

Intrinsic and extrinsic sources of variation in the dynamics of large herbivore populations

J.P. Marshal, J.W. Cain III, V.C. Bleich, and S.S. Rosenstock

Abstract: We evaluated the relative importance of intrinsic (density-dependent) and extrinsic (density-independent) sources of resource variability in the dynamics of bighorn sheep (*Ovis canadensis* Shaw, 1804) populations in southwestern USA. We tested the hypothesis that populations experiencing greater variation in forage availability are less likely to be at equilibrium density with forage supplies, and thus, would demonstrate weaker evidence of intraspecific competition. We used regression to relate population growth rate to rainfall (forage conditions) and to abundance (intraspecific competition) for 20 sheep populations, and we estimated the strength of the effects of density and rainfall for each population. Then we compared among populations to look for relationships between the strengths of rainfall and density effects and the variability in rainfall experienced by each population. Populations demonstrating a density effect were associated with environments having lower variability than those that did not. Populations showing a rainfall effect were associated with environments having a variability higher than those that lacked a rainfall effect. These findings are consistent with the hypothesis that populations experiencing higher variation in forage resources are less likely to achieve an equilibrium density with forage supplies where intraspecific competition would be a large determinant to the dynamics of that population.

Résumé : Nous avons évalué l'importance relative des sources intrinsèques (dépendantes de la densité) et extrinsèques (indépendantes de la densité) de variabilité des ressources dans la dynamique de populations de mouflons du Canada (*Ovis canadensis* Shaw, 1804) dans le sud-ouest des É.-U. Nous testons l'hypothèse qui veut que les populations qui connaissent une plus grande variabilité dans la disponibilité du fourrage sont moins susceptibles d'établir une densité d'équilibre avec leurs ressources fourragères et qu'ainsi elles présentent moins d'indications de compétition intraspécifique. La régression nous a servi à relier le taux de croissance de la population aux précipitations (condition du fourrage) et à l'abondance (compétition intraspécifique) chez 20 populations de mouflons; nous avons aussi estimé la force des effets de densité et des précipitations pour chaque population. Nous avons ensuite comparé les populations pour rechercher des relations entre la force des effets des précipitations et de la densité et la variabilité des précipitations éprouvée par chaque population. Les populations qui subissent un effet de densité sont plus souvent associées aux environnements qui ont une variabilité plus faible que celles qui ne connaissent pas d'effet de densité. Les populations qui éprouvent un effet des précipitations sont associées à des environnements qui possèdent une variabilité plus élevée que ceux fréquentés par les populations qui ne subissent pas l'effet des précipitations. Ces résultats s'accordent avec l'hypothèse selon laquelle les populations qui éprouvent une variation plus importante de leurs ressources fourragères sont moins susceptibles d'atteindre une densité d'équilibre avec leurs approvisionnements de fourrage, une situation dans laquelle la compétition intraspécifique serait un facteur déterminant majeur de leur dynamique de population.

[Traduit par la Rédaction]

Introduction

The influence of forage conditions on animal populations can originate from two sources: (1) intrinsic factors reflecting how animals affect their forage supplies through consumption and (2) extrinsic factors that are independent of foraging by animals (Andrewartha and Birch 1954, 1984). Intrinsic variation provides a mechanism whereby changes in per-capita food availability result in changes in animal

physiological condition, demographic rates, and population growth that lead to an equilibrium density with food availability; thus, it links intensity of intraspecific competition for forage to current or previous population density (Fowler 1981; Sinclair 1989; Choquet 1998). In environments where an animal population is not at equilibrium with its food supply, influence of such mechanisms would be reduced, and evidence for the patterns they produce (i.e., a density effect) would be weak or absent.

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In arid environments, forage conditions for large herbivores are highly variable, as a consequence of rainfall events that are unpredictable in spatial distribution, timing, or intensity (Noy-Meir 1973; Schwinning and Sala 2004). Changes in forage resources that occur via varying rainfall patterns can be substantial (Robertson 1987; Walker et al. 1987; Ellis and Swift 1988; Marshal et al. 2005). Such changes can happen over time scales short enough that demographic responses of a herbivore population, whether by increased survival or fecundity during periods of resource abundance or by increased mortality during periods of resource scarcity, lag resource conditions (Caughley and Gunn 1993; Sæther 1997). The population might exist rarely at an equilibrium abundance with forage, causing it to experience intraspecific competition for only brief periods, to demonstrate weak density effects where variation in dynamics are better explained by rainfall or forage patterns, or to lack evidence of intraspecific competition altogether (Caughley and Gunn 1993; Choquenot 1998).

The dual contribution of intrinsic and extrinsic sources of variation to dynamics of a population can be viewed as a tension between density-related and climate-related influences, the combination of which is unique to any particular population and determined by the variability of its environment (Post 2005). For temperate regions, environmental variability might express itself in the form of snow, temperature, or wind speed that alter a population's dynamics by affecting an individual's access to forage, or the energetic cost of locomotion or thermoregulation (Post and Stenseth 1998; Milner et al. 1999; Forchhammer et al. 2001). In arid mid-latitude environments, however, climate-driven variability is more likely to operate through annual rainfall, forage growth, and periodic droughts with associated forage scarcity (Caughley et al. 1985; Walker et al. 1987; Mduma et al. 1999). The consequence of these periodic severe perturbations are populations that can exhibit much greater rates of decrease than of increase, and thus, that spend much of their time below a density where limitation by food is apparent (Caughley and Gunn 1993).

An understanding of the contributions of intrinsic and extrinsic sources of variation to population dynamics, particularly in variable environments, is a critical aspect to understanding the consequences of changing resource conditions on animal populations under anthropogenic habitat loss, long-term climate cycles (e.g., El Niño Southern Oscillation), or changing global climate. Thus, our objectives were to investigate the relative importance of these sources in the dynamics of bighorn sheep (*Ovis canadensis* Shaw, 1804) populations inhabiting arid southwestern regions of the USA. Specifically, we used long-term survey and rainfall data to evaluate the following five predictions: (1) populations experiencing more variable rainfall are less likely to demonstrate relationships between density and population parameters and (2) are more likely to demonstrate relationships between rainfall and population parameters. Further, (3) populations demonstrating density relationships should show a weaker relationship with population parameters as rainfall becomes more variable. Populations demonstrating effects of both density and rainfall should (4) have a weaker relationship with density than populations demonstrating an effect of density alone. Moreover, when comparing across

populations for which there is evidence of effects of both rainfall and density on population parameters, (5) there should be an inverse relationship so that stronger density effects are associated with weaker rainfall effects.

Materials and methods

Study area

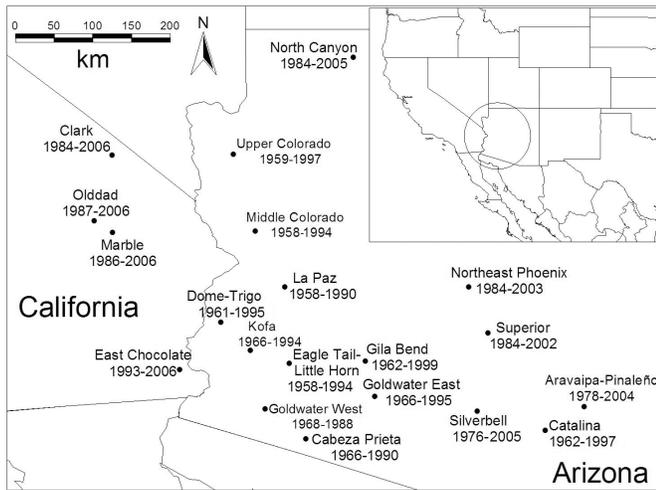
Data for this analysis came from bighorn sheep populations inhabiting mountain ranges in the Mojave and Sonoran deserts of southwestern USA, in the states of Arizona and California (Fig. 1). The region is typical for hot deserts, having low mean rainfall, high temporal and spatial variability in rainfall, and hot summer temperatures (>40 °C). Across the region, however, there is substantial variation in rainfall patterns and vegetation communities (Brown 1994). In general, regions to the east tend to have higher mean rainfall, lower interannual variability, and cooler temperatures, with the western regions being hotter, dryer, and more variable. The northern-most populations considered in this analysis occurred in the Mojave Desert, which generally had a higher elevation and cooler temperatures than the Sonoran Desert to the south. Throughout the region, seasonal rainfall tended to show a bimodal distribution, with rainy periods occurring in winter (January–March) and summer (July–September); however, there was substantial variation in the timing and amounts of precipitation, and in the driest areas, rainfall occasionally was absent during usually rainy periods (Brown 1994).

Bighorn sheep are habitat specialists, occupying mountainous regions with steep, rocky terrain that provides escape from predators (Krausman et al. 1999). They become reproductively active around August and give birth in February–March (Hass 1997). Their distribution frequently overlaps with native mule deer (*Odocoileus hemionus* (Rafinesque, 1817)) and exotic feral ass (*Equus asinus* L., 1758). Predators of bighorn sheep include mountain lion (*Puma concolor* (L., 1771)), bobcat (*Lynx rufus* (Schreber, 1777)), and coyote (*Canis latrans* Say, 1823). Many bighorn sheep populations were hunted, with legal harvest focussing exclusively on adult males, occurring in autumn and winter months (October–January), and removing a small number of individuals each year (≤ 10 per population).

Data sources

We analysed survey data for sheep populations ($n = 20$) in Arizona and California (Fig. 1) from 1958 to 2006. Regions in California were distinct mountain ranges; however, sheep populations in Arizona were divided into game management units that contained multiple ranges. Each geographic area was surveyed intensively by helicopter to count and classify sheep (Rabe et al. 2002). Survey polygons were delineated using identifiable ground features (Norton-Griffiths 1978) and ranged from 20 to 50 km² (mean ca. 40 km²). Survey teams covered each polygon by flying contour lines separated by ca. 150 m, at an altitude of 50–100 m, and a mean rate of 2.5 min/km² (Bleich et al. 1997; Hervert et al. 1998). Surveys for each area were typically conducted over a 2-day period during September–November with crews consisting of a pilot, a data recorder, and two observers. Observations of bighorn sheep were re-

Fig. 1. Locations of bighorn sheep (*Ovis canadensis*) populations, and years of data used in the current analysis, Sonoran and Mojave deserts, Arizona and California, USA.



corded, with surveys before 1984 identifying adult males, adult females, and juveniles (age <1 year). Thereafter, surveys classified males into horn size classes (I–IV) and identified male and female yearlings.

We obtained rainfall data from the US National Weather Service, Western Regional Climate Center (<http://wrcc.dri.edu/>, accessed 13 November 2008). We used stations representative of each region occupied by a focal sheep population, generally located within or a few kilometres away from the survey unit. We also attempted to select stations so that each population could be associated with an independent set of rainfall data; however, for some regions of southwestern USA, climate stations were scarce, so one station was associated with more than one population. In some cases, rainfall data for a particular station did not fully cover the period covered by sheep survey data; thus, we combined data sets of two nearby climate stations that had similar mean and variation in rainfall.

Data analysis

The population analysis was based on multiple linear regression models, the most complex of which took the form

$$[1] \quad \Delta N_t = \beta_0 + \beta_A A_t + \beta_{R0} R_t + \beta_{R1} R_{t-1} + \varepsilon_t$$

where ΔN_t is the population growth rate, A_t is the effective population abundance indexing intensity of intraspecific competition, R_t and R_{t-1} are rainfall for the current and previous years indexing forage resources over those periods, the β s are the intercept and slope estimates associated with each explanatory variable, and ε_t is the combination of process error and observation error (Owen-Smith and Mills 2006). Count results can be affected by survey conditions that influence visibility of animals (Caughley 1974; Hill et al. 1987), an effect that was apparent in our data from the unrealistically large rates of increase that were evident for some populations in some years. Thus, prior to analysis, we used a statistical filter to transform original count data. The filter produced a mean for each observation (N_t^*), based on the current, preceding, and succeeding years, with the transformations for the first and last years being $(5N_t + 2N_{t+1} -$

$N_{t+2})/6$ and $(5N_t + 2N_{t-1} - N_{t-2})/6$, respectively (Kendall and Ord 1990). This filter also removed serial autocorrelation in annual counts, a result we confirmed with the serial correlation coefficient and a nonparametric runs test on residuals from fitted models (Ramsey and Schafer 2002).

Using transformed counts, we estimated ΔN_t by $\log_e(N_t^*/N_{t-1}^*)$. Because of overlapping generations and the extended period over which density effects can occur for large herbivores (from before conception to time of the survey), A_t was calculated by $0.25N_t^* + 0.5N_{t-1}^* + 0.25N_{t-2}^*$ (Owen-Smith and Mills 2006). This formulation also reduces spurious density dependence that arises from observation error in N_t (Solow 2001). To facilitate comparison between sheep management units with differing areas, we standardized A_t for each unit by dividing by the long-term mean total sheep count for that unit (Owen-Smith and Mills 2006). Rainfall was used as an index to forage resource conditions. Current annual rainfall was summed backward from September of the year of the count to October of the previous year. We standardized rainfall for each population by dividing by the mean and then log-transforming that value (Owen-Smith and Mills 2006).

We used generalized least squares methods to fit regression models. For each population, we derived a separate set of eight candidate models, each based on a subset of variables from eq. 1, including a model containing only an intercept. We evaluated the fit of each model using Akaike’s information criterion corrected for small-sample bias (AIC_c ; Burnham and Anderson 2002), and identified best candidate models as those having a difference in AIC_c (Δ_i) of <2 when compared with the model with the lowest AIC_c (Burnham and Anderson 2002). We treated all models with $\Delta_i < 2$ as demonstrating evidence for an effect of the variables they contained, even if those variables occurred in separate models. If more than one model contained the same variable, our estimate of the effect associated with that variable was estimated using the Akaike weights (w_i), where we multiplied each estimate by its model’s w_i , summed the products, and then divided that sum by the sum of their weights.

An effect of abundance, if present, was assumed to be negative so that stronger effects of intraspecific competition were associated with more strongly negative estimates of the slope of A_t . Furthermore, because our study area was hot and arid, we assumed that rainfall would benefit sheep populations through growth of forage plants; thus, slopes estimated for R_t and R_{t-1} should be positive. If a contrary relationship emerged in the best candidate model set, and its support was not substantially different (i.e., within an AIC_c difference of 2) from the same model without that relationship, the relationship was assumed to be spurious and we dropped the associated model from further consideration. If an unexpected relationship did emerge and have support, we investigated the data further to identify other potential explanatory factors.

We compared populations to evaluate the influence of rainfall patterns, climate fluctuations, and intraspecific competition on population dynamics. We used linear regression to investigate relationships associated with each prediction listed in the Introduction. Response variables were rainfall coefficient of variation (CV; predictions 1–2) or slope coef-

ficient for the density effect (predictions 3–5) estimated for each population. Explanatory variables were presence of a density effect (0, 1; prediction 1), presence of a rainfall effect (0, 1; prediction 2), rainfall CV with presence of rainfall effect as a covariate (prediction 3), presence of a rainfall effect alone (prediction 4), and slope coefficient for the rainfall effect (prediction 5). Models were compared with intercept-only models using AIC_c to evaluate the strength of support for each prediction. We performed statistical analyses in R version 2.5.1 (R Development Core Team 2007) using functions from the library nlme (Pinheiro et al. 2007).

Results

Density and rainfall effects

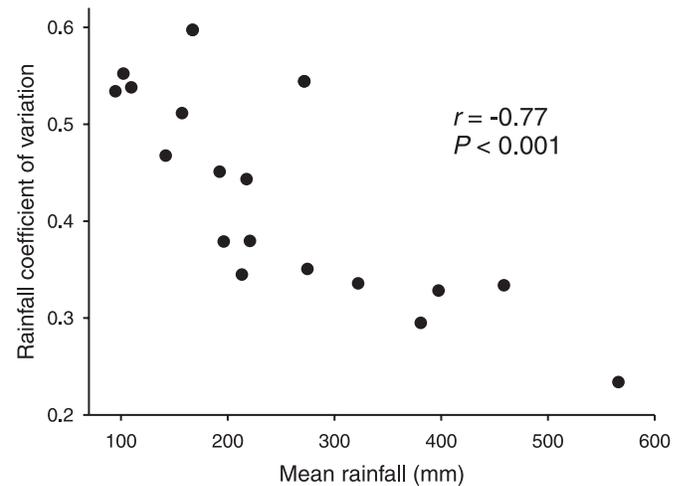
Mean annual rainfall varied substantially across the study area, ranging from 95 mm for East Chocolate to 566 mm for Catalina. Temporal variation in annual rainfall also varied substantially across the study area, with CV in annual rainfall ranging from 23% for Catalina to 60% for Superior. Variation in annual rainfall was negatively associated with the mean so that areas with lower mean rainfall also had higher interannual variation in rainfall (Pearson's $r = -0.77$, $P < 0.001$; Fig. 2). There was strong evidence of longitudinal gradients in mean and CV in rainfall (Fig. 3), where more eastern sheep units tended to experience higher rainfall, a pattern that would predict higher forage production in the eastern desert. Consistent with the inverse relationship between CV and mean rainfall, CV showed a negative relationship with longitude (Fig. 3), a pattern that would predict more variable forage production in the western desert. There was no evidence of latitudinal gradients in mean rainfall or CV (Fig. 3).

Five of the 20 populations considered in this analysis showed no indication of relationship between population growth and either density or rainfall (Table 1). Four populations demonstrated relationships between population growth and density alone, and there was evidence of relationships between current or previous year's rainfall and population growth for three populations. Eight populations exhibited relationships between population growth and density plus one of the rainfall variables. Among populations for which a density effect alone was evident, the strength of that effect ranged from -0.13 for Northeast Phoenix to -0.39 for East Chocolate (Table 1). Among those populations for which there was evidence of density and a single rainfall variable, the density effect ranged from -0.12 for Clark and Upper Colorado to -0.31 for Silverbell. Where an effect was evident, the influence of rainfall on population growth was always substantially lower than that of density, and ranged from 0.08 for Middle Colorado to 0.02 for Dome–Trigo.

Comparisons across populations

The intercept-only model had the lowest AIC_c value among all models used to evaluate predictions 1–5 (Table 2). In several cases, however, there were models representing predicted relationships for which $\Delta_i < 2$, leading us to conclude that there was suggestive evidence for the effects under consideration. A difference in rainfall CV was apparent between populations demonstrating and lacking a density effect ($\Delta_i = 1.57$), suggesting that populations having

Fig. 2. Relationship between mean rainfall and coefficient of variation in rainfall for bighorn sheep (*Ovis canadensis*) units in the Sonoran and Mojave deserts, Arizona and California, USA.



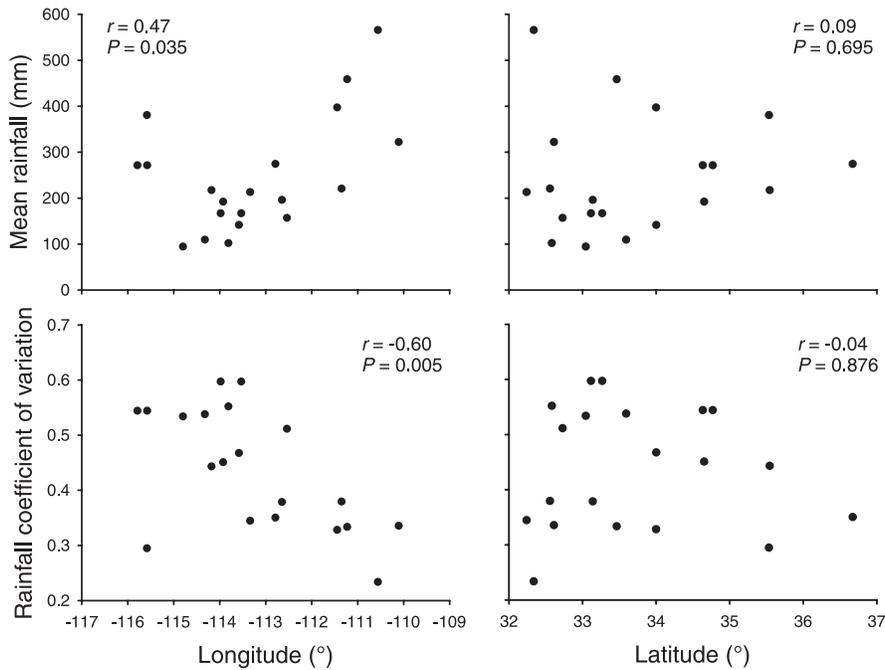
an effect of density experienced rainfall CV 0.0607 (SE = 0.0497) lower than populations that did not (Table 2). A further difference in rainfall CV emerged between populations affected by rainfall and those that were not ($\Delta_i = 0.05$): CV was 0.0834 (SE = 0.0478) higher for populations demonstrating a rainfall effect (Table 2). There was no evidence for a relationship between the strength of the density effect and rainfall CV ($\Delta_i = 2.14$). Strength of the density effect appeared weaker (difference = 0.0695, SE = 0.0474) for those populations demonstrating an effect of both density and rainfall when compared with populations having an effect density alone ($\Delta_i = 0.83$). Finally, for populations exhibiting both density and rainfall effects, there was no evidence that strength of the density effect weakened as the strength of the rainfall effect became stronger ($\Delta_i = 9.47$).

Discussion

Evaluation of predictions

Our first prediction was that populations experiencing more variable resource conditions would be less likely to demonstrate relationships between density and population growth. A comparison of variability in rainfall between populations demonstrating and lacking a density effect provided weak support for prediction 1. Although mean rainfall variability did appear to differ among populations with and without density effects, there were some notable exceptions to this pattern: East Chocolate demonstrated one of the highest effects of density on population growth (-0.39) and had relatively high variability in rainfall (0.53); Dome–Trigo showed similarly high rainfall variability (0.54) but a moderate effect of density (-0.15); and Kofa had very high rainfall variability (0.60) and a moderate effect of density (-0.17). For other high-variability systems (rainfall CV > 0.50), such as Eagle Tail–Little Horn (0.60), Goldwater East (0.51) and West (0.55), Old Dad (0.54), and Marble (0.54), the data did not support an effect of density on population growth. Thus, despite evidence of intraspecific competition in some high-variability systems, the tendency was

Fig. 3. Longitudinal and latitudinal variations in mean and coefficient of variation in rainfall for bighorn sheep (*Ovis canadensis*) units in the Sonoran and Mojave deserts, Arizona and California, USA.



for populations experiencing high environmental variability to lack evidence of a density effect.

Second, we predicted that systems with more variable rainfall would be more likely to show relationships with rainfall. A comparison of mean rainfall variability for populations demonstrating and lacking a rainfall effect provided evidence in support of prediction 2, where populations showing a rainfall effect appeared to experience higher environmental variability. The rainfall effect was apparent for the current or the previous year, but there was no evidence of an effect of rainfall from both years in the same model. For populations where current rainfall had the largest effect, rainfall generally would be expected to influence birth rate, neonatal survival, or yearling summer survival over the period between surveys for years $t - 1$ and t . For the previous year's rainfall, current dynamics could be influenced through condition of adult females and their capacity to become pregnant or nurse young, or through an effect of rainfall on yearling survival while those individuals were in the juvenile (<1 year) stage. Such patterns, particularly from lagged effects of resource availability on subsequent survival and reproduction (i.e., cohort effects), have been demonstrated for other large herbivores (e.g., red deer (*Cervus elaphus* L., 1758), Albon et al. 1987; western roe deer (*Capreolus capreolus* (L., 1758)), Gaillard et al. 1997). For bighorn sheep populations in southwest USA, higher variation in resources and periodic drought conditions should result in stronger influences of resource conditions during neonatal and juvenile development, cohort effects that are more apparent, and stronger effects on subsequent population dynamics.

Our third prediction stated that, for populations for which a density effect was evident, there should be a weaker effect of density (i.e., shallower slope) as rainfall variability increases. We detected no evidence of such a pattern for pop-

ulation growth. For systems dominated by variation in rainfall (e.g., kudu (*Tragelaphus strepsiceros* (Pallas, 1766)) in semiarid South Africa), evidence for intraspecific competition might only be apparent after statistically accounting for variation explained by rainfall (Owen-Smith 1990). It would be expected that the rainfall effect would need to be relatively large to obscure evidence of density-related processes, which was not evident for the bighorn sheep populations that we considered.

Fourth, we predicted that those populations showing a rainfall effect should also show a weaker overall influence of density because of the reduced role of intraspecific competition in affecting population dynamics in the presence of a rainfall effect. We found weak support for the notion that populations with both density and rainfall effects are subject to a lower mean density effect than those subject to effects of density but not rainfall. This is consistent with the idea that the stronger the effects of rainfall on dynamics of a population, particularly through periodic droughts and rapid rates of decrease, the less likely they are to be at equilibrium density where intraspecific competition for forage becomes evident (Caughley and Gunn 1993).

There was no support for our final prediction that addressed the hypothetical tension between the strength of density-related and climate-related factors. No relationship between slopes of the density and slopes of the rainfall effects were evident when comparing across populations.

Although there was some evidence that resource variation played a role in the relative contributions of intrinsic and extrinsic sources of variation to population dynamics for bighorn sheep, our capacity to detect such patterns likely was limited by the precision in the survey data, but also by the relatively narrow range of rainfall variability among our sample of bighorn sheep populations. Evidence of the tension between intrinsic and extrinsic sources of variation,

Table 1. Relationships between population growth and density of bighorn sheep (*Ovis canadensis*) populations and rainfall in the Sonoran and Mojave deserts of Arizona and California, USA.

Region	Intercept		Density		Current rain		Previous rain		AIC _c	Δ_i	w_i
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE			
Cabeza Prieta	0.0293	0.0494							3.12	0.00	0.32
Catalina	-0.0386	0.0613							30.25	0.00	0.40
Clark	-0.0316	0.0524							3.89	0.00	0.34
	-0.0436	0.0522			0.0712	0.0542			5.02	1.13	0.19
	0.0821	0.1132	-0.1207	0.1068					5.48	1.59	0.15
East Chocolate	0.3168	0.1376	-0.3877	0.1408					-9.98	0.00	0.54
Eagle Tail–Little Horn	0.0453	0.0366					0.0760	0.0377	-2.74	0.00	0.41
	0.0484	0.0381							-1.20	1.54	0.19
Superior	0.0129	0.0317							-16.37	0.00	0.49
	0.2426	0.1964	-0.2273	0.1918					-14.64	1.74	0.20
Gila Bend	0.0861	0.0824							55.12	0.00	0.35
	0.2356	0.1713	-0.1540	0.1547					56.60	1.47	0.17
	0.0766	0.0833			0.0726	0.0820			56.81	1.69	0.15
Goldwater East	0.0334	0.0577							16.92	0.10	0.31
Goldwater West	0.0324	0.0514							1.45	0.00	0.40
	0.0241	0.0509					0.0592	0.0459	2.77	1.32	0.21
Kofa	0.2276	0.0763	-0.1602	0.0704					-21.04	0.00	0.41
	0.2406	0.0765	-0.1766	0.0712	0.0335	0.0282			-19.64	1.40	0.20
La Paz	-0.0141	0.0473							9.00	0.00	0.46
Marble	-0.1690	0.0750	0.2186	0.0761					-39.21	0.00	0.53
	-0.1483	0.0759	0.1937	0.0777			0.0197	0.0162	-37.40	1.81	0.21
Middle Colorado	0.3012	0.1300	-0.2184	0.1205					10.76	0.00	0.26
	0.2897	0.1282	-0.2109	0.1187	0.0785	0.0563			11.37	0.60	0.19
	0.0818	0.0493							11.57	0.80	0.18
	0.0776	0.0486			0.0831	0.0583			11.99	1.23	0.14
North Canyon	0.3096	0.0804	-0.2428	0.0753					-27.67	0.00	0.54
Northeast Phoenix	0.0135	0.0395							-8.74	0.00	0.40
	0.1465	0.1165	-0.1279	0.1056					-7.15	1.59	0.18
Aravaipa–Pinalaño	0.0020	0.0318							-16.94	0.00	0.29
	0.2069	0.1254	-0.2105	0.1201			0.0556	0.0299	-16.13	0.81	0.20
	-0.0062	0.0320					0.0378	0.0294	-15.90	1.04	0.17
	0.1408	0.1265	-0.1347	0.1188					-15.53	1.42	0.14
Dome–Trigo	0.2235	0.0619	-0.1528	0.0539					-26.14	0.00	0.50
	0.2180	0.0626	-0.1510	0.0542	0.0247	0.0299			-24.15	1.99	0.19
Silverbell	0.3643	0.1704	-0.3107	0.1605					9.55	0.00	0.35
	0.0483	0.0516							10.65	1.09	0.20
	0.3397	0.1726	-0.2952	0.1615			0.0434	0.0452	11.44	1.89	0.14
Olddad	0.0092	0.0310			0.0600	0.0295			-15.40	0.00	0.43
	0.0108	0.0337							-14.42	0.98	0.26
Upper Colorado	0.2165	0.0313	-0.1249	0.0252			0.0315	0.0178	-52.04	0.00	0.45
	0.2165	0.0323	-0.1200	0.0260					-51.41	0.63	0.33

Note: Presented are the best models ($\Delta_i < 2$) selected from candidate models derived from a global model containing population density, current year's rainfall, and previous year's rainfall as explanatory variables, plus a candidate model containing an intercept only.

however, was apparent in harvest records and survey counts for reindeer and caribou (*Rangifer tarandus* (L., 1758)) across Greenland, northern Europe, and Russia (Post 2005), which likely had similar limitations. Comparisons across populations of those large herbivores revealed a negative relationship between the strength of density-dependent and density-independent effects (indexed by the North Atlantic Oscillation) so that stronger influences of climate factors were associated with weaker influences of intraspecific competition (Post 2005). There were also latitudinal effects, where the role of intraspecific competition appeared to decrease among more northern populations. Post (2005) attrib-

uted those patterns to increased importance of abiotic factors (e.g., snow depth, ice). The specific abiotic factors differ between those northern regions and southwest USA, but their influence on the balance between forage conditions and herbivore nutritional requirements should be similar, as should be their effects on population dynamics.

Rainfall versus density effects

In this paper, we present statistical models of relationships between population growth rate and factors we believe important in affecting growth rate. Importance, as defined here, is determined by measures such as the steepness of

Table 2. Model results to test relationships governing the role of intraspecific competition (via density) and rainfall variability in the population dynamics of bighorn sheep (*Ovis canadensis*) populations in the Sonoran and Mojave deserts of Arizona and California, USA.

Response	Model	Estimate	SE	AIC _c	Δ _i
Rainfall CV	Intercept only			-26.98	0.00
	Presence of density effect (0,1)	-0.0607	0.0497	-25.40	1.57
	Presence of rainfall effect (0,1)	0.0834	0.0478	-26.93	0.05
Density effect	Intercept only			-21.70	0.00
	Rainfall CV + presence of current rainfall effect (0,1)	-0.3373, 0.0882	0.2423, 0.0462	-19.55	2.14
	Presence of rainfall effect (0,1)	0.0695	0.0474	-20.87	0.83
	Current rainfall effect	-0.2943	0.7600	-12.23	9.47

the slope of relationships and by statistical support for variables used to explain variation in each population parameter. Those factors were relative abundance and rainfall, which we identified as most important in describing intrinsic and extrinsic sources of variation for bighorn sheep in arid environments. Statistical models of this nature permit investigation of correlative relationships in dynamics of large herbivore populations. Nonetheless, they produce hypotheses of causation only, which should be investigated further through studies of interactions between herbivores and forage availability or quality, and the influence each has on the other's abundance (Choquenot and McLeod 1997). Such investigations would permit the development of mechanistic models that represent plant-herbivore interactions explicitly. That exercise is necessary to understand the role of intraspecific competition and environmental variability where food resources and carrying capacity cannot be assumed to be constant or population growth rate to be density-dependent (Caughley and Gunn 1993).

We treated density and rainfall as two separate factors. Alternatively, they can be treated as components of the same effect, that of forage available per animal. Caughley (1976) described that as arising from three separate components, which he represented explicitly in an interactive plant-herbivore model: rate of change in edible plant biomass as a function of relevant environmental factors such as rainfall and temperature (plant growth response); per-herbivore intake rate of food as a function of edible plant biomass (herbivore feeding or functional response); and herbivore population growth rate as a function of edible plant biomass (herbivore numerical response). In such a system, the effect of per-herbivore forage arises through the sum of edible plant biomass for the population divided by the product of the herbivore feeding and numerical responses.

A "density effect" on population growth arises through variation in the numerical response alone and assumes variation in forage availability is small or zero. As a population increases, food per herbivore decreases, as does physiological condition, fecundity, survival, and population growth rate; as a result, population growth rate appears to be density-dependent. "Climate effects" or "rainfall effects" in arid systems influence the plant growth response. High-rainfall years yield high plant biomass and high per-herbivore food availability, and low-rainfall years result in a decrease in plant biomass and low per-herbivore food availability.

An alternative to an analysis based on the interactive plant-herbivore model is an approach that investigates the direct relationships between population parameters and per-

herbivore food supply. Using rainfall as an index to forage supply, Owen-Smith (1990) found strong relationships between demographic parameters of kudu and rainfall per biomass (*R/B*) of the population. In that case, climate effects occurred via the numerator and density effect through the denominator, but the importance of modelling the causal factor (i.e., forage per herbivore) remains clear. Further analysis indicated that the primary factor affecting population dynamics of kudu was rainfall and its influence on forage availability, whereas intraspecific competition modified the relationship between those dynamics and rainfall. For African savannas, the total amount of forage available is determined by rainfall, but density of herbivores influences the rate of consumption and the rate at which forage is depleted during the dormant (low-rainfall) season (Owen-Smith 1990; Mduma et al. 1999). A similar situation also might exist among large herbivores in North American deserts.

Comparisons among fundamentally different systems could produce patterns that are more easily detectable. Choquenot's (1998) conceptual model of a plant-herbivore continuum was based on systems differing substantially in environmental variability, capacity of the herbivore to influence its food supply (i.e., efficiency), and the strength of feedback between fluctuations in vegetation and herbivore population responses. At one extreme, an inefficient herbivore in a highly stochastic system would demonstrate weak feedback with forage fluctuations and abundance would be primarily determined by density-independent fluctuations in rainfall (e.g., feral pigs in semiarid rangeland; Choquenot 1998). At the other extreme, an efficient herbivore in a predictable system would demonstrate strong feedback to forage fluctuations and be primarily determined by intraspecific competition for forage and by density-dependent changes in demographic and population growth rates (e.g., white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) in temperate forest; Caughley 1976). Bighorn sheep in arid southwestern USA tend to the middle of this continuum, having an efficiency similar to that of white-tailed deer in a system that is highly stochastic. Compared with the extremes, one might expect bighorn sheep abundance to fluctuate in response to rainfall and resource conditions, as would occur via strong feedback. This feedback loop might be strong enough to dampen some of the variation caused by rainfall, but some variation would persist and population abundance would lag behind equilibrium density. Thus, as demonstrated for some of the sheep populations analysed here, both density-dependent and density-independent factors would be expected to play a role in the dynamics of bighorn sheep populations.

Other limiting factors

Our focus on density and rainfall effects presumes that no other factors (e.g., hunting, predation, disease, habitat changes, availability of drinking water) influence the dynamics of the sheep populations that we investigated. Our choice of relative abundance and rainfall as explanatory variables were based on the assumption that the influence of other factors was minor by comparison. Among these sheep populations, several demonstrated dynamics that were apparently related to neither rainfall nor density. This finding raises the question: what else might be the main determinant of dynamics for those populations? Predation and hunting are factors commonly cited in the literature. Predation by large carnivores has been proposed as an important factor limiting large-herbivore populations to densities below their food-resource ceilings for temperate (Skogland 1991; Messier 1994) and tropical species (Fryxell et al. 1988). Furthermore, predation and forage can have an interactive influence on populations of large herbivores (Sinclair and Arcese 1995). In situations where resources are scarce or energetic costs high, herbivores have poor nutritional intake relative to their requirements, resulting in poor physiological condition that predisposes them to mortality from other causes. Alternatively, predation might remove female adults that would otherwise survive and contribute to the reproductive potential of a population. Bighorn sheep can experience stochastic predation events, during which elevated predation pressure strongly affects adult survival, and consequently, population trend (Festa-Bianchet et al. 2006). Although bighorn sheep generally are not the preferred prey of large carnivores in southwestern USA, such episodes could occur among bighorn sheep in deserts (Rominger et al. 2004), and as a result, obscure relationships between population dynamics and forage or density feedback that otherwise would be apparent.

Anthropogenic effects, such as harvest or removal for translocations, could have a similar influence on relationships between population parameters and rainfall or density. Current harvest of bighorn sheep populations in southwestern USA is minimal and it focuses on a small number of adult males in each population. But unregulated harvest historically has been far greater (Monson 1980). Diseases such as infectious keratoconjunctivitis, caused by contact with domestic livestock, are capable of having a large effect on bighorn sheep populations (e.g., Jansen et al. 2007). Competition with feral ass also can impact the dynamics of bighorn sheep (Marshall et al. 2008). Harvest, disease, and competition with exotic ungulates affect population dynamics in a manner that could alter the relationships between population growth rate, forage resources, and density, making their estimation more difficult and less accurate.

Evidence presented here suggests a balance in the roles of intrinsic and extrinsic sources of variation on population dynamics of bighorn sheep in arid southwestern USA. Those populations demonstrating density effects appeared to be associated with lower variability environments than those that did not, whereas those showing a rainfall effect appeared to be associated with higher variability environments. The contribution of each source of variation to the population dynamics of those large herbivores, then, is likely influenced by the variability in rainfall and resultant forage resources.

However, other factors also might have influenced those dynamics and obscured forage–herbivore relationships in this arid environment.

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