



Effects of a Severe Drought on the Population Biology of a Tropical Hummingbird

Author(s): F. Gary Stiles

Source: *Ecology*, Vol. 73, No. 4 (Aug., 1992), pp. 1375-1390

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/1940683>

Accessed: 02-08-2015 18:52 UTC

REFERENCES

Linked references are available on JSTOR for this article:

http://www.jstor.org/stable/1940683?seq=1&cid=pdf-reference#references_tab_contents

You may need to log in to JSTOR to access the linked references.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Ecological Society of America is collaborating with JSTOR to digitize, preserve and extend access to *Ecology*.

<http://www.jstor.org>

EFFECTS OF A SEVERE DROUGHT ON THE POPULATION BIOLOGY OF A TROPICAL HUMMINGBIRD¹

F. GARY STILES

Museo de Historia Natural, Instituto de Ciencias Naturales,
Universidad Nacional de Colombia, Bogota, Colombia

Abstract. At Finca La Selva, in the Caribbean lowlands of Costa Rica, the Long-tailed Hermit (*Phaethornis superciliosus*) has a long breeding season (December or January through August or September) during which flowers are abundant, followed by a severe but predictable season of flower scarcity in late October–November, during which most of the annual mortality normally occurs. In 1973, the third of a 4-yr population study of marked lek males, an unusual drought caused a severe flower shortage at the height of the breeding season. During the latter part of the breeding season lek activity of males was reduced, successful breeding by females was drastically curtailed, and masses of both sexes dropped to levels lower than those of the lean season. Interrupted molt, an indicator of energy stress normally seen only in a minority of breeding females, was observed in 25% of adult males, and 50% of females, in 1973. Survivorship of lek males through the breeding season dropped from 90% in normal years to $\approx 60\%$, and the total lek population at the start of the 1974 breeding season was one-third lower than before the drought in 1973; the cohort of yearling males was most strongly affected. Recovery of numbers and age structure of the lek male population to pre-1973 levels required 3–4 yr. Jolly-Seber analyses showed close agreement with survivorship as determined by direct observation (possible because of the lek social system), and permitted estimation of other parameters of interest: populations of marked and unmarked males, probability of recapture of marked males, and recruitment. The average annual survivorship of male *P. superciliosus* (in normal years) is near the mean value reported for a series of tropical species. A simple model of the reproductive output of female *P. superciliosus*, assuming no sexual differences in survivorship, suggests that a female breeding only in the prime breeding season (roughly February–July, when over 80% of the fledglings are normally produced) will no more than replace herself in the population; breeding throughout 8–9 mo will permit her to increase her reproductive output by up to 10%, which agrees well with the 3+ yr required by the (male) population to recover from the drought. Possible implications of these findings for tropical bird demography and conservation are discussed.

Key words: Costa Rica; demography; hummingbirds; lek social systems; Long-tailed Hermit; *Phaethornis superciliosus*; population biology; survivorship.

INTRODUCTION

Compared to their temperate-zone relatives, many birds of the humid tropics supposedly can be characterized by more sedentary populations at or near carrying capacity, small clutches, and long breeding seasons but low nesting success, and relatively intense and prolonged parental care (reviews in MacArthur 1972, Skutch 1975, 1985, Ricklefs 1983, and Faaborg 1988). High adult survivorship is also often included in this list (e.g., Snow and Lill 1974, but see Karr et al., *in press*). Many of these features are presumably related to less extreme fluctuations of climate and resources in the wet tropics, in comparison with higher latitudes; conversely, many tropical birds may be sensitive to relatively small resource fluctuations in the scheduling of energy-demanding activities (cf. Worthington 1982,

Stiles 1985). However, predictability of resource levels may be as important as absolute resource abundance in the ultimate programming of a bird's annual cycle. A normally reliable season of abundant resources might select for proximate mechanisms to ensure that costly activities like breeding and molt will occur at this time (Lack 1968). Conversely, a predictable season of scarcity might select for timing mechanisms that preclude overlap of breeding or molt with this "lean season" (Fogden 1972, Stiles 1980; see also Terborgh 1983). The stresses of such a lean season could be cushioned by shifts in daily time and energy budgets, shifts in resource use, or emigration (review in Foster 1977).

Such a tropical bird population, whose annual cycle is scheduled around a predictable lean season, might be especially vulnerable to rare, unpredictable energy shortages during a season of normally abundant resources, when energy-demanding activities like breeding or molt have been programmed. With low reproductive rate and without a large population of

¹ Manuscript received 26 November 1990; revised 13 June 1991; accepted 26 June 1991; final version received 8 September 1991.

nonbreeding floaters, such a population might require considerably longer to recover from such a crisis than would populations of temperate-zone birds with opposite characteristics (cf. Brown 1969, Holmes and Sturges 1975).

Few long-term studies of tropical birds have identified such stressful periods and attempted to determine their effects upon the populations concerned. Faaborg (1982) found that mist-net captures of frugivores and nectarivores declined more than did those of insectivores following a drought during the breeding season in Puerto Rico, but he did not conduct detailed censuses, determine breeding success or resource abundance directly, nor monitor populations on a year-round basis. On Barro Colorado Island, Panama, periodic fruit shortages have been documented, with anecdotal evidence of severe effects upon mammalian frugivores, but with few data for birds (Foster 1982). The possible effects of an unusual shortage of ripe fruit during the breeding season upon the nutrition and time budget of a tropical manakin were discussed by M. S. Foster (1977), but she was unable to document any appreciable impact on the bird's population biology. Possible population changes of several species of lowland tropical birds in Panama during El Niño years were discussed by Karr (*in press*), but neither populations nor resources were monitored on a year-round basis. Although abundance of foliage and litter arthropods was estimated quantitatively by Karr and Brawn (1991) during and after an El Niño year, no consistent correlations between these parameters and captures of understory birds were found. However, the correspondence between the arthropods monitored and the specific resources required by particular bird species was unknown.

The assumption that tropical bird populations exist at or near carrying capacity seems to be based mainly upon theoretical considerations: quantitative data relating populations of neotropical bird species with fluctuations in their particular resources over long periods are virtually nonexistent. Worthington's (1982) study of two manakin species on a small island in Panama suggests that populations were continuously at or near carrying capacity, such that only when fruit availability was high was breeding possible. However, she did not monitor survivorship, her study only lasted 1 yr, and the insular nature of her study site may have affected her results: elsewhere, small frugivores like manakins make seasonal movements between habitats or elevations (cf. Levey 1988, Rosselli 1989, Loiselle and Blake 1991). Many studies have demonstrated seasonal fluctuations in food resources of tropical birds, including regular periods of scarcity (e.g., Fogden 1972, Stiles 1978, Levey 1988; see also Skutch 1950, 1985, and Karr and Brawn, *in press*). However, most studies have focused on the community level, comparing abundance of a general class of resource (e.g., fruit or flowers) with that of a general class of consumers (frugivorous or

nectarivorous birds). Conclusions reached at this level might be misleading for particular species if consumers specialize upon particular resources to any degree, and if particular consumers and their sets of critical resources show different seasonal patterns (Stiles 1985, Rosselli 1989).

Thus, there is a need for studies in which quantitative data on resource availability and population biology of particular species of tropical birds are combined to document the effects of unpredictable resource scarcity. Without such data, the supposed vulnerability of tropical species remains hypothetical, and theoretical and management implications of such vulnerability (e.g., Wilson and Willis 1975, Diamond 1976) lack a solid foundation. This paper presents such data for a hummingbird population of the wet lowland tropics.

Between 1971 and 1975, I studied the population biology of the Long-tailed Hermit (*Phaethornis superciliosus*) in the Caribbean lowlands of Costa Rica, an extension of a study of lek behavior (Stiles and Wolf 1979). During the 1973 breeding season a severe drought occurred, presenting me with the opportunity to observe how the bird's population biology and floral food resources were affected. Intermittent observations through 1981 allowed an assessment of the long-term effects of the drought. This study thus evaluates the extent to which *P. superciliosus*, a sedentary tropical bird faced by a predictable annual lean season, is vulnerable to an unpredictable food shortage during a season when flowers are normally abundant and reproductive activity is intense.

STUDY AREA

This study was carried out at Finca La Selva, a biological station of the Organization for Tropical Studies, at 10°26'N, 84°1'W, at an elevation of ≈75 m, in the lowlands of northeast Costa Rica. The climate and vegetation of La Selva are described in Petriceks (1956), Holdridge et al. (1971), and Janzen (1983); the avifauna is discussed in general terms by Slud (1960), Blake et al. 1990, and Levey and Stiles (*in press*). The phenology of the food plants of *P. superciliosus* was discussed by Stiles (1977, 1978); the annual cycle, lek behavior, and selected aspects of the population biology of this species have been treated by Stiles and Wolf (1974, 1979) and Stiles (1980). The climate of La Selva features a dry season from late December or January through March or early April, but even in the driest month, February, rainfall averages over 150 mm; between May and December, monthly rainfall averages 300–500 mm (Fig. 1).

THE BIRD

P. superciliosus is a typical dull-colored member of the hermit subfamily Phaethorninae. Males and females are identical in plumage, although males are larger and heavier on the average; most individuals can be reliably sexed by measurements (Stiles and Wol

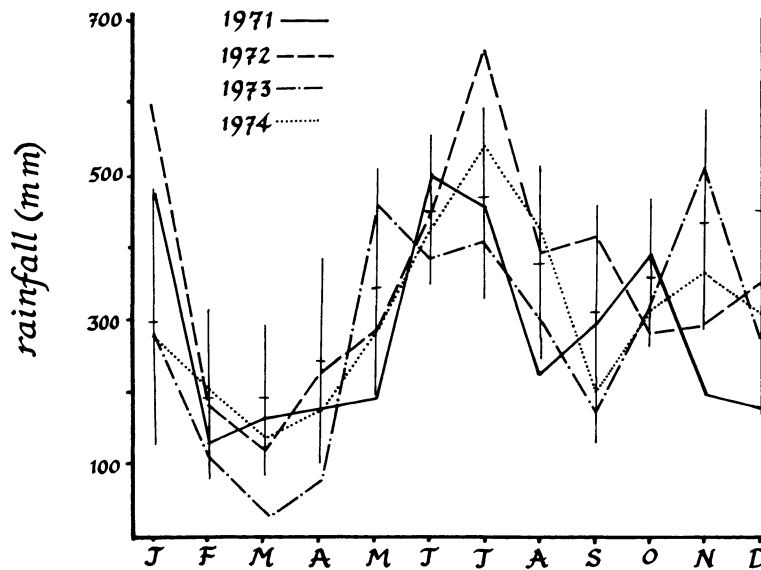


FIG. 1. Monthly rainfall at Finca La Selva, Costa Rica: 18-yr (1957–1975) means ± 1 SD, and monthly totals, 1971–1975.

1979). During the long breeding season, males spend most of their time defending territories on leks. At La Selva there is roughly one lek per square kilometre. Females range widely and nest in the areas between leks, and may visit several leks in the course of a breeding season. Both sexes visit scattered, nectar-rich flowers along regular foraging routes; males often range $\frac{1}{2}$ –1 km from leks to forage on a daily basis (Stiles and Wolf 1979; see also Gill 1988). There is a single annual molt, which overlaps breeding to varying extents in different individuals, molt timing in each bird apparently being keyed by its hatching date (Stiles and Wolf 1974). The peaks of breeding and molt in the *P. superciliosus* population coincide with peaks of flower availability in the dry and early wet seasons, respectively. A very pronounced period of flower scarcity occurs regularly between about late October and early December of each year; most of the annual mortality falls in this “lean season” (Stiles and Wolf 1979, Stiles 1980).

METHODS

Flowering phenology.—Between February 1971 and March 1975 I made monthly counts of the numbers of fresh, open flowers on 5–10 marked plants or clones of most species of hermit food plants at La Selva. I paid particular attention to the genus *Heliconia*, species of which are the most important food plants of *P. superciliosus*. For these species, I also monitored the production of new inflorescences. In particular, *H. pogonantha* (Fig. 2) is the bird’s mainstay during the first half of the breeding season, and usually produces abundant flowers over a period of 5–6 mo (Stiles 1975, Stiles and Wolf 1979). For other species of hermit food plants with relatively scarce, scattered flowers, I made month-

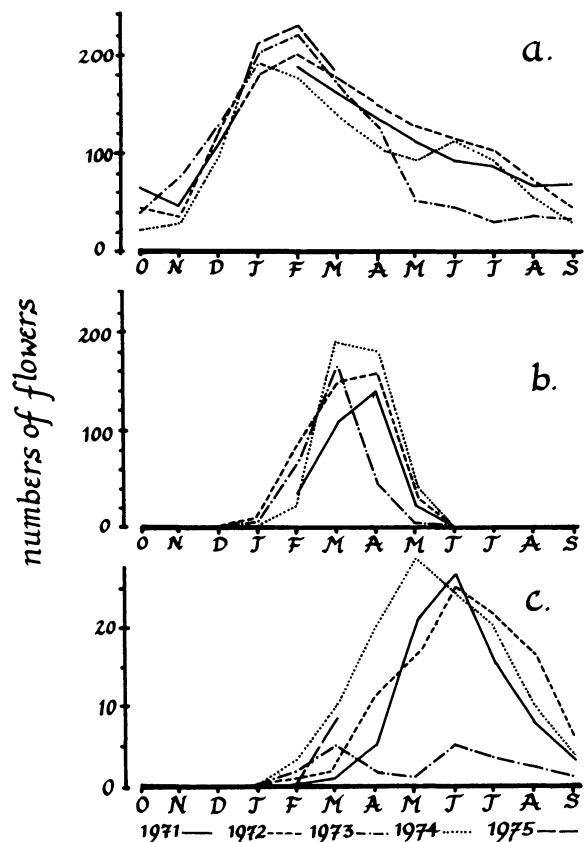


FIG. 2. Flowering of the three major dry season food plants of *Phaethornis superciliosus* at Finca La Selva, 1971–1975. (a) *Heliconia pogonantha*; (b) *H. wagneriana* (for these species counts of the numbers of flowers on 10 census clumps are given); and (c) *Costus pulverulentus*, for which numbers of flowers counted on 2.5 km of trails in the northern part of La Selva are given.

TABLE 1. Aspects of flowering of two species of *Heliconia*, 1971–1975.

A) Production of new inflorescences per trimester on 10 census clumps of <i>Heliconia pogonantha</i> .					
Trimester	Year				
	1971	1972	1973	1974	1975
January–March	31	25	37	24	28
April–June	29	24	9	23	25
July–September	11	8	13	7	...
October–December	10	56	62	73	...
B) Numbers of shoots and maximum number of flowers counted each year on 10 census clumps of two species.					
<i>Heliconia pogonantha</i>					
No. shoots start of blooming season	278	265	273	258	249
Max. no. flowers in blooming season	189	198	216	192	188
Max. no. flowers/shoot	0.68	0.75	0.79	0.74	0.76
<i>Heliconia wagneriana</i>					
No. shoots start of blooming season	105	115	137	132	120
Max. no. flowers in blooming season	136	156	177	187	...
Max. no. flowers/shoot	1.29	1.36	1.32	1.42	...

ly counts of flowers along ≈ 4 km of trails in the northern half of the La Selva property.

Unfortunately, only the latter method directly estimates absolute flower availability. The former method provides precise data on the distribution of flowering through the year on the individuals (or clones) censused, but is only an approximation to the total numbers of flowers available in the habitat, especially in comparing different years. However, the total number of shoots censused, and the maximum flower counts, were quite similar between years (Table 1), and I detected no pronounced changes in overall abundance of any *Heliconia* species during the study period. It is also my strong (albeit subjective) opinion that the plants or clones I censused were typical of their populations in terms of flowering; since the census clumps were scattered along ≈ 4 km of trails, I perforce observed most of these populations during each census. I therefore conclude that flower counts on 10 census clumps are quite representative of absolute flower availability to *P. superciliosus*, but emphasize that they are not a direct measurement thereof; this problem should be taken into account when choosing a method for quantifying resource availability (cf. Blake et al. 1990).

Hummingbird survivorship and population trends.—Because I could not observe or recapture female *P. superciliosus* consistently, I base my population estimates upon censuses of lek males. All males were individually color marked with back paint and acetate leg tags (Stiles and Wolf 1973); between 1971 and 1975 I marked 415 *P. superciliosus*, including 192 known lek males. In addition, L. Wolf and I marked ≈ 70 males in 1969 and 1970, some of which figure in the present study. I monitored survival and lek residence of most of these males through the study period; males were recaptured at intervals to refurbish their markings and to obtain data on mass and molt. My most reliable data were taken on Lek I (cf. Stiles and Wolf 1979),

where censuses and mist-netting were conducted nearly monthly through mid-1974, and less frequently thereafter. During 1971 and 1972, I censused and netted at Lek II several times per year; from 1973 to 1975, I censused and netted at Lek III at 3-mo intervals. Because of the longer intervals between marking sessions on Leks II and III, a few birds undoubtedly lost their markings between censuses, making survival data less reliable for these leks. Following the main study period, counts of the numbers of males singing on each lek were made in January or February of 1976, 1978, and 1981; marking was not attempted except on Lek I in 1981.

I consider survival within and between breeding seasons separately. Previous study (Stiles and Wolf 1979) has shown that survival is high through the long breeding season (December or January through July or August), but mortality increases sharply between breeding season, and is mainly concentrated in the “lean season” between about mid-October through early December.

Lek activity of male *P. superciliosus*.—Through early 1972, song activity on *P. superciliosus* leks was measured quantitatively (cf. Stiles and Wolf 1979), but these measurements were discontinued after February 1972. However, an approximate measure of lek activity for later months is provided by mist-net captures. For those months in which both types of data are available, the number of *P. superciliosus* captured per net-hour (one 12 m net open for 1 hour) was found to be significantly correlated with total singing activity (Spearman $r_s = 0.712$, $P < .05$, $n = 13$). Given comparable weather conditions, capture rates on different leks were quite similar, hence data for all leks were combined, giving a measure of lek activity for most months throughout the study. For purposes of analysis, capture rates for 1973 were compared with those for 1971, 1972, and 1974 using Mann-Whitney tests for early breeding season (late December–April), late

breeding season (May–August), and nonbreeding season (September–early December) separately.

Hummingbird masses and molt.—All *P. superciliosus* captured at leks or feeding areas were weighed to the nearest 0.1 g with a 10-g Pesola spring balance. Body condition was not otherwise monitored directly, but in a previous study (Stiles 1980), I found that fat reserves paralleled body mass for most of the year, save that during the lean season, apparently not only fat but also muscle protein was consumed. Monthly mean masses were analyzed with one-way analyses of variance, first comparing all months for each year separately, and then comparing the same month across years. I adopted this procedure instead of two-way ANOVA because of the rather large number of missing data (months), especially towards the end of the study. When significant results were obtained with ANOVA, Tukey tests (Zar 1988) were used to determine which monthly mean masses were significantly different.

All birds captured were also scored for molt, as in Stiles and Wolf (1974). I was particularly interested in the occurrence of interrupted molt, as indicated by a bird's having both fresh and worn primary feathers in its wing, but none in intermediate stages of growth. A molt in progress often may be interrupted in response to a sudden energy stress, or when the bird undertakes some energetically demanding activity like nesting or migration (Stresemann and Stresemann 1966).

Nesting success.—I was unable to obtain extensive direct data on nesting success; of the 30 nests found during the study, I could only determine the fate of 10 (2 succeeded in producing fledglings). An indirect measure of reproductive output, and hence of nesting success, is provided by the ratio of juveniles to adults in mist-net samples. Since such data are available for most months of the study, they provide a way to compare nesting success between years. Moreover, the approximate distribution of successful nestings through different breeding seasons can also be compared, since hatching dates of juveniles can be estimated from the degree of corrugation of the horny sheath of the maxilla (Stiles and Wolf 1974; cf. Ortiz-Crespo 1972). This method does not, however, give information on unsuccessful nests, or on the intensity of nesting effort per se.

Jolly-Seber analyses.—The combined visual and netting data of each monthly lek census were considered to represent capture-recapture data for the purpose of performing a Jolly-Seber analysis (cf. Poole 1974). This analysis provides estimates, with confidence intervals suitable for statistical testing, of the following parameters for each sampling period: sizes of the total (N) and marked (M) populations at the i^{th} census, probability that a marked individual alive during the i^{th} census will be recorded on that census (p), survivorship rate between census $i - 1$ and census i (ϕ), and the number of individuals added to the population at census i that are still alive at census $i + 1$

(B), a measure of recruitment. Also provided for each census period is an estimate of annual survivorship; the mean of these measures, adjusted for differing period lengths, provides an estimate of annual survivorship. From the lek censuses and additional observations (e.g., at feeding areas), some of these parameters are known with considerable accuracy for most censuses, hence comparison with the Jolly-Seber results provides a good check on the latter; other parameters estimated by the Jolly-Seber analysis are interesting in themselves, and not easily quantified by other methods (e.g., detection probabilities).

For purposes of the analysis, whenever a male *P. superciliosus* was seen and/or netted during a regular lek census, the bird was scored as 1; if neither seen nor netted it was scored as 0, irrespective of whether it had been seen or netted away from the lek during the sampling period. Thus, the analysis refers strictly to the population of males on the leks, and not to the total male population. This restriction was necessary because lek censuses were made at fairly regular intervals but other types of observations were not, making delimitation of sampling periods all but impossible.

The various Jolly-Seber models, with their respective assumptions, degrees of precision, and biases in estimating demographic parameters, are reviewed in detail by Karr et al. (*in press*). The *P. superciliosus* data were found to fit the most general Jolly-Seber model (Model A), with variable capture and survival probabilities, by goodness-of-fit tests (cf. also Karr, *in press*). The analyses was carried out by J. R. Karr using program JOLLY (Brownie et al. 1985, Pollock et al. 1990).

RESULTS

The 1973 drought.—The dry season of 1973 was one of the severest in the 30-yr history of the La Selva weather station: between late February and mid-April, only a single shower of 37 mm fell. In open areas the ground baked and cracked, and many herbaceous plants turned brown and lost their leaves. Leaf fall in the forest canopy, normally heaviest in the dry season (Frankie et al. 1974), was unusually so in 1973, although the canopy as a whole remained evergreen. The unusually heavy leaf litter crackled underfoot, making silent movement through the understory impossible for any terrestrial vertebrate, and even under the canopy the ground cracked in many places and many understory plants wilted. Flowering of many hummingbird food plants was affected to varying degrees (Stiles 1978). In the latter half of April the rains resumed, and May 1973 was quite wet. Rainfall for 1974 was essentially normal (Fig. 1).

Flowering of hummingbird food plants.—Several of the major food plants of *Phaethornis superciliosus* were affected by the 1973 drought to varying degrees. The most important, *Heliconia pogonantha* (Fig. 2), reaches its peak of flowering in January–February, and in most years declines slowly thereafter, not reaching low levels

(<50% of full bloom) before July or August. The large, heavy inflorescences of this species last for several months, and in most years flowering is kept high through at least early July by a flush of new inflorescences in April–May (cf. Stiles 1975). In 1973, however, no such flush occurred (Table 1), and flowering fell to 25% by late April and 10% by July (Fig. 2).

H. wagneriana, another important food plant through the breeding season, normally is in good bloom from mid-March through early May. In 1973 inflorescence production was curtailed and flower production dropped off rapidly, reaching low levels by late March (Fig. 2). In normal years the deep, boat-shaped bracts of this species are filled with water, which protects the flowers and developing fruits (Stiles 1979), and which is secreted largely (if not entirely, cf. Bronstein 1987) by the plant itself, with perhaps some contribution from rainwater. In 1973, most bracts were dry and cracking by late March, and many flowers were pierced and robbed of nectar by ants and bees, making actual nectar availability to hummingbirds even lower than flower counts would suggest (Fig. 2).

A third important food plant, *Costus pulverulentus* (called *C. ruber* in Stiles 1978), normally in good bloom from about April through August, scarcely flowered at all in 1973: its peak of flowering was $\leq 20\%$ of that of other years (Fig. 2). Another species similarly affected was *Justicia aurea*, whose flowering at peak in March–April was much less abundant than in other years (cf. Stiles 1978). However, this species is known at La Selva from only two large stands beside trails, and may be introduced; it certainly is much less important to *P. superciliosus* than the preceding three species.

Two less important species in the diet of *P. superciliosus* at La Selva were little affected by the 1973 drought. *Passiflora vitifolia* bloomed at about the same intensity in 1973 as in other years, and *Malvaviscus arboreus* actually bloomed more intensely in March 1973 than in any other year, but had declined to low levels by May. The major rainy season food plants of *P. superciliosus* (*Heliconia irrasa*, *H. mathiasae*, *H. umbrophila*, and *H. imbricata*, *Aphelandra storkii*, and *Costus malorteanus*) bloomed approximately on schedule in 1973 following a rainy May, and provided abundant flowers from July onward (Stiles 1978). The period of acute flower shortage to *P. superciliosus* at La Selva in 1973 was thus from late April or early May through June, when no major food plant was in good bloom; total flower availability during these months was probably only 20–30% that of normal years, and was quite similar to that of the October–November lean season.

Body mass.—In 1971, 1972, and 1974, mean monthly masses of lek male *P. superciliosus* fluctuated between ≈ 6.0 and 6.2 g. The only consistent pattern in all years was for masses to reach their annual minimum in November, corresponding to the lean season; masses tended to be highest between about April or May and

August, but with considerable interyear variation (Fig. 3). In none of these years was there significant variation among monthly mean masses (1971: $F_{10, 211} = 1.26$; 1972: $F_{9, 221} = 0.66$; 1974: $F_{5, 98} = 1.49$; all $P > .50$). Part of the variability in masses was undoubtedly due to the amount of nectar in the crop, hence time since last feeding (cf. Hainsworth and Wolf 1972). Because monthly sample sizes were virtually always ≥ 10 –15, I doubt that this factor affected the relationships between monthly means, but it certainly increased the variation within monthly samples.

In 1973, male masses plummeted between April and June, attaining levels even lower than during the lean season (Fig. 3). In this year there was highly significant variation among monthly mean masses of lek males ($F_{10, 185} = 40.56$, $P < .001$); this was due to significant differences between masses for May and June, and those for most other months (Tukey tests).

When the mass data were analyzed by month across years, no significant differences among mean masses of lek males between years were found for most months (all F values give $P > .50$). The exceptions were April, May, and June (respective F values: $F_{2, 64} = 6.23$, $F_{3, 93} = 8.41$, $F_{2, 63} = 6.21$, all $P < .01$); in all cases, the mean masses for 1973 were significantly lower than those for all other years, which did not differ among themselves (Tukey tests).

Masses of female *P. superciliosus* show trends similar to those of males in normal years, save that they tend to be highest rather earlier (March–May) and fall through the breeding season, showing a partial recovery in August–September before declining to minimum levels in November or December (Fig. 3). The more pronounced fluctuations in female masses mainly reflect smaller sample sizes (usually < 10). As in males, no significant variation among monthly mean masses was evident in 1971, 1972, or 1974. In 1973, mean masses from May through August were lower than for other years, although only for May was the difference significant ($F_{3, 22} = 3.92$, $P < .05$). As in males mean masses in May and June 1973 were lower than those of the lean season (Fig. 3).

The rapid recovery of mass by females at the start of the breeding season may reflect the fact that they evidently start to nest a month or more after males initiate lek activity, when flowers (especially those of *H. pogonantha*) are abundant. Males, on the other hand, must begin to establish lek territories as early as possible to be ready to fertilize the first females to appear (Lack 1968). That females evidently do not recover maximum masses before the lean season may reflect the greater costs of nesting as opposed to lek activity.

Lek activity.—In 1971, 1972, and 1974, levels of song and territorial activity on Leks I, II, and III (as indicated by mist-net captures) were variable but generally high between January and August, sharply lower from September to November, and increasing again in December, with the start of the next breeding season.

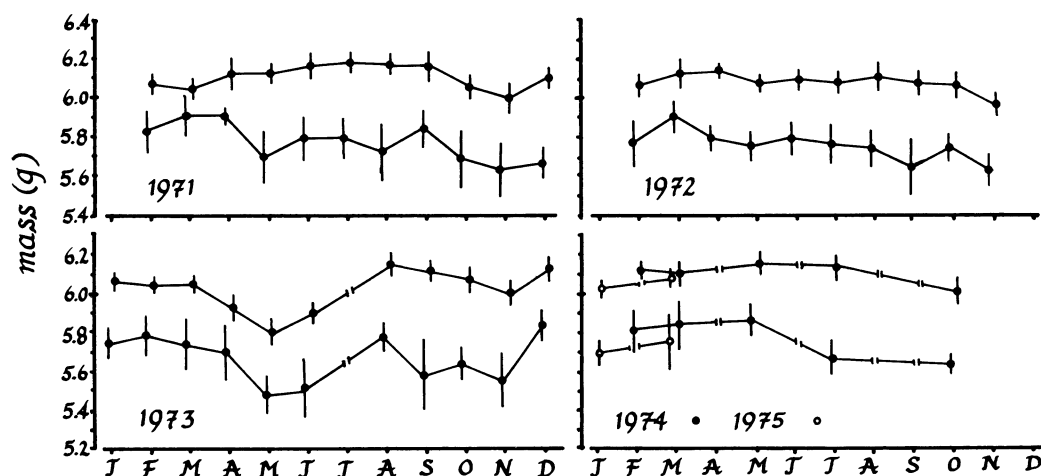


FIG. 3. Monthly mean masses, ± 1 SE, of male (above) and female (below) *Phaethornis superciliosus* at La Selva, 1971–1975.

Lek activity typically declined somewhat from March through June, with a resurgence in July–August as many juvenile males appeared on the leks (Stiles and Wolf 1979).

In 1973, capture rates were high through April, but dropped precipitously in May; no recovery was evident in June or August (no data are available for July). My field notes describe Lek I as “amazingly dead” during these months. Capture rates differed significantly between 1973 and other years for the late breeding season (means were 0.25 birds per net-hour in 1973 and 0.36 birds per net-hour for 1971, 1972, 1973, and 1974 combined; $U = 33$, $n = 11$, 3; $P = .01$), but not for the early breeding season or the nonbreeding season (the respective means were 0.41 and 0.37, and 0.17 and 0.19 birds per net-hour). Lack of a second peak of lek activity evidently reflects both the deaths or early departures of many resident males, and a lack of young males on the lek towards the end of the season.

Reproductive chronology and recruitment.—During 1971 and 1972, the great majority of fledged young were produced from eggs that hatched between March and July, although some were hatched as early as December or as late as October (Table 2). The chronological pattern of successful nesting was similar in the two years (Kolmogorov-Smirnov two-sample test, $D_{\max} = 0.04$, $P > .50$). In 1973, the number of eggs producing fledged young dropped sharply after March, and reproduction had practically ceased by June, although a

small number of successful eggs hatched in August, after flowering had resumed (Table 2). The difference in chronology of successful nesting between 1973 and 1971–1972 was highly significant ($D_{\max} = 0.28$, $P < .01$). I cannot say whether this drop in reproductive output was due to widespread nesting failure in May and June, or whether females simply ceased to initiate nesting attempts between about April and early July.

A further indication that reproductive success in 1973 was far below normal is provided by the ratios of juveniles to adults in mist-net captures through the breeding season (Fig. 4). Normally the proportion of juveniles in monthly samples rose steadily through the breeding season, reaching $\approx 50\%$ in July–August, then declining as young birds attained adult plumage and bill characteristics, or died. In 1973 the proportion of juveniles was far below normal in every month from June onward except October, indicating that few young birds were produced over the latter half or more of the breeding season.

In 1974, I did relatively little mist-netting after May, and so undoubtedly failed to capture many of the juveniles produced during the latter half of the breeding season. Thus, the apparent drop in fledglings produced from eggs hatching later than March 1974 (Table 2) almost certainly reflects insufficient sampling rather than any curtailment in reproduction, especially as juvenile:adult ratios in late 1974 were normal (Fig. 4).

Molt.—In all years, molt in the La Selva population

TABLE 2. Estimated hatching dates of juvenile Long-tailed Hermits (*Phaethornis superciliosus*) aged by bill corrugations, in different years.

Year	Estimated month of hatching											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1971	3	6	12	10	9	11	7	5	3	0	0	1
1972	8	7	11	15	17	13	9	8	4	1	0	2
1973	8	9	12	6	3	1	4	5	2	0	0	1
1974	4	9	11	7	5	4	4	3	1	0	0	0

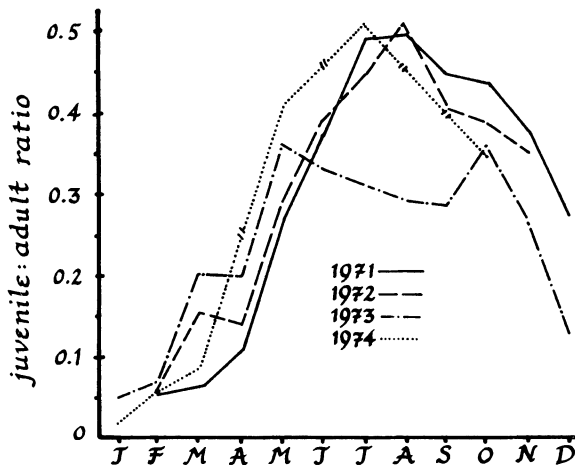


FIG. 4. Ratios of juveniles to adults in monthly mist-net samples of *Phaethornis superciliosus*, 1971–1975.

of *P. superciliosus* was most intense in June and July, when $\geq 50\%$ of all adults captured were undergoing primary molt; the annual low point of molt was December–January, with $\leq 5\%$ of the adults molting (cf. Stiles 1980). The 1973 drought did not affect the timing of molt in the population, but in 1974 the proportion of adult *P. superciliosus* in molt was higher between February and May than in any other year, rising from 20% in February (vs. 5–8% in other years) to 45% in May (vs. 25–30%). This reflects the fact that most of the young produced in 1973 hatched very early in the season, hence molted early as well (cf. Stiles and Wolf 1974). Also, adult males starting molt well before the drought survived somewhat better than males initiating molt during or after it (8 of 16 = 50% vs. 7 of 19 = 36%). In early 1975, the molt schedule of the population was partway back to the 1971–1973 pattern, with $\approx 15\%$ of adults molting in March.

In most years, interrupted molt was detected in 20–33% of the females: these had probably suspended molt after commencing a nesting attempt. Interrupted molt was only detected in males in 1973, never in 1971, 1972, or 1974, a highly significant difference ($\chi^2 = 25.2$, $P < .001$; Table 3). Most instances of interrupted molt in females were noted between June and September, or when most successful nests probably held nestlings (cf. Table 2). The 1973 drought definitely affected the proportion of individuals of both sexes showing interrupted molt. In this year, fully 25% of the males, and 50% of the females, showed interrupted molt (Table 3). This difference between the sexes was not significant ($\chi^2 = 1.13$, $P > .25$), but combining the data for both sexes, a highly significant difference between 1973 and other years in the incidence of interrupted molt was noted ($\chi^2 = 16.4$, $P < .001$).

Survival.—I define survival as the number of males known to be alive based on observations and captures both on and away from the lek, both during and after

a given census. At this point I should emphasize that disappearance of a regular lek resident during the breeding season is equivalent to death: during intensive censusing and netting operations on all the leks in the northern half of the La Selva property ($\approx 5 \text{ km}^2$) during 6 yr (Stiles and Wolf 1979 and present study), no lek resident ever changed leks, nor was such a bird ever seen again following disappearance from the lek. Conversely, if a male failed to appear on the lek at the start of a breeding season, he was never seen later in the season either; thus his death during the preceding nonbreeding season seems certain. The slow molt of this species, permitting lek activity and molt to occur simultaneously, makes it virtually certain that if a male is alive during the breeding season, he will be detected on the lek (Stiles and Wolf 1979).

In 1971, 1972, and 1974, survival of male *P. superciliosus* on Lek I was $\approx 90\%$ over the 8-mo breeding season. In the 3–4 mo between lekking seasons, survivorship declined to $\approx 60\%$ in each year (Table 4). Data from Lek II between 1969 and 1972, Lek III in 1974–1975, and Lek I in 1969 and 1970, show a similar pattern but with slightly lower survivorship values (≈ 80 – 85% through the breeding season, 50–55% during the nonbreeding season), probably due to loss of markings by a small proportion of the males.

Adult males apparently survived the breeding season slightly better than did juvenile males arriving on the lek early in the season (≈ 86 – 93% vs. 80–90%; Table 4), although disappearance of the latter could reflect transfer to another lek, which was never observed among adult males (Stiles and Wolf 1979). By contrast, survival through the nonbreeding season was slightly higher for juveniles than for adults (≈ 60 – 63% vs. 50–58%), although neither age-related difference was statistically significant (G tests; $P > .50$). For both age classes combined, survival was highly significantly lower in the nonbreeding season in these years ($\chi^2 = 18.6$, $P < .001$).

In 1973, survivorship through the breeding season dropped significantly (to 62–72%) for both early ju-

TABLE 3. Frequency of normal and interrupted molt in different years in male and female *Phaethornis superciliosus*.

Year	Sex	Number of individuals showing	
		Normal molt	Interrupted molt
1971	Males	48	0
	Females	20	6
1972	Males	58	0
	Females	17	5
1973	Males	21	7
	Females	5	5
1974	Males	21	0
	Females	8	1

TABLE 4. Survival of adult and immature marked male *Phaethornis superciliosus* on Lek I during nonbreeding (NB) and breeding (B) seasons, 1971–1975, as determined from lek census and netting.

Season	Adults		Immatures		All males		Annual proportion surviving
	Survived	Died	Survived	Died	Survived	Died	
NB 1970–1971					7	5	
B 1971	14	1	9	1	23	2	
NB 1971–1972	8	6	14	8	22	14	0.579
B 1972	20	2	8	2	28	4	
NB 1972–1973	11	8	13	7	24	15	0.558
B 1973* a	13	5	5	3	18	8	
b	9	9			14	12	
NB 1973–1974* a	7	6	8	6	15	12	0.429
b	7	2			15	8	
B 1974	12	2	6	1	18	21	
NB 1974–1975	6	6	11	7	17	13	0.515

* a and b for 1973–1974: a = assuming that 4 males whose date of death is uncertain died during nonbreeding season, 1973–1974; b = assuming these males died at end of breeding season of 1973.

veniles and adults ($\chi^2 = 5.27$, $P < .05$ for both age classes combined; see Table 4). Most adult males that definitely disappeared during the breeding season were last seen in April, suggesting that the May–June flower shortage was also the period of highest mortality. In fact, mortality might have been even greater towards the end of the breeding season, as four adult males disappeared between June and August 1973. I tentatively ascribed the deaths of these males to the nonbreeding season, during which survival was apparently normal (Table 4). However, in previous years, three of these males had remained active on the lek through late July or early August; thus breeding season survival might have been as low as 50%, while that during the nonbreeding season might have been as high as 77%. Unfortunately, I lack data for July 1973.

Seven of the nine adult males that definitely survived the 1973 breeding season lost no more than 0.2 g during May and June, whereas five of the eight definite ca-

sualties of this period were 0.3–0.6 g lighter than their previous average masses when last captured; two of the casualties also showed interrupted molt. Although the small sample size precludes statistical significance (Fisher's exact test, $P = .106$), loss of 0.3 g or more during the flower shortage of May and June seems to be associated with death during or shortly after the 1973 breeding season.

Population size and age structure of the leks.—Despite at least normal survival between the 1973 and 1974 breeding seasons, the number of territorial males on Lek I early in 1974 was fully one-third lower than in 1973; similar declines were noted in other leks (Fig. 5). Recovery of the population of lek males was slow: no overall increase was noted in 1975, and there was only a moderate increase in 1976. No data are available for 1977, but by 1978 the population had attained pre-1973 levels. All leks observed showed the same trends (for all leks 1973–1976, Kendall concordance coefficient $W = 0.9$, $s = 72$, $P < .01$; cf. Siegel 1956).

In any given breeding season, about half the adult males active on Lek I were 1 yr old; normally birds ≥ 2 , 3, or 4 yr of age were progressively less numerous (Table 5). The 1973 drought changed this, evidently producing especially heavy mortality in males in their

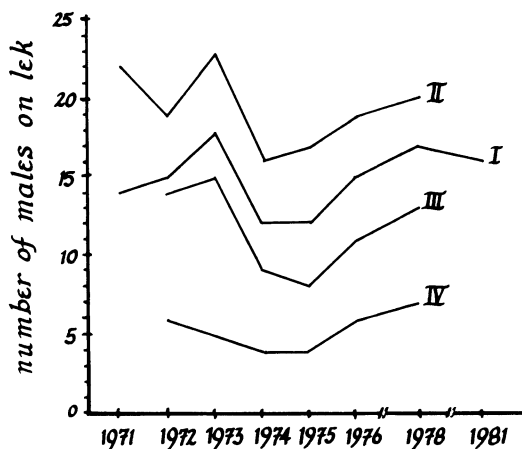


FIG. 5. Numbers of resident male *Phaethornis superciliosus* censused early in breeding season on four leks at La Selva, 1971–1978 or 1981.

TABLE 5. Age structure of territorial male *Phaethornis superciliosus* on Lek I, 1971–1975.

	Age in years*							
	1	1+	2	2+	3	3+	4	4+
1971	7	5	2	2	0	1	0	0
1972	14	0	5	2	0	0	0	1
1973	11	0	7	0	2	0	0	0
1974	8	0	2	0	5	0	0	0
1975	8	0	4	0	1	0	3	0

* Age in calendar years at start of lekking season. Ages 1+, 2+, etc. indicate that the bird was at least 1, 2, . . . yr old but exact age not known.

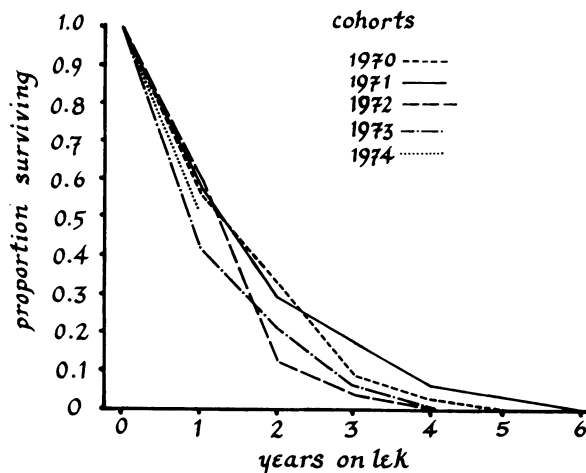


FIG. 6. Annual survivorship curve of five cohorts of male *P. superciliosus* on Lek I, 1970–1976.

first full season of lek activity. Thus, in 1974 there were actually more 3 yr olds than 2 yr olds on the lek. Age structure began to shift back toward normal in 1975, but there were still more very old males than in previous years (Table 5).

This can be further clarified by comparing survivorship curves of different cohorts of Lek I males through the study (Fig. 6). Typically $\approx 60\%$ of juvenile males reached the start of their first full breeding season, and about half of these attained their second. Thereafter, survival rates were more variable, doubtless reflecting the small sample of older males; only one male in the study reached 6 yr of age (five lekking seasons). The effects of the 1973 drought are seen in the strikingly low survival of the yearling (1972) cohort, and the moderately lower survival of the juvenile (1973) cohort, into the 1974 breeding season. Survivorship of these cohorts in succeeding years appeared to be essentially normal. Interestingly, the 1971 cohort appeared to be little affected by the drought, in fact, several males that survived it went on to become the longest lived of the entire study.

Jolly-Seber analyses.—During normal years, estimates of survival of Lek I males between monthly censuses during the breeding season were generally close to 1, but fluctuated widely, often falling to 0.7 or lower, during the nonbreeding season. Recall that “mortality” in this context is best interpreted as “permanent disappearance from the lek.” In several cases, birds that left the lek in July or August were seen at feeding areas a month or two later, but evidently died thereafter; these differences in estimation of dates of decease did not affect estimates of annual survival, but resulted in lower, more fluctuating ϕ values early in the nonbreeding season, especially in 1971 and 1974. In any case, because of long intervals between censuses, values for late 1974 are less reliable.

In 1973, survival dropped sharply after April, reach-

ing 0.65, the lowest value recorded, between June and August. The large standard errors and 95% confidence intervals of most estimates (except those for periods in which all birds were known to have survived, and the standard error was zero) preclude statistical significance for most differences in ϕ , but the estimates for June and August 1973, in particular, do differ significantly from most breeding-season estimates (confidence intervals do not overlap opposing means; cf. Zar 1988). Because standard errors are significantly larger during the nonbreeding season (Mann-Whitney test, $U = 226.5$, $n_1 = 25$, $n_2 = 10$, $P < .001$), the estimates of ϕ mostly do not differ significantly between seasons. This increase in standard errors of estimates for ϕ in the nonbreeding season is due to the decrease in p , the probability of detecting a marked individual alive in the population, which drops from ≈ 1.0 in the breeding season to ≈ 0.2 – 0.4 late in the nonbreeding season (Fig. 7a), as the males leave the leks at the end of the breeding season; p is in effect another measure of consistency of lek attendance in this system, and is in fact significantly correlated with mist-net captures throughout the study (Spearman $r_s = 0.393$, $n = 35$, $P < .05$, with correction for ties). Note that poor survival during the 1973 breeding season is not a reflection of departure of lek males, since p values during this period remained high (Fig. 7a).

Estimates of annual survivorship of lek males of *P. superciliosus* produced by Jolly-Seber analyses (Table 6) average slightly higher than those derived from direct observation (Table 4), but the latter values are well within the 95% confidence intervals surrounding the former. The difference in estimated annual survivorship for 1973 is 10–15% lower than for the other years, although the rather large variance of these estimates precludes statistical significance of the difference. Survival of males on Lek III was similar to that for males on the more intensively censused Lek I (Table 6).

In normal years, estimates of both the total population of lek males (N) and the number of marked males (M) peaked near the end of the breeding season (August–October), as expected. Recruitment (B) of young

TABLE 6. Estimates of annual survivorship (ϕ) of lek males *Phaethornis superciliosus* by Jolly-Seber analysis.

Lek	Year	No. sampling periods	Survivorship (mean \pm 1 SD)
I	1971	9 (10)*	0.62 \pm 0.42
	1972	11	0.57 \pm 0.37
	1973	10	0.49 \pm 0.45
	1974	7 (8)	0.61 \pm 0.40
	1971–1974	37 (39)*	0.57 \pm 0.40
III	1972–1974	11 (14)*†	0.58 \pm 0.36

* Initial and final sampling periods truncated due to need for previous and subsequent time periods to make estimates.

† One sampling period eliminated (Oct 1973) because only one bird was censused; this requires dividing by 0; hence, survivorship probably slightly overestimated.

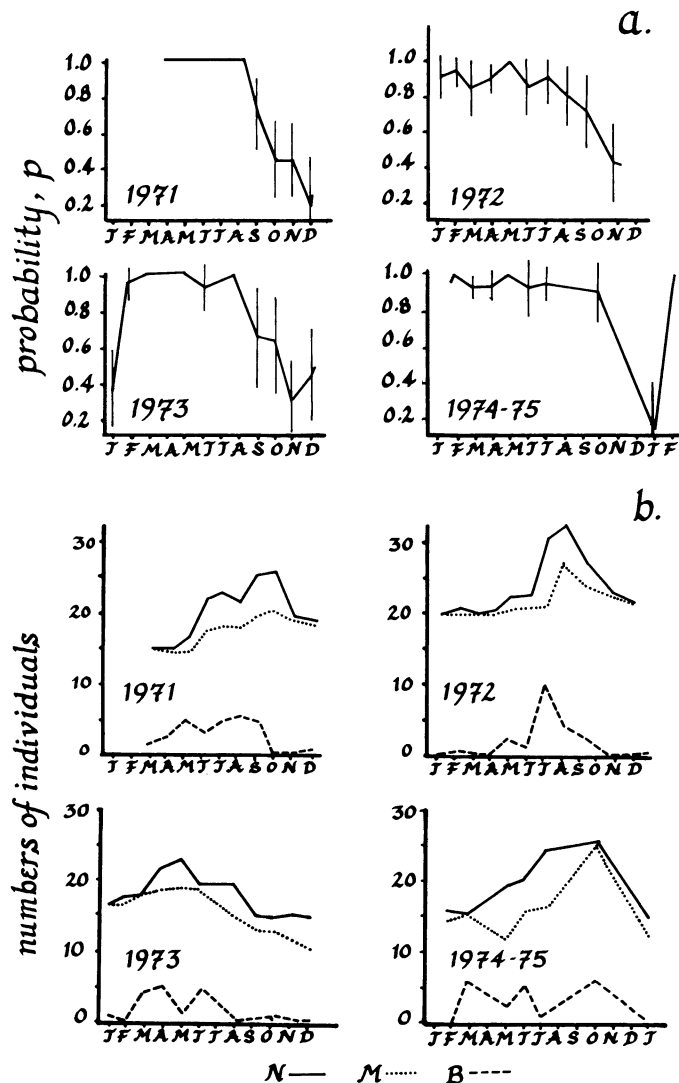


FIG. 7. Estimates of population parameters of male *Phaethornis superciliosus* on Lek I for each sample period, 1971–1974, derived for each sample period, 1971–1974, by Jolly-Seber analysis. (a) Probability that a marked male alive in the population will be included in any given sample (p) (mean and 95% confidence intervals). (b) Mean values of total (N) and marked (M) population of male *P. superciliosus*, and recruitment (B) for each sample period.

males onto the leks was highest between about May and October 1972 with a sharp peak in July (Fig. 7b). The peak of recruitment in March 1974 is due to movement onto the leks of several yearlings that in most years might not have obtained territories, but did so in this year due to the many vacancies created by high mortality in 1973. The apparent drop in recruitment in late 1974 is best ascribed to lack of sampling in August and September. Confidence intervals around these mean estimates show the same pattern as for other parameters: very narrow during the breeding season, much wider during the nonbreeding season as p declines (Fig. 7a). The wide confidence intervals during this period again preclude obtaining statistically significant differences between breeding and nonbreeding seasons in any of these parameters; on the other hand,

increases in N and M through the breeding season are significant.

In 1973, the population (N) peaked in June and declined thereafter, a very different pattern from that of the two previous years. In 1973, recruitment peaked in June, evidently due to the early movement onto the leks by several young males, permitted by the high mortality of lek residents following the drought. Recruitment dropped to near zero for the rest of the year, doubtless reflecting the virtual cessation of nesting after June 1973 (cf. Table 2).

DISCUSSION

Population dynamics of P. superciliosus

Through its curtailment of the flowering of several key food plants, the 1973 drought affected the lek ac-

tivity, molt, body mass, and survival of male *P. superciliosus* at La Selva, and the mass, molt, and timing of successful nesting of females. The total size and age structure of the population of lek males required at least 3 yr to return to pre-1973 levels. To better evaluate the effects of the drought, I shall now incorporate available life history data for *P. superciliosus* into a simple model of reproductive output on a seasonal and lifetime basis. However, because demographic models treat females and survivorship data are available only for males, I will assume that survival of females is similar to that of males. Although female survival is higher in the one hummingbird species for which such data exist (Calder et al. 1983), the reverse might be true in *P. superciliosus*, judging from the higher incidence of interrupted molt and hence, probably, energy stress in females. Survival of the sexes was also similar in most of the small birds discussed by Newton (1989). The general form of the model is similar to that proposed by Murray (1979, 1985).

Like all hummingbirds, *P. superciliosus* virtually invariably lays a clutch of two eggs. However, because some eggs are infertile, two young will not always be produced. Of a sample of 64 incubated hummingbird eggs collected by myself and M. Marin in Costa Rica, six were infertile, hence I will assume an infertility rate of 10% for eggs of *P. superciliosus*. This value is close to the mean of 9.4% of incubated eggs of several species of hummingbirds that failed to hatch, given by Skutch (1985). This would mean that the average successful nest produces 1.8 fledglings. From Table 4 I estimate that these will have a probability of 0.9 of surviving to the end of the breeding season, and 0.6 of surviving until the start of the next breeding season, when they enter the breeding population per se. Thus, a successful nesting will produce 0.972, or ≈ 1 adult that survives to reproduce. (Use of the slightly higher annual survivorship estimates from the Jolly-Seber analysis raises this value to ≈ 1.02 , scarcely a notable difference.)

In *P. superciliosus*, the incubation period is ≈ 21 d, and the nestling period 22–23 d (Skutch 1964); it probably takes a female a week or more to build a nest, and she will continue to care for the young for at least 8–10 d after they fledge (cf. Ruschi 1950, Snow and Snow 1964). Thus, a successful nesting attempt will require ≈ 2 mo in all. However, only ≈ 1 in 5 attempts succeed in this species (see *Results* and Skutch 1966). If the probability of failure is independent of the stage of the nesting attempt, and the success rate is 20%, I calculate by iteration that the time required for the average nesting attempt will be 60% of that for a successful attempt, or ≈ 36 d.

The starting point of the model is a female beginning her first breeding season. In a stable population, she must exactly replace herself by producing one female offspring that in turn survives to reproduce (or two young in all, assuming a 1:1 sex ratio). The model first calculates the number of young a female will produce

per season and over her lifetime under normal circumstances, then examines several of the parameters to determine how she might feasibly increase her reproductive output, for example, following a bad year like 1973.

The lifetime reproductive success of this female will be the sum of her probable production in each breeding season, times her probability of surviving through that season, and adjusted for her probability of survival through the preceding nonbreeding season. Thus,

$$R_T = 1 = \sum s \cdot R_s,$$

where R_T = total and R_s = seasonal reproductive output and s is the probability of survival through the end of the i^{th} breeding season. If survivorship through the breeding season is 0.9, and through the nonbreeding season is 0.6, such that annual survivorship is 0.54,

$$R_T = 0.9R_1 + 0.49R_2 + 0.25R_3 + 0.14R_4 \\ + 0.08R_5 \dots$$

If there are no age-related fecundity effects, $R_1 = R_2 = R_3 = \dots$ and we can solve for seasonal reproductive output R_s .

$$R_T = 1 = 1.95R_s.$$

Thus, $R_s = 0.51$, the number of surviving females she must produce per breeding season. Dividing this by the probability that the young female will in fact survive to her first breeding season, or 0.54, gives 0.94, the number of female fledglings that our hypothetical female must produce per breeding season. Since a successful nesting produces 0.9 female fledglings on average, in effect or female must have one successful nesting per year to exactly replace herself in the population. This, in turn, means that she must make on average five nesting attempts, given a success rate of 0.2. The question now becomes, how many attempts can she reasonably make in a breeding season?

The total nesting season of *P. superciliosus* at La Selva extends from December to October, a span of over 10 mo, but over 80% of the young that fledge hatch in a span of ≈ 6 mo, roughly between February and July, which we might call the "prime nesting season." With a prime nesting season of ≈ 183 d and with an average nesting attempt requiring ≈ 36 d, a female will have time for ≈ 5.1 nesting attempts during the prime season, or almost exactly what is required for her to produce, on average, the one successful nesting per season that will replace her in the breeding population!

If the parameters used in this simulation are anywhere near correct, a female with normal life-span and average breeding success, and breeding only in the prime breeding season, will no more than replace herself, thus barely maintaining a stable population; there would appear to be no large pool of nonbreeding "floaters" produced, that could join the breeding population in years following population crashes and thus speed the

population's recovery, in effect serving as a "buffer" against such crashes (cf. Brown 1969, Holmes and Sturges 1975). It is thus not surprising that the *P. superciliosus* population of La Selva apparently required at least 3 yr to recover from the 1973 drought. In fact, if the population's capacity to recover is really so limited, it becomes necessary to explore how recovery could occur at all.

Several of the parameters in the model seem unlikely to change, or to vary inversely with population size. Clutch size is invariable in hummingbirds; the proportion of infertile eggs seems unlikely to change given the mating system (cf. Stiles and Wolf 1979). Predation is the main cause of nest failure, and is mainly a function of habitat (Skutch 1966); thus, nesting success is not likely to increase as long as *P. superciliosus* continues to nest in the forest understory. Hermit nests are so thinly scattered and cryptic that it seems most improbable that a predator could form a search image for them; however, nothing is known regarding how predation rates might vary with hermit population density, nor about possible effects of the drought on potential nest predators.

Perhaps the parameter most susceptible to change would be the length of the nesting season: by making nesting attempts throughout a 9-mo span, a female could on average make 2–3 more attempts. The fact that relatively few young are produced at the extremes of the season suggests, however, that either relatively few females in fact attempt to nest over the entire 9-mo span, or that nesting success is lower toward the ends of this span (or both). Lowered nesting success late in the season seems likely on two counts: few adult males remain on the leks after August and many young males may not be reproductively mature (Stiles and Wolf 1979), and declining flower availability at this time might make provisioning nestlings difficult, and might impair survival of fledglings or even of the female herself (cf. Stiles 1980, Martin 1987, Nur 1989). A female nesting throughout 9 mo (50% more time) would probably produce considerably less than 50% more young than one nesting only in the 6-mo "prime" season. In fact, 15–20% of a normal year's young are produced outside the prime season; if 60% survive to the next breeding season, the "extra" breeding months make possible an annual increase of ≈ 8 –12% in the population. This agrees rather well with the 3+ yr the *P. superciliosus* population needed to recover from a 30% decrease due to the 1973 drought. Also consistent with this estimate is the small number of males that fail to obtain lek territories in any given year (Stiles and Wolf 1979). Recall, however, that the validity of these calculations rests upon several unproven assumptions, the most important of which is that survivorship of females is similar to that of males.

The single factor most limiting the *P. superciliosus* population of La Selva is survivorship through the October–November lean season. This presumably re-

flects a low ratio of energy supplies (few flowers in bloom) to demands (population levels high due to presence of many young birds). An increase in this ratio and hence presumably in survivorship, could be effected through either increasing flowering during the lean season, or decreasing population size before it. The latter certainly occurred in 1973, while the former probably did not (Stiles 1978). Unfortunately, because data are lacking for July 1973 I cannot determine to what extent survivorship through the 1973–1974 nonbreeding season might have been enhanced.

Judging from the numbers of lek males, the *P. superciliosus* population showed little or no recovery from 1974 to 1975, and a moderate increase from 1975 to 1976. The lack of increase through the 1974 breeding season could have resulted from many individuals being in poor condition at the start of this season; alternatively, females could have been even more severely affected than males by the 1973 drought, resulting in lower reproductive output in 1974 than expected from the number of lek males present. Body masses at the start of the 1974 season were normal, arguing against the first hypothesis, while the very high incidence of interrupted molt in females in 1973, implying greater energy stress, is consistent with the second.

The Long-tailed Hermit and other tropical birds

The data presented here suggest that the *P. superciliosus* population of La Selva is at or near the carrying capacity, as determined by floral resources, during much or all of the year. The increased nectar availability following the lean season is absorbed by the higher energy requirements of the adults for lek behavior, nesting, and molt, and increasingly by the young birds added to the population. Evidence, albeit indirect, that the population is near carrying capacity during the breeding season is provided by the effects of the drought itself: the decline in lek males was at least of similar magnitude to the decline in flower availability. However, it is impossible to be more precise than this because survivorship of females was not studied, and I lack data on absolute flower abundance for several key species. The fact that very few males that survive the lean season fail to obtain lek territories (Stiles and Wolf 1979) indicates that no large nonbreeding "floater" population exists. Finally, lek size over a 20-yr span has varied in parallel with nectar resources in the general vicinity of each lek (L. L. Wolf and F. G. Stiles, *unpublished manuscript*).

Low rates of nest success, small clutch sizes, and long incubation and nestling periods, such as those shown by *P. superciliosus*, are typical of small, forest-inhabiting, open-nesting neotropical birds (review in Skutch 1985). However, in view of these parameters, high adult survivorship has also been attributed to these birds (e.g., Snow 1962, Skutch 1966, 1985); indeed, it is virtually required by some theoretical models (Murray 1985), such that the 55% annual survivorship of

P. superciliosus at La Selva was considered "very exceptional" by Skutch (1985).

The entire question of the supposed high annual survivorship of birds of the humid neotropics has been reopened by Karr et al. (*in press*). Using Jolly-Seber analyses of large multiyear samples, these authors determined that mean annual survivorship estimates for birds of the eastern United States ($n = 10$ species) and central Panama ($n = 25$ species) were nearly identical. Interestingly, the mean annual survivorship for *P. superciliosus* estimated by Jolly-Seber analysis (0.57) is virtually identical to the mean of 0.56 for 25 Panama passerines, and somewhat lower than that obtained for the temperate-zone Broad-tailed Hummingbird (Calder et al. 1983). Values for a variety of cooperatively breeding temperate, subtropical, and tropical species summarized by Smith (1989) are similar or slightly higher, but high annual adult survival is often associated with cooperative breeding (Smith 1989). Data on annual survival presented in Newton (1989), mainly for small temperate-zone passerines, suggest similar or slightly lower (but often quite variable) values for annual adult survival.

Karr et al. (*in press*) point out potential flaws in previous analyses that suggested 0.9 as a typical value for annual survivorship of small tropical birds: short sample periods that might not have included both good and bad years; use of only maximum longevities to calculate average life expectancies; exclusion of individuals not recaptured from the estimates; or limitation of the estimates to particular age-sex categories that might not be typical of the species as a whole. I agree, but nevertheless suspect that considerable heterogeneity in survivorship may exist between different areas of the Neotropics. For instance, the largest and most reliable set of population data available is that of Snow (1962; see also Snow and Lill 1974) for the manakin *Manacus manacus* on Trinidad. Even when all nonrecaptured individuals are included, annual survivorship was estimated at 0.79, higher than for any species in the sample of Karr et al. (*in press*) and much higher than the latter's estimate for the closely related *M. vitellinus*. The only other study of a tropical hummingbird to present information on survivorship, that by Snow (1974) on the Green Hermit (*Phaethornis guy*), also on Trinidad, suggested on annual survivorship of $\approx 90\%$ for lek males (as calculated by Stiles and Wolf [1979] from Snow's data). While some of the difference between the estimates of survivorship of *P. guy* and *P. superciliosus* is undoubtedly due to methods of estimate (see Stiles and Wolf [1979] for a detailed critique), a real difference may exist. From the limited data presented by Snow and Snow (1972), it appears that *P. guy* does not encounter a severe "lean season" like that confronting *P. superciliosus* at La Selva. At least one major group of plants whose fruits were used heavily by *M. manacus*, those of the genus *Miconia*, had species in fruit throughout the year (Snow 1965).

In central Panama, rainfall is somewhat more seasonal than in Trinidad; in particular, the dry season is more extreme (cf. Snow and Snow 1964, Karr 1971). Hence, some critical resources might fluctuate more over the year in Panama than in Trinidad. Unfortunately, quantitative data on resources of the species studied by Karr et al. (*in press*) do not exist, nor do data on absolute resource abundance for Trinidad, such that any relationship between resource seasonality and survivorship in neotropical birds must be considered speculative for the present.

If annual survivorship rates on the order of that of *P. superciliosus* are indeed common among neotropical birds, then some current ideas and models of reproductive rates among these birds (e.g., Murray 1985, Skutch 1985) may require modification. At the very least, it seems high time to shift the emphasis from clutch size per se, and to pay more attention to differences in such parameters as length of breeding season, rate of renesting, molt, nest success, and seasonal distribution of resources among tropical species, rather than simply contrast "tropical" and "temperate" birds (see also Skutch 1985, Karr et al., *in press*).

As an example of the kinds of differences that will have to be accommodated in the next generation of models of population dynamics of neotropical birds, we need look no farther than the other hummingbirds that coexist with *P. superciliosus* at La Selva. With the possible exception of the Little Hermit *P. longuemareus* (which actually may breed year-round?), no other forest hummer at La Selva has a breeding season longer than 4–6 mo, or shows such complete overlap between molt and breeding (Stiles 1980). Many other species emigrate wholly or in part during the "lean season," whereas *P. superciliosus* apparently does not (Stiles and Wolf 1979). Do these other species survive better than *P. superciliosus*? Or have higher nesting success? Might the long breeding season, molt–breeding overlap, slow molt, and individualistic mechanism of molt timing (cf. Stiles and Wolf 1974) be a coadapted suite of characters enabling *P. superciliosus* to maintain a stable population at La Selva in the face of high mortality during the lean season and high nest predation? How do other species without these adaptations maintain their populations? Clearly, as Murray (1985) puts it, the comparative demography of hummingbirds promises to be interesting!

Although *P. superciliosus* is usually considered "abundant" at La Selva (e.g., Slud 1960), this may be in part because individuals are seen and netted often due to their wide-ranging foraging behavior (Stiles and Wolf 1979). In fact, given the observed density of leks, few or no floaters, and assuming a 1:1 sex ratio, then there are probably only a few hundred individuals of *P. superciliosus* in the entire 1500 ha of the La Selva property. Extinction of a population of this size is by no means inconceivable (cf. MacArthur 1972), especially if its capacity for rapid increase is limited by

such factors as nest predation. Monthly rainfall data from La Selva compiled over a 30-yr period reveal only two other years with droughts comparable in severity to that of 1973: 1961 and 1983. The *P. superciliosus* population of La Selva may thus be subjected to an acute flower shortage during the breeding season about once every 10 yr. This greatly exceeds the average life expectancy of this species, making unlikely the evolution of immediate response mechanisms such as a programmed cessation of reproduction should flower availability fall below some critical value. On the other hand, 10 yr is more than ample time for the population to regain its former numbers following a crash of the magnitude of that of 1973. Several bad years in a row might serve to reduce the La Selva population of *P. superciliosus* to still lower levels, but unless populations of important food plants, notably *H. pogonantha*, were severely decimated, which evidently did not occur in 1973, as flowering of all major food plants was nearly normal, except for possible small differences in timing (cf. Stiles 1978) in 1974, the hermit population should be able to recover.

I should emphasize that it remains a plausible but untested assumption that censuses of lek males accurately reflect the *P. superciliosus* population as a whole. Data presented here on masses, molt, etc. of females constitute circumstantial support for this assumption, but data on mortality of females are needed. Ideally, lek censuses combined with a long-term banding study conducted away from the leks, should be attempted. Because Jolly-Seber analyses give excellent agreement with direct observations of survivorship of lek males, banding data from females also might be analyzed by this method. It should be noted, however, that male *P. superciliosus* are nearly ideal animals for such an analysis, in that detection of individuals is virtually certain during the breeding season, but the seasonal departure of the males from the leks reduces the power of statistical analyses through its effects on confidence intervals. Any banding effort with females would have to be very intensive to generate *p* values close to 1, to reduce this problem. Confirmation of lek censuses as a reliable estimator of overall population size would have important management implications. Since such censuses can be accomplished relatively quickly and efficiently in terms of time and effort, they might make it possible to monitor populations of a variety of frugivorous and nectarivorous birds of tropical forests on a long-term basis.

ACKNOWLEDGMENTS

I am grateful to the Frank M. Chapman Fund of the American Museum of Natural History and the Vicerrectoria de Investigacion, Universidad de Costa Rica, for financial aid, and to the Organization for Tropical Studies, especially Ing. Jorge Campabadal and Liliana Echeverria, for logistic help. Rafael Chavarria, Lloyd Kiff, Paul Opler, Susan Smith, and Larry Wolf provided help in the field, while Gary Hartshorn made available the rainfall data; I especially thank James Karr for performing the Jolly-Seber analyses, and for extensive

comments on the manuscript. Rita Leon provided secretarial assistance at the Instituto de Ciencias Naturales.

LITERATURE CITED

- Blake, J. G., B. A. Loiselle, T. C. Moermond, D. J. Levey, and J. S. Denslow. 1990. Quantifying abundance of fruits for birds in tropical habitats. *Studies in Avian Biology* **13**: 73–79.
- Bronstein, J. L. 1986. Origin of bract liquid in a neotropical *Heliconia*. *Biotropica* **18**:111–114.
- Brown, J. L. 1969. Territorial behavior and population regulation in birds. *Wilson Bulletin* **81**:293–329.
- Brownie, C., D. R. Anderson, K. P. Burnham, and D. S. Robson. 1985. Statistical inference from band recovery data: a handbook. Second edition. United States Fish and Wildlife Service Resource Publication **156**.
- Calder, W. A., S. M. Hiebert, N. M. Waser, D. W. Inouye, and S. J. Miller. 1983. Site fidelity, longevity, and population dynamics of Broad-tailed Hummingbirds: a ten-year study. *Oecologia (Berlin)* **56**:359–364.
- Diamond, J. M. 1976. Island biogeography and conservation: strategy and limitations. *Science* **193**:1027–1032.
- Faaborg, J. 1982. Avian population fluctuations during drought conditions in Puerto Rico. *Wilson Bulletin* **94**:20–30.
- . 1988. Ornithology: an ecological approach. Prentice Hall, Englewood Cliffs, New Jersey, USA.
- Fogden, M. P. L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. *Ibis* **114**: 307–343.
- Foster, M. S. 1977. Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit source. *Ecology* **58**:73–85.
- Foster, R. B. 1982. Famine on Barro Colorado Island. Pages 201–212 in E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor, editors. The ecology of a tropical forest: seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, D. C., USA.
- Frankie, G. B., H. G. Baker, and P. A. Opler. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology* **62**:881–919.
- Gill, F. B. 1988. Trapline foraging by hermit hummingbirds: competition for an undefended, renewable resource. *Ecology* **69**:1933–1942.
- Hainsworth, F. R., and L. L. Wolf. 1972. Crop volume, nectar concentration, and hummingbird energetics. *Comparative Biochemistry and Physiology* **42**:359–366.
- Holdridge, L. R., W. C. Grenke, W. T. Hatheway, T. Laing, and J. R. Tosi, Jr. 1971. Forest environments in tropical life zones: a pilot study. Pergamon, Oxford, England.
- Holmes, R. T., and F. C. Sturges. 1975. Bird community dynamics in a northern hardwoods community. *Journal of Animal Ecology* **44**:175–200.
- Janzen, D. H., editor. 1983. Costa Rican natural history. University of Chicago Press, Chicago, Illinois, USA.
- Karr, J. R. 1971. Structure of avian communities in selected Illinois and Panama habitats. *Ecological Monographs* **41**: 207–233.
- . 1990. The avifauna of Barro Colorado Island and the Pipeline Road, Panama. Pages 183–198 in A. H. Gentry, editor. Four neotropical rain forests. Missouri Botanical Garden, St. Louis, Missouri, USA.
- . *In press*. Avian survival rates and the extinction process on Barro Colorado Island. *Conservation Biology*.
- Karr, J. R., and J. D. Brawn. 1991. Food resources of understory birds in central Panama: quantification and effects on avian populations. *Studies in Avian Biology* **13**:58–65.
- Karr, J. R., J. D. Nichols, M. K. Klimciewicz, and J. D. Brawn.

- In press.* Survival rates of temperate and tropical forest birds: will the dogma survive? *American Naturalist*.
- Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London, England.
- Levey, D. J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecological Monographs* **59**:126–147.
- Levey, D. J., and F. G. Stiles. *In press.* Birds of La Selva. In K. Bawa, G. S. Hartshorn, H. A. Hespenheide, L. McDade, editors. *La Selva: ecology and natural history of a tropical rainforest*. Sinauer, Sunderland, Massachusetts, USA.
- Loiselle, B. A., and J. G. Blake. 1991. Diets of understory fruit-eating birds in Costa Rica: seasonality and resource abundance. *Studies in Avian Biology* **13**:91–104.
- MacArthur, R. H. 1972. Geographical ecology. Harper & Row, New York, New York, USA.
- Martin, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. *Annual Review of Ecology and Systematics* **18**:453–487.
- Murray, B. G., Jr. 1979. Population dynamics: alternative models. Academic Press, New York, New York, USA.
- . 1985. Evolution of clutch size in tropical species of birds. Pages 505–519 in P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, editors. *Neotropical ornithology*. Ornithological Monographs **36**.
- Newton, I. 1989. Synthesis. Pages 441–469 in I. Newton, editor. *Lifetime reproductive success in birds*. Cambridge University Press, Cambridge, England.
- Nur, N. 1989. The cost of reproduction in birds: an examination of the evidence. *Ardea* **76**:155–178.
- Ortiz-Crespo, F. I. 1972. A new method to separate adult and immature hummingbirds. *Auk* **89**:851–857.
- Petrickes, J. 1956. Plan de ordenacion del bosque de Finca “La Selva.” Instituto Interamericano de Ciencias Agrícolas, Turrialba, Costa Rica.
- Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs*.
- Poole, R. W. 1974. An introduction to quantitative ecology. McGraw-Hill, New York, New York, USA.
- Ricklefs, R. E. 1983. Comparative avian demography. *Current Ornithology* **1**:1–32.
- Rosselli, L. 1989. El ciclo anual de un ave frugívora migratoria altitudinal, *Corapipo leucorrhoa* (Pipridae), y los frutos que consume. Thesis. Universidad de Costa Rica, San José, Costa Rica.
- Ruschi, A. 1950. O território y as áreas de alimentação e de nidificação de *Anisoterus pretrei* (DeLattre & Lesson) observadas através algumas gerações. *Boletim do Museu do Biologia “Mello-Leitão”* **8**:1–20.
- Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, New York, USA.
- Skutch, A. F. 1950. The nesting seasons of Central American birds in relation to climate and food supply. *Ibis* **92**:185–222.
- . 1964. Life histories of hermit hummingbirds. *Auk* **81**:5–25.
- . 1966. A breeding bird census and nesting success in Central America. *Ibis* **108**:1–16.
- . 1975. Parent birds and their young. University of Texas Press, Austin, Texas, USA.
- . 1985. Clutch size, nesting success, and predation on nests of neotropical birds, reviewed. Pages 575–594 in P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, editors. *Neotropical ornithology*. Ornithological Monographs **36**.
- Slud, P. 1960. The birds of Finca “La Selva,” a tropical wet forest locality. *Bulletin of the American Museum of Natural History* **121**:49–148.
- Smith, J. N. M. 1989. Summary. Pages 593–611 in P. B. Stacey and W. D. Koenig, editors. *Cooperative breeding in birds: long-term studies of ecology and behavior*. Cambridge University Press, Cambridge, England.
- Snow, B. K. 1974. Lek behavior and breeding of Guy’s Hermit hummingbird *Phaethornis guy*. *Ibis* **116**:258–279.
- Snow, B. K., and D. W. Snow. 1972. Feeding niches of hummingbirds in a Trinidad valley. *Journal of Animal Ecology* **41**:471–485.
- Snow, D. W. 1962. A field study of the Black and White Manakin, *Manacus manacus*, in Trinidad. *Zoologica* **47**:65–104.
- . 1965. A possible selective factor in the evolution of fruiting seasons in a tropical forest. *Oikos* **15**:274–281.
- Snow, D. W., and A. Lill. 1974. Longevity records for some neotropical land birds. *Condor* **76**:262–267.
- Snow, D. W., and B. K. Snow. 1964. Breeding seasons and annual cycles of Trinidad land-birds. *Zoologica* **49**:1–39.
- Stiles, F. G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology* **56**:285–301.
- . 1977. Coadapted competitors: flowering seasons of hummingbird-pollinated plants in a tropical forest. *Science* **198**:1177–1178.
- . 1978. Temporal organization of flowering among the hummingbird foodplants of a tropical forest. *Biotropica* **10**:194–210.
- . 1979. Notes on the natural history of *Heliconia* (Musaceae) in Costa Rica. *Brenesia* **15**:151–180.
- . 1980. The annual cycle in a tropical wet forest hummingbird community. *Ibis* **122**:322–343.
- . 1985. Seasonal patterns and coevolution in the hummingbird-flower community of a Costa Rican subtropical forest. Pages 757–787 in P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, editors. *Neotropical ornithology*. Ornithological Monographs **36**.
- Stiles, F. G., and A. F. Skutch. 1989. A guide to the birds of Costa Rica. Cornell University Press, Ithaca, New York, USA.
- Stiles, F. G., and L. L. Wolf. 1973. Methods of color-marking hummingbirds. *Condor* **75**:244–245.
- Stiles, F. G., and L. L. Wolf. 1974. A possible circannual molt rhythm in a tropical hummingbird. *American Naturalist* **108**:341–354.
- Stiles, F. G., and L. L. Wolf. 1979. Ecology and evolution of a lek mating system in the long-tailed Hermit Hummingbird. Ornithological Monographs **27**.
- Stresemann, E., and V. Stresemann. 1966. Die Mauser der Vogel. *Journal of Ornithology* **107**.
- Terborgh, J. 1974. Preservation of natural diversity: the problem of extinction-prone species. *BioScience* **24**:715–722.
- . 1983. Five New World primates. Princeton University Press, Princeton, New Jersey, USA.
- Wilson, E. O., and E. O. Willis. 1975. Applied biogeography. Pages 522–534 in M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. Belknap, Cambridge, Massachusetts, USA.
- Worthington, A. 1982. Population size and breeding rhythms of two species of manakins in relation to food supply. Pages 213–226 in E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor, editors. *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, D.C., USA.
- Zar, J. H. 1988. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey, USA.