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RESEARCH ARTICLE

Can livestock grazing dampen density-dependent fluctuations in wild herbivore populations?

Manvi Sharma[1,2] | **Munib Khanyari**[1,3,4] | **Abhirup Khara**[1] | **Ajay Bijoor**[1,5] | **Charudutt Mishra**[1,5] | **Kulbhushansingh Ramesh Suryawanshi**[1,5,6]

[1]Nature Conservation Foundation, Mysuru, India; [2]Ashoka University, Sonipat, India; [3]Interdisciplinary Center for Conservation Sciences, University of Oxford, Oxford, UK; [4]School of Biological Sciences, University of Bristol, Bristol, UK; [5]Snow Leopard Trust, Seattle, Washington, USA and [6]Wissenschaftskolleg zu Berlin, Berlin, Germany

Correspondence
Manvi Sharma
Email: manvigsharma@gmail.com

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Abstract

1. Conservation policy for the high mountains of Asia increasingly recognises the need to encompass large multi-use landscapes beyond the protected area network. Due to limited long-term research in this region, our understanding of even fundamental processes, such as factors regulating large mammal populations is poor.
2. Understanding the factors that regulate animal populations, especially those generating cyclicity, is a long-standing problem in ecology. Long-term research across multiple taxa (mainly from Europe and North America) has focussed on the relative roles of food and predation in generating cyclicity in population dynamics. It remains unclear how trophic interactions that are influenced by anthropogenic stressors can affect population dynamics in human-modified landscapes.
3. We present a 10-year study to compare the effects of livestock grazing on density-dependent dynamics in two populations of bharal, *Pseudois nayaur*, in the Himalayas. We combine this with a mechanistic understanding of whether density dependence in these two sites acts predominantly by affecting adult survival or recruitment. We compared and quantified density dependence in the bharal population by fitting Bayesian Gompertz state-space models.
4. We found evidence for negative density dependence which indicates possible cyclic dynamics in the bharal population of the site (Tabo) with low livestock density. The population dynamics of this site were driven by recruited offspring—with a 2-year density-dependent lag effect—rather than adult survival. In the site with high livestock density (Kibber), this density dependence was not detected. We postulate the potential role of excessive grazing by livestock in affecting offspring recruitment, thereby affecting the bharal population in Kibber.
5. *Synthesis and applications*: Our results suggest that conservation action to facilitate wild herbivore population recovery, such as the development of protected areas and village reserves, needs to account for density-dependent regulation. Sites

with trophy hunting require continuous monitoring to understand the effects of density dependence so that appropriate hunting quotas can be formulated.

KEYWORDS
competition, Gompertz state-space model, Himalaya, livestock, long-term study, negative density dependence, recruitment

1 | INTRODUCTION

Rangelands cover over 40% of the global land area, and a growing proportion of the world's poor people depend on livestock grazing for livelihoods (Otte et al., 2012). These rangelands also provide important habitat to support wildlife populations (du Toit et al., 2010). Understanding the consequences of the interactions between livestock grazing and wildlife populations is important for the effective management of these rangelands. Direct interactions between livestock and wild herbivores, such as competition and pathogen transmission, have received a fair amount of attention over the past 50 years (Pozo et al., 2021). However, effects of these interactions on the long-term population dynamics of wild herbivores have received less enquiry.

One of the interesting aspects of wild herbivore population dynamics is their cyclicity. Long-term research on the population cycles of multiple taxa has improved our understanding of how wild herbivore populations are regulated (Grenfell et al., 1992; Krebs et al., 2018; Myers & Cory, 2013). Cyclic population dynamics can arise from both extrinsic and intrinsic factors, and considerable research has focussed on the relative roles of resource depletion as well as direct predation in generating cyclicity in animal populations (Krebs et al., 2018; Majchrzak et al., 2022; Myers, 2018). While much research has focussed on population cyclicity driven by predation, it is unclear how other interactions that strongly affect density-dependent growth, such as competition from a co-occurring species, can affect cyclic population dynamics. Competition with livestock is likely to have strong population-level consequences for wild herbivores because livestock typically have a competitive edge. Livestock populations tend to be larger in size and receive veterinary care and supplemental feed (McNaughton, 1993). Additionally, the negative impacts of livestock production on wildlife can manifest through ancillary activities associated with livestock production, such as land-use change which could spatially displace livestock (Gordon, 2018). Currently, we lack both an empirical and theoretical understanding of how competitive interactions that manifest due to anthropogenic stressors could influence population cycles of co-occurring wild animals.

A fundamental feature of population cyclicity is density dependence—manifested in the form of density-dependent growth, followed by a density-dependent decline that stalls the population growth, and then a delayed recovery of the population (Myers & Cory, 2013). Interestingly, considerable variation has been reported in the strength of density dependence, its seasonal timing and the life stages or sub-populations at which it could operate (Albon et al., 2017; Lehman et al., 2018; McCullough, 1999; Stewart & Johnson, 2005). Anthropogenic stressors can influence density-dependent regulation in animal populations and this can be mediated via multiple different demographic parameters including birth rates, survival and dispersal (Cayuela et al., 2019; Sullivan et al., 2017).

Resource-linked density dependence has been documented to affect reproductive fitness in many ungulate species (reviewed in Bonenfant et al., 2009) by acting on different vital rates, such as birth rates, juvenile survival and adult survival. Gaillard et al. (1998) reported that ungulate populations from a range of environments have relatively less variation in adult survival, but juvenile survival tends to be highly variable (Gaillard et al., 1998). Many other studies have reported that birth rates are crucial in shaping population dynamics. Birth rates might get affected through reduced female fecundity or through the reduced proportion of females giving birth (Bonenfant et al., 2009; Mishra et al., 2004; Suryawanshi et al., 2010). Recent studies, however, have highlighted the important role of adult survival for ungulate population growth (Lee et al., 2016; Lehman et al., 2018). Lehman et al. (2018) reported that elk (*Cervus canadensis nelsoni*) asymptotic population growth rates were most sensitive to proportional changes in adult survival (Lehman et al., 2018). It is not clear which demographic variables primarily drive ungulate population change and if anthropogenic stressors act on these variables differently and shape population regulation.

The high-elevation regions of the Indian Trans-Himalayas support a multi-species assemblage of wild ungulates that share habitat with many domestic ungulate species. These cold deserts consist of sparsely vegetated steppes, small patches of moist sedge meadows near water bodies, and vast mountainous areas that are barren and under permafrost and glaciers (Bagchi & Ritchie, 2010; Champion & Seth, 1968). These Trans-Himalayan pastures are inhabited by wild ungulates, such as the bharal (*Pseudois nayaur*), important prey for the charismatic snow leopard (*Panthera uncia*) found in these regions. There is a high overlap in the diets of bharal and the Trans-Himalayan livestock (Bhattacharya et al., 2012; Mishra, 2001; Mishra et al., 2004). At high densities of livestock, the diet and offspring to female ratio of bharal are affected due to competition for forage. The offspring to female ratio was reported to be 1.5 times higher in mildly grazed landscapes than in intensely grazed landscapes (Mishra et al., 2004). The diet overlap between livestock and bharal is higher in summer (growing season); however, this overlap is reduced in the winter (Mishra et al., 2004). The high-elevation regions are highly seasonal regions with low annual precipitation. These areas have low primary productivity with high livestock stocking density with livestock biomass as high as 4000 kg/sq.km. in rangelands in the Spiti Valley (Mishra, 2001). Competition from livestock is reported to lead to shifts in the bharal diet as graminoid availability has been shown to be limited in winter (Suryawanshi et al., 2010) suggesting the presence of intense resource-linked competition from livestock.

Long-term population and demographic monitoring can provide insights into the dynamics of species populations and help understand the mechanisms through which competition and density dependence can affect populations. However, long-term studies of mountain ungulate populations in the Himalayas are challenging because of the remote terrain and poor logistical support (Singh & Milner-Gulland, 2011). While studies have reported seasonal variation in bharal density (Liu et al., 2008) and group size and composition (Oli & Rogers, 1996), we have little understanding of the effect of livestock on bharal population dynamics and regulation due to the absence of long-term population data. Here, we examine 10-year annual time series datasets of bharal abundance and demographic structure from two study sites that differ in the intensity of livestock grazing. The livestock density of one site was twice the density of the other site. The primary productivity in the landscape is extremely low. The annual maximum NDVI in Kibber was 0.19 (95% CI: 0.17–0.21) and in Tabo, it was 0.11 (95% CI: 0.09–0.13) (see Supporting Information for details). We quantified the nature and strength of density dependence in bharal populations from these two sites using recently developed Bayesian state space methods (Kéry & Schaub, 2011) and examined the demographic parameters that respond to changes in population size. Our long-term study contributes to the understanding of how artificially managed populations (livestock) affect density-dependent regulation in wild bharal populations. Our findings bring to light the role of livestock grazing in disrupting density dependence in bharal populations and demonstrate that anthropogenic stressors, such as livestock density potentially act through affecting offspring recruitment and not adult survival. Our study has implications for the management of wild ungulate populations as identifying population declines and growth during low and high phases can better inform management decisions, such as management of hunting quotas, or setting of grazing-free reserves.

2 | MATERIALS AND METHODS

The long-term monitoring programme for bharal populations in the Spiti river valley was set up in 2010 by researchers based at Nature Conservation Foundation (NCF). The field work was done under permits granted to NCF through a memorandum of understanding (MOU) signed between NCF and the Himachal Pradesh Forest Department (HPFD). We obtained oral consent from all participants for collecting livestock information as the surveys were part of a monitoring programme setup in 2010.

Our past work from these landscapes has shown that all available rangelands in this region are grazed by livestock and have a long history of pastoral association and that high densities of livestock affect the diet and reproduction of wild bharal populations (Mishra et al., 2004). The primary goal of the monitoring programme was to understand the long-term effects of competition from livestock on the populations of the primary prey of the charismatic snow leopard—a flagship species for conservation (Mallon et al., 2016). This study was carried out in the Spiti river valley, Lahaul-Spiti district, Himachal Pradesh, India (32.61° N 77.37° E), over a region that is approximately 12,000 km^2 in size and falls within the Indian Trans-Himalayan mountains in the rain-shadow of the Greater Himalayas. In this larger landscape, we worked in two sites, namely Kibber (411 km^2) and Tabo (341 km^2; Figure 1). These two sites are close to each other and are similar in the ecology, hydrology and climate. In the past, Mishra et al. (2004) describe the similarities between these sites and used them for comparative studies of effects of scramble competition between

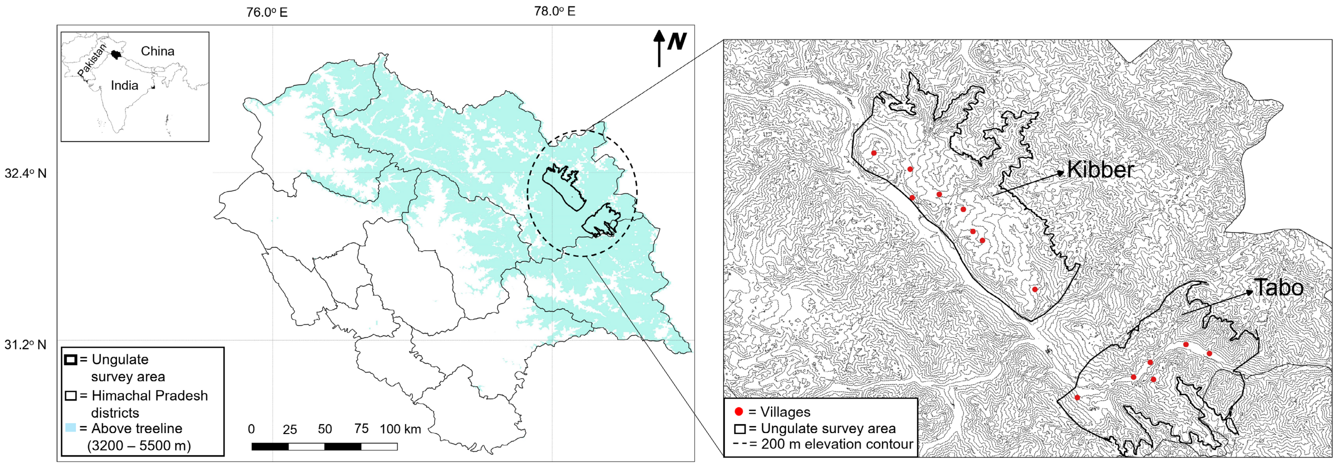

FIGURE 1 The left panel shows a map of the location of our study sites within the trans-Himalayan Lahaul-Spiti district of Himachal Pradesh. The right panel is a zoomed-in map showing Kibber (411 km^2) and Tabo (341 km^2) with 200 m contours lines. Red dots represent villages within each site.

blue sheep and livestock on blue sheep diet and reproductivity. The region is characterised by low precipitation, a short growing season, low primary productivity and varying livestock densities (Suryawanshi et al., 2013).

2.1 | Double-observer surveys

We used the double-observer survey method to estimate bharal abundance (Forsyth & Hickling, 1997; Suryawanshi et al., 2012). This method employs two observer teams separated in time and/or space, and models the data from the two surveys within the mark–recapture framework to estimate detection probability and population size. Ungulate groups are the unit that are 'marked' and 'recaptured', since groups, albeit temporary, can be identified during the surveys based on various characteristics including group size and age-sex classification. The study site was further divided into blocks which were surveyed keeping three primary assumptions of the method in mind: (i) entire visual coverage of the study site was possible during the survey, (ii) the two observer teams surveyed the area independently and (iii) individual herds could be uniquely identified based on information such as the age-sex composition of each herd, location and any other peculiarity that was observed. The population data collected included the number of groups sighted, group sizes and group detection or non-detection by the two observer teams.

The survey area of Kibber was 411 km^2 divided into nine survey blocks requiring 99 km of survey effort by each observer team every year and the survey area for Tabo was 341 km^2 divided into eight survey blocks requiring 87 km of survey effort by each observer team every year. In Kibber, the effort in each of the nine blocks ranged from 7 to 15 km, while in each of the eight blocks in Tabo it ranged from 5 to 14 km. Usually, each block was covered between 1.5 and 3 h. Each block was surveyed by two teams following recommendations of Suryawanshi et al. (2012). Each team comprised of either a single observer or two observers and we ensured that the same number of observers per team per survey across years were maintained to ensure standardised effort. Each observer used a 8 × 42 binocular. A total of eight observers were involved in the surveys, including six trained observers who participated in surveys across all years, supported by KS and MK as two trained observers who took part during some of the years. The second team maintained a separation of *c.* 15–30 min from the first team. Suryawanshi et al., 2012 report that a separation of 15–30 min between observers is appropriate for sampling and does not get impacted by changes in group sizes. Both sites were surveyed annually towards the end of May and the beginning of June. This time of the year was chosen for the surveys because it is just before the birthing pulse of the bharal. We avoided sampling during the birthing phase as that would lead to counting the kids born to only a section of the population. Additionally, the field sites are not easily accessible after the birthing pulse as the landscapes are covered in snow, making it extremely challenging to conduct surveys. The young bharal encountered during the survey had survived one winter and were approaching 1 year in age. On the rare occasion, we did observe newly born bharal but they were less than one or two individuals each year and were not considered for the analysis.

The surveys started at sunrise or immediately after, to control for any effect of time related impact on grouping and activity pattern of the study species (Fattorini et al., 2019). Each team used a pair of binoculars to locate and classify bharal. Bharal age-sex classification was done based on their body size and horn characteristics (Mishra et al., 2004). Male horns are in a crescent formation, curving outwards, backwards and then downwards. In older males (over 8 years of age), tips of the horns once again point upwards at the end. Compared to female horns, male horns are much thicker and diverge from a much closer base. Class 1 males (2–3 years) are as big as females with a horn size around 25 cm. Horn size reaches *c.* 35 cm in class 2 (4–5 years), and over 40 cm in class 3 and class 4 males (with an upward turn at the end; older than 5 years). Class 4 males have larger horns and body sizes than class 3 males. Adult rams (class 2, 3, and 4) have dark brown to black markings on the neck, chest and legs, and a flank stripe that merges with the colour of the legs.

Females are smaller compared to males and have relatively shorter and thinner horns that diverge out (rather than in parallel) with a gap between them. Sub-adult females (2–3 years) are similar to adult females, but of smaller body size with smaller and thinner horns. Visible scrotal sacs can particularly help distinguish younger males from the females. Given the timing of our surveys in early spring, yearlings were between 10 and 12 months in age (although as a stage yearling ranges from 0.5 to 1.5 years). They are roughly two-thirds the size of females, with horn sizes of around 15 cm. Their horns are smaller and thinner than those of sub-adult females.

2.2 | Surveys to estimate livestock populations

We conducted interview surveys across all the villages within each site, 11 within Kibber and 11 within Tabo (Figure 1). Village herders and key informants who maintained records for the village were interviewed to enumerate the number of livestock of each kind. We interviewed the same key informants each year. Livestock censuses were conducted each year in December and we have been collecting these data from the Spiti Valley from 2010 as part of our long-term monitoring programme. Additionally, we also compared the livestock density between the two sites in terms of bharal units using existing literature on livestock equivalent for bharals in terms of forage removal. For details, see Appendix S1 in Supporting Information.

2.3 | Estimating bharal abundance

The analysis was conducted in R statistical and programming environment using the 'BBRecapture' package which uses the Bayesian framework (Fegatelli & Tardella, 2013; Version 3.3.4, R Core Team, 2018). As recommended by Suryawanshi et al. (2012), the analysis was conducted on a number of groups. Based on the capture–recapture framework, a group was coded '11' if recorded by both teams, '10' if only the first team recorded it and '01' if only the second team recorded it. As detection probability was expected to vary across the two surveys, we used the 'mt' model to model the detection for the two teams separately (Suryawanshi et al., 2012). The estimated detection probability by model 'mt' for occasions one and two was interpreted as the detection probability for observer teams one and two.

To estimate the total number of bharal groups ($\hat{G}$) within each of our study areas, we fit the 'mt' model using the function BBRecap with a 'uniform prior'. We used uninformed uniform priors and did 10,000 Monte Carlo Markov Chain (mcmc) iterations with 1000 burn-in. The total estimated population (N_{est}) for each site was calculated as a product of the estimated group number ($\hat{G}$) and the estimated mean group size (μ). To estimate the confidence intervals of the population using the variance in $\hat{G}$ and μ, we generated a distribution of $\hat{G}$ by bootstrapping it 10,000 times with replacement. A distribution of N_{est} was generated by multiplying 10,000 random draws of $\hat{G}$ weighted by the posterior probability and draws of μ. The median of the resultant distribution was the estimated ungulate population (N_{est}) and the 2.5 and 97.5 percentiles were used as the confidence intervals. Densities were obtained by dividing the N_{est} by the total area sampled. The sampled area was calculated by summing areas of surveyed blocks demarcated on Google Earth.

We examined the year-to-year variation in key demographic parameters to understand the parameters that could contribute to observed changes in bharal abundance. Specifically, we tested if the potential density-dependent feedback structure was a consequence of a similar structure in the abundance of a demographic sub-group, that is, adult males, adult females or recruited offspring. For this, we calculated the mean proportion of adult females, adult males and recruited offspring across groups for each year. The recruited offspring included the total number of yearlings observed in the survey of a given year. The proportion was calculated by taking a ratio of the number of the demographic sub-group and the number of total individuals. We then estimated the number of individuals belonging to each demographic sub-group by multiplying the proportion with the estimated total population of that year.

2.4 | Examining density dependence in bharal population dynamics

We visualised the time series abundance data and the variation around the mean abundance estimate for overall bharal populations in Tabo and Kibber. Because clear positive or negative population trends were not discernible, we fitted autocorrelation function (ACF) and partial autocorrelation function (PACF) to the time series data to evaluate density dependence. ACF informs about the period of a time series data, whereas to identify the feedback structure in time series data, PACF is commonly used (Berryman & Turchin, Berryman & Turchin, 2003). Similarly, PACF functions were also fitted to each of the three categories, that is, males, females and offspring (yearling), to examine whether populations of individual categories follow similar density dependence as the overall population. Interpretation for the PACF was done by comparison with 95% confidence intervals on the autocorrelations derived from a white noise input.

Partial autocorrelation function analysis for the overall bharal time series suggested that both 1- and 2-year lag were important in explaining the dynamics in the population of Tabo. Whereas, for the population in Kibber, we could not detect any significant lag effect from the PACF analysis. Following the PACF analysis, we quantified the effect of density dependence on the overall population growth rate of bharal in Tabo and Kibber by fitting a Gompertz state-space (GSS) model to the data (Băncilă et al., 2015; de Valpine & Hastings, 2002; Dennis et al., 2006). We interpreted the 1-year lag effect as direct density dependence and the 2-year lag effect as delayed density dependence. Both direct and delayed density dependence was modelled using the GSS model. In the GSS, we modelled density dependence influencing bharal population as the following equation on log scale:

$$N_{e,t} \sim N_{t-1} + a + b_1{}^{*}N_{t-1} + b_2{}^{*}N_{t-2} \quad (1)$$

where $N_{e,t}$ is the expected population size at time t, a is the intercept, b_1 estimates the strength of density dependence and b_2 estimates the strength of delayed density dependence. The modelling framework was based on the approach used by Dennis et al. (2006) and Băncilă et al. (2015). The process leading to expected population size is described by the following two equations:

$$X_t \sim \text{Normal}\left(N_t, \sigma^2{}_{\text{obs}}\right) \quad (2)$$

$$N_t \sim \text{Normal}\left(N_{e,t}, \sigma^2{}_{\text{proc}}\right) \quad (3)$$

where N_t is the actual population size that depends on the process variance and the expected population size at time t. $N_{e,t}$ is the expected population size at time t and $\sigma^2{}_{\text{proc}}$ represents the process variance, that is, unexplained error in bharal abundance. $\sigma^2{}_{\text{obs}}$ is the observation variance that represents observation error under the assumption that counts sometimes are overestimated or underestimated with a mean of 0 (Kéry & Schaub, 2011). Altogether, Equations (1)–(3) were used to model the population dynamics using the R2WinBUGS package in R to operate WinBUGS (Sturtz et al., 2005).

To fit the models, we used vague normal priors with a mean zero and precision of 0.0001 for the parameters a, b_1 and b_2. We used vague uniform priors in the interval 0–10 for the standard deviations of $\sigma^2{}_{\text{obs}}$ and $\sigma^2{}_{\text{proc}}$. We ran three parallel MCMC chains with 200,000 iterations. Convergence was assessed using the Gelman–Rubin statistic R-hat. Convergence was satisfactory when R-hat values were smaller than 1 (Brooks & Gelman, 1998; Gelman & Hill, 2006).

3 | RESULTS

3.1 | Bharal and domestic ungulate population in Tabo and Kibber

Population size in the bharal population of both Tabo and Kibber changed considerably over the 10-year period—in Tabo, the population size ranged from 316 (95% CI: 305–349) to 572 (572–594) individuals and in Kibber, the population size ranged from 616 (95% CI: 599–662) to 971 (971–1013) individuals (Figure 2). The density ranged from 1.49 (95% CI: 1.46–1.61) to 2.36 (2.36–2.47) bharal km^{-2} in Kibber and from 0.93 (95% CI: 0.89–1.02) to 1.68 (1.67–1.74) bharal km^{-2} in Tabo. Overall, the average population density (pooled across all years) of bharal in Kibber was higher than the population density in Tabo. The average across all years was 1.27 bharal km^{-2} (95% CI: 1.12–1.41) for Tabo and 1.9 bharal km^{-2} (95% CI: 1.74–2.08) for Kibber.

The mean livestock density at Kibber was 1.9 times higher than Tabo. The mean livestock density over the years was 1.22 (95% CI: 1.15–1.29) in Kibber and 0.654 (95% CI: 0.617–0.707) in Tabo (Figure S1). Among the herded livestock, the density of sheep was 7.6 times higher in Kibber than in Tabo. Among the free-ranging livestock, the density of yak was 8.6 times higher in Kibber than in Tabo. For further information see Supporting Information.

3.2 | Direct and delayed-density dependence

Gompertz state-space model showed that in the case of Tabo, the estimated population size counts with the direct and delayed density dependence coefficients were close to the observed population counts (Figure 2c). The mean estimate for both 1- and 2-year lag (b1 and b2 in Equation 1) effect was negative suggesting the presence of negative density dependence feedback. The mean estimate for b1 was −0.49 (SD = 0.40) and the mean estimate for b2 was −0.92 (SD = 0.44) (Table S1). As expected from the PACF results, in the case of Kibber, the GSS model with direct and delayed density dependence coefficients could not explain the variation in population (Table S1).

Our study found evidence for direct and delayed density-dependent feedback structuring in bharal population of Tabo but this is impeded in the population of Kibber. For the bharal population

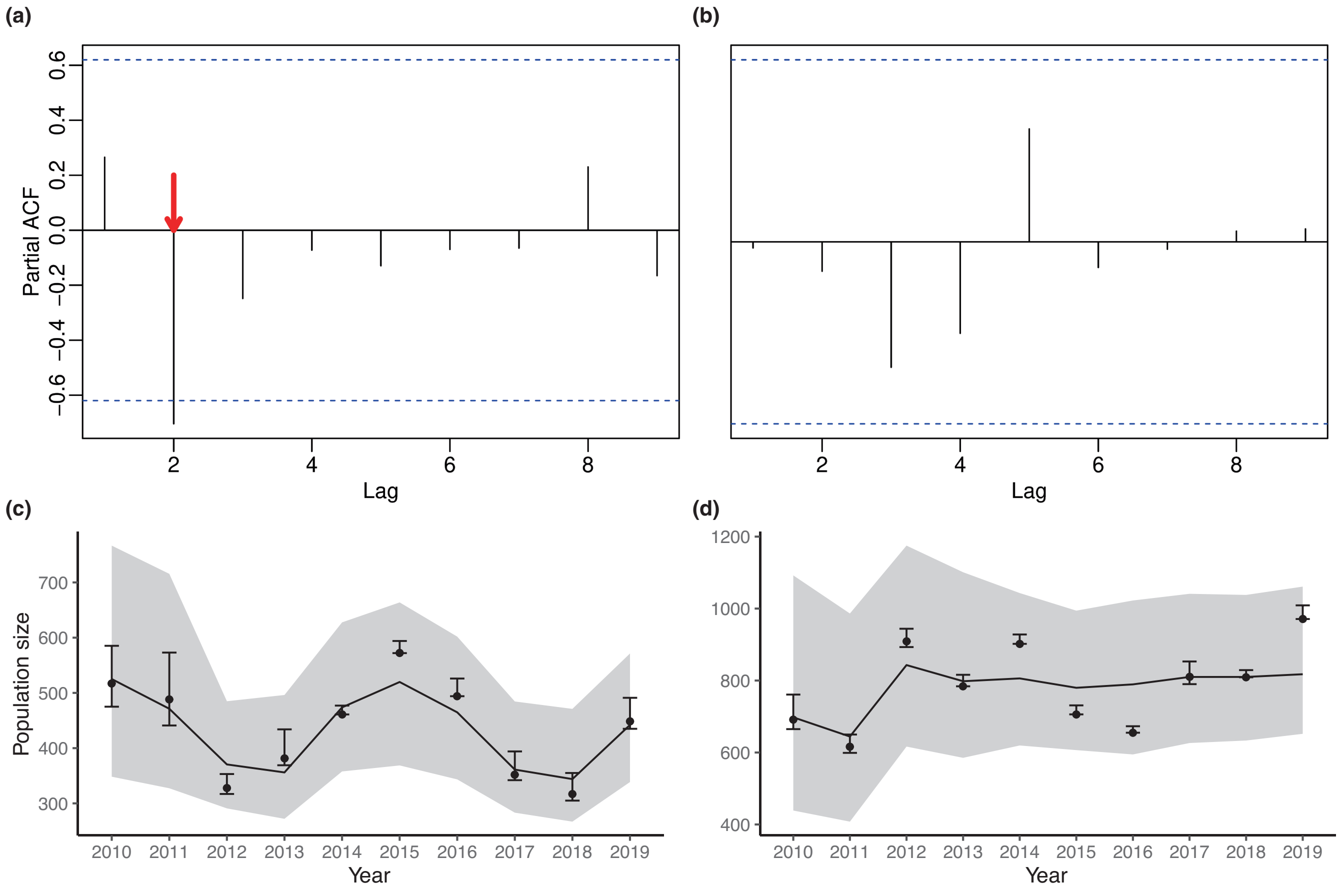

FIGURE 2 Bharal *Pseudois nayaur* time series data for Tabo and Kibber. The top panel shows the partial autocorrelation function (PACF) for bharal time series data for Tabo (a) and Kibber (b). The PACF of Tabo shows a statistically significant 2-year lag effect (red arrow), which was absent in Kibber. The horizontal blue lines are the approximate 95% credible interval (CI). The bottom panel shows the observed population size of the bharal *Pseudois nayaur* from 2010 to 2019 for Tabo (c) and Kibber (d). The estimated abundance based on the GSS model with 1- and 2-year lag is shown by the solid line. The shaded area is 95% CI.

of Tabo, PACF showed the presence of significant negative feedback at 1- and 2-year lag period (Figure 2) and the ACF analysis suggested a pattern of periodicity with a signal for a time period of 5 years suggesting that the populations potentially show cyclicity with a period of 5 years. For the bharal population of Kibber, the PACF analysis suggested the absence of any feedback structuring in explaining the population dynamics (Figure 2) and the ACF analysis indicated no pattern of periodicity. For details of ACF and PACF results, see Supporting Information.

3.3 | Role of recruitment in bharal population dynamics

The estimated number of adult females in both Tabo and Kibber seemed to show an increase over time. This increase was more consistent in Tabo (Figure 3) where the estimated number of adult females was the lowest in 2013 (mean = 71, 95% CI: 39–108) and the highest in 2019 (mean = 183, 95% CI: 155–213). In Kibber, the estimated number of adult females was the highest in 2018 (mean = 302, 95% CI: 259–350) and the lowest in 2010 (mean = 118, 95% CI: 74–168; Figure 4). Interestingly, we observed that the female to male ratio varied over time during the course of our study, but largely remained male-biased (Figure S6). For Tabo, the female to male ratio ranged from 0.55 in 2014 to 1.61 in 2019, while in Kibber, it ranged from 0.53 in 2014 to 1.01 in 2015. The number of adult males and the number of offspring (yearlings) did not show any increasing trends in Tabo or Kibber. We calculated the PACF for the time series data for each demographic sub-group to examine if feedback structures similar to the overall population could be detected. For Tabo, the PACF for offspring showed a statistically significant 1- and 2-year lag effect (Figure 3). We detected a weak effect for a similar lag effect in male numbers (Figure 3), although not statistically significant. We did not find any signal for a lag effect for females. In Kibber, we did not detect any significant lag effect for any demographic sub-group (Figure 4).

4 | DISCUSSION

Our long-term study shows that local differences in the intensity of anthropogenic stressors, such as livestock grazing pressure can have consequences for population dynamics in wild ungulate populations. We quantified the density-dependent feedback structuring in the long-term population dynamics in bharal populations from two sites that varied in livestock density. We found that bharal population from site with low livestock densities (in Tabo) showed negative density dependence with 1- and 2-year lag effects. Second, we found that this effect is mediated via recruitment of offspring and not adult survival. The density-dependent feedback structure was absent in Kibber which had higher livestock densities suggesting that

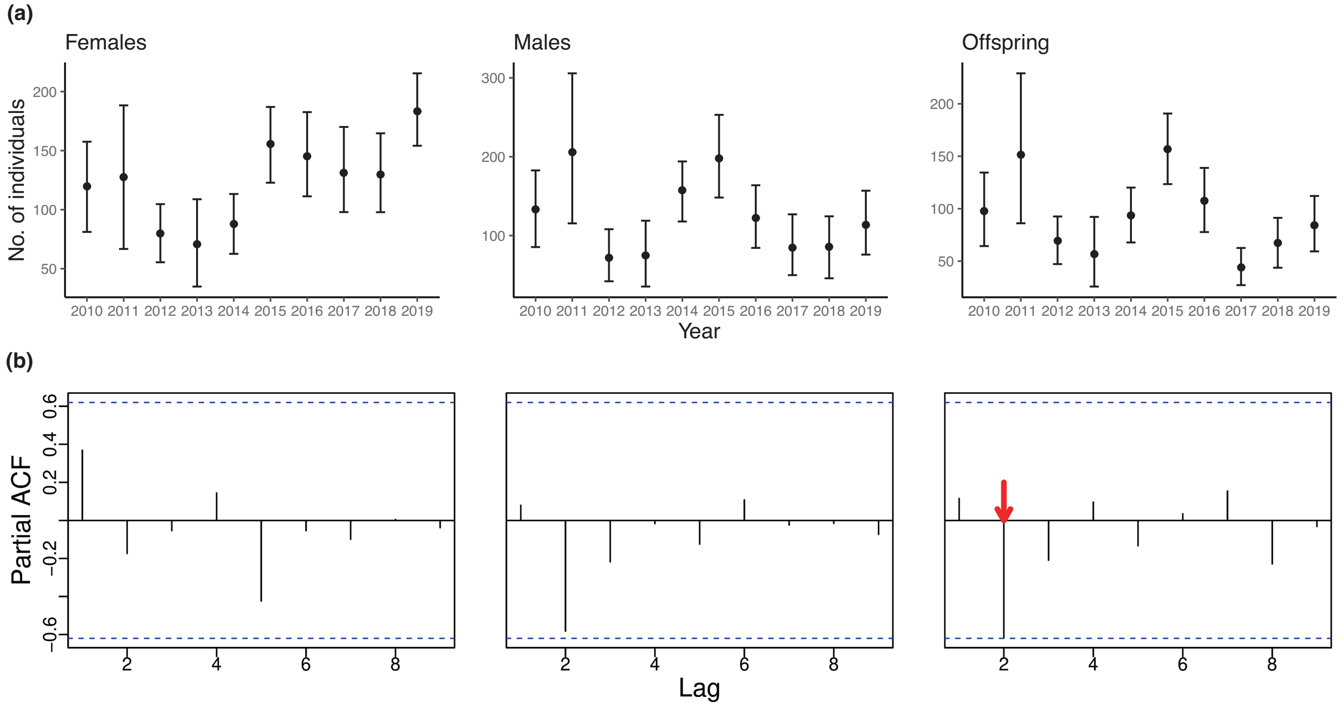

FIGURE 3 Year-to-year variation in the estimate of the number of females, males and recruited offspring (yearling) bharal in Tabo. The top panel (a) shows the mean number of individuals belonging to each sub-group and error bars represent 95% bootstrapped credible intervals (CIs). The bottom panel (b) shows the partial autocorrelation function (PACF) for each sub-group. The horizontal blue lines are the approximate 95% CIs. PACF of offspring shows a statistically significant 2-year lag period (red arrow). This 2-year lag effect is absent for females and males.

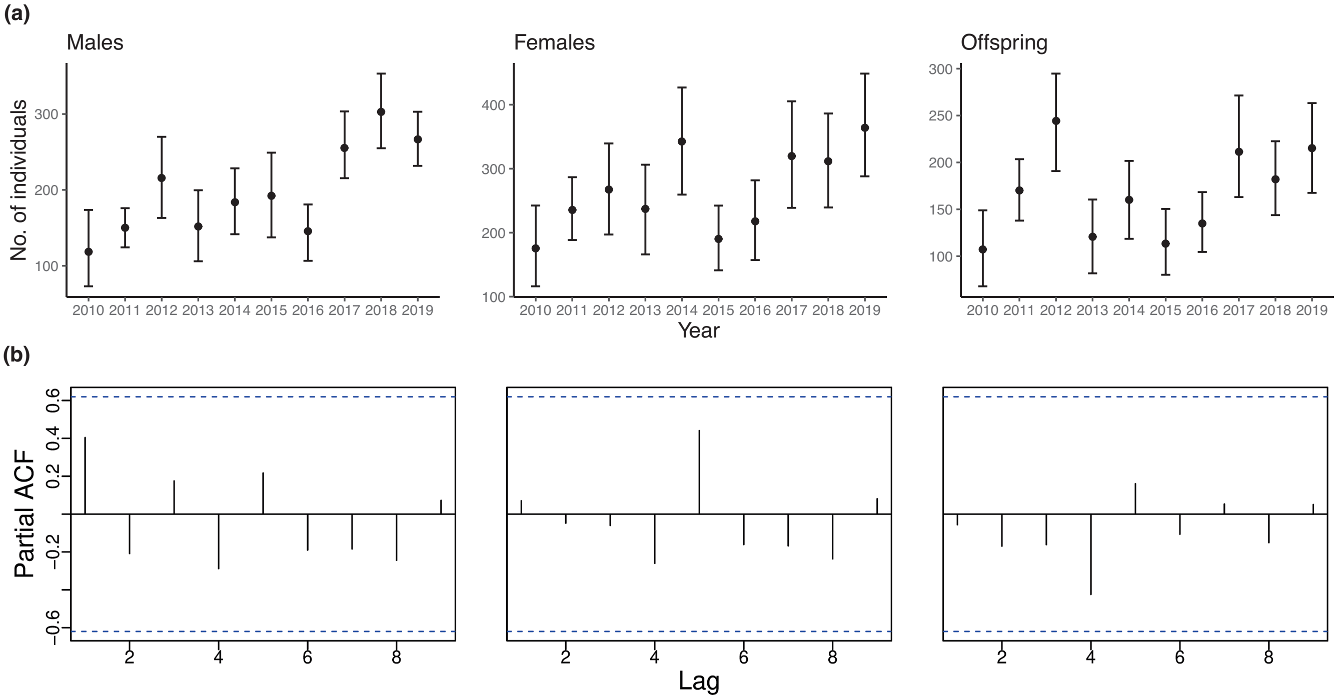

FIGURE 4 Year-to-year variation in the estimate of the number of females, males and recruited offspring (yearling) bharal in Kibber. The top panel (a) shows the mean number of individuals belonging to each sub-group and error bars represent 95% bootstrapped credible intervals (CIs). The bottom panel (b) shows the partial autocorrelation function (PACF) for each sub-group. The horizontal blue lines are the approximate 95% CIs. The PACF for all three categories showed no significant lag period effects.

anthropogenic stressors can have population-level consequences, potentially affecting cyclic dynamics in wild ungulates.

The population dynamics of bharal from Tabo are structured through a feedback effect. But what is driving population change in Kibber? We explicitly modelled the impact of density of bharal from previous years on population growth and found that this density dependence arises due to changes in bharal densities when livestock densities are low. But, when livestock densities are high, there are large fluctuations in the bharal populations which cannot be explained through the intrinsic process of density dependence. The large fluctuations at the site with high livestock density arise likely due to a combination of high degree of seasonality in resources and overstocking, given the extensive evidence for overstocking and competition from livestock from this region (Bagchi et al., 2004; Mishra, 2001; Mishra et al., 2004; Suryawanshi et al., 2010). The manner in which grazing pressure can cause disruption of density dependence is unknown. For example, consequences of competition from large-bodied livestock (yak and horses) might be different from the consequences of competition from small-bodied livestock (sheep and goats), as their forage requirements are different (Mishra et al., 2004). Livestock density was significantly higher in Kibber than in Tabo for five out of seven types of livestock. Sheep and yak densities are 7.6 and 8.6 times higher in Kibber than in Tabo respectively (Appendix S1). Future studies need to explore the effects of livestock composition on vegetation dynamics at a finer temporal scale. Building an understanding of temporal dynamics of vegetation will help in understanding the large fluctuations of wild ungulate populations. Both these study sites in the Spiti Valley had similar densities of snow leopards (Kibber: 0.3 (0.15–0.59); Tabo 0.37 (0.18–0.72); Suryawanshi et al., 2021)—the primary predator of bharal in these regions. Therefore, the role of predation in shaping different population dynamics for these two sites is limited. While the predator density is similar at these two sites, it is still possible that similar predator density does not necessarily translate to a similar functional response for both Tabo and Kibber. The functional response might depend on habitat characteristics that could affect predator–prey relationship.

Studies show that anthropogenic stressors, such as hunting or pollution, can disrupt animal population dynamics, a phenomenon articulated as the ‘risk-disturbance hypothesis’ (Frid & Dill, 2002; Hunter & Kozlov, 2019; Schuttler et al., 2017) and can often obscure density-dependent effects in populations dynamics (Pauli & Buskirk, 2007). There is evidence from many studies demonstrating that competition from livestock can negatively affect the body condition of wild ungulates. In white-tailed deer, *Odocoileus virginianus*, high stocking density has been shown to have detrimental effects on the nutritional condition of females and reduced the number of yearlings that survive to the next stage (Jenks & Leslie, 2003; Schieltz & Rubenstein, 2016). Studies from the Indian Trans-Himalayan region have shown that high livestock density can negatively impact bharal young to female ratios, through resource-driven competition (Mishra et al., 2004; Suryawanshi et al., 2010). Our study goes beyond traits and demonstrates how an anthropogenic stressor can affect population dynamics of wild fauna, potentially through disruption of density-dependent processes. We report that overall, the bharal population densities are low across both sites. The highest bharal density estimated from our study site was 2.36 (95% CI: 2.36–2.47) bharal km^{-2} in Kibber and 1.68 (1.67–1.74) bharal km^{-2} in Tabo. In the Ningxia and Inner-Mongolia Helan Mountain Nature Reserves, the bharal density was estimated to be 5.144 ind./km^2 on the east slope and 2.532 ind./km^2 on the west slope (Liu et al., 2008). In the Manang District of Nepal, the density was estimated to be 6.6–10.2 ind./km^2 (Oli, 1994). This low bharal density is perhaps due to the low primary productivity in this landscape—the annual maximum normalised difference vegetation index (NDVI) values rarely fall above 0.2 and the average forage available was estimated to be similar at both Kibber (207 kg/ha) and Tabo (206 kg/ha; Appendix S2). This region has one of the lowest above-ground graminoid biomass for any ecosystem in the world (Mishra, 2001). It is likely that ungulate populations from regions of low primary productivity are more likely to experience population-level consequences of anthropogenic stressors, while ungulate populations from regions with high primary productivity might buffer against these stressors. Negative density dependence in populations occurs when population growth is curtailed, and this is typically due to resource limitation. However other processes, such as disease spread, can potentially also lead to negative density dependence. Studies on livestock and ungulate disease ecology from Spiti Valley show the presence of parasitic nematodes in ungulate gut but these have not been linked to mortality (Khanyari et al., 2021). These pathogens might still impact the birth rate of ungulates but this negative impact on fecundity has not been demonstrated yet.

Ungulate populations typically show stable adult survival rates and variable juvenile survival rates, hence the expectation that ungulate population regulation might occur through recruitment-related processes (Bowyer et al., 2021; Kiffner & Lee, 2019). We found that female numbers were not sensitive to bharal population size, but the number of adult males (weak evidence) and the recruited offspring varied with population size in a manner similar to the abundance. Ungulate populations have been found to experience later primiparity and reduced maternal care when resources are scarce (Festa-Bianchet et al., 2019). In bharal, resource availability for females in year t is known to affect fecundity in the year $t+1$ and the survival of offspring to year $t+2$ (Mishra et al., 2004; Suryawanshi et al., 2010). This could explain the 2-year lag that we observed in offspring recruitment that is driving the density dependence. Our results suggest that offspring recruitment in bharal, and not adult female survival, is likely to contribute towards the population dynamics in bharal populations when livestock density is low. When livestock density was high, this recruitment related effect disappeared, indicating perhaps that livestock density affects offspring recruitment and not adult survival. However, a future study that directly measures the effects of livestock density on these two rates is needed to confirm this conclusively. Ungulates typically show female-biased populations and this is attributed to greater rates of predation and hunting on males (Berger & Gompper, 1999). Our results regarding the survival of adult males were unclear, and this needs to be explored further through studies on marked individuals.

5 | CONCLUSIONS

We demonstrate the role of livestock grazing in shaping long-term population dynamics of a wild ungulate through negative density dependence. In primarily bottom-up controlled systems, artificially managed populations (livestock) have population-level consequences for wild ungulates and predation by snow leopards may not significantly affect bharal population dynamics and regulation. Given our finding, we suspect that traditional conservation interventions to safeguard wild mountain ungulate populations such as the creation of livestock-free area, such as village reserves or strict protected areas, can increase the possibility of cyclicity in the populations of the bharal. Protected area and reserve managers are always under pressure to show an increase in ungulate populations. However, our work shows that wild herbivore populations may experience temporary declines due to density dependence. Our results also highlight the need for similar work on the many sympatric ungulates species (e.g. Ibex *Capra sibirica*; argali *Ovis ammon*; markhor *Capra falconeri*) in the region. Our results indicate that it is critical for conservationists and managers to explicitly investigate the population dynamic impacts of conservation interventions that restrict the co-occurrence of sympatric livestock. This can inform the management of species that are relevant for the trophy hunting economy (hunting permits can cost from 70USD to 62,000USD), such as deciding on dynamic hunting quotas and for ensuring the conservation of vulnerable carnivores such as the snow leopard whose population is directly determined by the availability of wild mountain ungulates.

AUTHOR CONTRIBUTIONS

The idea was conceived by Manvi Sharma, Kulbhushansingh Ramesh Suryawanshi, Munib Khanyari and Charudutt Mishra; the study was designed by Kulbhushansingh Ramesh Suryawanshi, Munib Khanyari, Ajay Bijoor and Charudutt Mishra; data were collected by Munib Khanyari, Abhirup Khara, Kulbhushansingh Ramesh Suryawanshi and Ajay Bijoor; data were analysed by Manvi Sharma, Munib Khanyari and Abhirup Khara; The first draft of the manuscript was written by Manvi Sharma, and all authors contributed substantially to improving it.

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CONFLICT OF INTEREST STATEMENT

None of the authors have a conflict of interest. Munib Khanyari and Kulbhushansingh R. Suryawanshi are Associate Editors of Journal of Applied Ecology, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.f7m0cfz4g (Sharma et al., 2024).

ORCID

Manvi Sharma https://orcid.org/0000-0002-8236-6342
Munib Khanyari https://orcid.org/0000-0003-4624-5073

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SUPPORTING INFORMATION

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

Appendix S1. Livestock density differences between the two sites.

Appendix S2. Analyses to compare productivity in Tabo and Kibber.

Figure S1. Mean livestock density in Kibber was 1.9 times higher than in Tabo.

Figure S2. Mean of annual maximum NDVI was slightly higher in Kibber when compared to Tabo.

Figure S3. The figure shows the within year and year-to-year variation in NDVI for Tabo and Kibber.

Figure S4. (a) Estimated above ground plant biomass (kg/ha) from NDVI for Kibber and Tabo from Guo et al 2018. (b) Livestock density converted to bharal units for Kibber and Tabo based on existing literature. (c) Above ground plant biomass per bharal unit (kg/ha) for Kibber and Tabo.

Figure S5. ACF for bharal populations of Tabo (A) and Kibber (B).

Figure S6. Female to male ratio in Tabo and Kibber across years.

Table S1. Parameter estimates from MCMC chains fitted for the Gompertz state space model.

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