

LONG-TERM STUDIES OF THE GREEN-RUMPED PARROTLET (*FORPUS PASSERINUS*) IN VENEZUELA: HATCHING ASYNCHRONY, SOCIAL SYSTEM AND POPULATION STRUCTURE

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Resumen. – Estudios de largo plazo del Periquito Mastranero (*Forpus passerinus*) en Venezuela: La eclosión sincronizada, sistema social y estructura poblacional. – Pocas aves tropicales han sido el enfoque de investigación a largo plazo sobre su ecología y comportamiento. A continuación presento los resultados más sobresalientes obtenidos en 19 años de estudios del Periquito Mastranero (*Forpus passerinus*) en los llanos de Venezuela, basados en el marcaje y revistamiento de más que 7500 individuos y 2500 intentos de anidación provenientes de dos poblaciones reproductivas establecidas en cajas para anidar. El trabajo inicial se enfocó en las causas y consecuencias de la eclosión extremadamente asincronizada exhibida por los periquitos. Un examen exhaustivo de un conjunto de atributos correlacionados con el éxito reproductivo en nidos experimentalmente sincronizados y asincronizados no dió pruebas de que la asincronía brindó algún beneficio a los patrones de la eclosión. Las consecuencias de no cuidar a los huevos durante su postura fueron severas – a medida que los huevos dejaron de estar incubados perdieron rápidamente su viabilidad y los huevos no vigilados fueron atacados frecuentemente por parejas no reproductivas. El trabajo durante la última década se ha enfocado en el entendimiento del sistema social y la dinámica poblacional. Los periquitos tienen un sistema social complejo, compuesto de parejas reproductivas hembra-macho, parejas no reproductivas hembra-macho, parejas macho-macho, y machos no reproductivos que ocurren solos o en grupos que a veces molestan a las parejas reproductivas. Los individuos no reproductivos comprendieron hasta el 50% de los machos que fueron revistados durante años cuando las poblaciones estaban grandes. Las fertilizaciones extra-parejas no fueron comunes (< 8% de los pichones). El divorcio raramente ocurre en las parejas reproductivas, pero parejas típicamente se reproducen juntas solo 1–2 años. Las parejas macho-macho fueron individuos jóvenes que viajaron juntos, se acicalaron mutuamente, y entraron juntos a las cajas. Los periquitos son fieles a su sitio y forman dos poblaciones reproductivas que se conectan gracias a la dispersión de los juveniles. Los sitios están separados por 600 m, pero se diferencian por 1–2 m de elevación, tipo de suelo y régimen de inundación. Estos factores pueden resultar en diferencias de hasta 6 semanas en el comienzo de la anidación en años lluviosos, pero no en años secos. Los estudios de largo plazo son críticos para entender la ecología de aves tropicales y los efectos que los cambios climáticos pueden tener en ellas.

Abstract. – Few Neotropical birds have been the subject of long-term ecological and behavioral research. I present highlights from 19 years of studies on the Green-rumped Parrotlet (*Forpus passerinus*) in the llanos of Venezuela, based on marking and resighting over 7500 individuals and monitoring of 2500 nesting attempts in two populations breeding in nest boxes. Initial work focused on the causes and consequences of the extreme hatching asynchrony exhibited by parrotlets. Examining an exhaustive set of fitness correlates at experimentally synchronized or asynchronized nests found no evidence that asynchrony benefited

hatching patterns. The consequences of not caring for eggs during laying were severe, as unincubated eggs lost their viability rapidly and eggs left in unguarded nests were frequently destroyed by nonbreeding pairs. Work over the past decade has focused on understanding parrotlet social system and population dynamics. Parrotlets have a complex social system composed of male-female nesting pairs, nonbreeding male-female pairs, male-male pairs, and nonbreeding males occurring primarily alone or in groups that sometimes molest breeders. Nonbreeders composed up to 50% of the males that are resighted during years when populations are large. Extra pair fertilizations were uncommon (< 8% of young). Divorce rarely occurs in breeding pairs, but pairs typically breed together for only 1–2 years. Male-male pairs were young individuals that traveled together, allopreened each other, and entered nest boxes together. Parrotlets have strong site fidelity and form two breeding populations connected by dispersing juveniles. The two sites are 600 m apart, but differ in elevation by 1–2 m, in soil type, and flooding regime. These differences can result in differences of up to 6 weeks in the onset of nesting in rainy years, but not in dry years. Long-term studies are critical to understand the ecology of tropical birds and the effects of climate change on them. *Accepted 1 November 2007.*

Key words: Social system, extra-pair fertilization, hatching asynchrony, parrot, breeding season, population structure, geographic variation, *Forpus passerinus*, Green-rumped Parrotlet.

INTRODUCTION

Despite the tremendous diversity of tropical ecosystems and their conservation importance, there is little long-term data on the social system and demography data of tropical birds based on studies of marked individuals (Stutchbury & Morton 2001). Most long-term studies of tropical bird behavior have chosen species with relatively closed populations that experience limited immigration or emigration, such as island residents or cooperative or lek breeders (Grant 1986, Rabenold *et al.* 1990, McDonald 1993). A notable exception was work on antbirds (Greenberg & Gradwohl 1985). While these species have fostered elegant work, birds are characteristically vagile and typically have open populations.

In 1985 I began studies of Green-rumped Parrotlets (*Forpus passerinus*) while conducting other research in Venezuela (Beissinger *et al.* 1988, Beissinger 1990a, 1990b). At the time few details were known about the behavior and ecology of wild parrots, aside from the exceptional studies of Puerto Rican Parrots (*Amazona vittata*) by Snyder *et al.* (1987), and detailed work on Australian cockatoos

(Rowley 1990), even though parrots had been kept in captivity for centuries. The biology of parrots continues to be poorly known because most species are monomorphic, are difficult to catch (Meyers 1994), cannot wear standard bird bands because of damage done to their legs when clamped by their strong beaks (Meyers 1995), nest in cavities high above the ground in the canopy of tropical forests, and have large home ranges. Yet parrots are one of the most threatened avian families, with one-third of the New World species considered at risk of extinction due to habitat destruction and harvest for the international trade (Beissinger & Snyder 1992).

Studying the Green-rumped Parrotlet seemed like an opportunity to rectify the lack of knowledge about parrots. Parrotlet nests were easily observed and accessible in hollow wooden fence posts set along pastures and forest edges, and adults would accept nest boxes (E. S. Morton, pers. com.). Birds could be easily captured in mist nets near nests, and would wear colored, aluminum or plastic bands without injury. Both adults and nestlings are plumage dimorphic (Forshaw 1989). Moreover, I was fascinated by the large clutch

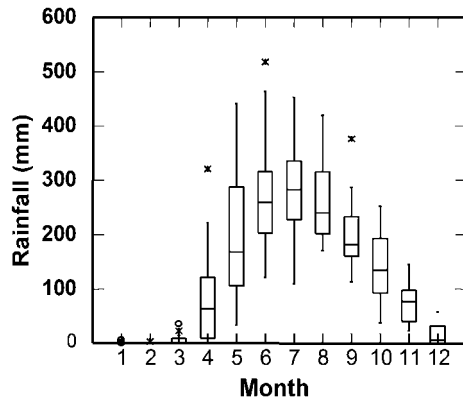


FIG. 1. Monthly rainfall at Hato Masaguaral, Guaraico, Venezuela from 1988–2006. Each box incorporates the central 50% of values and vertical lines show median values. Outliers are indicated by asterisks.

size and extreme hatching asynchrony exhibited by this species.

Here I present highlights from 19 years of studies on the Green-rumped Parrotlet conducted with students and collaborators in the llanos of Venezuela. I begin by reviewing the biology of Green-rumped Parrotlets and the study system, and then summarize results from the first decade of work on hatching patterns. Next I present recent data on the complex social system of parrotlets. I conclude by revealing small-scale structuring of parrotlet populations and how it effects the onset of breeding. Throughout this paper, I emphasize the value of long-term study and the results that it has generated.

STUDY SPECIES AND ENVIRONMENT

The Green-rumped Parrotlet is one of seven species in a genus of small Neotropical parrots (Forshaw 1989). It inhabits forest edge, savannas and pastures in northeastern South America, the sexes are plumage dimorphic, and adult size is small (24–36 g). The parrotlet

feeds principally on the seeds of herbaceous plants or fruits (Waltman & Beissinger 1992). From 1985–1987, I studied the breeding biology of parrotlets in Venezuela in “natural” cavities in fence posts. In 1988, I installed 40 nest boxes (1 m deep pvc tubes) hung on fence posts based on dimensions of fence post sites. Nest boxes were rapidly accepted and became the most frequently used nesting site (Beissinger & Bucher 1992a, 1992b). In 1989 the study was expanded by placing 100 boxes over a 4-km² area separated by distances exceeding those between adjacent natural nests. Six more boxes were added in 1994.

This work has been conducted at Hato Masaguaral (8°34' N, 67°35' W), a research station, cattle ranch, and nature reserve in Venezuela. The habitat is a mosaic of open grasslands with scattered clumps of large trees, patches of palm or deciduous forests with < 30% canopy closure, and dense stands of gallery forests along water courses with closed canopy (Troth 1978). Although annual temperature varies little (Sarmiento 1984), the llanos are highly seasonal environments (Fig. 1): six months of rain flood low-lying areas (May–October), four months of drought change the landscape to brown (December–March), and two months are transitional (April and November). This seasonal regime differs from the general perception of aseasonal tropical environments and allows many interesting comparisons with other tropical and temperate species.

CAUSES AND CONSEQUENCES OF HATCHING ASYNCHRONY

The early emphasis of our long-term research from 1989–1997 was to understand the factors that select for an extremely early onset of incubation in the parrotlet. Birds are unusual, compared to other vertebrates, in having some control over hatching patterns but often

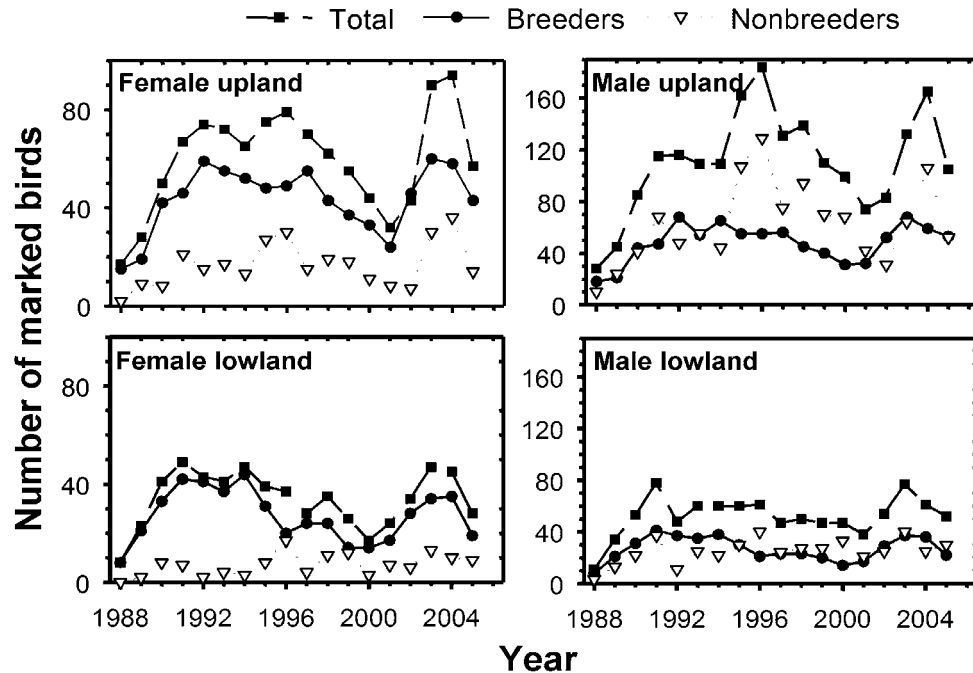


FIG. 2. Number of breeding and nonbreeding parrotlets resighted for each sex in the upland and lowland populations.

select a pattern that leads to mortality of last hatched young (Clark & Wilson 1981, Stoleson & Beissinger 1995). Unlike most Neotropical birds, parrotlets lay very large clutches (Mean = 7 eggs, range 3–14) that hatch and fledge very asynchronously (up to 18 days between first and last chicks in a brood), and this leads to low survivorship of penultimate- and last-laid eggs primarily due to starvation (Beissinger & Waltman 1991, Budden & Beissinger 2004).

We began by measuring an exhaustive set of fitness correlates at experimentally synchronized and asynchronized nests, and could find no evidence that asynchrony benefited hatching patterns (Beissinger & Waltman 1991, Stoleson & Beissinger 1997). Experimentally synchronized broods generally fledged as many or more young than asynchronized broods, especially in large broods of

eight young. Survival of fledged young and parents did not differ by synchrony treatment. Females from synchronous and asynchronous broods did not differ in the likelihood, timing, or success of their next breeding attempts. We also used doubly-labeled water to determine that peak metabolic rates did not differ between parrotlets rearing synchronous and asynchronous broods (Siegel *et al.* 1999). Working with Venezuelan counterparts, we found that the long nestling period and slow growth of parrotlet chicks may be an adaptation to a low protein diet of seeds (Pachecho 2000). Giving protein supplement to chicks did not increase growth rates.

Finding little evidence that asynchrony benefited nestlings or adults after hatching, we examined the consequences of not caring for eggs during laying. The Egg Viability Hypothesis proposes that avian parents may

TABLE 1. Social status assigned to 1113 Green-rumped Parrotlets observed repeatedly within a breeding season (June–November) and the percent of occasions (mean \pm 1 SE) they were observed in each category.

Sex	Social status assigned	N	Percent of sightings in each category			
			MF pair	MM pair	Group	Lone bird
Male	Breeding pair	438	86.57 \pm 0.88	1.08 \pm 0.25	6.21 \pm 0.50	6.15 \pm 0.52
	Male-female nonbreeding pair	84	72.97 \pm 2.36	2.66 \pm 0.65	13.28 \pm 1.46	11.10 \pm 1.33
	Male-male pair	37	3.52 \pm 1.14	65.65 \pm 2.51	18.48 \pm 1.86	12.36 \pm 1.71
	Group of males	61	7.88 \pm 1.52	13.00 \pm 1.72	62.02 \pm 2.04	17.11 \pm 1.72
	Lone male	36	8.03 \pm 1.90	8.11 \pm 1.91	22.54 \pm 2.53	61.31 \pm 2.84
	Undetermined	15	11.25 \pm 2.05	21.63 \pm 3.73	34.50 \pm 2.57	32.63 \pm 2.64
Female	Breeding pair	397	93.45 \pm 0.62	-	3.14 \pm 0.35	3.42 \pm 0.48
	Male-female nonbreeding pair	45	92.28 \pm 1.33	-	4.39 \pm 0.99	3.32 \pm 0.83

maximize the hatchability of eggs by initiating incubation before their clutch is completed because the viability of unincubated eggs declines over time (Arnold *et al.* 1987, Beissinger *et al.* 2005). Embryos are especially susceptible to death from overheating, are less affected by exposure to cool temperatures, and are susceptible to developmental failure under moderate temperature conditions (Webb 1987). Prolonged exposure to temperatures above physiological zero (24–26°C) yet below normal incubation levels (34–36°C) results in unsynchronized growth, abnormal development, and embryo mortality.

We tested the ability of newly laid parrotlet eggs to survive when exposed to ambient temperatures (Stoleson & Beissinger 1999). Hatchability declined to 70% after 3 days of exposure, was reduced to 59% after 5 days, and to 14% after 9 days, compared to high hatchability (86%) of control eggs that were not exposed to ambient conditions prior to incubation. This work led to direct tests of the egg viability hypothesis in Puerto Rico with Pearly-eyed Thrashers (*Margarops fuscatus*) and domestic fowl eggs using a climate gradient along the slope of a mountain (Beissinger *et al.* 2005) that identified an additional mechanism affecting egg viability – trans-shell infection by microbes – which could have important implications for clutch size of trop-

ical birds (Cook *et al.* 2003, Cook *et al.* 2005a, 2005b).

We also examined the consequences to pairs of not guarding nests during egg-laying (Beissinger *et al.* 1998). Unguarded eggs were destroyed at 60% of experimental boxes compared to 3% of nests guarded by laying pairs. The most frequent destroyers of eggs were prospecting male-female parrotlet pairs and, secondarily, male-male pairs, an unusual feature of avian social systems discussed further in the next section. Cavities are in short supply and parrotlets appear to have an incubation strategy adapted to limited breeding opportunities (Beissinger & Waltman 1991, Martin 1993, Beissinger 1996).

SOCIAL SYSTEM OF GREEN-RUMPED PARROTLETS

While conducting studies on hatching patterns and demography, we color-banded over 7500 parrotlets (1300 adults and 6200 nestlings). Marking adults concentrated on pairs near nest boxes, but we also captured as many other individuals as possible (Fig. 2). Nearly each day of the breeding season, we systematically walked the study area with spotting scopes to resight banded birds.

A glimpse of the complex social system of the Green-rumped Parrotlet emerges from

1113 parrotlets that we resighted ≥ 5 times during a breeding season (Table 1). Male Green-rumped Parrotlets were seen in five social groupings: breeding male-female pairs, male-female pairs that did not breed on the study area, male-male pairs, lone males, and groups of males (3–15 birds). In most years, the number of nonbreeding males resighted equaled or exceeded the number of breeding males in the population (Fig. 2); in some years male nonbreeders outnumbered breeders 2:1. Females were almost never observed without an accompanying male. Most male-female pairs lay eggs, but up to one-quarter of the pairs did not secure a nest site and never appeared to reproduce (Fig. 2). While individuals did change social status between years, within a year we typically observed individuals repeatedly in one social status category (Table 1). We were unable to reliably assign social status to only 1.3% (15/1113) of parrotlets observed repeatedly.

Male-female pairs have strong fidelity and behave as a cohesive unit. Males accompany their mates closely throughout the entire breeding season, and arrive and depart the nest together (Waltman & Beissinger 1992). Males feed females most of their food from prior to egg-laying, when females gain large amounts of mass for egg-laying and sit in the nest cavity, through hatching, when females finally begin to lose mass (Curlee & Beissinger 1995). Pair bond fidelity is very high, as only 1–2% of pairs divorce within and between years ($N = 877$ and 699 pairs, respectively). However, 75% of 738 marked pairs nested together for only one year due to mortality of a pair member as a result of a mean annual survival rate of 62% (Sandercock *et al.* 2000).

While Green-rumped Parrotlet pairs are apparently monogamous, extra-pair paternity occurs (Melland 2000). Extra-pair fertilizations (EPFs) occurred in 7.7% of the young and 14.4% of the 160 families and 827 nest-

lings sampled by Melland (2000), identified on the basis of 10 polymorphic microsatellite loci that had 115 alleles. This moderate frequency of EPFs appears typical of tropical birds (Stutchbury & Morton 2001). Genotypes matched those of social females in all cases, which indicates that conspecific brood parasitism does not occur often in this species. Sixty percent of the broods that contained extra-pair young had multiple chicks sired by extra-pair males. Occurrence of EPFs did not differ by laying order, whether the nest was located in upland or lowland populations in the study area, or by month within the nesting season (Melland 2000).

Male-male pairs are perhaps the most unusual affiliation of nonbreeders. Male-male pairs were resighted irregularly throughout the nesting season but affiliate closely. They travel throughout the study area together, allopreen each other, and enter nest boxes together. Male-male pairs appear to comprise 10% of the nonbreeding males that we resighted repeatedly, but nonbreeding males were difficult to detect and follow. We have documented repeatedly 48 male-male pairs. Male-male pairs were typically young individuals of <1 (79%) or 1–2 (16%) years of age. Only 6% were composed of siblings, although we did not know the relatedness of half of the pairs. Male-male pairs were seen together for up to a year, but most affiliations lasted only two months. Most pairs split when one male obtained a female (63%) or when one died (19%). However, 12% of the male-male pairs terminated when one member began affiliating with a new male.

Nonbreeding males also occur in groups or gangs that may harass prospecting and egg-laying pairs near nest sites. Such events are uncommon but can last 1–5 days. Groups of up to a dozen nonbreeding males also form at nests where a female's mate has died. Here they compete and fight for the opportunity to pair with the widowed female, and may guard

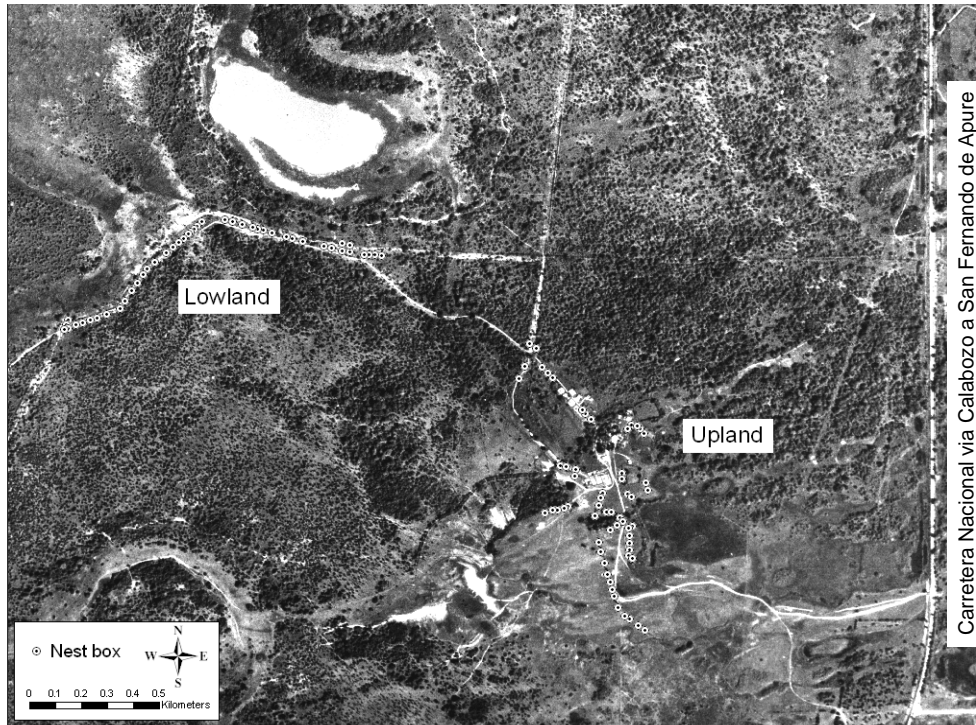


FIG. 3. Aerial photograph of the study area taken during March 1998 showing the location of nest boxes, and the upland and lowland populations.

and feed her young, or commit infanticide (Waltman & Beissinger 1992). Composition of groups appears to be fluid and membership determined by the home range or population of a nonbreeding individual.

SMALL-SCALE STRUCTURING OF PARROTTLET POPULATIONS AND EFFECTS ON THE ONSET OF BREEDING

Tropical ecosystems differ from temperate ecosystems in that they support a greater amount of biodiversity that persists at lower densities, possibly as a result of a higher degree of spatial heterogeneity of resources. The effect of spatial heterogeneity on the life histories of tropical vertebrates has rarely

been investigated and requires long-term study.

Our study area consists of two sites 600 m apart that differ in elevation by 1–2 m and in soil type, but not in rainfall or air temperature (Fig. 3). This slight difference in elevation and soil type results in remarkably different flooding regimes and vegetation that appear to be typical of this region (Troth 1978, Sarmiento 1984). There is an “upland” site dominated by grasslands interspersed with a mosaic of shrubs, woodlands without extensive canopies, and lightly grazed pastures (medano vegetation type). It occurs on sandy soils and retains standing water in few locations. The “lowland” site is about 1–2 m lower in elevation, but is composed of clay soils that hold water during the rainy season and flood from

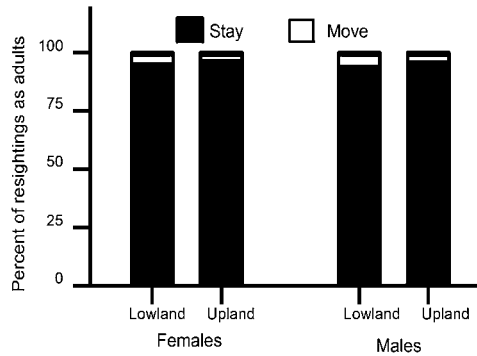


FIG. 4. Percent of adults (> 1 year of age) that were resighted in the population where they first settled (stay) or that later moved later to the other population (moved).

a few cm to 1 m deep in some spots. The lowland site consists of: (1) “bajío” vegetation composed of a mosaic of fewer patches of grasslands and more patches of open palm

savannas and open-canopy forests, and (2) “estero” vegetation that is seasonally flooded with water up to one meter deep and few trees.

Despite the proximity of these two sites, they function as distinct breeding populations connected as part of a metapopulation because adult parrotlets exhibit very high site fidelity. Only 24 of 799 females (3.0%) and 75 of 1516 males (4.7%) have bred at both sites. Furthermore, very few adults (birds > 1 year of age) have been resighted in both populations (Fig. 4). Elsewhere, we have shown that median inter-year movements of adults are < 250 m, regardless of breeding status (Sandercock *et al.* 2000). Nevertheless, the upland and lowland sites regularly exchange dispersing juveniles; 25% of 1092 juveniles recruited into the study area dispersed from one population to the other.

We have found that small-scale spatial het-

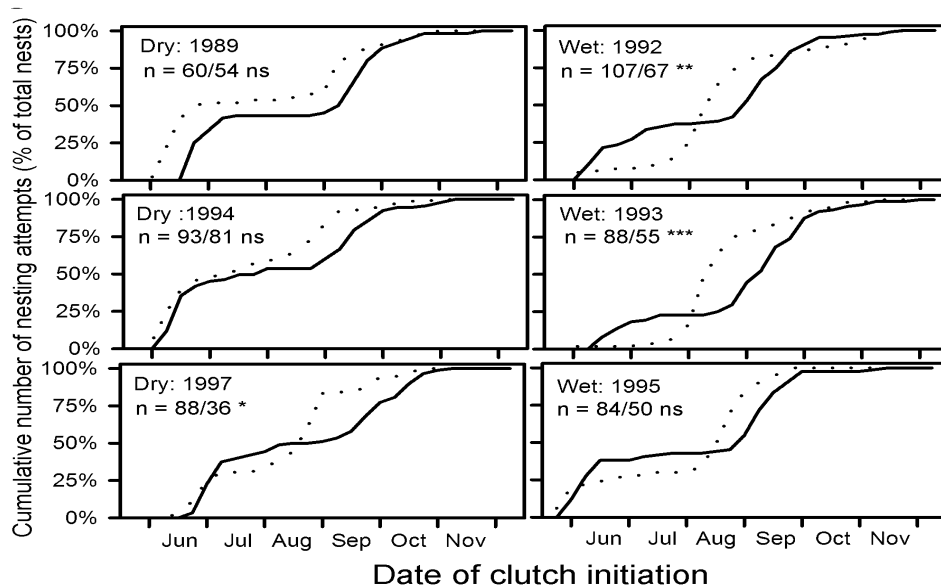


FIG. 5. Spatial heterogeneity in the onset of laying in representative years of low (dry) and high (wet) annual rainfall for the upland (solid line) and lowland (dotted line) populations. Number of nests (upland/lowland) and the results of Kolmogorov-Smirnov tests for differences between distributions are given (ns indicates $P > 0.05$, * indicates $P < 0.05$, ** indicates $P < 0.01$).

erogeneity plays an important role in the onset of nesting in parrotlets. The slight differences in elevation and vegetation between the upland and lowland populations can result in significant differences in the onset of nesting (Fig. 5), which coincides with the beginning of the rainy season. Parrotlets nested in two phases, which resulted in cumulative distributions of initiation dates that resemble step functions. Birds nesting in the second half of the breeding season included older individuals that were producing a second brood, and both young and old birds that had formed new pairs and were nesting for the first time that year. Total annual rainfall has ranged from relatively dry (1018 mm) to very wet (1995 mm) years. In years of heavy rainfall (Fig. 5), the onset of laying at the lowland site was significantly delayed (Kolmogorov-Smirnov test, $P < 0.05$), and the first quartile of nest initiations at the lowland site occurred 6–8 weeks later than the upland site. In years of low rainfall (e.g., 1994 and 1997), however, there was little difference in the timing of laying between the two sites (Fig. 5). Investigations have documented spatial heterogeneity in the onset of breeding among vertebrate populations, but often these populations were orders of magnitude farther apart than in our sites and experienced different climatic regimes (Adler 1994, Young 1994, Blondel 1999, Moore *et al.* 2005).

CONCLUSIONS

Long-term study of the behavior and demography of Green-rumped Parrotlets has produced a number of important advances for our understanding of tropical birds. The continuous study of annual and individual variation has allowed us to uncover a complex social system, microgeographic structuring of populations, and large annual and spatial variation in the onset of nesting. Studies of long duration are critical to understand

the factors that shape the ecology of birds in tropical environments and will become especially important as we seek to understand the effects of climate change on tropical birds.

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