Cast away on Mindoro island: lack of space limits population growth of the endangered tamaraw

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Abstract
Endangered species, despite often living at low population densities, may undergo unexpected density-dependent feedbacks in the case of successful recovery or marked reduction in range. Because density-dependence dynamics can increase risk of extinction, these effects can hamper conservation efforts. In this study, we analyze the dynamics of the largest population of the tamaraw Bubalus mindorensis, a critically endangered ungulate species endemic to Mindoro island, Philippines. The population is located within a <3000 ha area in Mounts Iglit-Baco Natural Park, with limited expansion possibilities. We took advantage of a 22 year time series of tamaraw counts to estimate annual population growth rate and possible density-dependence, accounting for sampling errors in the counts. The tamaraw population has been increasing at an average rate of +5% per year, as would be expected given its protected status by law. Population growth showed strong spatial structuring, with a population growth close to +10% in the core area of protection, and a reduction of abundance of −5% at the periphery of its range, inside the protected area. This range constriction is concerning because our best population dynamics model suggests significant negative density-dependence (Bayes factor = 0.9). The contraction of tamaraw range is likely caused by anthropogenic pressures forcing the species to live at relatively high densities in the core zone where protection is most effective, creating source-sink dynamics. Our study highlights the fact that, despite the continuous population growth over the last two decades, the long-term viability of the Mounts Iglit-Baco Natural Park tamaraw population remains uncertain.

Introduction
Assessing population abundance is an important component of conservation planning because of the strong link between population size and likelihood of extinction (Boyce, 1992). Accordingly, low population abundance is one of the primary criteria used for the evaluation of conservation status (Mace et al., 2008; Neel et al., 2012). Indeed, the effects of small population size on species persistence has been identified as one of the two central paradigms of conservation biology (Caughley, 1994). Research has shown that the population dynamics of small populations differ in several ways from what is reported at higher abundance (Caughley, 1994; Mugabo et al., 2013). When population size is small, demographic stochasticity – the random death of a few individuals – is more influential on the population dynamics and its viability than in populations that are larger in size (Shaffer, 1981; Lande, 1993). Similarly, when mating partners are too few to meet and reproduction fails, demographic stochasticity generates the so-called Allee effect (Courchamp, Clutton-Brock, & Grenfell, 1999), characterized by a decrease of population growth at low population abundance (i.e. demographic component, see Stephens, Sutherland, & Freckleton, 1999). Yet demographic stochasticity and the Allee effect are not the only considerations for the conservation of small populations; other density-dependent effects may also put these vulnerable populations at risk.

Classically, negative density-dependence describes situations where population growth rate is altered by increasing animal density (Nicholson, 1933), with crowding driving the
fate and viability of populations at risk of extinction (Beissinger & Westphal, 1998; Henle, Sarre, & Wiegand, 2004). Negative density-dependent effects on population dynamics and demographic rates are often overlooked in conservation for a simple reason: they are a priori expected to occur at high population abundance, a counter-intuitive situation for threatened populations. Yet, even in small populations, increasing abundance can occur rapidly as the result of (1) a range contraction caused by habitat loss, (2) the reintroduction of individuals for population reinforcement, (3) the disruption of natural emigration due to habitat fragmentation, or (4) following successful protection measures without the possibility for the population to expand geographically. In situations where there is low carrying capacity and limited connectivity for animals to seek less crowded areas, negative density-dependence may hinder some conservation goals. Achieving long-term population growth, or the removal of animals for reinforcement, for instance, may deemed to be difficult when negative density-dependence is at work.

There are multiple well-documented density-dependence effects on vital rates (Eberhardt, 1977, 2002; Fowler, 1987; Bonenfant et al., 2009), most of which are the result of behavior and life history trait changes as population density approaches carrying capacity (Choquenot, 1991; Bonenfant et al., 2009; van der Wal, Laforge, & McLoughlin, 2014). First, with increasing population density, individuals may die from starvation because of a reduction in the availability and accessibility of food resources by conspecifics. Increasing antagonistic interactions among individuals at high density may further generate high stress levels which, in turn, magnify the effect of other mortality sources (Peterson & Black, 1988; Hone & Clutton-Brock, 2007). For instance, at high population density, epizootics are more likely to emerge and to spread quickly in populations (Langwig et al., 2012). Second, 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). Given its numerous biological consequences, early detection of density-dependence is important for the management of threatened species because its evidence from data would suggest that the population is approaching the carrying capacity of the environment and starts to be limited by food resources (Eberhardt, 2002).

The tamaraw Bubalus mindorensis is a large ungulate endemic to the island of Mindoro, Philippines (Heude, 1888; Custodio, Lepitten, & Heaney, 1996). The species was originally found across the entire island of Mindoro, with a total estimate of 10 000 individuals in 1900 (Long et al., 2018). Since then, tamaraw populations suffered from land conversion for agriculture and logging, trophy hunting, disease outbreaks spread by domestic cattle (Maala, 2001), and traditional hunting conducted by upland indigenous communities who share their living space with the species (Long et al., 2018). Despite being officially protected by law since 1954, as well as the creation of the sizeable Mounts Iglit-Baco Natural Park (hereafter noted MIBNP) protected area in 1970 to protect its key habitat (Maala, 2001), tamaraw range has decreased substantially over the last decades. As a consequence, the tamaraw is now found in a few isolated populations scattered across Mindoro, with MIBNP holding the largest population (Matsubayashi et al., 2010; Wilson & Mittermeier, 2011; Long et al., 2018), restricted to a single location <3000 ha hereafter referred to as the core zone of monitoring (CZM).

Given its importance for the conservation of this iconic species, the MIBNP tamaraw population has been the cornerstone of past, present, and future conservation plans (Maala, 2001; Long et al., 2018). In an attempt to reinforce tamaraw protection, wildlife managers came to an agreement with residing indigenous communities in 2016, declaring a 1600 ha no-hunting zone area within the CZM. Unfortunately, one unforeseen consequence of the no-hunting area establishment is an increase in hunting pressure at its boundaries. Park rangers regularly report the setting of snares and spear traps in the border areas, and violation of the no-hunting zone agreement is not uncommon, with several deaths of tamaraws confirmed in the last years (R. Boyles pers. comm.). Furthermore, field observations by rangers suggest that tamaraw population density is growing within the no-hunting zone, which could increase the risks of crowding. In this context, it is possible that negative density-dependence combined with the source-sink dynamics will affect the population in the near future, undermining long-term conservation strategies.

Here, we took advantage of a 22 year time series of abundance data to provide a detailed analysis of the tamaraw population dynamics in the CZM of MIBNP. We predict (1) that because of the substantial conservation effort in the last decade, overall population growth rate (noted $r$) should be statistically >0. Yet (2), 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 $r$ in areas further from the main rangers’ base camps and patrolling routes. Finally (3), given the intensive conservation efforts and relative safety of tamaraw in the CZM, we predict a negative association between $r$ and tamaraw abundance within the no-hunting zone as a result of negative density dependence effects. To test the first two hypotheses, we computed the population growth rate of the tamaraw population at two spatial scales: over the entire CZM, and at specific locations used in annual tamaraw counts (hereafter referred to as vantage points). To test our third hypothesis of density-dependent demographic responses, we fitted and compared three population dynamics models: the baseline exponential model (no density-dependence), a Ricker model to test for a linear relationship between $r$ and annual abundance, and a particular formulation of Gompertz model to test for a decrease of $r$ through time.

**Materials and methods**

**Study site**

The Mounts Iglit-Baco Natural Park is a 106 655 ha protected area of the Philippines in the south-central part of the island of Mindoro (N12°54′, E121°13′). The MIBNP harbors
the largest population of tamaraw, found in a single 3000 ha area located on the south-west edge of the protected area. This 3000 ha area demarcates our study site, and is where most patrolling and observation activities are carried out (hence the so-called CZM). There are currently around 15 park rangers, which are divided into two or three teams to monitor the area on a regular basis. The teams patrol routes within the CZM, centered around the three permanent base camps. The CZM and no-hunting zone represent approx. 3 and 1.5% of MIBNP, respectively.

The CZM area is a rolling grassland plateau with an average elevation of 800 m 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. Introduced from Borneo to Mindoro in the early 60s (Pancho & Plucknett, 1971), the invasive Siam weed *Chromolaena odorata* has been rapidly spreading in the grassland area and now covers an unknown fraction of the tamaraw habitat. The tropical climate is strongly seasonal with a rainy season 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 tamaraw is the reticulated python *Malayopython reticulatus* that is capable of preying upon calves or yearlings, though no such predation observations have been made so far.

### Tamaraw counts

Every year since 2000, the Tamaraw Conservation Program (TCP), a program of the Philippine Department of Environment and Natural Resources (DENR), has conducted tamaraw counts across the CZM, yielding an annual index of relative population abundance. The tamaraw counting area consists of 18 vantage points, covering nearly 2200 ha within the CZM (Fig. 2). The tamaraw counting process is rather invasive for the MIBNP ecosystem because it involves the burning of grasslands a few weeks ahead of each count to increase visibility and to retain tamaraw to areas with nutrient-rich young grasses. For the past 22 years, between 1200 and 1500 ha of grasslands were intentionally burned each year for the purpose of monitoring tamaraw abundance.

During the annual counts, individual tamaraws were counted simultaneously at the 18 vantage points for 1 h and a half at dusk and dawn over a period of four consecutive days in late March or early April. For the eight sessions and at each vantage point, at least two observers spotted and recorded all animals seen, writing down observation time, approximate location, and sex and age-category of individuals (split into calves, yearlings, sub-adults, and adults). This sampling design remained unchanged for the 22 years, though the number of observers could vary from year to year. Immediately after the completion of the eight sessions, raw data were cross-checked and cleaned for potential multiple observations. Rangers observing at neighboring vantage points decided together if a group of tamaraws was previously seen or not based on the timing, moving direction and composition of the group. When timing, moving direction and composition did match, then those individuals were withdrawn once from the total number of sightings. We derived the total number of different animals corrected for multiple counts for each vantage point and year, and constitute the consolidated counts C. These annual counts comprise the only available source of information about tamaraw population trends and dynamics for officials to use for conservation management decisions. Note that, because of the COVID-19 pandemic, the tamaraw counts in 2020 did not take place and we missed detailed counts (vantage point level) for years 2000–2003 and 2005 following the loss of field data sheets. We considered all these missing values as not available to be estimated by our statistical models (see below for details).

### Data analyses

For populations of long-lived and endangered species, robust and accurate estimations of the population growth rate (r) remain 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-term series of population abundance (Royama, 1992), preferably on an annual basis. Because we were unable to mark tamaraw, both for legal and ethical reasons (Putman, 1995), we could not individually identify animals, and thus it was not possible to apply methods of abundance estimations based on capture–recapture (see Schwarz & Seber, 1999, for a review). We therefore used auto-regressive statistical models to analyze the annual counts. Working with abundance index data to derive an empirical estimates of r, however, comes with serious methodological issues (Ito, 1972; Lindley, 2003). Over the last decades, population counts have repeatedly been associated with a large sampling variance (e.g. Caughley, 1977; Morelet et al., 2007), and coefficients of variation for population abundance close to 30% have been reported for various large mammal species (Lubow & Ransom, 2016). From a conservation perspective, a large sampling variance in the input data for estimating r is a major pitfall because it leads to over-optimistic results, usually from an over-estimation of both the point estimate and its precision (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 in conservation.

Here, we analyzed the consolidated number of observed tamaraws (C), as judged by observers to be different individuals, for each of the 18 vantage points, split by years (Cs,t), where index s ∈ {1,…,18} stands for the vantage point identifier, and t ∈ {2000,…,2022} stands for the time in years. We implemented a state-space model to tease apart process from sampling variance, making the assumption that over- and under-counts cancel out and are randomly distributed from year to year. 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 (De Valpine & Hastings, 2002). To do so, we defined Ns,t as the...
The observation model was:

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

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, thus returning an unbiased estimation of the population growth rate provided there is no long-term trend in the detection probability of tamaraws. The overall population growth of the tamaraw population of MIBNP is then given by:

$$\bar{r} = \frac{1}{21} \sum_{t=1}^{21} \log \frac{N_{t+1}}{N_t}$$

where \( N_t = \sum_{i=1}^{18} N_{i,t} \). We input missing values at the vantage point level (years 2000–2003 and 2005) thanks to the sum constraint on \( N_{i,t} \), and the recursive equation linking \( N_{i,t} \) and \( N_{i,t+1} \). By backcasting missing values of tamaraw abundance, we could estimate the mean population growth at each vantage point \( \bar{r} \) with the same number of years and, in turn, correctly test for the effect of human disturbance at the periphery of the CZM on the population dynamics.

To test our third hypothesis we investigated potential density dependence in the annual growth rate by fitting two models classically used to detect negative density dependence (Dennis & Taper, 1994): a Ricker and a Gompertz growth model, to be compared with an exponential growth model, the exponential, Gompertz and Ricker model was the most likely underlying model given the data by taking the value one and zero otherwise. We estimated the three probabilities \( \pi \) as the number of times each models received a one divided by the number of MCMC iterations.

We fitted our statistical model to the tamaraw count data with JAGS 4.0 (Plummer, 2003), with three 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 (therefore giving a total of 6000 MCMC samples). We checked model convergence visually by investigating the mixing of MCMC chains, along with the R statistics that should be <1.1 at convergence (Brooks & Gelman, 1998). With the exception of \( r_m \) and \( \beta \) (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 parameter 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 analyzed the number of tamaraws as described above, we chose not to display such numbers on figures and to report a standardized abundance \( C_t' = C_t/\max(C_t) \) instead. This transformation applies to the estimated carrying capacities of the Gompertz and Ricker models, \( K' = K/\max(C) \). We did not provide raw counts to avoid confusion between the index of relative tamaraw abundance we worked with, and a real population size estimator that was not implemented at MIBNP. With this variable transformation \( K_R \) and \( K_G \) are unitless and can no longer be interpreted as the maximum number of tamaraws but the maximum relative abundance \( C_t' \) we can expect to observe at MIBNP. Reported values of the carrying capacities \( K_R \) and \( K_G \) can hence take values >1 because the carrying capacity has not yet been reached. Biologically speaking, we put more emphasis on how far from the carrying capacity the current abundance of tamaraws is \( C_t/K \) than on the number on animals per se.

### Results

From our baseline model of tamaraw counts, we estimated a mean annual growth rate of \( \bar{r} = 0.01 \; 0.05 \; 0.09 \) for the MIBNP population from 2000 to 2021, with an associated variance...
Table 1 Estimated annual growth rates (r) of some large bovinae populations with body size comparable to the endangered tamaraw

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
<th>r</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bison bison</td>
<td>Mackenzie Bison Sanctuary, Canada</td>
<td>0.21</td>
<td>Gates &amp; Larter (1990)*</td>
</tr>
<tr>
<td>Bison bison</td>
<td>Mackenzie Bison Sanctuary, Canada</td>
<td>0.20</td>
<td>Larter et al. (2000)*</td>
</tr>
<tr>
<td>Bison bison</td>
<td>Yellowstone, Wyomng, USA</td>
<td>0.07</td>
<td>Fuller et al. (2007)</td>
</tr>
<tr>
<td>Bison bison</td>
<td>Yellowstone, Wyomng, USA</td>
<td>0.30</td>
<td>Singer &amp; Norland (1994)</td>
</tr>
<tr>
<td>Bison bonasus</td>
<td>Biawowiez, Poland</td>
<td>0.07</td>
<td>Mysterud et al. (2007)*</td>
</tr>
<tr>
<td>Bison bonasus</td>
<td>Biawowiez, Poland</td>
<td>0.18</td>
<td>Krasiński (1978)*</td>
</tr>
<tr>
<td>Bos gaurus</td>
<td>Thung Yai Naresuan Sanctuary, Thailand</td>
<td>0.31</td>
<td>Steinmetz et al. (2010)</td>
</tr>
<tr>
<td>Bos javanicus</td>
<td>Not applicable, model prediction</td>
<td>0.32</td>
<td>Hone, Duncan, &amp; Forsyth (2010)</td>
</tr>
<tr>
<td>Bos javanicus</td>
<td>Cobourg peninsula, Australia</td>
<td>0.00</td>
<td>Choquenot (1993)</td>
</tr>
<tr>
<td>Boselaphus tragocamelus</td>
<td>Kanha National Park, India</td>
<td>0.18</td>
<td>Mathur (1991)</td>
</tr>
<tr>
<td>Boselaphus tragocamelus</td>
<td>Keoladoe National Park, India</td>
<td>[0.02; 0.06]</td>
<td>Haque (1990)</td>
</tr>
<tr>
<td>Bubalus arnee</td>
<td>Koshi Tappu Wildlife Reserve, Nepal</td>
<td>[0.02; 0.06]</td>
<td>Khatri et al. (2012)*</td>
</tr>
<tr>
<td>Bubalus arnee</td>
<td>Koshi Tappu Wildlife Reserve, Nepal</td>
<td>0.03</td>
<td>Heinen &amp; Paudel (2015)*</td>
</tr>
<tr>
<td>Bubalus bubalis</td>
<td>Top End, Northern Territory, Australia</td>
<td>[−0.81; 0.24]</td>
<td>Freeland &amp; Boulton (1990)</td>
</tr>
<tr>
<td>Bubalus mindorensis</td>
<td>Mount Iglit-Baco Natural Park, Philippines</td>
<td>0.05</td>
<td>This study</td>
</tr>
<tr>
<td>Pseudoryx nghetinhensis</td>
<td>Vietnam &amp; Laos</td>
<td>0.05</td>
<td>Kemp et al. (1997)</td>
</tr>
<tr>
<td>Syncerus caffer</td>
<td>Hluhluwe-iMfolozi Park, South Africa</td>
<td>0.12</td>
<td>Jolles (2007)</td>
</tr>
<tr>
<td>Syncerus caffer</td>
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<td>0.08</td>
<td>Cornélis et al. (2014)</td>
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<tr>
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<td>Lombard Nature Reserve, South Africa</td>
<td>0.12</td>
<td>Buys &amp; Dott (1991)</td>
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<tr>
<td>Taurotragus oryx</td>
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<td>0.16</td>
<td>van Houtan et al. (2009)</td>
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<td>Kruger National Park, South Africa</td>
<td>−0.02</td>
<td>Nicholls et al. (1996)</td>
</tr>
<tr>
<td>Taurotragus oryx</td>
<td>Masai Mara Ecosystem, Kenya</td>
<td>[−0.11; −0.07]</td>
<td>Ottichilo et al. (2000)</td>
</tr>
<tr>
<td>Taurotragus derbianus</td>
<td>Senegal</td>
<td>0.31</td>
<td>Koláčková et al. (2011)</td>
</tr>
</tbody>
</table>

The observed population growth rate of tamaraws at Mounts Iglit-Baco Natural Park, Mindoro, Philippines, between 2000 and 2021 of r = 0.05 lies at the lower range of reported values. Note some populations may be in a very different ecological context (colonization, saturation) making comparisons challenging.

*Same population with updated data.

process equal to \( \bar{s}_{\text{proc}} = 0.25 \times 0.31 \) (Fig. 1). It means the observed abundance increased 2.41 times over the course of the study. As expected for count data, the sampling variance was large \( \bar{s}_v = 7.18 \times 9.21 \times 9.98 \), suggesting frequent multiple counts of the same individuals. For the vantage point-specific growth rates \((r_v)\), we observed a marked variability in space (Fig. 2; see Supporting Information, Table S1) as shown by the fact that growth rates ranged between \( \bar{r}_v = -0.42 \times 0.18 \times 0.20 \) at Tarzan and \( \bar{r}_v = 0.06 \times 0.14 \times 0.26 \) at Bato Fidel and Bayombok vantage points. Without exception, \( \bar{r}_v < 0 \) were located at the periphery of the no-hunting area (Iyan, Tarzan, Saligue East, Mibluan, Fangandatan), although \( \bar{r}_v \) of a few vantage points were >0 despite being located on the no-hunting zone border (Nagbobong, Malabayong, Talafu West and East). The mean growth rate outside of the no-hunting area was \( \bar{r} = -0.14 \times -0.05 \times 0.08 \) (9 vantage points) while tamaraw abundance increased at rate of \( \bar{r}_v = 0.04 \times 0.09 \times 0.15 \) inside (9 vantage points).

We explicitly estimated the probabilities \( p_i \) that the exponential, Ricker, or Gompertz models would be the underlying process generating the observed variation in tamaraw abundance (proxy of Bayes factor). The estimated probabilities for the three population dynamics models given our count data were \( \bar{x}_1 = 0.10 \), \( \bar{x}_2 = 0.90 \), and \( \bar{x}_3 = 0.00 \), respectively, supporting our hypothesis of density-dependence feedbacks in the tamaraw population. Point estimates for the two parameters of the Ricker model were \( \hat{r}_{\text{R}} = 0.07 \times 0.08 \), and \( \hat{K} = 1.16 \times 1.37 \times 1.62 \) for the carrying capacity. Although the Gompertz model received no statistical support, the estimated coefficients were statistically significant and read \( \hat{\beta} = 0.03 \times 0.05 \times 0.07 \), and \( \hat{K} = 1.20 \times 1.41 \times 1.66 \) (Table S1) for the carrying capacity. Note that the statistical support for the Ricker model held for the dynamics of the core area only, that is, when considering only the 9 vantage points inside the no-hunting area (\( \bar{x}_1 = 0.02 \), \( \bar{x}_2 = 0.83 \) and \( \bar{x}_3 = 0.15 \)).

**Discussion**

The isolated tamaraw population in MIBNP has been increasing in size since 2000 (Fig. 1). Undoubtedly, a positive growth rate of 0.05 over 22 years of monitoring is a noteworthy success for such a highly endangered species, both for local populations and for global conservation efforts. However, the devil lies in the details, and two additional results darken this otherwise positive picture. First, we found support for a source-sink dynamic of the tamaraw population linked to poaching and evidenced by a clear spatially structured pattern in the local population growth rates. Second, our results highlight a progressive decrease of the average growth rate in time, suggesting density-dependent effects at the population level. The recent population dynamics of...
by competitive pioneer plant species such as cogon and wild sugarcane. Historical observations by Talbot & Talbot (1966) and more direct evidences (E. Schütz pers. obs.) at the Gene Pool Farm breeding center, Mindoro Island, also suggest that both invasive grasses make part of the tamaraw diet. Although these grasses likely provide tamaraws with abundant and high-quality forage at the early stages of plant growth (Talbot & Talbot, 1966), after burning for instance, in later stages of development these species are characterized by much lower nutritive value, especially during the dry season. Observations in the field indicate that once grass growth is complete, the stems exceed tamaraw height (300 cm vs. <120 cm, respectively) and dry out, thus becoming both inaccessible and unpalatable. It is therefore possible that lack of food resource accessibility and availability could be limiting the growth rate of the population.

The annual burning of the grassland habitat for population count may also be impacting plant composition in the CZM, with implications for tamaraw population dynamics. Previous observations suggest that regular burning could promote the expansion of Siam weed Chromolaena odorata (Nath et al., 2019), which appears to be rapidly spreading throughout our study site. The consumption of Siam weed by large herbivores is unclear. While some authors suggested potential toxicity of Siam weed leaves for consumers (Sajise et al., 1974; Aterrado & Talatala-Sanico, 1988), it makes a substantial part of the gaur Bos gaurus diet (Chaiyarat, Prasopsin, & Blumphakphan, 2021). Unlike its consumption, evidence for the avoidance of heavily invaded habitats by large herbivores is clearer. In African savannas, the induced changes in plant community and the reduced detection of predators following the growth of Siam weed shifted habitat selection of grazing and browsing mammalian species (Rozen-Rechels et al., 2017). If, like other African large herbivores, tamaraw avoid Siam weed when foraging, its increasing dominance in grasslands at MIBNP could ultimately decrease the CZM carrying capacity. Although burning creates high-quality forage in the short term, such an intensive habitat management practice is likely to cause a progressive decrease in habitat quality for tamaraws over the long term (see Dumalisile & Somers, 2017, for an example of long-term effects of Siam weed on large herbivores in African savannas).

**Long-term positive growth of tamaraws**

The average population growth rate of \( r = 0.05 \) – corresponding to a 2.5 fold increase in abundance between 2000 and 2021 – gives strong evidence that successful conservation policies over the past two decades have led to an increase in tamaraw abundance. Nonetheless, an annual growth of 5% is relatively low compared with other similar-sized or even larger cattle species (Table 1). For instance, a population of African buffalo Syncerus caffer in South Africa grew at a rate of 12% per year for 28 years (Jolles, 2007), and values close to 30% per year have been recorded for bison Bison bison and banteng Bos javanicus, despite the fact that these species are between 2 and 2.5 times larger in size than the tamaraw (Wilson & Mittermeier, 2011). From this brief comparative approach, we would expect a substantially higher average growth rate for tamaraws if the population was in a colonizing phase. Given that the tamaraw is secured within the no-hunting area, our results suggest that specific environmental factors are limiting its growth in the CZM.

A first limiting factor could be related to the fact that the most available and accessible habitat for the tamaraw in MIBNP is grassland (83% of the CZM), which is dominated by competitive pioneer plant species such as cogon and wild herbi-...
In the early years of the tamaraw monitoring, the apparent population growth (Fig. 1) likely resulted from immigrating individuals from outside of the CZM, and a high survival and reproduction rate inside. Today a different demographic process could be at work, with adult females gradually concentrating at the heart of the no-hunting area to avoid human disturbance. Conversely, a limited number of young individuals and adult males may venture outside of the no-hunting area, putting themselves at greater risk of dying. The net movements of animals in and out of the no-hunting area could lead to an apparent continuous growth of tamaraw abundance since the beginning of monitoring efforts, despite a shift in the underlying population dynamics.

The marked spatial heterogeneity we document, with negative growth rates at the periphery of the counting area, could indeed indicate a lower protection efficiency in areas further away from the main patrolling routes and ranger base camps. Such a result supports our second hypothesis, suggesting an unexpected contraction of the tamaraw range at MIBNP, and the disappearance of individuals at the periphery of the CZM. In other words, the CZM area may function like a source–sink system (Pulliam, 1988), with the more central and better patrolled areas exhibiting positive growth rates, and more peripheral areas with higher hunting pressure serving as population sinks. Again, our findings provide some support for this idea, as local growth rates in the core area of the no-hunting zone have values as high as 14% (Fig. 2), which is more in line with the average growth rates that we reviewed for large bovids (Table 1).

Source–sink dynamics were documented in populations of apex predators (wolves Canis lupus: O’Neil et al., 2020, lion Panthera leo: Mosser et al., 2009) and other large herbivores of varying body size (red brocket Mazama americana: Narango & Bodmer, 2007, Giraffa camelopardalis: Lee & Bolger, 2017) though at much larger spatial scales than for the tamaraw where source and sink areas are a couple of hundreds meters apart. The role of trophy or subsistence hunting (official or illegal) in source–sink dynamics is pervasive, particularly between protected and unprotected areas (Creel et al., 2016; Durant et al., 2017; Heurich et al., 2018), making human harvest the main target of conservation policies. Tamaraw is no exception and the observed source–sink dynamics stress the need for an improved control of poaching, and a further geographical expansion of the current 1600 ha no-hunting agreement area.

Figure 2 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 2021.
Space needed for sustaining population growth

The gradual decrease of the tamaraw population growth rate in MIBNP, coupled with the overall abundance in the CZM, suggests a type of density-dependence is occurring, where a change in demographic rates lowers 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 $r = 0.08$ and $r = 0.01$ for tamaraw. From the current data, our best model suggests a carrying capacity of 1.4, meaning that only 40% of growth is left possible before reaching the carrying capacity. If competition for food or mating becomes strong then the main tamaraw population may experience an increased net loss of animals in the near future. Tamaraws may already be experiencing a food resource shortage, which could make the population more prone to parasitism (Stien et al., 2002) or epizootics (Davidson & Doster, 1997). More generally, density-dependence should be of concern and investigated for large herbivores living in protected environments lacking apex predators, which contributes to limit abundance and reduces annual growth of prey species (Sinclair, Mduma, & Brahshares, 2003; Ripple & Beschta, 2012).

Another behavior associated with high population abundance is dispersal (Matthysen, 2005). In mammals, sub-adult individuals are more likely to disperse at high than low population abundance (e.g. Loe et al., 2009, for an example on red deer Cervus elaphus). At the high population abundance we documented in MIBNP, we would expect a greater number of dispersing individuals to venture outside of the no-hunting zone, where the risk of mortality is high because of hunting or poaching. In addition to jeopardizing the fate of the population by decreasing survival probabilities of subadults that are key to maintaining the future of the population, the empirical evidence for density-dependence that we report would limit the ability of this population to act as a source. With a combination of low recruitment and low survival of subadults, old individuals would quickly become over-represented in the population, which could depress growth even further in the future.

Unfortunately, in the absence of individual monitoring of tamaraws to estimate demographic rates independently of abundance, the real cause of the density-dependence we report is uncertain. We are currently unable to determine if the gradual decrease in growth rate is the consequence of an increased mortality or dispersal rate, a reduced reproduction, or some combination of these factors. The difficulty of teasing apart different demographic processes is a well-known limit of the so-called pattern-oriented approach (sensu Krebs, 2002) when working with time series of abundance. Further investigation of these possibilities is needed, as each situation would require different management approaches.

Implications for conservation

The main conservation goals for the tamaraw are (1) to ensure its long-term viability, and (2) support the expansion of the population within MIBNP and potentially in other sites. Current conservation measures assume that tamaraw population growth will continue in the next decade. The detection of density-dependence, however, suggests continued population growth will not be the case. In this situation, the dynamics of the tamaraw will change in the years to come if resources become the main limiting factor inside the no-hunting zone, forcing animals to disperse to, and potentially get killed in the outer zone. Several actions must be implemented by managers and authorities to address this issue in the short term. The priorities should be to expand the no-hunting zone or to create safety corridors through consensual agreement with indigenous people, both implemented in the context of creating a more sustainable land-use and traditional hunting system. Arriving at such an agreement with indigenous people will be a long process, but these conversations are already ongoing. Extending the no-hunting area will ultimately increase the sustainable population size, thus making it more viable and maintaining more genetic diversity. Likewise, allowing for dispersing individuals to leave the CZM and possibly settle in distant areas would relieve density-dependence pressure on the core population.

However, one could argue that such conservation actions only represent a short-term solution, as even if the size of the no-hunting area was increased, the tamaraw population would eventually grow toward the carrying capacity. We acknowledge this, but believe that these short-term conservation actions are still important, as they would help buy valuable time that is necessary to devise more long-term strategies. Any long-term strategy will likely involve active population management through translocation. Two of the four known populations of tamaraw on Mindoro (Aruyan Malate and Mount Calavite) have extremely small population sizes, and are thus believed to be non-viable. Transporting a small number of animals to these populations would improve their viability, while simultaneously reducing the effects of density-dependence for the main population at MIBNP. The number of tamaraw that are translocated should be determined by the number of recruited individuals each year, so that ultimately there is no decrease in population size in the MIBNP. Translocation of tamaraw may be perceived by stakeholders as a risky proposition, but a preliminary feasibility study for translocation and captive breeding is a realistic option and an appropriate next step. Ultimately, however, preventing the extinction of tamaraw will require decision makers to balance short-term actions with long-term strategies that involve active population management.

Conclusion

Securing large areas of habitat is often an effective conservation approach, but may not always be a viable strategy to protect highly threatened species, as illustrated by our study on the tamaraw population in MIBNP. More generally, we show that positive growth rates could potentially hide a less optimistic picture for some threatened species. First, the growth of a population that is confined to a small
conservation area may reflect a range contraction as a result of anthropogenic pressures, rather than the effect of increased abundance per se. Second, because of this, the population could face important demographic challenges that, in the long-term, lead to unusual problems for conservation. In this context, there is an increasing need to understand the interaction between anthropogenic activities and the population dynamics of threatened species. Our results suggest that, in some situations, conservation strategies designed to protect small, isolated populations may lead to long-term demographic issues that undermine species recovery. On the positive side, our findings also show how detailed analyses of relative population abundance data, even without absolute population size estimators, can help provide valuable information that assists in the development of conservation measures that are essential for large mammal conservation.

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References


**Supporting information**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table S1.** Estimates and 95% credible intervals of tamaraw local growth rate ($r_s$) as observed on the 18 vantage points used to count the tamaraw population at Mounts Iglit-Baco Natural Park (Mindoro Island, Philippines) between 2000 and 2021.