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The Population Ecology of Despotism

Concessions and Migration Between Central and Peripheral Habitats

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Abstract Since despotism is a common evolutionary development in human history, we seek to understand the conditions under which it can originate, persist, and affect population trajectories. We describe a general system of population ecology equations representing the Ideal Free and Despotic Distributions for one and two habitats, one of which contains a despotic class that controls the distribution of resources. Using analytical and numerical solutions we derive the optimal concession strategy by despots with and without subordinate migration to an alternative habitat. We show that low concessions exponentially increase the time it takes for the despotic habitat to fill, and we discuss the trade-offs despots and subordinates confront at various levels of exploitation. Contrary to previous hypotheses, higher levels of despotism do not necessarily cause faster migration to alternative habitats. We further show how, during colonization, divergent population trajectories may arise if despotic systems experience Allee-type economies of scale.

Keywords Despotism · Social stratification · Human population dynamics · Migration · Human behavioral ecology

Despotism is a common form of human social organization of interest among anthropologists because of its importance to the origins of modern societies (Johnson and Earle 2000; Kennett et al. 2009; Kennett and Winterhalder 2008; Kennett et al. 2006; Summers 2005). However, its role is less well understood, and its influence competes with other hypotheses in the evolution of the state. Arguing for a more prominent role

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in state formation, our analysis aims at building an understanding of despotic systems through mathematical modeling and illustrations through empirical cases.

The Role of Despotism in State Formation

Egyptian state formation circa 3000 BC is an example that highlights common social science explanations of the evolution of social hierarchy. The Nile Valley was underpopulated through the predynastic and early periods of state formation, mooting the possibility that political centralization was a direct organizational response to population pressure and declining marginal yields of agriculture. Egypt's irrigation technology was small in scale and locally managed, challenging theories by Steward (1949) and Wittfogel (1957) that the state arose through the advantages of large-scale water management. Fostered by warfare and maintained through class-based exploitation, the coalescence of the Egyptian state cannot be reconciled with ecosystemic theories entailing economic benefits that states might provide their subject populations. With mobile farmers able to relocate down river across the frontier into fertile areas of low-density settlement, the leaders of nascent Upper Egypt were constrained in their ability to expropriate the surplus production hypothesized to underwrite political theories of state-building.

Allen (1997) describes these features of the Egyptian situation, arguing that Upper Egypt successfully pursued broad political unification and state-building by controlling the outmigration of farmers seeking to avoid taxes. The leadership was aided in this tactic by the narrow, linear geography of the agrarian habitat available to the mobile population seeking resettlement. By expanding control over population movement into Lower Egypt, elites were able to capture surplus even at low levels of population density. Allen's hypothesis is similar to Carneiro's (1970) circumscription theory, in which geographic boundaries—the desert wastelands surrounding and isolating the fertile valleys of coastal Peru are a prime example—set a constraint on outmigration. Carneiro hypothesized that as population density grew, villages came into conflict over productive land. Those villages losing the territorial competitions were subjugated on unfavorable terms, a process that repeated itself and steadily differentiated the population into the powerful elites able to extract surplus resources and subjugated farmers who produced them.

Carneiro's and Allen's theories have in common the following variables and interactions: (a) endogenous population growth; (b) marginal returns to land and labor; (c) the availability and relative attractiveness (or unattractiveness) of migration to frontier or escape habitats; and (d) the ability of nascent elites to establish control over subordinate labor and surplus production through warfare and boundary maintenance. In both theories the farmer-producers acquiesce to exploitation only because constraints on relocation make it preferable to any alternatives. Similar mechanisms have been invoked to explain cases of social differentiation as diverse as the origins of serfdom in seventeenth-century Russia (Domar 1970) and chiefdoms among the Chumash of the southern California coast (Kennett et al. 2009). In some form or another, the variables listed above enter into a majority of theories of state origins (Trigger 2003).

Better understanding of interactions among these variables will emerge from formal models that incorporate the constraints and options facing elites and their agrarian



subjects. Two modeling frameworks—the Ideal Free (IFD) and Ideal Despotic (IDD) Distributions—have great potential in this regard, but they are underdeveloped for analysis of the origins of despotism. In this paper we take initial steps to better understand how the IFD and IDD might illuminate evolutionary mechanisms promoting the evolution of political hierarchy.

Modeling Framework: Ideal Despotic Distribution

Despite despotism's salience, few models of despotism are consistent with more established approaches in human behavioral ecology. Anthropologists typically rely on the Ideal Free Distribution (Fretwell and Lucas 1970) to predict the distribution of foragers and horticulturalists across a landscape (Winterhalder et al. 2010). In this model all individuals have similar capacities and they are affected equally by density-dependent changes in habitat suitability as population size grows or shrinks. However, the IFD in principle is inadequate to describe the demographics of societies under a despot, where the uneven distribution of resources affects resource production, population growth, and habitat selection. Clearly, a new approach should be formalized to describe despotic systems.

In their original description of the IFD, Fretwell and Lucas (1970) named a despotic variant, the Ideal Despotic Distribution, although they did not pursue its dynamics. In the IDD some individuals are presumed able to defend a disproportionate share of resources. The effects on consumer distributions are significantly different from the distributions in the IFD. Although the IFD has become the subject of a substantial biological literature, both theoretical and empirical, the IDD has received relatively little attention from biologists (see Hakoyama and Iguchi 2001; Zimmerman et al. 2003 for empirical examples). The IDD and similar models such as reproductive skew (Buston and Zink 2009) may offer us insights into the evolution of social differentiation and, ultimately, hierarchical despotic forms of human political organization. Carneiro's and Allen's models share features we can examine within an IDD framework and are among the theories that would benefit from formalization.

Empirical examples, such as the Egypt case, beg major questions surrounding the evolution of despotism. How, for instance, does a level of despotism evolve, and how does it affect demographic outcomes? In this paper we address two questions stemming from these investigations: (1) What is the optimal amount of concession by dominants? (2) How do concessions and habitat quality affect population growth and the flow of emigrants from the despotic habitat? We focus on the limiting case of an environment typical of growing human societies that contain a resource-rich habitat with social stratification, or a population center, and peripheral, resource-poor "escape" habitats without social stratification, a frontier.

The general IDD approach prescribes a modeling framework that includes density-dependent resource availability, differential resource control, migration, and the endogenous dynamics of population growth as habitats fill with producers and consumers. For transparency, we describe, analyze, and discuss three model variations of increasing complexity with these qualities. Assuming that ecological feedbacks are fast enough to influence decisions by despots and subordinates, we (mostly) use equilibrium analysis. Although we give no formal test of the model, we mean it to illustrate linkages among



the key variables incorporated into social evolutionary theories such as those of Allen (1997) and Carneiro (1970). Our objective, then, is to develop a simple model with properties realistic enough to serve as the basis, with suitable elaboration, for formal investigation of the origins of social stratification, exploitation, and state origins.

Ecological Models of Despotism

Model I: How Much Should Despots Concede?

Let P and Q be the population densities of subordinates and dominants occupying the same habitat. These populations grow depending on the per capita amount of resources produced by subordinates, π . The total flow of resources (πP) is controlled by dominants, who allocate it so that each subordinate experiences $c\pi$ amount of resources, where $c \in (0,1)$, and each dominant experiences $(1-c)\pi P/Q$. This is a strict taxation system for dominants, who concede a fraction, c, of resources to subordinates and divide the rest equally among themselves. Dominants cannot increase in numbers without obtaining resources produced by subordinates. Akin to Lokta-Volterra predator–prey models, the population dynamics of dominants and subordinates can be expressed in a standard continuous growth equation

$$\frac{dP}{dt} = gP(c\pi - \gamma) \tag{1a}$$

$$\frac{dQ}{dt} = gQ\left(\frac{(1-c)\pi P}{Q} - \gamma\right) \tag{1b}$$

where g translates net resources into population growth rate and γ is the per capita amount of resources needed for metabolic maintenance of both subordinates and dominants. Subordinates produce resources ultimately used for growth. We assume that per capita resource yield is a decreasing linear function of subordinate density,

$$\pi(t) = \max\{0, b - aP(t)\},$$
 (2)

where b is the basic habitat quality and a measures the rate of the decline in resources with increasing subordinate density. Setting dP/dt=0 and dQ/dt=0 we solve for the nontrivial steady-state densities of subordinates (\widehat{P}) and dominants (\widehat{Q}) :

$$\widehat{P} = \frac{bc - \gamma}{ac}, \widehat{Q} = \frac{(1 - c)}{c} \frac{bc - \gamma}{ac}$$
(3)

These equilibria are determined by the producer's net gain from basic habitat quality $(bc-\gamma)$, scaled by the concession-adjusted density-dependent effect (ac). This scaling occurs because a determines how quickly a growing population reaches its carrying capacity, which results when the concession-adjusted resource availability equals metabolic maintenance $(c\pi=\gamma)$. The equilibrium expressions also show that the dominant equilibrium density is always a proportion, (1-c)/c, of the subordinate equilibrium density.



We assume dominants have no interest in subordinate welfare per se, being concerned only with the role of subordinates in generating the net production that underwrites their own growth and persistence. Here, the chief concern of dominants is to extract resources from producers with the goal of maximizing their own population density at equilibrium, thereby fostering the largest possible oligarchy. Size matters to the oligarchy in order to secure social control over producers and to successfully compete with external groups. Other goals could be accommodated in the model (see Discussion). Thus, by adjusting the concession level (c), despots can distribute resources to maximize political control or competitiveness among groups. By setting $d\widehat{Q}/dc = 0$ and solving for c we find the optimal concession strategy for dominants as

$$c_{\text{opt}} = \frac{2\gamma}{b + \gamma} \tag{4}$$

Deviations from this level of concession result in a reduced dominant population.

This result shows that elevated metabolic maintenance costs (γ) increase optimal concession whereas elevated basic habitat quality (b) exponentially decreases concession. Environmental suitability scales the amount of concession increase that will be prompted by higher maintenance costs. This result highlights trade-offs influencing the despot's best strategy: an oligarchy needs a subordinate population to produce goods, so higher metabolic costs of these producers must be offset by higher concessions. On the other hand, ceding too much from a resource-rich habitat produces a suboptimally high population growth rate of subordinates. In response, as basic habitat suitability grows, despots will concede less to avoid depletion of resources by subordinate producers and increase the resource share and size of the oligarchy (assuming that their objective is to do so).

Absent from the optimal despotic strategy is the parameter that defines how much subordinate population growth depletes resources (a). This is because the optimal concession value only changes in response to parameters that change the relative growth rates of subordinates and dominants. The parameter a scales the absolute equilibrium densities of subordinates and dominants as shown in (3) but does not change their relative equilibrium densities, $\widehat{P}:\widehat{Q},\ [1:(1-c)/c]$.

In this model dominants succeed according to how effectively they use concessions to manage the size of the subordinate population that supports them. However, faced with such exploitation, subordinates may choose to migrate. It is this basic IFD/IDD dynamics of migration between habitats that we begin to consider in the next section.

Model II: How Much Emigration?

A simple extension of our Model (I) considers the consequences of out-migration by subordinates, such that

$$\frac{dP}{dt} = gP(c\pi - \gamma) - mP \tag{5}$$

where m is the fraction of the subordinate population migrating out of the habitat. It then follows that the nontrivial equilibrium densities become



$$\widehat{P} = \frac{g(bc - \gamma) - m}{acg}, \ \widehat{Q} = \left(\frac{1 - c}{c} \left(1 + \frac{m}{g\gamma}\right)\right) \left(\frac{g(bc - \gamma) - m}{acg}\right) \tag{6}$$

As in the previous section, the dominant equilibrium (\widehat{Q}) is a fraction of the equilibrium subordinate density (\widehat{P}) , though this fraction is now larger owing to the effects of migration. Since $(1+m/g\gamma)>1$, migration increases relative dominant densities and would perhaps increase concessions if subordinate densities are kept at optimal levels through migration rather than through reduced concessions. We see this is true when we solve for the optimal despotic concession strategy:

$$c_{\text{opt}} = \frac{2(m + g\gamma)}{g(b + \gamma) + m} \tag{7}$$

It can be shown that this level of concession results in the largest dominant population size. Concessions increase with migration rates m, and, as in the previous section, the absolute increase is scaled primarily by the initial resource quality of the habitat b multiplied by the resource-to-growth conversion parameter g. The increase in optimal concession c with migration rates is instructive. It shows that optimal subordinate densities (from a despot's point of view of maintaining a large oligarchy) can be maintained through emigration rather than reducing concessions to prevent subordinate overpopulation. This implies that a despotic group might tolerate or even promote some leakage of population across the frontier and out of their control. The growth rate g, not found in the case without migration, enters into the equilibrium solution since subordinate growth within a habitat is the difference between migration (m) and subordinate intrinsic growth. We find an approximate solution to subordinate population growth in the despotic habitat using a second-order Taylor series expansion of (5):

$$P(t) \approx \frac{z}{ac + \exp\left(-\frac{y^2}{z}P(0) + y - zt\right)}$$
(8)

where

$$y = 1 + acg$$
, $z = g(bc - \gamma) - m$

The expressions y and z represent the factors that limit and promote population growth, respectively. If dominants control the amount of out-migration by subordinates in the habitat, the optimal subordinate emigration rate is

$$m_{\text{opt}} = \frac{1}{2}g(bc - 2\gamma),\tag{9}$$

which we get by maximizing result \widehat{Q} from (6) with respect to the migration rate, m. This result suggests that under despotic control the number of migrants evicted or released from the habitat decreases with lower concessions to subordinates. Two mechanisms promote this effect. First, subordinate population sizes are smaller with reduced concession; thus the pool of potential migrants is fewer. Second, the despot would require lower levels of migration with lower concessions in order to maintain the optimal number of resource producers. This is contrary to what subordinates may do if they have the option of initiating migration. Previous hypotheses (e.g., Kennett and



Winterhalder 2008) and reproductive skew models (Buston and Zink 2009) have suggested that subordinate migration rates should increase in harsher despotic conditions.

When subordinates control the option to migrate to better opportunities elsewhere, the despotic strategy probably must take into account not only the resource and population dynamics of their own habitat, but the same features of the alternative habitats available to subordinates. We introduce this possibility in the next section by more explicitly considering the effect of alternative habitat suitability.

Model III: Effects of Subordinate Habitat Choice

Let i index habitats 1 and 2, P_i be the population density of subordinates in habitat i, and Q be the population density of dominants found only in habitat 1 (Fig. 1). In habitat 2 surplus is divided equally among subordinates such that they always experience amount π_2 . The availability of resources in habitat i is a linear density-dependent function of subordinate density in the habitat, such that $\pi_i(t) = b - a P_i(t)$. Migration of subordinates between the habitats depends on the relative suitability or resource intake they would experience in each habitat: $c\pi_1$ in habitat 1 and π_2 in habitat 2.

We include subordinate habitat choice in this two-habitat setting by expanding our standard continuous growth and migration model:

$$\frac{dP_1}{dt} = gP_1(c\pi_1 - \gamma) - mP_1 \frac{\pi_2^{\nu}}{(c\pi_1)^{\nu} + \pi_2^{\nu}} + mP_2 \frac{(c\pi_1)^{\nu}}{(c\pi_1)^{\nu} + \pi_2^{\nu}}$$
(10a)

$$\frac{dP_2}{dt} = gP_2(\pi_2 - \gamma) + mP_1 \frac{\pi_2^{\nu}}{(c\pi_1)^{\nu} + \pi_2^{\nu}} - mP_2 \frac{(c\pi_1)^{\nu}}{(c\pi_1)^{\nu} + \pi_2^{\nu}}$$
(10b)

$$\frac{dQ}{dt} = gQ\left(\frac{(1-c)\pi_1 P_1}{Q} - \gamma\right) \tag{10c}$$

The two right-most terms in Eqs. (10a) and (10b) determine the impact of per capita resource availability on the rate and direction of migration by subordinates, P_i . We assume that individuals have information about habitat suitabilities and that they migrate so as to settle in the best habitat available to them, expressed as their opportunity to convert resources into reproduction. These two terms are a switching function for the direction of migration. The migration parameter m converts differences in habitat suitability into a rate of migration; we assume it to be the same regardless of the direction of

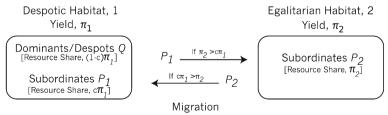


Fig. 1 Schematic of the two habitat model with subordinate habitat choice



movement. For a fixed value of v>1, as the concession-adjusted yield to subordinates in habitat 1, $c\pi_1$, increases over that in habitat 2, π_2 , the middle term of (10a) takes on a value approaching zero and the last term a value approaching 1. The effect is to add migrants to habitat 1 at a rate of mP_2 . Emigrants are simultaneously reducing the rate of population change in habitat 2 (10b) to the same degree, balancing migratory in-flow and out-flow between habitats. If the relative suitability of the habitats is reversed, migrants move in the opposite direction according to the same principles.

The parameter v>1 determines the precision with which this switchover is effected in the vicinity of $c\pi_1=\pi_2$. The higher the value of v, the more precise the switching behavior of individuals in response to a reversal of concession-adjusted habitat suitability. Larger values of v thus signify greater sensitivity to habitat differences. Low values of v allow for odds of migration around $c\pi_1=\pi_2$ less pronounced than a zero—one reversal and might represent habitat loyalty or "stickiness", cognitive limitations generating uncertainty in habitat assessment, or a probabilistic avoidance of migratory cost until disparities between habitats rise above a threshold. It can be shown through simulation that the long-run states of the system (10) do not change significantly at values of v>10.

In the following analysis we assume parameter values g=0.1, v=10, m=0.01, b=100, a=1, and $\gamma=1$ unless otherwise stated. Since an analytical solution to system (10) is unavailable, we simulated the system numerically using Matlab (2002).

How Much Should Despots Concede?

With two habitats and subordinates able to exercise habitat choice, what level of concession is optimal from the perspective of a despotic oligarchy intent on maximizing its numbers? Figure 2 shows that dominants should concede slightly less than 20% of total subordinate production. Further, simulations show that the analytical result in the one-habitat case, Eq. (4), predicts almost perfectly the simulated optimum in this two-habitat case (Fig. 2). Thus the analytical intuitions from the one-habitat case remain instructive, presumably because at equilibrium there is no significant migration, reducing the more complex optimal concession based on a system with migration (result (7)) to a simpler case with none (result (4)).

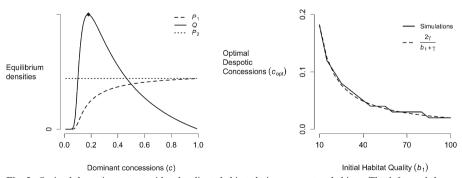


Fig. 2 Optimal despotic strategy with subordinate habitat choice among two habitats. The *left panel* shows equilibrium densities for all possible concession levels, with the filled diamond showing the optimal despotic concession. The *right panel* shows the results of numerical simulations of system (10), finding the optimal despotic concession for different qualities of the despotic habitat. It also shows how the analytical result from the one-habitat case approximates the simulated optimum in the two-habitat scenario. For both panels we assumed parameter values g=0.1, v=10, m=0.01, a=1, and $\gamma=1$. For the left panel we assumed b=10



Although a low concession level generates the greatest number of dominants at equilibrium, it also exponentially increases the time required to reach these equilibria (Fig. 3). Despots face an interesting trade-off: if it is tactically important to consolidate an oligarchy quickly, perhaps because of threats from a growing subordinate population in the egalitarian habitat 2 or from another despotic group not envisioned in our two-habitat model, then more generous concessions and acceptance of somewhat fewer oligarchs would be recommended. Elevating concessions dramatically increases the rate of population increase for both despots and subordinates in the despotic habitat. The despotic oligarchy whose reign depends on quickly securing a population advantage will be well advised to be more generous in their concession than the value 20%, that would in the very long run, produce the largest oligarchy.

Despotism as Migratory Push

Various authors have argued that the unusually rapid colonizations of Europe, the Pacific Islands, and Australia by humans can be explained in part by the IDD (Allen and O'Connell 2008; Kennett et al. 2009; Kennett and Winterhalder 2008; Shennan 2008). In this view, by monopolizing disproportionate shares of the best intra-habitat resources on an expansionary frontier, despots would drive more rapid emigration of subordinates to adjacent regions, where, in this view, the process repeats. If declining suitability of a habitat was shared equitably, as in the IFD, it would take longer for infill of one habitat to push emigrants to an adjacent, less-desirable one. Our model does not support this hypothesis.

Greater despotism instead slightly *increases* the time required to reach an arbitrary population level of subordinates (P_2) in habitat 2 (Fig. 4, left panel). The explanation for this counterintuitive pattern is instructive. The initial population of subordinates in habitat 2 must migrate there from habitat 1. Two opposing factors determine the timing

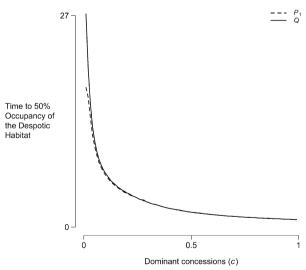


Fig. 3 The cost of low concessions. Shows the time to reaching 50% of steady-state density plotted against levels of dominant concessions. Generated from numerical simulations of system (10) assuming parameter values g=0.1, v=10, m=0.01, a=1, $b_1=50$, and $\gamma=1$



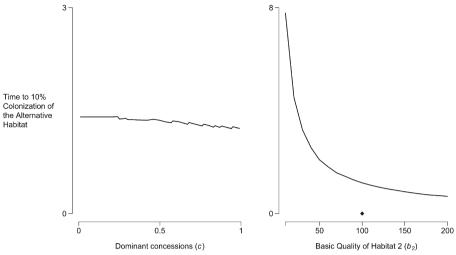


Fig. 4 The timing of colonization. The *left panel* plots the timing of colonization of an alternative habitat against dominant concessions (c). The basic habitat quality of the two habitats is the same $(b_1=b_2=100)$. The *right panel* plots of the timing of colonization against the basic habitat quality of the alternative habitat, with the *diamond* showing the basic habitat quality of the despotic habitat $(b_1=100)$. Both panels were generated from numerical simulations of system (10) assuming parameter values g=0.1, v=10, m=0.01, a=1, and $\gamma=1$. Initial population densities were $P_1(0)=0.01$, Q(0)=0.01, and $P_2(0)=0$. For the right panel, we further assumed the optimal despotic concession of $c=2\gamma/(b_1+\gamma)$

of this migration: (a) high levels of despotism make habitat 1 relatively unattractive by lowering concessions, but (b) despotism also suppresses population growth in habitat 1. The first, economic, force would shorten the time to the start of emigration (and is the basis of the "push" hypothesis mentioned earlier); however, the second, demographic, force lengthens the time it takes to grow a viable migrant population (Fig. 3). By a small margin the second force prevails. Rapid spread of a migration frontier requires not only a reason to migrate, but that a pool of potential migrants be produced at a sufficiently high rate. Despotism suppresses the population growth necessary to see an acceleration of migration to the alternative habitat.

Consistent with standard IFD interpretations, as the basic suitability of the alternative habitat declines subordinates will be more reluctant to emigrate there (right panel of Fig. 4). Simulations show that when the alternative habitat has less inherent resource quality than the despotic habitat, a further decrease in its relative quality has an exponential effect on time to colonization (region to the left of the diamond in the right panel of Fig. 4). However, if the alternative habitat has greater inherent resource quality, a further increase in quality has a diminishing effect: a 100% increase in alternate habitat value induces a small reduction in time to colonization. This arises because population density controls marginal suitability and thus emigration thresholds. Because subordinate densities experience exponential growth earlier in the population trajectory, especially in resource-rich habitats, density inflates rapidly relative to time.

Despotism and Path Dependence

Theories of state origins tend to fall into two broad categories: those arguing that subordinates receive few or no benefits and accept the relative deprivations of their role



owing to coercion by elites, and those that argue instead that despots provide compensating benefits in the form of redistribution of resources, defense, or enhancements to production. The latter theory amounts to the claim that a despot may solve economic or social coordination problems to the advantage of his or her subjects, despite their involuntary subjection and taxation. At this point we have examined aspects of the IDD model consistent with the former theory. Examination of the latter possibility provides further insight into the role of hierarchy in resource production and distribution, and their relationship to the evolution of despotic strategies. Economies of scale (Allee effects, in biology) introduced or organized by despots are an obvious possibility.

Up to now we have assumed that per capita resource yield is a declining linear function of subordinate density. We now introduce an Allee effect, in which the per capita resource yield peaks at an intermediate density of subordinates:

$$\pi(t) = \beta \left((1 + P(t))e^{-\alpha P(t)} \right) \tag{11}$$

where α scales the negative effects of population density and β is initial resource availability. We assume this economy of scale is present only in the despotic habitat, and the egalitarian habitat experiences the linear production function (Eq. 2).

We relax the standard behavioral ecology assumption of perfect information and optimal choice during initial colonization, and we allow for initial settlement groups of different sizes. Figure 5 demonstrates the consequences of this type of random founder effect. With uninformed or erroneous settlement choice, an Allee effect can significantly alter the population in-fill pattern, introducing the possibility of historical effects and path dependence.

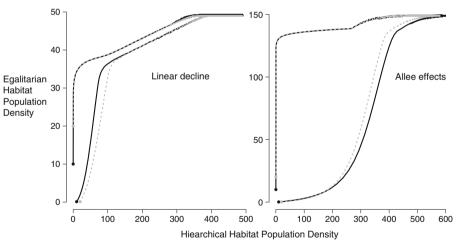


Fig. 5 Parametric plots of system (10) illustrating path dependence. Left panel shows simulations where both habitats experience a linear production function. The right panel has an Allee type production function in the hierarchical habitat and a linear decline production function in the egalitarian habitat. To illustrate the effects of initial conditions, four curves are plotted in each panel with contrasting initial densities of subordinates $(P_1, P_2) = \{(10,0), (20,0), (0,10), (0,20)\}$, where subscripts 1 and 2 denote the despotic and egalitarian habitat, respectively. The left panel plots simulations where the linear production function (2) is parameterized $b_1 = 100, a_1 = 1, b_2 = 50,$ and $a_2 = 1$. For the right panel, the parameter values for the Allee effect function (11) are $\alpha = 0.06, \beta = 100,$ and for the linear decline function, $a_2 = 1$ and $b_2 = 150$. Other parameters values for the system (10) are c = 0.2, g = 0.01, m = 0.1, and v = 20



In both panels in Fig. 5 the parameter values make the egalitarian habitat initially more attractive to subordinates than the hierarchical habitat. In the left panel both the despotic and the egalitarian habitats are characterized by a linear decline in per capita resource yield as the population of producers grows. Founding populations of 10 and 20 making the optimal, egalitarian choice of location fill that habitat exclusively until the marginal suitability drops sufficiently (at around 34 individuals) to provoke migration into the despotic habitat. Founding populations of the same size which suboptimally elect to settle in the hierarchical habitat instantly produce out-migrants who initiate rapid infill of the better, egalitarian habitat. Thus, in the linear case, wherever the founders initially reside, the overall tendency is a convergence of growth paths.

In the right panel we introduce an Allee effect in the despotic but not egalitarian habitat, on the assumption that the despotic regime is able to solve coordination problems and thus provide economies of scale not available to the egalitarian population. It is notable that mistaken settlers to that habitat find out-migration disadvantageous until their numbers have increased significantly and the returns to scale of the Allee effect are exhausted. Although the hierarchical habitat is lower in basic suitability, the Allee effect associated with a founding group elevates its value sufficient that it holds the growing population. The overall effect is for a divergent pattern based on initial settlement. This divergence is amplified if we introduce an Allee effect into both the hierarchical and egalitarian habitats. Allee effects act to hold populations in both the suboptimal and optimal habitat, only to see them eventually drain rapidly into the other.

These phase diagrams show us that (a) If migratory equalization is not instantaneous, then distinct pathways to equilibrium will result from different starting conditions; (b) With linear decline in yields, migration acts immediately to bend paths toward those that would result from strict adherence to IFD/IDD assumptions (settlement first in the optimal habitat, by a very small population), the adjustment constrained only by migration rate (m); (c) with Allee effects a population may tend to "stick" in the habitat it first occupies, even if that is the suboptimal choice, making path dependence most evident during early population growth stages in the Allee case. The shifting balance of positive and negative density dependence in habitats characterized by Allee yields produce complex and historically specific pathways.

Discussion

We introduce in three steps a general mathematical model capable of representing within a common framework both the Ideal Free and the Ideal Despotic Distributions. The parameter distinguishing the cases is the amount of concession, c. If c=1, then we recover the IFD; if c<1, then we have the IDD. Further, the model allows for habitat-specific population growth from two sources: (a) endogenous reproduction of subordinates from their own production and of dominants via capture of subordinate production and (b) migration of subordinates to their own advantage between habitats.

Analysis of the IDD reveals intuitive and counterintuitive properties of despotism, possibly important to its evolution and its consequences for despots, oligarchies and subordinates. (a) A one-habitat system of dominants and subordinates (Model I) reveals that elevated maintenance costs increase concessions whereas elevated habitat suitability reduces them, for despots optimizing their own population size. (b) If subordinates



can leave this system (Model II), the concessions granted by despots optimizing their population size will increase with out-migration rate. (c) Despotic concessions optimizing the equilibrium size of the despotic population typically are quite stingy, and they steeply depress the growth rate of the subordinate and despotic population living there ("How much should despots concede?"). (d) This implies a trade-off such that that a despot needing to establish a resident population quickly will favor more generous concessions. Despots must choose between slow subordinate growth yielding a large oligarchy or fast subordinate growth leading to a smaller oligarchy. Despotism has counterbalancing effects on emigration ("Despotism as migratory push"). High levels of despotism (low concession) give subordinates an economic incentive to migrate away, but they also depress growth rates sufficiently that demographic incentives to depart are delayed. Finally (e), If resource production has Allee-like properties and initial settlement is by a small group, then the IFD/IDD system exhibits strong path dependence. Allee habitats tend to capture and hold a growing settlement group, even though the alternative habitat has a higher basic suitability.

Future Work

The results presented here make several assumptions that can be addressed within the current framework. For example, by assigning the same parameter converting resources to reproduction, g, we implicitly assume that subordinates and despots require the same quantity of resources to reproduce themselves and their status. By differentiating this parameter such that $g_s \ll g_d$ (d = dominant; s = subordinate), the model can allow for elevated consumption needs of the despots, more consistent with the realities of political domination. Likewise, we assume that the dominant can control the allocation of production but cannot prevent emigration. This too can be examined within the present model, in this case by reducing the parameter controlling migration rates (m). As the despot approaches complete control of the border, m potentially drops to zero. Likewise, we have assumed no relatedness between the dominants and subordinates. Reproductive skew models (Buston and Zink 2009) suggest that relatedness gives subordinates an additional reason to stay with dominants, a feature that could be modeled by introducing parameters that bias the migration switch.

Further, an important effect not modeled here is competition among separated subpopulations of despots. Building population density quickly to compete with other groups (e.g., in warfare) may require more concessions than suggested in this analysis. In a multi-despot system, despots might compete for subordinates with concession inducements. Another possibility is that the despot may choose to concede more to the producing class by investing in statecraft (public works and entertainments such as feasting, monuments, bureaucracies, and armies) instead of expanding the oligarchy. In addition, concessions may be better viewed as dynamic, requiring a more complex dynamic programming analysis. This and other possible objectives of a controlling despot are possible adaptations of our approach.

We believe the IFD/IDD modeling approach formalized here is sufficiently promising and adaptable that it can build on classic theory (e.g., Carneiro 1970) and ultimately lead to empirical tests to help us understand the origins, persistence, and periodic failure of the hierarchical chiefdom and state-level societies.



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