MANAKINS (PIPRIDAE) IN SECOND-GROWTH AND OLD-GROWTH FORESTS: PATTERNS OF HABITAT USE, MOVEMENT, AND SURVIVAL

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ABSTRACT.—We used capture and recapture data (1985 to 1994) to examine seasonal variation in habitat use, movements within and among habitats, and survival rates of manakins (*Manacus candei, Corapipo altera, Pipra mentalis, P. pipra*) in northeastern Costa Rica. Manakins were captured in young and old second-growth woodlands in the lowlands and in old-growth forest at approximately 50, 500, and 1,000 m. Manakin species differed in their use of habitats, with old-growth forest species showing large and predictable seasonal variation in capture rates. *Corapipo* capture rates in lowland (nonbreeding) habitats were greater during the wet season than during the dry season and were greater in old-growth forest than in second growth. Capture rates at 500 m were higher in the dry season. *Pipra mentalis* capture rates were high in second growth and old growth. Capture rates were higher in the wet season and were correlated with capture rates of *Corapipo*, indicating that at least some individual *P. mentalis* migrate along the elevational gradient. *P. pipra* capture rates were highest at 1,000 m; few individuals descended to lowlands in the wet season. *Manacus* capture rates were highest in young second growth and did not vary between wet and dry seasons. Use of second-growth habitats by species typically associated with old-growth forests illustrates the value of maintaining a mosaic of habitats to accommodate seasonal changes in use of habitats. Contrary to expectations based on lek mating systems, there was little evidence that movements within habitats (i.e. recapture distances) varied between sexes. Yet, recapture percentages were higher in all species for adult females than males. Adult survival rates were ~0.75 for *Manacus* in young second growth, 0.62 for *Corapipo* in old-growth forest at 50 m and 0.66 at 500 m, and 0.70 for *Pipra mentalis* in lowland old-growth forest. Results support the suggestion that geographic variation in survival rates may be common in the tropics and illustrate the need for examining survival rates separately by age and sex. *Received 29 June 2000, accepted 8 October 2001.*

RESUMEN.—Con base en datos de capturas y recapturas recolectados entre 1985 y 1994, examinamos la variación estacional en el uso de hábitat, los movimientos dentro y entre hábitats y las tasas de supervivencia de saltarines (*Manacus candei, Corapipo altera, Pipra mentalis, P. pipra*) en el noreste de Costa Rica. Los saltarines fueron capturados en bosques sucesionales jóvenes y viejos y en bosques maduros a aproximadamente 50, 500 y 1,000 m de elevación. Las especies difirieron en términos de uso de hábitat y las tasas de captura de las especies de bosques maduros presentaron grandes variaciones estacionales predecibles. Las tasas de captura de *Corapipo* en áreas de tierras bajas (no reproductivas) fueron mayores en la estación lluviosa que en la estación seca y mayores en bosques maduros que en bosques secundarios. Las tasas de captura a 500 m fueron mayores en la estación seca. Las tasas de captura de *Pipra mentalis* fueron altas en bosques secundarios y maduros. Éstas fueron mayores en la estación lluviosa y se correlacionaron con las tasas de captura de *Corapipo*, lo que indica que al menos algunos individuos de *P. mentalis* migran a lo largo del gradiente altitudinal. Las máximas tasas de captura de *P. pipra* se presentaron a 1,000 m; algunos pocos individuos descendieron hacia las tierras bajas en la estación lluviosa. Las tasas de captura de *Manacus* fueron máximas en crecimiento secundario joven y no presentaron variación entre la estación lluviosa y la estación seca. El uso de hábitats secundarios por parte de especies típicamente asociadas a bosques maduros demuestra la importancia de mantener un

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mosaico de hábitats para permitir la variación estacional en el uso de éstos. A diferencia de lo que se esperaría con base en los sistemas de apareamiento en leks de estas aves, existe poca evidencia para sugerir que los movimientos dentro de hábitats (i.e. distancias de recaptura) varían entre sexos. Sin embargo, en todas las especies los porcentajes de recaptura de las hembras adultas fueron mayores que los de los machos. Las tasas de supervivencia de los adultos fueron de ~0.75 para *Manacus* en crecimiento secundario joven, 0.62 para *Corapipo* en bosque primario a 50 m y 0.66 a 500 m, y 0.70 para *Pipra mentalis* en bosque maduro de tierras bajas. Los resultados apoyan la sugerencia que la variación geográfica en tasas de supervivencia puede ser común en el trópico e ilustran la necesidad de examinar las tasas de supervivencia de las distintas edades y sexos por separado.

A BETTER UNDERSTANDING of population dynamics of individual species is a prerequisite for advancing our knowledge of factors that shape the dynamics of tropical bird communities. Such an understanding requires both pattern (e.g. habitat use) and process (e.g. survival) information (Marra and Holmes 2001). Unfortunately, most species in tropical forests are rare (Terborgh et al. 1990, Thiollay 1999), making it difficult to obtain data sufficient to document those patterns and processes. In contrast to most other members of tropical bird communities, manakins (Pipridae) typically are common to abundant in the understory of tropical forests (Karr, Robinson et al. 1990) and, as a consequence, are excellent candidates for studies on various aspects of population dynamics (Worthington 1982, Théry 1992, Graham 1996). Surprisingly, although the breeding biology and behavior of many species of manakins are relatively well known (e.g. Chapman 1935; Snow 1962; Lill 1974a, b; Foster 1977, 1981; Robbins 1985; McDonald 1989, 1993a, b; Tello 2001), detailed, long-term comparative studies on population dynamics of manakins are lacking. The paucity of such critical information for one of the more common elements of tropical forest bird communities was a major stimulus for this paper.

There are several major objectives to this study that relate to population dynamics of manakins. The first objective is to describe seasonal patterns of habitat use and how those patterns vary among and within species. Although many general aspects of habitat use by manakins are well know (e.g. Skutch 1967, Hilty and Brown 1986, Stiles and Skutch 1989), most previous studies that focused on aspects of population dynamics of manakins (e.g. Worthington 1982, Théry 1992, Graham 1996) have been relatively short (<5 years). Many species of manakins, including all species studied here, are heavily dependent on fruit (Levey 1988, Loiselle and Blake 1990, Marini 1992, Rosselli 1994). Fruit abundance varies markedly in space and time (Wheelwright 1983, Blake and Loiselle 1991, Loiselle and Blake 1994, Rosselli 1994) and, consequently, abundances of manakins are hypothesized to exhibit temporal and spatial variation in use of habitats (Martin and Karr 1986, Levey 1988, Loiselle and Blake 1991). Knowing the relative importance or use of different habitats and how that use varies over time has implications for ecology (e.g. seed dispersal) and conservation. For example, loss of important seed dispersers may, over time, affect the composition of forests (Chapman and Chapman 1995, Cardoso da Silva and Tabarelli 2000, Loiselle and Blake 2001) whereas loss of specific habitats may have consequences for long-term survival of birds, particularly those that require more than one habitat during their annual cycle (e.g. elevational migrants; Stiles and Clark 1989).

A second objective is to compare and contrast patterns of movement among and within species, among habitats, and between seasons. Manakins are the primary seed dispersers for many shrubs and treelets in tropical forests (Loiselle and Blake 1999) and variation in movement patterns can affect seed dispersal (Murray 1988, Graham et al. 1995, Sun et al. 1997, Jordano and Schupp 2000). Yet, despite the potential importance of frugivore movements for seed dispersal and plant recruitment, we know relatively little about actual movement patterns and home-range sizes of most frugivores. The lek mating system of manakins (Lill 1974a, b; McDonald 1989; Tello 2001) is hypothesized to result in sexual and age-related differences in movements and recaptures (Graves et al. 1983). Adult male manakins, because of their attachments to lek sites, are more sedentary (i.e. smaller home ranges) than fe-

males and young males (Snow 1962, Lill 1974a, Graves et al. 1983, Théry 1992) and may not disperse seeds as widely or into as many microhabitats as do females and young males (Graham 1996, Krijger et al. 1997).

A third objective is to compare survival rates among species and, when possible between sexes and age-classes. High estimates of survival for adult male manakins (e.g. Snow 1962) contributed support to the hypothesis that tropical birds live longer than comparable temperate species. Later estimates of survival rates of tropical birds that were based on capture–recapture data (e.g. Karr et al. 1990, Johnston et al. 1997, Jullien and Clobert 2000) generally have been lower than those reported by Snow (1962) but still relatively high compared to many temperate species. Interpretation of survival-rate estimates can be complicated by whether or not transients (i.e. birds moving through an area that are not likely to be captured more than once) are accounted for or not (Pradel et al. 1997). When effects of transients are included, estimated survival rates (excluding the first recapture interval) generally are higher (e.g. Brawn et al. 1999). Nonetheless, differences in average survival rates among different tropical localities (e.g. Panama, Trinidad, Peru; see Francis et al. 1999) have led to the hypothesis that survival rates of tropical birds may vary geographically, with rates lower in Panama than elsewhere. Thus, we evaluate that hypothesis from the standpoint of manakins, with the prediction that survival rates in Costa Rica should be more similar to those of Panama (i.e. both sites are in Central America). The degree to which individuals are transients may be influenced by age and sex (e.g. Graves et al. 1983). Consequently, determining whether or not tropical birds do indeed have higher survival rates than temperate birds is an issue likely to be complicated by intraspecific variation in survival. Therefore, survival estimates should be calculated separately for different demographic groups (Francis and Piper 1999) but that has rarely been done.

To address these three objectives and their associated hypotheses, we answer a series of relatively specific questions. (1) Are there distinct seasonal patterns of abundance (as indexed by capture rate) in manakin populations, and do those differ predictably among species and habitats? (2) Do male and female manakins differ in rate of accumulation of new individuals, recapture percentages, and distances between recaptures? (3) Do survival rates vary among species, sexes, or habitats?

STUDY AREA

We conducted our research at Estacion Biológica La Selva, in the lowlands of northeastern Costa Rica (10°25′N, 84°01′W), and in the adjacent Parque Nacional Braulio Carrillo. La Selva encompasses ~1,500 ha, of which ~67% is old-growth forest. Braulio Carrillo (~45,000 ha) borders La Selva to the south; continuous forest extends from 36 m at La Selva to over 2,900 m atop Volcán Barva. Our main study sites were at approximately 40 to 75 m elevation at La Selva (referred to collectively as "lowland sites") and at about 500 and 1,000 m in Braulio Carrillo.

Lowland study sites included young second growth (YSG; pasture until about 1981), older second growth (OSG; approximately 25 to 35 years growth at the start of this study), and old-growth forest (OGF). The youngest plot was located within an ~40 ha tract of former pasture bordered by older second growth. Vegetation on that plot averaged 5 to 8 m in height at the start of this study (1985) but changed considerably over time (Loiselle and Blake 1994). The OSG plot was located within a relatively even-aged tract of approximately 20 to 25 ha bordered by old-growth forest and younger second growth. Trees averaged 15 to 20 m over much of the plot in 1985. Two OGF sites were within the main block of undisturbed forest of La Selva where canopy height reaches 30 to 40 m (Hartshorn and Peralta 1988). Sites in Braulio Carrillo were in old-growth forest. Canopy heights ranged from about 35 to 40 m at 500 m, to 30 to 35 m at 1,000 m. Further descriptions of those sites are in Blake and Loiselle (1991, 2000, 2001), McDade et al. (1994), and Lieberman et al. (1996).

La Selva receives ~4,000 mm rain annually (Sanford et al. 1994). The dry season typically lasts from about late January or early February to March or April, with a second, less-pronounced dry season in September and October. The seasonal pattern of rainfall in Braulio Carrillo is similar to that at La Selva, but the dry season is shorter and less pronounced. Mean monthly temperature at La Selva ranges from 29.7°C in January to 31.1°C in April and September (Sanford et al. 1994).

STUDY SPECIES

When we began our studies, six species of "manakins" occurred in La Selva and Braulio Carrillo: *Manacus candei*, *Pipra mentalis*, *P. pipra*, *Corapipo altera*, *Piprites griseiceps*, and *Schiffornis turdinus*. The taxonomic relationships of the latter two species, and their placement within the tyrannoid superfamily, is

TABLE 1.   Sample effort (number of years, number of mist-net hours per season, number of nets per site) for study sites in La Selva (lowlands) and Braulio Carrillo (elevations >100 m).

Site	Elevation (m)	Nets	Season	Years	Net hours
Young second growth (YSG)	36	30	Wet	8	3,248
			Dry	6	4,899
			Breeding	1	844
			Postbreeding	1	1,186
Old second growth (OSG)	45	30	Wet	2	826
			Dry	3	3,128
			Breeding	1	838
			Postbreeding	1	806
Tropical wet forest	50	60[a]	Wet	9	9,542
			Dry	7	7,419
			Breeding	1	1,193
			Postbreeding	1	1,449
Tropical wet forest	75	30	Wet	2	799
			Dry	2	1,202
Tropical wet forest	250	20	Wet	1	343
			Dry	1	949
Tropical wet, cool transition forest	500[b]	20	Wet	4	1,166
			Dry	5	2,499
			Breeding	1	288
			Postbreeding	1	872
Tropical premontane rain forest	1,000[c]	20	Wet	4	1,348
			Dry	5	2,712
			Breeding	1	520
			Postbreeding	1	1,007

[a] We used 30 nets during the first two seasons in 1985, expanding to 60 nets during the postbreeding season.

[b] Samples from 1985 and 1986 were from one site at 500 m; subsequent samples were from a second site at ~450 m, approximately 1–2 km north of the first site.

[c] Samples from 1985 and 1986 were from one site at 1,000 m; subsequent samples were from a second site at ~1,060 m, approximately 1–2 km south of the first site.

uncertain (American Ornithologists' Union 1998) but they likely are not Pipridae (Prum 1990). Because these two species were captured only five times each (*Piprites*—three times in old second growth, once each in old-growth forest at 50 m and 500 m; *Schiffornis*—five times in forest at 500 m), they will not be considered further. *Manacus* typically breeds in second-growth habitats of various kinds, including sufficiently large disturbed areas within old-growth forest (e.g. regrowth following landslides or large treefalls (Levey 1988, Stiles and Skutch 1989, J. G. Blake pers. obs.). *Corapipo* primarily breeds from 400 to 900 m and moves to lower elevations during the wet season (Skutch 1967, Stiles and Skutch 1989). *P. pipra* breeds from about 800 to 1,500 m in old-growth forest and rarely descends to lowland forest during the wet season (Levey 1988, Blake et al. 1990). *P. mentalis* prefers old-growth wet forest in lowlands but also occurs in taller second growth (Stiles and Skutch 1989, J. G. Blake and B. A. Loiselle pers. obs.).

METHODS

Birds.—We used mist nets (12 × 2.8 m, 36 mm mesh) to sample birds occurring in forest undergrowth at various times over the period from January 1985 to January 1994 (Table 1). Logistical and monetary constraints prevented us from maintaining a consistent sampling scheme across all years and sites so sample effort varied among sites and years; YSG and the OGF site at 50 m were sampled most often. Despite various known biases (Karr 1981, Remsen and Good 1996, Young et al. 1998), mist nets are an effective way to sample birds that occur in the understory (Karr et al. 1990; Young et al. 1998; Zakaria and Francis 1999; Blake and Loiselle 2000, 2001). Mist nets do not necessarily provide a true indication of abundance in different habitats because likelihood of capture may vary with habitat, species, and behavior. Mist nets do, however, provide an indication of the level of activity of birds in the lowest levels of the habitat being sampled, facilitating comparisons of species (e.g. manakins) that commonly occur at that level. Further, mist nets are particularly useful for species that are not well represented by other methods of sampling. For example, we recorded few manakins during point counts: 166 *Manacus*, 15 *Corapipo*, 4 *Pipra pipra*, and 179 *P. mentalis* in 19,908 observations (i.e. 0.83, 0.08, 0.02, and 0.90 %, respectively, of observations; Blake and Loiselle 2000, 2001). Comparable values for capture data are 4.8, 4.9, 0.6, and 9.2 %, respectively, of 12,054 captures.

Mist nets (Table 1) were placed 40 m apart in a grid arrangement (30 nets covering ~5 ha in YSG and OSG sites; 60 nets covering ~10 ha in one lowland OGF site) or along narrow trails (30 nets covering 4 to 5 ha at the second lowland OGF site; 20 nets per site at higher elevations, over approximately the same area). Differences in arrangement of nets might influence likelihood of recapturing individuals, particularly transients (D. J. Levey pers. comm.). We doubt that this is a substantial problem because recaptures within 1 h were ignored, percentage recaptures within a sampling period were comparable among sites, and overall recapture percentages were not related to arrangements of nets. Nets typically were opened from dawn to about 1300 CTZ (i.e. 7 h day^{-1}) on an average of two days during each sampling period at each site. When multiple sample periods occurred during a year, samples were approximately five to six weeks apart. All birds were banded with numbered aluminum leg bands and identified by sex and age (if possible). Recaptures of birds initially classified as "unknown" sex frequently allowed later determination of sex on the basis of plumage or presence of brood patches or cloacal protuberances. Birds that could not be aged or sexed were classified as "young or female" and were treated separately in analyses that included consideration of sex or age; otherwise, all birds were included in analyses.

Analyses.—Samples were divided into seasons ("late wet," December through January; "dry," February through April; "breeding," May through July; "postbreeding," August through October) based on average monthly rainfall totals at La Selva and on breeding phenology of birds (Levey and Stiles 1994). Most data presented here are based on captures during the late wet (hereafter referred to simply as "wet" season) and dry seasons as breeding and postbreeding samples were collected only during 1985. Total sample effort varied among seasons and years (Table 1) so comparisons (e.g. among species, between seasons) typically are based on capture rates (capture rate = number of birds captured per 100 mist-net hours, where 1 mist net open for 1 h is equivalent to 1 mist-net hour) per sample or season; for the latter, samples within a year were combined by season. Because we were interested in comparing levels of activity of manakins, all recaptures that were separated by at least 1 h were included; recaptures within a single day were not common, however.

We used chi-square contingency analyses to compare numbers of recaptures by sex or between seasons. Expected values for numbers of recaptures were based on number of mist-net hours and assumed no difference between seasons or sex. We used correlation analyses to determine if capture rates within a species followed similar patterns between sites and whether capture rates of different species showed similar patterns within a site. Correlations in capture rates between species or sites were based on data from all sample periods (i.e. not combined by season). All variables were tested for normality (Wilk-Shapiro test) and homogeneity of variances (Bartlett's test) prior to statistical analyses. Nonparametric tests (e.g. Spearman's correlation) were used when necessary (i.e. when variables violated assumptions of parametric tests, even after transformations—e.g. ln + 1). Degrees of freedom varied with comparison because of different numbers of sample periods per site. We used the Dunn-Šidák procedure (Sokal and Rohlf 1995) to adjust the error rate when multiple tests were performed on related data. All reported *P*-values reflect those adjustments.

We used capture–recapture analyses for open populations to estimate annual survival rates (Pollock et al. 1990); data from each sample period were included in the calculations. We used program MARK (White and Burnham 1999, White 2001) to evaluate four different models (notations follow Cooch and White [1998] and Francis et al. [1999]) that differed in assumptions regarding constancy of survival (φ) and capture (ρ) rates. Previous unpublished analyses that used program JOLLY (Pollock et al. 1990; see also Brawn et al. 1995) indicated that a reduced-parameter model with constant capture ($\rho.$) and survival ($\varphi.$) rates fit the data in most cases so we included that model (model $\varphi.\rho.$) in all analyses. Because number of mist-net hours (sample effort) varied somewhat among samples, we followed Francis et al. (1999) and also included a model with constant survival but time-specific capture rates (model $\varphi.\rho t$). Transients (and young birds) may affect survival-rate estimates (Johnston et al. 1997, Pradel et al. 1997, Brawn et al. 1999, Francis et al. 1999), so we included two models that incorporated two "age" classes (first capture and subsequent captures) and that assumed either constant (model $\varphi a2\rho.$) or time-specific (model $\varphi a2\rho t$) capture probabilities. Model selection was based on Akaike's Information Criterion adjusted (QAIC$_c$), when necessary, for over-dispersion in the data (described in Cooch and White 1998). We used program CONTRAST (Hines and Sauer 1989) to compare survival rates.

RESULTS

CAPTURE RATES

We accumulated 2,304 captures of 1,537 manakins during 49,083 mist-net hours.

Within species comparisons.—We captured *Manacus* 535 times (220 recaptures). Most captures were in YSG (75%) and OSG (19%); few individuals were captured in old-growth forest. Capture rates were higher in YSG than in OSG during all samples and were slightly higher
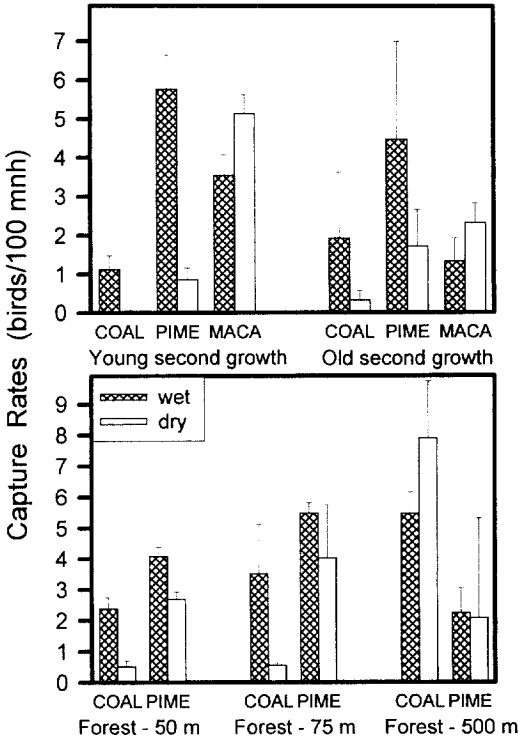
FIG. 1. Seasonal (wet season, dry season) capture rates (number of birds captured per 100 mist-net hours) in second growth and old-growth forest in La Selva Biological Station and Braulio Carrillo National Park, Costa Rica. COAL = *Corapipo altera*; PIME = *Pipra mentalis*; MACA = *Manacus candei*.

during the dry season than during the wet season (Fig. 1). Too few *Manacus* were captured in old-growth forests to warrant comparisons.

Corapipo (586 captures, 216 recaptures) capture rates in YSG and OGF sites at 50 and 500 m varied by site and season (Fig. 1). Capture rates were highest in OGF at about 500 m and lowest in YSG in both seasons. Capture rates declined from wet to dry seasons at both lowland sites but not at the 500 m site. Capture rates of *Corapipo* were correlated between YSG and OSG (r_s = 0.803, n = 9, P < 0.05) and between YSG and lowland OGF (r_s = 0.726, n = 20, P < 0.01) but not between other pairs of sites.

Most (92%) of the 73 *Pipra pipra* captures (26 recaptures) were in forest at ~1,000 m, where no other manakins were captured with any regularity (5 captures of *Corapipo*). Capture rates for *P. pipra* at 1,000 m were highest during the dry season in three of five years. Some *P.*

pipra moved to lowlands during the wet season where individuals were captured in YSG (1991, three captures) and lowland OGF (1992, three captures). Four individuals were captured at 500 m, including one during the wet and three during the dry season (1986).

Pipra mentalis was the most frequently captured species (1,110 captures, 305 recaptures). Capture rates were high both in second growth (YSG and OSG) and lowland OGF (Fig. 1). Capture rates declined from wet to dry seasons in all lowland sites but not in forest at 500 m; declines were stronger in YSG than in OGF at 50 m. Capture rates of *P. mentalis* were correlated between YSG and OSG (r_s = 0.746, n = 9, 0.10 < P < 0.05) and between YSG and lowland OGF (r_s = 0.551, n = 20, 0.10 < P < 0.05).

Between species comparisons.—Capture rates of *Corapipo, Manacus,* and *Pipra mentalis* varied by season in YSG but patterns of change were not similar (Fig. 1); *Manacus* showed no decline in capture rates from wet to dry season, in contrast to the other two species. Capture rates of *P. mentalis* and *Corapipo* varied between seasons in similar ways in YSG and in OGF at 50 and 500 m (Fig. 1). Capture rates of *P. mentalis* were greater than for *Corapipo* in lowland OGF and YSG in both wet and dry seasons, whereas *Corapipo* capture rates were higher than *P. mentalis* at 500 m during both seasons. Capture rates of *P. mentalis* and *Corapipo* were correlated in YSG (r_s = 0.816, n = 20, P < 0.01), lowland OGF (r_s = 0.613, n = 22, P < 0.01), and OGF at 500 m (r_s = 0.626, n = 13, 0.10 < P < 0.05). Capture rates of *Manacus* were not correlated with *P. mentalis* or *Corapipo*. Too few *P. pipra* were captured at sites below 1,000 m to require comparisons with other species.

ACCUMULATION OF INDIVIDUALS

Accumulation rates for male manakins were higher than for females except for *Manacus* in YSG (Fig. 2) in most cases. Sharp increases in numbers of new male (but not female) *Pipra mentalis* and *Corapipo* in lowland sites typically were associated with wet-season samples (Fig. 2). No such increases were noted for *Manacus* in YSG. The biggest increases for *Corapipo* males at 500 m typically occurred in dry-season (beginning of breeding) sampling.
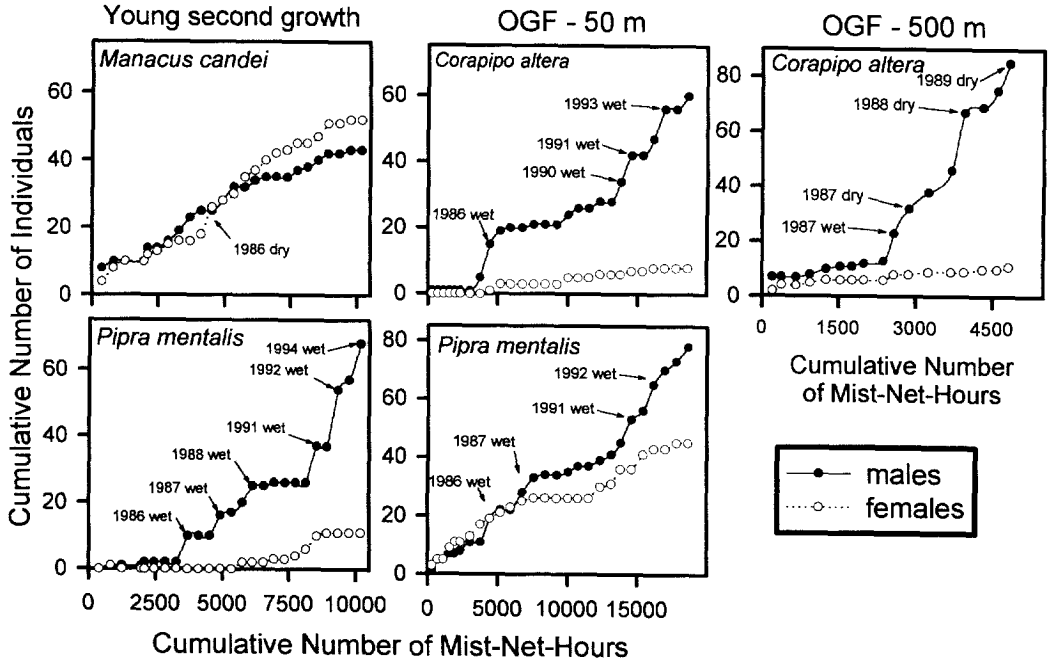
FIG. 2. Cumulative number of individuals (i.e. no recaptures) captured in young second growth (YSG) and old-growth forest (OGF). Season (wet or dry) and year of sample are indicated where large increases in numbers of individuals were noted.

RECAPTURES

Percentage recaptures.—Recaptures, as a percentage of total captures, increased rapidly in most cases but typically began to stabilize after 50 to 75 total captures. Total recapture percentage was lower for males (approximately 20 to 40%) than females (approximately 45 to 80%; $\chi^2 > 20.0$, df = 1, $P < 0.001$, all comparisons) except *Pipra pipra* at 1,000 m.

Differences in recapture percentages between sexes varied by species, season, and habitat. Recapture percentages for *Manacus* in YSG (Fig. 3) did not differ between wet and dry seasons for either sex and were significantly higher for females than males only in the dry season ($\chi^2 = 11.7$, df = 1, $P < 0.01$). Too few individuals were recaptured in OSG for analysis. Few *Corapipo* were recaptured in YSG. Recaptures accounted for a greater percentage of female than male *Corapipo* captured in lowland OGF during the wet ($\chi^2 = 15.1$, df = 1, $P < 0.01$) season but not during the dry season. Neither sex showed a difference in recaptures between wet and dry seasons. Female *Corapipo* were recap-

tured more frequently than males during the wet season at 500 m ($\chi^2 = 5.4$, df = 1, $0.10 < P < 0.05$) but not during the dry season ($\chi^2 = 3.24$, df = 1, $P > 0.10$). There was no difference in recaptures between seasons for either sex.

Recaptures of *Pipra mentalis* in YSG were higher in the wet season (Fig. 3) and were higher for females than for males ($\chi^2 = 14.0$, df = 1, $P < 0.01$). Recapture percentage was greater in lowland OGF for female than for male *P. mentalis* during the wet season ($\chi^2 = 15.2$, df = 1, $P < 0.01$) but not during the dry season. Males were more likely to be recaptured during the dry season ($\chi^2 = 11.3$, df = 1, $P < 0.01$) but females showed no difference between seasons in lowland OGF. Recapture percentages of *P. pipra* were higher for females than males at 1,000 m (70 vs. 62%) but the difference was not significant.

Recapture distances.—Most recaptures were within ~100 m of the previous capture (i.e. within a 2 to 3 net distance from one capture to the next; Table 2). That was true for movements within a sample (i.e. between days), between
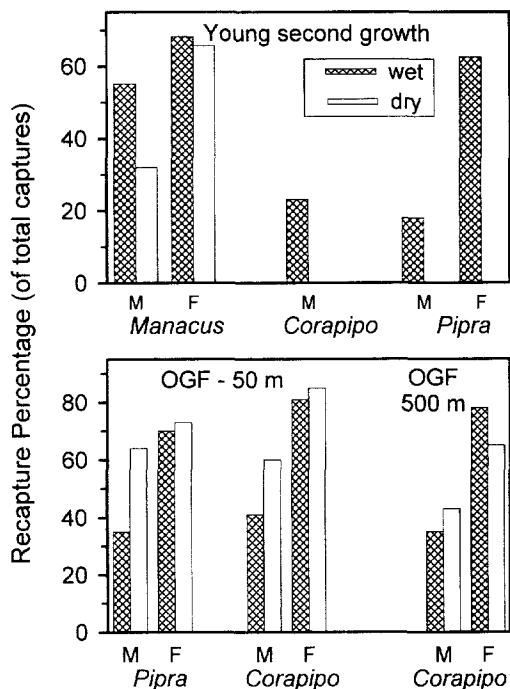
FIG. 3. Percentage of captures accounted for by recaptured individuals of *Manacus candei*, *Corapipo altera*, and *Pipra mentalis* during wet and dry seasons in second growth and old-growth forest (OGF). M = male; F = female.

samples, or between years (i.e. distance from the net the bird was last caught during one year to the distance from the net it was first caught during the subsequent year). Recapture distances were lower for male *Corapipo* and *Manacus* than for females, but differences were not significant (except for *Manacus* between sample distances, $t = 2.25$, df $= 21$, $0.10 < P < 0.05$). In contrast, recapture distances for male *P. mentalis* were not consistently less than for females. Mean between-year recapture distance for *Corapipo* in lowland OGF (i.e. nonbreeding site) was ~80 m for both males and females. Lowest between-year recapture distances were seen for *Manacus* in YSG (Table 2). Recapture distances for birds of unknown sex were variable for all species and not consistently greater or less than those for males and females.

Recaptures between habitats were relatively uncommon. Two *P. mentalis* (one female, one unknown sex) were recaptured between second-growth sites (~0.8 km apart) and between

second-growth and lowland old-growth forest (approximately 2 to 2.5 km apart). One male *P. mentalis* was originally captured in YSG in 1985 and subsequently caught (twice) in 1987 in OGF at 250 m (~6 km apart). One female *Corapipo* was captured in lowland OGF in 1988 and 1989 (i.e. with one migration interval), later captured at 500 m in 1989, and then recaptured at the lowland site in 1990, 1991, and 1994 (highland sites were not sampled after 1989). Ten *Manacus* (eight females, two unknown sex) were recaptured between the two second-growth sites.

SURVIVAL RATES

When analyses included all individuals (i.e. including individuals that could not be sexed), models that allowed survival rates in the first recapture interval to differ from those in subsequent intervals (model $\varphi a2\rho.$, model $\varphi a2\rho t$) were selected for all three species (Table 3). There was substantially greater support (based on Akaike weights) for the selected model for *Manacus* and *Corapipo* but not for *Pipra mentalis*. Survival rates for the first class ($\varphi 1$) were significantly less than for subsequent periods ($\varphi 2$) for both *Manacus* ($\chi^2 = 44.3$, df $= 1$, $P < 0.001$) and *P. mentalis* ($\chi^2 = 9.97$, df $= 1$, $P < 0.001$) but not for *Corapipo*. There was, however, no difference between $\varphi 2$ and $\varphi.$ for *Manacus* or *P. mentalis*; differences were greater but not significant for *Corapipo*.

Model $\varphi.\rho.$ (i.e. constant survival and capture probabilities) was selected for *Manacus* and *Pipra mentalis* when analyses were based on individuals of known sex (Table 3); support for the selected model relative to models that incorporated two classes for survival was typically greater for *P. mentalis* than for *Manacus*. Survival rates did not differ between sexes for *Manacus* (males, 0.76; females, 0.78) but was greater for female *P. mentalis* (0.81) than for males (0.61; $\chi^2 = 7.69$, df $= 1$, $P < 0.01$).

Models incorporating differences in survival between first and subsequent recapture intervals were selected for male and female *Corapipo*; selected models had substantially greater support than other models (Table 3). Survival rates for the first interval ($\varphi 1$) were higher than for subsequent intervals ($\varphi 2$) for manakins in forest at 50 m but the reverse was true at 500 m. In no case, however, was the difference signif-

TABLE 2. Mean distances (meters) between subsequent captures of the same individual within a sample, between samples within a year, and between years. Species: MACA—*Manacus candei*; PIME—*Pipra mentalis*; COAL—*Corapipo altera*. Sites: YSG—young second growth; OSG—old second growth; 50 m-old-growth forest at ~50 m. Ind.—number of individuals; Rec.—number of recaptures across all individuals.

Species	Site	Sex	Recaptures within sample				Recaptures between samples				Recaptures between years			
			Mean	SE	Ind.	Rec.	Mean	SE	Ind.	Rec.	Mean	SE	Ind.	Rec.
MACA	YSG	M	58	15.2	6	7	38	12.1	6	7	58	18.4	13	14
		F	74	20.2	13	22	77	8.6	17	25	69	8.3	30	61
		U	53	8.9	17	21	79	16.1	10	10				
MACA	OSG	F	70	11.6	11	20	69	23.1	5	7	59	13.0	10	14
		U	59	10.1	4	4	48	23.6	4	4				
PIME	YSG	M	92	17.3	7	7					100	20.8	5	7
		F	64	24.5	2	2	80		1	1	107	26.8	5	7
		U	88	15.7	11	14	117	27.5	2	2				
PIME	OSG	M									148	14.3	3	3
		F	68		1	2	80		1	1	83	3.0	3	3
		U	39	10.7	3	3	40		1	1				
PIME	50 m	M	83	11.2	17	19	111	17.7	14	19	115	17.2	21	33
		F	86	10.6	12	15	88	11.6	14	27	94	12.7	30	50
		U	100	12.3	27	31	198	37.7	10	11				
COAL	50 m	M	88	14.3	13	19	85	22.5	7	7	78	12.2	16	19
		F	92	15.9	4	14	93	26.7	3	5	79	9.9	8	18
		U	99	21.4	8	9	49	26.0	3	3				

icant. Too few adult female *Corapipo* were captured to allow separate analyses, but estimates for adult males were lower (but not significantly) than estimates based on males and females combined in lowland OGF (Table 3), suggesting that female rates were higher than males. Survival rates of *Corapipo* in lowland OGF (i.e. for migratory individuals on nonbreeding grounds) were comparable to those from forest at 500 m, where the species breeds. Analyses for *Corapipo* in lowland OGF were based on samples conducted only during the period when *Corapipo* occurs at that elevation.

DISCUSSION

Habitat use and patterns of movement.—Capture rates of the four species of manakins considered in this study varied both among and within habitats; such variation certainly reflected variation in actual abundance to a very large extent (i.e. as opposed to reflecting variation in use of different foraging strata, which has been suggested by some authors as a cause of variation in capture rates [e.g. Greenberg and Gradwohl 1986, Remsen and Good 1996]). Differences in capture rates among species and habitats largely reflected known (e.g. Stiles and Skutch 1989) breeding-habitat preferences of these species in Costa Rica (i.e. *Manacus* in second growth; *Pipra mentalis* in lowland oldgrowth forest; *P. pipra* and *Corapipo* in higher elevation old-growth forests) but also reflected seasonal variation in patterns of habitat use. Such variation, the extent of which differed among species and between sexes within a species, was associated with short-term (among habitats) and seasonal (among elevations) movements.

Elevational movements were evident for all species in this study except *Manacus*, but extent of such movements varied substantially among and within species. *Pipra pipra*, although primarily restricted to higher (1,000 m) elevations, occasionally descended to lowland old-growth forest during the wet season (Levey 1988), when other frugivores also migrate to lower elevations (Loiselle and Blake 1991). Periodic movements to lower elevations by normally sedentary species have been noted elsewhere (e.g. *Chlorospingus opthalmicus*; Winker et al. 1997) and may reflect annual variation in either fruit supplies or abiotic conditions (Levey and Stiles 1992, Loiselle and Blake 1992).

Corapipo altera is well known for its migration to lower elevations during the nonbreeding season (i.e. November to March; e.g. Slud 1960, Skutch 1967) and results from this study pro-

TABLE 3. Estimated apparent survival rates for three species of manakins in young second growth (YSG) and old-growth forest (50 m) in La Selva Biological Station and old-growth forest (500 m) in Braulio Carrillo National Park, Costa Rica. Survival rates (and standard errors) are estimated (using program MARK; White 2001) for all individuals and separately, when possible, by sex. Model $\phi a2,\rho t$ assumes survival rates differ between the first ($\phi1$) and subsequent (ϕ) capture periods and that capture rate is time dependent; Model $\phi a2\rho.$ assumes capture rate is constant; Model $\phi.\rho.$ assumes constant survival and capture rate. The model selected by AIC_c is in bold. EH—number of distinct encounter histories; Ind's—number of individuals captured; A-wt.—Akaike weight.

Species	Site	Sex	EH	Ind's	$\phi(a2),\rho(t)$			$\phi(a2),\rho(.)$			$\phi(.),\rho(.)$	
					$\phi1$(SE)	ϕ(SE)	A-wt.	$\phi1$(SE)	ϕ(SE)	A-wt.	ϕ(SE)	A-wt.
Manacus candei	YSG	all	77	336	**0.11(0.06)**	**0.59(0.04)**	**0.686**	0.12(0.07)	0.65(0.04)	0.308	0.60(0.04)	0.004
		M&F	66	191	0.47(0.17)	0.73(0.04)	0.001	0.50(0.19)	0.77(0.04)	0.411	**0.75(0.04)**	**0.587**
		M	31	62	0.60(0.77)	0.79(0.13)	0.00	0.70(0.81)	0.76(0.09)	0.249	**0.76(0.09)**	**0.751**
		F	41	129	0.53(0.18)	0.78(0.05)	0.062	0.52(0.17)	0.82(0.05)	0.385	**0.78(0.04)**	**0.397**
Pipra mentalis	50 m	all	84	478	0.15(0.06)	0.55(0.04)	0.437	**0.22(0.10)**	**0.56(0.04)**	**0.444**	0.53(0.04)	0.406
		M&F	72	244	0.75(0.21)	0.68(0.04)	0.00	0.92(0.24)	0.69(0.04)	0.371	**0.70(0.04)**	**0.625**
		M	42	121	0.47(0.23)	0.57(0.07)	0.00	0.73(0.34)	0.60(0.07)	0.274	**0.61(0.06)**	**0.726**
		F	37	123	0.45(0.00)	0.93(0.23)	0.00	1.00(0.00)	0.79(0.05)	0.361	**0.81(0.04)**	**0.639**
Corapipo altera	50 m	all	36	149	**0.43(0.14)**	**0.56(0.06)**	**0.996**	0.60(0.21)	0.62(0.06)	0.001	0.62(0.06)	0.002
		M&F	32	104	**0.71(0.19)**	**0.62(0.07)**	**0.846**	0.81(0.24)	0.66(0.06)	0.046	0.67(0.06)	0.108
		M	26	79	1.00(0.00)	0.47(0.10)	0.004	**1.00(0.00)**	**0.49(0.09)**	**0.795**	0.58(0.08)	0.200
	500 m	all	26	120	**037(0.25)**	**0.59(0.18)**	**0.905**	0.50(0.36)	0.42(0.12)	0.025	0.43(0.11)	0.070
		M&F	26	99	**0.49(0.28)**	**0.66(0.19)**	**0.774**	0.59(0.36)	0.47(0.12)	0.060	0.48(0.12)	0.166
		M	24	88	**0.21(0.19)**	**0.66(0.21)**	**0.479**	0.25(0.26)	0.48(0.14)	0.153	0.44(0.12)	0.368

vide further and direct evidence (i.e. recaptures between elevations) of such movements (see also Levey 1988). Capture rates in lowland habitats were much higher during the wet season than during the dry season, reflecting the timing of movements downslope and back to breeding grounds at higher elevations. *Corapipo* breeds in old-growth forest and prefers old-growth forest during the nonbreeding season as well; capture rates in younger habitats typically were lower than in older forests and also were more variable. Although second-growth habitats may not be preferred, they may provide an important alternative habitat during some periods because of abundance of fruit typically found in such habitats (Levey 1988, Blake and Loiselle 1991).

Pipra mentalis is a common breeding resident in lowland old-growth forest at La Selva. Individuals of this species also regularly occur in disturbed habitats (Levey 1988) although such occurrences are not necessarily related to breeding; no leks, for example, were found on or near our second-growth plots. Recaptures of individuals between old-growth and young forests demonstrate that *P. mentalis* moves among habitats at La Selva, presumably to take advantage of abundant supplies of fruit found in younger areas (see Graham 1996).

Regular seasonal changes in capture rates of *Pipra mentalis* in both young and old-growth forest in the lowlands likely reflect elevational movements by some individuals (Levey 1988). Capture rates of *P. mentalis* and *Corapipo*, the latter of which does not breed in lowlands and which is, with rare exceptions, completely absent from lowlands during the breeding season (Slud 1960, Skutch 1967, Levey 1988, J. G. Blake and B. A. Loiselle pers. obs.), followed similar patterns in lowland sites and in forest at 500 m, indicating that *P. mentalis* makes regular elevational movements during the same time periods as *Corapipo*. In contrast, capture rates of *Manacus* did not display the same seasonal variation and were not correlated with capture rates of other species, providing no evidence for or suggestion of seasonal movements.

Accumulation rates and recaptures.—New individuals (i.e. individuals not previously captured; Fig. 2) continued to be captured throughout this study. Such individuals likely reflect movement of transients through the study sites as well as production of young birds

within the sites. Rates of accumulation of male *Pipra mentalis* and *Corapipo altera* likely reflected movements by elevational migrants. The largest increases in captures of new individuals in lowland forests occurred each year in the wet season (i.e. during the period when frugivorous elevational migrants descend to lowland old-growth forests). Although an increase in captures of new individuals could represent production of young during the previous breeding season, that is not a likely explanation for the observed increases. First, no comparable increase in captures was noted during 1985 in the period after the main breeding season. Second, increases were noted in adult males as well as green-plumaged birds (i.e. juveniles and adult females). Third, there were corresponding increases for *Corapipo* but not for *Manacus*. Large increases in male *Corapipo* at 500 m tended to occur in dry-season samples, which coincided with the period when many individuals were moving to higher elevations to breed. Thus, many of the newly captured individuals likely were transients.

Differences between males and females in accumulation of new individuals may reflect both sex and age-related differences in movement patterns (Graves et al. 1983). The greater accumulation of males versus female *Pipra mentalis* and *Corapipo* could be a consequence of young males wandering over larger areas (Graves et al. 1983) or greater representation of males among elevational migrants. However, the difference also may be, at least partially, a reflection of the fact that not all birds were sexed, likely resulting in an under-estimate in the number of females captured (see below). *Manacus*, however, displayed a somewhat greater accumulation rate for females. *Manacus* are resident and do not make elevational movements so any sex-related differences in elevational movements would not affect results for this species.

Previous studies have suggested or found that adult male manakins are more sedentary (have smaller home ranges) than females (Snow 1962, Lill 1974b, Graves et al. 1983, Théry 1992; but see Graham 1996). In this study, recapture percentages were higher for females in all four species, suggesting that females concentrate their activities in restricted areas as well. Several factors may influence the likelihood of being recaptured. First, if adult

males are more sedentary, they may move less often and over shorter distances, which could reduce the possibility of being captured (Remsen and Good 1996). They may learn the locations of nets and simply avoid them, or, by moving less often, they may simply decrease the chance of hitting a net. Females, by contrast, may be more likely to encounter a net simply because they move more often or over greater distances. A potentially greater problem is caused by our inability to sex all individuals when first captured. Recapture percentages apply only to birds whose sex is known and, thus, probably overestimate the actual percentage of recaptures by sex because of the occurrence of unknown sex birds. A large proportion of captured individuals were in "female" plumage; that is, they were either adult females, juvenile females, or first year males. Such birds, if never recaptured, remained classified as unknown with respect to sex. What proportion of those transients were males or females is unknown. If a majority was, in fact, females, then recapture percentage of females would drop; male recapture percentage would drop by a smaller amount. Radio-tracking data from Théry (1992) and Graham (1996) indicate, however, that juvenile males wander over much greater distances, decreasing the chance of recapture and causing inflated estimates for males as well. Thus, our data on recaptures may be an overestimate for both males and females. Without determining sex of all birds when first captured, it is difficult to determine how much estimates may vary. Some previous studies have estimated sex ratios at 1:1 for some species of manakins (e.g. Snow 1962) but that may not always be true (e.g. *Corapipo altera*—2.85:1 male to female ratio, including one month [February] with a 26:1 ratio, Rosselli 1994; *Chiroxiphia pareola*—1:1.75, Graves et al. 1983). Thus, we can not simply assume that a majority of unsexed birds in our study were, in fact, female.

The recapture data do provide evidence for philopatry by residents and elevational migrants. The former is not unexpected given that lek locations are consistent across years (J. G. Blake and B. A. Loiselle pers. obs.). Data from *Corapipo* provide the strongest evidence for philopatry to nonbreeding sites. Sixteen males and eight females were recaptured between years (often multiple years) in lowland old-growth forest; most recaptures were in the same or adjacent net sites, indicating that individuals had the ability to return to the same location year after year. A similar pattern has been noted for some latitudinal migrants (e.g. *Hylochicla mustelina, Oporornis formosus, Seiurus aurocapillus*) at La Selva (Blake and Loiselle 1992).

Survival rates.—Early estimates of higher survival rates in tropical versus temperate species were based, in large part, on data from adult male manakins at leks (e.g. 89% survival for adult male *M. manacus*, Snow 1962; 79% when all nonrecaptured individuals were included in the estimates, Skutch 1985). The hypothesis that tropical species experience greater survival was challenged by Karr et al. (1990) who reported much lower survival rates for 25 species of tropical birds. Survival rate estimates (based on program JOLLY) for manakins in Panama (Brawn et al. 1995) were 0.51 for *Pipra coronata*, 0.72 for adult and 0.22 for juvenile *P. mentalis*, and 0.47 for *Manacus vitellinus*. These estimates were later criticized because they did not fully account for the influence of transient individuals (Johnston et al. 1997). Using such models, survival rates for manakins have ranged from 0.74 for female *M. manacus* on Trinidad to 0.56 for *P. serena* adults in French Guiana (Table 4). Estimates for *M. candei* in Costa Rica were higher than for *M. vitellinus* in Panama (although effects of transients were not included in that estimate) and comparable (considering females or males) to *M. manacus* on Trinidad (Table 4). Our estimates for *P. mentalis* (0.70 for adults, 0.56 for all individuals) are comparable to those of *P. mentalis* in Panama and to those of other *Pipra* as well (Table 4). Thus, data from manakins are not consistent with the suggestion that survival rates of birds from Panama are, overall, less than for other areas is South America (see Brawn et al. 1999, Francis et al. 1999).

Several factors may influence survival rates, including variation in resource abundance, climate, and predation risk. Our estimates for *Manacus candei* are based on samples collected in YSG habitats whereas estimates for *M. vitellinus* in Panama come from older forest. Both species prefer younger habitats (Ridgely and Gwynne 1989, Stiles and Skutch 1989, J. G. Blake and B. A. Loiselle pers. obs.) and the lower survival for *M. vitellinus* may reflect habitat differences in survival rates (see Winker et al. 1995). Brawn

TABLE 4. Summary of survival rates estimated for *Manacus* and *Pipra* species. Models assumed Estimated survival (ϕ) rates were either constant (.), time-specific (*t*), or differed between first and subsequent recapture periods (*a2*); capture (ρ) rates were assumed to be either constant (.) or time-specific (*t*). For models assuming two survival rates ($\phi a2$), survival rate is given only for the subsequent periods (i.e. not including the first recapture interval).

Species	Group	Model	ϕ	Location	Source
Manacus manacus	Females	$\phi.\rho t$	0.74	Trinidad	Johnston et al. 1997
Manacus vitellinus	All birds	$\phi.\rho$	0.47	Panama	Brawn et al. 1995
Manacus candei	All birds	$\phi a2\rho t$	0.59	Costa Rica	This study
Manacus candei	Adults	$\phi.\rho.$	0.75	Costa Rica	This study
Pipra coronata	All birds	$\phi t\rho t$	0.51	Panama	Brawn et al. 1995
Pipra mentalis	Adults	$\phi a2\rho t$	0.66	Panama	Brawn et al. 1999
Pipra mentalis	All birds	$\phi a2\rho$	0.56	Costa Rica	This study
Pipra mentalis	Males & females	$\phi.\rho.$	0.70	Costa Rica	This study
Pipra erythocephala	All birds?	$\phi a2\rho t$	0.69	Trinidad	Johnston et al. 1997
Pipra serena	Adults	$\phi.\rho$	0.56	French Guiana	Jullien and Clobert 2000
Pipra fasciicauda	All birds?	$\phi a2\rho t$	0.77	Peru	Francis et al. 1999

et al. (1999) suggest that lower survival rates in Panama compared to Trinidad might be related to the absence of *Micrastur* species from Trinidad; three species of forest-falcons are present in the Panama site. However, our survival rates for *Manacus* and *Pipra* are comparable to those from Trinidad and there are three species of *Micrastur* at La Selva (the same three as in Panama).

High variation in resources may lower survival rates as well (Stiles 1992). For example, annual survival rates for the lek-breeding hummingbird *Phaethornis superciliosus* was 57% at La Selva. Seasonal variation in availability of flowers is marked and mortality during the nonbreeding season can be substantially higher than during the breeding season when flowers are more abundant (Stiles 1992). In contrast, *Ph. guy* had an estimated survival rate of 90% on Trinidad (Snow 1974) where suitable flowers are available throughout the year. Similarly, differences in fruit availability may underlie differences in survival between *Manacus vitellinus* in Panama and *M. candei* in Costa Rica. Rainfall and fruit abundance are more seasonal in Panama than in La Selva. Fruits are available throughout the year in second growth at La Selva (Blake and Loiselle 1991) and may, at least partially, account for the higher survival rate of *M. candei*. The same may be true on Trinidad for *M. manacus* (see Stiles 1992).

Higher survival on nonbreeding versus breeding grounds is one suggested reason for evolution of migration (e.g. Nichols 1996). Similarly, fidelity to a particular nonbreeding site may produce greater familiarity with that site and lead to greater survival (Nichols et al. 1983, Diefenbach et al. 1988, Rappole 1995, Winker et al. 1995). Survival rates for *Corapipo altera* on nonbreeding grounds (i.e. lowland OGF at La Selva) were as high or higher than survival rates of individuals at 500 m, where *Corapipo* breeds. Not all individuals migrate (Rosselli 1994) or migrate as far, so captures during the nonbreeding season at breeding elevations may include residents as well as individuals from higher elevations.

Summary.—In summary, manakins display considerable intra- and interspecific variation in use of second-growth and old-growth habitats. At La Selva, elevational movments by *Pipra* and *Corapipo* are pronounced and contribute to the observed variation in capture rates of these species. Increased use by these species of lowland second-growth habitats during the nonbreeding season illustrate the potential value of maintaining a mix of both young and old habitats. Differences between males and females in recapture rates and rates of accumulation of individuals illustrate the need for further studies that more closely examine population dynamics for separate demographic groups. Similarly, differences in survival rates between species and sexes clearly warrant further, more detailed studies if we are to fully comprehend the population dynamics of tropical bird species.

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