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CONSERVATION ECOLOGY – ORIGINAL RESEARCH

# Decline in territory size and fecundity as a response to carrying capacity in an endangered songbird

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**Abstract** Density-dependent processes are fundamental mechanisms for the regulation of populations. Ecological theories differ in their predictions on whether increasing population density leads to individual adjustments of survival and reproductive output or to dominance and monopolization of resources. Here, we use a natural experiment to examine which factors limit population growth in the only remaining population of the endangered pale-headed brush finch (*Atlapetes pallidiceps*). For three distinct phases (a phase of population suppression, 2001–2002; expansion due to conservation management, 2003–2008; and equilibrium phase, 2009–2014), we estimated demographic parameters with an integrated population model using population size, the proportion of successfully breeding pairs and their productivity, territory size, and mark-recapture data of adult birds. A low proportion of successful breeders due to brood parasitism (0.42, 95% credible interval 0.26–0.59) limited population growth before 2003; subsequent culling of the brood parasite resulted in a two-fold increase of the proportion of successful breeders during the 'expansion phase'. When the population approached the carrying capacity of its habitat, territory size declined by more than 50% and fecundity declined from 1.9 (1.54–2.27) to 1.3 (1.12–1.53) chicks per breeding pair, but the proportion of successful breeders remained constant (expansion phase: 0.85; 0.76–0.93; equilibrium phase: 0.86; 0.79–0.92). This study demonstrates that limiting resources can lead to individual adjustments instead of despotic behavior, and the individual reduction of reproductive output at high population densities is consistent with the slow life-history of many tropical species.

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## Introduction

An important goal in ecology is to increase our understanding of the various factors that regulate natural populations (Fretwell and Lucas 1970; Ashmole 1963). Population changes depend mainly on four central demographic parameters: Fecundity, mortality, immigration, and emigration (Sibly and Hone 2002), which together determine whether a population is stable or not. Whether resources (bottom-up forces) or predators and parasites (top-down forces) play a stronger role in population regulation has been an important research topic in ecology (Hunter and Price 1992; Walker and Jones 2001). Fecundity and mortality are frequently influenced by a variety of extrinsic and intrinsic factors (Coughenour and Singer 1996). As

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finite resources impose limits on the size of plant and animal populations, many populations are ultimately regulated by the carrying capacity of the environment which they inhabit (Hanski et al. 1993; Turchin 2001). Whereas extrinsic factors, such as weather (White 2001), predators (Choquenot 2006; Krebs 2009), or parasites (Woodworth 1999), act independent of population density, intrinsic population regulation typically involves a negative feedback between population size and population growth rate as a consequence of decreasing per capita resource availability (Carrete et al. 2006; Ferrer et al. 2004; Nicoll et al. 2003).

Two important concepts in ecology differ in the question whether population regulation is affecting all individuals within a population similarly. The 'ideal free distribution' and 'individual adjustment hypothesis' posit that increasing population size decreases available resources for all individuals, resulting in lower per capita productivity, but constant proportion of breeders (Ashmole 1963; Ferrer and Donazar 1996; Fretwell and Lucas 1970). Alternatively, the 'ideal despotic hypothesis' predicts superior individuals to monopolize resources and to maintain the same per capita productivity as at low population sizes (Fretwell and Lucas 1970), whereas an increasing proportion of individuals is excluded from critical resources and either cannot breed or survive, a pattern which is common among territorial bird species (Andren 1990; Janiszewski et al. 2013; Sergio et al. 2007).

While resource availability and territoriality mediate regulation at the population level, individuals within populations will strive to maximize their lifetime reproductive success given the resources available to them. This frequently leads to trade-offs between current reproduction, time of breeding, and survival (Charnov and Schaffer 1973; Stearns 1976). Due to a lower amplitude of seasonal resource pulses, many tropical bird species follow a 'slow pace of life' (Hau et al. 2010; Williams et al. 2010) which manifests itself in smaller clutch sizes (Cardillo 2002; Jetz et al. 2008; Martin et al. 2006) and higher survival probabilities than in temperate congeners (Allcorn et al. 2012; McGregor et al. 2007; Peach et al. 2001). Experimental evidence from tropical passerines suggests that a limitation of natural resources does not affect survival but decreases fecundity (Brouwer et al. 2009; Ghalambor and Martin 2001), for example through the colonization of a larger amount of suboptimal habitat with increasing population size (Armstrong et al. 2005). However, whether this decrease in fecundity at the population level is a consequence of lower clutch size or breeding success for every individual in the population (hereafter referred to as 'individual adjustments'), or despotic behavior that displaces and prevents inferior individuals from reproducing is still poorly understood for tropical species.

Here, we took advantage of a recovery program as a natural experiment to test which reproductive parameter responded to changes in population density in a tropical bird population that has recently reached carrying capacity. Successful species recovery programs, where the external forces suppressing a population are actively manipulated, can serve as excellent case studies to examine aspects of population regulation, as management activities that have an important influence on the life-history parameters of a species are clearly identified (Nicoll et al. 2006). The globally threatened pale-headed brush finch (*Atlapetes pallidiceps*), a territorial passerine, is a suitable species to investigate the mechanisms of population regulation, because the entire global population is restricted to a small reserve and represents a closed, simplified study system where the effects of immigration and emigration are negligible. Recent management activities controlling a brood parasite (the shiny cowbird *Molothrus bonariensis*) and habitat maintenance have led to a fivefold population increase over the past 15 years (Krabbe et al. 2011). We examined how territory sizes, the proportion of successful breeders, and the number of raised offspring for successful pairs varied over three distinct phases of population development: an initial phase prior to management intervention when the population was suppressed by shiny cowbirds (Oppel et al. 2004a); a rapid expansion phase following the implementation of conservation management; and, most recently, a stagnating phase indicating that the carrying capacity of the environment was reached and the population approached equilibrium. Based on the mechanisms of population regulation in other territorial bird species (Andren 1990; Janiszewski et al. 2013; Sergio et al. 2007), we expected patterns consistent with despotic behavior. We hypothesized that with increasing population size, territory sizes would remain stable, and the proportion of successful breeders would decrease, as more birds would be excluded from good breeding habitat by dominant individuals.

## Materials and methods

### Study species and study site

The pale-headed brush finch is an omnivorous territorial songbird endemic to dry valleys along the central Andes in Ecuador, and a small reserve was established in Yunguilla (3°13′59.33″S, 79°16′52.97″W) in 2001 to protect the last population of that species. The reserve covers 160 ha of heterogeneous semi-open scrubland, the preferred habitat of the species (Oppel et al. 2004b). The region has a pronounced wet season from January through May, and the pale-headed brush finch exhibits seasonal breeding behavior during which territorial pairs can nest repeatedly after

failure, but generally only raise one successful clutch of up to three offspring per season (Oppel et al. 2003). Until 2003, brood parasitism by the shiny cowbird, which has colonized the valley following habitat modification by humans, was likely the most imminent threat to the population, because the majority of pairs raised shiny cowbirds rather than pale-headed brush finch offspring (Oppel et al. 2004a). If a shiny cowbird chick was successfully raised, no further breeding was attempted.

Conservation management started in 2003 and consisted of two aspects: First, a yearly cowbird control program during the breeding season of the pale-headed brush finch, where shiny cowbirds entering the reserve from adjacent agricultural fields were shot while perching on large exotic trees that formed a natural gateway for cowbirds to enter the reserve. Second, habitat management by removing bushes and trees higher than 2 m was implemented within the reserve to preserve the semi-open bushlands preferred by the species. Following this conservation management, the population increased fivefold until 2008 (Krabbe et al. 2011).

Since 2008, the population has increased only marginally and appears to have reached the carrying capacity of the small reserve which is surrounded by largely unsuitable agricultural habitat (according to habitat preferences described in Oppel et al. 2004c). We refer to the distinct phases in the population trajectory of the pale-headed brush finch as the suppression phase (2001–2002), the expansion phase (2003–2008), and the equilibrium phase (2009–2014).

### Field data collection for demographic parameters

Population size was monitored yearly since 2001 by an intensive territory mapping approach, during which all male individuals were counted based on their characteristic songs. The number of singing males was then doubled for the population size estimation, based on an approximately 50% sex ratio in the species (Krabbe 2004). Since 2002, detailed monitoring throughout the breeding season resulted in information on territory size, breeding success, and the number of fledglings produced by each pair (for details see Oppel et al. 2003, 2004a). Reproductive success was monitored for 26 pairs in 2002 (suppression phase), a total of 46 pairs in 2003–2006 (expansion phase), and a total of 120 pairs in 2013–2014 (equilibrium phase); the increase in sample size was a direct consequence of the increasing population.

To estimate adult survival probabilities, we individually color-ringed a third of the global population during the equilibrium phase ($n = 36$ individuals in 2012 and $n = 37$ in 2013). We captured birds by mist-netting before or after breeding (between January and June, depending

on the exact breeding phase of the respective pair) to keep possible disturbance at a minimum. In 2013 and 2014, we searched for ringed individuals among all breeding pairs during the phase of territory establishment to ensure that individuals were detected even outside of the territories in which they were ringed. We considered individuals which could not be detected in a given year as 'missing', because successful emigration from the study area is extremely unlikely for this species. No second population is known, and searches for pale-headed brush finches in other potentially suitable habitat patches outside the reserve (up to 20 km away) remained unsuccessful.

### Measurement of territory size

Pale-headed brush finches use prominent song perches from which they demarcate breeding territories, and we mapped territorial boundaries by intensively following individual birds (Oppel et al. 2004c). Well-known territory boundaries located in the same part of the reserve ($n = 16$ in 2003 and $n = 54$ territories in 2014) were digitized in Google Earth™ by following conspicuous landmarks, such as bushes and emergent trees. Territory polygons were exported into ArcGIS and converted to a projected coordinate system (UTM, Zone 17S) to facilitate consistent measurements of territory size.

### Assessment of temporal changes in demographic parameters

Our goal was to assess how population regulation was mediated during the distinct phases of population recovery: specifically, how different reproductive parameters changed once limiting factors were removed or emerged. This required us to estimate all demographic parameters of interest for each phase of the population trajectory. Because intrusive monitoring approaches, such as capture and individual marking, were avoided, while the population was at precariously low levels (i.e., below 70 individuals during the suppression phase), there were insufficient data to estimate all demographic parameters for each time period directly from field data. We, therefore, took advantage of recent advances in population modelling to estimate demographic parameters for which limited or no field data existed (Freeman and Besbeas 2012; Kéry and Schaub 2012; Schaub and Abadi 2011; Schaub et al. 2007).

We estimated demographic parameters of the pale-headed brush finch using an integrated population model, which has recently become an important tool to integrate population count data into a demographic model (Abadi et al. 2010; Besbeas et al. 2004; Oppel et al. 2014). We parameterized the model with a temporal structure, so that reproductive success and proportion of successful breeders
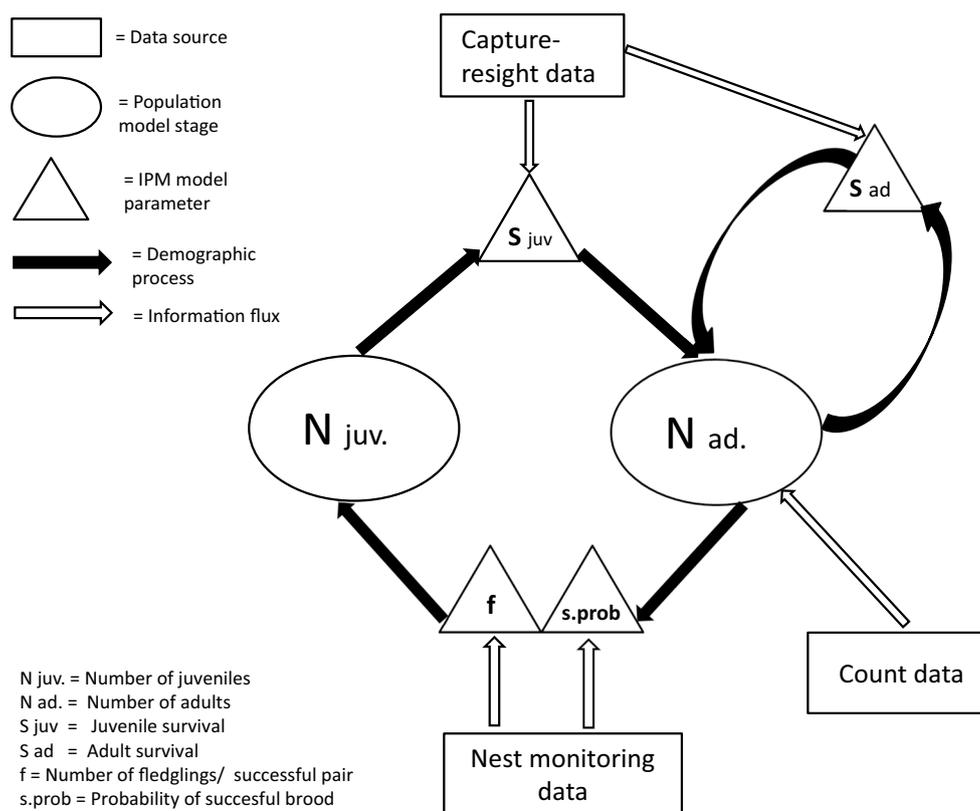
**Fig. 1** Schematic outline of the data sources and demographic parameters incorporated into the integrated population model (IPM) used to estimate the population trajectory of the Pale-headed brush finch

varied between the suppression phase, the expansion phase, and the equilibrium phase. The integrated population model was constructed with two age classes, juveniles, and adults, and assumed that the sex ratio at hatching was 0.5, and that all females started breeding at the age of 1 year. We decomposed population dynamics into a state process that was described by adult and juvenile survival probability, and annual fecundity, which was, in turn, decomposed into a process determining breeding success and the quantity of offspring produced if breeding was successful. The state process was based on the survey data and accounted for potential observation error during the monitoring (Fig. 1). We used a hierarchical state-space model to decompose the observed time series of pale-headed brush finch counts into a population process and an observation error component (Clark and Bjørnstad 2004; De Valpine 2003; Kéry and Schaub 2012). To estimate adult survival probabilities from individual capture–recapture data, we used Cormack–Jolly–Seber open population live recapture models (Cormack 1964; Jolly 1965; Seber 1965). Per capita productivity of successful pairs was defined as the number of fledglings per successfully breeding female in each year, and was assumed to follow a Poisson distribution constrained by the number of successful breeders in each

year. The number of successful breeders was derived from a binomial distribution based on the number of observed pairs and the number of pairs that raised offspring in a given year.

We used a Leslie matrix (Vaughan and Saila 1976) to describe the transition probabilities of juveniles and adults from 1 year to the next, and estimated those transition probabilities with the parameters for survival, breeding success probability, and productivity of successful breeders (Fig. 1). We assumed that annual survival during the first year of life (juvenile survival) was different from annual survival for birds that were older than 1 year (adult survival), but that both survival probabilities would not be affected by changes in population density and thus remained constant over time (Brouwer et al. 2009). In preliminary models, we included temporal variation in survival probabilities, but because these models yielded extremely imprecise estimates due to the lack of survival data prior to 2012, we did not incorporate temporal variation in survival probability in the model presented here. Although temporal variation in survival is possible, our model is still a valid evaluation of whether temporal variation in reproductive parameters can explain the observed population trend.

We fitted the integrated population model using a Bayesian approach to combine the joint likelihood with prior probability distributions of the parameters to draw inferences about all demographic parameters (Kéry and Schaub 2012; Schaub et al. 2010, 2007). We used informative priors for adult and juvenile survival probabilities, because few empirical field data were available for these parameters. We expected annual adult survival probability to vary between 0.32 and 0.95. This range covered the 95% confidence interval of an intensive mark-recapture study of a congeneric species (Ruiz-Gutierrez et al. 2012). For juvenile survival, we assumed a range between 0.05 and 0.85 given that pale-headed brush finches have a long post-fledging parental care interval (Oppel et al. 2003) which results in high juvenile survival in other tropical songbird species (Ricklefs et al. 2011; Tarwater and Brawn 2010; Tarwater et al. 2011). Priors for breeding success, probability (uniform prior 0–1) and the number of fledglings per successful pair (normal prior with mean 0) were uninformative. We ran three Markov chains with 150,000 iterations each and discarded the first 50,000 iterations. From the remaining iterations, we only used every second iteration for inference, and we tested for convergence using the Gelman–Rubin diagnostic (Brooks and Gelman 1998); all estimated parameters had values of R-hat <1.002. To calculate the posterior distributions of the parameters of interest, we used Markov chain Monte Carlo methods in JAGS 3.3 (Plummer 2012) via the R2jags library (Su and Yajima 2012) in R 3.0.1 (R Core Team 2013).

We report the proportion of successful breeders, average number of fledged chicks, and adult and juvenile survival probabilities estimated from the integrated population model together with 95% credible intervals. To assess differences in demographic parameters between time periods, we calculated the proportion of all simulations where the estimate from one time period was greater or smaller than the estimate from another time period, resulting in a Bayesian equivalent of a *p* value, and we considered these differences significant if the proportion exceeded 97.5%. Territory size was not a part of the integrated population model and was only measured during the suppression and equilibrium phases. We tested whether territory sizes differed between these two phases with a Wilcoxon rank-sum test in R 3.0.1 (R Core Team 2013).

## Results

### Field data and population trajectory

The pale-headed brush finch population increased from an estimated 68 to 220 individuals between 2001 and 2014 (Fig. 2). Of all 26 observed breeding events in 2002
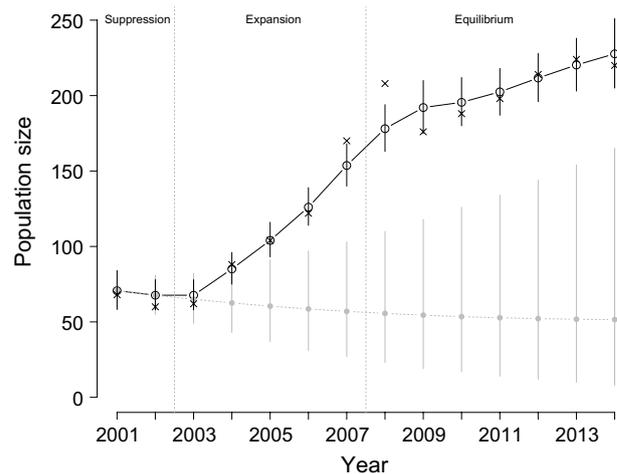


**Fig. 2** Population trajectory of the global population of the pale-headed brush finch confined to a small reserve in the Ecuadorian Andes. Population size derived from territory mapping (*crosses*) facilitated the development of an integrated population model (estimates presented as *white circles* with 95% credible intervals) to estimate demographic parameters during the phase of population suppression, expansion, and approaching equilibrium. *Grey circles* represent hypothetical population size estimates if no conservation management had been implemented from 2003 onwards (assuming a constant 61% parasitism rate and fecundity as found in 2002/2003). *Vertical dashed lines* demarcate the three distinct phases of the study period

(suppression phase), 10 pairs bred successfully (38%) and a total of 17 fledglings were produced. Of all 46 breeding pairs monitored between 2003 and 2006 (expansion phase), 39 pairs (85%) were successful and produced a total of 67 fledglings. Two pairs (4.4%) raised three chicks, 24 pairs (52.2%) raised two chicks, and 13 pairs (28.2%) raised one chick. Of all 120 breeding pairs monitored in 2013–2014 (equilibrium phase), 105 (87.5%) were successful; 42 pairs (35%) raised two chicks, 63 pairs (52.5%) raised one chick, but no pair raised more than two chicks, and no breeding failure in 2013 and 2014 was caused by cowbird parasitism. Of all 37 birds ringed in 2012, 21 (57%) were resighted in both 2013 and 2014, 7 (19%) were resighted in only 1 year, and 9 (24%) were not seen. Of all 36 birds ringed in 2013, 22 (61%) were resighted in 2014.

### Temporal changes in demographic parameters

The integrated population model successfully replicated the population trajectory of the pale-headed brush finch (Fig. 2), and indicated that two component parameters of seasonal fecundity had changed substantially over time. During the suppression phase, the population was regulated by reproductive failure owing to brood parasitism resulting in a very low probability of successful breeding (0.42; 95% CRI 0.26–0.59), which would have eventually
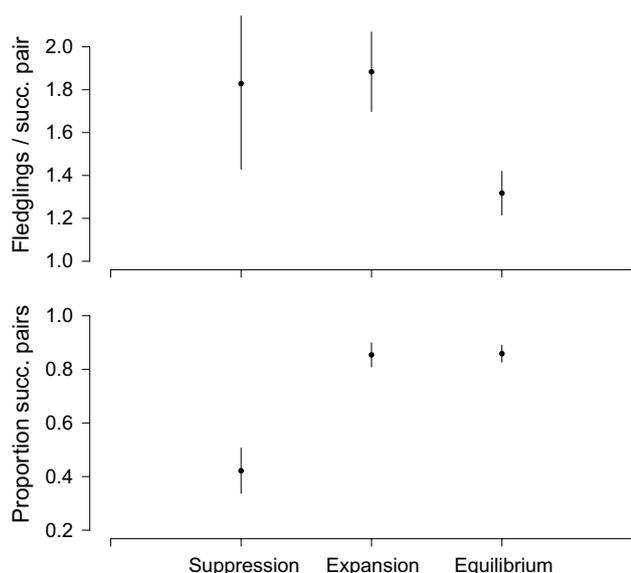
**Fig. 3** Demographic parameters (mean ± SD) of the global population of the pale-headed brush finch in central Ecuador derived from an integrated population model during three distinct phases of population recovery between 2001 and 2014: suppression (2001–2002), expansion (2003–2008), equilibrium (2009–2014)
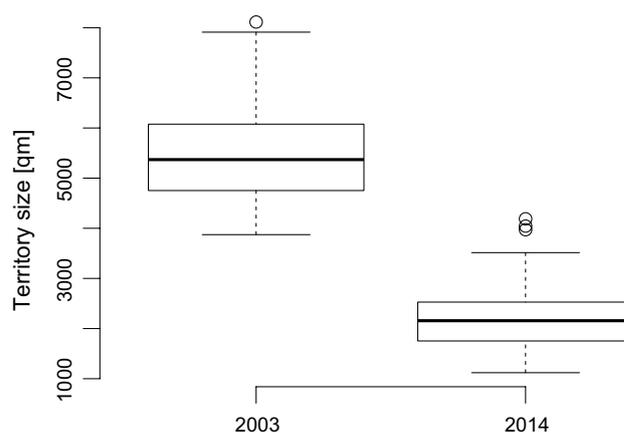


**Fig. 4** Territory size of the pale-headed brush finch in central Ecuador has decreased by more than half between 2003 (suppression phase, $n = 16$ territories) and 2014 (equilibrium phase, $n = 54$ territories)

led to extinction (Fig. 2). After cowbird control, probability of successful breeding doubled during the expansion phase (0.85; 0.75–0.93, Fig. 3) and remained equally high during the equilibrium phase (0.86; 0.79–0.92). Conversely, the number of fledglings produced by successfully breeding pairs was similar during the suppression (1.83; 1.12–2.68) and expansion phase (1.89; 1.54–2.27), but lower during the equilibrium phase (1.32; 1.12–1.52) in 99.97% of 150,000 simulations (Fig. 3). Adult survival probability was estimated at 0.77 (0.67–0.87) and juvenile survival probability was estimated at 0.49 (0.32–0.69), and these estimates were not constrained by the chosen priors for survival parameters (Appendix S1). The overall mean population growth rate $\lambda$ was 1.095 (1.077–1.113) over the entire study period, but varied substantially between years from a minimum of 0.962 (0.825–1.117) in 2001 to 1.261 (1.108–1.435) in 2003 immediately after the adoption of conservation measures. The mean population growth rates for the suppression, expansion, and equilibrium phases were 0.981 (0.877–1.095), 1.191 (1.155–1.228), and 1.035 (1.006–1.065), respectively.

Territory sizes during the equilibrium phase in 2014 (0.22 ha ± 0.07, $n = 54$) were less than half the size of territories during the suppression phase when the population was at very low density (0.56 ha ± 0.13, $n = 54$; $W = 859$; $p < 0.01$, Fig. 4).

## Discussion

Our data provide evidence for decreased territory size and fewer fledglings per successful breeding attempt as mechanisms of population regulation in a territorial bird species. While the population was limited by the proportion of pairs that managed to breed successfully during the suppression phase, the application of conservation management has resulted in a much higher probability of successful breeding since 2003. Both during the expansion phase and also while the population approached equilibrium, more than 80% of pairs bred successfully, indicating that population regulation is not achieved by superior individuals monopolizing available resources to the detriment of others. Thus, the 'ideal despotic hypothesis' is not supported in the pale-headed brush finch, which is in contrast to our expectations. Instead, we found that territories became much smaller, which typically results in food limitation and possibly decreased fertility (Brouwer et al. 2009; Dobson and Oli 2001; Sibly et al. 2005). This pattern was supported in our study species, where each successful pair raised fewer fledglings during the equilibrium phase than during the suppression or expansion phase.

As most studies concerning life-history variation have been conducted in temperate zones (Arnold 2011; Banbura et al. 2008; Hainstock et al. 2010; Wilson et al. 2016), the value of studies of tropical species such as ours is high (Bulit et al. 2014). Our estimates of adult and juvenile survival are consistent with the previous estimates of related species (Ruiz-Gutierrez et al. 2012), and further strengthen the evidence that tropical species have relatively high adult

survival probabilities (Allcorn et al. 2012; McGregor et al. 2007; Peach et al. 2001). Although we were not able to examine temporal variation in survival probabilities, other studies of tropical birds have also found that changes in population density were primarily regulated by a reduction of breeding investment and not by a reduction in life span (Ghalambor and Martin 2001; Brouwer et al. 2009). Our study is, therefore, fully consistent with the 'slow pace' characteristics of a tropical bird species predicted by the 'Pace of Life' hypothesis (Ricklefs and Wikelski 2002), even though the mechanism of reducing productivity via individual adjustments rather than despotic behavior is unexpected.

Individual adjustments are an unusual finding in territorial songbirds which have been described only once before (Hache et al. 2013), but alluded to in another tropical passerine (Brouwer et al. 2009). We found that adjustments concerned all breeding individuals in the study area, including those from high-quality habitats (Hartmann et al. 2015). We can thus exclude the possibility that individual despots were able to maintain high productivity and that only inferior individuals had to adjust territory size and ultimately productivity. We propose that an explanation for this pattern in the pale-headed brush finch could be the restriction to a small reserve within a matrix of unsuitable land, where an expansion of the increasing population to the surroundings of the reserve was equally impossible as for populations of birds restricted to small oceanic islands (Brouwer et al. 2009). Territory defense thus probably became energetically more costly with increasing population size and a higher number of neighboring territory holders, which can impose individual survival costs (see Drent and Daan 1980). The time and energy spent in territory defense can also be lacking for parental care (Duckworth 2006; Ros et al. 2004), which could increase the risk of nest failure through predation or parasitism in case of the pale-headed brush finch. Individual birds might, therefore, benefit from decreased territory and brood size, decreased defense costs, and better survival prospects, which again supports the 'slow pace of life' in this species.

A possible confounding factor for our study was natural succession of the vegetation towards more densely vegetated scrubland in approx. 50% of the area after the conversion of former agricultural land into a reserve, which coincided with the increase in population size (Hartmann et al. 2015). Although the species management program maintained high-quality habitat by active intervention and vegetation removal since 2003, the benefit of vegetation removal appeared to increase over time, indicating that habitat quality in unmanaged territories might have decreased (Hartmann et al. 2015). Although some of the reduction in productivity may have been due to slightly deteriorating vegetation structure, the persistent high breeding success across all individuals is more consistent with individual adjustments than with despotic behavior by dominant individuals.

The finding of individual adjustments in an endangered species has important implications for its conservation. The shrinkage of territories facilitated the increase of the population to an unexpected size: the small reserve now holds a population almost 2.5 times larger than originally predicted (Oppel et al. 2004c). Individual adjustments could furthermore have contributed to the preservation of genetic diversity despite the past bottleneck: If all animals rather than a few despotic individuals reproduce and thus pass on their genes, a larger overall genetic diversity can be preserved in the population because of an increased effective population size (Greenwald 2010; Wang et al. 2014). The unusual lack of despotic behavior could thus explain the surprisingly high microsatellite diversity found in the pale-headed brush finch (Hartmann et al. 2014). In addition, the finding of individual adjustments together with a lack of cowbird parasitism in the latter years demonstrates that the limitation to population growth is no longer a top-down suppression via brood parasitism, but a bottom-up limitation via the carrying capacity of the reserve. In contrast to other endangered species with cowbird parasitism, e.g., the black-capped vireo (*Vireo atricapilla*) (Wilsey et al. 2014), the pale-headed brush finch is, therefore, no longer dependent on permanent cowbird control. Future conservation activities should now focus on providing more habitat rather than cowbird control to allow a future population increase.

In summary, we provide insights how the demographic parameters of a remnant population suppressed by an external (top-down) factor have changed due to management activities to become a bottom-up regulated population with insufficient resources for further expansion. We furthermore show that individual adjustments instead of despotic behavior appear to regulate the population in this territorial bird species, and our finding of decreased fecundity and high survival in a tropical species is in concordance with the 'Pace of Life' hypothesis (Ricklefs and Wikelski 2002). Population dynamics in our study system depend strongly on how density-dependent population growth translates into individual life-history parameters, and that the respective life-history strategy is contingent upon the environment a species inhabits. The understanding of population regulatory processes has become increasingly important during the biodiversity extinction crisis (Hixon et al. 2002). Our study adds to other positive examples showing that integrated population models are a valuable tool that can help evaluate past management strategies and thus inform future management decisions (Oppel et al. 2014; Schaub et al. 2010; Wilson et al. 2016). Our results thus contribute to a better ecological understanding and more effective management of this globally threatened species as well as

to deeper ecological insights into population regulatory patterns, in general.

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