

Counts of unique females with cubs in the Apennine brown bear population, 2006–2014

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Abstract: Brown bears (*Ursus arctos marsicanus*) in the Apennines, central Italy, survive in a precarious conservation status but the reproductive performance of the population has never been formally assessed. Each year, from 2006 to 2014, we conducted surveys of females with cubs (FWC) to estimate the minimum number of female bears that reproduced and annual productivity in this bear population. We discriminated unique family groups based on simultaneity of sightings, presence of individually recognizable bears, and ad hoc distance-based rules developed using Global Positioning System relocations from 11 adult female bears in our study population. To estimate the true number of FWC from unique counts, we applied 2 estimators (Chao2, Capwire) known to handle heterogeneity in sighting probabilities relatively well at small sample sizes. Annually, we estimated 1–6 ($\bar{x} = 3.9 \pm 1.5$ SD) unique FWC and tallied a minimum of 3–11 ($\bar{x} = 7.4 \pm 3.0$ SD) cubs in the population. No temporal trend in FWC was observed and the mean estimate of reproductive females corresponded well with an independent estimate of total population size obtained in 2011. Although we confirmed that the population is still reproductively functional, the small number of reproducing females and their year-to-year fluctuations dramatically underlined the precarious status of Apennine bears. We concur with previous authors that counts of unique FWC are an effective means to assess reproductive output in small bear populations, although it is advisable that more in-depth demographic studies complement this technique.

Key words: Capwire, Chao estimator, demography, distance-based criteria, females with cubs, FWC counts, Italy, small populations, *Ursus arctos marsicanus*

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Robust estimation of population size and assessment of long-term reproductive potential are essential to evaluate factors that might limit growth of bear (*Ursidae*) populations (Schwartz et al. 2006). In brown bears (*Ursus arctos*), estimates of population size and trends have been obtained from application of mark–resight protocols (Mace et al. 1994, Miller et al. 1997, Solberg et al. 2006), longitudinal studies of radiocollared individuals (Schwartz et al. 2006, Brodie and Gibeau 2007), and mark–recapture estimates based on noninvasive samples (Boulanger et al. 2002, Bellemain et al. 2005, Kendall et al. 2008, Pérez et al. 2009, Sawaya et al. 2012, Ciucci et al. 2015a).

Bear family groups are more conspicuous relative to other segments of the population, so annual counts of unique females with cubs (FWC, hereby used excluding

yearlings and other dependent offspring; Knight et al. 1995, Keating et al. 2002) have been used as a practical index to approximate population abundance and trends (Schwartz et al. 2008, Interagency Grizzly Bear Study Team 2012). This technique has been adopted to assess year-to-year reproductive performance (e.g., Palomero et al. 1997) or, by assuming that the rate of change in FWC reflects the rate of change in the actual population size, to evaluate population size and trends in many brown bear populations (North America: Knight et al. 1995, Eberhardt and Knight 1996, Brodie and Gibeau 2007, Harris et al. 2007, Schwartz et al. 2008, Eberhardt and Breiwick 2010, Interagency Grizzly Bear Study Team 2012; Europe: Wiegand et al. 1998, Solberg et al. 2006, Palomero et al. 2007, Gonzalez et al. 2016).

However, FWC sighting rates have been recognized to be seriously affected by annual fluctuations in food conditions, habitat use, and social interactions (Wielgus and Bunnell 1995, Mattson 1997), as well as by

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year-to-year variability in search effort (Mattson 1997, Fernández-Gil et al. 2010, Doak and Cutler 2014). As a consequence, counts of unique FWC are recognized to be of limited utility unless they are corrected using adequate estimators of the true number of FWC in the population (Boyce et al. 2001b, Keating et al. 2002, Cherry et al. 2007).

Although field protocols to obtain sightings of FWC are relatively simple to adopt (Knight et al. 1995), the correct assignment of sequential sightings to the same group or different groups plays a fundamental role in the application of the technique. Misidentification of family groups may in fact lead either to Type I or Type II errors (i.e., false and missed distinction, respectively; Keating et al. 2002), in both cases strongly affecting counts of unique FWC (Schwartz et al. 2008, Interagency Grizzly Bear Study Team 2012). In most applications, the criteria used to discriminate among bear family groups are based on the distance between sequential sightings, their detailed description, or the presence of individually recognizable bears (Knight et al. 1995, Solberg et al. 2006, Schwartz et al. 2008). Rules based on the distance separating sequential sightings rely on movement data of radiocollared family groups related to the timing between successive sightings, providing for a maximum distance (e.g., twice the mean annual home range; Blanchard and Knight 1991) beyond which it is unlikely that 2 sequential sightings are from the same family group. Ordiz et al. (2007) improved these rule sets (i.e., distance-based criteria) for European bear populations by statistically relating the very high frequency (VHF)-revealed distance separating 2 sequential sightings of family groups to the lag between them. Today, Global Positioning System (GPS) movement data make it possible to further refine distance-based criteria both by accounting for the specific ecological and demographic conditions of a given bear population, and by taking advantage of the increased temporal resolution of GPS movement data (e.g., hourly relocation intervals).

Another critical aspect concerning the interpretation of counts of unique FWC is related to the estimators used to inflate FWC data into the true number of FWC in the population (Keating et al. 2002). Counts of unique FWC are expected to underestimate the true number of bear family groups in the population, whose detection probability will be <1 in most cases (Keating et al. 2002, Schwartz et al. 2008, Van Manen et al. 2014). Both parametric and nonparametric estimators have been evaluated to provide a reliable estimate based on the frequency of independent FWC sightings (Eberhardt and Knight 1996; Boyce et al. 2001a, b; Keating et al. 2002, Cherry et al. 2007). Specifi-

cally, the biased-corrected Chao estimator (Chao2; Chao 1989) appears to perform relatively better than others under variation in sighting heterogeneity, sample size, and sampling effort (Cherry et al. 2007). Nevertheless, unstable estimates are expected when applying this estimator to small bear populations because a small sample size may correspond to non-ideal estimation conditions (Cherry et al. 2007, Fernández-Gil et al. 2010, Interagency Grizzly Bear Study Team 2012). Using estimators that combine data across years (Boyce et al. 2001b) or allow the use of covariates to model detection probability (Cherry et al. 2007) are options to correct for small sample size, but theoretical and practical limitations still persist when these estimators are used with particularly limited data sets (Keating et al. 2002, Cherry et al. 2007, Interagency Grizzly Bear Study Team 2012).

The Apennine brown bear (*U. a. marsicanus*; Altobello 1921) is 1 of 4 very small and isolated bear populations in western Europe (Zedrosser et al. 2001). Although it is recognized as critically endangered by the Italian Red List (Rondinini et al. 2013), reliable data on the productivity of this bear population are still lacking (Ciucci and Boitani 2008). To fill this knowledge gap, concurrently with ongoing demographic monitoring (Gervasi et al. 2008, 2012; Ciucci et al. 2015a), we conducted surveys of FWC to assess reproductive output and minimum productivity in the Apennine bear population during 2006–2014. Specifically, by using ad hoc developed, GPS-derived distance-based criteria to facilitate distinction of FWC in the Apennine brown bear population, the aims of our study were to (1) adapt counts of unique FWC to local settings, and define ideal conditions for the long-term application of the technique to this bear population; (2) estimate number and trends of reproducing female bears and their minimum annual productivity; and (3) discuss the implications of the reproductive performance of Apennine bears for the conservation of this relict and imperiled population.

Study area

Our study area (Fig. 1), coincident with the stable range of reproductive female bears, is included in the core range of Apennine bears (Central Apennines, Italy; Ciucci et al. 2017). Comprising the Abruzzo, Lazio and Molise National Park (PNALM; 507 km²) and its outer buffer zone (787 km²), we defined the study area by including (1) the outermost locations of all verified sightings of bear family groups during the study period; (2) telemetry locations ($n = 22,268$ VHF- and GPS-locations) of 6 female bears for whom we had evidence of reproduction from

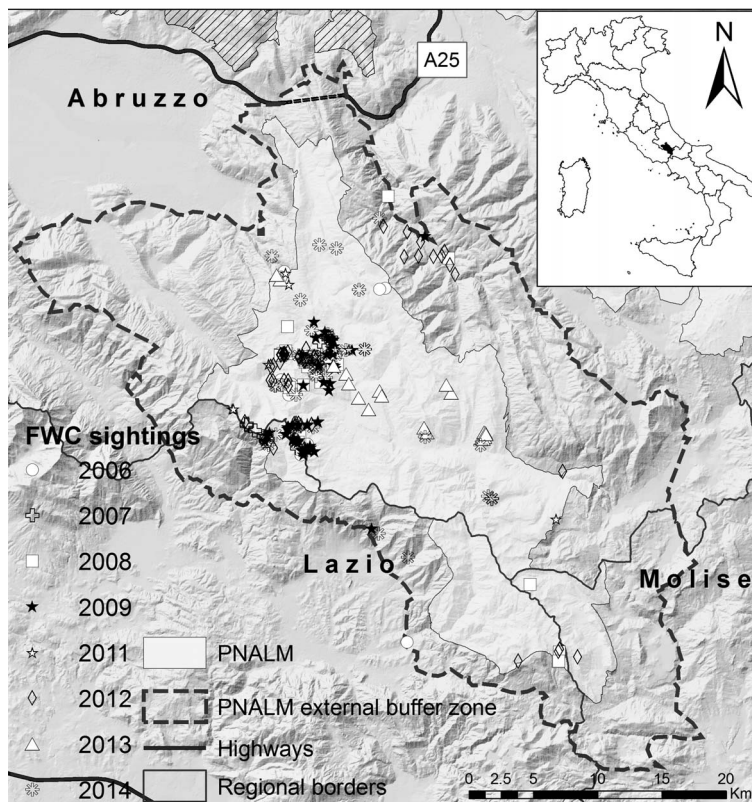


Fig. 1. Location of the study area in the Central Apennines (Abruzzo, Lazio and Molise National Park [PNALM], Italy, inset), and spatial distribution of all verified sightings ($n = 323$) of 31 unique female brown bears (*Ursus arctos marsicanus*) with cubs (FWC) recorded from 2006 to 2014.

2004 to 2014; and (3) locations of bear family groups occasionally reported since the 1970s (Zunino and Herrero 1972; Zunino 1976; C. Sulli, PNALM, unpublished data). The study area is typically mountainous, with elevations of 400–2,285 m. The climate is Mediterranean montane, with dry summers, cold winters (Piovesan et al. 2003), and snow cover extending from mid-December to March. The largest share (55.6%) of the study area is covered by forests, primarily beech (*Fagus sylvatica*), followed by grasslands and subalpine meadows (14.5%), and agricultural areas (8.4%; EEA 2006). High-elevation grasslands are attractive to bears during spring and summer. In particular, buckthorn (*Rhamnus alpinus*) patches are intensively used by bears in August–September when they heavily feed on buckthorn berries (Ciucci et al. 2014). Additional details of the study area have been reported elsewhere (Falcucci et al. 2009; Ciucci et al. 2014, 2015a).

In 2011, 51 bears of all ages (95% CI = 47–66 bears) were estimated in the core population, including 28 (95%

CI = 26–35) females (Ciucci et al. 2015a). Prior to 2006, FWC were only incidentally reported. A minimum 4–6 FWC were believed to be present in the population in the early 1970s (Zunino and Herrero 1972, Zunino 1976), but these and similar reports in the following years rested on unsubstantiated field methods and undefined criteria to distinguish family groups (Zunino and Herrero 1972, Ciucci and Boitani 2008). During the period of our study, bears in the core distribution showed a marked geographic closure (Gervasi et al. 2012); however, we cannot discount that a few dispersing female bears might have occasionally produced cubs in the much wider peripheral portion of the range.

Methods

Field methods

From 2006 to 2014, we used ground-based surveys from stationary vantage points to conduct annual counts of unique FWC during July–September to account for

Table 1. Characteristics of concurrent observation sessions conducted to detect female brown bears (*Ursus arctos marsicanus*) with cubs (FWC) in the Abruzzo, Lazio and Molise National Park, Italy, 2006–2014. n.a., not applicable.

Year	No. of sessions	Month	No. of vantage points	Sampled areas		Operators (min.-max.)	Observation hr			Effort ^a	Sightability index ^b		No. of unique FWC ^c
				No.	km ²		Dusk	Dawn	Total		All bears	FWC	
2006	4	Jul–Sep	62	31	93	12–36	30	126	641	2,745	12.5	2.0	3
2007	3	Jul–Sep	91	37	137	30–65	82	207	969	3,465	11.6	0.9	3
2008	7	Jul–Sep	105	40	147	21–42	101	279	1,113	3,205	7.5	1.5	5
2009	4	Aug–Sep	79	33	114	32–59	31	185	611	2,401	14.4	3.3	3
2010	n.a.	-	-	-	-	-	-	-	-	-	-	-	3 ^d
2011	5	Aug–Sep	56	25	117	22–56	80	209	810	2,486	15.1	0.4	1
2012	5	Aug–Sep	56	25	95	44–58	68	256	888	2,794	14.0	1.8	3
2013	6	Aug–Sep	46	25	94	66–78	108	425	1,638	5,709	8.8	0.0	0
2014	4	Aug–Sep	60	24	95	62–74	104	235	931	3,174	9.7	1.9	4

^a $\sum_{j=1}^n \{[\sum_{i=1}^N (Km_i^2 \times hrs_i)] \times \log(0.01 \times N)\}$ (see text).

^bNo. bears sightings/100 hr, and no. FWC sightings/100 hr.

^cCounts of unique FWC referring to simultaneous sessions only; for cumulative counts of unique FWC, see Table 4.

^dEstimated from unduplicated counts in all years, except those following hard-mast yield years (i.e., 2008, 2012, and 2014).

their increased visibility. We adopted 3 complementary observation strategies to increase coverage, probability of sightings, and accuracy in discriminating family groups. First, we relied on concurrent observation sessions to ensure distinction of family groups based on simultaneity of sightings (see below). Using 8–10 × binoculars and 20–60 × spotting scopes, we conducted 3–7 seasonal replicates of simultaneous sessions each year, involving 12–78 trained observers concurrently scanning 93–147 km² of open areas from 46 to 105 vantage points (Table 1). We selected sampled areas to embrace as many large meadows, alpine pastures, clear cuts, and avalanche chutes as possible, including buckthorn meadows where bears congregate in late summer to forage on berries (Ciucci et al. 2014). Each simultaneous session comprised 3-hour observation bouts replicated at dusk and dawn each day for 2–3 consecutive days. We annually adjusted the onset of simultaneous sessions to the prevalent phenology of seasonal key foods, in particular to the ripening of buckthorn berries. Second, we conducted observations opportunistically using a team of 1–10 observers who repetitively scanned areas with high probability of being used by family groups, or to verify sightings reported by third parties. Since 2011, we supplemented opportunistic sightings with 7–17 camera traps (UOVISION UV572; Uovision Europe, Kangasniemi, Finland) in up to 36 forested sites. Third, we also considered sightings of bear family groups incidentally reported by trained observers during other field and/or patrolling activities; sightings reported by untrained individuals were only considered if

promptly verified by trained observers, or otherwise supported by reliable evidences (e.g., videos or photographs whose date and location could be proven). Upon sighting a bear family group, each observer recorded date, time, the number of bears in the group, and any recognizable individual trait (e.g., collar, ear-tags, or natural markings). To record the geographic coordinates of a sighted family group, operators marked its approximate location on a 1:10,000 scale aerial photo. For the scope of this analysis we did not consider sightings of marked females that were aided by telemetry because they departed from random sampling (Keating et al. 2002, Brodie and Gibeau 2007).

To translate the raw sighting data to estimated total number of FWC, we adhered to the following steps (illustrated in the sections below): (1) application of rules, including ad hoc developed distance-based criteria, to assign raw sightings to unique FWC and obtain minimum counts of unique FWC; (2) subsampling of raw sighting data, according to temporal autocorrelation rules, to obtain a sample of independent sightings for each unique FWC; and (3) application of estimators to independent sighting frequencies to estimate total FWC.

Rules for discriminating family groups

A basic assumption of counts of unique FWC is that each family group is correctly identified (Knight et al. 1995, Keating et al. 2002). Following Knight et al. (1995), we classified a group of bears as a family unit according to the bears' association, social interactions, and relative

Table 2. Criteria used to discriminate among brown bear (*Ursus arctos marsicanus*) family groups seen during concurrent and opportunistic observation sessions (Abruzzo, Lazio and Molise National Park, Italy, 2006–2014).

Observation strategy		Criteria to distinguish bear family groups
Simultaneous sightings		Family groups are distinct if seen simultaneously (± 5 min) in different locations by ≥ 1 observer
Non-simultaneous sightings	Family groups include marked or tagged bears	Family groups are distinct if ≥ 1 include individually recognizable bears based on clearly detectable marks or tags
	Family groups do not include marked or tagged bears	Using ad hoc developed distance-based criteria, family groups are distinct if observed beyond the distance threshold at a time lag equal to the time elapsed between the sightings.

body size. Cubs and yearlings were distinguished based on their relative size, facial development, and behavior (Craighead et al. 1995, O’Brien and Lindzey 1998). We did not distinguish family groups based on the number of cubs because of their possible mortality during the survey period; we also did not rely on pelage color or size variation because these can change with condition of light, perspective, and growth (Knight et al. 1995). We differentiated among family groups by (1) simultaneity of sightings, (2) presence within family groups of individually recognizable bears, hereby defined as those with obvious natural markings (e.g., visible scars, injured ears, missing foot) or as instrumented (i.e., colored ear tags and/or collars), and (3) ad hoc developed distance-based rules (Table 2).

Distance-based criteria

Similarly to Ordiz et al. (2007), we modeled the relationship between the Euclidean distance travelled and the corresponding time lag using GPS movement data ($n = 18,988$ locations) acquired at a rate of 4–24 fixes/day from 11 adult female bears in our study area (2006–2010); we then used this relationship to predict spatio-temporal thresholds beyond which it is highly unlikely that 2 sequential sightings belong to the same family group. We based our model choice on a cross-validation approach compared with the R^2 statistics (Ordiz et al. 2007) because we were more interested in the model’s prediction performance than in fitting the observed data (Arlot and Celisse 2010). Movement rates and sightability of female bears are expected to vary seasonally (Dahle and Swenson 2003, Ordiz et al. 2007), so we developed regression functions for 3 bi-monthly seasons: spring (Apr–May: including den emergence and the start of the mating period), early summer (Jun–Jul: the mating season), and late summer (Aug–Sep: including hyperphagia and ripening of *Rhamnus* berries). For each female

bear and each bi-monthly season we compiled a data set containing all Euclidean distances travelled at increasing time lags, accounting for all possible permutations from time lags of 1–1,440 hours (i.e., 60 days). In particular, letting s_i and z_i , with $i = 1, 2, \dots, n$, be the coordinates and time, respectively, of the i th GPS location of a given female bear; from the sets $\{s_i\}_{i=1}^n$ and $\{z_i\}_{i=1}^n$, we then computed the vector of distances $\{d_i\}_{i=1}^n$ and associated elapsed times $\{t_i\}_{i=1}^n$ (hr). We then merged the distance data sets of all individual females and tallied the distances by the corresponding time interval. For each seasonal data set, we then computed a quantile (q) of the distances, with $q \in (0.50, 0.55, 0.60, \dots, 0.95)$, and for each q we randomly split in half the subset of distances above q into a training and a validation subset to be used in a cross-validation approach. We then used the training subset to fit several power and logarithmic regression functions of distance versus time (Table 3), based on which we predicted the distances of the validation subset. We repeated the above procedure for all combinations of regression functions and quantiles, and for each of them we finally computed the mean squared difference between observed and predicted distances using the cross-validation mean

Table 3. Logarithmic and power regression equations used to describe distances travelled (d) as a function of time (t) by 11 adult Global Positioning System-collared female brown bears (*Ursus arctos marsicanus* [i]; Abruzzo, Lazio and Molise National Park, Italy, 2006–2010).

Model	Equation
Mod. 1	$E(d_i) = \alpha + \beta t_i$
Mod. 2	$E(d_i) = \alpha + \beta t_i^2$
Mod. 3	$E(d_i) = \alpha + \beta_1 t_i^2 + \beta_2 t_i^3$
Mod. 4	$E(d_i) = \alpha + \beta \log(t_i)$
Mod. 5	$E(d_i) = \alpha + \beta t_i^{1/2}$

squared error (CVMSE); we repeated the whole procedure described above 200 times and, in the c th iteration, we computed the CVMSE as

$$\text{CVMSE}_c = \frac{\sum_{i \in N_c} (\hat{d}_i - d_i)^2}{n_c}$$

where N_c is the set of observation indices of the validation subset, n_c is the number of observations in the validation subset, and d_i and \hat{d}_i are the observed and the predicted distance, respectively, at time-lag i . We then chose the regression function and corresponding quantile that yielded the overall lowest mean CVMSE, computed as

$$\frac{\sum_{c=1}^{200} (\text{CVMSE}_c)}{200}$$

However, differently from Ordiz et al. (2007), none of our GPS-collared adult females had cubs during the tracking period, whereas females with cubs are known to move shorter distances during the mating period (Dahle and Swenson 2003, Martin et al. 2013, Graham and Stenhouse 2014). By recognizing that this may introduce a serious bias into our analysis (see also Discussion), we accordingly (1) increased observation effort to the enhance the likelihood of simultaneous sightings among different FWC, thereby reducing the number of FWC sightings whose assignment into distinct family groups required distance-based criteria; (2) used a more conservative method than Ordiz et al. (2007) to define distance-based thresholds (see above); and (3) empirically calibrated the distance-based criteria against a sample of known (i.e., marked) females with cubs in our bear population. In particular, with reference to the latter, we first calculated the upper limit of the prediction intervals, $CI_{\text{upp}} \in (0.75, 0.80, 0.85, 0.90, 0.95)$ for the lowest CVMSE models; we then applied these thresholds to observed distances among sightings of known FWC (i.e., natural marks, ear tags, or non-functioning radiocollars; see Tosoni et al. 2017) among our sample ($n = 91$ pairwise comparisons between all sightings, ranging from 1 to 36/year, of 6 known FWC corresponding to 12 unique FWC, including litters produced in multiple years). Finally, we chose the prediction interval that held Type I error (i.e., false distinction) the lowest while minimizing Type II error (missed distinctions). Whereas Type I error should be avoided to favor a conservative management approach (Keating et al. 2002, Cherry et al. 2007), Type II error should be controlled for because it may potentially lead one to underestimate cubs' mortality by first underestimating the number of reproducing females, and in turn the total number of cubs born, in the population each year. Finally, using the same pooled sample of

known FWC in our bear population, we also compared the performance of the distance-based criteria developed by Ordiz et al. (2007) with that of our ad hoc developed criteria. Data set development, model fitting, and cross-validations were all performed using Program R (R Core Team 2016; the code is available from GM upon request).

Counts and estimates of females with cubs

We used univariate Generalized Linear Models with a Poisson distribution, and Log Linear Models (R Core Team 2016) to explore the yearly relationship between counts of unique FWC and proxies of sightability and sampling effort (cf. Knight et al. 1995, Mattson 1997). For concurrent observation sessions, we related the annual number of unique FWC to both sighting effort and the number of bears sightings/100 hours, the latter being a proxy of bear mobility possibly related to food conditions (e.g., Doak and Cutler 2014). We quantified sighting effort as

$$\sum_{j=1}^n \left\{ \left[\sum_{i=1}^N (Km_i^2 \times hrs_i) \right] \times \log(0.01 \times N) \right\}$$

with $i = 1, 2, \dots, N$ being the number of sample (i.e., open) areas included in each session, and $j = 1, 2, \dots, n$ being the number of sessions implemented in each year (Table 1). Annual sighting rate during opportunistic sessions may be positively correlated both with search effort and an increased knowledge of places to search for FWC (Boyce et al. 2001b, Doak and Cutler 2014); therefore, we would expect both an increase in the fraction of FWC seen ≥ 1 and a positive relationship between counts of unique FWC and mean frequency of raw FWC sightings through the years (Knight et al. 1995, Doak and Cutler 2014). We accordingly tested for these relationships by using Generalized Linear Models based on Poisson and quasi-Poisson distributions, with counts of unique FWC as the dependent variable and year as a covariate (R Core Team 2016).

Conversion of raw sighting data to counts of unique FWC (above) included corresponding resight observations for each FWC summarized by date. Resight data were used with 2 estimators to predict the true number of FWC in the population: (1) the biased-corrected Chao estimator (Chao2; Chao 1989, Cherry et al. 2007), using Program SPADE (Chao et al. 2016), and (2) the estimator implemented in Program Capwire (Miller et al. 2005, Pennel et al. 2012). Whereas the former has been demonstrated to be robust to heterogeneity in sighting probabilities and variability in sighting effort (Cherry

et al. 2007), the latter handles heterogeneity and is also expected to perform well at small sample size (Miller et al. 2005). Capwire, to our knowledge, has never been applied to counts of unique FWC before, even though simulation work suggests that it outperforms the Chao estimator when used with small populations (Miller et al. 2005). The closed population assumption, required by both estimators, represents a negligible problem in our bear population, especially for the female segment (Gervasi et al. 2012: fig. 4). Both the Chao2 and the Capwire estimators assume that sightings of family groups are independent and randomly obtained (Boyce et al. 2001b, Cherry et al. 2007). However, multiple sightings of the same bear during our 2–3-day concurrent sessions, some opportunistic sampling periods, and multi-day camera sessions deviate from this assumption. In these cases, we therefore subsampled our raw sightings of FWC to reduce their temporal autocorrelation and geographic clustering. In particular, for simultaneous observations we retained only the first sighting of a given FWC in each session; for opportunistic observations that involved successive sessions on a daily basis at the same general location, we subsampled sightings of the same FWC according to a time lag between successive sessions. The time lag to subsample successful opportunistic sightings was derived from seasonal (i.e., Jun–Jul and Aug–Sep) autocorrelation functions (Boyce et al. 2010), using GPS-movement data of our sample of adult female bears. Specifically, we averaged across females the daily distances travelled by each female at increasing time lags (days), and used the R-package *Stats* (R Core Team 2016) to estimate an autocorrelation function of distance versus time from which we derived the first time lag whose autocorrelation value was included within 95% confidence intervals around the zero value. We then used time lag (i.e., 2 days in Jun–Jul, and 5 days in Aug–Sep; Fig. S1) as a minimum time interval to subsample sequential sightings of the same FWC. Overall, to apply the 2 estimators, each year we subsampled raw sightings at rates ranging from 31% to 80% and 0% to 77% of concurrent and opportunistic observations, respectively.

Finally, to obtain a rough estimate of the minimum number of female bears of reproductive age in the population each year, we calculated a 3-year running sum (Eberhardt and Knight 1996) corresponding with the mean inter-birth interval in our population (3–4 yr; Tosoni et al. 2017). Data were missing for 2010; therefore, we substituted the mean FWC for all years except those following mast years (i.e., 2008, 2012, and 2014).

Results

Distance-based criteria

In all seasons, the best performing model based on CVMSE was logarithmic (Mod. 4, Table 3), with q -values of 0.50 in spring, 0.60 in early summer, and 0.65 in late summer (Fig. S2; Table S1). Based on these models, and using data from 6 marked FWC re-sighted during the annual surveys, the upper limit of the 80% prediction interval minimized both Type I and Type II error rates, averaging across seasons 0% and 6% ($\pm 3\%$ SD), respectively, with the latter corresponding to just one known FWC omitted in the whole study period. Type I and II error increased at lower (i.e., 75%) and higher (i.e., 95%) prediction intervals, respectively (Table S2). Following the same numerical example provided by Ordiz et al. (2007:161) and using our distance-based criteria, we assigned 2 sequential sightings 30 days apart to 2 distinct family groups if they were >11 km apart in spring and early summer, and >10 km apart in late summer.

Counts and estimates of females with cubs

From 2006 to 2014, 90% of simultaneous sessions ($n = 38$) were conducted during August–September and 10% in July. Concurrent observation effort was 611–1,638 hours each year, corresponding to 0–3.3 FWC/100 hours/year (Table 1). Combining concurrent, opportunistic, and incidental observations, we recorded on average $35 (\pm 20$ SD, range = 6–58) FWC sightings/year. Approximately half of these ($49\% \pm 28\%$ SD, $n = 141$) were attributable to opportunistic observations, whereas $44\% (\pm 26\%$ SD, $n = 96$), and $15\% (\pm 14\%$ SD, $n = 36$) were attributable to concurrent and incidental observations, respectively. In addition, we recorded 1–24 sightings of family units with yearlings each year, 88% of which ($n = 46$) by means of opportunistic or incidental observations. Sightings of FWC were annually grouped in 3–16 pairwise unique contrasts; overall, 16% ($n = 9$ pairwise contrasts) of these were resolved using simultaneity of observation, 59% ($n = 33$) using individual recognition due to artificial or natural marks, and 25% ($n = 14$) using our ad hoc distance criteria.

We estimated 1–6 unique FWC in the population each year (Fig. 2), corresponding to an average of $3.9 (\pm 1.5$ SD)/year. We tallied 3–11 cubs annually for a mean of $7.4 (\pm 3.0$ SD; Fig. 2). For simultaneous and opportunistic observations, we failed to find significant relationships between annual counts of unique FWC and sampling factors or their correlates ($0.17 \leq P \leq 0.49$). Both the Chao2 and the Capwire estimators provided very similar estimates of FWC, and both were correlated with observed

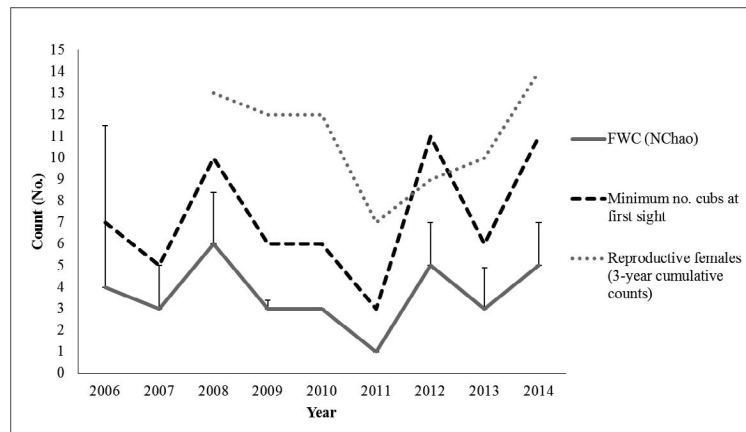


Fig. 2. Time series of estimated total number of female bears with cubs (FWC) and related parameters in the Apennine brown bear (*Ursus arctos marsicanus*) population (Central Apennines, Italy, 2006–2014). Error bars around FWC estimates represent 95% confidence intervals for \hat{N}_{Chao} .

counts (Table 4). The 3-year running sum indicated there were 7–14 reproductive females in the population annually, with a mean of 11 (± 2.4 SD)/year (Fig. 2). We failed to detect any annual linear trend in the number of FWC from 2006 to 2014 ($P \geq 0.56$).

Discussion

Our findings allow us to reject previous informal hypotheses depicting the Apennine bear population as being reproductively inefficient (cf. Ciucci and Boitani 2008).

However, the small number of reproducing females and their year-to-year fluctuations accentuate the extent to which human-caused mortality and/or stochastic factors are critically affecting this isolated bear population.

Our temporal series of unique FWC was not affected by annual variation in sampling effort and sightability, but issues regarding sampling, the application of distance-based criteria, or the use of estimators with FWC count data require some cautionary notes. Although the ideal period to observe bear family groups would be across

Table 4. Number of unique females with cubs (FWC) observed (N_{obs}), and their estimated total number using the Chao2 (\hat{N}_{Chao}) and Capwire (\hat{N}_{Cap}) estimators in the Apennine brown bear (*Ursus arctos marsicanus*) population (Central Apennines, Italy, 2006–2014). We also report the number of raw sightings of FWC attributable to simultaneous (n_{sim}) and opportunistic (n_{opp}) observations, and the number of subsampled sightings (n) used to estimate \hat{N} . Frequencies of sightings (f_i) are also reported (i.e., family groups observed 1, 2, 3, or >4 times).

Year ^a	N_{obs}	\hat{N}_{Chao} ^b	\hat{N}_{Cap} ^{b,c}	n_{sim}	n_{opp}	n	f_1	f_2	f_3	$f_{\geq 4}$
2006	4	4.4 (4–11.5)	5 (4–9)	11	14	9	2	1	0	1
2007	3	3 (3–5)	3 (3–5)	9	2	6	1	1	1	0
2008	6	6 (6–8)	6 (6–8)	16	26	20	1	2	2	1
2009	3	3 (3–3)	3 (3–3)	20	21	14	0	0	0	3
2011	1	-	-	3	3	5	-	-	-	-
2012	5	5 (5–7)	5 (5–8)	15	44	13	1	1	2	1
2013	3 ^d	3 (3–5)	3 (3–5)	0	23	8	1	1	0	1
2014	5	5 (5–7)	5 (5–6)	17	34	18	1	1	1	2

^aFWC counts were not available for 2010.

^b95% CIs in parentheses.

^cEstimated imposing the 2 innate rates model (TIRM; Miller et al. 2005).

^dAlthough we originally tallied 3 FWC in 2013, the actual number includes a family group with yearlings that was seen in 2014 only, and it was distinguished from the other FWC seen in 2013 using distance-based criteria.

the mating season (Knight et al. 1995), in our study area bear family groups are much less visible in spring; for practical reasons we therefore conducted most successful observation sessions during August–September, when bears congregate in high-altitude pastures to forage at buckthorn patches (Ciucci et al. 2014). By this time of the year some family groups may have lost the entire litter, and at high bear densities there is also the risk of undercounting unique FWC if they are not individually recognizable (Ordiz et al. 2007, 2008; Schwartz et al. 2008).

We developed our distance-based criteria using GPS movement data from adult females without cubs, which are not expected to restrict their movements during the mating season as females with cubs do (Dahle and Swenson 2003, Martin et al. 2013, Graham and Stenhouse 2014); therefore, we might have overestimated distance thresholds for family groups in this period. Accordingly, our distance thresholds in spring and summer were on average 46% higher than those developed by Ordiz et al. (2007), possibly reflecting the tendency of the single females we tracked to roam more extensively than females with cubs during the mating season. On the contrary, however, our distance thresholds were 48% lower than those of Ordiz et al. (2007) in late summer, when movement patterns of female bears with and without cubs are less differentiated (Dahle and Swenson 2003, Graham and Stenhouse 2014). We conducted the large majority of FWC sightings in late summer. Therefore, based on our sample of known FWC, had we used the rule set by Ordiz et al. (2007: figs. 1c, 2c), we would have omitted 0–2 FWC each year, corresponding to a cumulative Type II error of 29%. Therefore, by using a cross-validation approach calibrated on a sample of known FWC and because of the seasonal distribution of our FWC sightings, we believe we mitigated the risk that our distance-based criteria would inflate Type II error rates. Nevertheless, we acknowledge that developing population-specific distance-based criteria using GPS movement data from female bears with cubs would be ideal, and this should be regarded a priority for future monitoring of this, as well as of other, small bear populations. We also acknowledge that our FWC counts may be slightly conservative as indicated by an empirically derived Type II error of 6%, but we also argue that the overall effect of a few missed distinctions of unique FWC is probably negligible because distance-based criteria were used alone to assign no more than 25% of the pairwise contrasts between FWC sightings. Accordingly, we maintain that the precarious status of this bear population justifies our conservative approach in the absence of ideal movement data of females with

cubs. Still, we recommend for future monitoring that our ad hoc developed distance-based criteria be applied only if additional clues, such as simultaneity of sightings or presence of individually recognizable marks, are not applicable.

Similar to other applications to small bear populations (Brodie and Gibeau 2007, Palomero et al. 2007), the estimates of FWC we obtained were correlated and only marginally larger than FWC counts, indicating that relatively few FWC escaped detection. This may be a relatively common scenario for small bear populations in well-studied areas (Brodie and Gibeau 2007), where most family groups should be expected to have high enough sighting probabilities provided sufficient search effort is ensured and sampling coverage is enhanced by the adoption of different observation methods. Opportunistic observations, long valued in applications of counts of unique FWC elsewhere (e.g., Palomero et al. 2007, Schwartz et al. 2008), proved particularly useful in our case to enhance detection of FWC in remote areas, increase re-sighting frequency, and allow verification of otherwise equivocal cases. On the other hand, by using multiple sampling methods and, in particular, by including a large share of opportunistic sightings, we increased heterogeneity in sighting probabilities, and opportunistic observations clearly deviated from random sampling. Both estimators we used are known to perform well under substantial heterogeneity provided adequate sampling effort and sampling size are ensured (Miller et al. 2005, Cherry et al. 2007). Our sampling effort, measured as the ratio of the initial number of sightings to estimated population size (n/\hat{N} ; Keating et al. 2002), reflects ideal conditions for the Chao2 estimator (Cherry et al. 2007). Nevertheless, although the Chao2 is known to perform relatively well with a low proportion of animals seen at least once (Cherry et al. 2007), our sighting data fell in the lower end of the spectrum evaluated by Cherry et al. (2007), likely corresponding to unstable estimates and a slight negative bias. However, this should not equally affect Capwire estimates because, given the expected number of FWC in our population, our sampling effort is expected to correspond to a biologically negligible bias (Miller et al. 2005: fig. 2). It should be noted, however, that because both estimators require sighting data to be independent and randomly sampled, we had to heavily subsample our raw sighting data to mitigate any deviation from these assumptions.

Assuming the proportion of adult females in our bear population would be similar to other protected bear populations (i.e., 0.274–0.280; Eberhardt and Knight 1996, Nawaz et al. 2008), we would expect approximately 14

females of reproductive age in a population of 51 (95% CI = 47–66) bears of all ages (Ciucci et al. 2015a). This estimate closely matches the 3-year running sum that we obtained for 2008 and 2014. Accordingly, accounting for approximately 22% of adult female bears who might fail to reproduce in our bear population (based on 2 out of 9 ad F annually tracked for 6–10 yr; Tosoni et al. 2017), on average 3–4 adult female bears should be expected to reproduce each year, equal to the average number of FWC that we estimated annually. In addition, the lack of annual trends in number of FWC that we detected is consistent with a stable population size during the study period, as determined by concurrent demographic monitoring (Ciucci et al. 2015a, b).

Indeed, a minimum of 1–6 females reproducing/year is indicative of conditions well below population viability thresholds (Wiegand et al. 1998, Chapron et al. 2003, but see Sæther et al. 1998). Besides reinforcing previous recommendations to promote a rapid expansion of this bear population (Ciucci and Boitani 2008, Falcucci et al. 2009, Ciucci et al. 2015a), the limited number of reproducing females that we estimated demands timely efforts to reduce human-caused mortality. Survival of adult, reproductive females has long been known to dramatically affect population growth in brown bears (Eberhardt and Knight 1996, Garshelis et al. 2005, Harris et al. 2006). Nevertheless, human-caused mortality of adult females has been repeatedly reported in the Apennine brown bear core population in recent years (Ciucci and Boitani 2008, Falcucci et al. 2009). A minimum of 6 female bears (4 of reproductive age) were retrieved dead during 2008–2011—of which 3 deaths were human-related and 2 were from unknown causes (L. Gentile, Abruzzo, Lazio and Molise National Park, personal communication)—likely accounting for the observed decrease in the number of reproductive females from 2007 to 2011. Not only may this mortality significantly contribute to population decline in the long term (Wielgus et al. 2001) but it also may negatively affect the effective population size (N_e) through an increase in reproductive variance, hence accelerating further allelic erosion in an already genetically depleted bear population (Lorenzini et al. 2004).

Notwithstanding the small number of reproductive female bears, with an average productivity of ≥ 7 cubs/year, this otherwise isolated bear population seems still capable through recruitment of short-term compensation of adult female mortality, as suggested by the recovery of 14 reproductive females in 2014 after the 2011 minimum. The largest number of reproductive females in 2008, 2012, and 2014 followed 3 mast years in 2007, 2011, and

2013 (Ciucci et al. 2014; M. Posillico, National Forest Service, personal communication), possibly accounting for reproductive synchronization among females (Ordiz et al. 2008). Hard mast (*Fagus sylvatica* and *Quercus* spp.) is a key seasonal food for hyperphagic bears in our study area (Ciucci et al. 2014); therefore, it is expected to contribute to reproductive synchronization as reported in other bear populations thriving on hard mast (McLaughlin et al. 1994, Seger et al. 2013). Although our data did not allow a formal test of such a relationship, we indeed noticed a close correspondence between hard mast yield years and FWC estimates in the following years. This highlights the critical value of forestry practices for the maintenance, if not improvement, of current habitat productivity across the whole Apennine bear range (Ciucci et al. 2014).

Implications for future monitoring

Despite several authors emphasizing the need for more research on the biological, technical, and statistical aspects related to counts of unique FWC as a means to monitor bear populations (Craighead et al. 1995; Mattson 1997; Boyce et al. 2001a, b; Solberg et al. 2006; Intergovernmental Grizzly Bear Study Team 2012; Doak and Cutler 2014; Van Manen et al. 2014), there is general agreement that the technique should be supplemented by in-depth demographic analysis from complementary methods (Eberhardt and Knight 1996, Schwartz et al. 2006). This is particularly true for the Apennine bear population, whose demographic parameters are still largely unknown (Ciucci and Boitani 2008). By allowing for a large proportion of marked females in the population, a more in-depth study to assess reproductive and demographic traits of Apennine bears would also ensure accurate recognition of family groups in counts of unique FWC. In the meanwhile, we recommend that counts of unique FWC be conducted each year in the Apennine bear population using complementary observation strategies as hereby illustrated, possibly relying on an adequate number of marked adult females. Opportunistic strategies should take advantage of the increased availability of camera-trapping (e.g., Fisher et al. 2014), especially in remote and heavily forested areas, as well as from an increased participation of the public in the counts (e.g., Palomero et al. 2007). Parallel to unduplicated FWC counts, we also recommend monitoring yearly fluctuations of bear key foods, in particular buckthorn berries and hard mast, because their correlation with the vital rates of the Apennine bear population needs further, longer term investigation (Ciucci et al. 2014).

In dealing with such a small bear population, however, we caution relevant management authorities that monitoring by no means can be considered as a substitute for effective conservation management. The small number of reproducing female bears that we detected in the Apennine brown bear population requires more targeted and immediate recovery actions than are currently employed.

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Supplemental material

Fig. S1. Autocorrelation functions (ACF) of distance travelled versus time (days) during (A) June–July, and (B) August–September. Daily distance data were obtained by Global Positioning System relocations of 11 adult female brown bears (*Ursus arctos marsicanus*) tracked from 2006 to 2010 in the Apennine brown bear population (Central Apennines, Italy). Blue dashed lines indicate 95% confidence intervals.

Fig. S2. Box-plots with fitted curves (solid grey line) and upper 80% prediction interval (dashed black line) by regressing distance travelled (m) on elapsed time (hours) between successive Global Positioning System locations of 11 adult female brown bears (*Ursus arctos marsicanus*) tracked in the Abruzzo, Lazio and Molise National Park, central Italy, 2006–2010. Cross-validation mean squared error between observed and predicted values was minimized by the 0.50 quantile in spring (Apr–May; top panel); the 0.60 quantile in early summer (Jun–Jul; middle panel); and the 0.65

quantile in late summer (Aug–Sep; bottom panel). Mod. 4 (see Table 3) was the best performing model in all 3 seasons.

Table S1. Cross-validation mean squared error (CVMSE) across 200 validation sets for 11 adult GPS-collared female brown bears (*Ursus arctos marsicanus*; Central Apennines, Italy, 2006–2010). For each season, the CVMSE value (in bold) indicates the best combination of models (columns III–VII; cf. Table 3) and quantiles (in rows). CVMSE measures the difference between observed and predicted values of distance travelled using a training and a validation subset of distance data for each combination of regression model and quantile (see text).

Table S2. Calibration of distance-based criteria against a sample of 91 pairwise comparisons between sightings of 6 known adult female brown bears (*Ursus arctos marsicanus*) conducted in the Central Apennines, Italy, 2006–2010. For each season, Type I (false distinction) and Type II (missed distinction) error rates are reported based on increasing values of the upper prediction interval (CI_{upp}) of distance thresholds according to the lowest CVMSE model (see text and Table S1). We chose the lowest seasonal prediction interval that minimized both Type I and Type II error rates.