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The principle of self-reinforcement in nest building: evidence from abnormal nests of a weaverbird (*Ploceus cucullatus*)

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ABSTRACT. *The principle of self-reinforcement in nest building: evidence from abnormal nests of a weaverbird* (Ploceus cucullatus).- The male african village weaverbird *(Ploceus cucullatus)* normally weaves a roofed nest with a bottom entrance to which he adds a short entrance tube after a female has accepted his nest. The young male must practice a good deal before he can make a normal nest, and each appropriate species-typical building act may be self-reinforcing (self-rewarding). Different kinds of abnormal nests observed over some years can be interpreted by and give evidence for this principle of self-reinforcement which enters into the selection and preparation of nest materials, general organization of the nest and sequence of nest stages. The importance of weaving from a fixed spot is emphasized. A male was induced to build an entrance tube several times the normal length and this habit persisted in subsequent years in absence of further training, suggesting that the male develops a mental image of what a completed nest should look like. Evidence is presented from a novel abnormal nest that some reasoning may possibly enter into the conception of his nest by an experienced male.

KEY WORDS. Nest building, Abnormal nests, African village weaverbird, Ploceus cucullatus, Self reinforcement, Self-rewarding act

Introduction

The principle of self-reinforcement of behavioral responses is of basic importance in the development of species-typical behavior, as distinct from individual differences in behavior. By self- reinforcement is meant that the performance of a specific activity increases the probability that this activity will be repeated. An early example was the observation that the initial approach responses of baby chicks of the domestic fowl to specific stimuli from the parent or to siblings rapidly and greatly increase in frecuency and intensity with continued repetition of these acts themselves when the response brings the chick close to the parental stimuli or in contact with siblings (Collias, 1952, 1962; Ramsey & Hess, 1954).

In an important theoretical analysis based on an extensive review of the older literature, Thorpe (1963) long ago developed the view that in the variable and exploratory behavior of animals, a particular action is self-rewarding if it happens to lead to the next stage in an adaptive sequence of behavioral acts characteristic of the species, as in nest building. There seems to be some selective learning of the correct responses and such self-reinforced actions give the appearance of being goal-directed. Thorpe relied rather heavily on examples from nest building; however, the experimental evidence for this hypothesis was then rather sparse and somewhat tenous.

About that time we began an intensive analysis of the precise stimuli involved in nest-building behavior and its development in the african village weaverbird (*Ploceus cucullatus*), a species that we studied both in nature (Collias & Collias, 1970) and experimentally in aviaries. We found that during nest building each stage automatically provided the stimulus situation necessary for the next stage (Collias & Collias, 1984). The male weaves the nest in this species, and we also found that a young male must practice a good deal before he is able to build a nest (Collias & Collias, 1964, 1973). Much of this work is reviewed in a recent book (Collias & Collias, 1984).

Over a period of about 20 years we observed a variety of abnormal nests that the weaverbirds ocasionally built in our aviaries, and the present report adds additional evidence for understanding nest building from these abnormal nests with special reference to the principle of self-reinforcement of building responses. The photographs of these abnormal nests shown here have not been previously published.

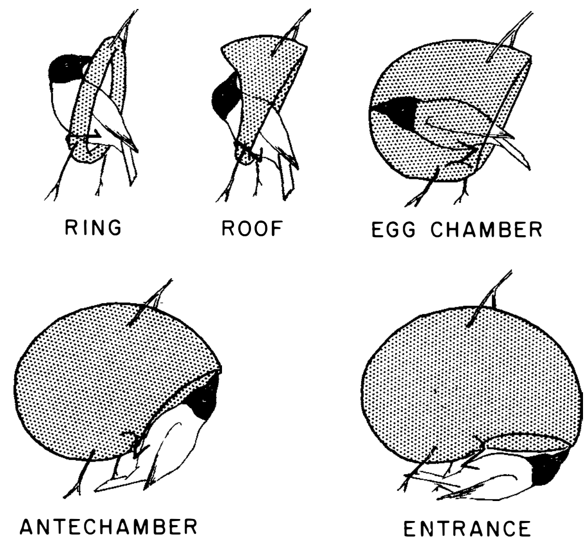

FIGURE 1. The different stages of weaving the nest with his beak by a male village weaverbird (N.E. Collias & E.C. Collias, 1962). [Diferentes etapas del tejido del nido con el pico por parte de un tejedor aldeano (N.E. Collias & E.C. Collias, 1962).]

Material and Methods

The birds used were all color banded with individually distinctive combinations. They were housed outdoors on the campus of our university in large outdoor aviaries (from 9.2 m long x 5.2 m wide x 5.2 m high, to 7.9 x 6.1 x 4.2 m) or during the winter in small aviaries (1.8 m^3 to 1.8 m x 3 m x 1.8 m high). They were furnished with a fresh source of nest materials, either tall reed grass or the fronds of palm trees. In the outdoor aviaries the birds built their nest in small trees or in branches nailed to the wooden supports.

The outer shell of the enclosed nest is woven in several stages by the male with his beak (fig. 1), using long strips that he tears from the leaves of tall grasses or palm trees. Once the outer shell is completed, the male displays it as part of his courtship to visiting unmated females. If a female accepts his nest she lines it with soft materials, mates with the male, does all of the incubating of the eggs and all or most of the care of the nestlings. A ridge in the floor of the nest between the egg or brood chamber and the nest entrance that opens downward helps keep the eggs and nestlings from falling out of the nest. In case no female accepts his nest the male tears it down when it becomes faded and he builds another fresh nest in its place. In this species, the male often builds several nests and may have more than one mate.

Results and Discussion

Selection and preparation of nest materials

The principle of self-reinforcing or self- rewarding species-typical acts was clearly shown when we first presented young male village weavers with nest materials of different colors simultaneously: green, yellow, blue, red, black and white (Collias & Collias, 1964). These materials were uniform in size, weight and shape. The birds at once showed the normal species preference for the green color characteristic of fresh vegetation. Their initial preference for green over other colors of nest materials doubled within the first week of the experiment, and this improvement was statistically significant.

The need for self-reinforcement of a nest- building act was also seen in the tearing of nest materials. Jacobs (pers. com.) reared a young male village weaver, providing him for about a year with long strips of nest material. When tested later as an adult he proved unable to tear a single strip for himself. We have also

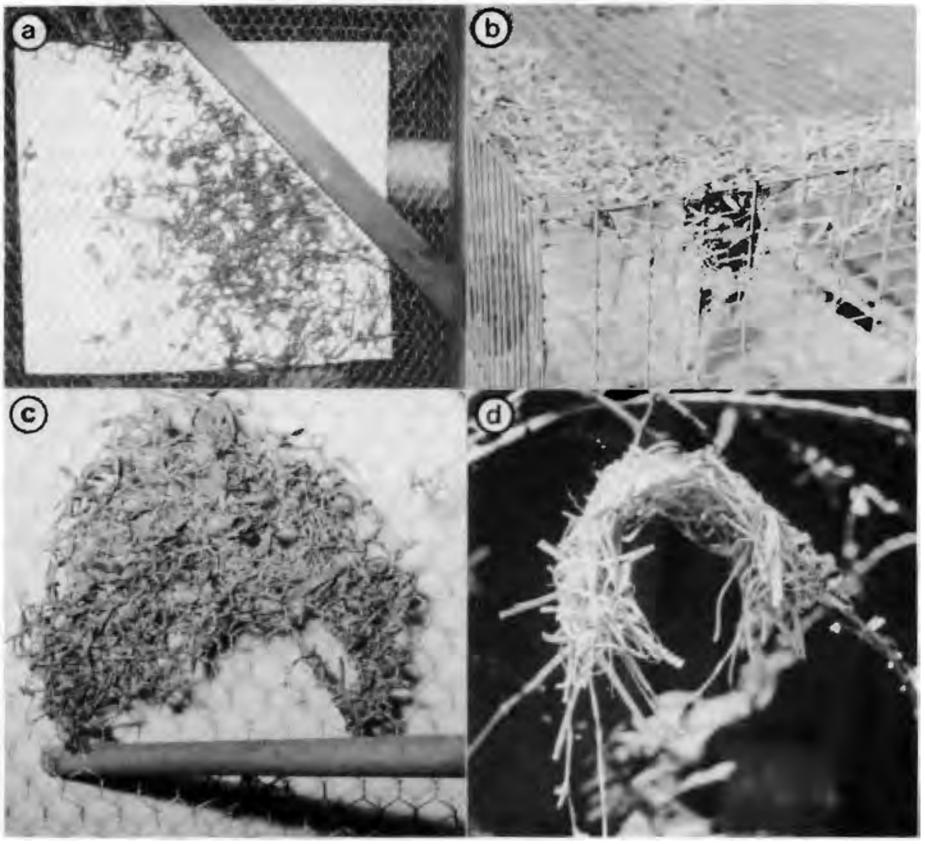

FIGURE 2. Importance of weaving from one place: a) Indiscriminate weaving from no fixed location over the wire frame wall of an aviary. b) A male in a cage weaves an elongated pattern on the roof over his head as he moves from side to side along the adjacent wall. c) Incomplete disc woven within reach of his beak by a male from one place on the perch. d) Incomplete ring built by a male given only nest materials too short to enable him to close the bottom of the ring.

[Importancia del tejido a partir de un emplazamiento. a) Tejido indiscriminado sin un punto de partida fijo sobre la pared de tela metálica de una pajarera; b) un macho enjaulado teje según un patrón alargado en el techo por encima de su cabeza a medida que se desplaza por la pared contigua; c) disco incompleto tejido dentro del radio de alcance del pico por un macho a partir de un punto de la percha; d) anillo incompleto construido por un macho provisto de materiales demasiado cortos como para poder cerrar el fondo.]

observed that a male village weaver greatly increases the length of strips that he tears and uses in his nest between his first and second year (Collias & Collias, 1973).

Importance of a fixed reference point from which to build

Young weaverbirds may at first weave a few strips indiscriminately in diferent places. Even an adult male, placed in a small aviary without any perches in it may weave over the wire framework of the wall of the aviary in an apparently random fashion (fig. 2a). A male in a cage where he has access to the wire framework of the roof while at the same time he can cling nearby to the adjacent sidewall reveals a preference for weaving over his head, but since he does not perch in any one spot he makes an elongated pattern of weaving to his left and to his right (fig. 2b), probably because there are no discontinuities in the wall or roof to either side of him that he can use as a reference point. A weaver building a normal nest weaves most of the roof of the egg chamber before he weaves the bottom.

If a male confined to a small aviary is given a perch he will stand on this perch as he weaves on the adjacent wall of the aviary wire frame. The result is a circular or disc-shaped mat like a flat projection of the egg chamber of the wire wall extending out as far as he can reach while standing on the perch next to the wall, but with a conspicuous gap in the disc at the botom which is the least preferred place for weaving (fig. 2c). Normally, the male builds a ring within which he perches as he weaves the egg chamber before himself. The globular form of the normal egg chamber results when the male pushes out with his beak as far as he can reach while consistently perching on the bottom of the ring (fig. 1).

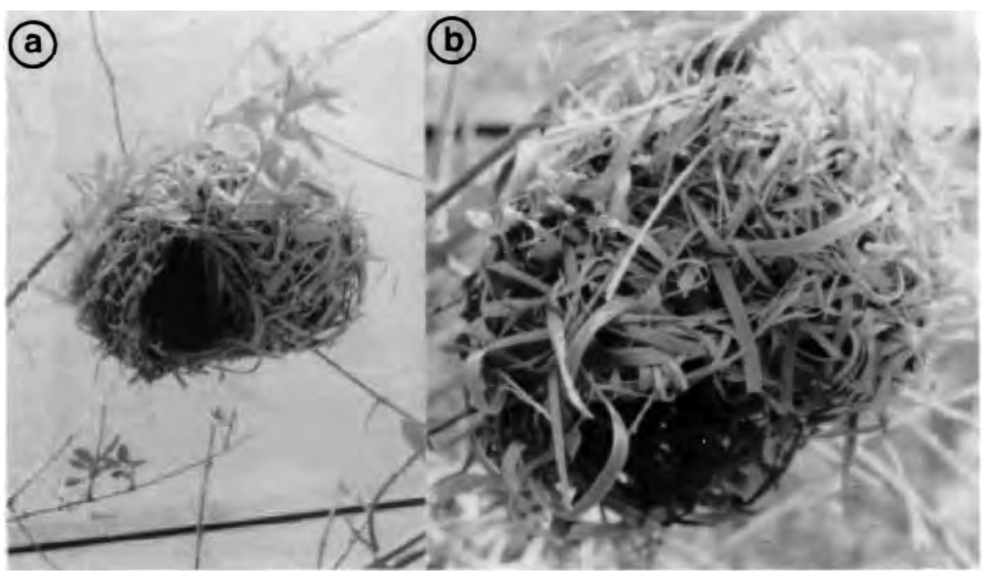

FIGURE 3. Shape of the egg chamber: a) Normal nest with a large rounded egg chamber; b) Nest with abnormally short and somewhat flattened egg chamber.

[Forma de la cámara de puesta: a) nido normal con cámara grande y redonda; b) nido con cámara anormalmente poco profunda y algo plana.]

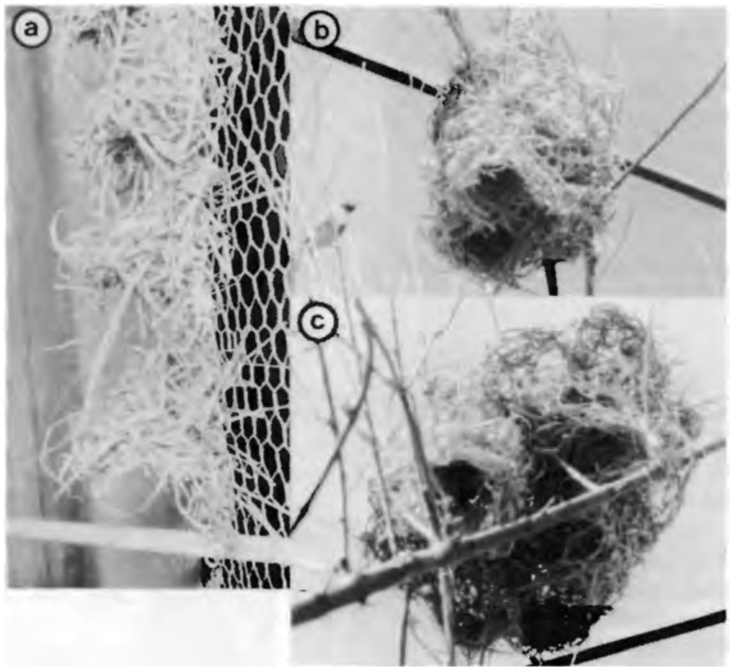

FIGURE 4. Abnormal antechambers: a) Series of antechambers built vertically along wire frame wall of aviary, starting from the perch below; b) A false, blind entrance and antechamber built alongside normal entrance (arrow); c) Six supernumerary, blind entrances and partial antechambers built after taking over another male's nest. The nest is viewed from beneath with arrow indicating the normal entrance into nest.

[Antecámaras anormales; a) serie de antecámaras construidas verticalmente a lo largo de la pared de tela metálica de la pajarera, comenzando por la percha situada por debajo; b) entrada falsa sin salida y antecámara construida junto a la entrada normal (flecha); c) seis entradas sin salida superfluas y antecámaras parciales construidas tras ocupar el nido de otro macho (vista del nido desde abajo, con la flecha indicando la entrada normal).]

Building of the ring

If a male is given the fork of a twig in which he can build his ring, he will still be unable to close the bottom of the ring beneath himself, if the strips with which he is provided are too short. The result is an incomplete ring without a bottom (fig. 2d), and the male proceeds no farther in his weaving. A few males apparently never learn to make a ring, posibly because they never learned to tear and prepare strips properly.

Some evidence for self-reinforcement in building the egg chamber

A normal egg chamber has a globular shape (fig. 3a), but occasionally we observed nests with an abnormally short egg chamber (fig. 3b). Sometimes, a male that has been in a small indoor aviary early in life builds a disc-like nest pad against the wire frame wall as described above, where the stiff unyielding wire frame blocks the normal pushing out reaction of the beak. When later placed in a large outdoor aviary with branches in which to build, the male sometimes produces a very short egg chamber as if his tendency to push out had failed to develop normally and had become cramped and abbreviated by his early experience in weaving on the unyielding wire frame of the aviary. Here again, I suggest there might be an illustration of the principle of self- reinforcement in nest building.

Building of the antechamber and abnormal supernumerary antechambers

In weaving the antechamber with his beak the male learns over backward from his customary stance on the bottom of the ring (fig. 1). The bottom of the ring becomes the threshold of the entrance of the egg chamber. When weaving on the wall of the aviary from a fixed site (perch) the male can build part of the roof over his head and then weave an antechamber away from the wall, even though he cannot build more than a flat projection of the egg chamber itself on the wire frame wall. After completing one antechamber he builds another, one above the other (fig. 4a).

We observed one male in a large outdoor aviary with ample building sites and opportunities, who seemed to have difficulty in making a ring. He would take over another male's nest and depending on its state of completion he would either complete the nest or satisfy part of his building drive by adding from one to six supernumerary antechambers to the outside of the nest (fig. 4b, 4c). These extra antechambers were all blind entrances and did not penetrate into the egg chamber of the commandeered nest. Having no fixed reference point the male might produce several antechambers. The presence of more than one antechamber suggests that in his early development, the male may have been directed by circumstances of the wire wall of the aviary to build antechambers rather than normal egg chambers, and the extra self-reinforcement for this stage of the nest may account for this abnormal predilection.

FIGURE 5. Abnormal nest with 60 cm long entrance tube, alongside normal nest built by the same male.
[Nido anormal con entrada en tubo de 60 cm de longitud, junto a la entrada normal construida por el mismo macho.]

Building of the entrance tube

After a female has accepted his nest the male generally adds a short vertical entrance tube about 5-10 cm long. If we repeatedly threaded into the rim of the entrance one end of long strips of nest materials leaving one end dangling, we found the male would weave up the dangling ends and endeavor to finish the rim. By this means we induced an adult male to weave an entrance tube three times (30 cm) the normal length (Collias & Collias, 1962). Over the next few years, with no subsequent experimental intervention on our part, this same male sometimes built nests with abnormally long entrance tubes, at first up to 20 cm, then 30 cm, and finally over 60 cm in length (fig. 5). It is as if his unusual experience, at first artificially induced, in being forced to build an abnormally long entrance tube, had been self-reinforced and continued to be self-rewarding resulting in his subsequent abnormal behavior as if the male now had a modified mental image of what a nest tube ought look like. None of the other male weavers in our aviaries ever built unusually long entrance tubes as this male did. But many of his nests continued to have entrance tubes of normal length (fig. 5), indicating there was some fluctuation in his building drive.

There is evidence of fluctuation in the general nest building drive which seems at times to be in balance with an increased drive to tear down an aging nest. After a male starts to tear down a nest, he will sometimes stop and instead begin to add fresh green materials to it. After the male described above built a few nests with very long tubes, he began to tear open the bottom of the egg chamber and add a short and second entrance tube to this opening (fig. 6a).

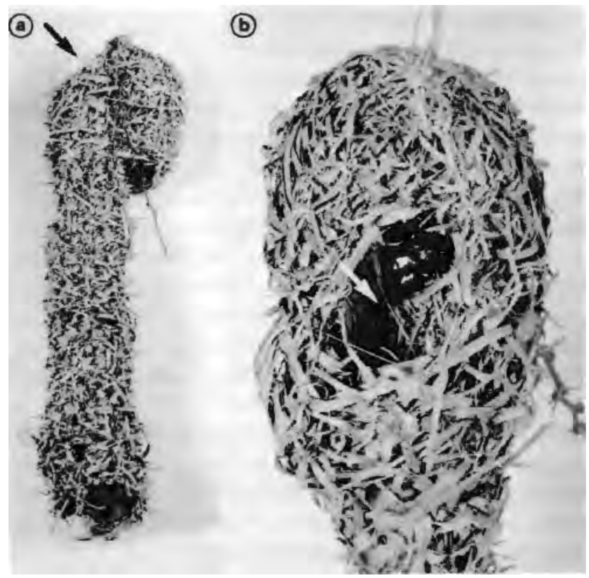

FIGURE 6. Abnormal extra entrances into egg chamber: a) Side view of abnormal nest with a second entrance with short entrance tube just below egg chamber, and a third entrance (arrow) at junction of antechamber with base of long tube; b) Closer view of the abnormal third entrance (arrow) in front view of nest. Photos by Clark Sumida.

[Entradas suplementarias anormales a la cámara de puesta: a) vista lateral de nido anormal con entrada en tubo de 60 cm de longitud, con una segunda entrada en tubo corto justo por debajo de la cámara de empolle, y una tercera entrada (flecha) en la intersección de la antecámara y la base del tubo largo; c) detalle de la tercera entrada anormal (flecha) en una vista frontal del nido.]

Possible cognition in nest building

Althrough the second entrance tube might be a purely automatic and mechanical response of the male's fluctuating building drive to a hole in the bottom of the nest, it does not explain why he made the opening at the bottom of the egg chamber instead of at the top where males usually began to tear down an old nest. Since it is considerable trouble for the bird to crawl up the abnormally long entrance tube, it is conceivable that the second entrance provided a short cut into the egg chamber. In the long tube nest that this male built last, he also tore open another hole at the outer surface of the long entrance tube at its junction with the antechamber (fig. 6b), providing still another extra entrance into the egg chamber. While the meaning of these extra entrances is obscure one possible interpretation is that the male had some comprehension that these extra and unique entrances provided more convenient access into the nest. The males sleep in their older nests leaving the fresh ones to the females.

Long ago, Fabre (1914), in an attempt to interpret the nest building instincts of insects, defined reason as "the faculty that connects the effect with its cause and directs the act by comforming it to the need of the accidental". In a recent general discussion of animal thinking, Griffin (1984) re-emphasized this criterion. Compared to stereotyped behavioral responses, he states, "conscious awareness is more plausibly inferred when an animal behaves appropriately in a novel situation - that requires specific actions not called for in ordinary circumstances". We have done some experiments (Collias & Collias, 1984) in which we found that any part of a male weaver's nest could be cut away and he would replace it, with the exception of the bottom of the ring which he needed to stand on while he wove. What this experiment shows is that the order of the stages in which a male builds is somewhat flexible but does not necessarily imply any ability to reason, since the male could be responding directly and automatically to the remaining parts of the mutilated nest, but cognition is still a possible alternative explanation. In the baya weaverbird (*Ploceus philippinus*) in India, experiments have also shown that holes of various sizes and shapes cut into different parts of the nest are repaired by the male owner (Ali & Ambedkar, 1956; Crook, 1964).

I conclude that the question as to whether or not a male weaver uses reason in building his nest is still an open question, but it does seem likely that he has some overall comprehension of what a nest ought to look like, based on selective learning.

Abnormal nest building by other species

There are widely scattered references describing instances of unusual, atypical or abnormal nest building in various species. A few examples will be given for birds from different continents.

Nests have been recorded that were built of such artificial materials as pieces of iron wire, spun glass, cotton, string, or cement (Collias & Collias, 1984). These strange materials presumably in some way resemble the normal nest materials.

Nests of the baya weaverbird have a long vertical entrance tube. In places where nest sites are limited the male may seal off the bottom entrance and build a second nest suspended from the first. Three or more such nests in series have been recorded (Ambedkar, 1964). Superabundant nest sites that appear exactly alike may confuse the builder. Individual american robins (*Turdus migratorius*) and european blackbirds (*Turdus merula*) have been several times reported to build numerous mostly incomplete nests in between the rungs of horizontally hung ladders (Welty, 1982).

The hornero or rufous ovenbird (*Furnarius rufus*) of Argentina and neighboring countries builds an oven-like nest of adobe with a side entrance. A photograph of a very unusual nest of this species which had two entrance holes is reproduced by Narosky et al., (1983).

The spectacled weaver (*Ploceus ocularis*) weaves a nest which like some other species of weavers has a long vertical entrance tube at the bottom. In southern Africa this tube is usually 25-30 cm long, but exceptionally may extend for 2 m (MacLean, 1985).

Acknowledgments

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Resumen

El principio de auto-refuerzo en la construcción del nido: pruebas obtenidas de nidos anormales de un tejedor (Ploceus cucullatus).

El tejedor aldeano macho (*Ploceus cucullatus*) teje el nido con el pico utilizando para ello tiras largas que arranca de la hierba o palmas. En la Figura 1 se ilustran las etapas normales del tejido del nido. Cada etapa es auto-reforzante (auto- gratificante) y, una vez terminada, sirve de estímulo para la siguiente. Un macho joven sin suficiente práctica en una determinada etapa de construcción del nido puede a la larga ser incapaz de completarla.

Los nidos anormales aportan pruebas del principio de auto-refuerzo en cada etapa de la construcción. En una pajarera sin perchas en las que construir, un macho teje una masa plana y amorfa (fig. 2a) o anormalmente alargada (fig. 2b) sobre la tela metálica. Pero a partir de un lugar fijo en una percha, alcanza con su pico tan lejos como puede en todas las direcciones y teje un disco plano sobre la tela; dicho disco, no obstante, queda incompleto por debajo (fig. 2c). En un lugar de nidificación normal, en una rama en horquilla, empieza por tejer un anillo, pero no consigue cerrar el fondo si sólo se le proporcionan materiales de nidificación muy cortos (fig. 2d). Normalmente, el macho cierra el anillo por debajo y se coloca en su interior mientras crea una cámara de puesta semiesférica tirando hacia fuera con el pico en todas direcciones, siempre de cara al interior de la cámara. Un macho que sólo haya podido tejer sobre la tela metálica de la pared de la pajarera, al disponer más tarde de un lugar normal para tejer entre ramas construye a veces un nido con una cámara anormalmente plana y poco profunda (fig. 3). Un macho joven que carezca de la suficiente experiencia en construir nidos puede ser incapaz de empezar un nido en su madurez y emplea su impulso constructor tejiendo antecámaras adicionales sobre nidos construidos por otros machos (fig. 4).

El macho generalmente añade una entrada tubular corta de hasta unos 10 cm alrededor de la entrada inferior mientras que la hembra se halla incubando. En uno de los experimentos, se indujo a un macho a construir una entrada de una longitud tres veces superior a la habitual. Años después, sin haber sido sometido a más adiestramiento, solía construir nidos con largos tubos de entrada (hasta 60 cm), lo que sugiere que su cerebro había desarrollado una imagen anormal del aspecto que debía tener el nido típico de su especie (fig. 5). En sus últimos nidos, dicho macho comenzó a abrir una o dos entradas suplementarias directamente sobre la cámara de empolle (fig. 6) con el objetivo aparente de evitar el impedimento del largísimo tubo de entrada al nido, sugiriendo de esta forma la posibilidad de haber ejecutado algún razonamiento o acto cognitivo en relación con la estructura del nido.

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