

## ECOLOGY AND BREEDING HABITS OF THE SAVANNA HAWK IN THE LLANOS OF VENEZUELA

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**ABSTRACT.**—The ecology of the Savanna Hawk (*Buteogallus meridionalis*) was studied in the palm-savannas of Venezuela in 1978–1980. Pairs produced only one egg per clutch, no more than one young per calendar year, and had eggs or young in nests from February to December, coinciding largely with the wet season. In comparison to North American Red-tailed Hawks (*Buteo jamaicensis*), Savanna Hawks had significantly fewer young per pair per year, lower nest success (47.1% vs. 82.5%), mainly due to lower hatching success (64.1% vs. 84.4%) and a lower proportion of pairs laying eggs (73.3% vs. 88.0%). Survival of young Savanna Hawks from hatching to near fledging was 70.4%, and the adult survival rate, 71.1%; these values are approximately equal to those for Red-tailed Hawks. The brood size was artificially doubled from one to two at 10 Savanna Hawk nests, but the adults could find only enough food to feed and raise one chick in most cases. Food appeared to be both the ultimate and proximate factor controlling the timing of breeding. The Savanna Hawk has evolved interrelated habits that counter its low fecundity: (1) the capability of renesting after the initial eggs or young have perished; (2) a post-fledging dependency period of four to seven months to help insure survival of the single young; and (3) permanent or long-lived pair-bonds. The ability to renest is enhanced by hunting versatility. Long-lived pair bonds may improve intra-pair activities thereby enhancing the reproductive success of experienced breeders.

Hawks and eagles in the tropics, in contrast to northern latitudes, may have evolved different reproductive habits in response to greater diversities of prey and predators, both avian and mammalian, and different climates. Little is known, however, about breeding habits and food relationships in neotropical falconiforms.

Tropical birds generally lay smaller clutches than their temperate counterparts (Lack 1947, 1948, 1954). Of the several hypotheses that have been proposed to explain this contrast, I investigated two dealing with the evolution of tropical clutch sizes: Lack's (1947) hypothesis of "maximum reproduction" and Skutch's (1967) of "readjusted reproduction." The former theory, which is more widely accepted, states that birds produce as many eggs and thus offspring as they can feed. The latter maintains that birds produce fewer young than they are capable of feeding because the adult survival rate is high and the need to recruit breeders is low. Additionally, Skutch believed that a smaller clutch size may, in part, be a result of heavy predation pressures in the tropics, such that smaller broods would require fewer feeding visits and therefore less risk of nest detection by predators. The question of what selects for a smaller clutch size in a predatory bird has not been addressed. Here, I present the results of a 16-month study of the Savanna Hawk (*Buteogallus meridionalis*, following Mayr and Cottrell 1979) in the llanos of Ven-

ezuela which examined: (1) a test of the hypotheses of Lack and Skutch, (2) what breeding habits exist to help offset a low reproductive potential inherent with a clutch size of one, and (3) how the timing and duration of breeding were related to rainfall and food resources.

### STUDY AREA AND METHODS

The Savanna Hawk ranges from Panama to central Argentina (Blake 1977). I studied a population for two breeding seasons and part of a third (15 January through 15 October 1978, 25 April through 3 October 1979, and 26 April through 3 May 1980) on a cattle ranch in Guarico State, Venezuela. Colleagues continued checking nests after I left, from October to December. The habitat was primarily palm savanna, although a few nests were found in tree savanna. The region (llanos) has one dry season (generally December through April) and one wet season (May through November), which have a pronounced effect on the land. In February for instance, the palm savannas were dry and dusty while in August they were sometimes covered with over a meter of standing water.

I chose a study area of 9.4 km<sup>2</sup> containing 23 pairs of hawks for which I determined the number of eggs and young produced each year. Additional data, including clutch size and nesting success, were gathered on nests located

outside the study area. Nest contents were checked periodically using a mirror attached to a pole. I travelled by motorcycle, horse, and on foot. Fifty adult Savanna Hawks were captured with balchatri traps (Berger and Mueller 1959). Forty-nine were individually color-banded, including 13 pairs in which both members were banded. I could not tell the sex of adults because they differ little in size and color (mean wing chord = 39.7 cm, range 31.5–42.3,  $n = 49$  adults; mean weight = 844 g, range 720–958,  $n = 50$  adults). Later, I determined the sex of several individuals by their behavior. Territories of five neighboring pairs (8 of 10 adults were initially color-banded) were determined during the dry and wet seasons by plotting 50 or more sightings for each pair from February to October 1978.

Lack's hypothesis of maximum reproduction was tested in 1978 by artificially doubling the normal brood size of one, at nine nests during the first week after hatching. The ages of the chicks did not differ by more than 1.5 days. Growth (weight) of two chicks in a manipulated nest and a chick in a control nest was measured every five days until fledging. I doubled the brood size at another nest in 1979 in order to observe chick interactions and to determine if doubling affected the amount of prey brought to the nest. In a blind placed level with the nest 85 m away, I watched the nest for about 44 h from 7 September to 2 October, and for 6 h before the second chick was added. The average period of observation was 2 h:5 min. (range 1:20–2:33). Another blind was erected at a nest with one chick in 1979 so that I could collect information about prey (30 h observation). Observations at both blinds were often interrupted because of storms and flooding. I estimated weights of prey from known weights of comparably sized animals. All observations were aided by a 32 $\times$  spotting scope.

Platforms were built at the top of nine palm trees (typical nesting sites) containing nests to allow a close inspection of chicks and prey remains. Flooding reduced the number of visits to some nests. Therefore, I considered a nest successful if a chick was raised to an age of at least five weeks, even though chicks fledged (left the nest) at roughly 6.5–7.5 weeks. I used an incubation period of 39 days (range 37–40,  $n = 4$ ) for back-dating some nests from known hatching dates to estimated laying dates.

Six immature hawks of known fledging dates were followed to determine the duration of the post-fledging dependency period. Dependency of a young bird on its parents was substantiated by continuous food begging calls by the former

and exchanges of prey from adult to immature birds.

## RESULTS

### PRODUCTIVITY

Savanna Hawks laid eggs from February to September ( $n = 116$  clutches, Figs. 1 and 2). Laying peaked in the first part of July 1978 but had no peak in 1979. The number of clutches in 1979 was nearly equal for each month from April to July, except for a low in June. In 1978, hatching occurred from March to October with a peak in mid-August. In 1979 nest failures caused two well-defined periods of hatching, the first in mid-May and the second in early September. In both years, I noted fledging from May to December. Individual hawks generally did not nest at the same time each year. In 1979, marked adults laid eggs, on the average, about 30 days from the date they laid in 1978 (Fig. 3). For both years the entire breeding season (egg laying–fledging) spanned about 250 days (260 days in 1978 and 240 days in 1979) and coincided to a large extent with the wet season (Figs. 1 and 2).

All clutches ( $n = 116$ ) had one egg. Nest success, from egg laying until a chick was at least 5 weeks old, both years combined, was 47.1% ( $n = 85$  nests, includes 10 renests). The number of young produced per nest attempt (started with a single egg) was 0.47 ( $n = 85$ ). Of 75 initial attempts in two years, 36 (48.0%) were successful; only 4 out of 10 renests proved successful (six other renests were noted but not checked to determine productivity). For 16 renests, 10 (62.5%) of the initial nests failed at the egg stage and 6 (37.5%) at the chick stage. Of 24 territories thoroughly checked after an initial nest failed, 16 (66.7%) pairs renested. No Savanna Hawks attempted to raise two young in one calendar year.

More nests were successful ( $P < 0.05$ ) in 1978 than in 1979. Of 44 initial nests in 1978, 25 (56.8%) were successful. Only three of seven (43%) renests were successful. In 1979, 11 (35.5%) of 31 initial nests were successful. Only one of three renests was successful. For both years combined, the time of nest failure was determined for 48 nests, including six renests. Thirty-two (66.7%) failed with eggs and 16 (33.3%) with young. Hatching success was 64.1% ( $n = 78$ ), while nestling success from hatching to at least five weeks of age was 70.4% ( $n = 54$ ).

Nests begun during the first half of the breeding season had about the same success as nests begun in the last half. Combining data from both years, 18 (62.1%) of 29 nests were suc-

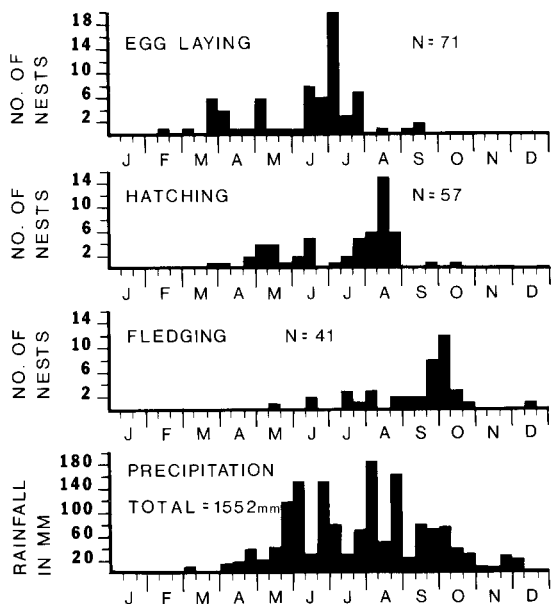


FIGURE 1. Breeding cycle of the Savanna Hawk in 1978 in the llanos of Venezuela showing peaks and spreads for major events in the cycle and their relation to annual precipitation. Renesting attempts are included. Flooding started in the last third of May and did not begin to subside until the middle of October.

cessful for the months before June while 29 (65.9%) were successful for June and after.

In 1978, 21 (91.3%) of the 23 pairs in the study area laid eggs resulting in 27 eggs, and 16 young survived to at least five weeks (1.17 eggs and 0.70 young per pair). This included six attempts at renesting, two of which were successful (0.26 renest attempts per pair). The number of laying pairs and production of eggs and young per pair were significantly lower ( $P < 0.01$ ) in 1979 than 1978. Twelve (54.5%) of the 22 pairs laid eggs resulting in 14 eggs and six young (0.64 eggs and 0.27 young per pair). In 1979, only three re-nests occurred, one of which was successful (0.14 renest attempts per pair, significantly less,  $P < 0.05$ , than in 1978). For both years combined, an average of 0.91 eggs and 0.53 young were produced per pair, including nonbreeders (non-layers).

#### ADULT SURVIVAL AND MOVEMENT

Forty-one adults were trapped and color-banded from 27 January to 13 March 1978, and 8 more from 5–10 October 1978, all of which were members of pairs. The first 41 were checked 3–18 April in 1979 and all were still present. For 45 of the 49, I determined how many had survived to approximately one year after capture. The territories of the January–March hawks were checked in 1979 from 26 April to 7 May, and the October hawks on 1

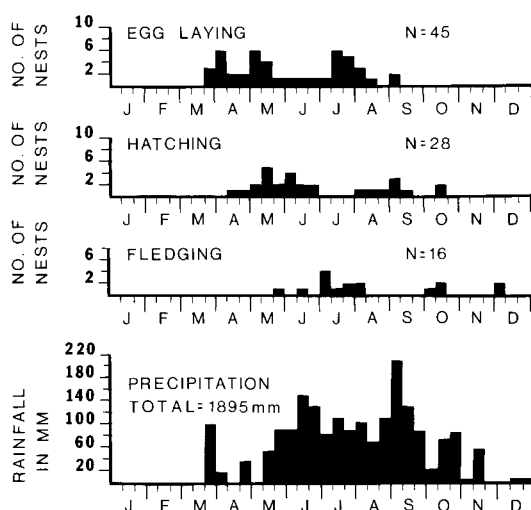


FIGURE 2. Breeding cycle of the Savanna Hawk in 1979 in the llanos of Venezuela showing peaks and spreads for major events in the cycle and their relation to annual precipitation. Renesting attempts are included. Although temporary flooding started in the last third of May, long-term flooding started in the middle of June and did not begin to subside until the last third of October.

October 1979. Thirty-five of the 45 adults were alive, giving a minimum yearly adult survival rate of 77.8% (assuming that they all remained in the area and none lost their bands). I also determined how many had survived to approximately two years after capture. Of 35 surviving adults in 1979, I checked 28 for survivorship in 1980 (26 April–3 May). Eighteen or 64.3% of the 28 adults were still alive, so the average annual adult survival rate over the two-year period was 71.1%. Since Savanna Hawks are resident and have eggs or young 11 months of the year, an approximate breeding replacement rate can be determined by subtracting the annual presumed survival rate of 71.1% from 100%, giving 28.9%.

Eleven of the 13 pairs with both mates banded were checked one year later and seven (64%) pairs were intact. Only one member of each of the other four pairs remained, although each had re-mated. Of the seven intact pairs left in 1979 only three (42.9%) remained intact in 1980. After two years then, 3 (27.3%) of 11 pairs were still together. I consider the adult annual survival and fidelity rates to be accurate because: (1) color-marked birds were not found outside their home ranges indicating little or no dispersal, (2) the location of territories in the study area remained essentially the same from 1978 to 1979, except for one pair, and (3) I saw no evidence that birds who had lost their bands were misidentified (based on 32 adults that received two bands each).

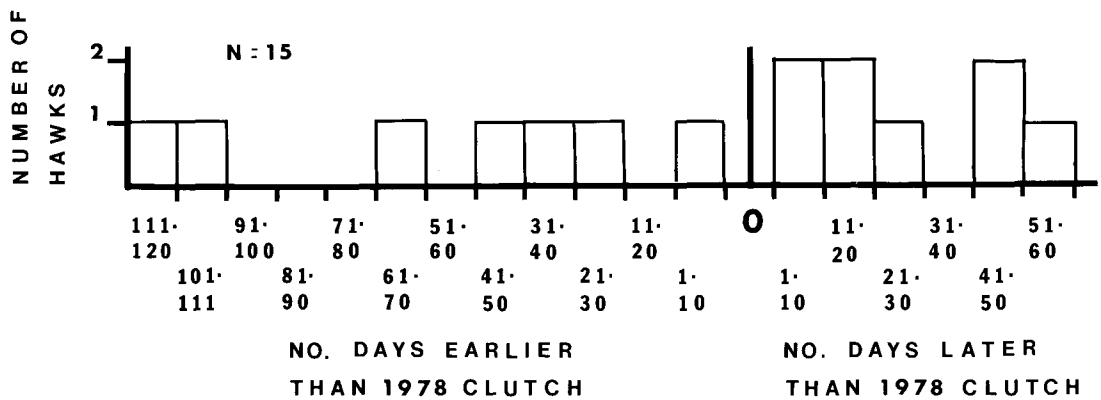


FIGURE 3. A comparison of laying dates in 1979 to those of 1978 for the same individually marked Savanna Hawks with the differences expressed in days earlier or later than 1978. Of 20 adults followed (all from different pairs), five did not produce eggs in 1979.

Twenty-three pairs averaged 0.41 km<sup>2</sup> of palm savanna per pair. This value includes some areas not used by the adults but by one- or two-year-olds in predominantly immature plumage. The home range included a hunting area that was defended against other hawks and a soaring range where the adults flew over their own area and their neighbor's as well. The home ranges of five neighboring pairs in palm savanna averaged 0.14 km<sup>2</sup> (range = 0.08–0.16 km<sup>2</sup>), none of which overlapped. Fledged hawks remained inside their parent's home range until they became independent four to seven months after fledging ( $n = 6$  young).

#### FOOD

The remains of prey at Savanna Hawk nests were chiefly semi-terrestrial fresh-water crabs (*Dilocarcinus dentatus*, 57.3%), birds (24.5%), and reptiles (10.7%) (Table 1). Sampling of remains was biased because large or partly inedible items such as crabs, lasted longer than small or entirely consumed prey (eels). Direct observation of prey delivery therefore gave more accurate data on food habits. Prey observed brought to two nests were mostly eels (44.9%), frogs (16.3%), crabs (12.3%), and birds (12.2%;  $n = 69$ , Table 2). All of these are wet-season prey. In the dry season, eels and crabs likely comprise little of the available food because so little water is present. Probably more mammals and birds are taken in the dry season; indeed, I saw two adults carrying rodents then.

I determined the rate of prey delivery at two nests during the nestling phase (Table 3)—one nest had one chick and the other two chicks (manipulation). Although incomplete, the data suggest that about the same amount of prey and number of items were brought to both

nests. The average weight of the prey (84% were whole) when delivered to the nests was 19 g.

#### CLUTCH SIZE MANIPULATIONS

The adults accepted and fed both chicks at the 10 manipulated nests. Of the nine nests in 1978, two failed from unknown causes, six produced only one young, and one produced two young. The latter chicks were lighter than average weight, fledged two weeks later than normal, and were severely infested with botfly larvae. Thus, only one of the nine nests produced two chicks; this is statistically significant (binomial test,  $P < 0.005$ ). In 1979, the parents at the single manipulated nest raised both young. For those six nests that lost one of two chicks, insufficient food was probably the cause. Starvation of one chick occurred at two nests, one at 48 days of age and the other at 44. The remaining chicks disappeared between 5–22 days of age. The weights of both chicks at one manipulated nest were compared to those obtained at a control nest containing only one chick (Fig. 4). Chicks in the manipulated nest grew significantly slower ( $P < 0.05$ , full model multiple regression test,  $F = 3.49$ ,  $df = 2, 20$ ) than the control and lost weight at 28–33 days of age, suggesting insufficient food. Delayed fledging was apparent at other manipulated nests in which only one chick survived (three to seven days late). At three nests, I marked both chicks to determine if adults raised their own or the introduced chick. At one nest, the adults raised only the introduced chick, while at two others the adults raised both (one each in 1978 and 1979).

Observations at the blind of the 1979 manipulated nest disclosed no sibling aggression even though chick two (C2) developed slower than the other (C1) and weighed only

TABLE 1. Prey remains found at Savanna Hawk nests in Guarico State, Venezuela.

Prey	No. individuals	% individuals
<b>Mammals</b>		
Unidentified rodents	4	2.5
<b>Birds</b>		
Purple Gallinule ( <i>Porphyryla martinica</i> )	5	3.1
Ani ( <i>Crotophaga</i> sp.)	2	1.3
Unidentified doves	15	9.4
Unidentified flycatchers	1	0.6
Unidentified birds	16	10.1
Total birds	39	24.5
<b>Reptiles</b>		
Rattlesnake ( <i>Crotalus</i> sp.)	1	0.6
Iguana ( <i>Iguana iguana</i> )	3	1.9
Unidentified lizards	8	5.0
Unidentified snakes	2	1.0
Unidentified reptiles	3	1.9
Total reptiles	17	10.7
<b>Amphibians</b>		
Unidentified frogs	5	3.1
<b>Crustaceans</b>		
Crab ( <i>Dilocarcinus dentatus</i> )	91	57.3
<b>Insects</b>		
Unidentified insects ( <i>Hemiptera</i> )	3	1.9
<b>TOTAL</b>	<b>159</b>	<b>100.0</b>

TABLE 2. Prey items observed brought to two Savanna Hawk nests and nearby areas in Guarico State, Venezuela.

Prey	No. individuals	% individuals	% biomass
Unidentified rodents	3	6.1	1.1
Cowbird ( <i>Molothrus</i> sp.)	1	2.0	2.7
Purple Gallinule	1	2.0	11.4
Unidentified birds	4	8.2	10.7
Total birds	6	12.2	24.8
Unidentified lizards	3	6.1	14.9
Unidentified snakes	1	2.0	5.3
Total reptiles	4	8.2	20.2
Unidentified frogs	8	16.3	7.3
Eel ( <i>Symbranchus marmoratus</i> )	22	44.9	42.0
Crab ( <i>Dilocarcinus dentatus</i> )	6	12.3	4.6
<b>TOTAL</b>	<b>49</b>	<b>100.0</b>	<b>100.0</b>

73.8% as much as C1 at 26 days of age. When the female fed one or both chicks (only the female fed chicks, sex was determined by copulation) during a visit to the nest, I defined this as a "feeding bout." When she offered food to a chick with her bill and it was accepted, I termed this a "bite." I witnessed 27 bouts for

a total of 1,453 bites up to 32 days of age (when I ceased watching from the blind). C1 consumed most of the food (63.5% of the bites) until the chicks were 21 days old, at which time C2 consumed the most until 32 days (57.5%). At 31 days, C2 weighed 586 g or 86.7% of C1's weight (676 g). Both chicks fledged, although C2 was underweight.

DISCUSSION

CONTROL OF CLUTCH SIZE

Many studies support Lack's theory that birds raise as many young as they can feed (see reviews by Lack 1954, 1968, Klomp 1970). However, this explanation appears inadequate for some species (see von Haartman 1971). Indeed, the converse, that clutch size is adjusted

TABLE 3. Comparative rates of prey delivery at two Savanna Hawk nests, one with one chick and the other with two chicks (manipulation).

	Age of chick(s) in days					Avg.	
	1-7	8-14	15-21	22-28	29-35		36-43
<b>One chick<sup>a</sup></b>							
Total period of observation (h)	6:05	—	—	7:05	10:30	12:20	—
Total no. of adult visits	8	—	—	7	6	12	—
No. visits per h of observation	1.32	—	—	0.99	0.57	0.97	0.96
No. prey items brought to nest	2	—	—	5	5	12	—
No. prey items per h of observation	0.33	—	—	0.71	0.48	0.97	0.62
Prey biomass brought to nest per h (g)	2	—	—	18	14	24	15
<b>Two chicks</b>							
Total period of observation (h)	—	17:03	12:43	10:30	4:00	—	—
Total no. of adult visits	—	18	18	8	2	—	—
No. visits per h of observation	—	1.06	1.42	0.76	0.50	—	0.94
No. prey items brought to nest	—	5	12	6	2	—	—
No. prey items per h of observation	—	0.29	0.95	0.57	0.50	—	0.58
Prey biomass brought to nest per h (g)	—	4	14	14	9	—	10

<sup>a</sup> The data are from two nests. The chick in age class 1-7 days is the same chick used in the manipulation for the second nest, but the data are prior to the addition of the second chick. The data for the other three age classes are from another nest with one chick.

to compensate for mortality is held by some (Wynne-Edwards 1962, Skutch 1976). Results of my brood manipulations with Savanna Hawks support Lack's explanation. Only one of nine manipulated broods that were experimentally increased to two chicks in 1978 actually raised both chicks, although the one nest manipulated in 1979 raised both chicks. In two cases the dead chick apparently died from starvation. That *both* manipulated chicks developed more slowly than normal and/or fledged later, supports the contention that inadequate food resources favored a clutch size of one. Additionally, a comparison of a brood of one chick to a manipulated brood of two indicated no significant differences in the rate of prey items delivered to the nest nor the amount of prey carried to the nest (Table 3). In short, the adults with two chicks brought no more food to their nest than the adults with one chick.

The above conclusion must also be discussed in terms of the "sibling aggression" theory proposed for certain species of African eagles. The Lesser Spotted Eagle (*Aquila pomarina*) and Verreaux's Eagle (*A. verreauxii*) typically lay two eggs; invariably when both hatch, only one chick survives, often because the first and larger kills the smaller (Meyburg 1974, Gargett 1977). Brown et al. (1977) reviewed this phenomenon and concluded that competition between siblings and survival are not affected by availability of food. These authors also rejected the idea that a second egg serves as a reserve if the first does not hatch, but other evidence supports this interpretation (Meyburg 1974, Stinson 1979). Thus, in these eagles, the survival of one chick appears to result from sibling aggression and not an immediate scarcity of food. However, it appears likely that fratricide avoids competition for a food supply that would ultimately be inadequate to feed two fledged nestlings (see discussion by Stinson 1979). During observations (44 h) at a manipulated nest of a Savanna Hawk, I saw no sibling aggression even though one chick was larger and developed faster than the other (both fledged). Also, I saw no physical injuries on the two starved chicks mentioned above or any of the other chicks at manipulated nests. Sibling aggression in eagles, and probably other raptors, often results in obvious injuries to the lesser chick (Meyburg 1974, Brown et al. 1977). My findings suggest, therefore, that the survival of only one Savanna Hawk chick at a manipulated nest was not a result of sibling aggression but inadequate food resources.

The rate of predation on bird nests appears to be much higher in tropical than in temperate

regions (Ricklefs 1969), although some recent evidence suggests otherwise (Oniki 1979). Skutch (1967) countered Lack's hypothesis of food limitation by presenting evidence that a small clutch and later small brood, reduces the risk of nest predation by requiring fewer feeding visits and less chance of nest detection by a predator. Skutch suggested that this was why food items brought to the nest are large and young do not often give begging calls.

I have no evidence to say that a clutch of one in the Savanna Hawk resulted from fewer feeding visits and a reduced chance of predation. First, Savanna Hawks bring prey items of smaller average size to nests (47 prey items brought to nests weighed an estimated average of 19 g at the time of arrival) than comparably sized North American buteonines, which generally bring squirrel- and rabbit-sized items (50–2,300 g; e.g., Red-tailed Hawk, *Buteo jamaicensis*, Fitch et al. 1946, Craighead and Craighead 1956, Seidensticker and Reynolds 1971, Luttich et al. 1971, Gates 1972, Smith and Murphy 1973, McInvaile and Keith 1974; Swainson's Hawk, *Buteo swainsoni*, Smith and Murphy 1973, Porton 1977, Dunkle 1977; Ferruginous Hawk, *Buteo regalis*, Smith and Murphy 1973, Woffinden and Murphy 1977; Harris' Hawk, *Parabuteo unicinctus*, Mader 1975). The Black Hawk (*Buteogallus anthracinus*) in Arizona differs from the foregoing because it catches reptiles and fish comparable in size to Savanna Hawk prey (Schnell 1979). Because Savanna Hawks bring less food to nests, they probably require as many or more feeding visits each day than temperate relatives, but I know of no comparable data on North American buteonines. Secondly, nestlings appeared to call for food as often as North American buteonines that I have observed (e.g., Red-tailed Hawk, Harris' Hawk).

Since Savanna Hawks have a greater nest success than non-raptorial open nesters in the wet tropics (47% vs. 34% respectively; see Skutch 1976 for latter), it is possible that predation is not an important cause of nest failures and that there is less need for larger prey items and less begging. However, circumstantial evidence suggests that most nest failures may indeed have resulted from predation. Savanna Hawks often chased Crested Caracaras (*Polyborus plancus*), Harris' Hawks, Crane Hawks (*Geranoospiza caerulescens*), and conspecifics away from nests. Also, tree nests, particularly those with vines to the ground, were probably preyed upon as easily by arboreal mammals and large snakes as other bird nests; snakes are thought to be the principal predators of tropical bird nests (Skutch 1976). John Robinson (pers. comm.) observed a group

of *Cebus* monkeys (*Cebus nigrivittatus*) surround and molest a nearly fledged Roadside Hawk (*Buteo magnirostris*) and Tropical Screech-Owl (*Otus choliba*) near my study area. Such monkeys are known nest robbers (Robinson, pers. comm.). Tayras (a weasel, *Eira barbara*), *Cebus* monkeys, ocelots (*Felis pardalis*), jaguarondi (*F. yagouaroundi*), opossums (*Didelphis* sp.), raccoons (*Procyon cancrivorus*), and other possible predators were seen in or near Savanna Hawk territories. It thus seems reasonable that predation contributed to nest failures.

In summary, I suggest that a clutch size of one evolved in the Savanna Hawk primarily because of a limited food supply. This supports Lack's idea of the control of clutch size, but does not exclude other factors that may have contributed indirectly, such as predator avoidance, or the effects of competition on food supply and clutch size (see Cody 1966 for a discussion).

#### TIMING OF BREEDING

Most Savanna Hawks (72% of 113 pairs) laid eggs during roughly the first half of the wet season, May to August (see Figs. 1 and 2). I have no data on prey abundance (surveys proved impractical because of flooding), but eels, crabs, and frogs seemed far more numerous during the wet season than the dry. Avian densities and frequency of breeding were also greatest during the wet season (Thomas 1979). The remaining hawks laid either before May (24%) or near the end of the wet season (4%, September through October). Laying thus occurred over many months, especially in 1979. Since Savanna Hawks have non-overlapping territories, such unsynchronized breeding cannot be the result of pairs trying to reduce intraspecific competition with their neighbors. Instead, pairs may become adequately nourished to breed at different times, possibly because prey availability differs within territories and some individuals hunt more efficiently than others. Fogden (1972) found that various tropical passerines laid eggs when their protein reserves and physiology were ready to bear the added stress of breeding, and not in response to rainfall. The absence of a clear correlation between the onset of the rains (or flooding) and laying in the Savanna Hawks (Figs. 1 and 2) suggests that rainfall was not a proximate cue to breeding. In short, for those hawks that breed in the wet season, it may not be the rains that trigger breeding but the increase in food supply that follows. Those hawks that breed before the rains may do so because they are already physiologically prepared. Food may therefore be both an ultimate

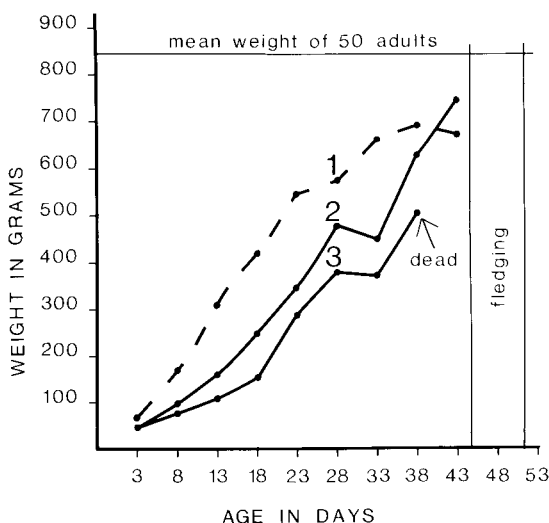


FIGURE 4. Weight increases of three young Savanna Hawks measured once every five days. The three development curves are from two nests. The first represents a control nest that contained a normal brood of one chick (1), while the second nest contained its original chick (3), plus an introduced one (2). Only the introduced chick survived at the manipulated nest.

and a proximate factor controlling the timing of breeding.

Two other factors that may influence the timing of breeding are: (1) the availability and exploitation of diverse prey types, and (2) time of initial nest failures. The length of a hawk's breeding season depends not only on how long prey is available (see review by Newton 1979) but also on how prey is exploited (Mader 1978). For example, neighboring Red-tailed and Harris' hawks in Arizona take the same types of prey (birds, mammals, reptiles) but the latter are more versatile in what they catch and their breeding season is twice as long (includes second broods, Mader 1978). Savanna Hawks are equally versatile, catching fish, crabs, snakes, iguanas, and birds (see Tables 1 and 2). Those pairs that nest before flooding or in locally unflooded savanna certainly take mostly terrestrial or arboreal prey. Exploitation of diverse types of prey probably provides a greater food base and helps insure adequate food supplies during renesting attempts, thereby contributing to a longer breeding season.

Laying dates are also influenced by failures of first nest attempts. When pairs of Savanna Hawks failed with eggs or young at the beginning of the rains they often renested a month or two later. The same may be true of other neotropical falconiforms. A pair of White-tailed Hawks that nested and failed in the dry season, renested in the wet, even though this species normally breeds in only the dry season in the llanos of Venezuela (Mader 1981). New-

TABLE 4. Breeding parameters in two North American buteonines and the South American Savanna Hawk.

	Red-tailed Hawk	Black Hawk	Savanna Hawk
Average incubation period in days	35	39	39
	Hardy 1939 Mader 1978	Schnell 1979	
Average clutch size ( <i>n</i> )	2.79 (476)	1.67 (12)	1.00 (108)
	Henny and Wight 1972 (476)	Schnell, pers. comm.	
Average hatching success % ( <i>n</i> )	84.4 (379)	—	64.1 (78)
	Fitch et al. 1946 (38) Craighead and Craighead 1956 (33) Seidensticker and Reynolds 1971 (22) Luttich et al. 1971 (172) Smith and Murphy 1979 (114)		
Average nestling success from hatching to fledging % ( <i>n</i> ) <sup>a</sup>	73.0 (152)	—	70.4 (54)
	Fitch et al. 1946 (26) Seidensticker and Reynolds 1971 (15) Smith and Murphy 1979 (84) Craighead and Craighead 1956 (27)		
Nestling period in days	41–47	43–50	45–50
	Fitch et al. 1946 Johnson 1973 Wiley 1975	Schnell 1979	
Average no. young/nest attempt ( <i>n</i> ) <sup>b</sup>	1.47 (281)	1.0 (58)	0.47 (85)
	Orians and Kuhlman 1956 (87) Gates 1972 (31) Johnson 1975 (121) Mader 1978 (42)	Schnell, pers. comm.	
Average nest success % ( <i>n</i> )	82.5 (309)	81.0 (58)	47.1 (85)
	Orians and Kuhlman 1956 (87) Gates 1972 (31) Johnson 1975 (78) Wiley 1975 (33) Mader 1978 (42) Smith and Murphy 1979 (38)	Schnell, pers. comm.	
Average no. pairs laying eggs % ( <i>n</i> )	88.0 (382)	—	73.3 (45)
	Craighead and Craighead 1956 (12) Orians and Kuhlman 1956 (60) Luttich et al. 1971 (66) McInvaile and Keith 1974 (107) Johnson 1975 (137)		
Approximate length of breeding season in days (laying to fledging)	114	100	250



TABLE 4. Continued.

	Red-tailed Hawk	Black Hawk	Savanna Hawk
	Smith and Murphy 1973 (83 days)	Schnell, pers. comm.	—
	Wiley 1975 (141 days)		
	Mader 1978 (118 days)		

<sup>a</sup> Fledging was not consistently defined in the references for Red-tailed Hawks and the criteria for fledging probably varied. Savanna Hawk chicks were followed to at least five weeks, and were assumed fledged (left the nest and perched nearby in same tree or flew) if they survived to this age. Of 28 chicks followed from five weeks to fledging, 27 (96%) fledged (does not include chicks from manipulated nests).

<sup>b</sup> Data for nest attempts and nest success include only those nests that began with at least one egg.

ton (1979:107) commented that it was not of much importance when large tropical raptors (kites to large eagles) with prolonged breeding seasons nested, since the breeding cycle was so long. I suggest that this is probably true only for those species that (a) do not renest after a failure within the same year, and (b) do not have to lay primarily in one season in regions that have one wet and one dry season. For those raptors that do renest and lay in principally one season such as the Savanna Hawk, a pair increases fitness by breeding as early as possible in a given season in order to renest during favorable conditions should the first clutch be lost.

REPRODUCTIVE RATES AND BREEDING PATTERNS

*Tropical vs. temperate hawks.* The reproductive rates (number of fledglings per adult per year) of land birds are generally lower in tropical than temperate species (Lack 1968, Skutch 1976). To find out if this is also true in hawks, I compared the reproductive rate of the Savanna Hawk with those of two related North American species, the Red-tailed Hawk and the Black Hawk. All are buteonines of comparable size (Red-tailed Hawk 1,126 g, Craighead and Craighead 1956; Black Hawk 945 g, Schnell in Newton 1979; Savanna Hawk 844 g); they occupy similar trophic levels, and live in largely open habitat. The Red-tailed Hawk is migratory in at least parts of its range but does not breed in South America. In contrast, the Black Hawk has a primarily neotropical distribution but does breed as far north as the southwestern United States where it is migratory (Blake 1977); the data below are from Arizona (Schnell 1979, pers. comm.).

Savanna Hawks average fewer eggs per clutch (1.0) than Red-tailed Hawks (2.79) and Black Hawks (1.67), and far fewer young per nest attempt (0.47 young) than Red-tailed (1.47) and Black (1.0). Savanna Hawks have significantly lower averages than Red-tailed Hawks for nest success (47.1% vs. 82.5%,  $P < 0.01$ ), hatching success (64.1% vs. 84.4%,  $P < 0.01$ ) and percentage of pairs in a popu-

lation that lay eggs (73.3% vs. 88.0%,  $P < 0.05$ ); the survival of young from hatching to near fledging is about the same (Table 4). Savanna Hawk nest success was also significantly less than that for Black Hawks (47.1% vs. 81.0%,  $P < 0.01$ ). Johnson (1975) found an average of 1.36 fledglings/pair/year ( $n = 137$ ) in Montana, and Craighead and Craighead (1956) 0.91 fledglings/pair/year ( $n = 22$  pairs) in Michigan. Savanna Hawks raised far fewer young/pair/year (avg. = 0.53 in 9.4 km<sup>2</sup> study area from 1978–1979) than did Red-tailed. While the annual survival rate of adult Red-tailed Hawks is estimated between 76.2–80.0% (Henny and Wight 1972), the Savanna Hawk has a rate of about 71.1%. Previous studies of tropical birds indicate that they usually have a greater adult survival rate than their temperate counterparts (Fogden 1972, Snow and Lill 1974).

Tropical hawks and eagles often have longer incubation and nestling periods than temperate latitude ones of comparable size and taxonomic group (Brown 1976, Newton 1979), even though it probably increases the chances of reproductive failure by storms, predation, or death of an adult. Indeed the Savanna Hawk has a longer incubation period than the Red-tailed and a slightly longer nestling period. However, the Savanna Hawk has incubation and nestling periods roughly equal to those of temperate populations of Black Hawks (Table 4). Black Hawks are primarily neotropical and their long incubation and nestling periods in Arizona may simply reflect their generally southern distribution.

Savanna Hawks have evolved at least the following interrelated habits that help counter low fecundity: (1) the ability to renest after eggs or young have perished in an initial nesting attempt, (2) a long fledgling dependency period of four to seven months to help insure survival of the single young, and (3) pair-bonds that remain intact from one breeding season to the next or until a member dies.

*Renesting.* Although Savanna Hawks renest after a nest failure with young, this behavior is rare among North America hawks. Of the

12 buteonines that breed in North America, only the Harris' Hawk is known to renest after the loss of young (Mader 1978); this species also ranges into the neotropics. However, renesting of buteonines after the loss of eggs is not uncommon. Little is known about renesting in tropical hawks after the loss of young. *Melierax* goshawks in equatorial East Africa breed twice a year (Smeenk and Smeenk-Enserink 1975), so presumably they renest after the loss of young. Thus it is not clear if renesting of this kind is a universal adaptation of tropical hawks, but it clearly increases the reproductive success of Savanna Hawks.

*Fledgling dependency.* The long post-fledgling dependency period of the Savanna Hawk is about two to three times longer than that of the Red-tailed Hawk (1–2.5 mo., Johnson 1973), Swainson's Hawk (1.0 mo., Fitzner in Newton 1979), or Black Hawk (1.5–2.0 mo., Schnell 1979). Hawks in Venezuela of comparable size to the Savanna Hawk show the same phenomenon. I found apparent dependency periods of ten months in the White-tailed Hawk and about seven months in the Great Black Hawk (*Buteogallus urubitinga*, Mader 1981). The onset of migration contributes to a shortened period of fledgling dependence in migratory North American hawks. Nevertheless, even those that are resident in parts of their range have shorter dependency periods than that of the Savanna Hawk. Red-shouldered Hawks (*Buteo lineatus*) in southern California have a fledgling dependency period of 2.0–2.5 months (Snyder and Wiley 1976) and Harris' Hawks in southern Arizona generally two to three months (Mader 1975). Taken together, these facts suggest that a long dependency may provide added parental care and increased chances of survival for small, infrequent broods in the tropics.

*Pair fidelity.* I tried to test the idea that prolonged pair-bonds increase reproductive success but could not find any information on pair fidelity for any North American buteonines. In areas where the individuals must migrate, pair bonds probably last only through the breeding season. However, since some migratory hawks have a high degree of nest-site fidelity, the same individuals may pair at the same nest-site year after year, creating a situation similar to permanent pair-bonds. Pair fidelity in sea birds improves intra-pair activities such as courtship and synchrony of mating and often increases successful reproduction (Coulson 1966, Mills 1973, Davis 1976). Long-term pair-bonds may help offset a low reproductive potential in the Savanna Hawk, principally by insuring fertilization and egg laying as soon as the adults are capable.

## SUMMARY

Savanna Hawks laid only one egg per clutch in the llanos of Venezuela because they usually cannot feed more than one chick. However, in contrast to all but one North American buteonine, Savanna Hawks renested after the loss of a chick. Although most nesting occurred in the wet season, rainfall by itself was probably not the cue that started Savanna Hawks breeding; rather it appeared to be the increase in food that followed. Home ranges were very small, averaging 0.14 km<sup>2</sup>, but pairs nevertheless took a great diversity of prey—fresh water eels, frogs, crabs, birds, reptiles and mammals. Fifteen marked adults laid eggs, on the average, about 30 days from the date they laid in the previous year. Nest success was about 47%, regardless of whether pairs bred in the first half of the wet season or the last. Little is known about the breeding ecology of other neotropical falconiforms.

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