

SEEKING TO UNDERSTAND THE LIVING BIRD The 1997 Margaret Morse Nice Lecture

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For over 50 years the classic study by Margaret Morse Nice on the life and behavior of the Song Sparrow (*Melospiza melodia*) has given a basic orientation and ideas for research to investigators of the natural behavior of birds. She made the first detailed, long-term study of the behavior of wild birds color-banded for individual identification (Nice 1933, 1934). She had an excellent education and the two volumes of her monograph on the Song Sparrow (Nice 1937, 1943), one on populations, one on behavior, are written from the viewpoint of basic biological problems, enlivened by her profound curiosity about the life of birds. Mrs. Nice was a firm believer in confirming for herself any important published fact about bird behavior, which is the reason why research was a passion with her (Nice 1979). In this spirit of direct scientific inquiry, we wish to present some highlights of our own research.

We have spent much of our lives trying to understand the biology of avian behavior, especially the function, causes, ontogeny and evolution of social behavior at the physiological, individual and population levels of organization (N. Collias 1991). The first part of this presentation will be given by Nicholas, the second by Elsie, but we have generally worked together.

Let me briefly introduce ourselves. My early childhood was in Chicago Heights, then a small town, where my family lived on the edge of town. Soon after learning to read, I discovered in the local library "The Burgess Bird Book for Children" (Burgess 1919) with its magnificent color plates by Louis Agassiz Fuertes. These plates gave me names for the common birds that I encountered in the nearby fields and woods. I vividly recall my first glimpse of a bluebird in an orchard. It seemed as if a fragment of the blue sky had fallen and was flying about on the back and wings of a

bird, an impression still fresh after three-quarters of a century. I was not then aware that anyone in my world had any real interest in birds aside from myself and Peter Rabbit, the hero of the bedtime stories by Thornton W. Burgess. It was far from my thoughts that anyone could make a living watching birds, until years later when a scholarship to the University of Chicago made possible for me a career in zoology and ornithology.

The situation was different for Elsie, some of whose ancestors, like those of Margaret Nice, arrived in New England in the 1600s. Eventually, Elsie's family settled in Tiffin, Ohio, near the Sandusky River. Her parents encouraged her early interests in nature and taught her the local birds. Her father, Heath K. Cole, was a lawyer with a strong interest in the natural sciences. Elsie, before she started school, developed a great interest in insect life, and readily prevailed on her father to make her an insect net. She eventually donated a substantial insect collection to Heidelberg College, her alma mater in Tiffin. After a year in research on malarial mosquitoes with the United States Public Health Service, Elsie went back to finish her Ph.D. work in zoology at the University of Wisconsin, where we met. Our friendship included getting up well before dawn to watch the prairie-chickens dance near Plainfield, Wisconsin, where we were two of the thousands of guests that Fran and Fred Hamerstrom introduced to these fascinating birds over the years. After Elsie and I were married we did our research together on birds.

UNIVERSITY OF CHICAGO (1937–1942). HORMONES AND BEHAVIOR

Mrs. Nice and her family moved to Chicago in 1936 and bought a house near the University of Chicago where I was a student, and we became friends.

My research career began after graduation in 1937 when Professor W. C. Allee of the University of Chicago zoology department hired me as his research assistant to work on the effects of hormones on the peck order of

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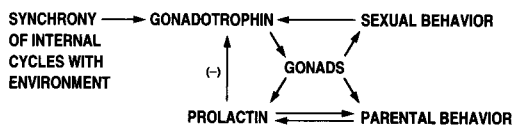


FIG. 1. Interactions between hormones and behavior in the control of breeding behavior in doves and pigeons. Inhibition indicated by minus (–) sign. (After N. E. Collias 1952 and Collias and Collias 1984).

hens. Testosterone and estradiol had been isolated in pure form in 1935 (Marrian 1950). In chickens, the cock's testes secrete testosterone, the hen's ovary secretes testosterone, estradiol, and progesterone (reviewed in Collias and Collias 1984).

We found that ovariectomized hens injected with testosterone became more aggressive and rose in the peck order, some from the bottom to the top (Allee et al. 1939). Ovariectomized hens injected with the female sex hormone, estradiol, became sexually receptive but they did not rise in the peck order (Allee and Collias 1940).

Rank in the peck order is decided by fighting or passive submission at the initial encounter of each pair of birds. Success in initial encounters between normal hens is correlated with larger comb size, a specific indicator of testosterone. In my Ph.D. thesis, using the path coefficient method of Professor Sewall Wright and with his advice, I found that a much greater percentage of the variance in success was determined by differences in comb size than in body weight or in previous success, while molt had a depressing effect on success (N. Collias 1943).

Mrs. Nice, who was president of the Chicago Ornithological Society from 1939 to 1941, invited me to speak before that society, and I spoke about hormones and behavior of birds as a self-regulating system with positive and negative feedback relations. Ten years later (N. Collias 1950), I reviewed the literature on the subject in some detail.

Figure 1 shows the interactions between the environment, hormones, and behavior. Originally it was based largely on pigeons and doves (N. Collias 1952), but indications now are that it may apply to many other birds as well. This figure was confirmed by a review of more recent literature in 1984 (Collias and Collias 1984), and I think is consistent in a

general way with more current evidence as critically reviewed in 1996 by Buntin, who also brings out the variation between different species of birds.

There are two general phases in the breeding cycle of birds, a sexual phase stimulated by pituitary gonadotrophin and gonadal steroid hormones, and a parental phase dominated by pituitary prolactin. The gonadal hormones stimulate pair formation, nest building and copulation. Male Ring Doves stimulate the females to lay eggs, as I found in a controlled experiment (N. Collias 1950), confirming Wallace Craig's demonstration of the same thing in 1911. Gonadal hormones, together with the mate, nest and eggs, also help bring about onset of incubation.

In 1935, Oscar Riddle and his colleagues discovered that prolactin injected into laying hens stimulates maternal behavior, i.e., incubation and care of chicks. Sitting on eggs in turn stimulates prolactin secretion. However, a hypophysectomized male pigeon that I injected with estradiol thereupon paired with a normal female and helped her incubate her eggs for over a month, showing that prolactin is not absolutely necessary for parental behavior (N. Collias 1950), although it normally stimulates it (Buntin 1996). By inhibiting gonadotrophin, rising prolactin levels help end the sexual phase of breeding.

Today, comparative endocrinology of wild birds in nature is a relatively new and flourishing field of research, made possible by such techniques as radioimmunoassay of minute hormone levels in the blood, a technique for which Rosalyn Yalow of New York received a Nobel Prize in 1977. For many species of birds it has now been amply confirmed that a sexual phase dominated by steroid sexual hormones is succeeded by a parental phase more or less dominated by prolactin (Buntin 1996), for example, in the Song Sparrow (Wingfield and Goldsmith 1990).

UNIVERSITY OF WISCONSIN (1947–1951). ANALYSIS OF FAMILY INTEGRATION AND VOCAL COMMUNICATION

I served as Instructor in Zoology at the University of Wisconsin for four years. After 3 and 1/2 years in the Army in World War II, I was more interested in family life than in peck

orders. Like Mrs. Nice, who as a young girl raised chickens, my first acquaintance with details of individual bird behavior was with chickens. The focus of my research at Wisconsin was on family integration, and this led to an interest in vocal communication.

Family integration and leadership.—When a baby chick is lost, cold, hungry, thirsty, or in pain, it utters distress cries (chirps). When the chick is returned to its mother or to its siblings, or the specific distress is relieved, the chick promptly switches to pleasure notes (twitters). To a newly hatched chick, the mother hen is a complex of warmth, physical contact, clucking sounds, and within about an hour, also a moving object. Loss of any one of these maternal stimuli may cause the chick to give distress cries and when the stimulus is restored it moves toward the source of the stimulus, normally the mother hen (N. Collias 1952).

In its social development the chick goes through a series of stages (N. Collias 1952, 1962):

- (1) Initial predisposition to response to certain key stimuli.
- (2) Self-reinforcement of these responses during an early sensitive period (filial imprinting).
- (3) Increasing social discrimination and recognition of individuals.
- (4) Social independence, exploration and social maturity with age and experience. Chicks on being isolated from companions give progressively fewer distress cries as they get older.

The first two stages depend especially on genetically determined predispositions, the last two stages involve learning to a greater extent.

In 1935, Lorenz graphically described filial imprinting of newly hatched Greylag Geese (*Anser anser*) that followed him about. In 1950, I confirmed in a controlled experiment that the day of hatching was a sensitive period in which chicks begin to follow the parent and that responsiveness fell off precipitously in succeeding days if first exposure to parental stimuli is delayed (N. Collias 1952).

Leadership among small chicks of a brood may contribute to family integration. Among recently hatched chicks of about the same age

(3–4 days) some specific individuals may lead the other chicks to maternal clucking (from a speaker) or to a source of warmth (warm lamp) in a cool room. A chick that forges very far ahead of the others, however, may utter distress cries and is likely to turn back to rejoin its companions. A good leader has both independence, and empathy with companions or young ones (N. Collias 1952).

Social guidance by the parent bird or other individuals enters into every stage of social development, and climaxes when birds learn traditional migration routes from experienced individuals, as has been indicated for geese and cranes (Lishman 1996). There has been a tremendous amount of work on social learning of the song of songbirds, including the Song Sparrow (Hauser 1996, Kroodasma and Miller 1996), and this is related to species identification.

A basic code of vocal communication.—During World War II, The Bell Telephone Company invented the sound spectrograph, a machine that makes precise visual pictures of sounds and gives a harmonic analysis of sounds (Potter 1945). This machine has revolutionized the study of animal communication. Professor Martin Joos, a linguist at the University of Wisconsin was one of the first to obtain a sound spectrograph for scientific studies. In 1953, he and I presented the first spectrographic study of the repertoire of vocal signals of an animal, the domestic fowl (Collias and Joos 1953).

We found that the spectrogram of chick pleasure notes emphasizes ascending frequencies, that of distress cries descending frequencies. The two opposed vocal signals apparently express states of security and insecurity, respectively. This is an example of what Darwin (1872) called the principle of antithesis, or that opposite states of mind as he put it, are accompanied by antithetical motor expressions. The different vocal signals of chickens, including those of their wild ancestor, the Red Junglefowl (*Gallus gallus*) are composed of elements that can be arranged in antithetical pairs, in effect a code (N. Collias 1987):

- (1) Pitch rises or falls.
- (2) Low versus high pitch.
- (3) Clear, distinct tones versus harsh sounds where harshness is defined

spectrographically as harmonic streaks combined with a wide and superimposed spread of frequencies.

- (4) Brief versus long notes.
- (5) Soft (low amplitude) versus loud notes.

In different vocal signals, the first element in pairs 2 to 5 above tends to attract chicks, the second element usually repels them. Different combinations of elements produce different vocal signals. For example, soft, low-pitched and brief notes as in clucking of a mother hen attract baby chicks, as was confirmed by experiments with comparable artificial sounds (Collias and Joos 1953). But harsh, loud, high-pitched and long sounds strongly repel them and cause chicks to rush to shelter. In the case of adults, loud, harsh and high-pitched sounds are also alarm cries, but harsh and lower-pitched sounds are threats. Quite similar elements in the vocal signals of the Village Weaver (*Ploceus cucullatus*), a passerine bird, indicate the generality of the code (N. Collias 1963).

The number of vocal signals or calls of birds has often been underestimated. Mrs. Nice (1943) described 21 "chief vocalizations" for the Song Sparrow, in the pre-spectrograph age. The Red Junglefowl has over 20 distinct and readily recognizable vocal signals, supported by spectrographic analysis (N. Collias 1987), as does the Village Weaver (Collias 1963 and unpubl. data). Not many birds have been observed sufficiently to yield such an extensive repertoire of vocal signals (Kroodsmma and Miller 1996). In species with a graded and overlapping repertoire of vocal signals, quantitative analysis shows that different vocal signals can be readily recognized, for example in the Brown Noddy, *Anous stolidus* (Riska 1986).

DELTA WATERFOWL RESEARCH STATION (1953–1955). FILIAL IMPRINTING OF WILD DUCKLINGS

On recommendation by Mrs. Nice to the director, H. Albert Hochbaum, we were able to spend three summers at this research station at the south end of Lake Manitoba, Canada.

The station operated a large incubator in which eggs collected from nests of various waterbirds in the wild were hatched and made available to investigators. With Redhead (Ay-

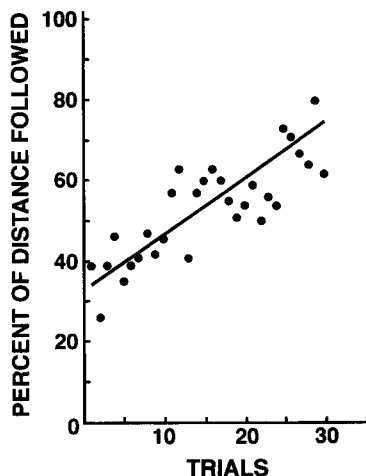


FIG. 2. Self-reinforcement of filial following. Red-head ducklings on day of hatching follow a person over standard course and distance better with each successive trial. Each dot is an average of 10 ducklings tested individually. (After Collias and Collias 1956).

thya americana) ducklings, we confirmed that the day of hatching is a sensitive period for imprinting as Fabricius (1951) had found for other ducks. We also found that ducklings followed a substitute parent better and better as imprinting proceeded (Fig. 2); i.e., filial imprinting is self-reinforced and a form of learning defined as improvement of performance with practice (Collias and Collias 1956). This means the day of hatching in ducks, as in chickens, is a critical time during which mother and young gradually develop strong social bonds to each other.

Observations on two species of ducks in nature showed that the ducklings spend most or all of the day of hatching in the nest with the mother. Thus, after the first young hatched, a Blue-winged Teal (*Anas discors*) hen led her brood from the nest about 18 hours later, a Canvasback (*Aythya valisineria*) hen only after 24 hours in the nest (Collias and Collias 1956).

For her graduate research at Clark University, Mrs. Nice (1910) had counted various natural foods eaten by a very tame Northern Bobwhite (*Colinus virginianus*) that was imprinted on her. Similarly, at Delta we imprinted several species of wild ducklings to ourselves as substitute parents so that we could watch details of their feeding behavior as

closely as we wished without disturbing the ducklings in the least. Different species of ducklings placed together in the same white enamel pan, with various small aquatic invertebrates that we collected from the marsh, preferred to feed on different species of invertebrates. For example, a Blue-winged Teal duckling placed in the pan along with small snails and *Daphnia* ate the snails first, whereas a Ruddy Duck (*Oxyura jamaicensis*) duckling ignored the snails and strained out all the *Daphnia* (Collias and Collias 1963). In theory, such different feeding specializations illustrate the idea of the ecological niche and the principle of competitive exclusion, whereby different species of animals can live together in a community (Hutchinson 1978).

WEAVERBIRDS AND EVOLUTION OF NEST-BUILDING BEHAVIOR

(From 1956)

At the end of her autobiography (1979), Mrs. Nice expressed a long cherished wish that she could have gone to the arctic and to the tropics. Modern travel facilities and greatly enhanced financial support for research have now made such things possible for many of us. The National Science Foundation was founded in 1950, and a few years later Elsie and I applied for a joint grant to go to Africa for a comparative study of nests and nesting behavior of weaverbirds. This was something that I had wanted to do ever since reading Alfred Emerson's (1938) classic monograph on termite nests as a study in the phylogeny of behavior. To our surprise, we received the grant and my dream was about to be realized.

Our friend, John Emlen, suggested we contact James Chapin of the American Museum of Natural History, who was then residing with his wife Ruth, in central Africa at a Belgian research station for tropical diseases. The Chapins were of inestimable help to us in many ways. The Belgians also helped us greatly. The director of the station even had a 12-m observation tower built for us next to a tree with a breeding colony of Village Weavers (*Ploceus cucullatus*). We caught many of these birds in mist nets and were able to make one of the first studies in Africa of birds color-banded as individuals (Collias and Collias 1959).

The male Village Weaver weaves the outer

shell of the nest and with special displays and calls endeavors to attract an unmated female to enter his nest. If she accepts, she lines the nest with fine grass tops and often also with feathers, mates with the male, incubates, and does most or all of the work of feeding the nestlings. The male builds more nests and tries to attract more mates in this polygynous species. But if his nest is rejected repeatedly by females, the male tears it down and weaves a fresh nest in its place. He may have to build many nests for each one that fledges a brood. Each brood leaves with the female.

Evolution of weaving (Collias and Collias 1964, 1984).—Small body size and ability to construct a nest and place it in a wide range of nest sites may have been key factors in the origin and evolution of passerine birds (Order Passeriformes; N. Collias 1997). Like many other tropical passerine birds, weavers build roofed nests (Collias and Collias 1964, 1984; N. Collias 1997). In Africa, we traveled about to places Jim Chapin recommended, and we found as many nests of weavers as we could (Collias and Collias 1964). We found that only the Ploceinae (true weavers) of the seven subfamilies of Ploceidae (weavers) then recognized by Chapin (1954) truly weaves the nest, using interlocking loops of long green flexible strips torn from the leaves of grasses or palms. Sibley and Monroe (1990) unite four of Chapin's subfamilies into one that they call Ploceinae, but recognize much the same relationships. Weaving is a primary adaptation that enables safer placement of the nest which is suspended from twigs or vines near the periphery of trees, or the nest is slung between upright reed stems over water. The other subfamilies recognized by Chapin thatch their nests of stiff, often dry grass stems or sometimes light twigs.

Some of the true weavers add a long entrance tube about the bottom entrance of the nest that probably helps protect from snakes. There is a convergent evolution of entrance tubes in African and Asiatic species of weavers.

In the lowland rain forest of eastern Zaire, I collected the nest of *Malimbus cassini*, Cassin's Malimbe, also now known as the Black-throated Malimbe. This nest, with its very long, neatly woven entrance tube, is I think the most finely constructed nest of any bird in

the world. I knew of no specimen of this nest at that time in any American museum.

The genus *Euplectes* consists of true weavers which include a variety of bishop birds and widowbirds. They have elaborate flight displays but their nests illustrate regressive evolution of weaving (Craig 1980). In South Africa, we found a ground nest of the Long-tailed Widowbird (*E. progne*); this nest had only a very thin woven outer shell over a thick nonwoven lining of brown grasses.

Evolution of gregarious nesting by weavers.—Whereas forest-dwelling weavers are often solitary nesters, weavers of open country with an abundance of grass seeds and insects frequently nest in a colony, often in isolated trees (Chapin 1954, Crook 1962). Other things that favor gregarious nesting include feeding in large flocks well away from the nesting grounds, social guidance to good food sources, scarcity of trees for nests, and special protection from enemies by cooperative defense, or nesting in very thorny trees, or close to nests of stinging insects (reviewed by Collias and Collias 1984; see also Siegel-Causey and Khartonov 1990).

Social stimulation may also play a role in gregarious nesting. In Senegal, we found that colonies of Village Weavers with fewer than ten adult males attracted disproportionately and significantly fewer females than did males of larger colonies (Collias and Collias 1969). This is an example of the F. Fraser Darling (1938) principle of social stimulation to breeding. At UCLA, we found that moderate crowding of Village Weavers in large aviaries stimulated renewed breeding and extended the breeding season (Victoria and Collias 1973).

Gregarious nesting culminates in the famous apartment-style nest of the Sociable Weaver (*Philetairus socius*) of southwestern Africa (Collias and Collias 1964, 1978; Maclean 1973). The huge compound nest is thatched of straws with light twigs added to the communally built roof that helps protect the birds from some enemies, sun and weather. The underside of a nest mass has numerous openings to the separate nest chambers. A colony we saw in South Africa was said by local farmers to have occupied the same two trees for over 100 years. Our colleagues at UCLA, Bartholomew, White, and Howell (1976) found that the larger the nest mass, the greater

the thermal homeostasis in the nest of this species (see also White et al. 1975).

The Sociable Weaver belongs to the subfamily Plocepasserinae (of Chapin 1954) as do the Grey-headed Social Weaver (*Pseudonigrita arnaudi*) and the White-browed Sparrow Weaver (*Plocepasseri mahali*), both of which we studied in Kenya (Collias and Collias 1978, 1980). The individual nests of the latter two species are often in physical contact, but lack a communal roof, and their sleeping nests have two entrance holes, an obvious defense against nocturnal predators. In contrast to the Sociable Weaver and the Grey-headed Social Weaver which may nest in large colonies and forage in large flocks well away from the nest trees, the White-browed Sparrow Weaver nests in small cooperatively breeding groups and defends a small group territory within which it feeds. The Plocepasserinae illustrate the Friedmann (1935) principle of colonial breeding in species of birds whose nesting and feeding grounds are spatially separated, whereas birds that feed in their reproductive area are generally solitary or less gregarious nesters.

Division of labor between male and female Village Weavers.—The division of labor between male and female birds in breeding behavior can be measured in terms of metabolic demands of the acts involved (Orians 1961; Collias and Collias 1967a, 1976; Paynter 1974). As a rough estimate of a very energy demanding act, flying by the Village Weaver takes about six times the energy as just resting under the same conditions. The male uses much flying energy for building nests that are unsuccessful. Putting the total amount of flying to gather nest materials into energy terms, we estimated for the central African race *P. c. nigriceps* that the male Village Weaver did 6–7 times as much work for nest building as did the female who merely lines the nest. By the same criterion of amount of flying required, the female did about twice as much work in foraging for food for the nestlings as did the male. Details of the analysis are given elsewhere (Collias and Collias 1967a, 1984:183–187).

The division of labor between male and female varies in different subspecies of Village Weaver (Table 1; Collias and Collias 1967a, 1970, 1971, 1984). In the west African race,

TABLE 1. Nests, polygyny, and nestling care in three races of Village Weaver, *Ploceus cucullatus*.^a

	Western Africa <i>cucullatus</i>	Central Africa <i>nigricaps</i>	Southern Africa <i>spilonotus</i>
Aver. min. temp. when breeding	24° C	11° C	14° C
Number of males	9	18	11
Nests built in two weeks	3.3	1.4	1.9
Mates per male	3.1	1.8	2.0
Feeding rate per hour per nest:			
by male	0.1	2.3	1.4
by female	4.1	4.7	4.2
number of nests	15	11	39

^a After Collias and Collias 1984:55.

the male scarcely feeds the nestlings and devotes his energy to building more nests and getting more mates, and he is more polygynous. The central African race was observed in a cool mountain habitat where the young apparently need more food, and the male often helped the female feed the nestlings, leaving him less time to build nests and get mates. The south African race is intermediate.

It is desirable to measure actual energy expenditure directly in the field. During the last two decades (Carey 1996), measurement of field metabolic rates has proved feasible with the doubly-labeled water technique, clearly described by Nagy (1989). This technique measures CO₂ production rate and therefore overall energy expenditure over a specific period of time. For example, Flint and Nagy (1984) of UCLA found that the metabolic rate during flight of free-ranging Sooty Terns (*Sterna fuscata*) was about five times the standard resting metabolic rate.

Mate selection by the female Village Weaver.—Darwin's (1871) theory of sexual selection has attracted renewed attention in the last two decades (Andersson 1994), but Darwin had little to say about the role of nest-building behavior in courtship and mate selection. Long ago, Mrs. Nice (1943:179) pointed out that for birds "Symbolic building is characteristic of courtship in many species." The male Village Weaver carries this process one step further in that he weaves the complete outer shell of the nest that he then displays to unmated females.

Over the years we and our associates at UCLA did many controlled experiments on

mate selection by the female Village Weaver in large outdoor aviaries. Doctoral and post-doctoral students on this problem have included Janice Victoria McClean, Catherine H. Jacobs, Florence McAlary McFarland and Cathleen R. Cox.

To attract an unmated female, each male of the colony hangs beneath the bottom entrance to his nest flapping his wings vigorously and uttering cries distinctive of each individual. It is a spectacular sight when all males of a colony display and call simultaneously. A visiting female inspects the nest interior and signifies her acceptance by lining the nest and copulating with the male.

Janice (Victoria 1969) found that both a male and his nest are essential for a female to choose a mate and lay eggs. Cathy (Jacobs et al. 1978) found that nests accepted by females were displayed by the male more than twice as often on the day of acceptance as nests that were rejected. The male's wing display reveals and is greatly enhanced by the bright yellow wing linings, and if we painted the wings black, such males attracted significantly fewer mates than did control males (E. Collias et al. 1979). Very young adult males and very old males are also discriminated against by the females (N. Collias et al. 1986). A female may change mates between broods, but she has a significant tendency to select her previous mate or a familiar territory for subsequent broods (McAlary 1985).

A nest has to last at least a month from the time the female accepts it until the young fledge. As a nest ages, it turns brown. The female prefers a fresh green nest, and she prefers a fresh nest painted green to a fresh nest painted brown (Jacobs et al. 1978), so color of the nest is one factor in her choice.

The strength of nest materials is very important to the female's choice. If a male's nest is repeatedly rejected, he tears it down and builds a fresh nest in its place, so fragmented materials from discarded old nests litter the ground. If the birds in an aviary are given no fresh nest materials, they will pick up and build nests of the old fragmented materials. A male displays his most recently built nest the most, and so may induce a female to temporarily accept such a trash nest. But we and our associates found that females laid eggs in significantly fewer trash nests than in still older

brown nests built of normal materials (Collias and Collias 1984).

In conclusion, the nest of the male Village Weaver, as well as the male himself, are both important considerations in the female's choice of a mate.

RED JUNGLEFOWL BEHAVIOR AND MECHANISMS OF EVOLUTION (From 1960)

Since my research career began with the analysis of behavior in domestic chickens, and, yet with a basic drive as a naturalist, it was understandable that I should be most curious as to the behavior in nature of the wild ancestor of the domestic fowl, i.e., the Red Junglefowl. During the academic year of 1962–1963, with financial support from the National Science Foundation and the Guggenheim Foundation, we were able to carry out a field study of this bird in nature (Collias and Collias 1967b), with special reference to its behavioral ecology and population breeding structure. We then tried to relate our results to mechanisms of evolution.

The principal theory relating genetics and evolution is the theory of Sewall Wright (1932, 1978a) that adaptative evolution depends most importantly on the shifting balance between the factors of evolution acting on a species that is subdivided into many partially isolated local populations. This theory is opposed to the idea that a species consists basically of a single randomly breeding population.

The significant question here is the nature of the breeding structure of populations in nature. One of the first attempts to relate the population structure of a wild bird species in nature to Wright's theory was in 1947 when Alden H. Miller plotted the population data of Mrs. Nice on the Song Sparrow to emphasize very limited dispersal distance of juvenile birds from their birthplace to breeding place. Miller (1947:139) concluded that the Song Sparrow, an abundant and widespread species, "actually is seen to exist in small effective breeding units" subject to considerable random differentiation in accord with Wright's theory. Wright (1940) considered especially important for evolution the case where local populations are liable to frequent extinction with restoration from a few stray immigrants,

TABLE 2. Principles of animal breeding in evolution theory.^a

Animal breeding	Evolution theory
1. Partially inbred lines	1. Random genetic drift in local populations
2. Mass selection	2. Selection between individuals and families
3. Cross breeding and line breeding	3. Differential emigration from local populations

^a After Sewall Wright.

a phenomenon shown recently to occur frequently in color-banded populations of the Song Sparrow on small islands off the coast of British Columbia (Smith et al. 1996).

Wright (1978b) states that he derived his theory of the mechanisms of evolution from the principles and history of animal breeding (Table 2). Evidence from the breeding of chickens supports his theory (Collias and Collias 1996). Many new breeds and varieties of chickens have been produced by a combination of cross breeding and line breeding. As the primary and perhaps sole ancestor of the much studied domestic fowl, the Red Junglefowl is eminently suited for a study of genetic mechanisms in evolution.

After making a preliminary study of a free-ranging population of this species on the grounds of the San Diego Zoo, we visited southeast Asia, and then we went on to India for a study of the bird during its breeding season. Dr. Salim Ali of the Bombay Natural History Society advised us that a good place to find Red Junglefowl was in the Saharanpur forest district in the Himalayan foothills. There we received much help from the Wildlife Preservation Society of India. We observed the junglefowl from a platform in a tree, from a car, through a telescope when they came to drink at a waterhole, by following them about from elephant back, and by capturing them in nets and nooses with the assistance of the local people. The appearance of chicks coincided with onset of the rains and of flights of termites, an important food for the chicks, and this coincidence may help determine the breeding season.

We located roosts when the cocks crowed at dawn. The roosts were located in or near small branch ravines in western Thailand

(Collias and Saichuae 1967), and along larger water courses in India. When the birds were not disturbed they occupied the same roosts throughout the breeding season in India (Collias and Collias 1967b).

There seemed to be little difference between the behavior of Red Junglefowl in nature and in the free-living population at the San Diego Zoo where the birds formed separate populations in different ravines with very little interchange between local populations (Collias et al. 1966). We had color-banded most of the junglefowl in the zoo, and now focused on one large ravine where over a 7-year period we were able to get the lifetime breeding success of many of the birds, something that would have been very difficult in the field. We found that only a very small proportion of the birds, including the most dominant cock and most dominant hens, produced most of the adults of succeeding generations (Collias et al. 1994, Collias and Collias 1996). Of 8 successive males at the top of the peck order of cocks, one male (Male AA) had a longer tenure and copulated more often than the other 7 despots combined. He also mated twice as often as his 19 subordinates put together. The three hens at the top the peck order of hens added more offspring of breeding age to the population than did the remaining 25 adult hens of the flock for which we had lifetime breeding success. These findings accord with the dynasty principle elucidated by Newton (1989) in his summary of long-term studies by various investigators of different bird species in nature. When allowance was made for differential production of progeny and isolation by distance, the genetically effective breeding size of our Red Junglefowl population was estimated at only about 13% of the adult population (Collias and Collias 1996).

In conclusion, the behavior of the Red Junglefowl can be related to Wright's shifting balance theory of evolution through the effect of behavior on the breeding structure of populations. Social behavior exerts a reciprocal effect on evolution by structuring the population into traditional roosts and by greatly reducing the genetically effective breeding size of local populations through competition among individuals and families. Therefore, considerable random differentiation in and among local

populations is expected, aside from local differences in conditions of selection. In a recent review of electrophoretic studies of allozyme variation in wild populations of 63 species of birds, Stangel (1991) found that island populations were significantly more differentiated than mainland populations, and that differences were significantly correlated with distance between sample localities.

The second part of this presentation of our research is given by Elsie, who describes some aspects of the development of behavior in birds, and also genetics of egg-color polymorphism as related to behavior.

I am honored to be asked along with my husband to give the first Margaret Morse Nice lecture. I grew up in northern Ohio during the period when Mrs. Nice did her classic field study of the Song Sparrow in Columbus, Ohio. However, I did not meet Mrs. Nice until after Nick and I were married.

As my husband mentioned we met at the University of Wisconsin where I was finishing my Ph.D. work. We were married the next year. Ever since we have worked as a team on the behavior of birds, in this country and overseas.

INHERITED AND LEARNED COLOR PREFERENCES

Initial response to parental bill color by chicks of Franklin's Gull (Larus pipixcan).—While at the Delta Waterfowl Research Station in 1955 we did an experiment on the initial response of incubator-hatched Franklin's Gull chicks to parental bill color (Collias and Collias 1957).

We presented two different bill colors simultaneously to a Franklin's Gull chick on the day it hatched in order to test the very first responses of the chick to parental bill color. The method used was to present to the chick a flat piece of immobile cardboard on which two simple models of adult Franklin's Gull heads were facing each other. Each head had a differently colored bill. The bills of the two heads were actually holes in the cardboard behind which different colors could be placed on both sides. The impression of motion was accomplished by having a light behind the heads flash on and off 85 times a minute,

stimulating the chicks to respond to the models. The chicks were taken right from the incubator and it was the first experience the chicks had with any color or the opportunity to peck at a bill or to even see a shape like that of an adult gull's head.

The colors tested were red, the color of an adult Franklin's Gull bill, versus white, or red versus green. The number of times a chick pecked at each color was recorded. Seventeen chicks each tested for six minutes, pecked the red bill 15 times more often than they pecked at the white bill and 4 times more often than they pecked at the green bill. Both results were statistically significant. We concluded that newly hatched Franklin's Gull chicks have a genetically determined predisposition to peck at a parental bill of the normal red color over white or green. We believe this experiment was the first confirmation with incubator-hatched young and without the use of hand-held models of the classic experiments by Tinbergen and Perdeck (1950) showing that the feeding responses of newly hatched Herring Gull (*Larus argentatus*) chicks are stimulated by the sight of the red spot on the lower mandible of the yellow bill of the parent.

Anna's Hummingbirds (*Calypte anna*) trained to select different colors in feeding.—Since most of the things one can buy for feeding hummingbirds are red, I decided to test if hummers really had a preference for red. I tested red, blue, yellow and colorless solutions of sugar water in various experiments (Collias and Collias 1968).

I trained hummers to come to a given color by presenting all four colors simultaneously, but only the solution to which the hummingbirds in our garden were being trained had sugar in it. All the other colors were just colored water.

When testing, I presented the same colors as in the training period but this time all colors were just water without sugar. In all cases the bird visited the color to which it had been trained by far the most often. This result showed a tendency to persist at a given color that indicates a good source of nectar before shifting to another color.

When I tested all four colors in different test tube feeders with the same concentration of sugar I found the hummers would start on

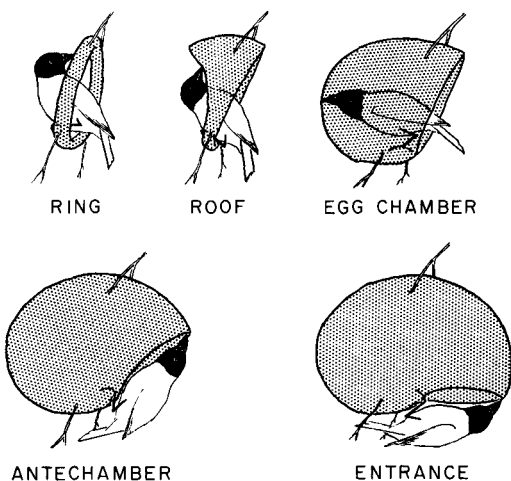


FIG. 3. Sequence of stages followed by a male Village Weaver in weaving his nest (Collias and Collias 1962).

one tube and finish that tube completely before they had finished half of any other color. This result shows a tendency to exploit a known source of nectar before exploring another regardless of color.

In conclusion, Anna's Hummingbirds can probably learn any flower color that indicates a good nectar flow.

WEAVING OF THE NEST BY THE MALE VILLAGE WEAVER

As you know we studied weaverbirds, particularly the Village Weaver for many years, and I am going to describe some phases of our work. First, I want to describe how a weaverbird makes a nest (Collias and Collias 1962, 1984).

A typical Village Weaverbird nest built by an experienced male adult weaver doesn't look much like a typical nest from North America. It is roofed, has a bottom entrance, and is woven of strips torn from the leaves of grasses or palms.

Figure 3 shows the various stages in building of a Village Weaverbird nest. Each stage of the nest provides the stimulus for the next stage.

- (1) Only the male weaves a nest and he selects a site which is quite far out on a small branch, and preferably at a fork. He first builds a ring. Then while standing in the ring he builds the rest of the nest. He

- always stands in the same place and always faces in the same direction.
- (2) He builds the roof over his head and in front of him pushing and building out as far as he can, and so ends up building the globular nest chamber.
 - (3) Then he builds over his head toward his back and forms the antechamber. When he gets the antechamber down to the horizontal he neatly finishes off the entrance. Then he thatches a ceiling of relatively short wide strips.
 - (4) His standing in one place and pushing out in all directions determines the size and shape of the nest.
 - (5) The threshold where he keeps his feet serves as a ridge to keep the eggs from rolling out of the bottom of the nest chamber.
 - (6) After a female accepts a nest he adds a short entrance tube 4–8 cm long. This is the only part of the nest he adds while outside the nest, probably because the female won't let the male enter the nest after she accepts it.

Figure 4 shows some of the motions a male goes through to push and pull a strip into his ring. Note that if the strip is too long for him to push all of it through, he brings the loop around and weaves it in. He then takes the loose end of the strip and weaves it in.

After studying how a weaver makes his nest we attempted to weave a nest ourselves with forceps, using as near as possible the same general techniques as the male, and we managed to make a nest that was a reasonable facsimile of a normal nest (illustrated in Collias and Collias 1962).

DEVELOPMENT OF NEST BUILDING BY THE MALE VILLAGE WEAVER (Collias and Collias 1964, 1973)

Reports in the literature indicate that a bird which was denied access to nest materials until it was an adult built a first nest that was just like that of an experienced bird. This is not true of the Village Weaverbird as we saw in Africa. Males do not get adult plumage until their second year, and we saw colonies of yearling males gathered in a tree practicing building nests. The nest of a young weaverbird doesn't look much like the nest of the

adult (Collias and Collias 1964). So we decided to see what a bird had to develop or learn in order to build a typical nest.

A young Village Weaver that I raised from before he had his eyes open we called Tex as a shortened form of *Textor* which means weaver and which at that time was the generic name of this group of weaverbirds. Little did I realize at the time that Tex was only the first of 41 weaverbirds I was going to hand rear.

After Tex could feed himself we kept him in a cage that was large enough that we could furnish him with giant reed grass (*Arundo donax*) for nest materials, as we did the adults in the outdoor aviary. A nest built by Tex in his second year was pretty good. At this point he had neither seen nor even heard another Village Weaver so neither tuition nor example is necessary for a male weaver to build a nest—then just what was necessary?

I reared some male weavers in the complete absence of any natural materials that could be used for building. When these birds were seven months old I tested their preference for different colors with colored toothpicks which gave a standard size, shape and weight, representing nest materials. During the first four days of testing, preference of the young weavers for green increased significantly ($P = 0.01$) from 38% to 71%.

At first the males will try to weave with any strip even if it is much too short. By measuring the length of all the strips in two nests of the same bird, we found that a male Village Weaver in his first breeding season as an adult builds with strips that average twice as long as those he used as a yearling.

The birds also have to learn the mechanics of weaving and where to weave. We found retarded development of weaving ability in young male Village Weavers that had been completely deprived of normal nest material until almost one year of age. As yearlings, the controls not only tore more strips, they wove a significantly bigger percentage of their strips (Collias and Collias 1973). However, both groups wove by far the majority of strips on the wire of the cage—an easier place to weave than on the twigs. In fact the deprived yearlings didn't weave anything on the twigs.

The next year, after considerable practice, the percentage of total strips woven by deprived and nondeprived birds was not signif-

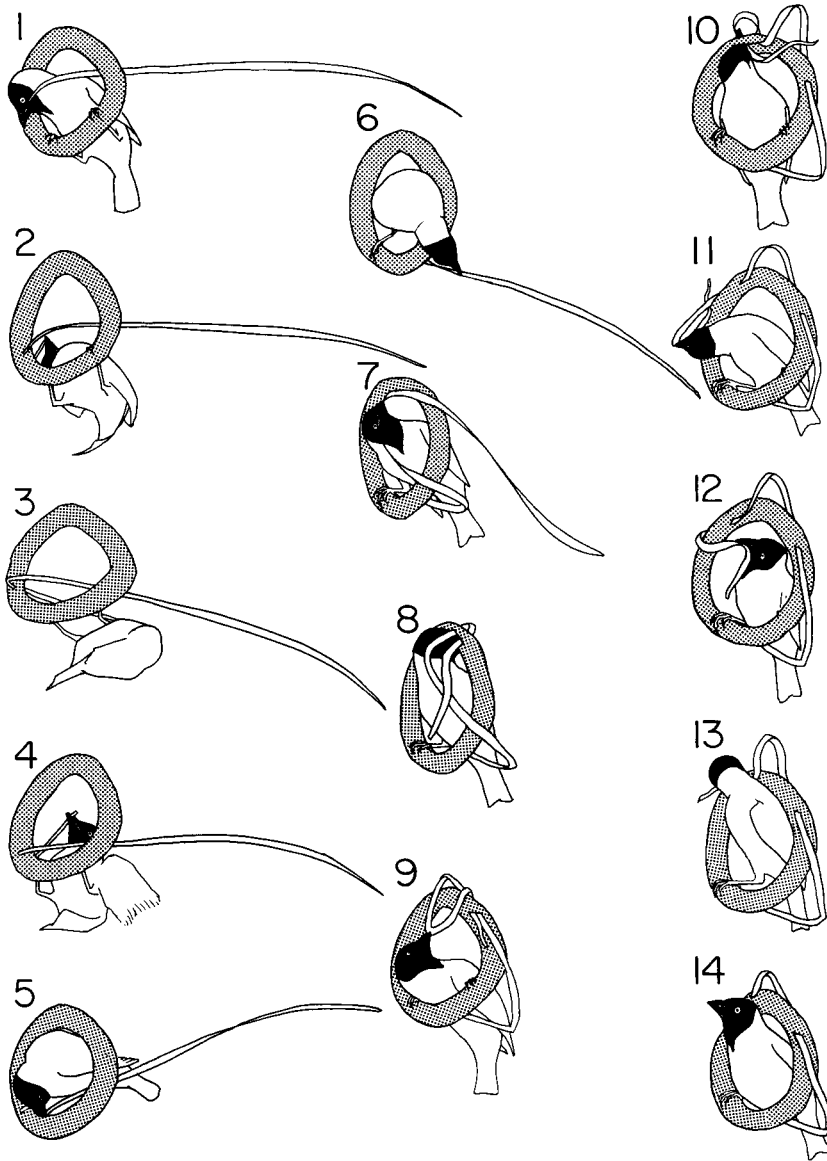


FIG. 4. Typical sequence of movements by a male Village Weaver as he weaves a single strip of grass or palm leaf into his ring (Collias and Collias 1962). Drawn by Nicholas Collias from motion picture frames.

icantly different. However, the number of strips woven on twigs was significantly different (Collias and Collias 1973).

When watching young Village Weavers learning to weave we have often seen a subordinate tear a strip and immediately have it taken away from him by a more dominant bird. The dominant bird often then used this strip to weave. Of course this means that the

dominant bird has much more opportunity to practice weaving. Since the young weavers need practice in order to perfect the skills used in weaving the dominant birds actually perfected their weaving skills and often went on to build a nest at a much earlier age than did the subordinate birds.

When matched with control birds that had a similar dominance level, the deprived young

wove a significantly smaller percentage of their strips (Collias and Collias 1973). The deprived birds in this case were only partially deprived in that they had access to nest material until they were seven weeks old and then were not given any nest material until the age of about one year when this test was done.

A long-term example of the effect of lack of practice on subsequent ability to build a nest was Male LL who was at the bottom of the peck order in his group which had been completely deprived of nest materials after seven weeks of age. He would tear a strip only to have it promptly taken away by one of his cage mates. As a result Male LL had almost no chance to practice weaving, and never learned to build a nest. He lived seven years, and spent several breeding seasons in a large outdoor aviary with a number of the other weavers. He changed to full breeding plumage each breeding season and held a territory, yet in all that time he never managed to build a nest. He would tear a strip and taking it to a perch spend hours playing with it but he never wove one strip. Thus weavers must have sufficient opportunity to weave when they are young or they never learn to weave.

Our colleague Cathy Jacobs who helped us a great deal in our studies on weaverbirds hand-reared a male Village Weaver she called Phineas. Cathy kept Phineas in her office for four years in a cage. Starting at about six months she supplied Phineas with many long strips she tore from palm fronds, at least once a week for a year and occasionally after that. He often wove his strips on the wire cage and wove a complete ring his second year. At four years he was put out in the large outdoor aviary. This aviary was supplied with a fresh palm frond daily for all the weavers. Phineas was unable to tear a single strip by himself although he did weave a crude nest from strips he took from other weavers. This shows that not only rather complicated weaving requires practice but also the more simple task of tearing a strip.

We induced an adult male weaver (RR) to build an abnormally long entrance tube on his nest by adding dangling strips with one end fastened to the entrance of his nest. Thereafter although he usually built a normal length tube he sometimes built a long one several times the normal length. None of these later nests

were built with any help or incentive from us so he had learned to build a very long entrance tube after he became an adult.

In conclusion, our experiments on development of nest building by the Village Weaver showed:

- (1) Self-reinforcement of inherited acts with experience.
- (2) Building a species-specific nest requires practice but not a tutor.
- (3) A young bird has a long sensitive period (months) for nest building.
- (4) Adults can learn new building habits.

INHERITANCE OF EGG-COLOR POLYMORPHISM IN THE VILLAGE WEAVER

Now I am going to shift from the building of a nest to egg-color polymorphism in the Village Weaver. It seems a bit far from behavior but as Ernst Mayr (1958) has pointed out, behavior often precedes related morphological evolution.

Most birds in North America lay only one color of egg, but that is not true of the Village Weaver, the eggs of which vary widely in both color and spotting. The four background colors found in the Village Weaverbird are white, turquoise, emerald turquoise, and emerald. Each female lays the same type of eggs over her lifetime (E. Collias 1984).

For fourteen years we did experiments that required the female to make a choice between the nests built by the males. To maximize the number of choices that females made we removed the eggs of a clutch one or two days after the last egg was laid. Each egg was identified as to the female who laid it, the date laid and the male to whom the female was mated at that time.

By this method we accumulated well over a thousand eggs. Suddenly one day I realized that now I had an opportunity to explore the genetics of egg color in a passerine bird (E. Collias 1993), something that had never been done before, for in addition to having the eggs, we had been breeding these birds for years and knew the parents and sibs of all our birds except, of course, our original flock. I identified the color of each egg from the *Villalobos Color Atlas* which divides the spectrum into 33 hues and then subdivides and

grades them by chromaticity (the amount of attenuation of the hue) and lightness (from black to white).

For example, examination of variation in 59 eggs laid by female ABA over nine years showed that all her eggs were of turquoise hue, most were fairly light in color (Grade 17), intermediate in chromaticity (Grade 6), and all were unspotted.

From 20 different crosses between 13 males and 15 females which resulted in at least one daughter from whom we also obtained eggs, I postulated five hypotheses as to the inheritance of egg color: two, three, or four alleles at one locus, or two pairs of sex-linked alleles, or two pairs of autosomal alleles at two loci. On checking each hypothesis against the data I ruled out the first four.

Since space is limited, I will summarize the hypothesis that appears to explain the inheritance of egg color and recommend that for more details on the crosses, how I tested the hypotheses, and my reasoning with regard to acceptance or rejection, one can check my 1993 paper in *The Auk*.

The last hypothesis for the inheritance of egg color is two pairs of autosomal alleles at two loci and postulates the following:

Emerald—at least one dominant gene for emerald (E-), and only recessive genes for turquoise (tt).

Turquoise—at least one dominant gene for turquoise (T-), and only recessive genes for emerald (ee).

Emerald turquoise—at least one dominant gene for both emerald and turquoise (E-T-).

White—only recessive genes at both loci (ee, tt).

This hypothesis worked in all 20 crosses. The other four hypotheses fail to explain the data.

I shall give an example of how Hypothesis 5 worked—two pairs of autosomal alleles at two loci (Figure 5):

Male 1 (Ee, Tt)—mated with Female 1 who laid emerald turquoise (Ee, Tt) eggs.

They had a daughter who laid white (ee, tt) eggs.

Male 1 (Ee, Tt)—also mated with Female 2 who laid white (ee, tt) eggs. They had two daughters one of whom laid tur-

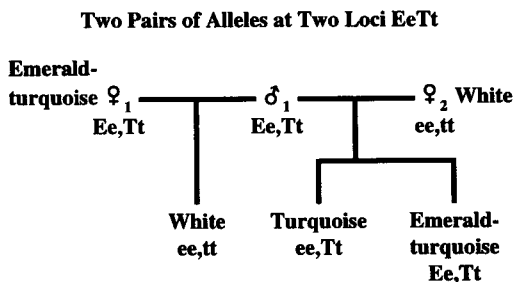


FIG. 5. Example of matings by Village Weavers and colors of eggs laid, consistent with hypothesis of a pair of alleles at each of two autosomal loci, with turquoise allele and emerald allele dominant over white allele but not over each other (emerald-turquoise egg; E. C. Collias 1993).

quoise (ee, Tt) eggs, the other laid emerald turquoise eggs (Ee, Tt).

Therefore, these results are consistent with a hypothesis of two pairs of autosomal alleles at two loci for the inheritance of egg-color polymorphism in the Village Weaver.

Now why do Village Weavers have so many different kinds of eggs? Our colleague, Janice McLean, answered that question. She put other weaverbird eggs into a nest already containing eggs. Unless the added egg very closely resembled that of the host the strange eggs were immediately tossed out regardless of whether the added egg was the odd one in the clutch or if the female's own egg was the odd one (Victoria 1972).

This egg variability probably arose as a defense against nest parasitism. Did this develop as a defense against intraspecific or interspecific parasitism? I do not rule out either completely. However, I do not think intraspecific parasitism played a big part in the Village Weaver. We never saw any evidence of this type of egg parasitism in three breeding seasons in Africa. However, it does occur. Janice, in four years of observation in our aviaries saw two cases both under rather unusual circumstances. In one case where the eggs differed, the strange egg was ejected. In the other case in which both females had very similar eggs, the parasitic egg was accepted.

I think interspecific parasitism probably played an important role because of the work of Cruz and Wiley (1989) on the Village Weavers which were introduced into Hispaniola by the early 18th century. These weavers

were without brood parasites until the 1970s when the Shiny Cowbird (*Molothrus bonariensis*) arrived and laid in the weaver nests. The weavers did not reject the cowbird eggs although these were quite different from the weaver eggs. Evidently weavers had lost the egg rejection behavior in the intervening 200 yrs, which they certainly would not have done if intraspecific nest parasitism was common.

To summarize egg-color polymorphism in the Village Weaver:

- (1) Each female weaver lays eggs with the same color characteristics all her life.
- (2) The inheritance of background color of eggs is consistent with a hypothesis of 2 autosomal alleles at 2 different loci.
- (3) A female will throw out any egg that differs markedly from her own eggs, a protection from brood parasitism.
- (4) This favors selection for uniformity of eggs of the same female and variability between females.

Our research on bird behavior has given us much enjoyment and intellectual satisfaction over the years, as has the consequent interaction with many friendly and helpful students of birds. Foremost among the latter has been Margaret Morse Nice and the inspiration and guidance given by her research on the life of birds in nature.

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