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ORIGINAL ARTICLE

Analyzing Taylor's Scaling Law: qualitative differences of social and territorial behavior on colonization/extinction dynamics

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Abstract The power law relation between the mean population count and its variance (Taylor's Power Law, TPL) is among the few general patterns in population ecology. While the TPL has been described to be pervasive across taxa, the causes of variation of the exponent describing this relation is not well understood. We compare the TPL exponents for two species with different social systems and behavior: Piñon jays (*Gymnorhinus cyanocephalus*) and Western scrub-jays (*Aphelocoma californica*). We analyze the underlying processes that generate the expected values of population size and its variance. Using a probabilistic model, we identify and estimate important processes involved in the generation of the TPL exponents. While both species show a scaling relationship between their mean and abundance, share a common negative relation between mean abundance and colonization–extinction rates, they differ greatly in the statistical distributions of colonization, extinction, the mean number of colonists, the probability of zero abundance and population sizes. We show how different aspects of the processes that generate abundance affect the TPL exponent, thereby providing empirical guidelines to interpret differences in the scaling relation between mean and variance of population size.

Keywords Invariant scaling · Mean–variance · Population dynamics · Population variability · Taylor's Power Law

Introduction

Populations in space and time exhibit an intriguing relationship between the mean abundance of individuals (M) and the variance (V), known as the Taylor's Power Law (TPL hereafter; Taylor 1961). In the TPL, M and V are related by a power law relation: $V = \gamma M^{\beta}$, such that the log-transformed variance in abundance plotted as a function of the log-transformed mean abundance exhibits a characteristic slope (β). The TPL has been documented both across many sampling sites (i.e., through space) and over many sampling periods (i.e., through time; Taylor 1961; Taylor and Taylor 1977; Taylor et al. 1978; Taylor and Woiwod 1982; Keitt et al. 2002; Kendal 2002; Kerkhoff and Ballantyne 2003; Krasnov et al. 2006).

The origin of the TPL has been under debate ever since Taylor's first description in 1961. The debate centers on the relative importance of density dependent processes, stochasticity, and mathematical artifacts inherent to population dynamics (Anderson et al. 1982; Soberón and Loevinsohn 1987; Hanski and Tiainen 1989; McArdle et al. 1990; Kendal 2004; Ballantyne and Kerkhoff 2007;

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Engen et al. 2008). Empirical evidence and theoretical arguments show that the range of possible values for β is constrained between approximately one and two depending on the degree of association between individuals within or among populations (Anderson et al. 1982; Taylor and Woiwod 1982; Gillis et al. 1986; Hanski and Tiainen 1989; Kendal 1992, 1995; Keeling and Grenfell 2000; Keitt et al. 2002; Ballantyne and Kerkhoff 2005); density dependent factors reduce the null expectation of a slope of two (Gillis et al. 1986; Keeling and Grenfell 2000; Kilpatrick and Ives 2003; Ballantyne and Kerkhoff 2007). The upper limit of $\beta = 2$ is determined by density independence or equivalently by a lack of association between individuals (Ballantyne 2005; Engen et al. 2008). Where individuals become independent, the slope of the TPL increases to its upper limit. In contrast, populations with high spatial or temporal correlation among individuals show low β values. The null expectation for the TPL is best understood via the coefficient of variation (CV). The CV, a normalized measure of dispersion, compares the magnitude of the fluctuation across populations of different sizes. When β approaches two, the mean population size becomes equal to the standard deviation, meaning that the fluctuations grow with population size. In other words, where $\beta = 2$, variations in population size are due to factors independent of the mean abundance (i.e., if $\beta = 2$, CV is independent of mean abundance, if $\beta < 2$, CV decreases with mean therefore $\mathrm{CV} \propto \sqrt{V[N]}/E[N] \propto \sqrt{E[N]^2}/E[N] \propto 1$; Ballantyne 2005). Deviations from the null expectation of $\beta = 2$ will occur when a reduction in the degrees of freedom affects the variance. For example, a reduction in the degrees of freedom may occur when populations are regulated by factors that induce correlation among individuals, as by territoriality or colonization–extinction processes and may partly be responsible for spatial patterns of aggregation.

Western scrub-jays (*Aphelocoma californica*, WESJ) and Piñon jays (*Gymnorhinus cyanocephalus*, PIJA) are two closely related species in the family Corvidae (Pitelka 1951; de los Monteros and Cracraft 1997; Saunders and Edwards 2000; de Kort and Clayton 2006). The two species exhibit several behavioral differences that we exploit to guide predictions regarding their temporal TPL. These two corvids occupy similar habitat, although WESJ are usually found in dryer habitats and lower elevations. PIJA are highly social, non-territorial birds that depend heavily on piñon seed (Balda et al 1997). WESJ caches a number of food types, breeds in pairs without helpers, is highly territorial year round and may even show aggressive behavior to the point of attacking by grappling and pecking same-sex individuals during contests over breeding vacancies (Ritter 1983; Peterson and Burt 1992; Burt 1996; Curry et al. 2002). PIJA is a less aggressive cooperative breeder with dispersal largely by females to adjacent flocks in search of males (Marzluff and Balda 1989). Occasionally young PIJA males wander to maximize their reproductive output (Marzluff and Balda 1992).

Several behavioral differences may affect the TPL. While PIJA are not known to defend a territory they may vigorously defend nesting materials once in place (Balda 2002). Overall, the individual home ranges of PIJA are remarkably stable through the year and remain mostly limited to the home range boundaries of the flock; boundaries are not defended conspicuously (Marzluff and Balda 1992). In contrast, WESJ actively defend a territory throughout the year but might tolerate “floaters” when not breeding (Curry et al. 2002). This presumably occurs because non-divisible resources are protected by WESJ (Brown 1964; Both and Visser 2003), leading to a spatial organization in which territory size is negatively correlated to population density (Curry et al. 2002; López-Sepulcre and Kokko 2005).

To assess differences in processes that generate TPL exponents we use local colonization and extinction rates to calibrate a Markov Chain (MC) framework to analyze TPL exponents for both PIJA and WESJ. The MC gives the dynamics with which we write a model for the expected abundance and variance. The model permits an analysis of β with respect to population parameters such as the mean number of colonists, $\hat{N}_c$, the probability of zero abundance, $P(N = 0)$, and the probability distribution of population size, $P(N > 0)$.

We generate and test specific predictions regarding measured parameters in terms of the behavioral differences between species that affect mean–variance scaling. We do not expect qualitative differences in colonization and extinction probabilities between PIJA and WESJ, as proximity among populations is critical to the local extinction and colonization of adjacent sites. We do expect the mean number of colonists, $\hat{N}_c$, to be higher for PIJA given the higher vagility described for this species. While we do not attempt to provide final explanations to the emergence of the mean–variance scaling among populations, we do show for the first time how differences in colonization–extinction dynamics can result in qualitatively different TPL exponent.

Materials and methods

We use annual abundance of PIJA and WESJ from the Breeding Bird Survey routes across the complete species geographic ranges (Fig. 1a; BBS, Sauer et al. 2005). The BBS consists of yearly censuses conducted during June

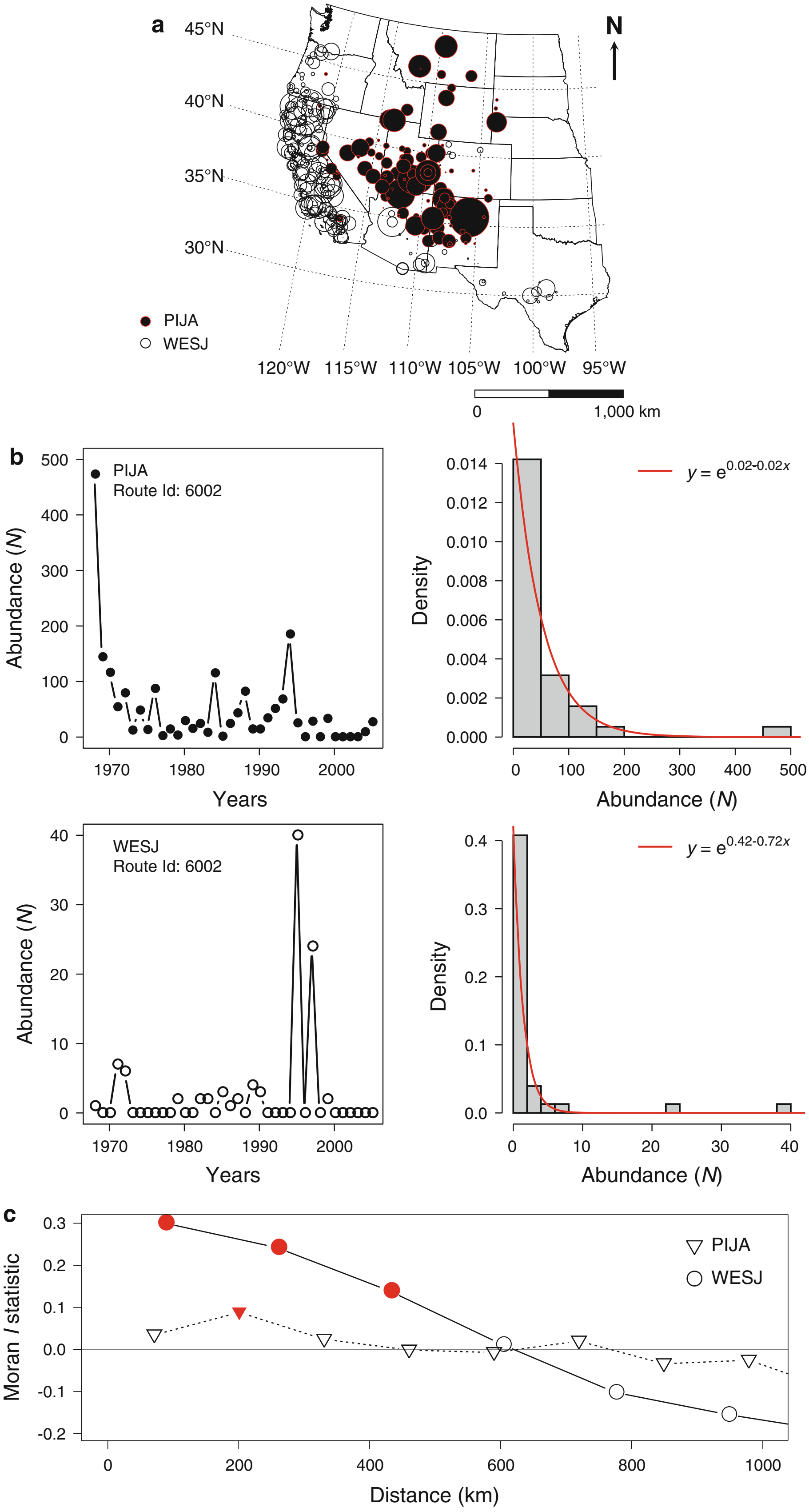

Fig. 1 Spatial distribution of routes considered in the analysis. **a** Spatial location of relative abundances per route; **b** Abundance for route 6002 (latitude 36°24′36″N, longitude 113°19′48″W) is portrayed for illustration purposes. *Top* and *lower panels* show time series and the distribution of abundance for PIJA and WESJ, respectively; **c** Moran's *I* is used to show spatial correlation between abundance across the species' range, significant spatial correlation is shown by *filled symbols*

across North America starting in 1966. Each route consists of a 40 km transect. An observer travels by vehicle along each transect and stops every 0.8 km to count all birds detected within a 0.4 km radius during 3 min. Survey results are widely accessible through the Internet. We also include a copy of the dataset employed in Appendix A in the Electronic Supplement Material (ESM).

Between 1968 and 2005, PIJA were present in a total of 244 routes and WESJ were sampled in at least 411 routes. Because routes have been added over the years, not all routes cover the same time span and could also harbor transient or non-stationary populations if few observations are recorded. We restricted our analysis to routes fulfilling the following two conditions: (1) were sampled for at least 10 consecutive years (i.e., at least 10 years separated the first and last population counts), and (2) had at least 5 years of positive abundance. This filtered routes to 111 and 256 routes for PIJA and WESJ, which are at least 8 km apart. Moran's *I* was used to characterize the spatial structure of abundance among routes (Fortin and Dale 2005). Mean and variance were calculated for each route and plotted on a logarithmic scale (base 10). TPL slopes and confidence intervals were calculated for each species separately using standardized major axis regression (also known as type II or reduced major axis regression; Legendre and Legendre 1998). Slopes were compared using a likelihood ratio test for common slopes (Warton et al. 2006).

We simulated scaling exponents for both species with a probabilistic model based on empirical population counts and on rates of route colonization and extinction. For each studied route the colonization–extinction process can be modeled by a two states Markov chain (Fig. 2). Each route can either be in an occupied state (State 1 in Fig. 2) or in a vacant state (State 0 in Fig. 2) with their respective probabilities $P(N_t > 0)$ and $P(N_t = 0)$. The alternance in time between these two states of occupancy can occur through four distinct mechanisms: persistence (transition *a*); local extinction (transition *b*); vacant persistence (transition *d*) or local colonization (transition *c*) and the probabilities for these four transitions can entirely be described by the colonization (δ) and extinction (λ) rates (Taylor and Karlin 1984) and are given by:

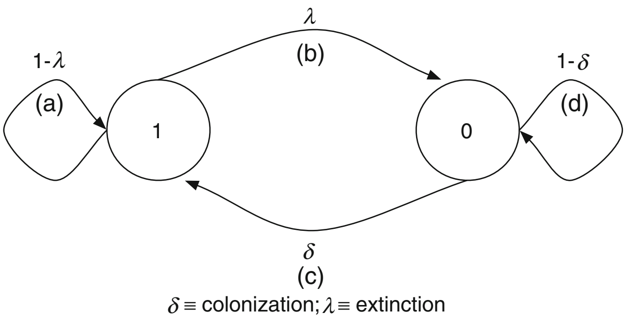

Fig. 2 Probabilistic model used to estimate expected population size ($E[N]$), and variance ($V[N]$), based on Markov chain framework of colonization and extinction rates

$$P(a) = (1 - \lambda)P(N_t > 0) \tag{1}$$

$$P(b) = \lambda P(N_t > 0) \tag{2}$$

$$P(c) = \delta P(N_t = 0) \tag{3}$$

$$P(d) = (1 - \delta)P(N_t = 0). \tag{4}$$

In order to account for an event that could only be observed as persistence but which in fact could involve extinction (i.e., extinction and colonization processes occur simultaneously), one must ensure that the calculated values for colonization (δ) and extinction (λ) rates do not violate the following condition $0 < \delta + \lambda < 1$ (Clark and Rosenzweig 1994). Assuming that at the initial state the route is occupied, such chain possesses stationary solutions of the form:

$$P(N_t > 0)(t) = \frac{\delta}{\delta + \lambda} \tag{5}$$

$$P(N_t = 0)(t) = \frac{\lambda}{\delta + \lambda} \tag{6}$$

As routes have been yearly sampled for at 10 to over 30 years, in some cases, the colonization (δ) and extinction (λ) rates can be accurately approximated by:

$$\delta = \frac{k}{k + l} \tag{7}$$

$$\lambda = \frac{m}{m + n} \tag{8}$$

where, for each route, *k*, *l*, *m* and *n* denote the number of times that each of the following transitions occur: a vacant state to an occupied state (local colonization), a vacant state to a vacant state (vacant persistence), an occupied state to a vacant state (extinction) and an occupied state to an occupied state (persistence), respectively (Clark and Rosenzweig 1994).

We may define $\hat{N}_a$, $\hat{N}_b$, $\hat{N}_c$ and $\hat{N}_d$ as the expected population size following each of the aforementioned transition. As the two transitions *b* (extinction) and *d* (vacant persistence) lead to a vacant state, it follows that $\hat{N}_b = \hat{N}_d = 0$. In the case of local colonization (transition *c*), the expected population size following this type of transition is defined as the mean value of non-zero population size following years with zero abundance. Therefore one can count the number of colonists, $N_C(i)$ for each transition from a vacant to an occupied state and approximate $\hat{N}_c$ as:

$$\hat{N}_c = \frac{1}{k}\sum_{i=1}^{k} N_C(i) \tag{9}$$

In the case of persistence (transition a), the empirical probability distribution of the population size N following such a transition is of the form $P(N) = e^{(\alpha+\rho N)}$, where the coefficients α and ρ are extracted from the empirical data using non-linear regression of the probability of finding a particular abundance (see Fig. 1b for an example route), against the number of birds for a route in the case of persistence (*nls* procedure in *R*, R Development Core Team 2010). Code is provided in Appendix B of ESM. α is an indicator of the probability of absence and ρ describes the rate of decay in the probability of occurrence with respect to the population size. Biologically, we interpret α as representing the habitat suitability for that particular route, and ρ an index of density dependence that may be affected by flocking behavior for example. The expected population size $\hat{N}_a$ can be approximated by the product of the population size N times its probability of occurrence $P(N)$ leading to:

$$\hat{N}_a = \sum_{N=1}^{M} N e^{(\alpha+\rho N)} \tag{10}$$

where M is the maximum population size observed.

This Markov framework permits to derive a theoretical mean abundance ($E[N]$) and its variance ($V[N]$) taking into account both dynamics of abundance and colonization–extinction processes. Consequently, we define $E[N]$, as the sum of the expected population size following each transition weighted by the probability of going through that same transition such that:

$$E[N] = P(a)\hat{N}_a + P(c)\hat{N}_c \tag{11}$$

and $V[N]$, as the expected value of the sum of squared deviations of population size from the expected:

$$V[N] = \sum_{N=0}^{M} (N - E[N])^2 e^{(\alpha+\rho N)} \tag{12}$$

As a first approach, we used quantile regression (Koenker and Bassett 1978) to assess whether simple differences in colonization and extinction alone could explain TPL exponent differences between species. Quantile regression determines the upper and lower bounds of the density-dependent colonization and extinction probabilities as a function of the log-transform of mean abundance (Cade et al. 1999). All analyses were performed using the open-source *R* statistical package (R Development Core Team 2010, version 2.8.0).

To ascertain how dynamics affect TPL exponents, we compare empirical and model-based mean–variance abundance relationship by assessing the distributions of population parameters including λ, δ, the mean number of colonists ($\hat{N}_c$), and the probability of zero abundance, $P(N = 0)$ (Fig. 2). We use Kolmogorov–Smirnov tests to compare the statistical distributions of α and ρ between species to test for differential effects of density dependence on the TPL. All comparisons were performed on the probability distributions generated from a density kernel estimator (Venables and Ripley 2002). This approach is an optimal non-parametric representation of variability that avoids error associated with bin size selection and location common in simple histogram estimation (Silverman 1986). A Wilcoxon rank-sum test was used to identify how differences in the medians agreed with our predictions based

Table 1 Model predictions and test based on parameters that reflect the behavioral differences between Piñon jays (PIJA) and Western scrub-jays (WESJ)

Parameter	PIJA vs. WESJ	Predictions explanation	Test	
			W	P value
δ	PIJA = WESJ	Sensitive to route density	11509.5	0.0045
λ	PIJA = WESJ	Sensitive to route density	18297.5	<0.0001
$\hat{N}_c$	PIJA > WESJ	Vagility	18793.5[a]	n.s.
$P(N = 0)$	PIJA < WESJ	Rescue effect	18562.0[a]	<0.0001
$P(N > 0)$	PIJA = WESJ	Population growth rate, flocking	15938.5	<0.0001
α	PIJA < WESJ	PIJA is less of a habitat specialist	4746.0[a]	<0.0001
ρ	PIJA > WESJ	Flocking tendency	19458.0[a]	<0.0001

A Wilcoxon rank sum test was used to assess predictions

δ colonization rate, λ extinction rate, $\hat{N}_c$ expected number of colonists, $P(N = 0)$ probability of zero abundance, $P(N > 0)$ probability of positive abundance, α habitat suitability index, ρ density dependence index, *n.s.* not significant

[a] Single tailed tests

on behavioral differences between species (Table 1). The alternative hypothesis was set to match the predictions using two-tailed tests for δ, λ and $P(N > 0)$ and single-tailed tests with their respective direction for the remaining parameters. For example, we used a Wilcoxon rank-sum test (Legendre and Legendre 1998) to test if the median of $P(N = 0)$ for PIJA was significantly smaller than for WESJ based on our predictions shown in Table 1.

Results

WESJ shows a strong spatial correlation up to about 500 km in mean abundance values for the time span studied (Fig. 1c). As opposed to WESJ, PIJA show no apparent correlation of mean abundance. Additional evaluation of the Ripley's K function for both species clearly shows differences in the aggregation patterns according to a stronger territorial behavior of WESJ as compared to PIJA (data not shown).

For both species, Taylor's Power Law relations are characterized by high correlation coefficients ($r = 0.948$; $t_{109} = 31.218$; $P < 0.0001$ and $r = 0.967$; $t_{254} = 60.671$; $P < 0.0001$ for PIJA and WESJ, respectively, Fig. 3). As expected, PIJA has a higher slope than WESJ ($\beta = 1.77$ for PIJA vs. $\beta = 1.50$ for WESJ, Fig. 3). Slopes differ significantly between species (Bartlett-corrected likelihood = 22.02, $P < 0.0001$), and from the null expectation of $\beta = 2$ (Bartlett-corrected likelihood = 6.28, $P = 0.0122$ for PIJA and Bartlett-corrected likelihood = 16.66, $P < 0.0001$ for WESJ; see Warton et al. 2006 for further explanation).

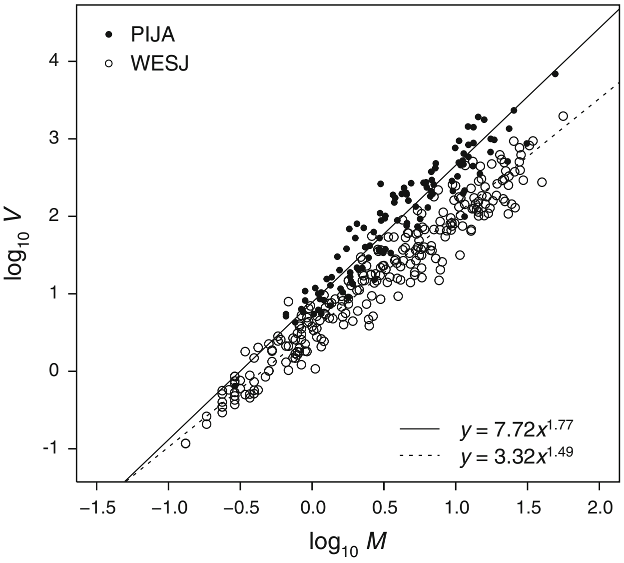

Fig. 3 Taylor's Power Law relation for Piñon jays (PIJA) and Western scrub-jays (WESJ)

Quantile regression analysis show a significant constraint at the upper and lower bounds of mean abundance (data not shown) where PIJA and WESJ show the same qualitative pattern in relation to extinction and colonization probabilities (Fig. 4). Mean abundance decreased as an exponential function of colonization probability for both species (Fig. 4). Additionally, extinction rates form a similar bounded negative relation for both species (Fig. 5) with a bounding slope of -1 for both species. This shows similar interdependence between colonization and extinction processes for both species, which makes extinction and colonization by themselves unable to explain differences in β.

The probability distributions of colonization and extinction rates differ significantly between species (Fig. 6; Table 2). The Kolmogorov–Smirnov tests of the probability distributions of mean abundance confirms the significant differences between species (Fig. 7a; Table 2). The distribution of mean number of colonists for both species differ while being strongly right-skewed for both species (Fig. 7b). The probability density of zero abundance is slightly left skewed for both species, but significantly different between species as well (Fig. 7c; Table 2).

For cases in which no directional change in the parameters is predicted (δ, λ and $P(N > 0)$; Table 1), the Wilcoxon sum-rank test corroborates the differences in the behavioral dynamics between species showing that both species have significant differences in the distribution of their parameters (Table 1). Except for $\hat{N}_c$, differences between parameter medians confirm the predictions generated from the species behavioral characteristics (Table 1). For the remaining parameters, the significance of the test, contingent on the direction in which the single-tail test was performed, validates our expectations (Table 1).

The mean and variance generated by our model accurately reproduce the TPL relation for both species with exponents that are statistically indistinguishable from the observed (Bartlett-corrected likelihood ratio for common slope: $LR = 1.433$; $P = 0.231$) for PIJA or nearly so for WESJ ($LR = 4.031$; $P = 0.045$). Equally, model-based results show that TPL exponents are significantly different between species ($LR = 16.041$; $P \ll 0.0001$). Nonetheless, the model TPL (Fig. 8) shows higher scatter than the observed TPL (cf. Fig. 3).

Discussion

We showed a significant difference between the Taylor Power Laws of two closely related species that have different social structures and behaviors (Fig. 3). Although density dependent factors are known to lower the TPL exponent (Anderson et al. 1982; Keeling and Grenfell

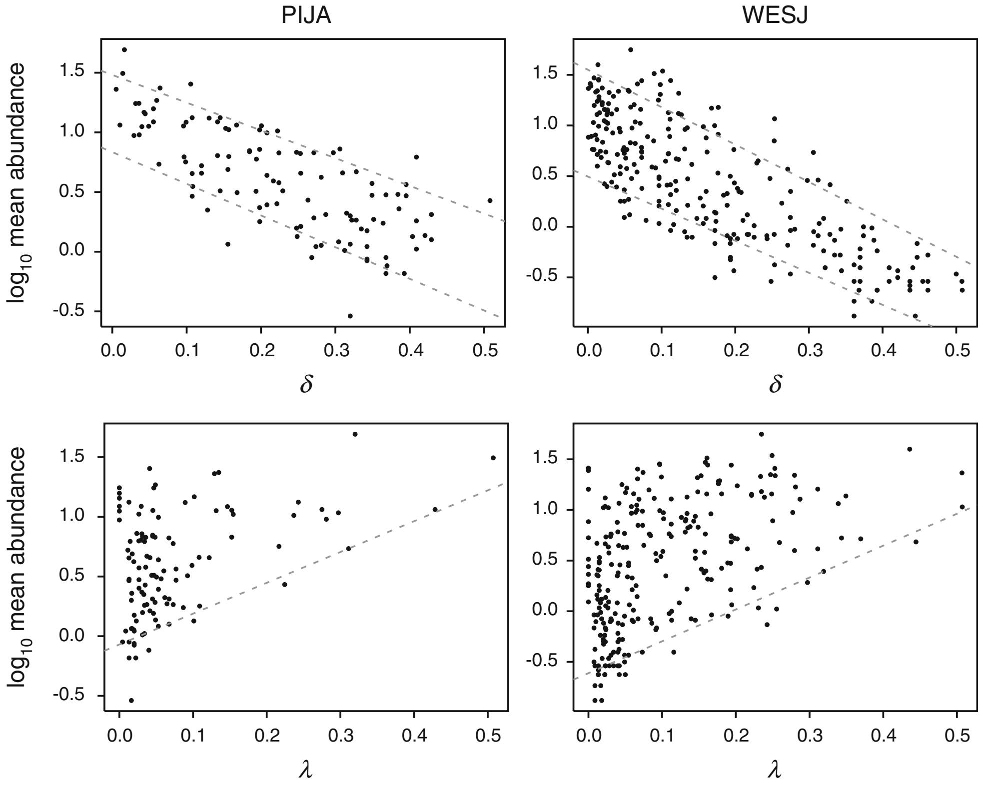

Fig. 4 Relation between mean abundance and colonization (δ) and extinction (λ) rates. The *broken lines* show the upper 90% quantile regression line for the relation between colonization and log-mean abundance and the lower 10% and upper 90% quantile regression lines for colonization

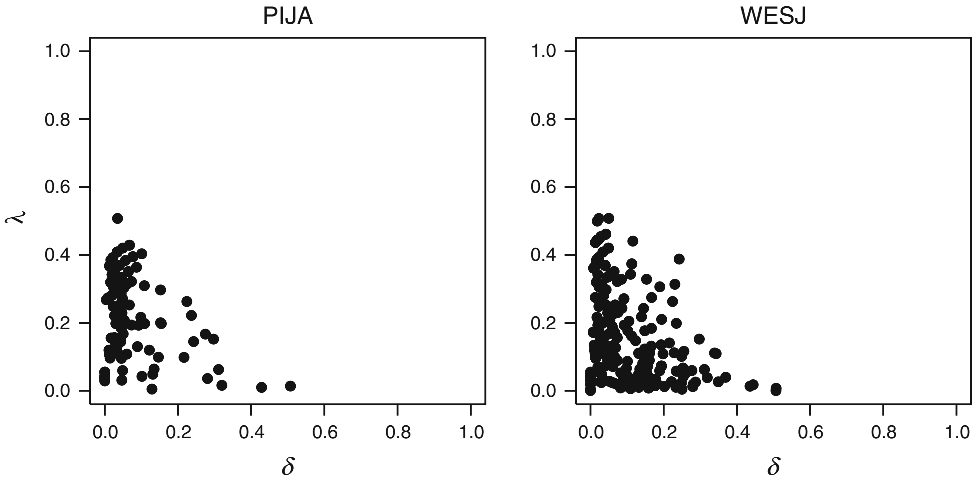

Fig. 5 Relation between colonization (δ) and extinction (λ) rates for BBS abundances of PIJA and WESJ

2000), few have attempted to relate empirical population processes to the exponent (e.g., Hanski and Tiainen 1989; Maurer and Taper 2002). We successfully relate empirical colonization–extinction dynamics that result in different TPL exponent.

Attempts to explain the origin of the TPL and to ascribe particular ecological processes to the slope of the relation entail conceptual, technical, and empirical issues. Conceptually, we recognized that rates of birth, death, immigration, and emigration map onto observable colonization and extinction processes in a complex fashion that may be consistent with alternative models. Thus, a lower exponent cannot be attributed uniquely to any particular explanation. The conceptual challenge of ascribing ecological causes to

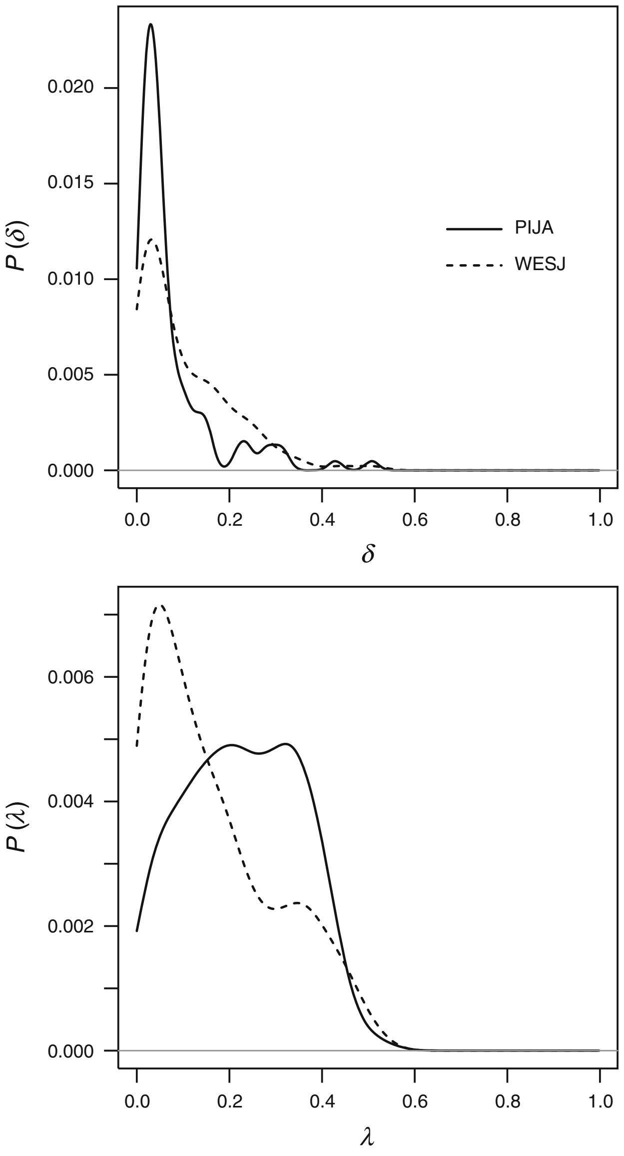

Fig. 6 Probability density functions for colonization (δ) and extinction (λ) rates

Table 2 Comparison of probability distributions for PIJA and WESJ using Kolmogorov–Smirnov two sample test

Distribution	D	P value
$E\,[N > 0]$	0.215	0.0016
$P\,(N = 0)$	0.271	<0.0001
$\hat{N}_c$	0.306	<0.0001
P (colonization)	0.211	0.021
P (extinction)	0.279	<0.0001
ρ	0.325	<0.0001
α	0.530	<0.0001

$P < 0.05$ show significant differences between the statistical distribution of evaluated parameters

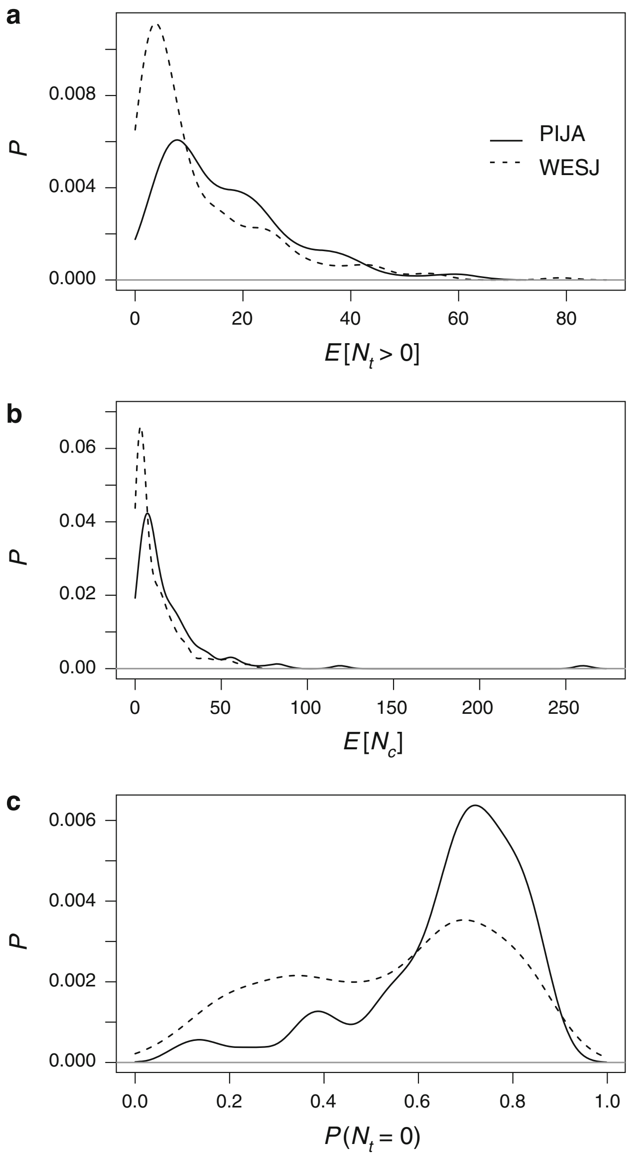

Fig. 7 Probability density functions of **a** the mean abundance for $N_t > 0$, **b** the mean number of colonists, $E(N_c)$ and **c** the probability of zero abundance $P(N_t = 0)$ for PIJA and WESJ

the slopes of empirical TPL relations benefits from recognition that the entire exercise is based on counts of birds. Under the assumption that particular dynamical rules pertain over the length of the record, counts assembled into statistical distributions contain all the information available about the populations. Our particular strategy for partitioning the counts (Eqs. 11, 12) was consistent with observation (Fig. 8) that we attribute to behavioral differences between species (Table 1). As recently noted by Engen et al. (2008), other conceptual frameworks may be consistent with observation as well. For example, using Taylor and Woiwod's (1982) records of moths, aphids and birds, Hanski and Tiainen (1989) posit territoriality as the only 'usable' framework to explain the TPL, a claim

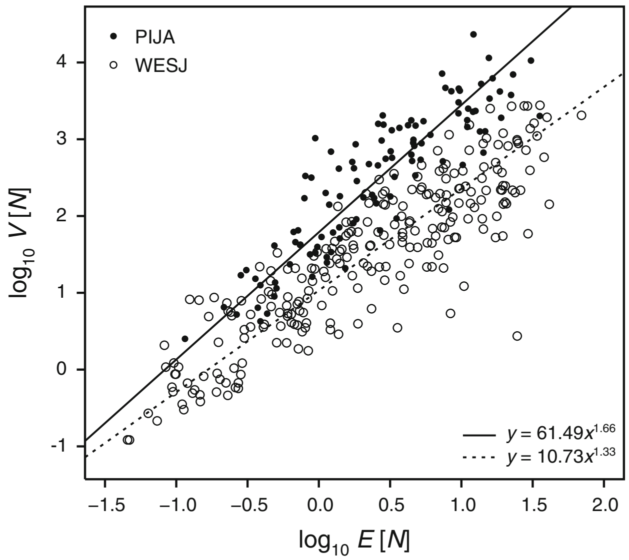

Fig. 8 Taylor's Power Law relation for Piñon jays (PIJA) and Western scrub-jays (WESJ) as estimated from our probability model

refuted by the successful mapping of other behavioral traits such as flocking, vagility and colonization onto the TPL for PIJA and WESJ (Table 1). Theoretical explanations that include predator–prey relations (Kilpatrick and Ives 2003) and reproductive variance (Ballantyne and Kerkhoff 2007) offer alternative conceptual frameworks for the TPL.

Technical aspects of power laws guided our examination of corvid abundances and variances to reveal support for the hypotheses that: (1) power laws exist for these species; (2) the slopes differ from the null expectation of $\beta = 2$; (3) a single slope is observed over the entire domain of population sizes that span three orders of magnitude (Fig. 8), rather than exhibiting a bend as expected where one source of density-dependent variation supersedes another (Ballantyne and Kerkhoff 2007; Kerkhoff and Enquist 2007; Engen et al. 2009). Empirically, the stochastic approach avoids logistical limitations that would make it extremely difficult to test parametric models over the extent of a species' range based on, for example, inter-pair correlations in fitness. Moreover, errors associated to the loss of degrees of freedom when only temporal variation across population is considered, as is presented here, limits the statistical power to differentiate the particular value of an observed exponent from that predicted by theory, in contrast to applications in physics where high precision is possible due to the elimination of extraneous factors that compromise assumptions, e.g., that governing rates are constant over the period of record or that counts are immune to sampling error. Thus, spatial considerations not accounted for in this study may certainly account for variation in TPL slope. Low spatial correlation may represent higher degree of independence yielding higher slope of the TPL. This is confirmed by Fig. 1c which clearly shows lower autocorrelation for PIJA, the species with steeper slopes in both empirical and modeled TPL. Autocorrelation of abundance may give valuable information on both spatial and temporal aspects of the species distribution by providing insights on the spatial synchrony among species, which in our case is coherent with the territorial behaviors described. PIJA shows low autocorrelation, if any, suggesting high independence between individuals resulting in higher TPL slopes. In contrast, the high autocorrelation in abundance of WESJ may only partly account for the more shallow slope of the TPL as high autocorrelation could be the outcome of either aggregate or regular occurrence across the landscape. However, while a deeper assessment of the combined study of how temporal and spatial dependence affect TPL is beyond the scope of this study, it represents an important aspect to explain species dynamics and the TPL. For example, a consequence of our simplification of the species dynamics to its temporal component may partly be responsible of the larger scatter shown by our model (cf. Figs. 3, 8).

Based on the empirical counts of individuals across the geographic range of PIJA and WESJ, we successfully predicted differences in the distributions of most of the parameters proposed to affect the slope of the TPL (Table 2). The mean number of colonists was the only parameter that did not follow prediction, most likely due to the annual time scale that could mix multiple colonization events. Likewise, the apparent number of colonists may be inflated by immigrants that arrive after the initial colonists or by subsequent recruitment. In spite of only assessing qualitative behavioral differences between species, we show that these differences may leave statistical imprints on the exponent of the TPL. In addition to the differences in social behavior, the dynamics that give PIJA and WESJ unequal TPL exponents relate to differences in the underlying demographic processes. The species share a complementary dependence between colonization and extinction that constrains mean abundance (Fig. 4) which is insufficient to explain the differences in β between species. Therefore, β can hardly be explained by the patterns obtained from raw counts alone (e.g., Fig. 4). Rather, a theoretical framework is needed to partition statistics according to dynamical processes that produce the observed counts.

Territoriality arises when animals match population density to resource availability (Fretwell and Lucas 1969), and is ultimately a form of density dependence that may account in part for differences in β among species (Hanski and Tiainen 1989). Territorial behavior occurs when limited resources are available to individuals within (or among) populations; a great variety of territorial systems have been found in nature (Brown 1964). At low population densities, we expect that all individuals will benefit from high quality resources and reproductive success should be largely density-independent. However, as mean population size increases, individuals relocate to lower quality habitats only when reproductive success in the high- and low-quality habitats become equal (Fretwell and Lucas 1969; Gillis et al. 1986; Holt and Barfield 2001). This shift in habitat occupancy occurs mostly through competitive exclusion and greatly hinders reproductive success. Therefore, and as Ballantyne and Kerkhoff (2007) show, density-dependent regulatory processes through differential reproduction are expected to play major roles once the population reaches carrying capacity. However, abundance of highly mobile populations, and those of ephemeral environments, remain below carrying capacity largely due to fluctuations in vital rates. Therefore, territoriality is clearly only one of several factors that generate differences in β, and may consequently fail to address other processes that generate the power law. In fact, PIJA and WESJ not only differ in how they use space, these species have radically different strategies to maximize reproductive success in limited resource environments. For example, in contrast to WESJ, PIJA is a cooperative breeder that benefits from helpers after the egg has hatched (Marzluff and Balda 1992).

Several factors contribute to the mean and variance of population size. For example, immigration into extant populations with positive abundance increases population variance (Fig. 2), and recurrent immigration may rescue the population from extinction (sensu Brown and Kodric-Brown 1977; Holt 1983) at sub-annual time scales. These implicit factors could influence the colonization/extinction dynamic, and thereby introduce variability in the exponent and normalization constant of our TPL estimation. In particular, we expect flocking differences between PIJA and WESJ to alter the estimation of γ because, contrary to WESJ colonization, PIJA colonization of vacant sites is most probably done by large flocks (Marzluff and Balda 1992). This could introduce variability not only in $\hat{N}_c$ but also in the estimation of the probability of zero-abundance, $P(N = 0)$, as our simple MC model is not able to emulate such behavioral differences. However, we retain the fact that the direction of the differences of the TPL relationship is correctly predicted by our model.

Explicit tracking of individual dispersal would verify the role of immigrants. However, such an exercise is beyond the scope and objectives of the model. Rather, the model identifies processes originating the TPL from the standpoint of colonization and extinction dynamics. As such, the model identifies a set of parameters that define the mean and variance of populations, thereby providing guidelines to interpret the difference in the TPL exponent between species. The explanation for the TPL exponent is found in the differences between underlying probability density functions that reflect behavioral differences between species. The distribution of colonization and extinction probabilities, the probability of non-zero abundance and the mean number of colonists are of particular importance in the creation of the TPL pattern. Thus, if similar processes govern the population dynamics in both species, we would expect the distribution of such factors to be equal in both species. This hypothesis is clearly rejected (Table 2; Fig. 7).

Conclusions

PIJA and WESJ exhibit a constant mean–variance scaling relation throughout their full range of population sizes. However, different scaling exponents define the relation for each species which we attribute, albeit non exclusively, to behavioral differences between species. We develop a probabilistic model that successfully recovers the TPL relation for each species from the empirical estimation of abundances.

However, the non-invertible mapping of counts onto population parameters attests that any given factor may hardly be taken as the unique explanation for the TPL. Having said that, our model provides important guidelines to interpret empirical differences in the TPL exponent between species. Moreover, the model provides a non-parametric approximation that successfully recreates the first two moments of population abundance.

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