# BREEDING BIOLOGY OF THE PUERTO RICAN SHARP-SHINNED HAWK (ACCIPITER STRIATUS VENATOR)

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ABSTRACT.-We studied the breeding biology of the Sharp-shinned Hawk (Accipiter striatus venator) in Maricao forest of western Puerto Rico from 1978 to 1985. Sharp-shinned Hawks are year-round residents and establish nesting territories only during the breeding season, which coincides with the dry and beginning of the wet seasons. Nesting sites were occupied in December and January every year and reoccupancy rates were 50% or higher. Prolonged and intense territorial conflicts between mated and unmated males were common. The onset of egg-laying was in late March or early April approximately 3-4 months after occupancy of nesting sites. Laying of first clutches peaked in early April and spanned 38 days (n = 19clutches). Laying of second clutches occurred irregularly and spanned 55 days (n = 8 clutches). Females renested only after the initial clutch or brood was lost. The incubation period was 32 days (n = 13 clutches), similar to the duration reported in temperate North America. Nestling females attained larger asymptotic mass than males, but the latter grew faster; although the slopes of the regression lines were statistically homogeneous. Males fledged at an average age of 28.2 days and females at 32.1 days. Young were slightly heavier than adults at fledging, but the wing chord and tail lengths were approximately 50% shorter than those of adults. Fledging occurred at the peak of prey abundance. The breeding cycle in Puerto Rico was approximately 2 months longer than that recorded in Oregon and Utah. The time that elapsed from occupancy of nesting sites to egg laying accounted for the differences. Juveniles departed from nesting sites when prey was still abundant but delivery rates had declined considerably. A total of 105 eggs was laid in 40 nests (average clutch size 2.6), of which 63% hatched and 47% of the nestlings fledged. A total of 0.8 young fledged per breeding attempt. Overall nest success was 29%, 36% (n = 33 nests) in first nesting attempts and 0% in second nesting attempts (n = 9 nests). Most reproductive losses in 28 nests resulted from nestling mortality from *Philornis* sp. (Diptera, Muscidae) (n = 9) and desertion of clutches (n = 11). Fecundity and reproductive success was lower in Puerto Rico than in Oregon, Utah, and Wyoming. Despite low reproductive success in Maricao forest, the breeding population did not decline during our study. Received 29 June 1987, accepted 9 May 1988.

RELATIVELY little is known about the breeding biology of raptors in tropical regions, particularly in the Neotropics. Due to the lack of detailed information on tropical species, only limited comparisons within and between geographic regions are possible. We selected the Sharp-shinned Hawk (Accipiter striatus) as a model species to examine reproductive adaptations in a tropical environment (Puerto Rico), relate breeding adaptations to its ecology, and compare breeding features with those of conspecifics in temperate North America (e.g. Bent 1937; Craighead and Craighead 1956; Platt 1973; Snyder and Wiley 1976; Hennessy 1978; Reynolds 1978, 1983; Reynolds and Wight 1978; Reynolds and Meslow 1984; Mueller et al. 1981).

Tropical birds of prey have longer breeding seasons and lower reproductive rates than their

temperate counterparts (Liversidge 1962; Benson et al. 1971; Smeenk 1974; Smeenk and Smeenk-Enserink 1975, 1977; Thiollay 1975; Brown 1976; Snyder and Wiley 1976; Faaborg et al. 1980; ffrench 1980; Mader 1981, 1982; Wiley and Wiley 1981). Breeding cycles are longer in tropical birds of prey, in part because laying occurs at almost any time of the year (Mader 1982). Furthermore, tropical species have breeding seasons that are restricted to either the wet or dry season (Benson et al. 1971; Mader 1981, 1982). The duration of some of the stages of the breeding cycle (such as incubation and nestling periods) are generally longer in the Tropics (Newton 1979, Mader 1982). Although reproductive rates and nest success are comparatively lower in tropical areas, survival of fledglings and adults is as high as in temperate

areas (Mader 1982). Also, some tropical raptors lay replacement clutches after losing eggs or young, which rarely occurs in temperate areas (Newton 1979, Mader 1982).

### STUDY AREA AND METHODS

Our study was in Maricao forest (4,150 ha), at the west end of the Cordillera Central (18°09'N, 66°58'W). Elevations ranged from 550 m in the subtropical moist forest to 900 m in the subtropical lower montane wet forest life zones. Precipitation ranged from 57 mm in January to 374 mm during October (annual mean 2345.4 mm, 1971-1982). Mean monthly temperatures ranged from 20.1°C in January to 23.2°C in August (annual mean 21.8°C; National Oceanic and Atmospheric Administration 1972-1982). The life zones and vegetation are described by Ewel and Whitmore (1973), and Cruz and Delannoy (1984).

The breeding grounds were visited regularly throughout the breeding season to find mated pairs. We defined nesting site as an area where aerial displays, mating and nest-building, adult incubating, brooding, and repeated prey-carrying occurred. An area with a mated pair was considered an occupied nesting site. Observations of Sharp-shinned Hawks on their breeding grounds were made from abovecanopy lookouts and ground blinds with the aid of binoculars and a spotting scope. To reduce difficulty in determining whether an observation pertained to courtship or territorial behavior, display flight was categorized as territorial only if followed by encounters between the resident and intruders.

The incubation period was the time (days) from laying to hatching (after clutch completion) of the last egg. We measured egg dimensions (length and width) to the nearest 0.1 mm with vernier calipers, and determined egg mass and body mass of nestlings to the nearest 0.1 g with a Pesola spring scale. Individual young were marked with an inert organic dye (food coloring) on the crown soon after hatching. Sex of nestlings was inferred from differences in body mass and size developed during growth. Growth patterns of male and female nestlings were described graphically. Ricklefs' (1967) method of fitting equations to growth curves was used to compare male and female growth patterns. Growth curves were fitted most closely by the logistic equation and logistic constants were used for comparisons. Shortly before fledging, young were banded with USFWS aluminum bands and colored leg bands. Mist nets were used to capture fledglings and adults, which were measured (length of tarsus, wing chord, culmen, and tail), weighed, and checked for ectoparasites. Tarsal length was measured from the intertarsal joint to the bend of the foot. Wing chord was the distance from the bend to the tip of the longest primary. Culmen length was measured from the cere to the bill tip. The tail length was taken from the base to the tip of the center rectrix.

Productivity was production of fledglings related to size of nesting population (including territorial nonbreeders). Reproductive output was the total number of fledglings produced over a period of time. Reproductive success was a general term that included several measures and components, expressed on a per pair, per breeding attempt, or per egg basis.

To determine bird-prey abundance in the Maricao forest, 3 transects (4 km total) were established (Cruz and Delannoy 1984). Bird densities were estimated by the variable strip method (Emlen 1971). Parallel lines on both sides of the transect routes, 5 m apart to a distance of 30 m, defined the strips of coverage. Lateral distance of bird species from the transect route was estimated by visual or aural detection. To reduce bird-count variability introduced by observers' bias, only Delannoy conducted the censuses. The transect count for a species was transformed into a density estimate by dividing the number of individuals per area covered by the coefficient of detectabililty (Emlen 1971, 1977). Each transect route was censused twice a month on consecutive days from June to August 1980 (18 counts), from January to August 1981 (48 counts), and from May to August 1982 (24 counts). Censuses were initiated 30 min after sunrise and completed within 1-2 h. Counts proceeded only when there was 30% overcast or less, little or no wind, and nonfoggy conditions.

A total of 333 h was spent at 4 nests to observe the movements and behavior of fledglings and determine the rate of prey delivery by adults. These observations were initiated midway through the nestling period and continued until young departed. All statistical procedures followed Sokal and Rohlf (1981).

# RESULTS

Reoccupancy of nesting sites.-Puerto Rican Sharp-shinned Hawks are year-round residents that establish nesting territories only during the breeding season. Nesting sites are reoccupied in December and January. Nesting sites had relatively high reoccupancy rates (Table 1). Nine sites were used at least twice. Five had reoccupancy rates of 80% or higher, while none of the remaining 4 nesting sites had reoccupancy rates of less than 50%. A banded adult female reoccupied the same nesting site in 1981, 1982, and 1983. Another banded female returned to the same nesting site in 1982, 1983, and 1985. Newton (1986) reported average periods of residence on nesting sites of 1.4 yr in male and 1.5 yr in female Eurasian Sparrowhawks (Accipiter nisus). Two males had residence periods of 4 and 5 yr, and 5 females had been

present 5-6 yr. A third female banded in 1981 moved 1.7 km to a different nesting site in 1982. A female banded as a nestling in 1979 used a nesting site 1.1 km away from her natal area in 1983. Eurasian Sparrowhawk females moved a median distance of 1.5 km and males 0.8 km, and maximum distances of 27 km and 19 km, respectively (Newton 1986). Of the 42 nests studied from 1978 to 1985, only 4 were occupied by immature-plumaged females, and none by immature males.

Courtship and territoriality.-Most Sharpshinned Hawk activities during December and January consisted of courtship and territorial display flights. Males and females initiated display flights shortly after sunrise and, in some sites, continued until mid-morning. A typical courtship flight began when the male circled above the nesting site; the female followed shortly afterwards. Adults mixed soaring and rapid flights, calling intermittently. The male used flapping flight more frequently, and circled higher, than the female. Birds reached estimated above-canopy heights of 20 to 200 m ( $\bar{x}$ = 140 m, n = 44). At irregular intervals male and female independently performed an undulating flight display that consisted of a repeated series of shallow and deep dives followed by a recovery of height. The hawks frequently held a stationary position in midair and plunged vertically, or nearly so, with closed wings accompanied by repeated quickening movements of the wings. On deep dives, they dropped for several seconds and recovered a short distance from the canopy. We did not observe the performer direct the latter display towards the other member of the pair. Display bouts lasted from 3-20 min ( $\bar{x} = 13$  min; n =44), and were repeated several times. All courtship flights (n = 44) ended with a deep dive into the forest. Courtship flights normally were followed by courtship-feeding, matings, and nest building.

We observed 19 territorial display flights between nonspecific males in 5 nesting sites in 1981. Resident males initiated territorial behavior from a perch (n = 3) or from the air (n =16). When intruder males entered air space near the nesting sites, resident males flew straight at them, chasing them. Both males normally called repeatedly. The resident males usually evicted the intruders (n = 15). Some intruders did not leave the nesting sites immediately, and the resident males responded with 2 different behav-

 TABLE 1.
 Reoccupancy rate of Sharp-shinned Hawk nesting sites in western Puerto Rico.

Nesting site	Years occupied/ years checked	Reoccupancy rate
Rio Grande	2/4	0.50
Rio Bonelli	4/4	1.00
Merenderos	7/7	1.00
Quinina	4/5	0.80
Casa de Piedra	5/6	0.83
Cain Alto	4/6	0.67
Buena Vista	4/7	0.57
Camping area	3/6	0.50
Descanso	5/6	0.83

iors. In one instance the resident male flew in circles above the intruder and dove twice until the intruder left. On three occasions conflicts reached high intensity, and males grappled talons and spun laterally to a few meters from the canopy before breaking loose (n = 1), or landed on the ground with locked talons, thrashed wings at each other, and finally broke loose (n = 2). In all three instances after separating, the resident chased and evicted the intruder from the nesting site. Conflict between males persisted for several months (February-May) in 2 nesting sites. We recorded 20 encounters between intruder and resident male, but only 2 (10%) ended in physical contact and thrashing wings in midair. Intruders were evicted in all 20 encounters. The rate of intrusion was 0.59/h of observations (20/34). The intruder male carried prey into the nesting site twice. The female accepted prey once in the absence of the resident male. At no time did the intruder male attempt to copulate with the female. The intruder also carried nest material and deposited it on the nest while the female was incubating (n = 4).

Nest building.—Most Sharp-shinned Hawks started nest construction shortly after permanently occupying their sites in January. However, the hawks added little nesting material (sticks and twigs) at this stage and construction proceeded slowly. Both sexes became more active in the nest-building process 3-4 weeks before laying eggs.

We observed the nest-building process in 1 pair. On 10 February 1981 the pair had laid the foundation of the nest platform (approximately 1-2% of the completed nest's size). During 4.5 h of observation on 20 February the male made 11 trips to the nest with nest material; the female made none. On 5 March, the male made 62% of trips and the female, 38% (n = 42) in 1 h. On 15 March, the male made 11% of trips while the female made 89% in 1 h (n = 36). In all, males made 46% of the trips and females 54% (n = 89).

Nests were built on trees; branches and twigs were gathered from the ground and nearby trees, and the nest bowl was lined with a layer of finer twigs. No additional nest material was added. Although most pairs built a new nest every year, some did not. In 2 nesting sites in 1983, for example, the banded pairs reused the same nests they built in 1982. Also, some pairs built alternate nests and used them after failing in their first nesting attempt. We observed this behavior at 2 sites in 1982. Near nest completion the pair gave shape to the nest bowl by trampling the layer of finer twigs with their talons and breast.

Egg laying, incubation, and hatching.—By February females stopped hunting and stayed near the nest. Three females settled permanently on their nesting sites on 14, 15, and 25 February 1981. They spent most of their time resting on branches ("pre-laying lethargy," Newton 1979). Males provided all the food at this stage and during the following months.

Eggs were laid during the dry season from March to July (n = 27 clutches) (Fig. 1). Laying of first clutches spanned 38 days (16 March to 22 April, n = 19 clutches). Earliest recorded laying dates were 9 April 1978, 21 March 1979, 24 March 1980, 18 March 1981, 15 March 1982. The number of first clutches peaked in early April. Females renested only after losing the first clutch or brood. Second clutches occurred irregularly from 12 May to 5 July, a span of 55 days (n =8). Second clutches peaked in late May and early June. It took 2 females approximately 27 and 30 days, respectively, to lay again after losing their first broods. Females laid most eggs on alternate days until clutch completion. We determined egg-laying sequences in 3 clutches (n = 8). Seven of 8 eggs were laid on alternate days, while 1 egg was laid the following day. The most common clutch was 3, and the average size of first clutches did not differ significantly from second clutches (Table 2).

Mean dimensions of Puerto Rican Sharpshinned Hawk eggs were 37.6 mm  $\times$  29.5 mm (n = 49, Table 3). Similarly, average dimensions of Sharp-shinned Hawks eggs in temperate North America were 37.5 mm  $\times$  30.4 mm (n = 58, Bent 1937). The average egg mass was 18.5 g, 10.8% of the female's body mass and 32% of her mass for a clutch of 3 eggs. Sharp-shinned Hawk eggs in temperate North America averaged 19 g, 11% of the female's body mass and 53% for the usual 5-egg clutch (Newton 1979).

Only females incubated while males provided food. Similar behavior has been reported for populations in temperate North America (Snyder and Wiley 1976). In 1981, we recorded the incubation pattern of a female during 12-h periods (0600-1800) for 3 consecutive days. The female incubated the first egg 27% of the observation period the first day, a clutch of 2 eggs 32% of the observation period the second day, and 42% the third day with still 2 eggs. Although the incubation period varied among females, it is possible that full incubation begins with the third egg. The incubation period from laying to hatching of the last egg was 32 days (n = 13 nests). In temperate North America, Sharp-shinned Hawks have incubation periods of 30-32 days (Platt 1973, Hennessy 1978, Reynolds and Wight 1978).

We determined the hatching sequence of 9 eggs in 3 nests. The first and second eggs laid (n = 6 eggs) hatched less than 24 h apart. Third eggs (n = 2 clutches) hatched between 36 and 48 h after the second-laid eggs. In the remaining clutch, the third egg laid hatched approximately 24 h after the second. Fifteen first clutches hatched over a period of 38 days from 20 April to 27 May (Fig. 1). Three second clutches hatched in the late dry and early wet season on 4 June, 16 June, and 5 July.

Nestling period.—Young emerged from the eggs with their eyes opened. A few hours later the white natal down dried. They uttered "peep" calls in response to the approach of the female or any object, such as a reaching hand. The young raised their heads and accepted tiny morsels of prey presented by the female. By the second and third day after hatching (day 0 at hatching) the young showed improved coordination in pecking at the food held above them by the female. At 4 days of age, the young performed poorly coordinated preening movements of the breast.

About a week after hatching, differences in plumage development between the male and female nestlings were apparent. The primary feather tips of males emerged from the sheaths at approximately 6–7 days and, in females, 8

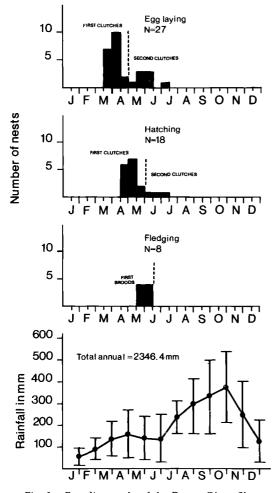


Fig. 1. Breeding cycle of the Puerto Rican Sharpshinned Hawk in Maricao forest relative to rainfall pattern. Vertical lines in rainfall graph represent 1 SD above and below mean values. There were no fledgings from second clutches.

days. The first tail feathers appeared at approximately 9–10 days in males, and 11 days in females. In the second week after hatching, a white down, "wooly" in appearance, began to replace the natal down. Young flapped their wings for the first time at 12 days and emitted "alarm calls" when we climbed the nest tree or reached into the nest. At age 13–15 days they showed defense displays to our reaching hand. They uttered "alarm calls," sat on their tarsometatarsi and, with spread wings, presented their claws.

During the nestling period, males hunted and delivered avian prey to the females, or dropped it in the nests and departed immediately. We

 TABLE 2.
 Average clutch size of Sharp-shinned Hawk first and second clutches.

	No. 1-egg nests	No. 2-egg nests	No. 3-egg nests	Average clutch size*
First clutches	4	2	25	2.68°
Second clutches	1	3	5	<b>2.44</b> <sup>a</sup>
Total	5	5	30	2.63

\* Mann Whitney test U = 172, P > 0.05.

did not observe males dismembering prey, feeding young, or brooding. Females brooded and fed prey to the young. Everytime the adult males arrived with prey, they gave a "contact call" from a nearby perch, stimulating the female to leave the nest to obtain the prey. Shortly after males surrendered the prey to the females, they typically flew to the nest, stared at the young momentarily, and then departed. Females normally returned to the nest, tore apart the prey and fed the young.

During the third week after hatching (16–23 days) females spent less time brooding. They perched near the nest and waited. When prey was delivered, they dismembered it for the young. In one nest the female brooded three 16-day-old young 57% of the time (n = 9.25 h), but decreased brooding to 5% (n = 4 h) when the young were 23 days old. They were last brooded at 26 days and brooding was limited to a period of rainy weather.

During the fourth week after hatching (24-31 days), the young squabbled over prey delivered by males and were able to dismember most of its soft parts. Upon her return to the nest the adult female assisted the young in dismembering the harder portions of the prey. At 25-27 days the young flapped their wings regularly and jumped across the nest or into nearby branches and began to roost overnight in branches.

The nestling period ended when the young flew short distances from the nest and roosted in trees 10-15 m distant. Eleven males fledged at an average age of 28.2 days (SD = 1.17, range

TABLE 3. Dimensions and mass of Sharp-shinnedHawk eggs.

Feature	n	Mean	SD	Range
Length (mm)	49	37.6	0.93	36.4-39.8
Width (mm)	49	29.5	0.57	28.1-31.2
Mass (g)	8	18.5	0.41	18.0-19.0

	Males	Females
Component	(n = 13)	(n = 11)
Nestling period (days)	28.2	32.1
Adult mass $(g) = W$	94.9	170.9
Asymptote $(g) = A$	102.0	172.0
R = A/W	1.07	1.01
К	0.28	0.24
t <sub>o</sub> (inflection point)	8.8	11.0
t10-t90	16.2	18.3
KR/4 × 100 (%/day)	7.4	6.1
KA/4 (g/day)	7.0	10.3

TABLE 4. Comparison of growth-rate parameters of male and female Sharp-shinned Hawk nestlings.

= 27-30), and 9 females at 32.1 days (SD = 1.05, range = 30-33), with a combined average fledging age of 30.0 days (SD = 2.28, range = 27-33).

Growth rate. - Male and female nestlings showed differences in growth patterns (Table 4). Females attained a higher asymptotic mass than males but the latter grew faster, although the slopes of the regression lines were statistically homogeneous (Fig. 2). K, a constant calculated from the slope of the regression line that represents the rate at which asymptotic mass was reached, was higher in males than females. The maximum growth rate in g/day (KA/4) was greater for females than males, but when expressed as a percentage of adult mass (KR/4  $\times$ 100), males attained adult mass 1.05 times faster than females. It took males 8.8 days to grow half their asymptotic mass (t<sub>0</sub>) but 11 days for females. The time interval of growth from 10-90% of the asymptote  $(t_{10}-t_{90})$  was shorter in males than females. Males fledged before females. The young at fledging were slightly heavier than adults.

Growth of body parts in young near-fledging to the age of recapture was compared to average adult body size (Table 5). All young lost mass from near fledging to the recapture age. The tarsi of all young also grew slightly between the intervals compared. The most notable difference in growth between these ages was in the length of the wing chord and tail, growth increments of 23, 35, 37, and 48% in wing-chord length, and of 40, 47, 50, and 53% in tail length.

Fledgling period and dispersal.—Observations of adults and young were continued at 4 nesting sites until young departed. Between 32 and 39 days from hatching, most activities of young

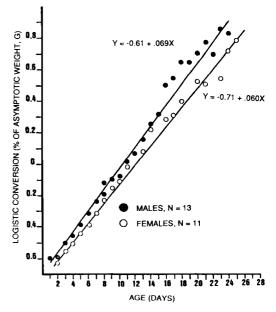


Fig. 2. Growth of nestling Sharp-shinned Hawks. Circles represent mean values. Slopes are statistically homogeneous. F = 0.003, P > 0.05.

occurred in or near the nest. Adults delivered prey to the nest.

By 40-47 days after hatching, the young became strong fliers, chased each other, and dispersed to 50-75 m from the nest. Adult females still fed young at this time. Adults were commonly intercepted immediately after being detected by young, and adults surrendered prey in midair to the first young to arrive. The young were capable of handling and carrying prey to a perch away from their siblings, where it was consumed.

Two young males each attempted to capture prey for the first time at an age of 47 days. One flew after a Grey Kingbird (Tyrannus dominicensis), the other, at an Emerald Hummingbird (Chlorostilbon maugaeus). Both attempts were unsuccessful. We observed 12 other attempts within 100 m of the nests to capture prey by young whose ages ranged between 51 and 68 days. Young males were involved in 9 of the attempts, females in 3. Young attempted to capture butterflies (5 attempts), Emerald Hummingbirds (3), Zenaida Doves (Zenaida aurita; 2), and Anolis lizards (2). They succeeded in catching only Anolis lizards. Although we tried to monitor movements of all young within the nest areas, at times we lost visual contact and other attempts

Age period (days)	Sex	% adult mass	% adult wing chord length	% adult tail length	% adult tarsus length
26-50	female	99-91	61-98	55-95	97-102
26-50	female	99-94	53-101	42-95	94-99
26-50	male	110-103	68-103	48-98	104-107
26-43	female	104-97	69-92	48-95	91-93

TABLE 5. Growth of Sharp-shinned Hawk young between two age periods relative to adult values,\* reported as percentage.

\* Average mass (g) and average body measurements (mm) of adults: male—mass = 94.9, wing chord = 141.0, tail length = 116.3, tarsus length = 45.7; female—mass = 170.9, wing chord = 174.4, tail length = 139.9, tarsus length = 56.4.

at predation were presumable unobserved. Twice when we lost visual contact of 2 young males for 45 min, their crops were full when spotted.

Young spent time away from the nest area 1-2 days before departing from the nesting site. In 1982 we monitored movements of 6 young at 2 nesting sites. Two young, 1 in each of the nesting sites, did not spend time away, but departed abruptly. Two to three days prior to their departure, the other young spent time away: 12% (female) and 16% (male) at one site; 43% (female) and 37% (male) at the second. The ages of young in 1 nesting site were 64 days (female), 68 days (male), and 72 days (male) when they departed at 62 days (male), 64 days (female), and 68 days (male).

There was a strong correlation between decrease in the prey-delivery rate and departure of young from the nest areas. Fledglings in 1 nest responded to decrease in prey-delivery rate by spending less time in the nest area (Fig. 3a). Decline of prey deliveries was abrupt, and was stopped altogether 5 days before the fledglings departed. However, the fledglings did not leave when prey deliveries stopped but gradually reduced time spent in the nest area. To the extent the bird densities in the areas censused can be extrapolated to the home range of this pair, prey abundance increased during the period when prey deliveries decreased and eventually stopped (Fig. 3b).

Adult and young did not stay together after the latter departed. We visited 2 nesting sites in 1982 and found the adults present, calling and flying, although the young had left. Adults normally entered nesting sites quietly when young were present.

Egg-laying and hatching occurred over extended periods due to laying and hatching of second clutches. Fledging occurred over a shorter period because no second nests were successful. Egg-laying and hatching occurred mostly during periods of low prey abundance (Fig. 4). Young fledged during the peak of prey abundance. No bird prey density data were available for the last quarter of the year. Despite these limitations, it appears that Sharp-shinned Hawks have nestlings and fledglings at periods of prey abundance.

*Molting.*—Observations on molting (n = 8 females) was limited to the breeding season, and indicated that breeding and molting overlapped. Early in the nestling period four females were missing either 1-4 primaries or tail feathers, or both. In some females molting may begin earlier, i.e. after egg-laying. One female began to molt primaries 5 days after clutch completion. Three other females were missing tail or wing feathers (3-7) during the fledging period. We believe that molt in females is slow and extends perhaps from 4-6 months. Breeding and molting also overlapped in a Sharpshinned Hawk population in northeastern Oregon (Henny et al. 1985). Females molted more than 60% of their primaries by mid-July, suggesting that molting began shortly after clutch completion.

Reproductive success.—From 1978–1982 and in 1985, 105 eggs were laid in 40 nests, an average clutch size of 2.6 (Table 6). Two nests were attended by non-laying pairs. Of 105 eggs 63% hatched and 47% of the nestlings fledged. A total of 0.8 young fledged/breeding attempt. Productivity was 0.9 and nest success 29%. All nesting attempts by immature-plumaged females failed (n = 4).

Reproductive success varied considerably between years (Table 6). We excluded the small number of nests sampled in 1978. All reproductive success parameters, with the exception of the proportion of eggs hatched, were lower in 1980 and 1981. Productivity and nest success

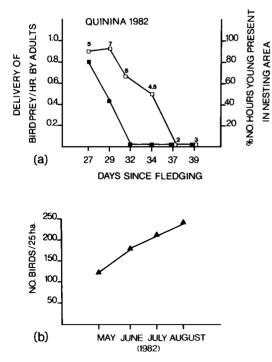


Fig. 3. (a) Relationship between departure of 3 Sharp-shinned Hawk young from nest area (open squares) and prey-delivery rate (solid squares). Numbers above open squares are hours of observations. (b) Bird-prey density in latter part of breeding season.

were considerably higher in 1979, 1982, and 1985, and highest in 1982. The number of fledglings/breeding attempt was also highest in 1982. However, reproductive output was highest in 1985.

We compared nest success and average number of fledglings produced between first and second nesting attempts. Nest success was 36% (n = 33 nests) in first attempts and 0% in second nesting attempts (n = 9 nests). First attempts produced 0.9 fledglings and second attempts none.

We determined nest failures in relation to nesting stage of first and second nesting attempts. Nest failures during the nestling stage were similar (36% in the first attempts and 33% in second nesting attempts). In contrast, nest failures during the egg stage were approximately 3 times higher in second nesting attempts (67%) than in first attempts (21%). Causes of nest failures in relation to stage of reproduction were determined in 28 nests and renests (Table 7). During incubation, desertions

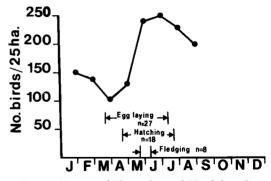


Fig. 4. Timing of Sharp-shinned Hawk breeding cycle relative to density of avian prey in Maricao forest (1981). Egg laying and hatching periods include second clutches. There were no fledgings from second clutches.

(73%) were the most important cause of nest failures. Seven of 11 desertions were of second nesting attempts. Nest failures related to deliberate human harassment (20%) were second in importance during incubation. Warble fly (*Philornis* sp., Diptera, Muscidae) parasitism accounted for most (69%) nest failures during nestling stage. Warble fly larvae feed subcutaneously and cause damage to tissues of nestlings, affect growth and development, and kill the host (Arendt 1985a, b; Uhazy and Arendt 1986). Nestling predation was second in importance (15%).

# DISCUSSION

Courtship and territoriality.—The courtship and territorial behavior of the Puerto Rican Sharpshinned Hawk did not differ significantly from other small Accipiter hawks (Brown 1976, Newton 1979). The "undulating flight display" of males prior to pair formation might serve both to attract potential mates and give an assertive message. When agonistic behavior between males during a territorial conflict reached high intensity levels, they rendered their talons ineffective by grappling each other. This ritualized aggression allowed the contestants to assess their strengths without inflicting damage.

Territory possession reduced disturbance during pair formation. The territorial conflicts in the Maricao forest suggest that nesting sites were in short supply or that there was an unbalanced adult sex ratio (more males than females). Unfortunately, we were unable to distinguish these to possibilities. Effects of intruder

Year	No. nests studied	No. active nestsª	No. eggs laid	Mean clutch size	No. (%) eggs hatched	No. (%) young fledged	Fledglings/ breeding attempt <sup>ь</sup>	Fledglings/ territorial pair (n)°	Nest success <sup>d</sup> (%)
1978	2	2	6	3.0	3 (50)	0 (0)	0	0 (2)	0
1979	7	7	18	2.6	10 (56)	9 (90)	1.3	1.5 (6)	43
1980	6	6	14	2.3	8 (57)	1 (13)	0.2	0.3 (3)	17
1981	11	11	29	2.6	18 (62)	1 (6)	0.1	0.1 (8)	9
1982	6	6	16	2.7	15 (94)	9 (60)	1.5	1.8 (5)	50
1985	10	8	22	2.8	12 (55)	11 (92)	1.4	1.2 (9)	40
Total	42	40	105	2.6	66 (63)	31 (47)	0.8	0.9 (33)	29

TABLE 6. Reproductive success of Sharp-shinned Hawks.

\* Active nest defined as a nest with at least one egg.

<sup>b</sup> Breeding attempt refers to a clutch initiated (first nests and renests).

<sup>c</sup> n = total number of breeding and nonbreeding pairs.

<sup>4</sup> Nest success is the proportion of nests that fledged at least one young.

males on the breeding activities and fitness of pairs were not determined.

Duration and timing of the breeding cycle.-The breeding cycle in Puerto Rico was approximately 2 months longer than in Oregon and Utah (Fig. 5). Similarly, tropical passerines (Ricklefs 1969a) and other raptors of comparable size and similar trophic requirements also have protracted breeding cycles compared to their temperate-latitude counterparts (Brown 1976; Newton 1977, 1979; Wiley and Wiley 1981; Mader 1981, 1982). Differences between tropical and temperate avian groups stem primarily from differences in the length of time required to complete various stages of the breeding cycle. However, duration of incubation, nestling, and fledgling stages is about the same in Puerto Rico, Oregon, and Utah. The elapsed time from occupancy of nesting sites to initiation of laying accounted for the differences in the duration of breeding cycles. Early occupancy of the breeding grounds in Puerto Rico may be advantageous if Sharp-shinned Hawks could detect spatial and temporal changes in distribution and abundance of prey resources. This may be particularly important if this information was a proximate cue to initiate egg laying.

The fledging period in Sharp-shinned Hawks was synchronized with the peak of prey abun-

dance, but females had to reach optimal body condition to lay during relatively low prey abundance. Perhaps females need a longer prelaying period to reach optimal body condition during low prey abundance than high prey abundance. Body condition of the female is crucial (Romanoff and Romanoff 1949, Ricklefs 1974, Alisaukas and Ankney 1985, Astheimer and Grau 1985). In the Eurasian Sparrowhawk only females that gain mass subsequently lay (Newton 1986). The reserves buffer females against erratic prey delivery by males and allow uninterrupted incubation and feeding of young. Tawny Owl (Strix aluco) showed similar differences in mass between laying and non-laying females (Hirons 1976). Some albatrosses, geese, and penguins arrive on their breeding grounds when feeding conditions are poor, and have long breeding seasons. Food intake is reduced, and body reserves are an important source of energy and nutrients for pre- and post-laying activities and egg synthesis (Frings and Frings 1961, Barry 1962, Fisher 1967, Ryder 1970, Warham 1974).

It is possible that the breeding season in Puerto Rico was restricted to a relatively brief period (dry season) by low food availability and extremely high precipitation in the wet season. Unfortunately, data on prey abundance were

TABLE 7. Causes and timing of Sharp-shinned Hawk nest failures.

Time of failure	Desertion of eggs <sup>a</sup>	Desertion of nestlings <sup>a</sup>	Predation on eggs	Predation on nestlings	Warble fly	Human related <sup>b</sup>	Total
Pre-hatching	11 (73%)	_	1 (7%)	_		3 (20%)	15
Post-hatching	_	1 (8%)	_	2 (15%)	9 (69%)	1 (8%)	13

\* Direct observations confirmed abandonment of viable eggs or young.

<sup>b</sup> Human related refers to deliberate human harassment of nests, their contents or adults which resulted in nest failure.

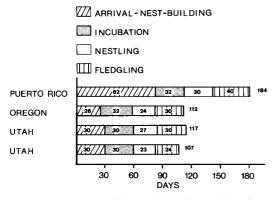


Fig. 5. Duration of Sharp-shinned Hawk breeding cycle in Puerto Rico and 3 populations in North America. Number inside breeding stage represents its duration. Data for Puerto Rico based on sample of 13 nests, Oregon on 12 nests (Reynolds 1978), and Utah on 7 and 34 nests (Hennessy 1978 and Platt 1973, respectively).

not available for the last quarter of the year in Maricao. If there were a period of reduced abundance or availability of prey in the last quarter of the year, it may have prevented the temporal separation of breeding and molting, which overlapped in Maricao forest. The hawks appeared to have a low rate of molt that lasted many months, which could reduce the energy requirements and insure adequate insulation and flight performance. Egg laying at 3 Sharpshinned Hawk nests in eastern Puerto Rico (Luquillo Forest) was also in the dry season (Snyder and Wiley 1979). Overall counts of small birds in that forest showed strong seasonality with a major peak in spring, a drop in summer, a lesser peak in autumn, and another drop in winter. Heavy rainfall might interfere with foraging activities of the hawks, which feed on relatively elusive avian prey. In fact, severe rainfall was suggested as a cause of Puerto Rican Sharpshinned Hawk nest failures in Luquillo (Snyder and Wiley 1976) and Toro Negro (Cruz and Delannoy MS) forests. In Great Britain, rainfall was the second most frequent cause of mortality of young Eurasian Sparrowhawks during the breeding season (Moss 1979). Rainfall affected prey delivery and forced the females to hunt, which left the young unattended and resulted in prolonged exposure and death.

Development and dispersal.—All growth parameters examined indicated that male nestlings grew faster than females. Sexual differences in growth rates have been found in other dimorphic raptors (Schnell 1958, Moss 1979, Picozzi 1980). Male Sharp-shinned Hawk in Puerto Rico became behaviorally advanced and feathered sooner than females. They left the nest earlier and developed flight skills sooner. In most dimorphic raptor species for which data are available, males fledge earlier than females (Newton 1979). These adaptations might help minimize competition of the larger females with the smaller male siblings. We found no information on Sharp-shinned Hawk growth rates in temperate North America. Eagle species vary in their growth pattern, not because of sibling competition for food as proposed by Werschkul and Jackson (1979), but because of selection to reduce peak energy requirements of nestlings (Bortolotti 1986).

Young hawks continued to grow after fledging and this apparently influenced the length of the dependency period afterwards. At fledging, young were slightly heavier than adults. Wing chord and tail lengths were approximately 50% shorter than those of adults. Allometric growth of body parts in young limited the flying capabilities at fledging. Delayed growth of wings and tail in young hawks forced them to develop their flight skills slowly and progressively. This is particularly important because Sharp-shinned Hawks feed primarily on elusive avian prey. During the dependency period, young hawks pursued birds, butterflies, and captured lizards. Young Peregrine Falcon (Falco peregrinus) learned to discriminate through trial and error which species were suitable as prey and which were most profitable to hunt (Sherrod 1983). Mueller and Berger (1970) showed that young North American Sharpshinned Hawks attacked birds too large as suitable prey more often than adults and attributed this difference to lack of experience. Newton (1986) reported young Eurasian Sparrowhawk females attacking bird prey larger than themselves and suggested that learning consisted of restricting attacks to smaller and more manageable prey. Learning presumably plays an important role in the development of Sharpshinned Hawk hunting skills.

Other investigators have reported a trend of declining prey deliveries towards the end of breeding season similar to that of the Sharpshinned Hawk. Snyder and Wiley (1976) observed declining prey deliveries late in the breeding season at 2 of 3 nests in Arizona and

4 h	A mania	

		Puerto Rico		regon*	Utah⁵	Utahs		Wyoming	
Mean clutch size	2.	6 (105/40)	4.6	6 (23/5)	4.3 (146/34)		_	3.	5 (7/2)
% eggs hatched									
(hatching success)	63	(66/105)	70	(16/23)	—		_	100	(7/7)
% of hatched chicks fledged									
(nestling survival)	47	(31/66)	81	(13/16)	_			100	(7/7)
% successful nests	29	(12/42)	92	(11/12)	_	62	(58/94)	100	(2/2)
Fledglings/breeding attempt	0.	8 (31/40)	2.2	7 (30/11)	_			3.	5(7/2)
Fledglings/nest		7 (31/42)	2.	5 (30/12)	4.5 (9/2)	2.3	l (197/94)	2.	5(7/2)
Fledglings/territorial pair		9 (31/33)	2.2	7 (30/11)	_			3.	5 (7/2)

TABLE 8. Reproductive success of Sharp-shinned Hawks in Puerto Rico and North America.

\* Reynolds and Wight (1978).

<sup>b</sup> Platt (1973).

<sup>c</sup> Hennessy (1978).

<sup>d</sup> Craighead and Craighead (1956).

felt these nests were stressed by food shortage. Mueller et al. (1981) reported 65% fewer prey deliveries/h and 63% fewer g/h to a nest towards the end of the dependency period and attributed the decline to reduced hunting by adults, rather than to depleted prey resources.

Alternatively, the gradual decrease of prey deliveries could have been a strategy of the adults to force the young to become independent. This proposition is consistent with the parent-offspring conflict theory developed by Trivers (1974). The fledglings, in order to maximize their inclusive fitness, may demand more parental investment than what the adults could possibly provide. Therefore, "the optimal strategy should involve flexibility in the behavior of adults with parental care being prolonged when food is scarce" (Mueller et al. 1981: 89). However, the length of parental care also depends on whether or not the population is migratory. Several studies have suggested that parental "meanness" (i.e. indifference, aggression, or both) is an important factor influencing offspring independence (Trivers 1974, Wilson 1975, Davies 1978). We do not know where immature individuals established residency.

Population ecology.—Despite the low reproductive success of the Sharp-shinned Hawk in Maricao forest, there is no indication that this population is declining. We censused an area of 29.1 km<sup>2</sup> and obtained breeding densities of 1.06 individuals/km<sup>2</sup> in 1981 and 1.03 individuals/km<sup>2</sup> in 1985 (unpubl. data). In addition, although reproductive success was very low at many nesting sites, the reoccupancy rate was relatively high. A low reoccupancy rate might indicate high adult mortality and very little recruitment, or emigration into adjacent habitats. Although the data on adult mortality are limited, some individuals were still alive 3 yr and up to 5 yr after being banded. Other indirect evidence suggestive of low adult mortality is that only 3 of 42 nesting females were in immature plumage. No immature-plumaged males occupied nesting sites. We surmise that recruitment of reproductive individuals into the population is low. There was no evidence that the Sharp-shinned Hawk population in Maricao is maintained by an influx of individuals from other populations. Individuals banded in Toro Negro and Luquillo forests have not been observed in Maricao. Most lands adjacent to the Maricao forest are under cultivation or in early secondary growth and may not be suitable for nesting.

In general, birds on tropical islands and in mainland regions have lower fecundity and reproductive success than their counterparts in temperate latitudes (Ricklefs 1969b, Klomp 1970, Cody 1971, Skutch 1976, Crowell and Rothstein 1981). We compared reproductive variables of Sharp-shinned Hawks in Puerto Rico with temperate North American areas (Oregon, Utah, Wyoming) to determine if the general tropicaltemperate reproductive trend held. In all variables examined, the averages in Puerto Rico were lower (Table 8). Egg losses in Puerto Rico were primarily due to desertions, while infertility, death of embryos, and egg breakage caused egg losses in Oregon, perhaps due to high levels of pesticides (Reynolds and Wight 1978). In the Maricao population some females may have sufficient body reserves to produce eggs, but they then experience shortage of body reserves and abort nesting attempts. Low body reserves and declining food resources were likely causes of desertions and were particularly common in second nesting attempts. The high incidence of nest desertions during incubation resulted in low hatching success of this population.

Lower fecundity in Puerto Rico could be related to high adult life expectancy in this population. We have provided evidence that adult survival was relatively high, recruitment to the breeding population was slow, and the population was at carrying capacity with existing nesting habitat. As suggested by Pianka (1978: 128), "current reproductive effort should be inversely proportional to adult life expectancy."

Some pairs in Maricao forest renested after losing their eggs or nestlings. This habit may help to offset the low fecundity of the population. However, none of the second nesting attempts fledged young. The Savanna Hawk (*Buteogallus meridionalis*), another tropical raptor with low fecundity and capacity to renest, had 40% success on second nesting attempts (Mader 1982). It is possible that in some years Sharpshinned Hawks in Puerto Rico have better success on second nesting attempts than during our study period. Renesting following loss of nestlings has not been reported for the Sharpshinned Hawk in North America.

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100 Years Ago in The Auk



From the review (1888, Auk 5: 414) of G. Trumbull's "Names and Portraits of Birds Which Interest Gunners with Descriptions in Language Understanding of the People" (1888. New York, Harper and Brothers. viii + 222 pp. [no price given]):

"Vernacular Ornithology.-This is a wonderful world of checks, balances, compensations, and reactionary running-gear. For example, the A.O.U. Committee has upset all the technical names of birds that could thus hardly be dealt with, and Mr. Trumbull has set up all the vernacular names that could be treated understandingly. Thus ornithology fattens and flourishes, as on loaves and fishes; for has not our author wrought a veritable miracle; namely, the filling of a 'long-felt want'? (Not that any one has actually felt that want until the void has been filled; but it existed, and only needed filling to be felt and grow by what it fed upon. Even ornithologists, however hopelessly mired down in the mazes of their 'shoptalk,' as our irreverent friend terms their technical vocabulary, may find in this book much to their profit. Seeing that theirs is not the only language that is weighted with synonymatic woe, they may take heart again. Many of them have 'viewed with alarm' as the politicians say, the great load of wordy rubbish that our science carries; the spectacle of a bird with half a dozen generic, a dozen specific names, and several dozen combinations of these two terms has a chastening effect upon the mind. But now, with risen spirits, we can 'point with pride,' like statesmen, to the synonymatic confusion worse confounded which our mother tongue offers to console us, if not to absolve us from our sins. For here we have a thousand and more names for three-score birds! Et tu Brute, Mr. Trumbull?

"But to be serious, as befits the rich embarrassment with which the author endows us, let us examine this remarkable work. It treats all the gamebirds of Eastern North America-the natatorial, gallinaceous, limicoline and paludicole birds ordinarily pursued, for sport by 'that helpless but interesting creature, "the true sportsman,"' or for profit by 'our gunners, a class of men who earn a livelihood by shooting birds.' These we find to be sixty-one in number. They are first named in strict accord with the rules and regulations for such cases and provided by the A.O.U. Committee, the dogmas of which deathless doers of deeds nomenclatural are accepted by Mr. Trumbull with orthodox humility. Then comes a brief description, in language 'understanded of the people,' together with a statement of habitat in each case, the range being usually drawn from the same fountain of infallibility whence the sacred scientific names issue: for in the beginning was the word, and the word was with the Committee. With these data comes a portrait in each case—a striking silhouette, or symphony in black and white, struck by the well-known hand of Mr. Edwin Sheppard, who has made better likenesses of more birds than any other American artist now living. Having thus marked down his bird, so to speak, Mr. Trumbull proceeds to bag his game with a wealth and ingenuity of device that excite our unbounded admiration. It is truly an infinite variety that neither age can stale nor custom wither-a bounteousness, a plentitude, a very plethora, the fullness whereof is exhaustless. Allah is said to be invoked by the pious Mussulman under ninety and nine aliases, and history but repeats itself in the myrionymy of the game birds of America. A thousand names, for three-score birds, by a single prophet!" ... -E.C.