Assessment of key reproductive traits in the Apennine brown bear population

Elisabetta Tosoni[1], Luigi Boitani[1], Leonardo Gentile[2], Vincenzo Gervasi[1], Roberta Latini[2], and Paolo Ciucci[1,3]

[1]*Department of Biology and Biotechnologies "Charles Darwin", University of Rome "La Sapienza", Roma 00185, Italy*
[2]*Abruzzo, Lazio and Molise National Park, Pescasseroli, l'Aquila, 67032, Italy*

Abstract: Although knowledge of reproductive parameters is critical to project the probability of persistence of small and endangered populations, no such data are available for the relict Apennine brown bear (*Ursus arctos marsicanus*) population (central Italy). From 2005 through 2014, we compiled re-sight data on marked adult female bears ($3 \leq n \leq 10$/yr, for 78 total bear-years) and unmarked, distinct family groups ($n = 17$) to estimate basic reproductive traits in Apennine bears. We had a high rate of radiocollar failure, so we included in our sample marked, adult female bears with non-functioning radiocollars and used multi-event models in a capture–recapture, robust-design framework to correct for their incomplete detection and potential classification error. We obtained annual detection probabilities of 0.77 and 0.82 for reproductive and non-reproductive female bears, respectively, and the classification error of their reproductive state was negligible ($P = 0.003$). Mean litter size was 1.9 (± 0.7 SD) cubs, weaning occurred at approximately 1.4 years, and the interbirth interval was 3.7 years. Based on our multi-event model, female bears had highest probability to reproduce 3–4 years after their last reproduction, and their average reproductive rate was 0.243 (95% CI = 0.072–0.594). Average survival of adult female bears was 0.93 (95% CI = 0.83–0.97) whereas apparent cub survival was 0.49, based on the proportion of cubs seen before weaning the year following birth. Our findings place reproductive parameters of the Apennine bear population at the lower bound along the spectrum reported for other non-hunted brown bear populations. Coupled with high levels of human-caused mortality, a relatively low reproductive performance may explain why Apennine bears have not expanded their range beyond their historical minimum. More in-depth demographic investigations are urgently needed to corroborate our results and to assess the relative role of density-dependence versus inbreeding depression in affecting the dynamics of this imperiled bear population.

Key words: Apennine brown bear, capture–recapture, demography, E-SURGE, inter-birth interval, multi-event modelling, reproductive rate, transition probability, *Ursus arctos marsicanus,* weaning

A few key demographic parameters act as main drivers of apex predators populations (Eberhardt 2002) and bears are no exception (Harris et al. 2006, McLellan 2015, van Manen et al. 2016). Specifically, survival of adult females, reproductive rate, and variance in juvenile survival are the main parameters that affect dynamics of bear populations (Knight et al. 1995, Garshelis et al. 2005, Harris et al. 2011). Lack of knowledge on basic reproductive traits impedes identification of factors limiting bear population recovery (McLellan 2015) and comprehensive evaluation of current conservation strategies (e.g., Ciarniello et al. 2009). In particular, when dealing with small and highly endangered bear populations, lack of knowledge on the basic reproductive parameters hampers projection of the probability of persistence under alternative management scenarios (Chapron et al. 2003, 2009).

Notwithstanding the precarious status of the Apennine brown bear (*Ursus arctos marsicanus*), with approximately 50 bears surviving in the last stronghold (the National Park of Abruzzo Lazio and Molise; hereafter, PNALM) of a once wider range across the central Apennines in Italy (Ciucci et al. 2017), no data exist on the basic reproductive traits of this relict and isolated population (Ciucci and Boitani 2008). Despite the establishment of PNALM in 1923 and protection of the species by Regional and National authorities since 1939,

[3]email: paolo.ciucci@uniroma1.it

this bear population has not expanded its range during the past decades (Boscagli 1999, Ciucci and Boitani 2008). The availability of suitable habitat at the landscape scale does not seem to be limiting (Posillico et al. 2004, Falcucci et al. 2009); therefore, a lack of demographic vigor, or excessive levels of human-induced mortality, or both have been advanced as possible causes for the lack of population expansion (Falcucci et al. 2009, Gervasi et al. 2012, Ciucci et al. 2015). Human-caused mortality may indeed be negatively affecting recovery of Apennine bears (i.e., min. known levels of 2.5 bears/yr; P. Ciucci, unpublished data), and recent demographic monitoring failed to obtain evidence of consistent population growth that would be compatible with population expansion (Ciucci et al. 2015, 2017, Gervasi et al. 2017). To develop effective conservation actions for this bear population, it is essential to obtain a mechanistic understanding of the factors responsible for the lack of population growth, first of all by estimating its basic reproductive traits. However, although substantial work has recently been done to unveil basic ecological parameters of Apennine bears, including diet, home ranges and habitat use, habitat relationships, population size, and trends and productivity (Falcucci et al. 2009; Tosoni 2010; Tosoni et al. 2017; Ciucci et al. 2014, 2015; Gervasi et al. 2008, 2012), knowledge regarding basic reproductive traits is lacking.

To fill this knowledge gap, we compiled re-sighting data of adult female bears marked within a broader ecological study and a subsequent monitoring project that we conducted on the Apennine brown bear population during 2005–2014. Combining various data sets comprising re-sights of marked adult female bears with both functioning and non-functioning radiocollars with observations of unmarked family groups, our aim was to produce estimates of interbirth interval, litter size, age at weaning, and reproductive rate. In-depth demographic methods and known-fate encounter histories have been used to accurately estimate these parameters (e.g., Schwartz et al. 2006a, b; Harris et al. 2011, Mace et al. 2012). Given our data sources, we chose multi-event modeling within a capture–recapture framework to produce robust estimates of reproductive rate and the likelihood of reproduction of adult female bears as a function of years since last reproduction. By using such a probabilistic framework, we also obtained the first estimate of adult female survival for this population. Finally, we also report an empirical approximation of apparent cub survival based on the proportion of cubs seen prior to weaning the year following birth. Whereas some of these estimates are preliminary, we offer a discussion of their implications

for the conservation and the demographic monitoring of Apennine bears.

Study area

The study area is located in the central Apennines and comprises the Abruzzo, Lazio, and Molise National Park (507 km^2; PNALM), and its external buffer zone (800 km^2). The topography of the study area is mountainous and rugged, with elevation ranging from 400 m to 2,285 m and a variety of vegetation communities from sub-alpine meadows to low-elevation grasslands and mature stands of hard-mast-producing forests (*Fagus sylvatica* and *Quercus* spp.). Although no formal estimate of carrying capacity has been produced to date, habitat productivity is currently judged adequate for bears, featuring seasonal abundance and diversity of key foods and availability of supplemental foods during hyperphagy (Ciucci et al. 2014). The study area generally corresponds to the core range of Apennine brown bears, excluding occasional bears, primarily males, in peripheral portions of the range that until now have been of little demographic relevance for the dynamics of the population (Ciucci et al. 2017). In 2011, 51 bears of all ages were estimated for the study area, at a density of 39.7 bears/1,000 km^2 (Ciucci et al. 2015) and a minimum of 1–6 females producing 3–11 cubs/year (Tosoni et al. 2017). Although brown bears are protected, their conservation is not always prioritized over resource use by humans, including livestock grazing, forestry, and tourism, especially in the external buffer zone of the PNALM where hunting with dogs is also allowed (Ciucci and Boitani 2008, Maiorano et al. 2015). Direct and indirect human-caused mortality comprises poaching, vehicle collisions, and also diseases transmitted by free-ranging livestock and pets (Di Sabatino et al. 2014, Di Francesco et al. 2015). Additional details of the study area have been reported elsewhere (Ciucci et al. 2014, 2015).

Methods
Field methods

To ascertain the reproductive status of adult female bears, we verified presence or absence of a litter by direct observations (8–10× binoculars and 20–60× spotting scopes), either aided by telemetry or opportunistically. During 2005–2010, we ear-tagged (color-coded tags) and radiocollared 9 adult (≥4 yr) and 3 subadult (3–4 yr) female bears, using very high frequency (VHF; Telonics Inc., Mesa, Arizona, USA) or Global Positioning System (GPS-Tellus, Televilt, Lindesberg, Sweden;

Table 1. Capture history of 14 female Apennine brown bears (*Ursus arctos marsicanus*) captured and equipped with very high frequency (VHF-) or Global Positioning System (GPS-) transmitters in the Abruzzo Lazio e Molise National Park, Italy, 2005−2014. We also ear-tagged 1 cub and 1 yearling, both males, in 2 additional family groups (not listed).

Bear ID	Capture date	Collar type	Age at first capture	Radiocollar-days[a]	Date last seen
FP01	24 Aug 2004[b]	VHF	Adult	485	Aug 2014
F10	13 Oct 2004[b]	VHF	Adult	547	
	25 Oct 2008	GPS		206	
	14 Sep 2009	GPS		424	Sep 2014
F02	28 Oct 2005	GPS	Adult	482	Aug 2012
F01	19 May 2006	GPS	Adult	237	Aug 2013
F03	11 Jul 2006	GPS	Subadult[c]	124	
	12 Nov 2006	GPS		201	Sep 2013
F04	25 Jul 2006	GPS	Adult	126	Aug 2012
F05	4 Sep 2006	GPS	Adult	658	Sep 2014
F06	8 Nov 2006	GPS	Subadult[c]	776	Aug 2009
F07	21 May 2007	GPS	Adult	204	
	26 May 2008	GPS		290	Sep 2014
F08	20 Oct 2008	GPS	Adult	581	Sep 2014
F11	25 Oct 2008	VHF[d]	Cub	576	Sep 2014
F12	18 May 2009	VHF[d]	Yearling	55	Jul 2009[e]
F09	2 Sep 2009	GPS	Subadult[c]	466	Jul 2014
F13	14 Oct 2009	GPS	Adult	398	Sep 2014

[a]Functioning period, including extension through the use of VHF beacon after GPS component or battery failure.
[b]Bears captured by the National Park of Abruzzo Lazio and Molise authority before the onset of our study.
[c]3−4 yr.
[d]VHF-transmitter ear-tags.
[e]Found dead from unknown causes.

and GPS Plus, Vectronic Aerospace GmbH, Berlin, Germany) collars, the latter including a VHF beacon (Table 1). We also equipped 2 cubs (1 M and 1 F) and 2 yearlings (1 M and 1 F) still associated with their mothers, for 4 total different family groups, with VHF-transmitting ear-tags (ATS Inc., Isanti, Minnesota, USA). Each year, 3–10 adult females were marked in our bear population, including 1–7 wearing functioning GPS or VHF radiocollars annually (Table S1). Assuming a stable population size of 51 (95% CI = 47–66) bears of all ages as estimated in 2011 (Ciucci et al. 2015), and that adult females represent a stable proportion of 0.274–0.280 as in other protected brown bear populations (Eberhardt and Knight 1996, Nawaz et al. 2008), our annual sample of adult marked female bears represented approximately 21.5–71.6% (95% CIs = 16.6–77.7%) of all adult females expected in the studied population.

As soon as adult female bears with functioning radiocollars emerged from the den, we used VHF-aided homing techniques (Mech 1983) to verify presence of cubs and estimate litter size, either through direct observations or intercepting their tracks in the snow. After den emergence, we attempted to locate radiocollared family groups with yearlings at weekly intervals to assess weaning time. Excluding 7 collars that were scheduled to drop off, we purposely left 5 other non-functioning radiocollars on adult females until the completion of the study to facilitate monitoring of their reproductive status by resight. Recapture efforts by the PNALM Authority ensured removal of remaining radiocollars after the study was completed. Each year, from spring to late summer, we therefore also attempted to ascertain the reproductive status of female bears with non-functioning radiocollars by opportunistically scanning open areas within their known home ranges, or during annual counts of females with cubs (FWC) conducted from 2006 to 2014 (Tosoni et al. 2017).

Reproductive parameters

We had high rates of premature collar failure (mean tracking period: 256 ±148 SD days/ad F bear) and none of the GPS collars were functional for ≥2 years (Table 1), so our sample of tracked female bears was insufficient to produce a precise estimate of most reproductive traits. Therefore, to estimate interbirth interval and reproductive rate, we integrated our sample of female bears with functioning radiocollars with resightings of those wearing non-functioning radiocollars. In addition,

to estimate litter size, we also used sightings of distinct, unmarked family groups detected during annual counts of FWC (Tosoni et al. 2017); we treated each litter as a sample and estimated litter size based on the largest count of cubs upon first sighting (Craighead et al. 1995, Garshelis et al. 2005). We explored whether litter size was affected by the date of first sighting using generalized linear mixed models with a Poisson distribution (R package *lme4*; Bates et al. 2016), with female identification as a random factor and Julian date as a covariate. To assess age at weaning, we only used sightings of family groups comprising marked females with functioning radiocollars or dependent bears with transmitting ear tags. We calculated weaning time as the mid date between the last day we observed the family group together and the first day of ≥2 successive sightings in which the adult female was seen without cubs (Dahle and Swenson 2003b). Limited to one family group in which only 1 of 2 yearlings was tagged, we assessed weaning after ≥2 sightings in which the litter was not observed any longer in the company of the mother.

By using resight data of marked adult female bears with both functioning and non-functioning radiocollars, we estimated interbirth interval as the number of years between subsequent litters for each female, considering both complete and incomplete cycles. We followed the procedure suggested by Garshelis et al. (2005) and treated each interval, rather than each female, as the unit and summed the proportions of monitoring periods of different length (≥1 yr), resulting in cub production weighted by the corresponding proportion of those available during the study period (see table 3 in Garshelis et al. 2005).

Female bears with non-functioning radiocollars in our data set had an annual detection probability <1, and depending on when and at what frequency they had been seen in any given year, their reproductive state may have been erroneously determined. We therefore applied multi-event capture–recapture models (Pradel 2005) using Program E-SURGE (Choquet et al. 2009) to produce a more robust estimate of reproductive rate. Multi-event models are hierarchical models that allow estimation of the dynamics of a hidden process through a series of observations (events) that are affected by some error or uncertainty (Pradel 2005). As applied to our case, the hidden process was the annual transition of adult female bears from reproductive to non-reproductive state (and vice-versa) and from both these conditions to death; this process was observed with uncertainty through a series of resights (events), which were potentially affected by classification error. We used only 2 transition states (reproductive vs. non-reproductive) considering that, in our

bear population, the majority of family units split up during their second year of life; this was different from the approach of Schwartz and White (2008). To run multi-event models on our 10-year data set, we binned it into 8 monthly sessions from March to October each year, and classified female bear detections as 0 if a given female was not observed, 1 if it was observed alone, and 2 if it was observed with cubs. The data were organized in a robust design fashion, with open sessions between years ($n = 10$) and closed sessions within each year ($n = 8$). Female bears in our sample ($n = 12$) were allowed to survive, die, or reproduce between open sessions, although their state was kept fixed between closed ones, thus assuming that no mortality occurred during our sampling period each year. With E-SURGE we then used the encounter histories, the structure of 4 matrices used to describe model structure (see Text S1), and a maximum likelihood procedure to estimate both sampling and biological parameters. Sampling parameters comprised marked females' individual observation probability and the probability of misclassification of their reproductive state, whereas biological parameters included the annual transition probabilities among all states (i.e., reproductive, non-reproductive, dead) and average yearly survival rates. We used the resulting matrix of transition probabilities (matrix **T**, see Text S1), assuming they were constant across time and age, to estimate the proportion of individuals in reproductive state at each occasion, which corresponded to the annual reproductive rate (sensu Schwartz and White 2008). Similarly to Schwartz and White (2008), we multiplied the vector [1, 0] (i.e., the initial values for the stage distribution) by the matrix of transition probabilities 1,000 times, until reaching an asymptotic stable-state distribution, which corresponded to the annual proportion of reproductive and non-reproductive adult female bears in the population. To obtain an estimate of fecundity (no. of F cubs/ad F/yr), we multiplied the proportion of reproductive female bears by mean litter size (female cubs only; assuming a 50:50 sex ratio of cubs), based on all litters. Being based on the estimation of transition probabilities between alternative reproductive states, our method was robust to the bias associated with the initial reproductive structure of the sample of captured female bears (Schwartz and White 2008). Such bias may underestimate reproductive rates using traditional approaches based on actual proportions in the captured sample because of capture heterogeneity of reproductive versus non-reproductive female bears (e.g., Miller et al. 1997, Schwartz and White 2008). We entered all marked female bears in the data set when they reached sexual maturity, which we assumed to be at

4 years of age. However, to account for uncertainty about the age of first reproduction, we conducted a sensitivity analysis of our multi-event parameter estimation assuming that females did not reproduce until 5 or 6 years of age. This affected 3 marked females in the data set (F03, F06, F09), whose first year and first 2 years of resights were deleted from the data set, respectively. More details about the parameterization and estimation procedures of multi-event models are provided in Text S1.

We also estimated fecundity using the method of Chapron et al. (2013: method M4; see also Garshelis et al. 2005), where yearly ratios of the number of female cubs to the number of marked adult female bears are averaged across years (Table S1). We again assumed a 50:50 sex ratio of cubs. Compared with other standard methods (see Schwartz and White 2008 for a review), this method is unbiased because it is not dependent on the duration of the study and allows inclusion of female bears with open cycles and non-reproducing females (Chapron et al. 2013). This method is based on the actual proportion of reproductive female bears directly estimated from the captured sample; therefore, contrasting the 2 estimates of fecundity allowed us to determine whether our sample of female bears was cumulatively affected by 2 main sources of bias: heterogeneity in capture probability among females of different reproductive states (Schwartz and White 2008) and imperfect detection of female bears wearing non-functioning radiocollars.

In addition to the reproductive parameters described previously, we also grossly estimated the apparent survival of cubs by computing the proportion of cubs that were seen again as yearlings the following spring, prior to weaning (Schwartz et al. 2006c, McLellan 2015). Although this procedure is robust only if applied to female bears with functioning radiocollars, we included marked female bears with non-functioning radiocollars, as well as unmarked family groups observed in successive years, to provide a preliminary approximation of cub survival. Identification of unmarked family groups from one year to the next has been based on the spatial distance thresholds that we developed to discriminate among different FWC during annual counts (Tosoni et al. 2017). Anecdotally, based on 4 yearlings equipped with transmitting ear tags, we also report the proportion of them that survived from weaning to denning in the second year of life (Schwartz et al. 2006c, McLellan 2015).

Results

From 2005 to 2014, we annually detected 1–6 family groups, 33–100% of which were unmarked (Table 2). We failed to detect age of first reproduction for the 3 female bears captured as subadults because they never reproduced during our study (Table 1; Table S1). Excluding the tagged cub and yearling females (Table 1), we detected reproduction in 7 out of 12 adult marked female bears ($n = 80$ bear-years), for 29 total cubs produced (Table S1). We could verify reproductive status soon after den emergence (on average 15 $\pm$19 SD days) only in the 9 female bears with functioning radiocollars ($n = 14$ bear-years), and only 1 of them had cubs (FP01 in 2005; Table S1). The remaining female bears (82.5% or $n = 66$ bear-years) wore non-functioning radiocollars, and we assessed their reproductive state based on the first sighting each year, on average by 12 July (range = 6 Mar–28 Oct; Table S1).

Based on 31 total family groups (including distinct, unmarked family groups; $n = 17$), first observed on average by 27 July (range = 3 Apr–12 Dec; Table 2), we estimated mean litter size at 1.9 ($\pm$0.7 SD; range = 1–3) cubs/litter (Tables S1, S2). We did not detect a relationship between litter size and date of first sighting. Twenty-six percent of litters comprised 1 cub, 55% comprised 2 cubs, and 19% comprised 3 cubs. The range of weaning dates was 7 May–6 June in the yearlings' second year of life, averaging 26 May ($\pm$ 14 days SD) or at 1.4 years of age ($n = 4$ bear-years). Based on 7 female bears ($n = 42$ bear-years), 5 of which had right-censored open cycles, interval between litters was 3.7 years (Tables 3, S2).

Using capture–recapture multi-event modeling, we estimated that reproductive and non-reproductive marked females had an annual probability of being observed of 0.77 (95% CI = 0.70–0.84) and 0.82 (95% CI = 0.66–0.93), respectively. The monthly probability of reproductive females to be observed without cubs was 0.01 (95% CI = 0.00–0.10), which corresponded to a negligible probability of 0.003 (95% CI = 0.001–0.006) to be misclassified as non-reproductive females. Transition probabilities from non-reproductive to reproductive state were a function of the number of years since last reproduction, with female bears more likely to produce cubs 3 or 4 years after their last reproduction (Fig. 1). The model also provided an average annual survival probability of adult marked females of 0.93 (95% CI = 0.83–0.97). Based on the estimation of the proportion of females in reproductive state at each sampling occasion, and assuming transition probabilities remained constant across time and age, we estimated a reproductive rate of 0.243 (95% CI = 0.072–0.594). With age of first reproduction at 5 and 6 years, average reproductive rates were only marginally greater (0.254 and 0.261, respectively).

Table 2. Family groups of Apennine brown bears (*Ursus arctos marsicanus*) annually detected in the Abruzzo Lazio and Molise National Park, Italy, comprising marked adult females with functioning and non-functioning radiocollars (2005−2014), and those unmarked but distinguished based on distance-based criteria (2006−2014). We also report the cumulative number of cubs tallied each year and the number of yearlings still associated with their mothers within the first week of June (i.e., upper bound of weaning) of the following year. n.a.: not available.

	No. F with cubs					
Year	Functioning	Non-functioning	Unmarked	Total	No. cubs[a]	No. yearlings[a,b]
2005	1			1	2	n.a.
2006	1		3	4	7 (1)[c]	0
2007			3	3	5 (2)	4 (1)
2008		4	2	6	10	0
2009	1	1	1	3	6	7 (2)
2010			2[d]	2	4	5
2011		1		1	3	3
2012		3	2	5	11 (3)	1
2013		1	3[d]	4	6	1 (1)
2014		1	4	5	11 (1)	3

[a]No. of within-year verified mortalities in parentheses.

[b]Cubs born the previous year that have been detected still associated to their mothers within the upper bound of weaning (i.e., first week of Jun of current year).

[c]One cub was found dead in Jul 2006, before any females with cubs were sighted.

[d]Including 2 (2010) and 1 (2013) females with cubs (and corresponding cubs) gone undetected in current year but that were seen as family groups with yearlings the successive year, when they were distinguished using distance-based criteria (Tosoni et al. 2017).
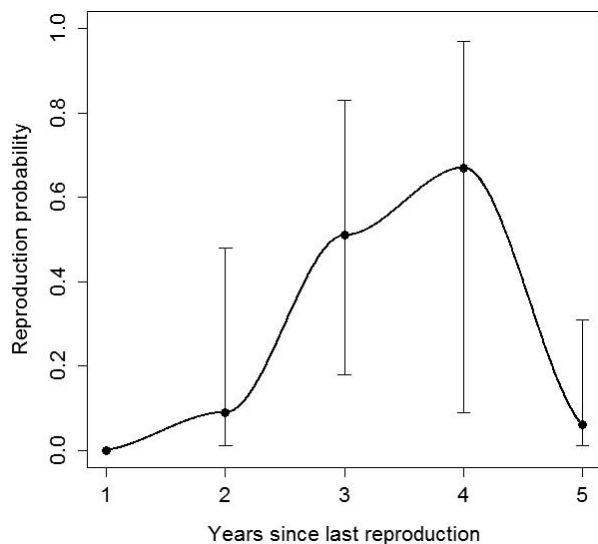

Fig. 1.   Probability for an adult (>4 yr old) female Apennine brown bear (*Ursus arctos marsicanus*) to be in reproductive state as a function of the number of years since last reproduction. Estimates derived from a multi-event, capture–recapture model using a sample of 12 marked adult female bears (2005–2014, central Apennines, Italy). Error bars represent 95% confidence intervals.

Multiplied by the number of female cubs based on average litter size and assuming a 50:50 sex ratio of cubs, the estimated reproductive rate corresponded to a fecundity estimate of 0.23 female cubs/adult female/year. In contrast, fecundity directly calculated from the captured sample using the method of Chapron et al. (2013) was 0.18 (± 0.13) female cubs/adult female/year, corresponding to a mean proportion of reproductive female bears of 0.179 (± 0.138; Table S1).

Considering 25 FWC tallied from 2006 to 2013, out of 47 total cubs, only 23 (*n* = 11 family groups) were re-sighted as yearlings associated to their mothers before weaning (i.e., within the first week of Jun), providing a crude approximation of apparent cub survival of 0.49. Although anecdotal, 2 (F12 and M14) of the 4 dependent bears equipped with VHF ear tags died during the summer, shortly after weaning. One of those bears (M15) was still associated with his mother after den emergence in its second year of life, just before the ear tags failed. Another (F11) survived until the completion of the study, at the age of 7 years, as confirmed by direct observation of her color-coded ear tags (Table 1).

Discussion

This study is a first attempt to estimate the reproductive characteristics of Apennine bears at the population

Table 3. Calculation of average interbirth interval of female Apennine brown bears (*Ursus arctos marsicanus*; Abruzzo Lazio and Molise National Park, Italy, 2005−2014) following Garshelis et al. (2005) to account for intervals that remained open when the female was last observed. Sightings data were obtained from marked female bears, including those with functioning and non-functioning radiocollars.

Time since last litter (yr)	No. periods observed	No. periods ending in cub production	No. incomplete periods not observed the next yr	Observed periods ending in cub production (%)	% of all periods available to end in cub production	% of all available periods ending in cub production	Interval length (yr) weighted by % producing
1	13	0	3	0.0	100.0	0.0	0.00
2	11	1	1	9.1	100.0	9.1	0.18
3	8	4	1	50.0	90.9	45.5	1.36
4	3	2	0	66.7	45.5	30.3	1.21
5	1	0	0	0.0	15.2	0.0	0.00
6	1	1[a]	0	100.0	15.2	15.2	0.91
Total		8	5			100.0	3.67

[a]Reproduction was assumed to reduce the risk of underestimation.

level, complementing previous and ongoing work on estimating size (Gervasi et al. 2012, Ciucci et al. 2015), trends (Gervasi et al. 2017), and productivity (Tosoni et al. 2017) in this small bear population. All reproductive traits that we estimated rank Apennine bears toward the lower spectrum of the reproductive performance of other, non-hunted brown bear populations in Europe, Asia, and North America (Table S2). An interbirth interval of 3.7 years, further confirmed by the relationship between transition probabilities and years since last reproduction, is longer in Apennine bears compared with other non-hunted, European bear populations (Table S2). Bears do not generally reproduce before dependent bears are weaned, and length of litter interval depends on length of family association with maternal care negatively correlated with frequency of litters (Schwartz et al. 2003; Zedrosser et al. 2009, 2013). The relatively long interbirth interval we estimated in Apennine bears was not expected based on the length of maternal care with respect to other European bear populations, and it may be an indication of adult females' reduced fecundity, even though the role of bias in our data should be taken into account. Also, mean litter size in Apennine bears was lower than other brown bear populations, such as the long-isolated Cantabrian population in Spain and the reintroduced population in the Eastern Alps of Italy (Table S2).

According to our estimate of weaning, family break-up occurred during the mating season of the litter's second year of life, similar to observations from other European brown bear populations (Swenson et al. 1997; Frković et al. 2001; Dahle and Swenson 2003a, b). Although our estimate of weaning rests on a particularly small sample size (*n* = 4 family groups with functioning radiocollars),

it is supported by sightings of 4 family groups with females wearing non-functioning radiocollars (*n* = 5 family group-years) associated with their yearlings up to March–May of the year following birth; the same females were then repeatedly seen alone by August–September of the same year. However, we would expect some additional variability of weaning time in Apennine bears, as indicated by 4 unmarked family groups (out of 25 tallied from 2006 to 2013), whose yearlings were still associated with their mothers through August–September of their second year of life.

The combination of a relatively long interbirth interval, a relatively small litter size, and a non-trivial proportion of non-reproducing adult female bears contributed to a relatively low reproductive rate in Apennine bears. Using multi-event modelling based on a stable-state distribution of transition probabilities, we estimated a reproductive rate of 0.24, which corresponds to fecundity of 0.23, ranking Apennine bears low compared with other European and North American brown bear populations (Table S2). As suggested by the sensitivity analysis, our estimate of reproductive rate was robust to uncertainty in the age of first reproduction. Our findings also indicated that, although some of the marked females wore non-functioning radiocollars, the overall detection probability of our sample of captured females was substantial and classification error of their reproductive state was negligible. Nevertheless, the lower estimate of fecundity (i.e., 0.18 F cubs/ad F/yr) obtained from the yearly proportion of reproductive females in the captured sample indicates that our sample of captured females was possibly biased. Likely sources of bias may have originated from a lower capture probability of parous females (Miller et al. 1997,

Schwartz and White 2008) and imperfect detection of captured female bears with non-functioning radiocollars.

Additional indications that the reproductive performance of Apennine bears may be low are provided by our failure to document reproduction in 5 adult female bears, each tracked for 5–9 years, and in 3 female bears captured as subadults and then tracked for 2–7 years. The latter, in particular, also suggests that age at first reproduction may be >4 years (Table S1). In addition, we failed to document reproduction the year after weaning in 4 marked females (F05, F10, F13, FP01) tracked for 2–5 years following reproduction for 8 total reproductive events (Table S1). Although failure to document reproduction could have originated from the imperfect detection of marked female bears (see below), based on the estimated detection probability and classification error we suspect that these cases likely reflect lack of reproduction rather than missed detection. At best, they represented cases in which reproduction occurred over unusually long interbirth intervals (i.e., ≥6 yr; Table S1).

Given our sampling context, we recommend that the results we hereby report be interpreted cautiously. Whereas robust estimates of reproductive parameters in bear populations are generally obtained using a known-fate sampling framework (i.e., through longitudinal monitoring of a sample of captured bears with functioning radiocollars; Schwartz et al. 2006a, b; Mace et al. 2012), we included marked females with non-functioning radiocollars to estimate interbirth interval and reproductive rate, and unmarked family groups to estimate litter size. This inclusion, although essential to increase sample size, introduced potential sources of bias due to incomplete detectability and lack of sampling control, in turn contributing to the potentially erroneous classification of reproductive state. To reduce this risk, we annually ensured an intensive and continuous search effort to anticipate the date of first sightings of marked female bears; however, any reproductive trait we estimated, including presence or absence of a litter, might be biased by the partial or total loss of cubs that might have occurred but gone unnoticed from parturition to first sighting (i.e., a female seen alone late in the summer could have lost a litter in the preceding months; Schwartz et al. 2006a). Accordingly, our estimates of litter size may be biased low, and interbirth interval may be biased high. In addition, we might have estimated a premature weaning time in case mortality of a litter was confounded with weaning. For these reasons, however, we used multi-event modelling to produce a more robust estimate of reproductive rate based on transition probabilities. Multi-event modelling indeed revealed that the probability of detection

of marked female bears in our study was <1. Nevertheless, we had a high detection probability of reproducing and non-reproducing marked female bears. The intense search effort in a relatively small study area, coupled with high visibility of adult females at buckthorn (*Rhamnus* spp.) patches during summer (Tosoni et al. 2017), likely increased the detection probability. We recognize that a violation of the closure assumption (i.e., no mortality occurred during closed sessions) would generate a negative bias in detection estimates, and hence an overestimation of survival probabilities. However, no marked, adult female bear was found dead during the study period, suggesting that such bias, if present, would have a negligible effect on our estimates.

Our multi-state capture–recapture application using a transition matrix for the estimation of a stable-state distribution confirms this is a useful tool to produce unbiased estimates (i.e., independent from the initial capture state) of reproductive rate. Schwartz and White (2008) previously used such a design to estimate reproductive rate in grizzly (*Ursus arctos*) and black (*U. americanus*) bear populations; compared with their work, we faced 2 additional problems: 1) we included captured female bears with non-functioning radiocollars, so we could not assume that detection and survival probabilities were known with certainty; and 2) using a limited number of observations, our definition of the reproductive state of some female bears was prone to misclassification. By making use of the multi-event approach, we both estimated detection and survival probability from the data and also incorporated state uncertainty into parameter estimation, although at the cost of reduced precision.

Although primarily affected by the species' evolutionary life history (Zedrosser et al. 2013), reproductive parameters within and among brown bear populations are expected to vary significantly (Steyaert et al. 2012). Reproductive performance in brown bears has been shown to be affected by nutritional status (Hilderbrand et al. 1999, Ferguson and McLoughlin 2000), environmental conditions (McLellan 1994, Nawaz et al. 2008), social behavior and population density (Wiegand et al. 1998; Miller et al. 2003; Schwartz et al. 2003, 2006a; Støen et al. 2006). In particular, in bear populations close to carrying capacity, density-dependent effects are expected to depress fecundity, through a delayed age of first reproduction, lowered cub production and recruitment, or reduction of cub survival (Schwartz et al. 2006a, van Manen et al. 2016). Underlying mechanisms of density-dependent effects may include several forms of competition, including interference competition through social dominance and displacement (Miller et al. 2003, Gende and Quin

2004, McLellan 2005, Nevin and Gielbert 2005, Rode et al. 2006, Steyaert et al. 2013), reproductive suppression (Støen et al. 2006, Ordiz et al. 2008), or intraspecific killing (Gosselin et al. 2015). The latter, in particular, has been recognized as a relevant factor affecting young survival (Swenson et al. 2001a, b) and potentially affecting reproductive performance (Chapron et al. 2009, Gosselin et al. 2015). Whereas adult female bears in our population did not appear to experience poor nutritional conditions (Ciucci et al. 2014), we anecdotally reported ≥2 verified cases of conspecific killing (P. Ciucci, unpublished data). Indeed, density-dependent factors may play a role in Apennine bears that occur at a relatively high density in a restricted core distribution (Ciucci et al. 2015), which could explain our low estimate of apparent cub survival. In contrast, our estimate of adult female survival is within the range expected for protected, non-declining brown bear populations (Harris et al. 2006). These observations suggest that low fertility and recruitment may currently be more limiting than adult survival in Apennine bears.

Given the small and long-isolated nature of our study population, the net effects of density-dependent factors may be confounded in Apennine bears with the expression of inbreeding depression. Although adequate reproductive performance is still observed in bear populations with low genetic diversity (Paetkau et al. 1998), reproductive traits in small and highly inbred bear populations are expected to reveal expressions of inbreeding depression (Laikre et al. 1996), primarily affecting body mass at birth, juvenile survival, and fecundity of adult females (Keller and Waller 2002). Although there is no genetic evidence of inbreeding in Apennine bears, the genetic diversity of this population is particularly low (Lorenzini et al. 2004). Therefore, relatively low reproductive performance and low cub survival may in part be due to inbreeding depression. Inbreeding depression and density-dependent effects may interact through human-caused mortality of juvenile bears, which is mostly unreported, possibly further depressing recruitment and population growth.

The density-dependent versus inbreeding depression hypotheses entail substantially different conservation scenarios. However, our results at this stage are not robust enough to definitively inform management in this respect. Clearly, the reduced reproductive performance of Apennine bears and low apparent cub survival are consistent with the lack of range expansion in this bear population during the recent decades (Boscagli 1999, Ciucci and Boitani 2008), particularly in light of persistent human-caused mortality (Falcucci et al. 2009). Al-

though we concur with previous recommendations that effective mitigation of human-caused mortality and conflict over multiple use be urgently achieved to facilitate population expansion (Lorenzini et al. 2004, Ciucci and Boitani 2008, Anonymous 2011, Ciucci et al. 2015), we also maintain that a deeper understanding of population dynamics requires longer term and more in-depth demographic studies (e.g., Garshelis et al. 2005, Schwartz et al. 2006d). In addition to raising concerns over the efficacy of current conservation measures for this imperiled bear population, our findings emphasize the urgent need for longitudinal demographic and ecological studies. Further investigations of the potential contribution of density-dependent or inbreeding depression effects on demographic parameters are needed to better understand the lack of growth and expansion of the Apennine brown bear population.

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Supplemental material

Text S1. Details about multi-event capture–recapture models developed in Program E-SURGE to estimate interbirth interval and reproductive rate of Apennine brown bear population using data set of marked adult female bears.

Table S1. Reproductive chronology of 14 marked female Apennine brown bears as reconstructed by direct observation during 2005–2014 in the Abruzzo Lazio and Molise National Park, Italy.

Table S2. Reproductive characteristics in hunted and non-hunted Apennine brown bear populations across Europe, Asia, and North America.