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ORIGINAL PAPER

# Spatial and temporal dynamics at manakin leks: reconciling lek traditionality with male turnover

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**Abstract** Leks, display grounds where males congregate and females visit to copulate, are typically traditional in location, despite often high turnover of individual males. How leks can persist in face of male turnover is not well understood, in part due to a lack of detailed field data allowing for a clear understanding of lek dynamics. We followed the fate of individual males at 11 to 15 leks of the blue-crowned manakin *Lepidothrix coronata* across four breeding seasons to gain insights on how leks are formed and changed in space and time. Between years, leks were traditional in location despite changes in territory ownership due to male disappearance and recruitment. New males were equally likely to recruit by taking over existing territories or by establishing new territories. Recruitment was influenced by age, as recruits were more likely to be adults than subadults. Lek size did not affect the probabilities of a male recruiting or persisting at a territory, and vocalization rate, a correlate of mating success in this population, did not affect male persistence. We used our field data to model changes in lek size and composition over longer periods of time (100 years) to understand how lek traditionality can be reconciled with high male turnover. Our simulations showed that leks in our population rapidly stabilize in size despite changes in territory ownership and that rates of male recruitment and disappearance compensate each other, such that leks have the potential to persist for several decades after the original males have disappeared from them.

**Keywords** Ecuador · Lek dynamics · *Lepidothrix coronata* · Male turnover · Pipridae · Population dynamics · Territoriality

## Introduction

Lekking is a type of promiscuous mating system in which males aggregate at display grounds, the “leks,” to attract females for copulation (Bradbury and Gibson 1983; Wiley 1991). Leks of birds and mammals typically are traditional in location over time, as males congregate at the same sites in successive years and recruiting males tend to join existing leks rather than establish new, isolated territories (Lill 1976; Hovi et al. 1996; Wiley 1991). Yet, turnover of individual males via disappearance and recruitment at leks can be high (Höglund and Robertson 1990a; Gibson 1992; Westcott and Smith 1994). Leks can thus be viewed as dynamic mating foci where individual males are replaced over time.

Mechanisms maintaining lek traditionality in the face of high male turnover are not fully understood. Site traditionality suggests that there are spatial limitations for the establishment of leks, that males benefit by settling in pre-established leks, or both. In relation to the first alternative, there is evidence that creation of new leks may be limited to some extent by availability of suitable habitat, constraints on optimal spacing among males, or niche partitioning between the sexes or with other lekking species (Wegge and Rolstad 1986; Bradbury et al. 1989b; Gosling and Petrie

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1990; Westcott 1993; Durães et al. 2007; Loiselle et al. 2007). In relation to the second alternative, two main hypotheses address how males that occupy traditional lek sites would have increased fitness. First, if the species is long-lived and females tend to return to familiar sites to mate, new male recruits that occupy territories vacated by successful males or that join leks that receive a large number of female visits would "inherit" the mating history of these sites, a phenomenon known as "temporal spillover effect" (Apollonio et al. 1989; Gosling and Petrie 1990; Gibson et al. 1991; Gibson 1992; Jiguet and Bretagnolle 2006). Alternatively, traditionality could be maintained if successful males tend to hold the same territories across years, but there is turnover of lower-rank males that cluster around these "hotshot" males in an attempt to intercept copulations (the "hotshot" or "spatial spillover effect," Höglund and Robertson 1990b; Rintamäki et al. 1995; Lanctot et al. 1998).

All these are mechanisms by which lek site traditionality could be sustained with high turnover of individual males, at least up to some threshold level. Several factors may influence rates of male turnover at leks. The first and most obvious of these are the intrinsic rates of recruitment and mortality in the population (e.g., Bradbury et al. 1989a; Alatalo et al. 1992). However, male behavioral strategies may also play a role in modulating turnover at leks. For example, males may recruit into some leks at a higher rate due to female preferences for leks in a given size range (Lank and Smith 1992; Höglund et al. 1993; Hovi et al. 1996; Jiguet and Bretagnolle 2006, but see Lanctot et al. 1998). Individual competitive abilities of males may also affect turnover rates at leks because the optimal lek size and tenure time may differ in relation to relative competitive ability, affecting the probability that a given individual would recruit into or remain at a given lek (Alatalo et al. 1992; Widemo and Owens 1995; Westcott and Smith 1997; Hernandez et al. 1999; Apollonio et al. 2003). Finally, previous individual mating history may affect turnover at leks when successful males tend to return to the same territories between breeding seasons, and unsuccessful males are more likely to change territories (Höglund and Robertson 1990a; Gibson 1992; Westcott and Smith 1994; Rintamäki et al. 1995; Apollonio et al. 2003).

Although hypotheses have been proposed to reconcile individual turnover at leks with their long-term spatial stability, we currently lack a clear understanding of what drives this pattern. In part, this is due to a paucity of data from natural populations on rates of male turnover and lek stability: most reports are anecdotal and there have been few attempts to quantify turnover across years. Here, we provide such information based on observations at leks of the blue-crowned manakin *Lepidothrix coronata* in eastern Ecuador. Manakins (Pipridae) are lek-breeding, neotropical birds generally characterized by marked sexual dimorphism and elaborate male courtship displays (Sick 1967; Prum 1990; Snow 2004). Leks of manakins are typically traditional in location, and there are anecdotal reports of leks persisting on the same sites for several years and even decades (Sick 1967; Lill 1976; McDonald 1989; Tello 2001). In these long-lived species (at least 10–14 years, Snow and Lill 1974; McDonald 1993), spatial traditionality would suggest that individual males keep the same territories for several years, but too few studies have followed marked individuals across time to corroborate this. In this study, we first estimated rates of male recruitment and disappearance from leks by following the fate of banded territorial males over the course of four breeding seasons. Second, we tested for the influence of lek size, male age (a typical correlate of individual competitive ability), and vocalization rate (a correlate of mating success in the blue-crowned manakin, Durães 2008) on these rates. Third, we used the estimated rates of male recruitment and persistence at territories to model changes in lek size and composition over longer periods of time, in an attempt to understand how traditionality in lek location can be reconciled with high male turnover rates.

## Materials and methods

### Study species

The blue-crowned manakin is widespread in humid and unflooded forests below 1,000 m in northwestern Amazonia, the Chocó region west of the Andes, and southern Central America (Ridgely and Tudor 1994; Snow 2004). As in most manakins, males exhibit delayed plumage maturation; females and juveniles (<1 year old) are bright green; younger males ("subadults") have a predefinitive plumage with varying degrees of black and blue feathers mingled with green, and males >2 years of age ("adults") are sooty black with bright blue crowns (Ryder and Durães 2005). Adult and subadult males, but not green-plumaged juveniles, establish territories at leks or display solitarily (R. Durães, manuscript in preparation; for the sake of simplicity, the term "lek" will be used in this paper to describe both group and individual display sites). Leks are "dispersed" (sensu Prum 1994), being formed by individual, contiguous male territories, each ~1,000 $m^2$ in size (Durães et al. 2007). During the breeding season, territories are actively defended against other adult and subadult males, although juvenile males are usually tolerated and may form temporary coalitions with territorial males (R. Durães, unpublished data). Females make short visits to leks, usually alone, to observe male displays and to mate. As in all lekking species, nest building and parental care is completely maternal.

## Study site and mapping of male territories

Research was conducted at Tiputini Biodiversity Station (TBS), Orellana Province, Ecuador (00° 38′ S, 76° 08′ W, 190–270 m a.s.l.). TBS covers 650 ha of virtually undisturbed lowland, wet evergreen forests comprised primarily of unflooded *terra firme* and flooded *várzea* habitats (more details in Loiselle et al. 2007). Over the course of four breeding seasons (from December of the previous year to April 2004, 2005, 2006, and 2007), we systematically searched for and mapped leks within and immediately surrounding a 100-ha permanent study plot (Harpia plot). Harpia ranges in elevation from 201 to 233 m a.s.l., contains a grid at 100×200-m intervals, and is primarily characterized by upland forest (Loiselle et al. 2007). Each year, we attempted to capture all territorial males and to mark them with unique numbered aluminum bands and color band combinations. Individual territories were delimited by mapping song perches used by the resident male during repeated visits (≥3 visits per year). Territories were considered to belong to the same lek when males were within auditory contact and/or if interactions among neighboring males were observed. Territory ownership was confirmed each year and several times over the course of each breeding season by resighting of color bands; territory ownership was never observed to change within a breeding season. The same procedures were used to map all leks in a second 100-ha plot (Puma plot, 209–235 m a.s.l.) located ~1.5 km from Harpia. Puma leks were not included in the estimation of territory transitions (see below), and data from this plot are presented here mostly as a comparison with the size distribution of Harpia leks.

To test whether the distribution of lek sizes departs from random (e.g., if there is an excess of smaller or larger leks), we did simulations in which we reshuffled males holding territories on a plot in a given year at random among the existing leks, with the constraint that each lek should receive at least one male. We repeated this procedure 100 times and computed the average number of leks that should fall in each size class as expected by chance. We then compared the expected and observed distribution of leks per size class with two-sample Kolmogorov–Smirnov tests.

## Ownership transitions at territories

We established the transition in ownership status for each male territory in Harpia, from one breeding season to the next, for the three interannual periods studied (i.e., 2004–2005, 2005–2006, 2006–2007; in 2007, although we could establish the number of males at all leks, we were unable to determine confidently the identity of four territorial males and therefore we excluded these individuals when estimating rates of persistence or turnover at territories). For each territory, one of four transition classes were noted: (1) *maintained*, held the territory in a year ($t_x$) and also in the following year ($t_{x+1}$); if the initial male was not present at that territory in year $t_{x+1}$, the territory could either be (2) *vacated*, if it was unoccupied, or (3) *taken over*, if a different male occupied that territory in the second year (takeovers could potentially happen by passive occupation of vacated territories or by aggressive displacement of the resident male; we were unable to ascertain the frequency of these alternatives, although we have anecdotal evidence that aggressive takeovers do occur; R. Durães, unpublished data). In addition, territories could be (4) *new*, if a male occupied a site at the lek that was vacant the previous year. Each male–territory–year was treated as a unit and we estimated the probability that each of these transitions would occur. Given that $S$ (for "survival") is the probability that a male will persist at the same territory from time $t_x$ to time $t_{x+1}$ and $1-S$ is the probability that it will not, $TO$ ("takeover") is the probability that a new male will recruit into the lek by occupying that territory at $t_{x+1}$, and $B$ ("birth") is the probability that a male will recruit by establishing a new territory; the probabilities for each of the four transition classes can be described as:

1. $P_{\text{maintained}}=S$;
2. $P_{\text{vacated}}=(1-S)\times(1-TO)$;
3. $P_{\text{taken-over}}=(1-S)\times(TO)$;
4. $P_{\text{new}}=B$

The takeover rate, $TO$, was estimated empirically as: (number of territories taken over)/((number of territories taken over)+(number of territories vacated)), averaged across time intervals. Because $1-B$, the probability that a suitable, unoccupied lek site will remain unoccupied from time $t_x$ to time $t_{x+1}$, cannot be estimated accurately, $B$ could only be estimated at a *per* lek basis, as: (number of new territories established)/(number of observed leks). Therefore, in order to make the rate at which new territories arise comparable to the estimates of territory persistence, vacancy, and takeover for use in the simulations (see below), we assumed that males could recruit into leks via takeover or by establishing new territories with similar probabilities (i.e., $B=TO$; thus, Eq. 4 becomes $P_{\text{new}}=TO$). Although this may not always be true (e.g., if males establishing new territories face less resistance than males taking over preexisting territories), we did confirm with a Chi-square test that the frequencies of recruitment by either mechanism do not differ (see "Results"). Chi-square tests were also used to assess whether age (subadult vs. adult) influenced the way a male recruits into a lek (i.e., via takeover vs. establishment of new territory), with data combined across all years, and to test whether the probability that a male recruits into a lek was influenced by lek size, for each year separately.

*S*, the rate of male persistence at territories, was estimated using the "known fate" model implemented in program MARK (White and Burnham 1999). The sample unit was a male–territory association; thus, a territory that underwent a takeover, being occupied by a male at year $t_x$ and by a different male at year $t_{x+1}$, corresponded to two independent data points according to the different males that came to occupy that territory. For each of the four sampled breeding seasons, an entry of 1 was given if the territory was occupied by the focal male, and an entry of 0 was given if the territory was not occupied by the focal male. Lek sizes at year $t_x$, the first year of each time interval, were included as unstandardized covariates. Four competing models were evaluated, which included a general model assuming a constant *S* rate irrespective of year or lek size, plus three models incorporating year and/or lek size at year $t_x$ (Table 1). Logit or sine link options were used to build models with or without covariates, respectively. When lek size was included in a model, the real persistence parameters were estimated assuming the mean lek size in the population for that year. The relative likelihood of each model in the candidate set was estimated based on second-order Akaike's information criterion values, or $\mathrm{AIC}_c$ (Burnham and Anderson 2002). Models with $\mathrm{AIC}_c$ values differing by ≤2.00 units were considered equally supported, in which case *S* estimates were averaged across all models to account for uncertainty in model selection, with the contribution of each model to the final average being proportional to their $\mathrm{AIC}_c$ weight (Burnham and Anderson 2002; Johnson and Omland 2004).

Lacking sufficient data to test directly for the effect of previous mating history on the probability of a male persisting at a territory, we used vocalization rates as a correlate of mating success. Display rate has been repeatedly shown as an important correlate of male mating success in lekking species (reviewed in Fiske et al. 1998), and we have data showing that this is also the case for vocal display rates in our study population (Durães 2008). Vocalization rates were estimated for a subset of the territorial males during 30-min sessions (in 2005, 32 males observed) or 120-min sessions (in 2006, 25 males observed) conducted during early morning (0630–0830 hours) or mid-afternoon (1400–1600 hours), which are periods of peak lek activity. Identity of the focal male was confirmed by resighting of color bands during each observation session. Each individual was observed for a total of 132 (±39, 1 SD) min in 2005 and 713 (±271) min in 2006. A sitting observer recorded the number of calls given by a focal male during 5-min (2005) or 10-min (2006) intervals. Calls included advertisement songs, which are produced only by males and are used for territory defense and long-distance attraction of females, and whistle calls, which are uttered by both sexes and by birds of all ages and are much softer and propagate to shorter distances than songs (R. Durães, unpublished data). Data collection was halted while females or other males were present at the territory or when the focal male was displaying at his dance court. Vocalization rates were estimated as mean number of calls per minute and compared for males persisting vs. disappearing from a territory between years using a nonparametric Mann–Whitney test. Because individuals increase vocalization rates according to lek size (Durães 2008), we repeated this analysis after controlling for lek size with residual analysis and obtained similar qualitative results (recently, the use of residual analysis in ecology has come under criticism, e.g., Darlington and Smulders 2001, but visual inspection of scatterplots confirmed a lack of consistent direction in the differences in vocalization rates between persisting and nonpersisting males across lek size class). Due to the small number of males that were observed in 2006 and disappeared from territories in 2007, we combined data across years; qualitative results did not change when only data from 2005 were considered.

**Table 1** Candidate models describing *S*, the probability that a male holding a territory in year $t_x$ will persist at this same territory at year $t_{x+1}$ at leks of the blue-crowned manakin *L. coronata*, during 2004–2007, at TBS, Ecuador

| Model | $\mathrm{AIC}_c$ | $\Delta\ \mathrm{AIC}_c$ | $\mathrm{AIC}_c$ weight | No. parameters | Persistence estimates per period | | |
|---|---|---|---|---|---|---|---|
| | | | | | 2004–2005 | 2005–2006 | 2006–2007 |
| (1) *S* (lek size) | 128.194 | 0.00 | 0.371 | 2 | 0.769 (0.042) | 0.746 (0.042) | 0.772 (0.042 |
| (2) *S* (.) | 128.572 | 0.38 | 0.307 | 1 | 0.752 (0.041) | 0.752 (0.041) | 0.752 (0.041) |
| (3) *S* (lek size×year) | 129.561 | 1.37 | 0.187 | 4 | 0.817 (0.063) | 0.669 (0.067) | 0.816 (0.061) |
| (4) S (year) | 130.236 | 2.04 | 0.134 | 3 | 0.806 (0.071) | 0.674 (0.069) | 0.806 (0.066) |
| Weighted average | | | | | 0.778 (0.057) | 0.724 (0.063) | 0.779 (0.055) |

Model 1 allows *S* to vary with lek size, model 3 with year and lek size, and model 4 only with year, while model 2 assumes a constant persistence rate. Models are sorted in decreasing order of $\mathrm{AIC}_c$ values; $\Delta\ \mathrm{AIC}_c$ is the difference between the $\mathrm{AIC}_c$ value for the current model and the model with the lowest $\mathrm{AIC}_c$, and $\mathrm{AIC}_c$ weight is a relative measure of model support, given the model set. Mean estimates of *S* (and SE, between parentheses) for each interannual interval are presented for each model, as well as the weighted average across models.

### Simulations of lek dynamics

Estimated probabilities of male recruitment and persistence at territories were combined to model lek dynamics over periods of time longer than the 4-year span of this study, with the objective to understand how lek size and composition are modulated by these parameters and how long leks can remain traditional in location in the face of male turnover. A simulation started at time $t_x$=0 with a lek whose size was chosen at random from the natural range observed in our population (i.e., one to seven males). Each male in the lek had a probability $S$ of persisting in its territory until $t_{x+1}$ and $S-1$ of disappearing, in which case that territory had a probability $TO$ of being reoccupied by a different male and $1-TO$ of remaining unoccupied at $t_{x+1}$. In addition, during each time interval $t_x$ to $t_{x+1}$, one male could establish a new territory at the lek with probability $B=TO$. This process was iterated 1,000 times for 100 years. Leks that disappeared (i.e., reached a size of zero males) were not allowed to be recolonized; although recolonization may potentially happen in nature, we made this assumption because we never observed it in our population. Output measures were lek size at time $t_x$, proportion of original males still present at time $t_x$, and probability that a lek will persist up to $x$ years, which is given by the proportion of the initial 1,000 leks remaining at that time period. Statistical analyses were performed in SPSS 11.5 (SPSS 2002); unless stated otherwise, values are means±one SD.

## Results

### Lek sizes and ownership changes at territories

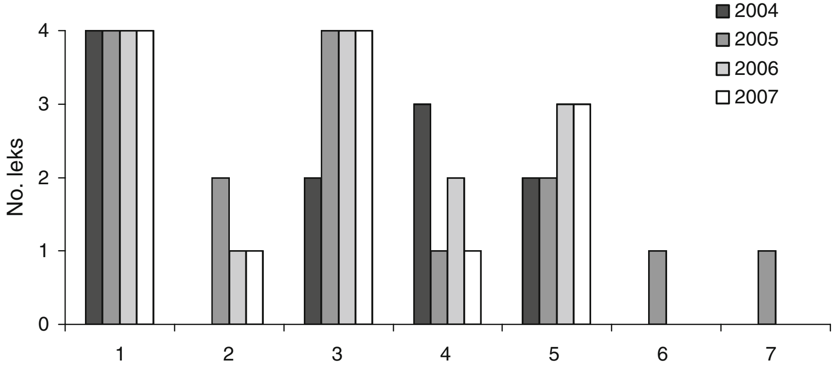
We located 11–15 leks each year on each study plot, though the true number of leks per study plot probably ranged from 13 to 15 (11 leks were located on the Harpia plot in 2004, but this number is almost certainly underestimated, as additional leks were located, with greater effort, in subsequent years). Leks were traditional in location, and lek centroids changed little in position between years (21± 26 m, range 0–89 m; $n$=26 interannual observations of 13 leks). The few exceptions were due to the disappearance of two leks (with one and three males in the previous year) and the establishment of a new lek by a solitary male. Leks were held between one and seven territorial males, with an average of 3.0±1.6 males per lek (Fig. 1). Mean size of leks was similar between plots (plots compared during 2006, $t_{26}$=0.16, $p$=0.91) and, in the Harpia plot, among years ($F_{3,\ 49}$=0.08, $p$=0.97). There was no indication that the number of leks in each size class departed from random for Harpia in any given year or for Puma in 2006 (Kolmogorov–Smirnov tests, all $p$ values >0.99).

Although leks were stable both in location and in mean size within the population, individual leks changed as a result of relatively high male turnover rates. Ownership status was unambiguously established each year for 34–47 territories in 12–15 leks, for a total of 117 observed territory transitions involving 65 different individual males over four seasons (Fig. 2a). In 68% of these cases ($n$=80), the territory was maintained by the same male between years; in 15% ($n$=17), the territory became vacant; in 9% ($n$=11), it was taken over by a different male, and in 8% of the cases ($n$=9) a new territory was established. During the observed period, 29% of the males ($n$=19) held a territory for 1 year, 28% ($n$=18) for 2, 26% ($n$=17) for 3, and 17% ($n$=11) for 4 years; however, because most of these histories were incomplete, it was not possible to make inferences about the average male tenure time in the population. Between consecutive years, leks changed in size in 32% of the cases ($n$=44 interannual lek comparisons) as a result of males disappearing and/or recruiting into the lek. These changes in size ranged from a gain of two to a loss of three males per lek (Fig. 2b), with an average net change of +0.4, −0.4, and −0.3 males per lek for the interannual periods of 2004–2005, 2005–2006, and 2006–2007, respectively. Among the males disappearing from their territories, only one was later resighted; this male held a territory for at least 2 years (2004–2005), and in 2006 he had taken over another male's territory on a neighboring lek.

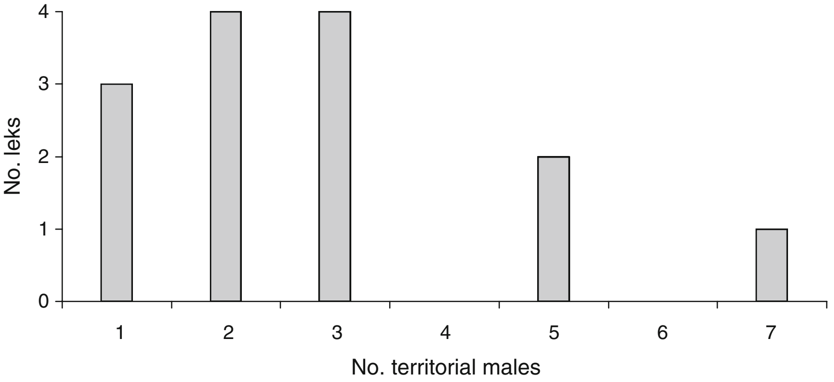
### Recruitment of males at leks

Each year, between zero and two new males were recruited at each lek, either via takeovers ($n$=11 events) or by establishing new territories ($n$=9). Combining data across years, recruitment by each of these mechanisms happened at similar frequencies ($\chi^2_1$=0.20, $p$=0.66). The average rate of takeovers, $TO$, was 0.39 (2004–2005 0.33; 2005–2006 0.40; 2006–2007 0.43). The average rate of establishment of new territories *per* lek was 0.23 new territories per lek per year, but it was highly variable across time intervals (0.50, 0.20, and 0). Males recruiting into leks were more likely to be adults ($n$=15) than subadults ($n$=5; $\chi^2_1$=5.00, $p$=0.025). This does not seem to be due to an excess of adult floaters in the population, as roughly similar proportions of unbanded adults and subadults not known to hold territories were captured each year during systematic mist-netting sampling at the plots (J. G. Blake and B. A. Loiselle, unpublished data; see Blake and Loiselle 2008 for details on the systematic mist-netting sampling). While age seems to influence the probability of a male to recruit into a lek, it did not influence the mode of recruitment: both adults and subadults recruited via takeovers or by establishing new territories with similar probabilities ($\chi^2_1$=1.68, $p$=

**Fig. 1** Distribution of lek sizes (in number of male territories) for the blue-crowned manakin, in **a** Harpia plot, 2004 (2.9±1.6 males; $n$=11 leks), 2005 (3.1±1.9; $n$=15), 2006 (2.9±1.5; $n$=14), and 2007 (2.9±1.7; $n$=13), and in **b** Puma plot, 2006 (2.9±1.7; $n$=14). Harpia and Puma are two 100-ha study plots located ~1.5 km apart between closest edges



(a) Harpia plot



(b) Puma plot, year 2006

0.19). The number of males recruiting into leks of a given size was proportional to the frequency of leks in that size class (2004: $\chi^2_3$=1.37, $p$=0.71; 2005: $\chi^2_6$=7.71, $p$=0.26; too few recruitments were observed in 2006 to allow for tests), indicating that the size of a lek does not affect the probability that a male will recruit into it.

### Male persistence at territories

The model incorporating lek size but not year had the lowest AIC$_c$ value amongst the four models being compared (Table 1). However, three of the four screened models, including the general model $S$(.), were equally supported based on AIC$_c$ values (i.e., $\Delta$ AIC$_c$ values <2), indicating that lek size or year are not good predictors of the probability that a male will persist at a territory between two breeding seasons. We thus averaged survival estimates across all models; the weighted average probability of male persistence at territories was 0.76 when averaged across years (Table 1). Vocalization rates did not differ between males persisting ($n$=40) or disappearing from a territory ($n$=13) in the next year ($U$=182.0, $p$=0.13). This same result held after controlling vocalization rate for lek size in that year ($U$=192.0, $p$=0.24).

### Modeling lek dynamics

Temporal changes in size and composition of leks were modeled assuming $S$=0.76 and both $TO$ and $B$=0.39. Each lek from the initial pool of 1,000 started with one to seven males and was allowed to undergo changes in size and composition according to these rates. Each year, a fraction of leks disappeared; persisting leks rapidly converged to a mean size of three males (Fig. 3). Male turnover rates, i.e., the rate at which individuals present at $t_0$ disappear from a lek, show that on average 21% of the original males are expected to have disappeared from the lek after 1 year, 39% after 2 years, and 53% after 3 years (Fig. 4a). These rates are in general agreement with the rates of territory turnover observed on the Harpia plot: on average, 23% males disappeared within a year (19%, 33%, and 17% for 2004–2005, 2005–2006, and 2006–2007, respectively), 46% disappeared within 2 years (52% and 39% for 2004–2006 and 2005–2007), and 61% within 3 years (2004–2007). Estimated tenure times (i.e., number of years an individual male is expected to retain a given territory) had a distribution strongly skewed towards short tenure times and a long right-side tail indicating that a small proportion of the males may hold territories for a long time (median=

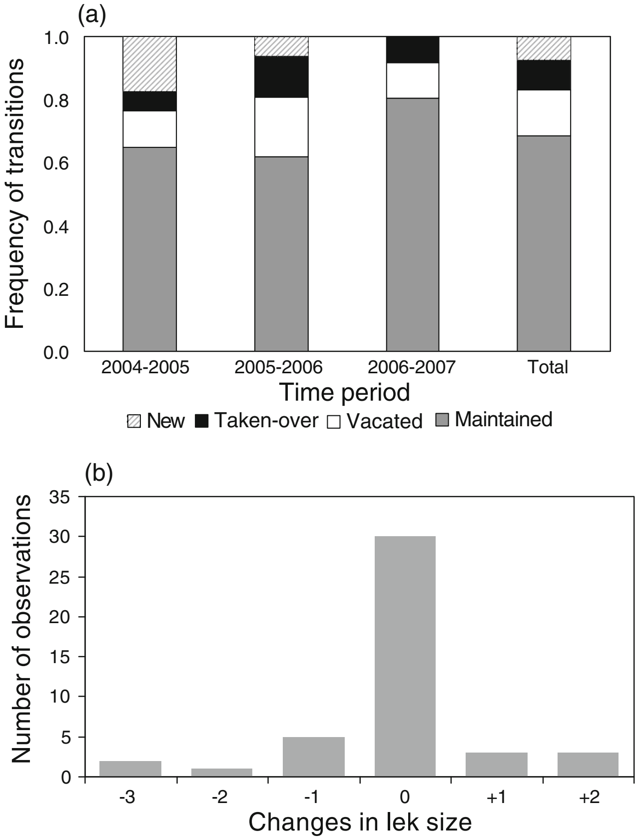


**Fig. 2** Changes in territory ownership and lek size observed between 2004 and 2007. In **a**, the frequency of each type of transition observed at territories between consecutive years is depicted; existing territories could be maintained by the same male, be taken over by a different male, or vacated; in addition, new territories could be established in previously unoccupied sites. Thirty-four transitions were recorded in 2004–2005, 47 in 2005–2006, and 36 in 2006–2007, for a total of 117 territory transitions observed in 54 territories belonging to 15 leks. In **b**, net changes observed between consecutive years in lek size are shown; observations were recorded between 2004 and 2007 for up to 15 leks each year, for a total of 44 interannual observations

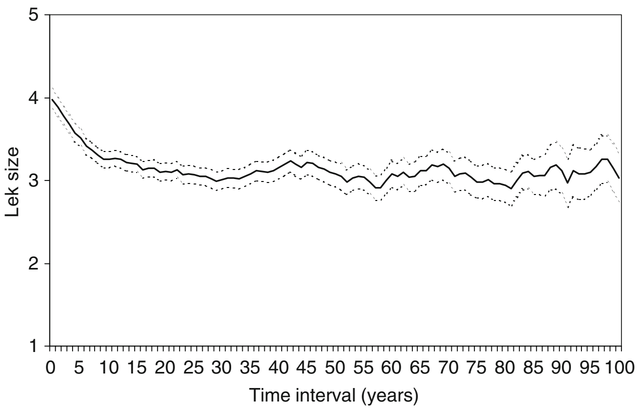


**Fig. 3** Predicted changes in lek size (in number of males) over time. Leks starting with one to seven males rapidly converge to a mean size of approximately three males; *solid* and *hatched lines* represent average and 95% confidence intervals, respectively

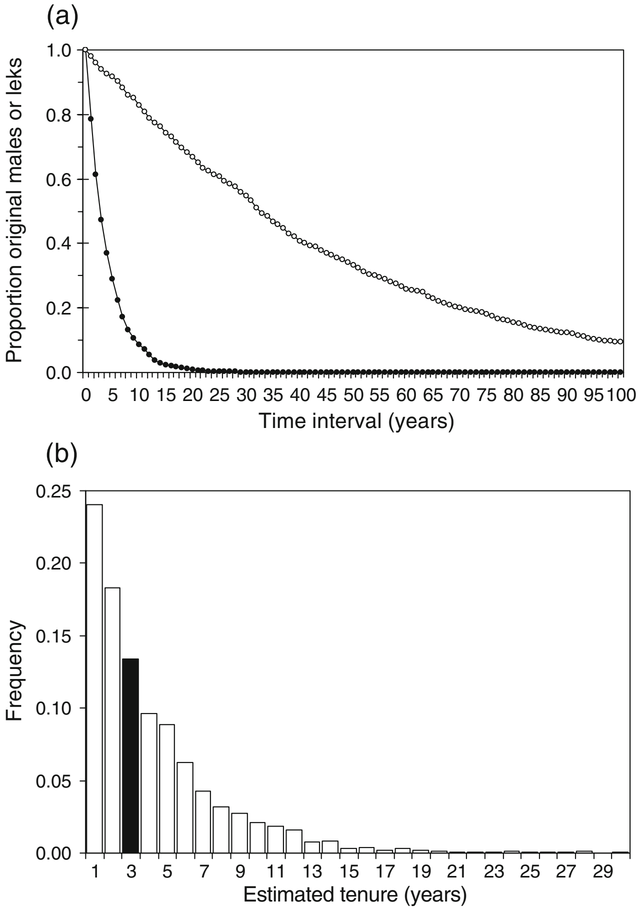


**Fig. 4** In **a**, proportion of leks (*open symbols*) present in the population at time=$t_0$ that are expected to persist (i.e., retain ≥1 male) after *t* years or proportion of males (*solid symbols*) initially present and that are expected to persist at those leks after *t* years. In **b**, expected tenure times for lekking males; no males were observed to hold a lek territory for more than 30 years during simulations; the median (3 years) is shown in *black*

3 years; 56% males expected to have tenures of ≤3 years, and 9% males expected to have tenures of ≥10 years; Fig. 4b). This small proportion of long-tenure males is also reflected by the long time taken, on average, for a complete turnover of males at leks (Fig. 4a, solid symbols). Due to the presence of these “anchor” males, and to the recruitment of new ones, leks are expected to persist for very long times; assuming that all the initial conditions remain unchanged, the average probability that a lek would persist for 100 years according to our simulation was 9% (Fig. 4a, open symbols).

## Discussion

Territoriality has a critical influence on male fitness in lek-breeding populations (e.g., Kokko et al. 1998). Floater males that are not able to secure a lek arena are expected to have reduced or nil mating success, as females are unlikely to mate away from leks; in the blue-crowned manakin, molecular analyses of paternity suggest that only territorial males sire young (Durães 2008). As such, attendance and display rates at leks are important correlates of male mating success across species (Mackenzie et al. 1995; Fiske et al. 1998). Holding territories for extended periods may also be important for securing copulations, as male mating success can increase with age or tenure time in some lekking birds (e.g., Tsuji et al. 1994; Lanctot et al. 1998), including manakins (McDonald 1993; Ryder et al. 2008). Manakin males show strong territory fidelity and at least some individuals exhibit long tenure times (Lill 1976; McDonald 1993; Castro-Astor et al. 2004; Ryder et al. 2008). On the other hand, there is at least anecdotal evidence suggesting that male turnover rates at leks can also be high (e.g., Foster 1981). Here, we provide what is, to our knowledge, the first detailed information on the temporal dynamics and male turnover at manakin leks and show that leks of the blue-crowned manakin are spatially traditional yet fairly dynamic in composition.

Our observations show that, on average, one fourth of the males present at a lek in any given year are not present in the following year, yet simulations suggest that individual leks can persist for many decades. The fate of most males observed disappearing from leks is unknown, with the exception of a single individual resighted holding a territory at a different lek in the subsequent year. However, the fact that this observed movement was very limited (the centroids of the first and the second territories held by that male were only 80 m apart) and that we surveyed systematically a large area (two 100-ha plots located ~1.5 km apart and their immediate surroundings) without recording other postjuvenile dispersal events suggests that most cases of male disappearance from leks are likely due to mortality. This is further supported by observations that adult manakins have small home ranges, with males being more sedentary than females (Graves et al. 1983; Blake and Loiselle 2002). In 5 years of systematic mist-netting capture–recapture studies at the two plots at TBS, long-distance dispersal was virtually unrecorded for adult blue-crowned males (recapture distances 121.4±97.5 m, range 0–281 m; J. G. Blake and B. A. Loiselle, unpublished data).

Our estimates of annual male persistence at territories (0.76 on average) were higher than estimates of survival based on capture–recapture. Blake and Loiselle (2008) report an average annual survival rate of 0.59 (range 0.58–0.64 depending on the model) for blue-crowned manakins in TBS, but their analyses included individuals of all ages and both sexes. When sexes were considered separately, survival rates were ~11% lower for males than for females (0.54 vs. 0.61, respectively; J. G. Blake and B. A. Loiselle, personal communication) and still below our estimates. Because our analyses considered only lekking individuals, they might have overestimated male survival, e.g., if floaters survive less than territorial males. On the other hand, due to the pronounced sedentarism of territorial males, direct resighting at leks may provide more accurate survival figures for this class of birds than recapture events. For example, fairly similar survival rates were recorded for males (0.78±0.03) and females (0.75±0.04) of the long-tailed manakin (*Chiroxiphia linearis*) when a combination of resightings at leks and systematic netting was applied (McDonald 1993).

At the same time that males disappear, new males recruit into the leks. Competitive ability for territory acquisition often increases with male age (Apollonio et al. 1989; McDonald 1993; Tsuji et al. 1994; Kokko et al. 1998), and our data suggest that this may be the case with blue-crowned manakins as well. For each three recruiting males in definitive plumage (adults), only one in predefinitive plumage (subadults) was observed recruiting into a lek. Green-plumaged juvenile males do not establish stable territories but may form loose associations with territorial males during which they practice display elements together (R. Durães, manuscript in preparation). This suggests that older males have an advantage over younger males when acquiring lek territories or that males delay establishment of stable territories and initiation of costly courtship displays until an age when they are more likely to successfully secure copulations.

We did not find evidence that the probability of a male recruiting into a lek or persisting in a given territory is influenced by lek size. An effect of lek size could be expected in at least two situations. First, larger leks could be more effective as recruiting foci due to the increased display activity levels. Second, if females prefer to mate at leks of a given size, as has been observed for other species (Lank and Smith 1992; Höglund et al. 1993; Hovi et al. 1996; Jiguet and Bretagnolle 2006, but see Lanctot et al. 1998), males could attempt to recruit preferentially into these leks. Likewise, if territories at larger leks are preferred, the pressure of takeover attempts could be higher at these leks. However, we have data showing that, although some females seem to favor larger leks over small ones, in the population at large, males at leks of all sizes, including individuals displaying solitarily, obtain copulations (Durães 2008).

Song rate is a strong correlate of male mating success in many lekking species (Fiske et al. 1998), including the blue-crowned manakin (Durães 2008). Males that are unsuccessful in acquiring mates in one season have been shown to change territories more often than successful ones for several lekking species (Höglund and Robertson 1990a; Gibson 1992; Westcott and Smith 1994; Rintamäki et al. 1995;Apollonio et al. 2003), and thus we hypothesized that blue-crowned males with higher vocal display rates would persist longer at their territories. As an alternative, it is also conceivable that a high energetic investment in costly lekking displays (e.g., Vehrencamp et al. 1989; Höglund et al. 1992) could reduce male survival, leading to a negative relationship between vocalization rate and persistence at leks. We, however, failed to detect an effect of vocalization rate on persistence probabilities at territories of the blue-crowned manakin, suggesting that previous mating history does not affect territoriality in this species and/or that vocal display is not costly enough to reduce survival (e.g., Dearborn et al. 2005).

## Stability in lek sizes and locations

The distribution of lek sizes in this population was constant both in time (across the 4 years of study) and space (between two study plots). In addition, the results of our model indicate that, regardless of their initial size, persisting leks converge rapidly to a mean size of three males, similar to what we observed in the field. At a first look, this might suggest that there is an "optimal" lek size that maximizes male fitness, perhaps due to a nonrandom female preference for leks of particular sizes (Lank and Smith 1992; Höglund et al. 1993; Hovi et al. 1996; Jiguet and Bretagnolle 2006). However, there are three lines of evidence that refute this idea: first, the distributions of observed lek sizes were not different from basic random expectations; second, males recruited into leks irrespective of their size; third, lek size did not affect the survival probabilities of males at territories. Thus, lek size seems to be more likely a by-product of the observed rates of recruitment and survival in this population rather than a selective force modulating lek structure.

Leks were also extremely traditional in location. Although our study had a short time frame, our model of lek dynamics showed that leks could persist for much longer periods (>100 years) even in the face of turnover of individual males. By projecting lek changes over time, we were thus able to show that, despite their dynamic nature, leks of the blue-crowned manakin seem to be at a balance where rates of male disappearance are compensated by male recruitment. How long leks will actually persist in nature will certainly be affected by other factors, such as changes in the forest structure, but our simulations show that, assuming that the initial conditions observed during this study are maintained, leks have the potential to persist long after all the original males have been replaced.

One possible mechanism allowing for the persistence of leks on the same locations is limitation of suitable lekking habitat or some other type of spatial constraint on lek establishment. We have previously shown that male settlement is not bounded by female spatial distribution (i.e., leks are not located at female "hotspots," Durães et al. 2007) and that, although location of leks seems to be influenced by male habitat selection and by niche partitioning with other manakins, suitable lekking habitat is not limited for blue-crowned manakin in the study area (Durães et al. 2007; Loiselle et al. 2007). On the other hand, leks are spatially distributed in an extremely regular pattern, which suggests that a settlement pattern that minimizes competition among leks may be favored (Durães et al. 2007; see also Wegge and Rolstad 1986). In addition, fruit availability is higher at manakin lek sites than at nonlek control sites (Ryder et al. 2006). Whether leks have been settled at those sites precisely because of their high fruit availability or whether seed deposition underneath display perches have created these patterns, the fact is that the presence of territorial males creates a positive feedback in resource levels that would promote traditionality in lek location. Thus, it is possible that increased availability of food resources and reduced competition with males from other leks play a part in maintaining lek locations.

An alternative explanation for lek traditionality is an increased fitness for males occupying traditional sites. The "spatial spillover" or "hotshot" model proposes that leks are formed when less successful males cluster around more successful males in an attempt to intercept copulations (Beehler and Foster 1988; Höglund and Robertson 1990b; Rintamäki et al. 1995; Lanctot et al. 1998). This model predicts that mating females are faithful to males, not to sites, and that at least the most successful males should hold territories for long periods of time. In contrast, the "temporal spillover" model proposes that leks are maintained because females tend to go back to familiar places to mate and, as a result, males tend to settle at traditional sites, where they would enjoy increased mating success (Apollonio et al. 1989; Gosling and Petrie 1990; Gibson et al. 1991; Gibson 1992; Jiguet and Bretagnolle 2006). This model predicts that females are faithful to sites, not males, and that males settled at more traditional sites would have higher mating success than males settled at more recently formed leks. At present, we lack sufficient data to tease apart these two possibilities, but we suggest that male recruitment at leks of the blue-crowned manakin is unlikely to be modulated in the long term by the presence of specific "hotshot" males. Our simulations suggest that, although most males have short tenure times (≤3 years), a small fraction can retain territories for long periods of time (9% of males expected to have tenures of ≥10 years). However, we did not find evidence that these "anchor" males are "hotshot" males, to the extent that persistence at territories was not higher for males with higher vocal display rates. We also have anecdotal data showing that females can mate repeatedly at the same leks within and between breeding seasons but not necessarily with the same individual males (R. Durães, unpublished data), lending circumstantial evidence for the temporal spillover hypothesis.

In conclusion, leks of the blue-crowned manakin are stable in relation to the distribution of lek sizes in the population and to their location. Stability of lek sizes seem to be a by-product of the intrinsic rates of mortality and recruitment of territorial males, which, coupled with the presence of a small fraction of males that have long tenure times and act as “anchors,” would allow leks to persist in the same locations for very long periods of time. That males tend to recruit into established leks rather than initiate new leks at unoccupied sites may be due, at least in part, to the increased food availability at leks, to a spatial pattern that minimizes competition among leks, and to a tendency of females to mate at familiar sites.

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