



Coupled Demographic Dynamics of Herds and Households Constrain Livestock Population Growth in Pastoral Systems

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Abstract

One of the dominant narratives about pastoral systems is that livestock populations have the potential to grow exponentially and destroy common-pool grazing resources. However, longitudinal, interdisciplinary research has shown that pastoralists are able to sustainably manage common-pool resources and that livestock populations are not growing exponentially. The common explanation for limits on livestock population growth is that reoccurring droughts, diseases, and other disasters keep populations in check. However, we hypothesize that coupled demographic processes at the level of the household also may keep livestock population growth in check. Our hypothesis is that two mechanisms at the herd-household level explain why livestock populations grow much slower in pastoral systems than predicted by conventional Malthusian models. The two mechanisms are: (1) the domestic cycle of the household, and (2) the effects of scale and stochasticity. We developed an agent-based model of a pastoral system to evaluate the hypothesis. The results from our simulations show that the couplings between herd and household do indeed constrain the growth of both human and livestock populations. In particular, the domestic cycle of the household limits herd growth and ultimately constrains the growth of livestock populations. The study shows that the misfortunes that affect individual households every day cumulatively have a major impact on the growth of human and livestock populations.

Keywords Pastoral systems · Agent-based modeling · Demography · Population growth · Livestock · Domestic cycle · Households · Family herds · Coupled system

Introduction

One of the dominant narratives about pastoral systems is that livestock populations have the potential to grow exponentially and destroy common-pool grazing resources. However, longitudinal and interdisciplinary research has shown that

pastoralists are able to sustainably manage common-pool resources (Coughenour et al., 1985; Little & Leslie, 1999; Moritz et al., 2014a, b) and that livestock populations are not growing exponentially (McCabe, 1990; Moritz et al., 2014a, b; Sandford, 2006; Sperling, 1987). The common explanation for limits on livestock population growth is that reoccurring droughts, diseases and other disasters keep populations in check (Ellis & Swift, 1988; Gilles & Jamtgaard, 1982). However, we hypothesize that demographic processes at the level of the herd and household are an important factor in constraining the growth of livestock populations. Our hypothesis is that two mechanisms at the herd and household level explain why livestock populations grow much slower in pastoral systems than predicted by conventional Malthusian models. The two mechanisms are: (1) the domestic cycle of the household, and (2) the effects of scale and stochasticity. These two mechanisms lead to the continuous removal of people and livestock from pastoral systems and are density independent, i.e., not shaped by ecological constraints.

One-sentence summary: Agent-based modeling simulations show that couplings between demographic dynamics of herd and household constrain the growth of human and cattle populations in pastoral systems.

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A brief example illustrates how the coupling between these two mechanisms may keep livestock populations in check. Among pastoralists in the Far North Region of Cameroon, the family herd is divided among sons when the patriarch dies. In the ideal scenario, the patriarch dies at an advanced age when the herd is large enough for each son to inherit a herd that can support their respective families. However, when a patriarch of an extended family dies prematurely and leaves each son with herds that are too small to support their respective families, there is a great chance that the herds will disappear over time. Two reasons drive this phenomenon. First, when the herds do not provide enough milk, the sons must sell reproductive animals to feed their families. Second, smaller herds have a greater chance of decreasing in size due to stochasticity in fertility and mortality. Eventually, a herd may become too small to provide enough milk and income, and this forces the family to sell the remaining cattle, leave pastoral society, and pursue other livelihoods to support themselves. We have seen these scenarios play out many times among pastoralists in Cameroon (Moritz, 2003, 2013) and it is common in other pastoral systems (Barth, 1961; Fratkin & Roth, 1990).

We developed an agent-based model to examine whether, how, and how much these mechanisms keep livestock population growth in check. Agent-based modeling is a particularly useful tool to examine these processes because the long-term, demographic dynamics of herds and households are difficult to study empirically, and we lack the longitudinal data sets of coupled herd and household demography in pastoral systems.

Agent-based modeling allows us to conduct multiple experiments on a computer to explore the long-term dynamics of coupled herd-household demographic processes. Agent-based modeling is particularly appropriate because it allows us to examine how stochasticity in demographic processes i.e., life events, affect household viability and overall population growth.

Domestic Cycle and Herd Dynamics

Herding animals is a commitment to a way of life in which the interdependence with their animals structures pastoralists' lives (Chang & Koster, 1994). This interdependence is also evident in the relationship between human and livestock demographic processes. Stenning explained in a classic paper on *Household Viability among the Pastoral Fulani* (1958) how pastoralists seek an equilibrium between herd and household. In an equilibrium, the herd provides enough milk to feed the household and the household provides enough labor to manage the herd. This equilibrium depends on the fertility of herd and household. In pastoral households there is often a strict division of labor in which

men are responsible for the fertility of the herd and women are responsible for the fertility of the household. If there are fertility problems in either one, the potential disequilibrium between herd and household may lead to the dissolution of the household.

Pastoral households regularly go through periods of disequilibrium because of the domestic cycle in which households expand and dissolve. In the domestic cycle, households start with a husband and wife, expand with the addition of children (and sometimes additional wives), and dissolve as children marry and set up their own independent households. Because of the domestic cycle, households regularly experience labor and/or food shortages. Pastoral societies across the world have developed strategies to resolve these imbalances between herd and household, for example through labor contracts and livestock exchanges. However, there are also imbalances between herd and household due to misfortunes, e.g., infertility problems may limit growth of the herd, or an early death of a patriarch may lead to an untimely division of the family herd among heirs. One of the main risks of these unfortunate events is that the herd may become too small to provide enough food and/or income to the household.

Studies on pastoral wealth have shown that the dynamics of herd growth are to the advantage of pastoralists with larger herds and that those same dynamics work against pastoralists whose herd are smaller (Bradburd, 1982; Fratkin & Roth, 1990; Lybbert et al., 2005). In other words, pastoralists with larger herds likely see their herds increase over time and pastoralists with smaller herds likely see their herd decrease in size (Grandin, 1989; Fratkin & Roth, 1990; Sieff, 1999; Borgerhoff Mulder & Sellen, 1994). Moreover, this inequality in livestock wealth persists over generations (Mulder et al., 2010). This is due to two processes. First, larger herds buffer households against risks of droughts, diseases and other disasters (Bradburd, 1982; Fratkin & Roth, 1990). Second, if herd size is too small, households have to sell reproductive animals to support their families, and this limits the natural growth potential of their herds. In our earlier agent-based modeling study we confirmed that scale and stochasticity matter and that larger herds have a greater chance of long-term survival (Buffington et al., 2016; Moritz et al., 2017), but we also found that there is no clear threshold and that even larger herds run the risk of disappearing due to stochasticity in fertility and mortality rates, i.e., bad luck.

When herd size becomes too small, it can no longer provide enough food and/or income for the household. Consequently, poor households have to leave the pastoral system and pursue other livelihood strategies like crop agriculture. This process has been called "sloughing off" by Barth (1961) and has been described for pastoral societies across the world (Bradburd, 1989; Fratkin & Roth, 1996;

Loftsdóttir, 2008). One of the consequences of the sloughing off of households is that animals are also removed from the pastoral system as impoverished households sell their animals at local and regional livestock markets. Most livestock sold at these markets is either consumed locally or exported for consumption elsewhere, and thus disappear from the pastoral system.

While the demographic processes at the herd and household level have been well described, the couplings between the two and its impacts on long-term growth of livestock populations have not been systematically studied. Our agent-based modeling approach allows us to examine whether, how, and how much coupled demographic dynamics impact the growth of human and livestock populations in pastoral systems.

Artificial Pastoral System

Pastoral systems are an excellent example of a complex social-ecological system because of the dynamic couplings among households, herds, and rangelands. Agent-based modeling is one of the tools of choice to study complex systems, and in the last twenty years, the number of agent-based modeling studies of pastoral systems has steadily increased (Moritz et al., 2023). Agent-based modeling allows researchers to build artificial pastoral systems that are spatially explicit and allow for examination of complex interactions between households, herds, and rangelands over long time periods.

To examine the impact of coupled herd-household demographics on the growth of livestock populations in pastoral systems, we developed an agent-based model of an artificial pastoral system that is a simple but meaningful representation of a wide range of pastoral systems. However, even a quick, cursory review shows that there is considerable variation across pastoral systems in terms of the species of livestock raised, the degree of market involvement, the livestock products sold, the organization of households, and the types of livestock exchanged, let alone the larger social, ecological, economic and political context (Barfield, 1993). Therefore, we have decided to model our artificial pastoral system after that of Fulani pastoralists in the Far North Region of Cameroon for which we have collected ethnographic and demographic data on households and herds in prior research projects (Moritz, 2003, 2010, 2012a, 2013). These pastoralists are part of a much larger and more diverse population of Fulani pastoralists that can be found across West and Central Africa.

The pastoral system of Fulani pastoralists in the Far North Region of Cameroon is complex and this required us to make decisions that simplify the empirical reality for our agent-based model. We reduced the complexity

of herd-household dynamics in five major ways. First, we did not consider livestock exchanges between households because we found that they contribute to short-term survival of households but not to long-term viability of family herds (Moritz, 2013). Second, we only model cattle and no other livestock, even though pastoralists in our study area also keep some small stock (goats, sheep) for minor expenses and a few animals for transportation (donkeys, horses) (Moritz, 2012b). Third, while we recognize that members of the households may have competing interests and do not necessarily pool their resources (Moritz, 2003), we treat the herd and the milk production as a common resource for the whole household. Fourth, even though in the Chad Basin large increases and decreases in cattle numbers are mostly due to changes in transhumance movements (Moritz et al., 2019), we did not consider migration in order to assess the effects of demographic couplings on herds and households. Finally, we modeled only herds and households but not the environment. However, the environment is represented indirectly in the model; herd mortality rates derived from the literature include different causes of death, including predation, diseases, and malnutrition. Similarly, milk production numbers represent the seasonal dynamics observed in West and Central African pastoral systems in which milk production is considerably higher in the rainy season than in the dry season.

Our artificial pastoral society has a patrilineal kinship system with an exogamous marriage system. The marriage system is simple: there is no polygyny and no divorce. Daughters marry out and are removed from the model. Widows return to their patrilineal kin with their young children, and all are removed from the model. The social system is simple: each household is an independent unit and there are no interactions between households. There is no adoption, no labor pooling, and no livestock exchanges. The inheritance rules are also simple. The herd is only divided when the patriarch dies, and only sons over 10 years of age inherit livestock, daughters do not inherit. The herd is equally divided among heirs. Sons only inherit livestock from their fathers, not from their grandfathers or other patrilineal kin. The patriarch is called herd-manager in the model as he is the one who executes the commands that link the herd and household.

While the artificial pastoral system is modeled after Fulani pastoralists in West and Central Africa, it is representative more broadly of mobile pastoralists who do not rely on agriculture or other sources of income, and whose access to resources is not severely constrained politically or otherwise. Moreover, because our modeling study examined the coupled dynamics of herd and household demography, we purposefully did not model the couplings between household, herd, and rangelands.

- (V) The fifth set of submodels is set in motion when a herd-manager dies. It executes a series of submodels that divide the herd among heirs (if any): (15) checks whether herd manager has any sons over ten years old, and if not, the herd will be removed; (16) divides the animals from all the sex/age classes among the heirs; (17) removes all sons less than ten years old; and (18) heirs that were not yet married, will be married.
- (VI) In the final submodel (19) households who have lost all the animals in their herd are removed from the model.

Parameterization

We derived the demographic parameters in the model from the literature (see Supplement 1 for a detailed discussion of all parameters, including milk production, caloric needs, caloric terms of trade, cattle weight, and labor costs). We derived the fertility rates, mortality rates, and herd composition in terms of age/sex classes from an earlier study and agent-based model (Buffington et al., 2016; Moritz et al., 2017). For the estimates of human fertility and mortality, we relied primarily on Randall's review of African pastoralist demography (2008). They note that there are few demographic data available for mobile pastoralist populations and the data that exists is from small communities studied by anthropologists (e.g., Mulder 1992; Little & Leslie, 1999). Randall's review is based on those community studies, including ones of West African pastoralists (Hampshire, 1998; Hill, 1985; Randall, 1984). The review of these studies shows that there is not one pastoral demographic regime, but that there is considerable variation across all demographic parameters among pastoralist populations (see also Mulder 1992).

Sensitivity Analysis

We conducted a local sensitivity analysis to examine the impact of small changes in nine parameters (cattle fertility, cattle mortality, initial herd size, human fertility, human mortality, caloric-terms-of-trade, human caloric needs, labor costs, and milk production) on three system-level outcomes (number of people, number of cattle, and number of herds) (Railsback & Grimm, 2012). As expected, the sensitivity analyses show that the model is most sensitive to changes in cattle fertility and calf mortality. Small changes in cattle fertility had major effects on the number of people, herds, and cattle in the simulations. Detailed results from the sensitivity analysis can be found in Supplement 2.

Experiments

To examine whether, how much, and how the coupled demographic dynamics at the herd-household level limit the growth of human and livestock populations in pastoral systems we conducted several experiments.

First, we compared 250-year simulations of the coupled herd-household model, a decoupled herd model, and a decoupled household model to examine *whether* and *how much* couplings constrained population growth. The decoupled models respectively represent households without herds and herds without households. In the decoupled household model, all the submodels for the herd and couplings were removed. The rules for the household submodels remained the same as in the coupled model. Households represent agricultural households with the same kinship and marriage systems in which sons only start independent households when the patriarch dies. In the decoupled herd model, all the submodels for the household and couplings were removed. Most of the rules for the herd submodels are the same, except for the herd-splitting submodel. In the coupled model, the herd-splitting procedure is initiated by the death of the herd-manager. In the decoupled model, the herd has a chance of splitting when it has more than 40 animals and all herds split when they have 80 or more animals. The herds represent feral herds of cattle with sizes that range from 18 to 81 animals with an average of 42.5 animals. These statistics were derived from the literature (Bouissou et al., 2001; Hall, 1989; Hall & Moore, 1986; Lazo, 1994). We limited these experiments to 250 years because the explosive growth of herds in the decoupled herd model as well as that of people in the decoupled household model required so much computing power and slowed down the simulations.

Second, we ran 900 simulations for 1,000 years with the coupled herd-household model to examine *how* the couplings between herd and household constrained population growth. In particular, we examined whether households sell more cattle to cover living costs of the household or to cover labor costs, whether herd division due to early death of the herd-manager affects population growth, and whether demographic dynamics in the herd or the household had a greater impact on removal of humans and cattle from the population. The 900 simulations resulted in 152 successful simulations with at least one household left after 1,000 years. These successful simulations yielded data for a total of 6,367 herds and households. One of the main reasons that only 16.9% of the simulations were successful is because each simulation starts with just one household that consists of a husband and wife and a small herd of 50 animals. Because both the herd and household are small, the impact of stochasticity in fertility and mortality rates for humans and cattle has a significant impact on the viability of households.

Table 1 Descriptive statistics for herds and households

Herd Size	1 – 50		51 – 100		101+	
	mean	sd	mean	sd	mean	sd
Number of households	14.51	14.73	18.86	17.45	11.1	10.1
Household size	4.85	0.98	4.89	1.16	6.66	1.51
Herd size	29.98	7.13	77.12	5.55	143.77	19.2
Cattle per person	7.68	2.72	20.78	7.69	27.35	7.2
Milk production (liters per day)	4.28	1.45	8.66	2.53	15.28	4.48
Production deficit (liters per day)	0.04	0.69	0.26	1.08	0.23	1.01
Number of cattle sold for living costs per year	2.47	0.72	1.75	0.6	1.86	0.62
Number of cattle sold for labor costs per year	0	0	0.12	0.21	0.90	0.81

Statistical Analyses

To compare whether differences in model outcomes between the coupled and decoupled herd and household models were statistically significant, we ran ANOVAs and non-parametric Mann-Whitney U tests. To analyze the correlations between starting herd size and ending herd size as well as age at herd-manager career start and ending herd size, we used linear models. We first calculated the statistics for each of the simulations separately and then calculated the statistics for all the simulations, which are presented in the tables and figures below. We ran all the analyses using R software (v.1.4.1106) (R Core Team, 2021).

Results

We will discuss four sets of results. First, we discuss the descriptive statistics for herds and households to assess whether they resemble those of pastoral systems and validate our artificial pastoral system. Second, we compare simulation results from the coupled and decoupled models to examine *whether* and *how much* the couplings between herd and household constrain the growth of human and livestock populations. Third, we examine *what couplings* had the greatest impact in constraining the growth of human and livestock populations. Fourth, we examine the growth of human and cattle population. We analyzed the data by wealth category

because there we found that there was considerable variation in most variables, e.g., milk production, livestock sales, and herd composition, across these wealth categories.

Artificial Herds and Households Resemble Those in Pastoral Systems

The results from the simulations show that the herds and the households in the artificial pastoral system resemble or are within the range of mobile pastoral systems in West and Central Africa (see Tables 1 and 2).

Herd-Household Couplings Constrain Population Growth

The demographic couplings between herd and household constrain the growth of both human and livestock populations in our artificial pastoral system (see Fig. 2). The number of households and the total human population are significantly higher in the decoupled household model than in the coupled herd-household model – more than three times as large. The number of herds and the total cattle population are also significantly higher in the decoupled herd model than in the coupled herd-household model. The total cattle population is almost more than 20 times larger in the decoupled model – the magnitude is surprising.

Table 2 Herd composition: percentage of animals in each sex and age class by herd size

Herd Size	0 – 50		51 – 100		101+	
	mean	sd	mean	sd	mean	sd
Sex and age classes (years)						
Female calves (0 – 1)	14.8	3.33	13.51	1.74	13.45	1.2
Male calves (0 – 1)	16.44	4.33	13.36	1.59	13.55	1.34
Heifer (2 – 3)	12.36	2.69	10.41	1.5	9.41	1.15
Bullock (2 – 3)	8.82	3.09	10.45	1.47	10.44	1.2
Cows (4 – 11)	35.82	4.27	28.39	1.65	27.85	1.43
Bulls (4 – 10)	10.77	5.9	22.72	3.52	24.18	2.45
Post-reproductive cows (12 – 14)	0.99	0.93	1.15	0.45	1.13	0.42

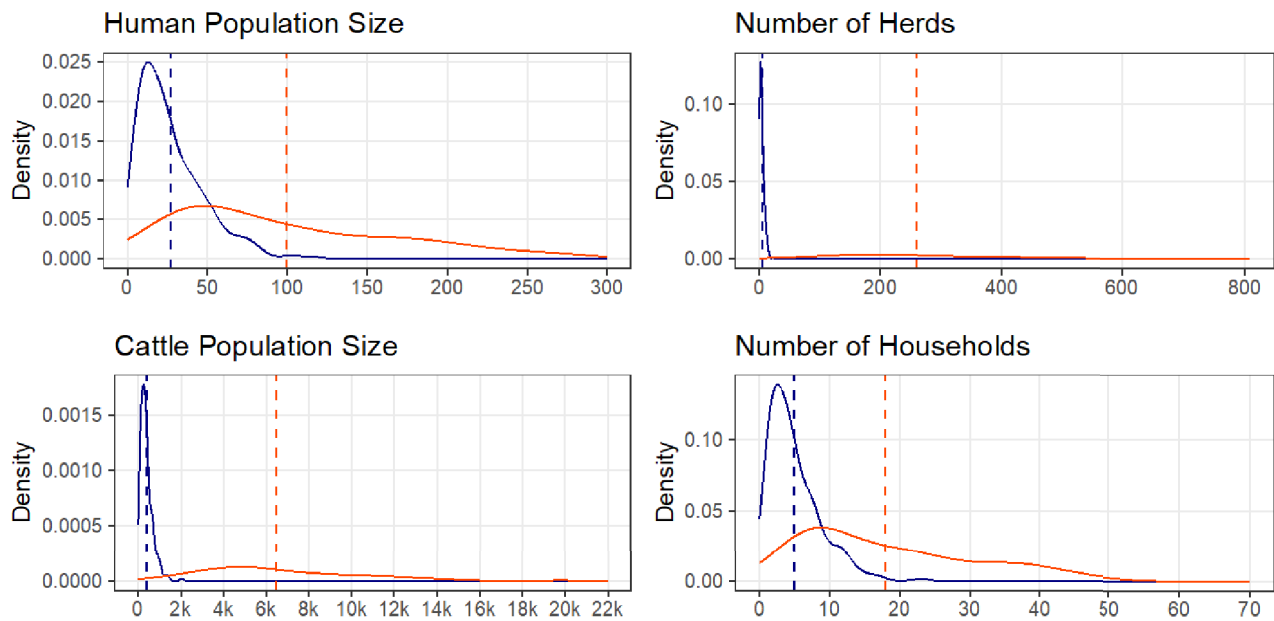


Fig. 2 Comparison of results from coupled and decoupled models. Note: The blue plots are from the coupled herd-household model and the orange plots are from the decoupled models. The figures show that the couplings strongly constrain the growth of human and cattle populations. The horizontal axes show the number of people, cattle, herds, and households. The vertical axes show the probability density.

Removal of Herds and Households From the Pastoral System

There are several couplings between herd and household that contribute to the removal of herds and households from the pastoral system and thus constrain the growth of human and livestock populations. First, herds and households may leave the pastoral system simply because stochasticity, i.e., misfortune. The death of a few reproductive cows in a small herd may quickly lead to the disappearance of the herd and thus the removal of the household. Similarly, the death of a herd-manager without heirs may also lead to the disappearance of the household and thus the herd. Our simulations show that on average the percentage of herds that are removed is higher than the percentage of households that are removed (see Table 3), which indicates that the scale and stochasticity

of household demographic dynamics are a stronger driver for the removal of herds than vice versa. In other words, it is more common that herds are removed because households faced misfortune than that households are removed because herds are too small.

The Effect of Livestock Sales

Other herd-household couplings that constrain the growth of livestock populations in pastoral systems are livestock sales to cover living costs and/or labor costs. When herds are small and do not provide enough milk to cover the nutritional needs of the household, the herd-manager must sell animals, and this constrains the growth of the herd. Second, when the household cannot provide enough labor, the herd-manager must sell animals to cover the costs of hiring a herder. On average, households are selling more livestock to cover living costs than to cover labor costs (see Tables 1 and 4). Not surprisingly, wealthier households with larger herds sell more livestock to cover labor costs than households with smaller herds. The number of livestock sold annually is relatively small for both living costs (1.86 to 2.47 animals per year) and labor costs (0 to 0.9 animals per year) (see Table 1). These numbers suggest

Table 3 Removal of herds and household from the pastoral system

	min	max	mean	sd
Sloughed households (%)	10.49	26.05	18.04	3.08
Sloughed herds (%)	14.29	28.1	21.16	2.34

The numbers represent the herds and households removed as a percentage of all the herds and households that ever existed over the course of a 1,000-year simulation

Table 4 Livestock sales to cover living costs and labor costs

Herd size	Living Costs			Labor Costs		
	max	mean	sd	max	mean	sd
0 – 50	109	31.40	15.60	12	0.35	1.50
51 – 100	145	29.61	15.17	44	7.45	6.28
101 +	90	35.43	13.41	32	10.51	6.44

The table shows the total number of animals sold for living and labor costs over the course of a herd manager's career

that livestock sales have a limited effect in constraining the growth of livestock populations in our artificial system, although the effect is much stronger for households with smaller herds because even a small number of livestock sold can lead to significant reduction of the herds' reproductive capacity. This is evident in the differences in composition between smaller and larger herds indicates that livestock sales have a major impact (see Table 2). Poorer households have to sell more animals to cover living costs and that is why the percentage of male animals is much lower in the smaller herds.

Herd-Manager Careers

In addition to herds that are removed from the pastoral system because a herd manager dies without heirs, there are also herd managers that leave too few animals to their heirs. This makes it more likely that the households of the heirs will not be able to make it and will be removed later. The average age at which sons become herd managers and the size of the starting herd vary by wealth class (see Table 5). Poorer households are headed by herd managers that started at a younger age (26.5 years) and with a smaller herd (32 animals), while wealthier households are headed by herd managers that started at a later age (30.5 years) with a much larger herd (107 animals). In other words, wealthier herd managers are set up for success from the start and the opposite is true for poor herd managers (Fig. 3). The intergenerational transfer of wealth is thus an important contributor to sustained economic inequality in this pastoral system.

Growth of Human and Livestock Populations

The percentage of successful runs for the simulations for the herd, household, and coupled model gives a good indication of how sensitive they are to the effects of scale and stochasticity in human and cattle demography. All of the simulations of the decoupled herd model succeeded (100 of 100), which is mainly due to the fact that the simulations start with one herd of 50 animals and there are no livestock sales or herd division due to the death of the herd manager. Only half of the simulations of the decoupled household model succeeded (101 of 200), which is primarily because the simulations start with one household with only two people. In that context, the misfortune of one or more untimely deaths can lead to the end of the simulation. An even smaller percentage (31.4%) of the simulations in the coupled herd-household model succeed after 250 years (283 of 900), which is due to the effects of scale and stochasticity and the couplings between herds and households. The small percentage of successful simulations underscores the precarity of households in pastoral systems. And when we ran simulations for 1,000 years, only 152 out of 900 (16.9%) simulations were successful.

The human and cattle annual population growth rates across the 152 successful simulations also emphasize the role of stochasticity and scale in demographic processes of pastoral systems (Figs. 4). Weighted means of both human and cattle annual growth rates average between -0.01% to 1.0%. Once again, the low growth rates demonstrate the precarity of households in pastoral systems as well as the

Table 5 Herd size and age of herd-managers at the start of their careers by herd size

Herd Size	Starting Herd Size				Age when becoming manager			
	min	max	mean	sd	min	max	mean	sd
0 – 50	12	61	31.75	8.31	14	44	26.56	4.73
51 – 100	11	112	68.27	12.94	10	45	25.91	4.5
101 +	62.83	265	107.31	22.62	12.5	52	30.48	5.66

The differences in starting herd size are statistically significant (ANOVA, $df = 1$, $F = 5228$, $p < 0.001$), as are the differences in starting age (ANOVA, $df = 1$, $F = 67.31$, $p < 0.001$), though with a weaker effect

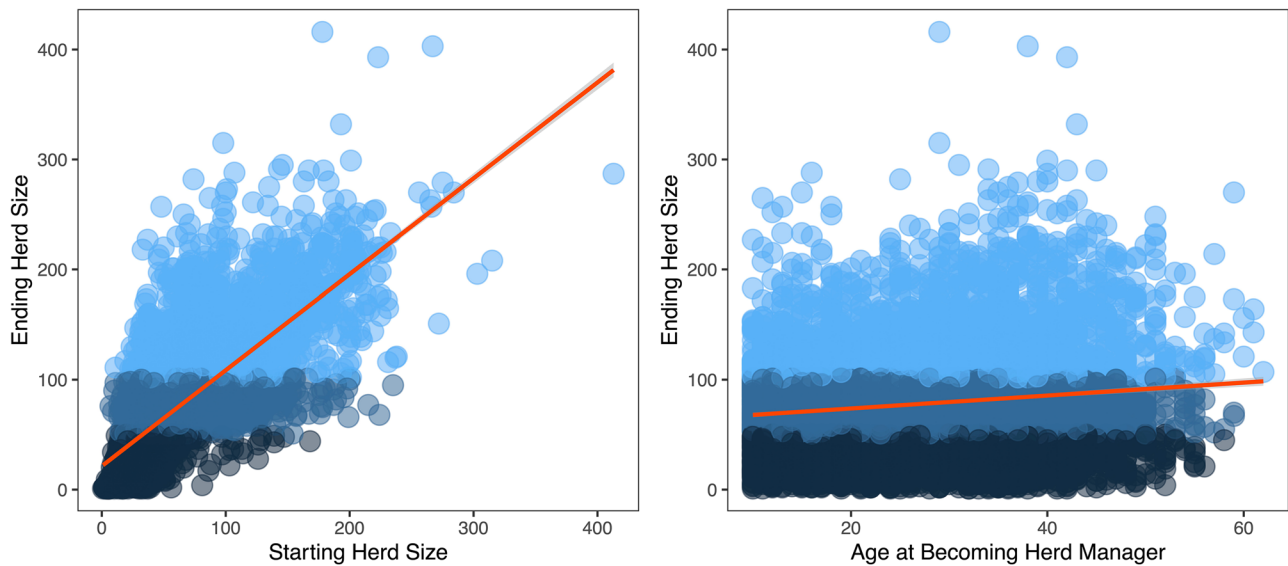


Fig. 3 Correlation between starting herd size and ending herd size (left) and age at becoming herd-manager and ending herd size (right). Note: Fig. 4 shows that there is a strong correlation between starting herd size and ending herd size ($df=6365$, $F=8167$, adjusted

$r^2=0.5619$, $p<0.001$), while Fig. 5 shows that age at career start is also correlated with ending herd size ($df=6365$, $F=114.6$, adjusted $r^2=.01753$, $p<0.001$). The different shades of blue represent the different herd-size categories

variation in outcomes due to stochasticity (see Supplementary Materials).

Discussion

The simulations show that the combined effects of the domestic cycle and the couplings between herd and household demography limit the growth of the family herds and

that the demographic dynamics of scale and stochasticity affect smaller herds to a much greater extent than large herds. The cumulative effect is that poorer households and their livestock are continuously removed from the pastoral system. In other words, the process of sloughing off – passing from nomadic to settled society – that Barth (1961) described for Basseri shepherds in Iran, is also what keeps human and cattle populations in check in our artificial pastoral system.

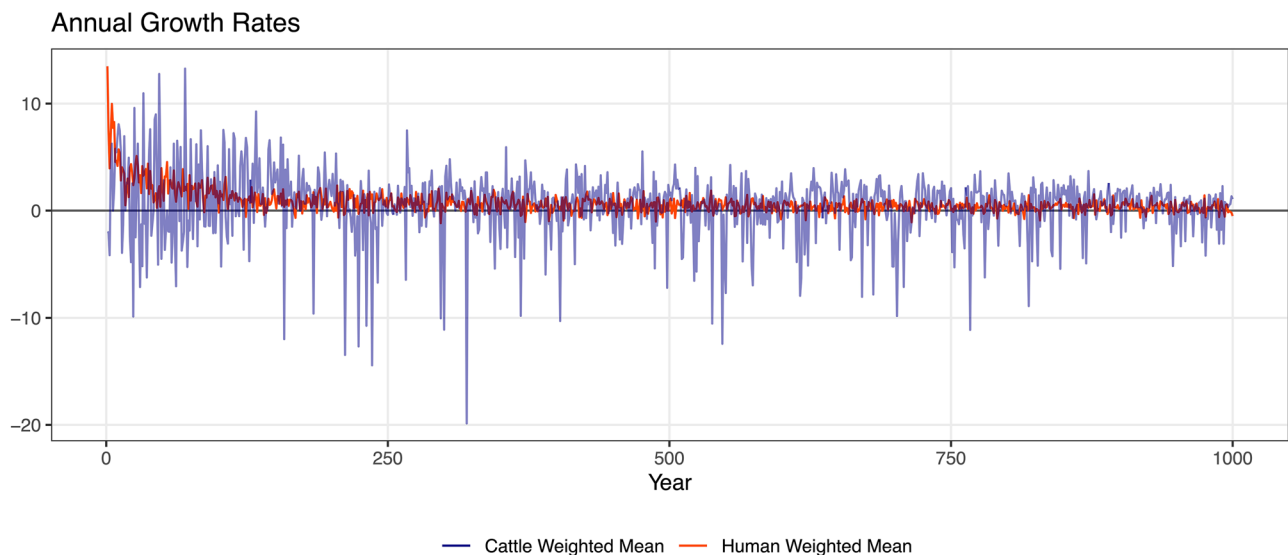


Fig. 4 Weighted mean annual growth rate of human and cattle populations. Note: Weighted average annual growth rates for human and cattle populations in the 152 simulations are relatively low, but there

is more variability in the growth rates from year to year for cattle than for human populations. There is also a considerable across simulations (see Supplementary Materials S3 and S4)

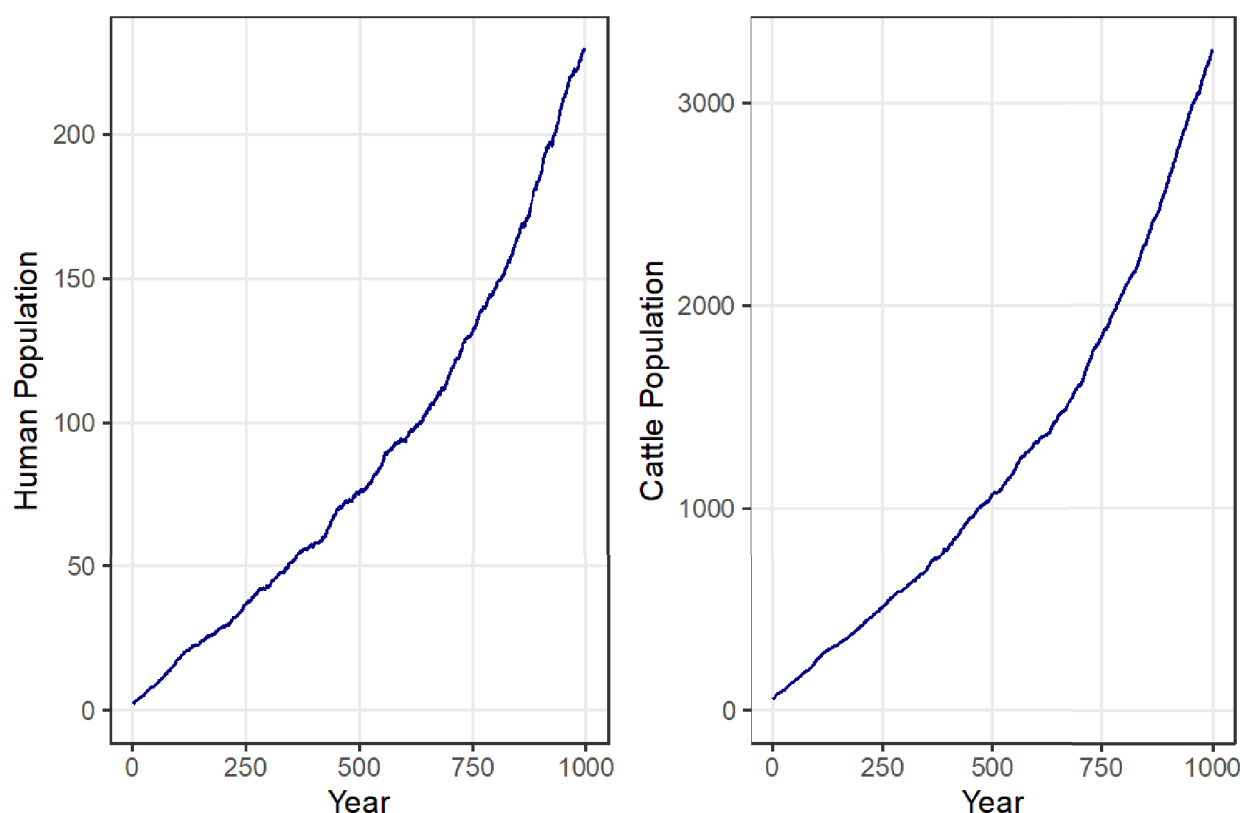


Fig. 5 Average growth of human and cattle population. Note: Because of the couplings between herd and household, human and cattle populations increase at similar rates, and herd and household size do not change much over time

When we started the simulations, we did not know whether the two mechanisms of the domestic cycle and scale and stochasticity would constrain the growth of livestock populations and we were prepared to do additional simulations in which a widespread drought, disease, or another disaster event would wipe out a large number of cattle. However, the results from our simulations show that the everyday events that affect households cumulatively have a major impact on the growth of human and livestock populations. This finding dovetails with what we observed among pastoralists in the Far North Region of Cameroon, who during our studies were not affected by widespread disasters, but whose lives were nevertheless seriously affected by everyday misfortunes that led to the removal of individual households from the pastoral system (Moritz, 2013). However, widespread disasters that affect whole regions populations generally get more attention than the smaller, everyday disasters that affect individual households, even though the cumulative effects may be similar in magnitude.

The interconnected problems of population growth, domestic cycle, and limited resources is not limited to pastoral societies. Netting (1972) describes how extended families in the Swiss village of Törbel work together and pool

resources as long as the parents are still alive – children receive equal shares of the inheritance, which means that over time, land-holdings would get smaller and smaller, and eventually too small to support families. However, this problem is solved by a steady process of out-migration. Netting describes how “only three men appear to have settled in Törbel, married, and had children there since 1700” (1981). Thus, in Törbel, steady outmigration maintains balance between natural resources and human populations in the Swiss valley. A similar process of sloughing off households keeps human and livestock populations in check in pastoral systems. In societies with primogeniture like the pastoral Rendille, in which the first-born son inherits all the livestock, there is a similar out-migration of poorer male pastoralists (Roth, 2000).

Understanding coupled herd-household dynamics has implications for our understanding of economic inequality in pastoral societies (Mulder et al., 2010; Salzman, 1999). While the emergence of economic inequality was not the focus of our current research project, the simulations allow us to conduct preliminary analyses of the impacts of the coupled demographic dynamics on the human population, and in particular, how many households leave the pastoral

sector, how many households are below the poverty line, and what the level of economic inequality is among remaining households. In Barth's original model, both poor and wealthy leave the pastoral system and the "middle-class" remains, but in our model only the poor are removed from the pastoral system. What is remarkable in our model is that the mechanisms of the domestic cycle, coupled demographic dynamics, and the effects of scale and stochasticity not only keep overall populations in check, but they also seem to prevent the accumulation of wealth. In our simulations, rarely does herd size go over 500 animals. It might well be that the lack of interactions among households is what limits wealth accumulation – wealthier pastoralists do not take the animals from the poor leaving the pastoral system. While considerable effort has been devoted to the study of social support and mutual aid in pastoral systems (Aktipis et al., 2011; Bollig, 1998; Moritz, 2013), researchers may have overlooked how these same interdependencies between households may benefit wealthy pastoralists more so than the poor (but see Bradburd, 1990).

Our artificial pastoral system was as simple as possible to examine the effects of demographic couplings between herd and household. The simplification comes with certain limitations, for example, in the current model, households are independent and do not form a pastoral society – it is better described as a population of isolated households. One of the next steps is to examine how interdependencies would affect the removal of households from the pastoral system. For example, how do livestock loans, labor arrangements, adoptions, and other social strategies allow poorer pastoralists to stay in this artificial pastoral system? And how may interdependencies between households benefit wealthier pastoralists? Finally, although we were careful in the use of the limited data on human and cattle demography to develop our model, we may have created an artificial pastoral system that may be more bleak than existing pastoral systems – about half of the households in our model leave the pastoral system. We would encourage other researchers to use our model and revisit the human demography parameters that we used in this model.

Conclusion

Our study makes theoretical, methodological, and political contributions. First, we show that coupled dynamics of herd and household demography constrain the growth of livestock populations and that everyday misfortunes cumulatively have a major impact. Second, we demonstrate how agent-based modeling is a useful approach to study long-term dynamics in complex systems that are difficult to study empirically. Third, our findings challenge conventional Malthusian models of population growth. The literature on pastoral systems is dominated by concerns about the Malthusian

specter of livestock populations growing exponentially in a situation of limited natural resources. We hypothesized that the domestic cycle of pastoral households limits the growth of livestock populations. We used the conceptual framework of coupled systems to examine how the domestic cycle of households affects the demography of family herds and vice versa, and what the cumulative effects are on the growth of human and livestock populations in pastoral systems. The results from our agent-based modeling approach simulations show that the misfortunes that affect individual households every day, cumulatively constrain the growth of human and livestock populations in pastoral systems.

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Authors' Contributions MM and CH wrote the manuscript. CH, DP, AB, AY, and MM developed the agent-based model. CH ran the simulations, analyzed the data, and created the figures. MM, RG, JT, and IH designed the study. All authors reviewed the manuscript.

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Availability of Data and Materials The agent-based model is available in the Computational Model Library of the CoMSES Network at: <https://www.comses.net/codebases/4db826be-85aa-47c0-93b1-5fcec2bef057/releases/1.0.0/>.

Declarations

Ethical Approval Not applicable. No humans or cattle were harmed in this artificial pastoral system.

Competing Interests There are no competing interests.

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