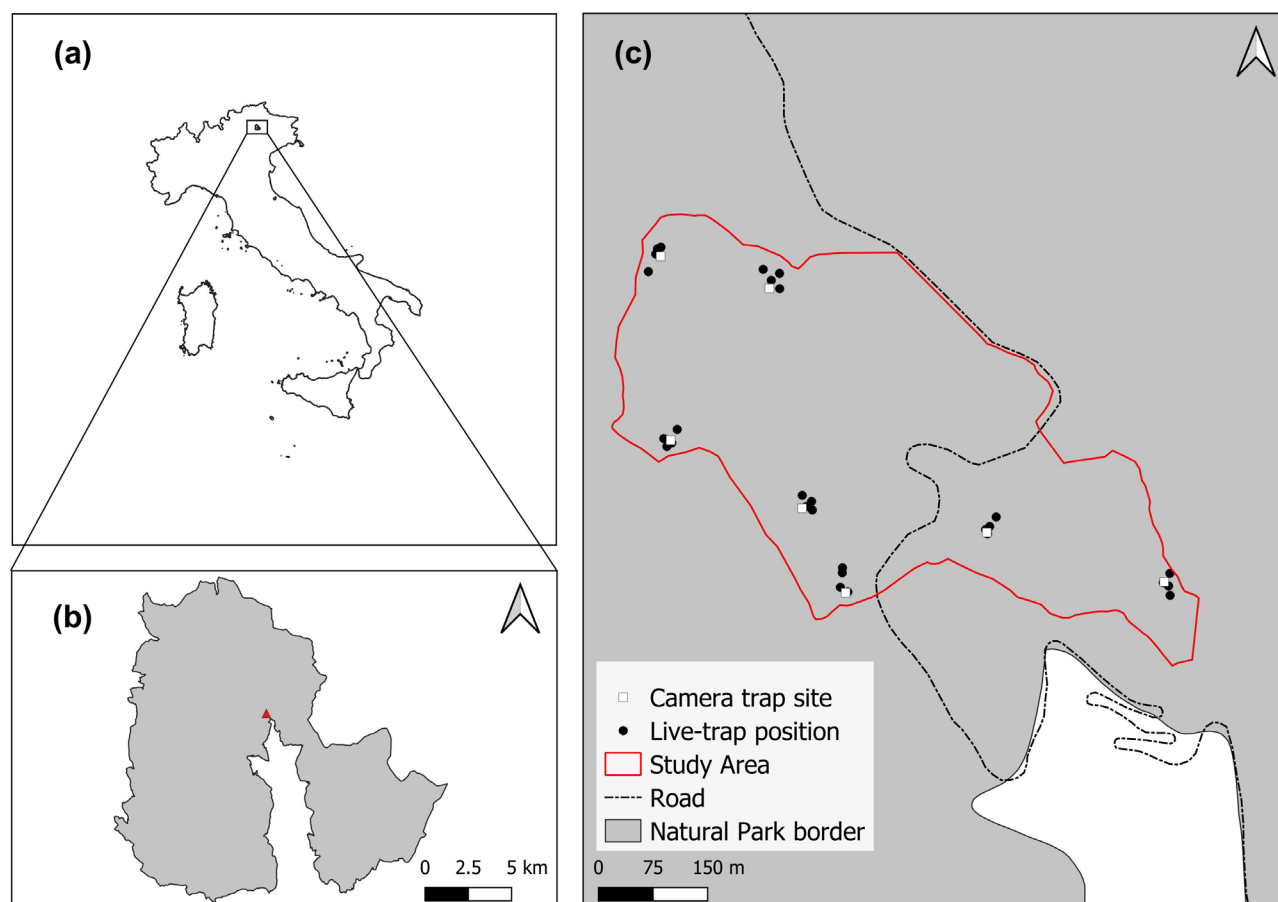


Fig. 1. (a) Location of the Paneveggio-Pale di San Martino Natural Park, located in the eastern Italian Alps; (b) the red triangle indicates the location of the study area into the Natural Park borders; (c) border of the study area (red line), live-traps (black dots) and camera trap (white squares) locations; the latter also represents the position of family group burrows and their distributions. We used Quantum GIS version 3.10.12 (QGIS Development Team 2021) graphics program to create this figure.

Based on the number of marked individuals, the sample population available for CMR analysis was assumed to be small (Table 1). When the population and sample sizes are small, the models based on multiple capture occasions (e.g. Otis et al. 1978) perform poorly and it is more appropriate to use a Lincoln-Petersen estimator by pooling data from multiple periods into two periods (Menkens

& Anderson 1988). Thus, for each year the seven sampling occasions were pooled on only two occasions (four + three, respectively). Therefore our capture-recapture design included two secondary sampling occasions within three primary occasions (year). The Alpine marmot population was expected to be open (i.e. with gains and losses) between these primary periods and assumed to

Table 1. Summary of results obtained from analysing data collected in three years of the Alpine marmot research program in Paneveggio-Pale di San Martino Natural Park, from 2019 to 2021. The table reports the total capture events (i.e. captures plus recaptures), the maximum number of different marmots caught each year (MNC), abundance estimates (n), with 95% confidence interval (CI) and coefficients of variation (CV) for both CMR and CTMR methods. Also reported for CTMR are: the known number of different individuals available for MR estimates within the study area (Available); the number of images of unmarked marmots (Unmarked observed) and the number of images recorded for Alpine marmots that were marked but not individually recognized (Marked unknown).

Year	Total capture events	CMR				CTMR					
		MNC	n	CI	CV (%)	Available	Unmarked observed	Marked unknown	n	CI	CV (%)
2019	62	18	19	18-27	8.80	18	935	237	24	18-30	11
2020	33	14	15	14-22	9.80	19	25	214	20	17-24	9.8
2021	68	22	24	22-32	8.10	22	104	441	22	21-24	2.4



be closed geographically (no movement in or off the study area) and demographically (no births or deaths) within secondary periods. To estimate marmot population size for all primary periods, we implemented the Lincoln-Petersen estimator in a robust-design fashion (Pollock 1982), using the package RMark (Laake 2013), an interface to program Mark (White & Burnham 1999), with R (R Core Team 2020) in RStudio (R Studio Team 2020).

After captures, one occasion of mark-resight (obtained by pooling six consecutive days of observations) with camera traps was conducted. A total of seven camera traps ($n = 5$ ScoutGuard SG-2060-X model and $n = 2$ Cuddeback C 123 model) were deployed in front of the family burrows (Fig. 1c). Each camera trap was mounted at a height of about 50 cm on a pole; this limited the possibility that marmots could pass beneath the camera passive infrared (PIR) or outside the detection zone. Cameras were set to take consecutive pictures, without delay. All images were processed using the open-access software Wild.ID (Fegraus & MacCarthy 2016) to distinguish between blank and non-blank images containing marmots or other species. The total number of “marked known”, “marked unknown” and “unmarked” individuals detected during the mark-resight occasion was noted down. Some animals were too far from the camera and too difficult to identify correctly and were classified as “unknown”, and equally redistributed between unmarked and marked unknown. Because the CTMR started soon after the end of CMR, the number of marked individuals available for resighting was assumed to be $n = 18, 19$ and 22 for 2019, 2020 and 2021 respectively (Table 1). For 2020, we added five available individuals to those captured in the same year (i.e. five marmots known and marked in 2019) because observed during captures. We are aware that this may bias the MR estimator. However, the small size of this study population should minimize this bias. Mark-resight estimates were obtained with the Bowden’s estimator through a user-defined function built in R (scripts are provided in Data S1 and Data S2) following Bowden & Kufeld (1995). In a closed population when the number of marked individuals is known there are several estimators available for assessing abundance, such as Bowden’s estimator, hypergeometric maximum likelihood estimator (Bartmann et al. 1987) and Minta-Mangel estimator (Minta & Mangel 1989). Bowden’s estimator assumes that (I) the total number of resightings for each animal constitutes a set of fixed values and (II) the animals

to be marked are selected from the population by means of simple random sampling without replacement. This latter assumption, however, can be relaxed as long as the marked individuals are proportionally distributed in groups (Fattorini et al. 2007). In this study we chose to use Bowden’s estimator because it relaxes several assumptions of MR (see above). Furthermore, it allows for heterogeneity in the probability of resightings; it does not assume independence among sighting trials and it allows for the inclusion of unidentified marked individuals in the estimate (Bowden & Kufeld 1995). Finally, Bowden’s estimator is used because of its computational ease and the possibility to obtain reliable estimates (Bowden & Kufeld 1995, Diefenbach 2009, Weckerly & Foster 2010). In accordance to Diefenbach (2009), who applied Bowden’s estimator to the uniquely marked birds that could be resighted multiple times during a single survey, we argue that the same method can be suitable to Alpine marmots resighted by camera traps.

To investigate whether there was any difference between estimates of CMR and CTMR within each year, we used a t-test (with alpha level = 0.05) applying the formula suggested by Schenker & Gentleman (2001): $(\overline{CMR} - \overline{CTMR}) \pm 1.96 \times \sqrt{SE_{CMR}^2 + SE_{CTMR}^2}$. Lastly, to investigate the precision of two abundance estimators we inspected their coefficients of variation (CV).

In the three years of survey, during capture-mark-recapture, 31 different marmots were captured and individually marked, for a total of 163 capture events (Table 1). The CMR model returned an abundance estimation for primary occasions of $n = 19$ with CV = 8.80% (95% CI = 18-27) individuals in 2019, $n = 15$ with CV = 9.8% (95% CI = 14-22) in 2020 and $n = 24$ with CV = 8.1% (95% CI = 22-32) in 2021.

Considering the three years together, we were able to identify 87% of the marked marmots in images based on combinations of coloured ear tags. During CTMR, in 2019 we observed 2,736 marked individuals, 2,499 identified and 237 not identified, 935 unmarked and zero unknown. In 2020 we observed 389 marked individuals, of which 175 identified and 214 not identified, 25 unmarked and zero unknown. Finally, in 2021, 4,838 marked individuals were observed, 4,483 identified and 355 not identified, 18 unmarked and 172 unknown. Table 1 shows how unknown individuals were redistributed. Bowden’s estimator returned an

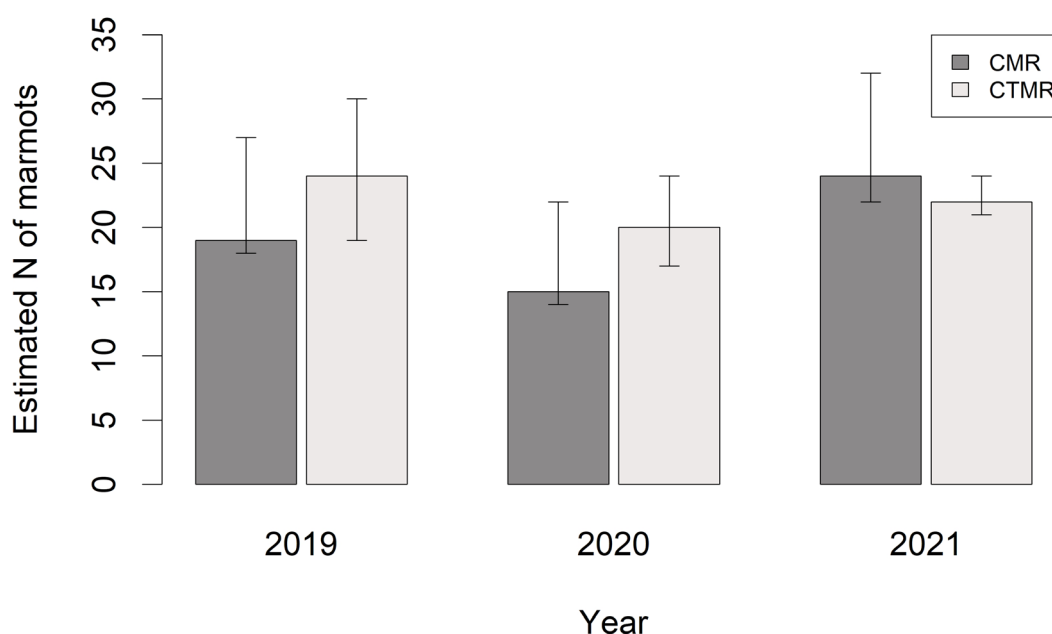


Fig. 2. Abundance estimates of the marmot populations in the study site obtained using two different sampling methods: capture-mark-recapture (CMR) and camera traps mark-resight (CTMR). Gray filled boxes represent the marmot abundance estimate with robust design estimator, the light gray filled boxes represent the marmot abundance estimate with Bowden's estimator. Vertical lines represents 95% confidence interval.

estimate of $n = 24$ with $CV = 11\%$ ($95\% CI = 18-30$) for 2019, $n = 20$ with $CV = 9.8\%$ ($95\% CI = 17-24$) for 2020 and $n = 22$ with $CV = 2.4\%$ ($95\% CI = 21-24$) Alpine marmots for 2021 (Table 1 and Fig. 2).

As expected, the estimates of marmot abundance obtained with CMR and CTMR were fairly similar within each year. The difference between CMR estimate and CTMR estimate were not significant for 2019 ($95\% CI = -10.9-0.9$) and 2021 ($95\% CI = -1.8-5.9$). However, this difference was significant in 2020, with CMR returning a lower estimate than CTMR ($95\% CI = -9.4--0.6$). From inspection of CVs, the CTMR estimator was slightly more precise than CMR only in 2021.

In 2019 and 2021, when the marmots emerged from the burrows, the harsh environmental conditions (i.e. heavy snow cover and reduced natural forage availability) increased live trapping rates. Conversely, in 2020 the spring season conditions (www.meteotrentino.it) and greater availability of food resulted in a reduction in trap efficiency (cf. Pawlina & Proulx 1999 for an overview). Consequently, total capture events in 2020 nearly halved compared to 2019 and 2021 (Table 1); this, in turn, likely made the 2020 CMR estimates questionable. It should be noted, however, that the formula used to calculate the t-score relies on symmetrical intervals, and that Fig. 2 does not suggest major differences between methods in all years.

In the absence of knowledge of the “true” population size, it is difficult to compare the results of different estimation methods. This is even more problematic with small sample sizes, which make the estimation of capture probability challenging (cf. Hammond & Anthony 2006). The reliability of abundance estimators depends on the possibility of satisfying the underlying assumptions. We accepted the assumption of demographic closure of the population because CMR and CTMR were conducted in a short time frame, before pups were born, thus immigration or losses (via death and emigration) could be assumed negligible. However, it cannot be excluded with certainty that some emigration events may have occurred between the CMR and CTMR sessions. A marmot upon reaching sexual maturity must choose between becoming a helper within a family group or disperse shortly after hibernation (Stephens et al. 2002). In our case, no individual was ever observed to disperse or was trapped as a floater. According to Keiter et al. (2017) the scale at which an animal moves (i.e. its home range) may affect abundance estimates through changes in the availability of an animal to be sampled. A marmot family group home range is between 0.9 and 2.8 ha (Perrin et al. 1993) and could be both fully or only partially included within the area effectively sampled. We argue that the assumption of geographic closure was correct for several reasons. First, our live traps were located at relatively large distances one



from one another (mean 396.4 m, range 130–823, SD 188.3). Additionally, the closest known family groups outside the study area are located farther than these distances. Moreover, capture-recapture of individuals from one live-trap group to another group did not occur. Predation episodes by golden eagles, the main avian predator in this area (Pedrini & Sergio 2001), and red foxes could be assumed negligible over such a short timeframe. In addition, the assumption of permanence and correct identification of marks was clearly valid. In the event that a marmot lost the coloured ear-tags, during CMR correct identification and the reapplication of ear-tags was possible thanks to the use of Tracer Bayer transponders.

Mark-resight models assume there is no loss or misidentification of marks (Bowden & Kufeld 1995). In our study, only one investigator classified all camera trap photos. We were not able to individually identify a few individuals by camera trap; in case of uncertainty Bowden's estimator still allowed for the inclusion of unidentified marked individuals in the estimate. Bowden's estimator provides high precision when the population investigated is not small or otherwise when a large percentage of the population is marked (Diefenbach 2009, Weckerly & Foster 2010). In our case, despite a small population, we marked almost all the marmots. Furthermore, according to Fattorini et al. (2007), one pivotal assumption of Bowden's estimator is that marks must be fairly evenly distributed among groups. A Spearman's rank correlation test was performed between group size (i.e. the number of marmots present in each picture) and the number of marked individuals within each group. We obtained a significant and positive correlation for all years: $\rho = 0.53$ ($P < 0.001$) in 2019, $\rho = 0.72$ ($P < 0.001$) in 2020 and $\rho = 0.94$ ($P < 0.001$) in 2021. This finding supports the assumptions.

According to Kendall (1999) the marmot's semifossorial behaviour generates a sort of temporary emigration (for an overview of this process see Kendall et al. 1997). Under a scenario of "completely random emigration" (Kendall et al. 1997), the time spent by marmots inside their burrows is equivalent to the time spent in an area not exposed to sampling efforts. This may bias estimators when the study period (for physical captures or resightings) is shorter than the time

animals spend inside their burrows, making some animals unavailable for capture. Following Corlatti et al. (2020), we considered this movement (inside and outside burrows) as random: during each primary period, capture occasions were conducted over a long enough period (roughly two weeks) so that all marmots would have a chance to be captured. Consequently, methods based on capture-recapture or resighting should be robust to this temporary unavailability (cf. Kendall et al. 1997, Kendall 1999) and the estimated closed "superpopulation" should reflect the true number of marmots present each year, inside and outside of the burrows.

Finally, our results agree with those of Corlatti et al. (2017) and, despite a different study area extent, we found a similar marmot density. In Corlatti et al. (2017, 2020) the MR estimator was more precise than CMR, while in our study we found very similar precision. Overall, our results support the claim that the (CT)MR approach could represent a reliable alternative for estimating Alpine marmot populations. Nevertheless, estimating the population size of Alpine marmot remains a challenging issue. We argue that CTMR estimates may be closer to the "true" number of animals present each year, because the low number of marmots caught in 2020 might have biased the CMR estimator. While the CMR method answers important ecological questions across long-term studies (Clutton-Brock & Sheldon 2010), it can be costly and may not always be sustainable over long periods. The (CT)MR approach also requires a sample of marmots to be individually marked. To make CTMR more sustainable than traditional CMR, future studies should investigate the extent to which the capture effort may be reduced, while ensuring robustness of CTMR. The small sample size of our study did not allow us to simulate the effects of a reduction in capture effort, and thus to evaluate if CTMR may be a less expensive and time-saving method than CMR, except for the time spent in classifying images (Yu et al. 2013). When only a subset of the animals photographed are uniquely identifiable from marks (i.e. where unidentified individuals are also present), as in this study, spatial mark-resight models (Chandler & Royle 2013, Sollmann et al. 2013, Bengsen et al. 2022) may be employed to estimate abundance. We encourage investigation of this method with Alpine marmots in future research.



Acknowledgements

We are grateful to Filippo Zibordi for sharing his experience in catching marmots. We thank Maurizio Salvadori and Silvia Sartore for their help during captures. We also thank Vittorio Ducoli (Director of Paneveggio-Pale di San Martino Natural Park) for the support given to this research. We are grateful to the Forest and Wildlife Service (Autonomous Province of Trento) for authorization to capture. We would also like to thank Pierre Dupont and one anonymous reviewer for their helpful comments on a previous version of the manuscript. This work was funded by Paneveggio Pale di San Martino Natural Park.

Author Contributions

L. Corlatti conceived the study. A. Forti, M.J. Orsingher, E. Dorigatti, G. Volcan and P. Partel collected data. L. Corlatti and A. Forti performed data analysis. P. Partel and L. Pedrotti administered the project. A. Forti and L. Corlatti wrote the first version of the manuscript and all authors contributed to the final draft. The authors declare no conflicts of interest.

Data Availability Statement

All required data/information is provided in the manuscript and related supplementary materials.



Literature

- Allredge M.W., Blecha T. & Lewis J.H. 2019: Less invasive monitoring of cougars in Colorado's front range. *Wildl. Soc. Bull.* 43: 222–230.
- Alonso R.S., McClintock B.T., Lyren L.M. et al. 2015: Mark-recapture and mark-resight methods for estimating abundance with remote cameras: a carnivore case study. *PLOS ONE*: 10: e0123032.
- Armitage K.B. 2013: Climate change and the conservation of marmots. *Nat. Sci.* 5: 36–43.
- Armitage K.B. 2014: Marmot biology: sociality, individual fitness and population dynamics. *Cambridge University Press, Cambridge, UK*.
- Bartmann R.M., White G.C., Carpenter L.H. & Garrott R.A. 1987: Aerial mark-recapture estimates of confined mule deer in pinyon-juniper woodland. *J. Wild. Manag.* 51: 41–46.
- Bassano B., Peracino V. & Montacchini F. 1996: Food habits of Alpine marmot (*Marmota marmota*, L.). In: Le Berre M., Ramousse R. & Le Guelte L. (eds.), *Proceedings of 2nd International Conference on Marmots. International Marmot Network, Moscow, Russia*: 135–140.
- Bengsen A.J., Forsyth D.M., Ramsey D.S.L. et al. 2022: Estimating deer density and abundance using spatial mark-resight models with camera trap data. *J. Mammal.* 103: 711–722.
- Borgo A., Vettorazzo E. & Martino N. 2009: Dynamics of the colonization process in reintroduced populations of the Alpine marmot. *Ethol. Ecol. Evol.* 21: 317–323.
- Bowden D.C. & Kufeld R.C. 1995: Generalized mark-sight population size estimation applied to Colorado moose. *J. Wildl. Manag.* 59: 840–851.
- Buckland S.T., Anderson D.R., Burnham K.P. et al. 2001: Introduction to distance sampling. *Oxford University Press, Oxford, UK*.
- Cassola F. 2016: *Marmota marmota*. The IUCN Red List of Threatened Species 2016: e.T12835A510082. Downloaded on 07 February 2022. <https://dx.doi.org/10.2305/IUCN.UK.2016-2.RLTS.T12835A510082.en>
- Chandler R.B. & Royle J.A. 2013: Spatially explicit models for inference about density in unmarked or partially marked populations. *Ann. Appl. Stat.* 7: 936–954.
- Clutton-Brock T. & Sheldon B.C. 2010: Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends Ecol. Evol.* 25: 562–573.
- Corlatti L., Nelli L., Bertolini M. et al. 2017: A comparison of four methods to estimate population size of Alpine marmot (*Marmota marmota*). *Hystrix* 28: 61–67.
- Corlatti L., Sivieri S., Sudolska B. et al. 2020: A field test of unconventional camera trap distance sampling to estimate abundance of marmot populations. *Wildl. Biol.* 2020: wlb.00652.
- Diefenbach D.R. 2009: Estimating avian population size using Bowden's estimator. *Auk* 126: 211–217.
- Doran-Myers D., Kenney A.J., Krebs C.J. et al. 2021: Density estimates for Canada lynx vary among estimation methods. *Ecosphere* 12: e03774.
- Fattorini L., Marcheselli M., Monaco A. & Pisani C. 2007: A critical look at some widely used estimators in mark-resighting experiments. *J. Anim. Ecol.* 76: 957–965.
- Fegraus E. & MacCarthy J. 2016: Camera trap data management and interoperability. In: Rovero F. & Zimmermann F. (eds.), *Camera trapping for wildlife research. Pelagic Publishing, Exeter, UK*: 33–42.
- Figueroa I., López B.C., López A. & Potrony D. 2009: What happens to ptarmigan when marmots arrive? *Ethol. Ecol. Evol.* 21: 251–260.
- Fryxell J.M., Sinclair A.R.E. & Caughley G. 2014. Wildlife ecology, conservation and management. *Wiley-Blackwell, Oxford, UK*.
- Gilbert N.A., Clare J.D.J., Stenglein J.L. & Zuckerberg B. 2020: Abundance estimation of unmarked animals based on camera-trap data. *Conserv. Biol.* 35: 88–100.
- Hammond E.L. & Anthony R.G. 2006: Mark-recapture estimates of population parameters for selected species of small mammals. *J. Mammal.* 87: 618–627.
- Hansson A., Dargusch P. & Shulmeister J. 2021: A review of modern treeline migration, the factors controlling it and the implications for carbon storage. *J. Mt. Sci.* 18: 291–306.
- Hariyadi A., Priambudi A., Setiawan R. et al. 2011: Estimating the population structure of Javan rhinos (*Rhinoceros sondaicus*) in Ujung Kulon National Park using the mark-recapture method based on video and camera trap identification. *Pachyderm* 49: 90–99.
- Holmberg J., Norman B. & Arzoumanian Z. 2008: Robust, comparable population metrics through collaborative photo-monitoring of whale sharks *Rhincodon typus*. *Ecol. Appl.* 18: 222–233.
- Jackson R.M., Roe J.D., Wangchuk R. & Hunter D.O. 2006: Estimating snow leopard population abundance using photography and capture-recapture techniques. *Wildl. Soc. Bull.* 34: 772–781.



- Karanth K.U., Nichols J.D., Kumar N.S. & Hines J.E. 2006: Assessing tiger population dynamics using photographic capture-recapture sampling. *Ecology* 87: 2925–2937.
- Keiter D.A., Davis A.J., Rhodes O.E. et al. 2017: Effects of scale of movement, detection probability, and true population density on common methods of estimating population density. *Sci. Rep.* 7: 9446.
- Kendall W.L. 1999: Robustness of closed capture-recapture methods to violations of the closure assumption. *Ecology* 80: 2517–2525.
- Kendall W.L., Nichols J.D. & Hines J.E. 1997: Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* 78: 563–578.
- Laake J.L. 2013: RMark: an R interface for analysis of capture-recapture data with MARK. *National Mammal Member Laboratory, Alaska Fish. Sci. Cent., Seattle, USA*.
- Mackey B.L., Durban J.W., Middlemas S.J. & Thompson P.M. 2008: A Bayesian estimate of harbour seal survival using sparse photo-identification data. *J. Zool. (Lond.)* 274: 18–27.
- McClintock B.T., Conn P.B., Alonso R.S. & Crooks K.R. 2013: Integrated modeling of bilateral photo-identification data in mark-recapture analyses. *Ecology* 94: 1464–1471.
- McClintock B.T., White G.C., Antolin M.F. & Tripp D.W. 2009: Estimating abundance using mark-resight when sampling is with replacement or the number of marked individuals is unknown. *Biometrics* 65: 237–246.
- McMahon C.R., van den Hoff J. & Burton H.R. 2005: Repeated handling and invasive research methods in wildlife research: impacts at the population level. *AMBIO* 34: 426–429.
- Menkens G.E. & Anderson S.H. 1988: Estimation of small-mammal population size. *Ecology* 69: 1952–1959.
- Minta S. & Mangel M. 1989: A simple population estimate based on simulation for capture-recapture and capture-resight data. *Ecology* 70: 1738–1751.
- Mowat G., Heard D.C., Seip D.R. et al. 2005: Grizzly *Ursus arctos* and black bear *U. americanus* densities in the interior mountains of North America. *Wildl. Biol.* 11: 31–48.
- Neal A.K., White G.C., Gill R.B. et al. 1993: Evaluation of mark-resight model assumptions for estimating mountain sheep numbers. *J. Wildl. Manag.* 57: 436–450.
- Otis D.L., Burnham K.P., White G.C. et al. 1978: Statistical inference from capture data on closed animal populations. *Wildl. Monogr.* 62: 3–135.
- Palencia P., Rowcliffe J.M., Vicente J. & Acevedo P. 2021: Assessing the camera trap methodologies used to estimate density of unmarked populations. *J. Appl. Ecol.* 58: 1583–1592.
- Parsons A.W., Simons T.R., Pollock K.H. et al. 2015: Camera traps and mark-resight models: the value of ancillary data for evaluating assumptions. *J. Wildl. Manag.* 79: 1163–1172.
- Pawlina I.M. & Proulx G. 1999: Factors affecting trap efficiency: a review. In: Proulx G. (ed.), *Mammal trapping. Alpha Wildlife Research and Management Ltd: Sherwood Park, USA*: 95–116.
- Pedrini P. & Sergio F. 2001: Density, productivity, diet, and human persecution of golden eagles (*Aquila chrysaetos*) in the central eastern Italian Alps. *J. Raptor Res.* 35: 40–48.
- Pelliccioli F. & Ferrari C. 2013: The use of point-transects distance sampling to estimate the density of Alpine marmot in the Gran Paradiso National Park. *J. Mt. Ecol.* 9: 47–60.
- Perrin C., Allainé D. & Le Berre M. 1993: Socio-spatial organization and activity distribution of the Alpine marmot *Marmota marmota*: preliminary results. *Ethology* 93: 21–30.
- Pollock K.H. 1982: A capture-recapture design robust to unequal probabilities of capture. *J. Wildl. Manag.* 46: 757–760.
- QGIS Development Team 2021: QGIS geographic information system. <http://qgis.osgeo.org>
- R Core Team 2020: R: a language and environment for statistical computing. *R foundation for statistical computing, Vienna, Austria*.
- R Studio Team 2020: RStudio: integrated development for R. *Rstudio Inc., Boston, USA*. <http://www.rstudio.com/>
- Rézouki C., Tafani M., Cohas A. et al. 2016: Socially mediated effects of climate change decrease survival of hibernating Alpine marmots. *J. Anim. Ecol.* 85: 761–773.
- Rivero M., De la Torre J., Camacho G. et al. 2022: Tapirs in trouble: estimating Baird's tapir densities in the Sierra Madre de Chiapas, Mexico. *Oryx* 56: 373–382.
- Rovero F. & Zimmermann F. 2016: Camera trapping for wildlife research. *Pelagic Publishing, Exeter, UK*.
- Rowcliffe J.M. 2017: Key frontiers in camera trapping research. *Remote Sens. Ecol. Conserv.* 3: 107–108.
- Royle J.A. & Converse S.J. 2020: Estimating abundance from capture-recapture data. In: Murray D.L. & Sandercock B. (eds.), *Population*



- ecology in practice. *Wiley-Blackwell, London, UK*: 103–122.
- Santangeli A., Pakanen V.-M., Bridgeford P. et al. 2020: The relative contribution of camera trap technology and citizen science for estimating survival of an endangered African vulture. *Biol. Conserv.* 246: 108593.
- Schenker N. & Gentleman J.F. 2001: On judging the significance of differences by examining the overlap between confidence intervals. *Am. Stat.* 55: 182–186.
- Schwarz C.J. & Seber G.A.F. 1999: Estimating animal abundance: review III. *Stat. Sci.* 14: 427–456.
- Semenov Y., Ramousse R. & Le Berre M. 2003: Alpine marmot (*Marmota marmota*) impact on floristic diversity of alpine meadows. In: Ramousse R., Allainé D. & Le Berre M. (eds.), *Adaptive strategies and diversity in marmots. International Marmot Network, Lyon, France*: 269–274.
- Singh N. & Milner-Gulland E. 2011: Monitoring ungulates in Central Asia: current constraints and future potential. *Oryx*: 45: 38–49.
- Sollmann R., Gardner B., Parsons A.W. et al. 2013: A spatial mark-resight model augmented with telemetry data. *Ecology* 94: 553–559.
- Stephens P.A., Frey-Roos F., Arnold W. & Sutherland W.J. 2002: Model complexity and population predictions. The Alpine marmot as a case study. *J. Anim. Ecol.* 71: 343–361.
- Tafari M., Cohas A., Bonenfant C. et al. 2013: Decreasing litter size of marmots over time: a life history response to climate change? *Ecology* 94: 580–586.
- Taylor J.C., Bates S.B., Whiting J.C. et al. 2021: Using camera traps to estimate ungulate abundance: a comparison of mark-resight methods. *Remote Sens. Ecol. Conserv.* 8: 32–44.
- Weckerly F.W. & Foster J.A. 2010: Blind count surveys of white-tailed deer and population estimates using Bowden's estimators. *J. Wild. Manag.* 74: 1367–1377.
- White G.C. & Burnham K.P. 1999: Program MARK: survival estimation from populations of marked individuals. *Bird Study* 46: 120–139.
- White G.C. & Schenk T.M. 2001: Population estimation with radio-marked animals. In: Millspaugh J.J. & Marzluff J.M. (eds.), *Radio tracking and animal populations. Academic Press, San Diego, USA*: 329–350.
- Williams B.K., Nichols J.D. & Conroy M.J. 2002: Analysis and management of animal populations. *Academic Press, New York, USA*.
- Yu X., Wang J., Kays R. et al. 2013: Automated identification of animal species in camera trap images. *EURASIP J. Image Video Process.* 2013: 52.
- Zimmermann F., Breitenmoser-Würsten C., Molinari-Jobin A. & Breitenmoser U. 2013: Optimizing the size of the area surveyed for monitoring a Eurasian lynx (*Lynx lynx*) population in the Swiss Alps by means of photographic capture-recapture. *Integr. Zool.* 8: 232–243.

Supplementary online material

Data S1. Supplementary material: individual capture history (<https://www.ivb.cz/wp-content/uploads/JVB-vol.-71-2022-Forti-et-al.-Data-S1.pdf>).

Data S2. Supplementary material: R script for repeat data analysis (<https://www.ivb.cz/wp-content/uploads/JVB-vol.-71-2022-Forti-et-al.-Data-S2.pdf>).