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Population reconstruction as an informative tool for monitoring chamois populations

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Knowledge of population trends is of key importance for sustainable management of wildlife and finding reliable and cost–effective monitoring methods is therefore of great interest. In two populations of Alpine chamois *Rupicapra rupicapra*, we collected data on mortality from 12 424 individuals hunted or found dead and population size data based on ground counts over a period of 28 years. Our study had three aims: 1) we investigated if changes in population size obtained with a simple deterministic population reconstruction (DPR) approach using hunting and natural mortality covary with population size estimates obtained from ground count data. 2) We investigated if the performance of DPR is affected by the removal of natural mortality data. 3) We assessed how many years of mortality data are needed to obtain consistent population trends using DPR. Our results suggested that 1) population abundance from mortality data using DPR significantly and positively correlated with population abundance obtained with ground counts. 2) DPR without natural mortality data performed similarly as compared to DPR using full data (hunting and natural mortality). 3) Consistent estimates of population trends can be obtained with ≥10 years of mortality data, however, this time span was influenced by the mean age at death, which in turn was affected by the local hunting regime. Our results suggest that DPR and ground counts perform similarly for the estimation of temporal trends in Alpine chamois abundance. The consistence of ground counts and DPR supports the use of these methods as reliable tools for tracking abundance of chamois populations over time. However, the reliability of abundance estimates using DPR may vary between populations and the influence of different hunting regimes must be considered for the correct interpretation of results.

Keywords: abundance estimation, chamois, cohort analysis, monitoring, *Rupicapra rupicapra*, ungulate

Sustainable wildlife management requires reliable estimates of absolute or relative population abundance (Msoffe et al. 2007, Soininen et al. 2016). Statistical estimators, such as capture–recapture (Lebreton et al. 1992) or distance sampling (Focardi et al. 2002, Koenen et al. 2002, Buckland et al. 2015), are widely used to obtain information about absolute population size, but the associated sampling costs often make these methods difficult to sustain in the long term. Relative abundance indices (RAIs) are often used as cost-effective methods to track long-term changes in wildlife populations, provided the relationship between RAIs and true abundance is known (Schwarz and Seber 1999). Alternatively, retrospective cohort analysis based on game bag statistics may be an inexpensive tool to obtain absolute or relative estimates of population abundance in the past (Fryxell 1988, Broms 2007, Clawson 2010).

Population reconstruction methods are based on the idea that age-at-death can be used to back-calculate year- and age-specific abundance. These methods, also known as cohort- or virtual population analyses, were originally developed in fisheries (Fry 1949) and later extended to other wildlife (Lowe 1969). In its simplest form, deterministic population reconstruction (DPR) allows to assess minimal population size, and the minimum number of individuals alive in one cohort for a given year is the sum of all individuals from that cohort found dead in subsequent years (Roseberry and Woolf 1991). Under the assumption that all mortality events are known, which is highly unlikely in wildlife populations, DPR should return the true population size. When only age-at-harvest data are used, however, absolute abundance is difficult to assess because harvest is usually not the only source of mortality in a population (Pope 1972). In such cases, DPR

is reduced to a RAI; however, harvest-based reconstruction can be ameliorated by adding estimates of natural mortality (Fryxell 1988, Solberg et al. 1999).

Although statistical reconstruction methods have been developed for cohort analysis (Gove et al. 2002, Skalski et al. 2007), these methods require the estimation of several population parameters (Gove et al. 2002) and are computationally challenging (Skalski et al. 2005). Simpler methods, such as DPR based on age-at-harvest data (Skalski et al. 2005), may therefore be preferable as quick and easy tools for practical wildlife management. Investigating whether DPR can be used as a reliable RAI to track population trends is thus of paramount importance for sustainable wildlife management. Ideally, the applicability of reconstruction methods should be cross-checked with other, independent monitoring methods (Solberg et al. 1999, Mysterud et al. 2007).

In hunted ungulate populations, several methods can be employed to monitor population trends over time. Direct methods include, e.g. transects counts (Vincent et al. 1991) or spotlight counts (Corlatti et al. 2016), while indirect methods include the analysis of age structure (Rughetti 2016), body mass (Gaillard et al. 1996, Toïgo et al. 2006), fecal pellet counts (ENETWILD 2020), DNA-based capture–recapture (Brinkman et al. 2011, Ebert et al. 2012) or density-dependent ecological indicators (Morellet et al. 2007). For mountain ungulates living in open areas, such as the ibex *Capra ibex* or the Alpine chamois *Rupicapra rupicapra*, ground counts from vantage points or transects are commonly used (Largo et al. 2008, Herrero et al. 2011). Long-term data sets based on ground counts have been extensively used to investigate ungulate population dynamics (Jacobson et al. 2004, Ciach and Pęksa 2018, Corlatti et al. 2019). The main drawback of ground counts is that true population size is underestimated by an unknown quantity (Corlatti et al. 2015a). Nonetheless, for chamois this method has low observation error (Corlatti et al. 2019) and has been shown to reliably track changes in ungulate population size, as long as several years of data are available (Loison et al. 2006, Largo et al. 2008).

Although reconstruction methods have been successfully applied to hunted ungulate populations (Lowe 1969, McCullough 1979, Raesfeld and Reulecke 1988) and age at death is easily determined in wild bovids, these methods are not commonly used in the monitoring of chamois. Taking advantage of data on 12 424 chamois (harvested or found dead) and long-term (28 years) ground count data from two populations, we aim to assess the reliability of DPR as a RAI to track chamois abundance over time by cross-checking reconstruction estimates with abundance data from ground counts. Specifically, we investigate 1) if DPR estimates of population abundance, based on harvest and natural mortality data, positively correlate with ground count data; 2) if DPR estimates of population abundance, based on harvest data only, positively correlate with ground count data; and 3) how many years of harvest data are necessary to obtain consistent estimates of population trend based on DPR.

Material and methods

Study areas and populations

Data were collected for two hunted chamois populations in the Austrian part of the eastern Alps. One population was located in the Tennen Mountains (TEN; 47°32′N, 13°16′E; overall area ca 250 km^2), a mountain range in the northern Limestone Alps in the province of Salzburg, Austria (Fig. 1). The study site extends over an area of about 200 km^2 with elevations from 500 to 2400 m a.s.l. The dominant tree species are Norway spruce *Picea abies*, Scots pine *Pinus sylvestris*, silver fir *Abies alba* and beech *Fagus sylvatica* at lower elevations, and European larch *Larix decidua* and dwarf mountain pine *Pinus mugo* at higher elevations. Above the treeline (approx. 1800 m a.s.l.), the habitat consists mainly of alpine meadows, sparsely vegetated areas and bare rocks at the highest elevations. Chamois can occur at any altitude, but due to the spatial distribution of hunting areas where most chamois were harvested, highest densities are expected between 800 and 2200 m.

The second population was located in the Seckau Tauern Mountains (SEC; 47°22′N, 14°37′E), which extend over an area of about 900 km^2 and at elevations between 800 and 2300 m a.s.l. in the province of Styria, Austria (Fig. 1). Data were collected in an area of about 200 km^2, reflecting the approximate distribution area of chamois within the Seckau Tauern Mountains. The forest at lower altitudes consists mainly of Norway spruce and silver fir, and of European larch, Swiss pine *Pinus cembra* and dwarf mountain pines at higher altitudes. Alpine meadows dominate the habitat above the treeline (approx. 1800 m a.s.l.), and chamois have been harvested at highest densities between 1600 and 2200 m.

The official chamois hunting season lasts from 16 July to 15 December in TEN, and from 1 August to 31 December in SEC; however, the highest monthly harvest rates are reported in November and December. Both study areas are subdivided into hunting areas (41 in TEN and 66 in SEC) for which annual sex and age-specific harvest quotas are set by local authorities. Harvest quotas for males and females are set at a ratio of 1:1–1:1.3 and at different percentages for the age classes. In TEN up to 30% of male harvest quota and up to 40% of female harvest quota are for the young age classes (1–3 years for females and 1–2 years for males). Up to 15% of the female harvest quota and up to 18% of the male harvest quota are for middle-age classes (4–9 years for females and 3–7 years for males) and the remaining part for old individuals (≥ 10 years for females, ≥ 8 years for males). In SEC, highest relative quotas are for young age classes (1–3 years – up to 45% of the total quota for both sexes), and the lowest quotas are for middle-age classes (4–10 years for females, 4–8 years for males – maximum 15% of total quota), while the remaining part of the quota is for old individuals (≥ 11 years for females, ≥ 9 years for males). In addition, sex-independent quotas are set for kids in both areas. The overall quota is set and adjusted based on how much of the annual harvest quotas of the last three years had been fulfilled, with the aim to always reach 100% of the quota (for additional

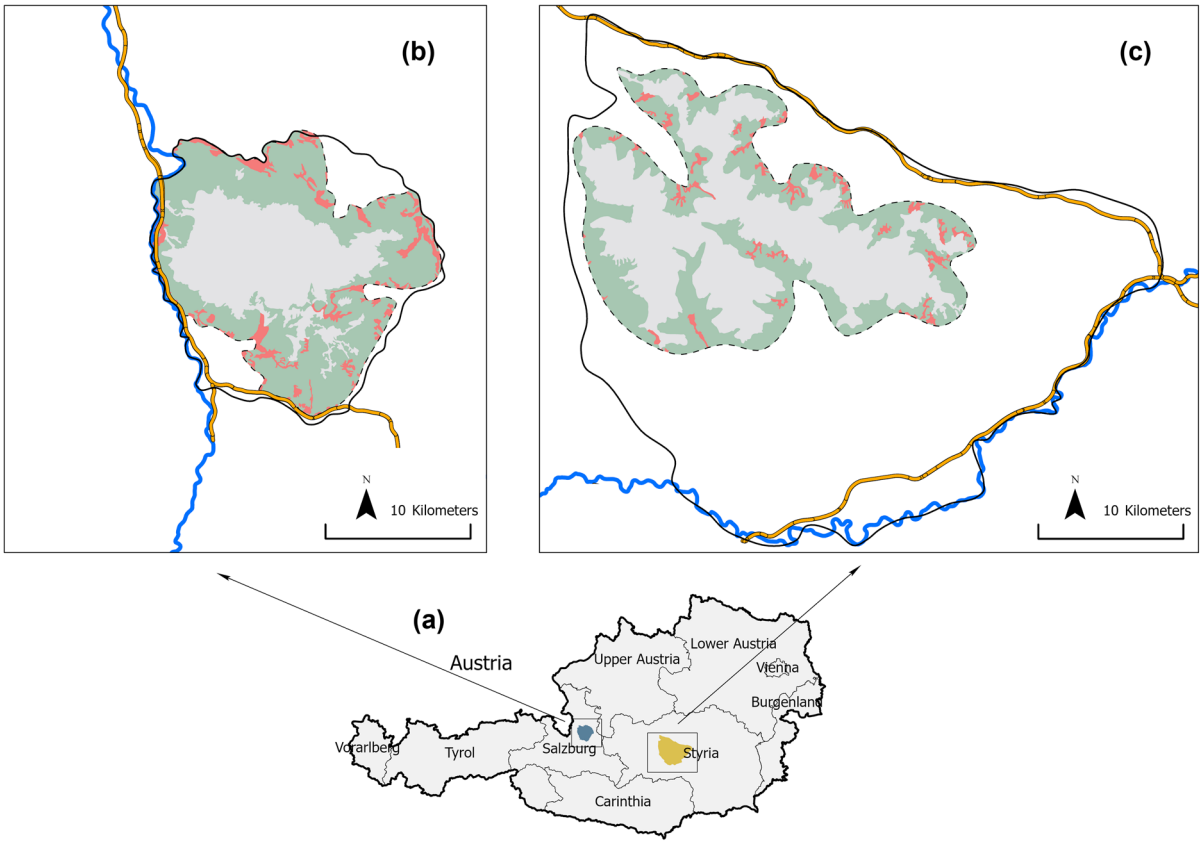

Figure 1. Map of the study areas. (a) External border of Austria and federal state borders with the locations of the Tennen Mountain Range (TEN = blue) and the Seckau Tauern Mountain subrange (SEC = yellow). Tennen Mountains (b) and Seckau Tauern Mountains (c). Solid lines indicate the extension of the moutain (sub)ranges, dashed lines indicate the study areas, blue lines are broad rivers (Salzach in TEN and Mur in SEC) and yellow lines show highways. Grey areas represent open alpine areas (alpine meadows, sparsely vegetated areas and bare rocks), green ares show forests within the study area and red areas are other landcover types (such as agricultural areas and settlements).

details on game management in Austria see Trouwborst and Hackländer 2018). Natural mortality mainly occurs during the winter (Rughetti et al. 2011) due to avalanches and food shortage. Negligible kid mortality might be caused by the golden eagle *Aquila chrysaetos* (Bertolino 2003). No large carnivores are permanently present in the study areas.

Population counts

Data on chamois abundance were collected using block counts (Chudik 1969, Caughley 1977, Corlatti et al. 2015a), since 1972 in TEN and 1976 in SEC, by regional hunting organizations. For this study, we used only count data between 1998 and 2019 for TEN and between 1992 and 2019 for SEC, to ensure consistency in the counting methodology in terms of survey sectors. Annual block counts were carried out in permanently established sectors in 60% (120 km^2; n = 17 sectors) of the study area in TEN and 85% (170 km^2; n = 23 sectors) of the study area of SEC (Fig. 1). Survey sectors were defined based on counting experience developed since the 1970s in both areas, and never changed ever since. Counts were carried out by teams of at least two observers on the same day in July or August, i.e. before the start of the hunting season in the respective area. The total number of observers varied between 34 and 40 in TEN and between 46 and 55 in SEC. For training purposes of new observers, the teams sometimes consisted of three persons. To reduce potential bias in data collection, at least one member of each team was an independent observer, i.e. a person who was not allowed to hunt in the sites included in a sector; furthermore, the second member of each team was an officially appointed game warden. Surveys took place between 6 a.m. and 10 p.m., when the highest chamois activity is expected (Aublet et al. 2008, Mason et al. 2014). Each team carried out observations from one vantage point per sector with the aid of 7 × 42 binoculars and spotting scopes with 60× magnification. For the entire study period, each sector was observed on a yearly basis, using the same vantage points, from which 56% (68 km^2) of open alpine areas in TEN and 46% (78 km^2) of open alpine areas in SEC could be observed (Supplementary material Appendix 1 Fig. A1). All the chamois observed in each sector were noted down according to their sex and age-class, or classified as unknown if sex or age could not be determined. Since only the absolute number of observed chamois was relevant for our investigations, incorrect determinations regarding sex and age had no effect on the analyses. To prevent multiple counts, observers also recorded whether chamois moved from or into an adjacent sector. On the same day of data collection, coordinators reconciled the data from each observation team and corrected the data set removing multiple counts. Because ground counts may be subject to variations in detection probability over time, possibly owing to different observers or weather conditions, raw count data were filtered using a

linear state-space model and a Kalman filter approach with the R-package '*MARSS*' (Holmes et al. 2012). State–space models allow to divide a population time series into process variation (assuming a Gompertz-like density-dependent growth with independently normally distributed errors) and observation errors (Dennis et al. 2006, Ahrestani et al. 2013, Corlatti et al. 2019, Kavčić et al. 2019). The Kalman filter approach also allowed to estimate the number of expected individuals in years when no ground counts were carried out due to foggy weather conditions (2000 in TEN, 2009 and 2010 in SEC). The goodness of fit of the state–space model was assess by inspecting the distribution of the residuals.

Deterministic population reconstruction

To reconstruct population size with cohort analysis, we used age-at-harvest data and natural mortality data for chamois collected each year between 1998 and 2019 in TEN and between 1992 and 2019 in SEC. While counts were carried out only in open alpine areas (i.e. alpine meadows, sparsely vegetated areas, bare rocks), harvest data and mortality data were collected in open alpine areas as well as in the surrounding forest habitats, because chamois commonly move between these habitat types (Miller and Corlatti 2009, Zeiler 2012). The comparison between ground counts and DPR assumes that the same population is assessed, i.e. that the population is geographically closed between summer (i.e. the time of counting) and late winter (i.e. the end of the main mortality period, see below). The demarcation of the populations is based on the division of the eastern Alps into mountain ranges (Grassler 1984, Grimm 2004). Although dispersal from and to adjacent populations cannot be entirely ruled out, the assumption of closure is reasonable because chamois movements are strongly restricted due to physical barriers (i.e. fenced highways (Fuchs et al. 2000), railways with sound protection walls) surrounding the study areas in the valley bottoms (Onderscheka et al. 1993, Reiner 2015). Specifically, chamois migration from or to the adjacent population in the west of TEN (i.e. the Hagen Mountains) is highly unlikely because of the barrier of the (fenced) four-lane highway A10 and the wide or fast flowing Salzach River which separates the two populations. Also, SEC is clearly divided to the south and south-east and to the north and north-east by (fenced) four-lane highways and the Mur River (south and south-east) (Fig. 1). Few dispersal, if any, may occur between the eastern border of the SEC and the Rottenmann and Wölz Tauern Mountain, but no chamois has been recorded between these sites during the study period. Although we assumed that all data came from the same closed populations, count and mortality data covered different types of habitat. Thus we expect a greater difference in abundance between count data and DPR with increasing proportion of mortality data coming from forest habitats.

By regulation, all harvested chamois must be reported (within three days of the harvest in SEC and five days in TEN) to the regional hunting authorities. For each animal (4086 in TEN, 6473 in SEC) the following data were recorded: hunting area, harvest date, eviscerated body mass (in kg), sex and age. Age was determined by counting horn growth annuli, a method that is commonly used in wild Bovidae (Geist 1966, Schröder and von Elsner-Schak 1985, Stevens and Houston 1989, Corlatti et al. 2015b). An independent group of hunters checked the age estimates of all harvested individuals at regular annual meetings. To avoid multiple recordings of the same individual, horns were permanently marked by drilling a small hole into their lower backside. Annual number of harvested chamois ranged between 135 and 253 in TEN and between 110 and 355 in SEC. Since chamois found dead also must be reported by law, we were able to include natural mortality data of 1165 chamois found in TEN (541 females and 624 males) and 700 chamois found in SEC (377 females and 323 males) into the analysis. If only the skeletons were found, males and females could still be distinguished by the shape of their horns (Blagojević and Svetlana 2015). The observed sex-ratio of found carcasses is in line with the nearly-unbiased sex specific survival in Alpine chamois (Bocci et al. 2010, Corlatti et al. 2012). Natural mortality carcasses are routinely recorded by hunters, and locations known as hotspots for natural mortality (mainly due to avalanches) are systematically searched once a year after snowmelt by hunters with the aid of dogs trained to search for wounded and dead animals. Although these systematic searches were conducted only once a year, the high presence of hunters in the study area from the snowmelt until the end of the year, during which also carcasses were found and recorded, suggests a high probability of carcass recovery. During systematic searches after snowmelt, 938 carcasses (81% of overall found carcasses) were found in TEN and 360 carcasses (51% of overall found carcasses) were found in SEC, whereas 227 (19% of overall found carcasses) in TEN and 340 (49% of overall found carcasses) in SEC were found by hunters by chance (Supplementary material Appendix 1 Table A1). The number of carcasses that may be removed entirely by scavengers like red fox *Vulpes vulpes* and golden eagle was assumed to be low.

Data analyses were conducted for the entire study period, between 1998 and 2019 for TEN and between 1992 and 2019 for SEC. The total sample size was 5251 individuals for TEN (2567 females and 2684 males) and 7173 individuals for SEC (3709 females and 3464 males) (Fig. 2). Age data from harvested chamois and natural mortality were used to perform simple DPR (Pope 1972, Solberg et al. 1999, Mysterud et al. 2007). DPR with age-at-death data is based on cohorts of individuals born in the same year. By summing up data from all previous birth-cohorts, the minimum number of individuals alive in a specific year can be reconstructed (Fryxell 1988, Solberg and Sæther 1999). In other words, if an individual was born prior to and harvested within or after a specific year, it was part of the population size estimate in this specific year. Because our data also include natural mortalities, we did not incorporate additional assumptions of natural mortality into our reconstruction. To investigate if reconstruction with and without natural mortality data performed similarly, we additionally reconstructed annual population size with harvest data only.

Counts versus deterministic population reconstruction

To investigate whether ground count data and DPR data covaried over time, we compared the within-year differences between the two methods separately for each study

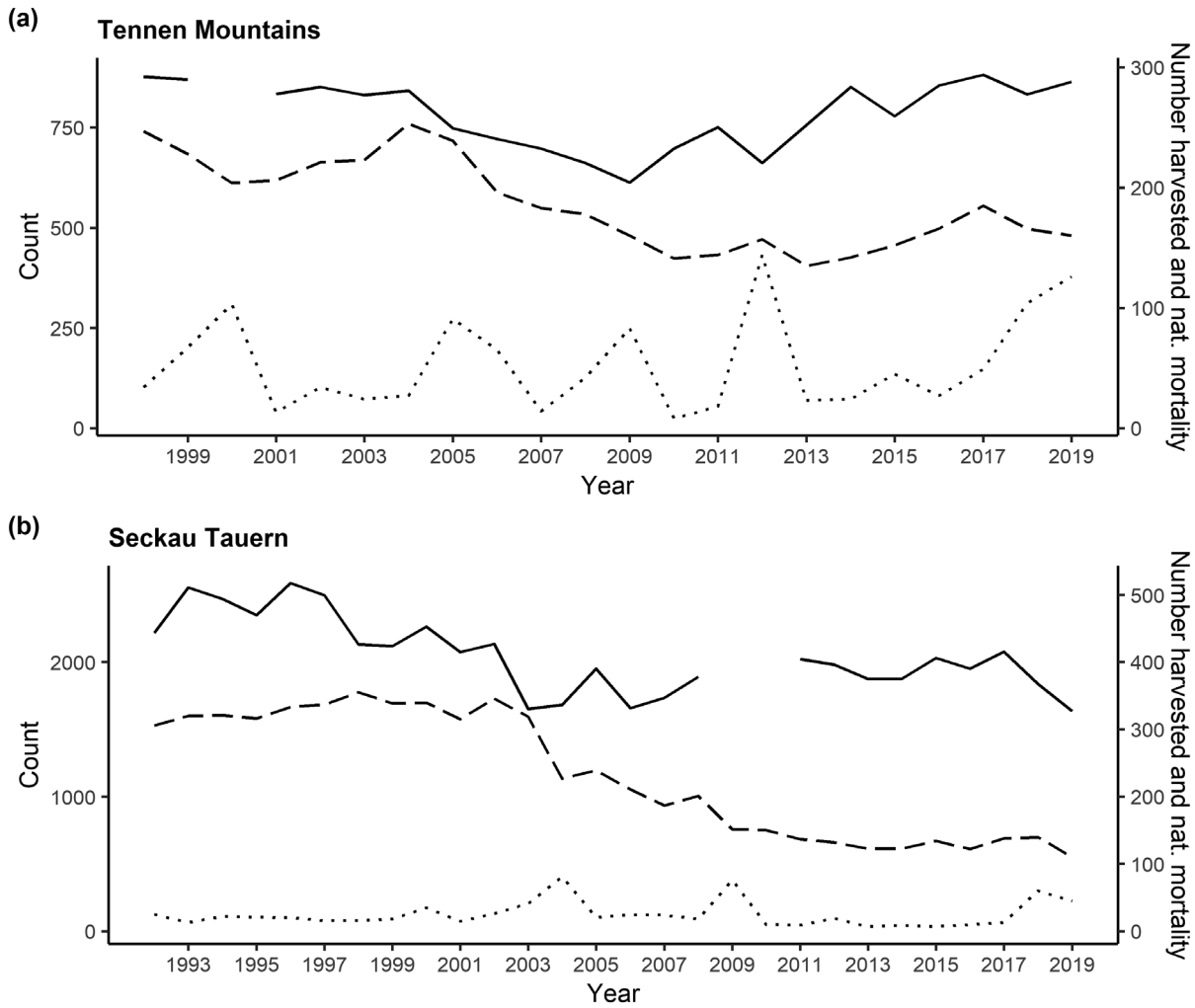

Figure 2. Data of annual abundance based on counts (solid line – no counts have been carried out in 2000 in TEN and 2009 and 2010 in SEC), harvest (dashed line) and natural mortality (dotted line) of chamois in (a) Tennen Mountains (1998–2019) and (b) Seckau Tauern Mountains (1992–2019), Austria. The primary y-axis depicts abundance based on counts, and the secondary y-axis depicts annual number of harvested chamois and natural mortality.

site with Buishand U-test (Buishand 1984) in the R-package '*trend*' (Pohlert 2020). The null hypothesis in the Buishand U-test for change-in-point assumes that the yearly difference between population sizes based on DPR and ground counts remains constant over time (Buishand 1984). We thus tested if the difference between the time series obtained by different methods remained constant over time, and also the point in time when the time series diverged (Jaiswal et al. 2015).

We computed the adjusted partial sum (S_k), i.e. the cumulative deviation from mean for kth observation of a series x_1, x_2, x_3 … x_k … x_n with mean ($\overline{x}$) as:

$$S_k = \sum_{i=1}^{k}\left(x_i - \overline{x}\right)$$

A series is considered constant without any change point if $S_k \cong 0$, where $x_i =$ is the difference between the number of individuals from ground counts and the number of individuals from reconstruction. The Buishand U-test statistic was defined as:

$$U = \left[n(n+1)\right]^{-1}\sum_{k=1}^{n-1}\left(\frac{S_k}{D_x}\right)^2$$

with

$$D_x = \sqrt{n^{-1}\sum_{i=1}^{n}(x_i - \overline{x})}$$

The p-value associated with the U-statistic was estimated with a Monte Carlo simulation using 2000 replicates (Pohlert 2020). Under the assumption that ground counts and DPR return consistent trends, the change point detected with the Buishand U-test (i.e. the year when the two time series diverged) indicates the minimum number of years necessary to obtain reliable DPR estimates. To further explore the relationship between count data and reliable DPR estimates, we fitted a log–log linear regression of abundance based on log-counts as a function of abun-

Table 1. Estimates of chamois abundance by age and year for the Tennen Mountains population (TEN, upper), Austria, 1998–2019, and for the Seckau Tauern population (SEC, lower), Austria, 1992–2019. Reconstruction using deterministic population reconstruction was based on harvest data and natural mortality. Shaded rows indicate years for which no reliable estimates of population abundance could be made since they lay after the detected change point (see text for details).

TEN	Age (in years)																	
Year	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16+	Yearly abundance
1998	190	166	193	148	163	157	133	97	92	90	78	35	24	21	14	5	7	1613
1999	237	138	132	162	137	144	143	116	74	73	76	61	25	18	17	8	5	1566
2000	265	182	106	113	150	124	125	125	100	46	60	57	48	15	9	11	9	1545
2001	224	226	140	94	108	146	115	115	110	83	38	49	45	39	7	8	10	1557
2002	226	187	179	133	87	102	138	107	95	93	71	30	37	38	25	4	12	1564
2003	251	187	136	165	121	82	94	130	99	79	76	50	23	31	23	22	9	1578
2004	214	214	148	115	157	117	76	86	109	86	68	53	39	18	25	11	17	1553
2005	186	160	145	137	107	137	106	71	75	88	69	56	38	29	14	19	14	1451
2006	200	136	116	126	127	102	129	99	59	69	73	47	34	25	20	9	16	1387
2007	181	174	97	106	118	113	93	120	86	54	60	57	32	21	17	12	17	1358
2008	119	147	143	88	96	112	102	87	104	76	47	49	45	25	11	13	9	1273
2009	125	97	113	123	78	87	97	88	74	87	58	34	38	32	22	6	13	1172
2010	117	106	71	101	117	71	83	93	76	65	75	45	27	25	20	13	14	1119
2011	133	97	77	68	98	110	68	78	85	62	57	65	38	23	22	13	18	1112
2012	83	92	74	68	60	86	99	66	67	74	50	44	56	29	18	11	14	991
2013	104	62	61	60	62	51	80	96	64	58	66	38	34	37	27	11	11	922
2014	88	86	37	55	54	61	47	73	83	55	53	56	34	25	25	20	16	868
2015	78	62	55	31	51	49	51	42	60	71	50	42	42	28	21	18	22	773
2016	75	61	33	45	26	42	41	46	36	48	60	41	35	29	18	16	25	677
2017	72	58	25	18	38	19	36	33	37	27	37	47	28	27	24	11	17	554
2018	45	38	19	14	14	29	12	28	28	22	24	19	30	16	13	10	11	372
2019	21	23	7	5	3	2	11	5	17	14	14	11	8	10	6	4	8	169

SEC	Age (in years)																	
Year	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16+	Yearly abundance
1992	359	226	276	352	262	155	151	120	88	94	74	56	29	25	18	14	25	2324
1993	318	293	192	235	314	244	145	137	101	81	85	61	42	22	20	13	19	2322
1994	297	252	239	174	209	279	215	131	122	94	73	71	52	32	18	13	18	2289
1995	348	238	209	200	149	190	255	193	116	110	82	62	55	43	26	13	16	2305
1996	342	275	206	170	175	135	176	232	168	102	96	71	52	48	31	17	17	2313
1997	300	261	216	174	153	158	124	164	201	153	92	82	56	41	36	23	22	2256
1998	289	241	211	184	156	137	140	112	144	172	130	78	72	44	35	24	27	2196
1999	246	222	187	170	167	150	120	124	98	131	145	106	61	58	33	22	31	2071
2000	336	187	183	158	148	155	133	104	105	89	113	111	85	47	46	22	32	2054
2001	258	286	154	149	138	133	134	117	88	90	76	92	86	64	32	28	29	1954
2002	280	209	253	130	129	117	118	118	103	69	76	61	72	64	40	24	40	1903
2003	219	204	167	214	114	119	100	105	107	82	61	61	48	54	43	20	32	1750
2004	199	130	156	139	180	100	109	87	86	91	62	46	41	27	40	22	26	1541
2005	161	161	105	134	116	166	92	98	70	78	77	55	33	31	20	23	27	1447
2006	204	116	133	92	117	99	152	79	86	62	67	59	44	23	23	18	23	1397
2007	158	171	97	111	81	100	88	136	69	73	55	50	49	35	10	12	26	1321
2008	95	120	151	81	97	78	90	82	121	61	66	42	42	34	25	6	7	1198

Table 1. Continued.

SEC	Age (in years)																Yearly abundance
Year	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16+	
2009	91	66	103	127	66	92	71	80	77	104	50	50	30	32	21	16	5	1081
2010	73	68	42	61	99	58	85	60	61	60	78	37	33	16	15	12	10	868
2011	85	51	61	54	60	91	55	76	58	56	54	56	31	27	15	13	15	858
2012	58	59	45	50	49	54	82	50	68	52	48	44	39	22	21	9	18	768
2013	68	31	46	34	46	45	50	74	42	61	43	41	37	25	15	12	13	683
2014	48	48	29	37	30	39	43	47	66	35	49	32	31	27	23	9	18	611
2015	60	34	32	24	24	29	36	41	40	56	29	40	28	21	15	18	17	544
2016	67	39	29	19	18	20	23	28	38	31	46	26	30	20	14	7	16	471
2017	83	46	26	19	14	14	13	18	26	33	27	36	15	20	9	9	13	421
2018	52	57	29	12	14	11	12	7	11	21	23	18	27	8	11	3	7	323
2019	24	5	3	10	4	4	6	2	4	3	6	8	5	13	2	5	5	109

dance based on log-DPR for the period prior to the change points. After the change point, the remaining number of years with mortality data would not be enough to obtain reliable estimates of abundance. Consequently, we expected the change point to be influenced by median age of death (due to harvest or natural mortality) within each population, because with a high proportion of individuals that die young, fewer years should be needed to reconstruct a population. Therefore, we also assessed the cumulative sex specific mortality curves by summing the relative frequency of harvested and found chamois for each age. To test if median age is significantly different between TEN and SEC we used the Mann–Whitney U test. All data handling and statistical analyses were carried out in the software R ver. 3.6.1 (<www.r-project.org>) in R Studio ver. 1.2.5001 (RStudio Team 2019).

Results

We used data of 12 424 chamois, of which 5251 (78% harvest, 22% natural mortality) were from TEN and 7173 (90% harvest, 10% natural mortality) were from SEC (Fig. 2). Age ranged from 0 to 22 years for females and from 0 to 18 years for males in TEN, and 0 to 22 years for females and 0 to 19 years for males in SEC.

Yearly abundance estimates based on DPR, including data from all known mortality sources, ranged between 1119 and 1613 in TEN and between 1397 and 2324 in SEC and generally suggested a decreasing trend in population abundance (Table 1, Fig. 3). Yearly abundance estimates based on ground count data varied between 644 and 874 in TEN and between 1746 and 2436 in SEC and also indicated a generally decreasing trend in population abundance (Fig. 3). The residuals diagnostic for the state–space models suggested no violations of model assumptions (normality and homogeneity of variance across fitted values).

Using the full data set (harvest plus natural mortality), the year 2011 in TEN and the year 2007 in SEC were suggested as change points by the Buishand U-test (TEN: $U=1.73$, $n=22$, $p < 0.001$; SEC: $U=2.44$, $n=28$, $p < 0.001$) (Fig. 4a–b). After excluding natural mortalities from this analysis, the change point was estimated as the year 2010 in TEN, while 2007 remained the point of change in SEC (TEN: $U=1.78$, $n=22$, $p < 0.001$; SEC: $U=2.47$, $n=28$, $p < 0.001$) (Fig. 4c–d). The mortality curves of the two populations showed different patterns (Fig. 6a). In TEN juvenile mortality (kids and yearlings) was higher than in SEC, especially in juvenile females (Fig. 6b). With three years, median age of female chamois in TEN was significantly lower than in SEC (six years; $U=4\ 748\ 018$; $p < 0.001$). Although median age for males was five years in TEN as well as in SEC, the Mann–Whitney U test indicated a significant lower median age in TEN than in SEC ($U=4\ 349\ 089$, $p=0.001$).

For the time periods prior to change points, results of the log–log linear regression of population abundance from counts as a function of population abundance from DPR showed a very high correlation in TEN and SEC either with or without natural mortality (Table 2, Fig. 5). The linear

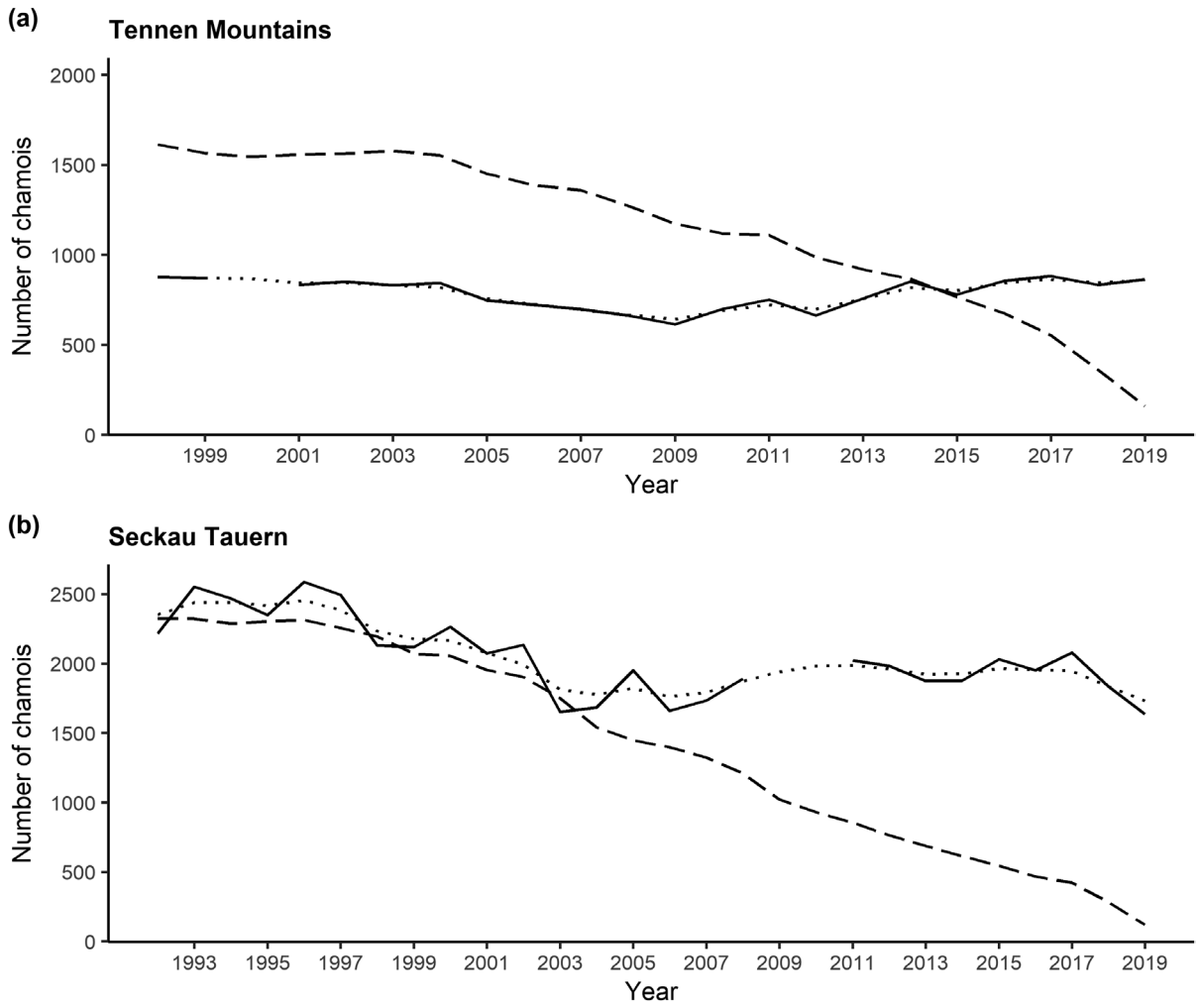

Figure 3. Population abundance trends of chamois in (a) Tennen Mountains (TEN; 1998–2019) and (b) Seckau Tauern Mountains (SEC; 1992–2019), Austria, based on ground counts (solid lines – no counts have been carried out in 2000 in TEN, and 2009 and 2010 in SEC), filtered counts using a linear state-space model and a Kalman filter (dotted lines), and abundance estimated with deterministic population reconstruction (dashed lines).

regression models showed a good fit, as the residuals diagnostics suggested no violations of assumptions.

Discussion

Our results show that chamois population abundance estimates based on DPR, with or without including natural mortality data, positively correlated with ground counts. The results suggest a population decline in both study areas, and their consistency supports the validity of these methods to track changes in chamois population size. Depending on the age structure of the study populations, a minimum of 10 and 14 years of mortality data were necessary to obtain reliable estimates of relative abundance using DPR.

The positive significant relationship between estimates obtained by DPRs with full data (harvest plus natural mortality) and estimates obtained with ground counts suggests that both methods performed similarly for the estimation of population trends. When DPRs are based on a populations' complete harvest and mortality data, the estimates should return true population size. Our data are unlikely to fully include mortality events, yet DPR can be generally considered an approximation of true population size. In turn, our results showed that ground counts underestimated abundance based on DPR by 46 ± 2.6% in TEN, whereas DPR slightly underestimates abundance based on ground counts by 7.2 ± 5.9% in SEC. These differences in the estimates between study areas can be explained by the fact that chamois in SEC mainly use open and sparsely forested areas around and above the tree line (cf. Bačkor 2010), i.e. there is a high degree of overlap between the area where chamois are counted for management purposes and the actual area where chamois are hunted. In comparison, forested areas are typically very steep and rocky and thus good chamois habitat in TEN (cf. Miller and Corlatti 2009, Zeiler 2012), and here chamois are hunted in both open and forested areas, but ground counts are carried out only in open areas. During the study period, 39% of chamois were shot in hunting areas which extend entirely below the tree line in TEN, whereas this was only 11% in SEC. This eventually resulted in a smaller overlap between the area for ground counts and the area that is used for the collection of harvest data in TEN compared to SEC. Notably, however, these differences did

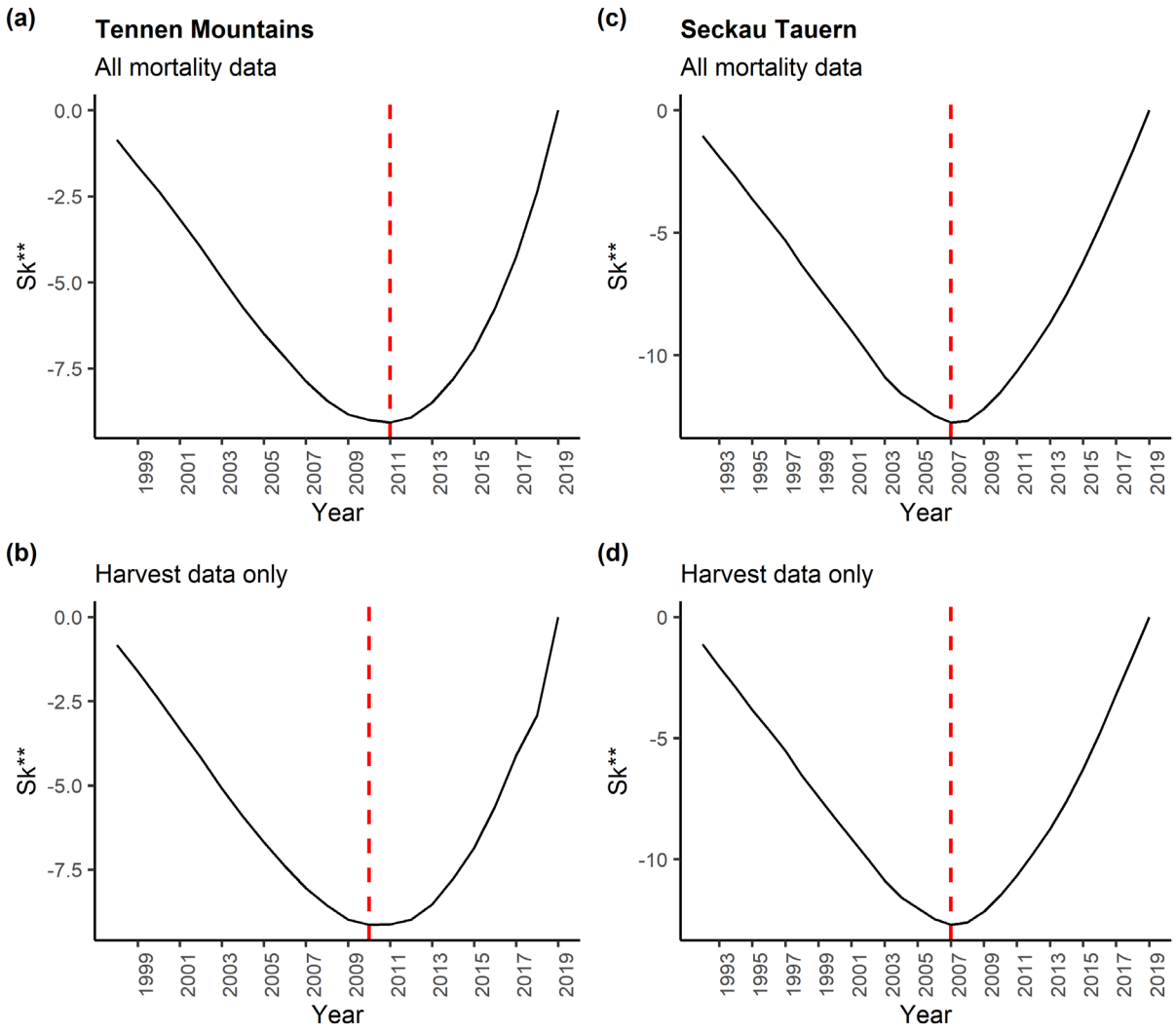

Figure 4. Rescaled adjusted partial sums (S_k^{**} – the cumulative deviation from mean for the difference between population abundance from counts and from deterministic population reconstruction) from Buishand U tests for chamois in (a, b) Tennen Mountains and (c, d) Seckau Tauern Mountains, Austria. (a) and (c) include harvest and natural mortality data, plots (b) and (d) show results for harvest data only. The red dashed lines indicate the change points.

not affect the agreement of trend estimates obtained with DPR and counts in the two areas: DPR estimates correlated well with ground counts in both populations, thereby suggesting that ground counts provided consistent information on size trend also when open areas were severely underrepresented compared to forests.

Table 2. Result of log–log linear regression of abundance from annual population counts as a function of abundance estimated by deterministic population reconstruction of chamois for Tennen Mountains (TEN) and Seckau Tauern Mountains (SEC), Austria. For TEN the data included both harvest and natural mortality data from 1998 to 2010, and harvest data only from 1998 to 2009. For SEC the data included both harvest and natural mortality data, and harvest data only from 1992 to 2006. β indicates the regression coefficients, 95% CI the 95% confidence intervals, R^2 the overall variation explained, and df the degrees of freedom.

Population	β	95% CI	R^2	df
TEN	0.84	0.60, 1.07	0.85	11
$TEN_{harvest\ only}$	0.95	0.83, 1.08	0.97	10
SEC	0.67	0.55, 0.77	0.92	13
$SEC_{harvest\ only}$	0.62	0.54, 0.71	0.94	13

One of the main challenges in population reconstruction methods is the integration of natural mortality estimates (Fryxell 1988, Gove et al. 2002, Skalski et al. 2007). Without data on natural mortality, the performance of DPR is expected to be hampered, unless harvest mortality accounts for the largest part of mortality events (Gilbert et al. 2007, Skalski et al. 2007). Natural mortality can be approximated with data collected in other areas and/or periods (Solberg and Sæther 1999, Solberg et al. 1999, Mysterud et al. 2007) or estimated by modelling (Gilbert et al. 2007, Skalski et al. 2007) and assumed to be constant across years (Roseberry and Woolf 1991, Solberg et al. 1999). Our results suggest that the performance of DPRs for tracking over-time variation in population size was not affected by the absence of natural mortality data; this, in turn supports a wide applicability of DPR for monitoring hunted chamois populations, even where detailed information on natural mortality is not available.

To obtain robust assessments of abundance, population reconstruction methods require that data are included up to an age where only a small proportion of a cohort is still alive within the population (Solberg et al. 1999, Mysterud et al.

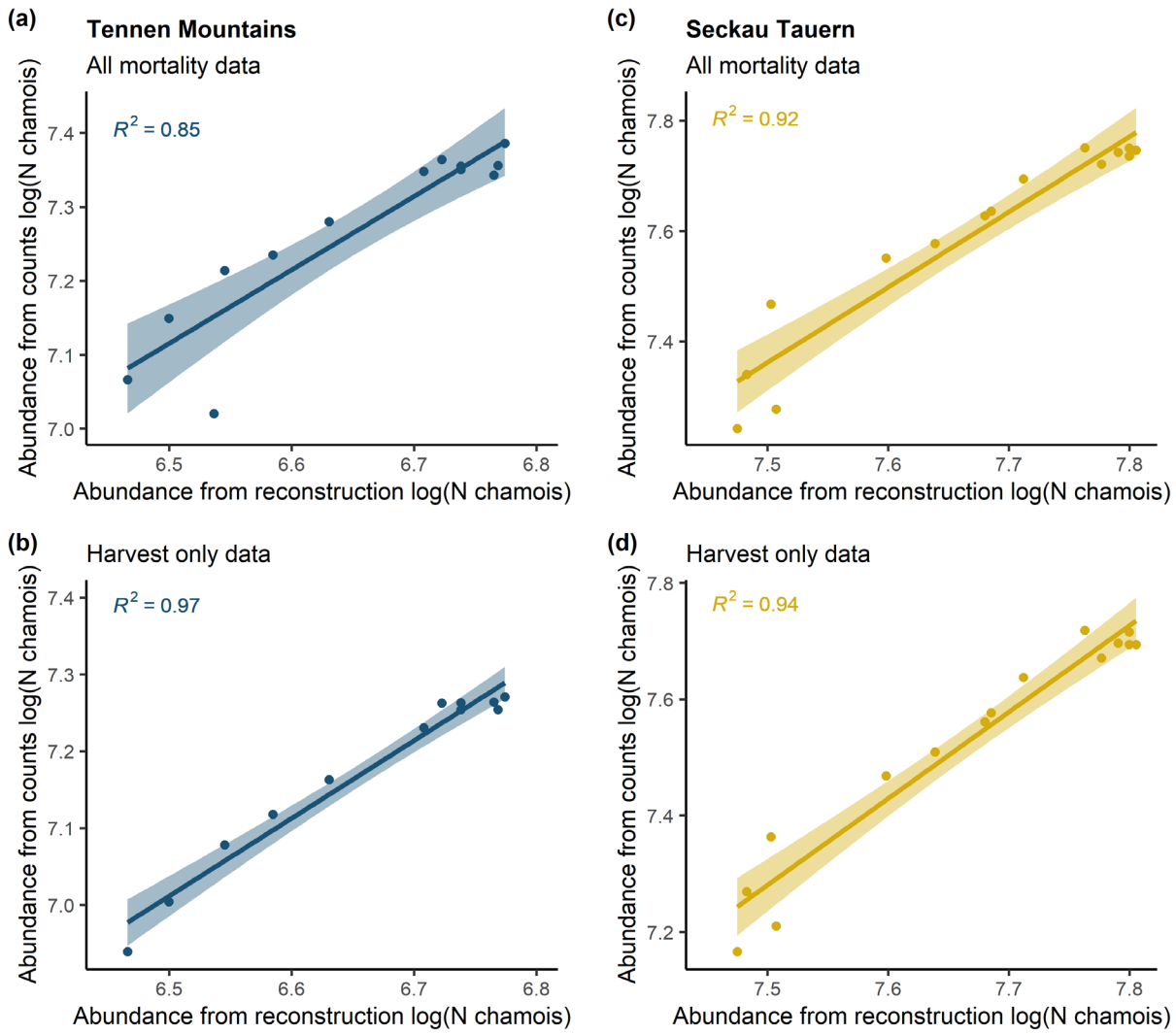

Figure 5. Log–log model of the relationship between population abundance based on yearly counts of chamois and from deterministic population reconstruction with harvest and natural mortality data for (a, b) Tennen Mountains (1998–2010) and (c, d) Seckau Tauern Mountains (1992–2006), Austria. Axes report log-transformed data, shaded areas correspond to 95% confidence intervals.

2007). In contrast to Solberg and Sæther (1999) and Mysterud et al. (2007), we did not pre-define an age until which data had to be included for population reconstruction, but rather we tested how many years of harvest data were necessary to obtain abundance estimates consistent with data from ground counts. Our results suggest that consistent estimates of chamois population abundance can be obtained with a minimum of 10 (11 for harvest data only) years of mortality data in TEN and a minimum of 14 years in SEC. The difference between study populations in the length of the data series necessary for consistent estimates, likely resulted from different age-specific mortality rates between populations. In TEN, 39% of mortality events affected kids and yearlings compared to 29% in SEC. In addition, the median age of chamois was lower in TEN than in SEC, which likely affected the change points and resulted in a shorter data series necessary to obtain consistent estimates in TEN compared to SEC. Age at harvest is influenced by local hunting regulations. In Austria, hunting quotas are set for sex-specific age classes, with the lowest harvest rates allowed in mid-age-class (see also Fig. 6b). An additional explanation for the differences in the length of data series needed could be the site-specific differences in natural mortality rates due to different climatic conditions. Our data show a higher natural mortality in TEN compared to SEC, likely due to harsher climatic conditions in TEN. Differences in the efforts to find and document cases of natural mortality may also affect the differences in the length of data series needed to obtain consistent abundance estimates.

The reliability of ground counts for tracking chamois populations over time depends on a constant probability of detecting animals. In turn, efforts should be made in order to maintain the methodology as consistent as possible in relation to other potential sources of variation, such as observers and weather conditions. Long term studies have shown that consistency in the used methodology leads to low observation errors in ungulate population trends (Ahrestani et al. 2013, Corlatti et al. 2019). While ground counts should be seen as simple RAIs, not as absolute abundance estimates, count data can be used to monitor changes in population size (Loison et al. 2006, Largo et al. 2008, Ciach and Pęksa 2018). Indeed, the consistency of the ground count

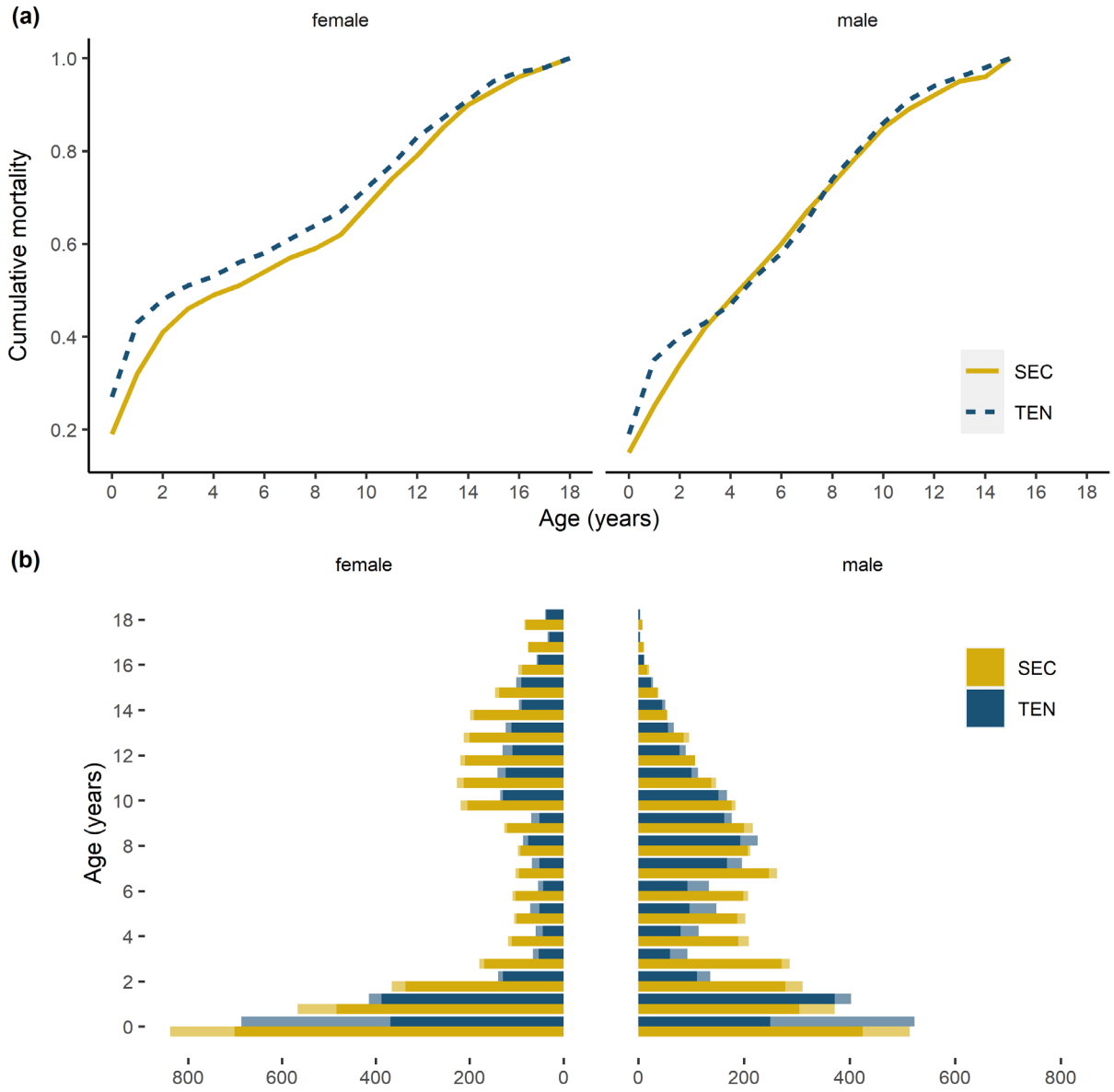

Figure 6. Age and sex specific cumulative mortality of chamois (a), and age specific frequency of mortality (solid bars indicate number of harvested chamois, shades bars indicate number of natural mortality) (b) in the Tennen Mountains population (TEN, 1998–2019) and Seckau Tauern Mountains population (SEC, 1992–2019), Austria.

methodology employed in this study is supported by the positive covariation of ground counts and DPR. The goodness of ground counts to track changes in chamois populations seemingly applies even if only a relatively small portion of the population can be visually detected (i.e. outside of forested areas), however this result needs to be interpreted with caution and further studies are required to support our findings.

DPR appears to be a useful and applicable method for wildlife managers to obtain reliable estimates of population abundance and trend. DPRs without natural mortality may provide robust indices of relative abundance in chamois, although information on natural mortality is necessary for the assessment of absolute abundance. One of the main advantages of DPR is its cost-effectiveness compared to other monitoring methods, as the necessary data are routinely collected by wildlife managers. Furthermore, since cohort analysis allows to reconstruct not only population size, but also age distribution (Table 1) and sex ratio, DPR can theoretically be used to obtain estimates of demographic parameters, such as recruitment rate (i.e. the ratio of offspring that did not die due to natural causes divided by mature females) (Uraguchi et al. 2014, Reiner 2015, Gilbert and Raedeke 2016). Reliable estimates of the true birth rate (all kids born in one year, regardless of whether they survived the first year, divided by mature females), however, crucially assume knowledge of the offspring's natural mortality rates (Gilbert and Raedeke 2016). For the wildlife manager this may be problematic, as natural mortality of young age classes is difficult to obtain, owing to the difficulty to find carcasses, especially of juveniles, since they are often removed by scavengers (Hoefs and Bayer 1983, Bocci et al. 2010). The main drawback of population reconstruction methods, especially for long-lived species, is that estimation of population

abundance is just possible in retrospect (Ueno et al. 2009). If real-time abundance index is of interest, ground counts may be preferable for chamois. More generally, for a robust monitoring of wildlife populations, a combination of several methods, such as direct counts, population reconstruction or density-dependent indices (Morellet et al. 2007), is desirable.

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Supplementary material (available online as Appendix wlb-00757 at <www.wildlifebiology.org/appendix/wlb-00757>). Appendix 1.