Cast away on Mindoro island: population dynamics of the critically endangered tamaraw (*Bubalus mindorensis*) at Mounts Iglit–Baco Natural Park

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Abstract

Endangered species, despite living at low population density, may undergo density-dependent feed-backs in case of successful recovery or marked reduction in range. When at work, density-dependence dynamics increases extinction risks and hamper conservation efforts. The largest population of the critically endangered tamaraw (*Bubalus mindorensis*) lives on a $< 3,000$ha in Mounts Iglit-Baco Natural Park (MIBNP) with very limited expansion possibilities. Tamaraw abundance has been monitored on a yearly basis from animal counts by Philippine authorities since the year 2000. Consistent with its protected status by law, the MIBNP tamaraw population has been increasing in size at an average rate of $+6\%$ per year, which we found to be relatively low compared to other similar-sized *Bovinea* species. Population growth was strikingly spatially structured within MIBNP with a population growth close to $+16\%$ in the core area of protection, while a reduction of abundance of -27% was measured at the periphery of the species range inside MIBNP. Highly concerning is the fact that the annual population growth rate progressively decreased significantly over the years since 2008, which we interpreted as an evidence of density-dependence. This isolated tamaraw population is currently experiencing a contraction of its range in MIBNP, likely caused by anthropogenic pressures forcing large herbivores to live at relatively high density in the core zone of the monitoring where protection is most effective. Our study highlights that beyond the encouraging results of a continuous growth over the last two decades, the MIBNP tamaraw population remains subject to uncertainty of its long term viability.

INTRODUCTION

In conservation planning, population abundance is critical and focuses the attention of field biologists and wildlife management institutions. Low population abundance is considered as one of the foremost criteria used for the evaluation of conservation statuses (Mace *et al.* 2008; Neel *et al.* 2012) . The International Union for Conservation of Nature (IUCN) would for instance classify any species with very small population sizes as threatened, and so without evidence for past, present or future decline (Mace *et al.* 2008). Also most populations of endangered wild species are indeed isolated and fragmented, and hence are of small size. The repeated focus on abundance in conservation biology has its roots in the fact that population viability strongly depends on the number of animals in a population (Lande *et al.* 2006). Overall, the ecology of small populations is particularly relevant to the genetics, evolution and demography of threatened species (Korn 1994).

In terms of populations dynamics, small populations differ in several ways from what is generally reported at higher abundance (Caughley 1994; Mugabo *et al.* 2013). When population size is small, the random death of a few individuals may precipitate the extinction of a population, a process referred to as demographic stochasticity (Shaffer 1981; Lande 1993). Similarly, when mating partners are too few to meet and reproduction fails, demographic stochasticity generates the so-called Allee effects (Courchamp *et al.* 1999), that is a decrease of the population growth at low population abundance (*i.e.* demographic component, see Stephens *et al.* (1999)). Yet vulnerable populations can also suffer from classical density-dependent effects whereby population

growth rate decreases with animal density (Nicholson 1933), driving the fate and viability of populations at risk of extinction (Beissinger & Westphal 1998; Henle *et al.* 2004) . The classical density-dependent effects on population dynamics and demographic rates are often overlooked in conservation because they are *a priori* expected to occur mainly at high population abundance. Although counter-intuitive for threatened populations, increasing abundance could, however, occur incidentally following a range contraction caused by habitat loss, the continuous and long-term reintroduction of individuals for reinforcement, or following successful protection measures. High abundance can potentially trigger undesirable ecological and demographic consequences for its conservation.

Density-dependence is a pervasive demographic responses among large mammals (Fowler 1987; Bonenfant *et al.* 2009). In addition to depressing recruitment rates rapidly, mortality of adults may increase as population density approaches the carrying capacity (Eberhardt 1977; 2002). Many changes in behaviour and life history traits of individuals account for those observed changes in demographic rates (Bonenfant *et al.* 2009; Choquenot 1991; Van der Wal *et al.* 2014). With rising density, individuals die from starvation because of reduction in the availability and accessibility of food resources by conspecifics. Agonistic interactions between individuals generate high stress levels which, in turns, magnify the effect of other mortality sources (Peterson & Black 1988). For instance, at high population density, epizootics are more likely to emerge and to spread quickly in populations (). Higher densities may also force non-dominant animals to occupy low-quality territories, ultimately decreasing the average productivity and survival of the population (Krüger & Lindström

2001). Finally, because high population density exacerbates the effect of environmental variation on demographic rates (Hones & Clutton-Brock 2007), the risks of massive mortality events are much higher if the population is maintained in this state on the long term. Given its numerous biological consequences, an early detection of density-dependence is of the upmost importance for the management and conservation of animal species to limit the risk of catastrophic events.

The tamaraw (*Bubalus mindorensis*) is a large mammalian herbivore endemic to the Island of Mindoro (Heude 1888; Custodio *et al.* 1996). Despite the tamaraw being officially protected by law in 1954 and the creation of the Mts Iglit-Baco Natural Park (MIBNP) protected area in 1970 (Maala 2001), its distribution range has been dramatically shrinking over the last decades. Originally found across the whole island of Mindoro with a gross estimate of 10,000 individuals in 1900 (Long *et al.* 2018), the tamaraw has suffered from intensive land conversion for agriculture and logging industry, trophy hunting, disease outbreaks spread out by domestic cattle (Maala 2001), and traditional hunting conducted by upland indigenous communities who share their living space with the large herbivore (Long *et al.* 2018). As a consequence, the species is now found in a few isolated populations scattered across Mindoro, with MIBNP hosting the largest number (Matsubayashi *et al.* 2010; Wilson & Mittermeier 2011; Long *et al.* 2018). The MIBNP tamaraw population has been restricted to one location of less than <3,000 ha in 2018, that we referred to as the Core Zone of the Monitoring (CZM, see Fig. 1).

Given its critical importance for the conservation of this iconic species, the MIBNP tamaraw population has been the cornerstone of all past, present and

future conservation plans (Maala 2001; Long *et al.* 2018). A better knowledge about its ecology and population dynamics is fundamental to assess its current conservation status, to strengthen protection measures and to guide future conservation strategy with evidence-based information (Caughley 1994; Norris 2004; Stewart *et al.* 2005; Sutherland *et al.* 2004). Unfortunately, the population dynamics of tamaraws in MIBNP has not been documented so far, nor do we have any estimation of its average population growth rate. Yet it is likely that density-dependence of demographic parameters will affect the population in the near future because hunting and human disturbance prevent this population from expanding outside of the CZM.

Here we took advantage of a 19 year-long time series of abundance data to present the first detailed analysis of the tamaraw population dynamics in the CZM of the MIBNP. We test the hypothesis that this population of large herbivores could be facing negative effects of density. We predict (*i*) that because of the substantial conservation effort in the last decade, overall population growth rate (noted r) should be statistically > 0. Yet (*ii*), because the no-hunting agreement area creates a spatial demarcation between risky and safe habitats, we expect local growth rates to differ in space and predict a decrease of r while getting away from the main rangers' base camps and patrolling routes. Finally (*iii*), given the absence of direct threats, we predict that the MIPBN tamaraw population could be approaching the carrying capacity of the CZM and expect a negative association between r and tamaraw abundance within the NHZ.

MATERIAL AND METHODS

Study site

The study area is located within the Mounts Iglit-Baco Natural Park (N12°54′ E121°13′) in the south-central part of Mindoro which, with 106,665 ha, is the island largest protected area. MIBNP shelters the largest number of tamaraw in a single site located on the south-west edge of the protected area (Fig. 1). Tamaraw distribution range is now restricted to less than 3,000 ha, which represents approx. 3% the MIBNP surface. This area is the Core Zone of the Monitoring because this is where most of the patrolling and observations are carried out by the Park's officers. There are currently 15 park rangers divided into two or three teams to monitor the area on a regular basis, following regular distinct patrolling routes centered around the three base camps.

In an attempt to reinforce tamaraw protection, wildlife managers came to a much needed agreement with residing indigenous people in 2016, declaring a 1,600 ha no-hunting zone area (NHZ) within the CZM (Fig. 1). An unforeseen consequence of the NHZ establishment for tamaraw seems to be an increase of pressure by traditional hunting at its direct boundaries. MIBNP rangers regularly report setting of snare and spear traps, and violation of the NHZ agreement in the last year is not uncommon with several deaths of tamaraws confirmed (Boyles comm. pers.). Another possible response of large herbivores to hunting is space use modification to reduce the risk of being killed (Chassagneux *et al.* 2019; Marantz *et al.* 2016).

The CZM area is a rolling grassland plateau with an average elevation of 800m a.s.l., dominated by cogon (*Imperata cylindrica*) and wild sugarcane

(*Saccharum spontaneum*), and interspersed with numerous wooded creeks, secondary forest fragments and steep hills. In recent years, the invasive Siam weed (*Chromolaena odorata*, locally called hagonoy) has been quickly spreading in the grassland and now covers an unknown fraction of the tamaraw habitat. The tropical climate is strongly seasonal with a rainy season spanning from June to October (mean temperature 26.5°C; mean rainfall: 150 mm), and a hot dry season from November to May (mean temperature 29.8°C; mean rainfall: 5 mm). Apart from humans, the only potential predator to the tamaraw is the reticulated python (*Malayopython reticulatus*) that is capable of preying upon calves or yearlings but no such observation have been made so far.

Tamaraw counts

Every year since 2000, the Tamaraw Conservation Program (TCP), a high profile program of the Philippine Department of Environment and Natural Resources (DENR), has been conducting tamaraw counts across the CZM in MIBNP, yielding an annual index of relative population abundance. The tamaraw counting area consists in 18 vantage points, covering nearly 2,200 ha within the CZM (Fig. 1). The method is rather invasive for the MIBNP ecosystem because it involves the burning of grasslands a few weeks ahead of each count, in order to increase visibility and to attract tamaraws to areas with highly palatable and attractive regrowing grasses. Each year, between 1,200 and 1,500 ha of grasslands were intentionally burned for the purpose of monitoring tamaraw abundance.

Individual tamaraws were counted simultaneously at the 18 vantage points for two hours at dusk and dawn, and for four consecutive days, in late March or

early April. For the 8 sessions and at each vantage points, at least two observers spotted and recorded all animal seen on field paper sheets, writing down observation time, approximate location, and assessed sex and age-category of individuals (split into calves, yearlings, sub-adults and adults). Right after the completion of the 8 sessions, count data were cross-checked and cleaned for obvious double observations, and the total number of different animals seen was then derived for each vantage point s and year t. These annual counts make the only available source of information about tamaraw population trends and dynamics for officials and conservation agencies.

Data analyses

For populations of long-lived and endangered species, robust and accurate estimations of r remains difficult to obtain. Knowledge about r requires either the estimation of demographic rates combined into a Leslie matrix (Leslie 1945) or the availability of long time series of population abundance, preferably on an annual basis. In the absence of natural marking, capturing individuals of an endangered species to make them identifiable with tags often face strong and justified resistance for ethical reasons, mostly because of unavoidable mortality risks. Consequently, in the best case the monitoring of the population abundance of endangered species relies on an estimator accounting for detection probability of animals (*e.g.* Kéry & Schmidt 2008), but most of time a simple index of abundance is carried out.

Working with abundance index such as annual counts to derive an empirical estimates of r however comes with some serious methodological issues (Îto 1972; Lindley 2003). Over the last decades, population counts have repeatedly

been associated with a large sampling variance (*e.g.* Caughley 1977), and coefficient of variation for population abundance as high as 30% were reported for species 1, species 2 for instance. From a conservation biologist viewpoint, a large sampling variance in the input data for estimating r is a major pitfall because of the over-optimistic results it leads to. Both the point estimate and its precision are overestimated in the presence of sampling variance (Lindley 2003). Despite the availability of appropriate statistical methods to account for the sampling variance of population counts (Kalman filter, De Valpine & Hastings 2002), such tools remain seldom used in practice for conservation.

Here we analyzed the number of observed tamaraws and judged as different individuals by observers for each of the 18 vantage points, split by years ($C_{s,t}$, where indice $s \in \{1,\ldots,18\}$ stands for the vantage point, and $t \in \{2000,\ldots,2019\}$ stands for the time in years. We implemented a state-space model to tease apart process from sampling variances, making the assumption that double and under-counts compensate and are randomly distributed from year to years. We worked in a Bayesian framework (*e.g.* Kéry & Schaub 2011) but note this is fully equivalent to a Kalman filter with a frequentist approach. To do so we defined $N_{s,t}$ as the unobserved 'true' abundance linked to $C_{s,t}$ by a random effect corresponding to the process variance (σ_c^2), on the log scale to ensure positive values for abundance. Our baseline model was:

$$\log(C_{s,t}) \sim \mathcal{N}(\log(N_{s,t}), \sigma_c^2)$$

Accordingly, we computed the population growth rate $r_{s,t}$ of the tamaraw population at each vantage points s, as:

$$r_{s,t} = \log\left(\frac{N_{s,t+1}}{N_{s,t}}\right),$$

from counts corrected for the sampling variance, hence returning an unbiased estimation of the population growth rate. The overall population growth of the tamaraw population of MIBNP is then given by:

$$\bar{r} = \frac{1}{19}\sum_{t=1}^{19}\log\left(\frac{N_{t+1}}{N_t}\right),$$

whereby $N_t = \sum_{s=1}^{18} N_{s,t}$. We informed N_t with the total number of animals seen each count session (C_{tot}) and linked counts at the VP and population levels with the following observation equation: $C_{tot} \sim \mathcal{N}(N_t/p, \sigma^2_{tot})$. The consolidated number of tamaraws C_t being much smaller than total number seen C_tot from which double-counts were removed, we included a constant proportion parameter p, similar to a ”detection rate” (which is not). By doing so, we could use the available information about tamaraw counts fully, including both the knowledge of experienced rangers and the raw number of detected tamaraws with no *a priori* interpretation. In addition, we could input missing values at the VP level for years 2000 to 2003 and 2005 thanks to the C_{tot} constrain on N_t.

To test our third hypothesis we investigated potential density-dependence in the annual growth rate by fitting a logistic growth model to the total number of tamaraws seen per year N_t:

$$\log(N_{t+1}) = \log(N_t) + r_m \times \left(1 - \frac{N_t}{K_l}\right),$$

where r_m is the maximum population growth for the tamaraw, and K is the carrying capacity of the MIBNP. Likewise, we tested if the annual population growth rate would decrease in time with population density by fitting a Gompertz model:

$$\log(N_{t+1}) = \log(N_1) + \log\left(\frac{K_G}{N_1}\right) \times \left(1 - e^{-\beta \times t}\right),$$

Because the pair of parameters r_m and K_l (logistic), and β and K_G (Gompertz), are not fully separately identifiable (Lebreton & Gimenez 2013), we used informative priors for r_m and β based on the reported maximum population growth for other large bovids (see Traill *et al.* 2007, for a similar approach). Accordingly, we set a moderately informative prior value of mean 0.3 and a precision of 0.1 in our models (Table 2). We assessed the different models by computing explicitly, during the model fit, the probability for our abundance time series to be generated by each of the three demographic models (exponential, Gompertz and logistic).

We fitted our statistical model to the tamaraw count data with JAGS 4.0 (Plummer *et al.* 2003), with 3 MCMC chains and a burn-in of 40,000 iterations. We obtained parameter estimates with an additional 30,000 iterations and a thinning factor of 5 (hence a total of 6,000 MCMC samples). We checked model convergence graphically by investigating the mixing of MCMC chains, along with the $\hat{R}$ statistics (Brooks & Gelman 1998). With the exception of r_m (see above), we set uninformative priors with large variance for all other parameters to be estimated, and checked the sensitivity of our results to the average value of the priors by replicating the analyses with variable mean and initial values for

prior distributions. We report all parameters estimates as the mean of the posterior distributions along with the 95% percentile for the credible intervals following Louis & Zeger (2008): $_{95\%low}\, estimate\, _{95\%up}$.

Note that despite the fact that we analysed the number of seen tamaraws as described above, we chose not to display such numbers on figures and to report a standardized abundance ($C_{z,t}/max(C_{z,t})$) instead. This transformation applies to the estimated carrying capacities of the Gompertz and logistic models, $K/max(C_{z,t})$, hence reported values for K are > 1. We did not provide raw counts to avoid a likely confusion between the index of relative tamaraw abundance we worked with, and a real population size estimator that was not implemented at MIBNP. Such a variable transformation has no incidence on the biological interpretation of the results though.

RESULTS

From our baseline model of tamaraw counts, we estimated an average annual growth rate of $\bar{r} = {}_{0.02}\,0.06\,_{0.12}$ for the MIBNP population from 2000 to 2019, which associated variance process equals $\sigma_{proc} = {}_{0.25}\,0.37\,_{0.49}$ (Fig. 2). As expected for count data, the sampling variance was large $\sigma_c = {}_{7.32}\,9.31\,_{9.98}$ suggesting frequent double counts of the same individuals. That the MIBNP tamaraw population increased in size by c.a. 6% per year and was statistically different from 0 is a clear support of our first hypothesis predicting increase of abundance thanks to successful protection efforts at MIBNP.

Considering the vantage point specific growth rates (r_s), we observed a marked variability in space (Table 2; Fig. 3) considering that growth rates ranged

between $r_s = {}_{-2.52}\,{-0.32}\,{}_{0.20}$ at Tarzan VP and $r_s = {}_{0.03}\,0.19\,{}_{0.35}$ at Inubon VP. Vantage point specific growth rates were spatially structured at MIBNP (Fig 3). With no exception, $r_s < 0$ were located at the periphery of the NHZ (Iyan, Tarzan, Saligue East, Mibluan, Fangandatan) although r_s of a few vantage points was > 0 despite being located on the NHZ limit too (Nagbobong, Malibayong, Talafu West and East). Together these results are in accordance with our hypothesis of an on-going contraction of the tamaraw range at MIBNP after 2000, and the disappearance of individuals at the periphery of the CZM.

Analytical evidence for density-dependence in the tamaraw dynamics between year 2008 and 2019 was moderate to high. We explicitly estimated the probability π that the exponential, Gompertz and logistic models would be the underlying process generating the observed variation in tamaraw abundance (proxy of Baye's factor). Our different models did have different probability to have generated to observed data with, respectively $\pi = 0.80$, $\pi = 0.00$ and $\pi = 0.20$ for the exponential, Gompertz and logistic model respectively. The estimated coefficients of the Gompertz model lent statistical support for the hypothesis of a gradual decrease in the annual population growth with time ($\beta = {}_{0.07}\,0.09\,{}_{0.11}$), and estimated carrying capacity to $K_G = {}_{1.12}\,1.33\,{}_{1.64}$. Similarly, point estimates for the two parameters of the logistic growth function were $r_m = {}_{0.09}\,0.11\,{}_{0.13}$ for the maximum population growth rate and $K_l = {}_{1.14}\,1.35\,{}_{1.61}$ for the carrying capacity, very close to K_G estimates.

DISCUSSION

The isolated tamaraw population in MIBNP has been increasing in size since 2000 (Fig. 2). Undoubtedly, for such an highly endangered species a positive growth rate of 0.06 over 19 years of monitoring is a great success, both locally and for the global conservation effort. Yet, the devil lies in the details though, and two additional results darken this otherwise positive picture of tamaraw population dynamics and conservation. First, our results highlight a progressive decrease of the average growth rate, suggesting density-dependent effects at the population level. Furthermore, we found support for the hypothesis of a contraction of the tamaraw distribution, evidenced by a clear spatially structured pattern of the population growth rates. The population dynamics we document is clearly calling for new and urgent conservation actions if the future of tamaraw is to be ensured.

Long-run Positive Growth of Tamaraws

The average population growth rate of $\bar{r} = 0.06$ we found gives strong evidence in favor of our hypothesis of successful conservation policies of tamaraw over the past two decades. Yet, an annual growth of 6% is relatively low compared to other similar-sized or even larger cattle (Table 2). For instance, a population of African buffalo (*Syncerus caffer*) in Southern Africa grew at a rate of 12% per year for 28 years (Jolles 2007), and values close to 30% per year have regularly been recorded for bison (*Bison bison*) or banteng (*Bos javanicus*) despite these species are between 2 and 2.5 times larger in size than the tamaraw. From this brief comparative approach, we could expect a substantially higher average

growth rate for tamaraws if the population was in a colonizing phase. Given the tamaraw is threatened, our results suggest that specific environmental factors are limiting its dynamic in MIBNP.

A first limiting factor could stand in the fact that the most available and accessible biotope for the tamaraw in MIBNP is grassland (83% of the CMZ) dominated by strong pioneer competitive species such as cogon and wild sugarcane; both grasses becoming *de facto* prominent in the tamaraw diet. While providing tamaraws with abundant and high quality forage at the early stages of plant growth, the grassland could rapidly become of much lower nutritive value during the dry season. Once grass growth is complete, stems exceeds tamaraw height (300cm vs. $<$ 120 cm respectively) and dry out to become unpalatable, raising the question of food resource accessibility and availability for a large population of tamaraws.

Dry vegetation also questions the ambivalent role of fire regime. On the one hand, regular burning rejuvenate vegetation and promote regeneration of attractive new grass shoots few months ahead of the rainy season, when animals might look for alternative marginal habitats such as forest or creeks for complementary feeding purposes. On the other hand, previous observation suggest that regular fire could promote Siam weed expansion (Nath *et al.* 2019), which is indeed rapidly spreading on the study site. Like other grazing herbivores (Rozen-Rechels *et al.* 2017), tamaraw avoid this invasive plant, an issue that could ultimately decrease the CMZ carrying capacity (Dumalisile & Somers 2017). More generally tamaraw feeding preference is not fully understood and the species might be a mixed-feeding or a browsing herbivore (*sensu* Hofmann 1989). While being *de facto* restricted on grassland habitats,

tamaraw are suspected to be ecologically flexible, as recent assessment of a new tamaraw population in mountain forest habitats in the upland inner Mindoro Island would suggest (Schütz 2019). In other words, the CZM might actually provide ecological conditions whose intrinsic limits are artificially reduced, so far, thanks to long lasting and highly disturbing habitat management policies;detrimental impact starting progressively to exceed beneficial effects.

Possible Impacts of Human Disturbance and Hunting

An additional factor, related to human activities, could also account for the low tamaraw population growth rate we report. Tamaraw has always been traditionally hunted by IPs and despite agreement of mutual effort of conservation, both intentional and unintentional casualties still happen. Besides tamaraw is sought after for bushmeat by lowlander poachers. Both threats are hard to control in the field, are likely pervasive across MIBNP, and lead to an increased mortality of all age-classes of tamaraws to an unknown extent. Positive growth over the past two decades is a clear sign of successful protection measures thanks to the constant presence of rangers and the recurrent patrols that have likely contributed to decrease harvesting pressure within the CZM. However, the marked spatial heterogeneity we document on the observed growth rates with negative values at the periphery of the counting area might reveal a lower protection efficiency when moving away from the main patrolling routes and base camps. Actually, the CZM area functions like a source-sink system with central areas nearby base camps concentrating most of the vantage points with positive growth rates, with local value as high as 16% (Table 1), more in line with the average growth we review for large bovids (Table 2).

Space Needed for Sustaining Population Growth

At first glance, the gradual decrease of the tamaraw population growth rate over the survey coupled with the overall abundance observed at MIBNP reflects the signature of some sort of density-dependence: a change in demographic rates lowering the number of individuals added to the population from year to year (Fowler 1987; Sinclair 1989). Predicted growth rates from the lowest to the highest abundance varied between $r_t = 0.11$ and $r_t = 0.01$ for tamaraw at MIBNP. Detection of density-dependence in MIBNP is worrying because it is usually the sign of increased competition between individuals for food or territorial space. In other word, our results suggest that tamaraws could already be suffering from food resource shortage. Similar to the tamaraw case is the banteng (*Bos javanicus*) population of Alas Purwo National Park, Indonesia. In spite of an increasing abundance, this population has become consolidated close to an artificially maintained grazing area, which may be causing increased predation pressure of juveniles, and the population dynamics and carrying capacity are not yet known (JB, pers. obs).

In absence of safe corridors for individuals to safely emigrate from the CZM and in the presence of adverse effects of Siam weed on forage quantity, we cannot expect this population to keep on increasing in size for the next decade as we report between 2000 and 2019. From current data, we could estimate a carrying capacity of 1.4 meaning the current MIBNP tamaraw abundance has already reached almost 2/3 of the carrying capacity. This explanation is the *biological* hypothesis of density-dependence, which is well known and repeatedly detected in many populations of large mammals (Bonenfant *et al.*

2009). Yet, in absence of trustful demographic rates estimations of tamaraws at MIBNP we hit the limits of the so-called pattern-oriented approach (Krebs 2002), with no way to assert real changes in demographic rates with abundance.

Consequently, an alternative interpretation of the density-dependence pattern that we report for tamaraw is possible, which we describe as the *count bias* hypothesis. Visual counts of animals, as it is conducted in MIBNP, are notoriously known to be inaccurate and prone to underestimation of the real abundance (Andersen 1953; **?**) (Andersen 1953; Laake et al. 1999). Tamaraw counts were not designed to be used with a population abundance estimator such as returned by the distance sampling (Buckland *et al.* 2004) or capture-recapture methods (Schwarz & Seber 1999), and therefore failed to account for the imperfect detection of individuals. The proportion of undetected tamaraws could increase with their overall abundance, a previously reported effect on red deer (*Cervus elaphus* Garel *et al.* 2010) and roe deer (*Capreolus capreolus*, Pellerin et al. 2018). Alternatively, different cognitive biases (Baddeley et al. 2004) could generate similar patterns if, for instance, observers unconsciously pull the total number of animals downward when consolidating count data. At this stage, counts at year t could likely influence the results of counts at year $t+1$, assuming observers are conservative in their expectation of the tamaraw annual population growth. The monitoring of additional biological variables in the field such as the reproductive success of females could help at teasing apart the two hypotheses (Morellet *et al.* 2007).

Implication for tamaraw conservation

Current conservation measures assume tamaraw population growth will continue in the next decade, without a need to mitigate increased pressures thought to be impacting the periphery of the CZM or to address the density dependence pressure on the population. Our results call for a adjustment to strategic planning for protection and management within MIBNP, as part of the MIBNP Management Plan and the island-wide Tamaraw Conservation Management and Action Plan (DENR 2019). Firstly, two main aspects must be urgently addressed: (*i*) increase the available space for the species so to mitigate density-dependence effect and maintain positive growth rate, that must be combined with (*ii*) increasing the effectiveness of ranger patrols in the periphery area of the CZM to reduce the recurrent poaching pressure from Filipino lowlanders and losses due to traditional hunting. Both targets request to collaborate closely with residing IP communities on a more sustainable land-use and traditional hunting system. Indeed, a more effective protection and suitable habitat management might in turn increase the average growth rate at MINBP, and exacerbate the observed density-dependence demographic responses of tamaraws. Secondly, when investigating the feasibility of translocating animals from this source population to other sites, estimated demographic rates should be incorporated into population modelling for extraction number that maintain a sustainable yield and the tamaraw population viability. Indeed, the maximum sustainable yield is found at $K/2$ in density-dependent models, not when population abundance reaches carrying capacity K.

Conclusion

Despite increased efforts of land conservation, range contractions and habitat fragmentation are still one of the most important threat to large animals population (Ripple *et al.* 2015). As a consequence, a greater proportion of wild herbivores (and their natural predators) are expected to be impacted by intensively managed landscapes. So far, conservation responses essentially consist in protecting large areas of land, a more than praiseworthy approach, that nevertheless have limits, as illustrated by our results. In any case, positive growth rates detected for a species in a conservation area could potentially hide a darker picture. First, the apparent growth of a population, trapped in a too small conservation area, can be the pervasive effect of range contraction rather than the effect of increased reproduction and survival. Second, because of this, the population could actually face important demographic challenges that, in the long term, could lead to new threats. In this context, there is an increasing need to understand the interaction between anthropogenic activities and the population dynamics of protected species. Clearly, the protection of large herbivores may hence come at the costs of undesirable ecological effects, rendering their conservation even more difficult. On the bright side, our findings also exemplifies how detailed analyses of relative population abundance data, even without absolute population size estimators, can contribute to determining future conservation measures and are essential for large mammal conservation.

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TABLE CAPTIONS

Table 1 Annual growth rate (r) of tamaraw abundance as estimated at each vantage counts in Mounts Iglit-Baco Natural Park located on Mindoro island, Philippines, between 2006 and 2019. We used a Bayesian state-space model to account for sampling variance in animal counts and reported the posterior mean estimation and its associated 95% credible interval (CI). Note the marked spatial variation in the temporal trend of tamaraw abundance, ranging from a rapid decline at Tarzan to a marked increase at Bato Fidel or Inubon (see also Fig 3).

Table 2 Estimated annual growth rates (r) of some large *bovinae* populations with body size comparable to the endangered tamaraw (*Bubalus mindorensis*). The observed population growth rate of tamaraws at Mounts Iglit-Baco Natural Park, Mindoro, Philippines, between 2000 and 2019 of $r = 0.06$ lies at the lower range of reported values.

Table 1

Vantage point	r	2.5%	97.5%
Loibfo	0.12	−0.01	0.25
Magawang	0.12	−0.02	0.24
Bayokbok	0.12	−0.01	0.25
Bato Fidel	0.15	0.01	0.27
Inubon	0.15	0.02	0.28
Mibluan	0.13	−0.01	0.26
Nagbobong	0.02	−0.14	0.19
Fangandatan	−0.03	−0.24	0.14
Anyayos	0.08	−0.06	0.21
Lanas I	0.10	−0.05	0.24
Lyan	−0.02	−0.24	0.16
Tarzan	−0.18	−0.42	0.02
Talafu East	0.06	−0.10	0.20
Talafu West	0.07	−0.08	0.21
Malitwang	0.08	−0.08	0.22
Lanas II	0.02	−0.13	0.17
Saligi East	−0.18	−0.45	0.04
Malibayong	0.02	−0.16	0.19
Saligi East	−0.46	−2.98	0.17

Table 2

Species	Location	*r*	Reference
Bison bison	Mackenzie Bison Sanctuary, Canada	0.21	Gates & Larter (1990)
Bison bison	Mackenzie Bison Sanctuary, Canada	0.20	Larter *et al.* (2000)
Bison bison	Yellowstone, Wyoming, USA	0.07	Fuller *et al.* (2007)
Bison bison	Yellowstone, Wyoming, USA	0.30	Singer & Norland (1994)
Bison bonasus	Białowieża, Poland	0.07	Mysterud *et al.* (2007)[1]
Bison bonasus	Białowieża, Poland	0.18	Krasiński (1978)[1]
Bos gaurus	Thung Yai Naresuan Sanctuary, Thailand	0.31	Steinmetz *et al.* (2010)
Bos javanicus	Not applicable, model prediction	0.32	Hone *et al.* (2010)
Bos javanicus	Cobourg peninsula, Australia	0.00	Choquenot (1993)
Boselaphus tragocamelus	Kanha National Park, India	0.18	Mathur (1991)
Boselaphus tragocamelus	Keoladoe National Park, India	0.02 - 0.06	Haque (1990)
Bubalus arnee		0.02 - 0.06	Khatri et al. (2012)
Bubalus arnee	Koshi Tappu Wildlife Reserve, Nepal	0.03	Heinen & Paudel (2015)
Bubalus bubalis		0.03	Heinen (1993)
Bubalus bubalis		?	Freeland and Boulton (1990)
Bubalus mindorensis	Mount Iglit-Baco National Park, Philipines	0.06	This study
Pseudoryx nghetinhensis	Vietnam & Laos	0.05	Kemp *et al.* (1997)[b]
Syncerus caffer	Hluhluwe-iMfolozi Park, South Africa	0.12	Jolles (2007)
Syncerus caffer	Zakouma National Park, Chad	0.08	Cornélis *et al.* (2014)
Taurotragus oryx	Lombard Nature Reserve, South Africa	0.12	Buys & Dott (1991)[c]
Taurotragus oryx	South Africa	0.16	Van Houtan *et al.* (2009)
Taurotragus oryx	Kruger National Park, South Africa	−0.02	Nicholls *et al.* (1996)
Taurotragus oryx	Masai Mara Ecosystem, Kenya	−0.11 - 0.07	Ottichilo *et al.* (2000)
Taurotragus derbianus	Senegal	0.31	Koláčková *et al.* (2011)

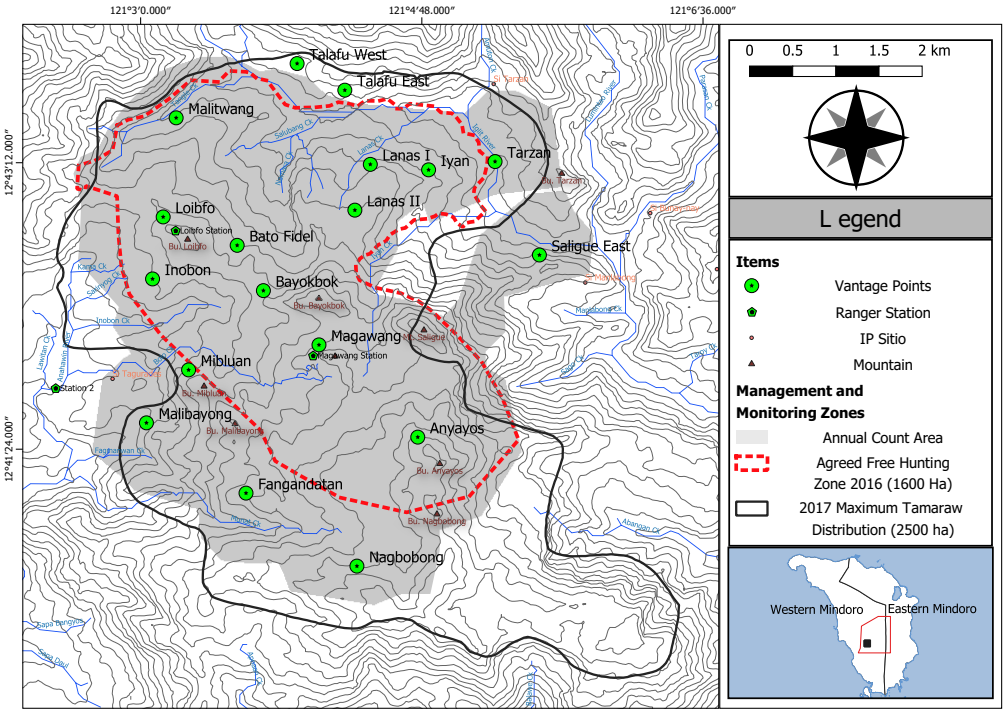
FIGURE CAPTIONS

Figure 1 General location of the Mounts Iglit-Baco Natural Park on Mindoro island, Philippines. The current geographical range of the endangered tamaraw (*Bubalus mindorensis*) population is limited to a 2,500ha area (salmon color area) of which 1,250ha consists in a no-hunting zone (red dotted line) since 2016, hence offering the highest level of protection for the species. Every year since 2000, taramaw counts have been carried out in March–April on 18 different vantage points (green circles) for the purpose of monitoring population abundance trends.

Figure 2 Time series of tamaraw (*Bubalus mindorensis*) abundance in Mounts Iglit-Baco Natural Park on Mindoro island, Philippines, from years 2000 to 2019. Raw counts (black solid line) and counts corrected for sampling variance (blue solid line) are presented with the associated 95% credible interval. Over the 13 years of monitoring, tamaraw abundance increased at a rate of 6% per year on average.

Figure 3 Spatial variation in the local growth rate of tamaraw (*Bubalus mindorensis*) abundance in Mounts Iglit-Baco Natural Park on Mindoro island, Philippines, from years 2000 to 2019. With a general positive growth since 2000, the situation in the core area of the monitoring zone is in sharp contrast with the important decrease in abundance observed at the periphery. Movement of animal toward less disturbed areas or illegal hunting outside of the no-hunting agreement zone could account for this marked spatial structure of the tamaraw population dynamics.

Figure 1


121°3'0.000"
121°4'48.000"
121°6'36.000"
12°43'12.000"
12°41'24.000"
Talafu West
Talafu East
Malitwang
Lanas I
Iyan
Tarzan
Lanas II
Loibfo
Loibfo Station
Bato Fidel
Saligue East
Inobon
Bayokbok
Magawang
Magawang Station
Mibluan
Station 2
Malibayong
Anyayos
Fangandatan
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Items
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Ranger Station
IP Sitio
Mountain
Management and Monitoring Zones
Annual Count Area
Agreed Free Hunting Zone 2016 (1600 Ha)
2017 Maximum Tamaraw Distribution (2500 ha)
Western Mindoro
Eastern Mindoro

Figure 2

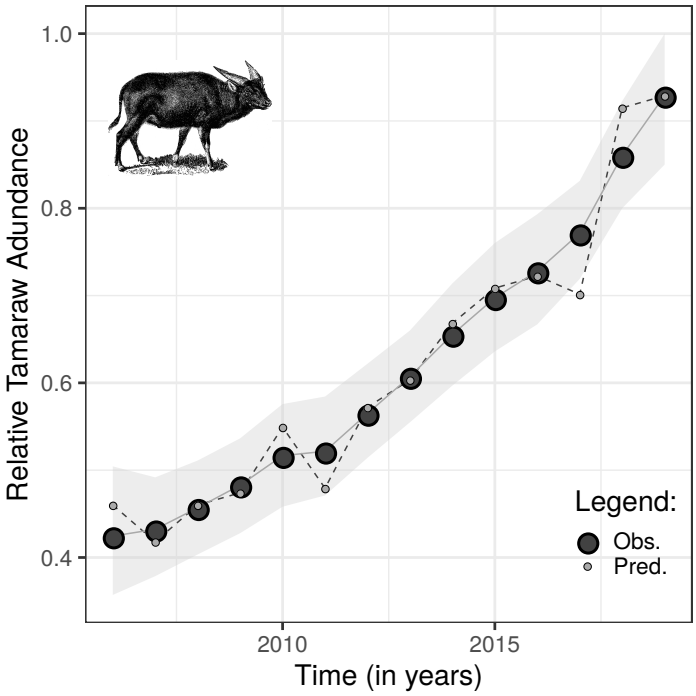
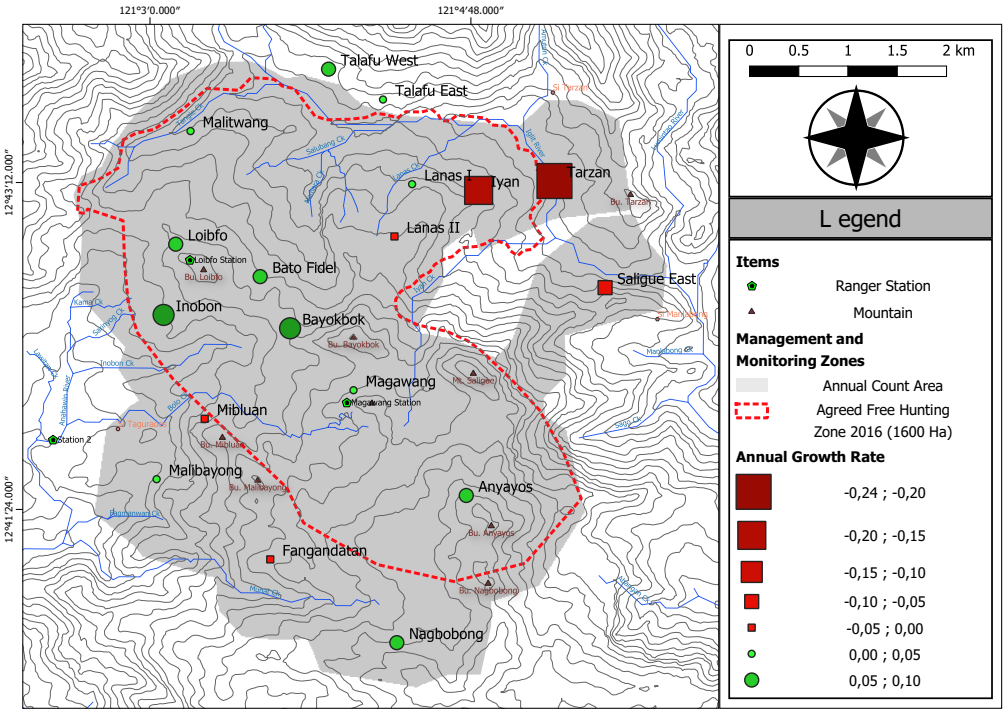

1.0
0.8
0.6
0.4
Relative Tamaraw Adundance
2010
2015
Time (in years)
Legend:
Obs.
Pred.

Figure 3


121°3'0.000"
121°4'48.000"
12°43'12.000"
12°41'24.000"
Talafu West
Talafu East
Malitwang
Lanas I
Tyan
Tarzan
Lanas II
Loibfo
Loibfo Station
Bato Fidel
Saligue East
Inobon
Bayokbok
Magawang
Magawang Station
Mibluan
Station 2
Malibayong
Anyayos
Fangandatan
Nagbobong
0 0.5 1 1.5 2 km
L egend
Items
Ranger Station
Mountain
Management and Monitoring Zones
Annual Count Area
Agreed Free Hunting Zone 2016 (1600 Ha)
Annual Growth Rate
-0,24 ; -0,20
-0,20 ; -0,15
-0,15 ; -0,10
-0,10 ; -0,05
-0,05 ; 0,00
0,00 ; 0,05
0,05 ; 0,10