

The Behavior of Lovebirds

The nine members of the genus Agapornis have different rituals for such activities as nest building. These differences shed light on the evolution of lovebirds and on the role of heredity in behavior

by William C. Dilger

All lovebirds display the behavior that gives them their anthropomorphic common name. They pair early, and once pairs are formed they normally endure for life. The partners exhibit their mutual interest with great constancy and in a variety of beguiling activities. For the student of the evolution of animal behavior the lovebirds have special interest. The genus comprises nine forms (species or subspecies). They show a pattern of differentiation in their behavior that corresponds to their differentiation in color and morphology. By comparative study of their behavior, therefore, one can hope to reconstruct its evolution and to observe how natural selection has brought about progressive variations on the same fundamental scheme.

Together with my colleagues in the Laboratory of Ornithology at Cornell University, I have been studying both the constants and the variables in lovebird behavior for the past five years. It is not too difficult to duplicate in the laboratory the basic features of the lovebirds' natural African environment, so the birds thrive in captivity. Our work has covered all the lovebirds except Swindern's lovebird; we have not been able to obtain any specimens of this species. Our findings in two areas—sexual behavior and the defense and construction of the nest—have been particularly fruitful, be-

cause in these areas the evolutionary changes in lovebird behavior stand out in sharp relief.

Lovebirds constitute the genus *Agapornis*, and are members of the parrot family. Their closest living relatives are the hanging parakeets of Asia (the genus *Loriculus*). Three species of lovebird—the Madagascar lovebird, the Abyssinian lovebird and the red-faced lovebird—resemble the hanging parakeets and differ from all other lovebirds in two major respects. The males and females of these three species differ in color and are easily distinguishable from each other. The male and female of the other lovebirds are the same color. In these three species the primary social unit is the pair and its immature offspring. The other lovebirds are highly social and tend to nest in colonies. In these respects, then, the Madagascar lovebird, the Abyssinian lovebird and the red-faced lovebird most closely resemble the ancestral form, and the other lovebirds are more divergent.

Our study of interspecies differentiation of behavior has begun to reveal the order in which the other species arrived on the scene. Next after the three "primitive" species is Swindern's lovebird. Then comes the peach-faced lovebird and finally the four subspecies of *Agapornis personata*, commonly referred to as the white-eye-ringed forms: Fischer's lovebird, the black-masked lovebird, the Nyasaland lovebird and the black-cheeked lovebird. There are significant differences in behavior between the peach-faced lovebird and the four white-eye-ringed forms.

Perhaps the sharpest contrasts in behavior are those that distinguish the three primitive species from the species that evolved later. Even the common generic characteristic of pairing at an

early age shows changes between the two groups that must be related to their contrasting patterns of life—nesting in pairs as opposed to nesting in colonies. Among the primitive species pair formation takes place when the birds are about four months old. At that time they are entirely independent of their parents and have already developed adult plumage. In the more recently evolved species, the colonial nesting pattern of which offers them access to their contemporaries virtually from the moment of their birth, pair formation takes place even earlier: the birds are about two months old and still have their juvenile plumage.

Among all the lovebird species pair formation is a rather undramatic event. Unpaired birds seek out the company of other unpaired birds and test them, as it were, by attempting to preen them and otherwise engage their interest. Couples quickly discover if they are compatible, and generally it takes no more than a few hours to establish lifelong pairs.

When the paired birds reach sexual maturity, their behavior with respect to each other becomes much more elaborate. This behavior as a whole is common to all lovebirds, and some activities are performed in the same way by all. Other activities, however, are not, and they show a gradation from the most primitive forms to the most recently evolved ones. One constant among all species is the female's frequent indifference to, and even active aggression against, the male each time he begins to woo her. Another is the essential pattern of the male's response—a combination of fear, sexual appetite, aggression and consequent frustration. Primarily motivated by both fear and sexual appetite, the male makes his first approach to his mate by sidling toward and then away from

NINE FORMS OF LOVEBIRD, as well as one hybrid (top left), are shown on the opposite page. They are arranged in their apparent order of evolution. The hybrid was bred in the laboratory for experiments on the inheritance of behavior. The letter A. at the beginning of each of the Latin species names stands for the genus *Agapornis*.

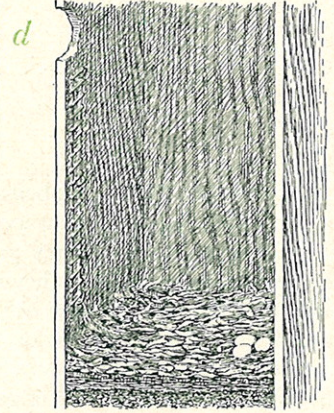
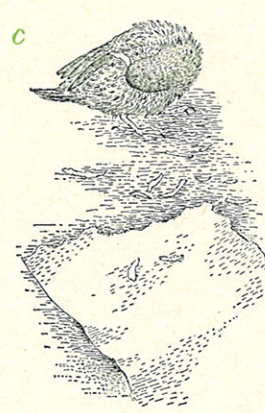
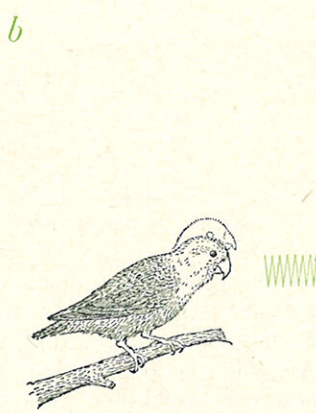
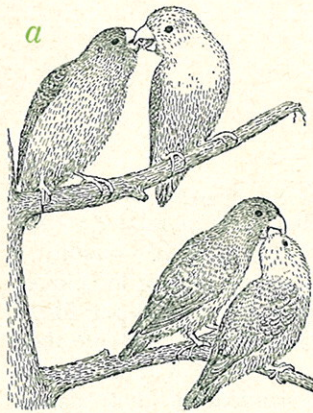
her while turning about on his perch. This switch-sidling, as it is called, is common to all species.

Two forms of male behavior initially associated with frustration, on the other hand, show a distinct evolutionary progression. The first of these activities is called squeak-twittering. Among the three primitive species—the Madagascar lovebird, the Abyssinian lovebird and the red-faced lovebird—the male utters a

series of high-pitched vocalizations when the female thwarts him by disappearing into the nest cavity. The sounds are quite variable in pitch and purity of tone and have no recognizable rhythm. In the more recently evolved species—the peach-faced and the four white-eyed forms—squeak-twittering is rather different. The sound is rhythmic, purer in tone and less variable in pitch. Nor does it occur only when the female has

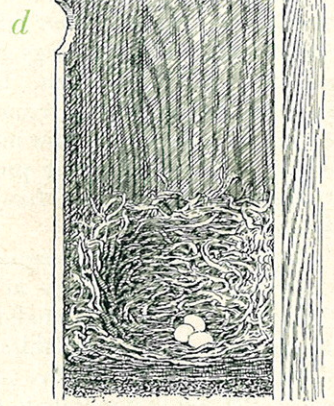
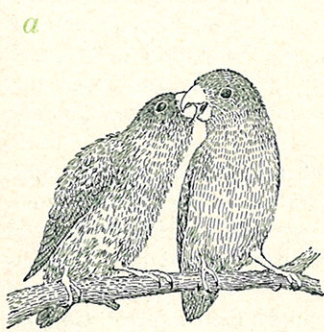
turned her back on the male and entered the nest cavity. The male usually vocalizes even when the female is present and gives no indication whatever of thwarting him. Squeak-twittering has undergone a progressive change not only in its physical characteristics but also in the context in which it appears.

A similar evolution toward more highly ritualized behavior has occurred in another sexual activity, displacement



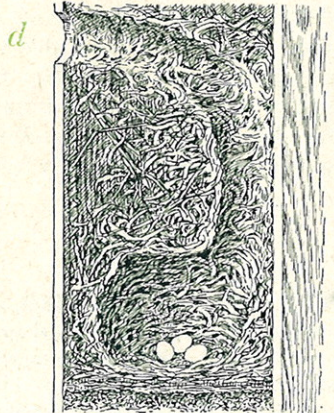
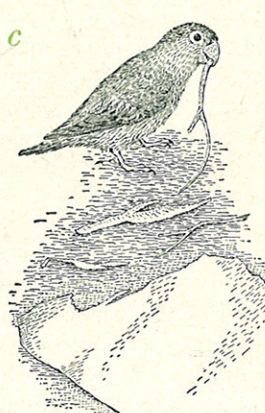
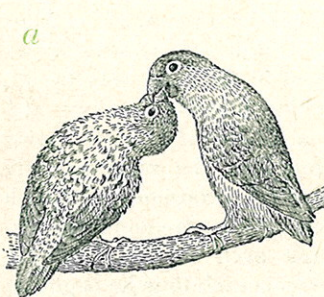
BEHAVIOR OF MADAGASCAR LOVEBIRD is outlined. Both sexes engage in courtship feeding (a). Accompanying head bobs

are rapid and trace small arc (b). Nest materials, generally bark and leaves, are carried several pieces at a time and tucked among



BEHAVIOR OF PEACH-FACED LOVEBIRD suggests higher evolutionary stage. Only males perform courtship feeding; females

fluff their feathers during this ritual (a). Slower head bobs trace wider arc (b). Nest materials, also bark and leaves, are



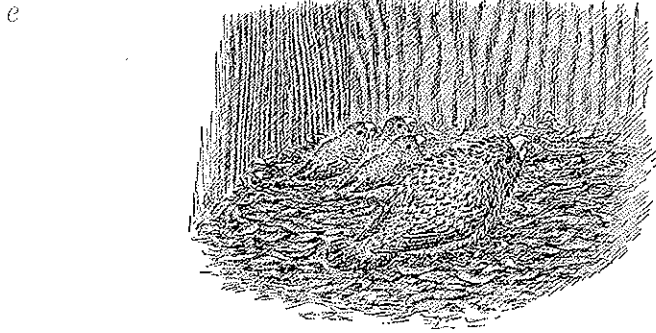
BEHAVIOR OF FISCHER'S LOVEBIRD indicates a further evolution. Courtship feeding (a), mobbing (e) and bill-fencing

(f) are performed much as they are by the peach-faced lovebird. But other kinds of behavior are significantly different. Head bobs

scratching. This response derives from the habit, common to all species, of scratching the head with the foot when frustrated. Among the three primitive species displacement scratching is still close to its origins. Only two things distinguish it from ordinary head-scratching: its context and the fact that it is always performed with the foot nearest the female. Purely practical considerations govern this behavior: the male al-

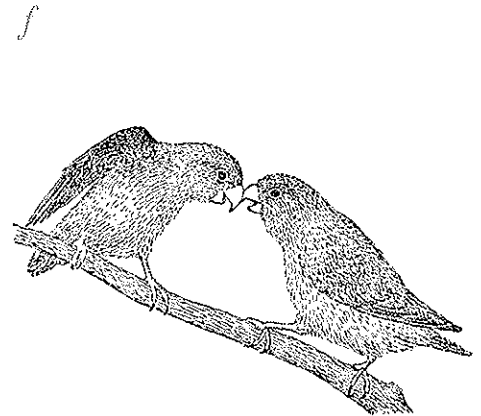
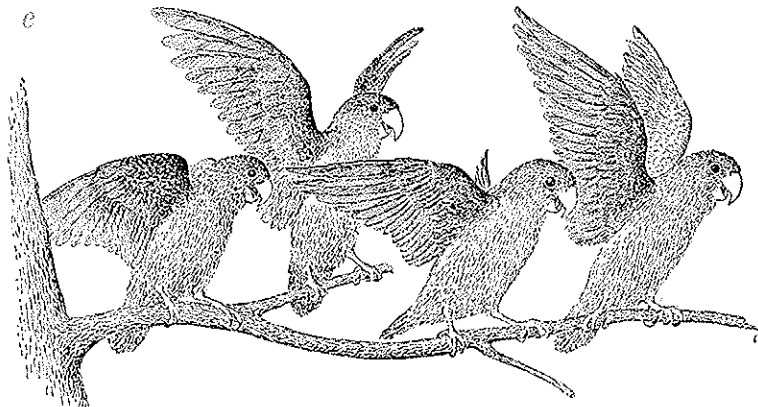
ready has that foot raised preparatory to mounting his mate. In the more recently evolved species, displacement scratching has become primarily a form of display. Its progressive emancipation from the original motivation with which it is associated becomes more and more apparent as one observes it in the species from the peach-faced lovebird through the white-eye-ringed forms. Among all these the scratching is far more rapid

and perfunctory than it is among the primitive species. Nor is it uniformly directed at the feathered portions of the head. In the peach-faced lovebird it is sometimes directed at the bill instead, and among the Nyasaland and black-cheeked lovebirds it is nearly always so directed. Moreover, these species use the far foot as well as the near one in displacement scratching; among the Nyasaland and black-cheeked lovebirds one is



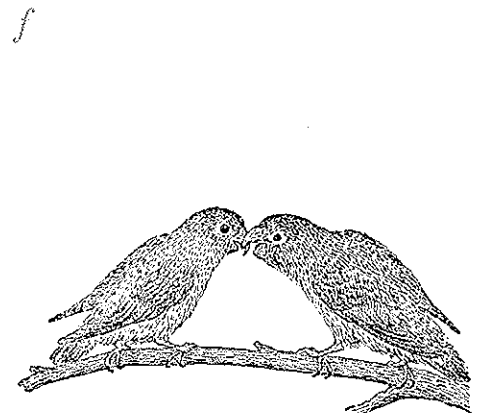
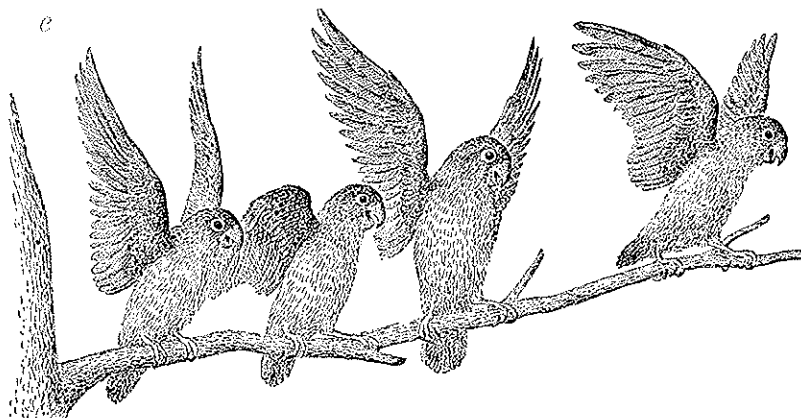
all feathers of the body (c). Short strips are used to make an unshaped nest pad (d). The young join the mother in cavity-

defense display (e). In f birds show threat and appeasement display. It usually averts combat; if it fails, the birds fight furiously.



carried several at a time in back plumage (c); long strips are used to make a well-shaped nest (d). Birds join in "mobbing" to

protect nest (e). Bill-fencing (f) has a display function. It never leads to real harm; the birds bite only their opponents' toes.



(b) are still slower and trace an even wider arc. Nest materials are carried in the bill, one piece at a time (c); twigs as well

as strips of bark and leaf are used. This permits construction of an elaborate covered nest, entered through a tunnel (d).

used as often as the other. Finally, as in the case of squeak-twittering, which is often performed at the same time as displacement scratching among these species, the display occurs even when the female does not seem to be thwarting her mate.

All species engage in courtship feeding: the transfer of regurgitated food from one member of the pair to the other. In the three primitive species the female often offers food to her mate. This behavior has never been observed among the peach-faced and white-eye-ringed forms; here courtship feeding seems exclusively a male prerogative.

One can also discern an evolutionary progression in the manner in which the birds carry out the rather convulsive bobbing of the head associated with the act of regurgitation that immediately precedes courtship feeding. Among the primitive species these head-bobbings describe a small arc, are rapid and numerous and are usually followed by rather prolonged bill contacts while the food is being transferred. In the other forms the head-bobbings are slower, fewer in

number and trace a wider arc; the bill contacts usually last for only a short time. Moreover, among the more recently evolved forms head-bobbing has become pure display; it is no longer accompanied by the feeding of the female. Unlike the females of the primitive lovebird species, which have no special display activity during courtship feeding, the females of the more recently evolved species play a distinctly ritualized role. They ruffle their plumage throughout the entire proceeding.

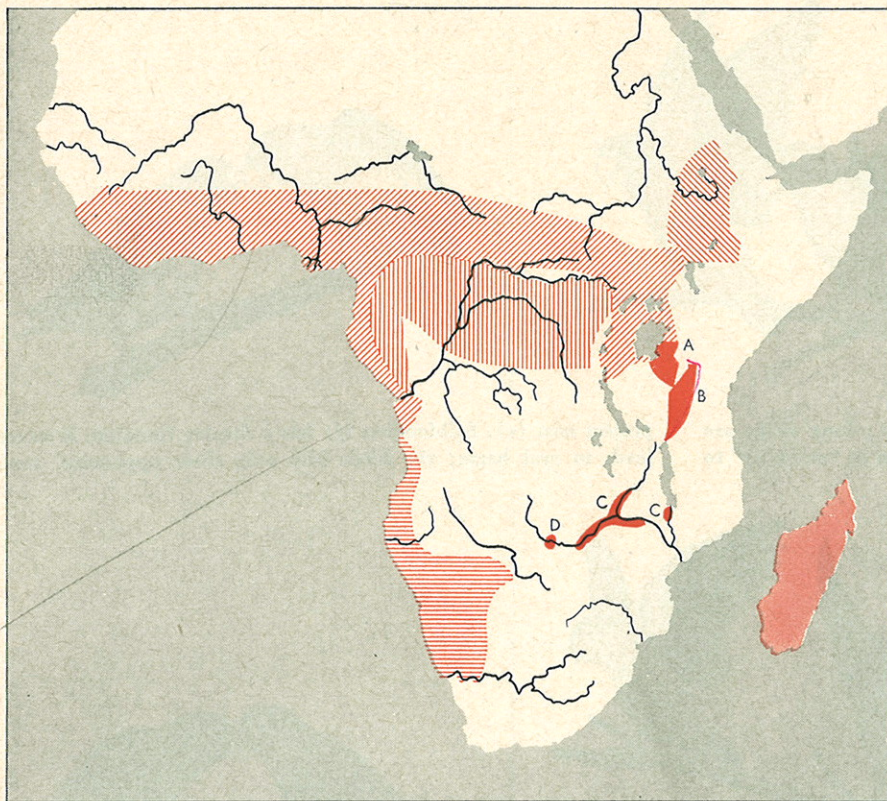
Females of all species indicate their fluctuating readiness to copulate by subtle adjustments of their plumage, particularly the feathers of the head. The more the female fluffs, the readier she is, and the more the male is encouraged. Finally she will solicit copulation by leaning forward and raising her head and tail. Females of the primitive species do not fluff their plumage during copulation; females of the more recently evolved species do. This is undoubtedly related to the morphological differences among the lovebirds. Since males and females of the more recently evolved species have the same coloring and patterning, the

females must reinforce their mates' recognition of them, both in courtship and in copulation, by some behavioral means.

Although the forms of precopulatory behavior seem to be innate among all species, learning appears to play a major role in producing the changes that occur as the members of a pair become more familiar with each other. Newly formed pairs are rather awkward. The males make many mistakes and are frequently threatened and thwarted by their mates. After they have had a few broods, however, and have acquired experience, they become more expert and tend more and more to perform the right activity at the right time. As a result the female responds with aggression far less often, and the male engages more rarely in the displays that are associated with frustration and thwarting. Squeak-twittering and displacement scratching in particular become less frequent. Switch-sidling is still performed, but with a perceptibly diminished intensity. Altogether precopulatory bouts become less protracted. In spite of the male's reduced activity, the female seems to become receptive fairly quickly.

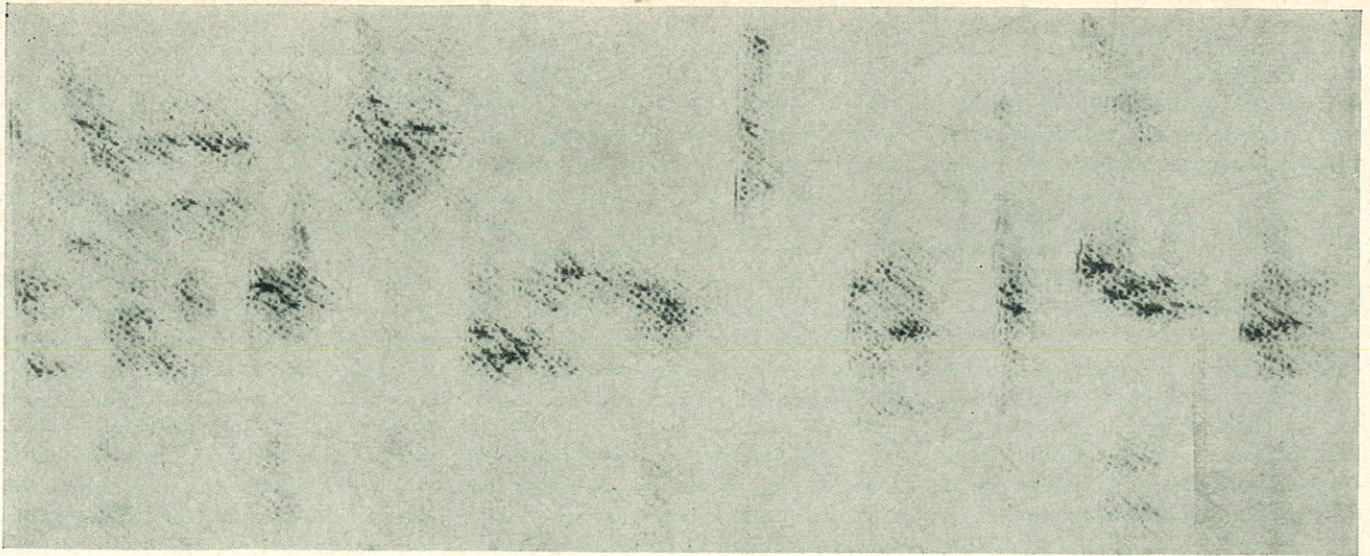
Disagreements among members of the same species are handled in quite different ways by those lovebirds that nest in pairs and those that nest colonially. Among the less social primitive species an elaborate pattern of threat and appeasement display has developed. For example, a formalized series of long, rapid strides toward an opponent signals aggression; a ruffling of the feathers, fear and the wish to escape. The loser in a bout of posturing may indicate submission by fleeing or by remaining quiet, turning its head away from its opponent and fluffing its plumage. By means of this code the birds can communicate rather exact items of information as to their readiness to attack or to flee. As a result actual fights seldom occur. When they do, however, the birds literally tear each other apart.

The peach-faced lovebird and the white-eye-ringed forms, which nest colonially, are thrown in contact with members of their own species much more often. This is undoubtedly related to the fact that they have developed a ritualized form of display fighting that goes far beyond a mere code of threat and appeasement and that replaces serious physical conflict. Display fighting among these more recently evolved species consists primarily of bill-fencing. The two birds parry and thrust with their bills and aim sharp nips at each other's toes.



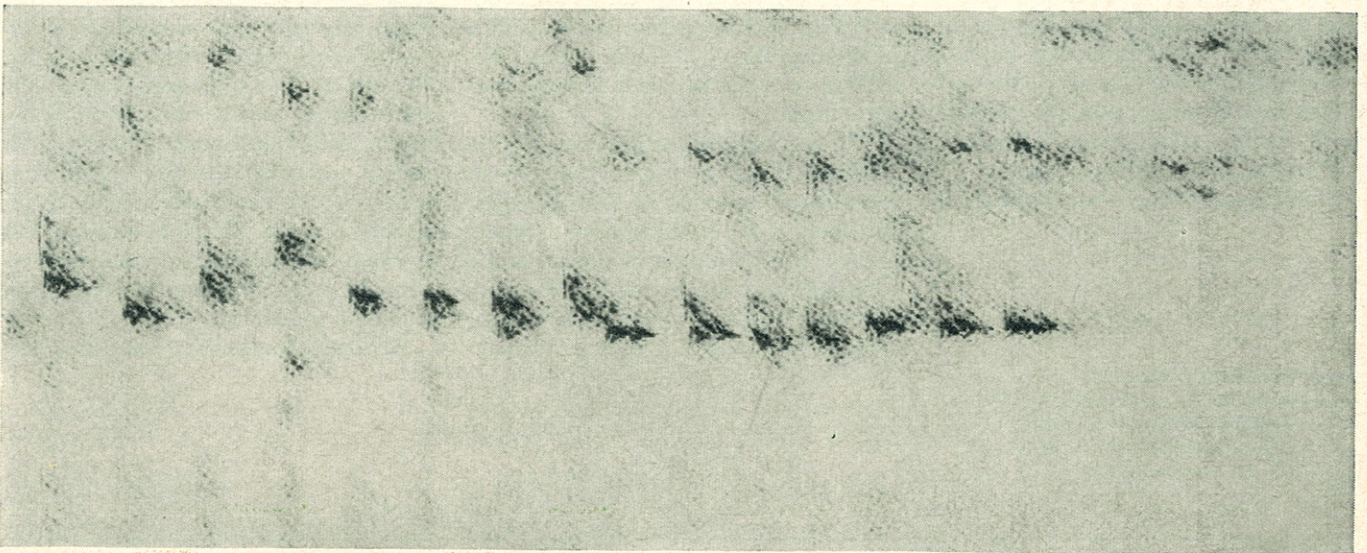
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|  MADAGASCAR LOVEBIRD |  A FISCHER'S LOVEBIRD |
|  ABYSSINIAN LOVEBIRD |  B BLACK-MASKED LOVEBIRD |
|  RED-FACED LOVEBIRD |  C NYASALAND LOVEBIRD |
|  SWINDERN'S LOVEBIRD |  D BLACK-CHEEKED LOVEBIRD |
|  PEACH-FACED LOVEBIRD | |

DISTRIBUTION OF LOVEBIRDS is shown on this map of Africa and the island of Madagascar. All nine of the lovebird species and subspecies inhabit different areas.



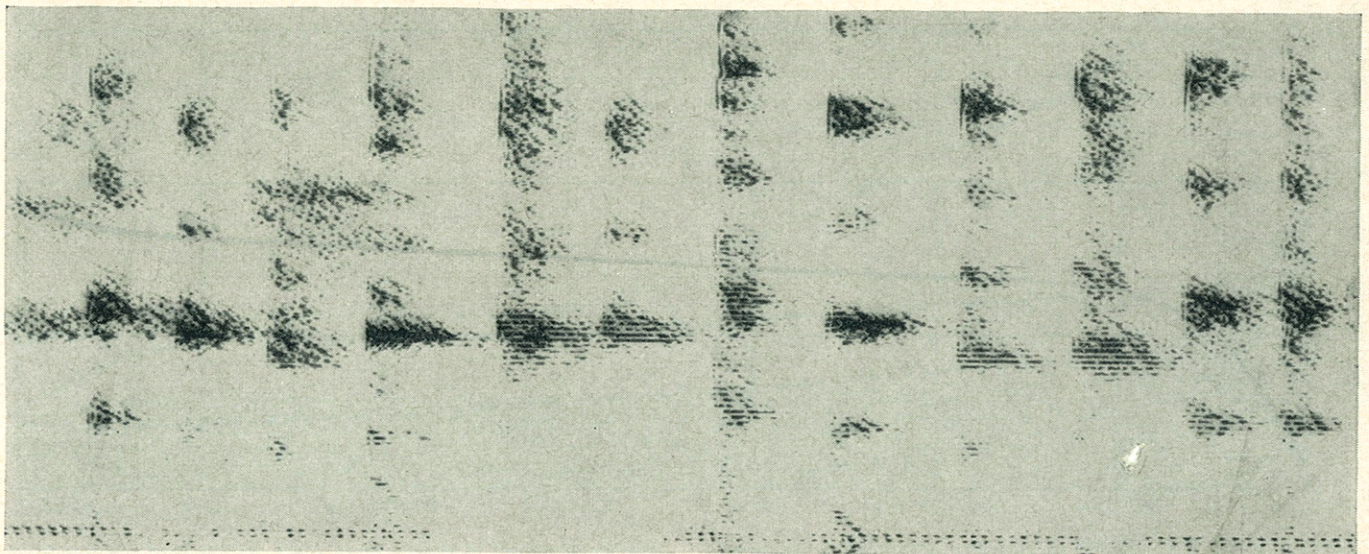
SQUEAK-TWITTERING in male Madagascar lovebird is seen on sound spectrogram. The horizontal axis represents time; the

vertical axis, frequency. Uneven distribution of spots along both axes shows an arhythmic quality and a wide variation in pitch.



SOUND SPECTROGRAM of squeak-twittering in peach-faced lovebird shows greater rhythmicity and less variation in pitch.

In Madagascar lovebird behavior is displayed only when female thwarts male. In peach-faced lovebird this is not always the case.



FURTHER EVOLUTION in squeak-twittering is seen in behavior of Nyasaland lovebird. Sounds are very rhythmic and show almost

no variation in pitch; wide vertical distribution of spots reflects the large number of harmonics contained in the monotonous note.

The toe is the only part the birds ever bite, and the inhibition against biting a member of the same species in any other place seems to be, like bill-fencing itself, an innate pattern. Though bill-fencing appears to be innate, it must be perfected by learning. The colonial nesting pattern offers young birds considerable practice with their contemporaries, and they quickly become skilled.

If lovebirds have had experience in rearing their own young, they will not rear the young of those other forms that have a natal down of a different color. On the other hand, a female that is given the egg of such a form at the time of her first egg-laying will rear the bird that emerges. Indeed, if a peach-faced lovebird has her first experience of motherhood with a newly hatched Madagascar lovebird, she will thereafter refuse to raise her own offspring. The down of the peach-faced lovebird's newly hatched young (like the down of the white-eye-ringed forms) is red, and the down of newly hatched Madagascar, Abyssinian and red-faced lovebirds is white.

Unlike most of the other members of

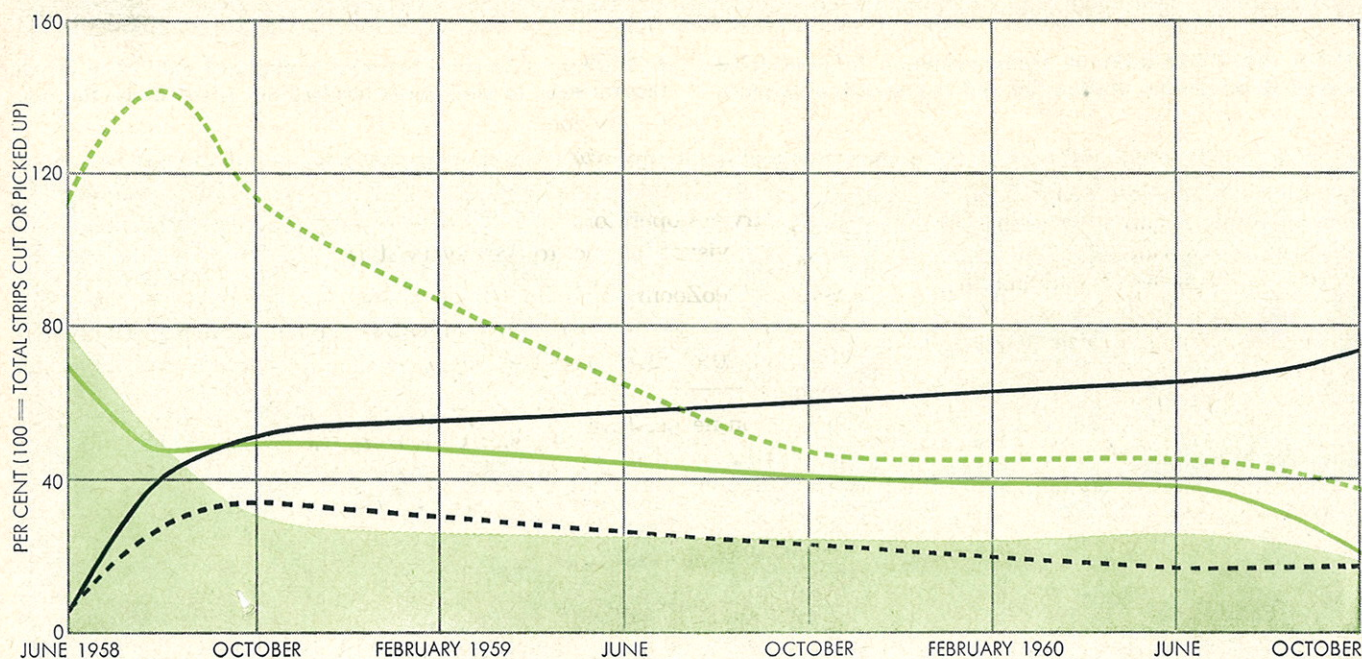
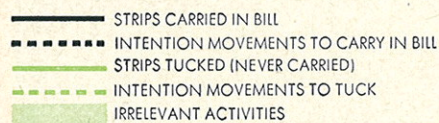
the parrot family, which simply lay their eggs in empty cavities, all lovebird species make nests. The red-faced lovebird constructs its nest in a hole it digs in the hard, earthy nests certain ants make in trees. All other species, however, make their nests in pre-existing cavities, which are usually reached through small entrances. The nests of the Madagascar lovebird, the Abyssinian lovebird and the red-faced lovebird are quite simple, consisting essentially of deposits of soft material on the cavity floor. These three species have developed an elaborate cavity-defense display. The moment an intruder appears, the female ruffles her feathers, partly spreads her wings and tail and utters a rapid series of harsh, buzzing sounds. If the intruder persists, she will suddenly compress her plumage, utter a piercing yip and lunge toward it. She does not bite, but she gives every indication of being about to do so. Her older offspring may join her at this time, ruffling their feathers and making grating sounds.

The effect of this performance is quite startling; it can even give pause to an experienced investigator! The Madagascar lovebird, the most primitive of all the species, is the quickest to engage in the cavity-defense display and is the only species we have seen carry the display through both stages. A stronger stimula-

tion is necessary before the Abyssinian lovebird engages in this behavior, and we have not seen the bird go any further than ruffling its body plumage and making the harsh, rasping sounds.

The white-eye-ringed lovebirds build rather elaborate nests, consisting of a roofed chamber at the end of a tunnel within the cavity. This fact and their strongly social nature combine to make their response to a threat to their nests different from the response of the primitive species. They have no cavity-defense displays at all. If a predator actually reaches the cavity, the birds within it will either cower or, if possible, flee through the entrance. But if the predator, encouraged by this show of fear, enters the cavity, it is likely to find that its troubles have just begun. It faces a journey down a narrow tunnel, defended at the end by a bird with a powerful and sharp bill. Moreover, a predator is seldom allowed to come close to the cavity. As soon as it is seen approaching, the entire colony engages in a form of behavior called mobbing: holding their bodies vertically, the birds beat their wings rapidly and utter loud, high-pitched squeaks. The sight and sound of a whole flock mobbing is quite impressive and probably serves to deter many would-be predators.

All female lovebirds prepare their nest



CONFLICTING PATTERNS of carrying nest-building materials are inherited by a hybrid lovebird, produced by mating the peach-faced and Fischer's lovebirds. The hybrid's behavior is charted

here for a period of almost three years. As the bird progressively learns to carry nest materials as Fischer's lovebird does, the number of irrelevant movements and inappropriate activities decreases.

materials in much the same way: by punching a series of closely spaced holes in some pliable material such as paper, bark or leaf. The material is held between the upper and lower portions of the bill, which then works like a train conductor's ticket punch. The pieces cut out in this way vary in size and shape among the various lovebirds. So do the forms of behavior that now ensue.

The three primitive species and the peach-faced lovebird tuck the pieces they have cut into the feathers of their bodies and fly off with them. The Madagascar lovebird, the Abyssinian lovebird and the red-faced lovebird use very small bits of material. (This is one of the reasons their nests are so unstructured.) The entire plumage of the bird is erected as it inserts the six to eight bits of material in place and remains erect during the whole operation. The peach-faced lovebird cuts strips that are considerably longer. (This permits the more elaborate structuring of its cuplike nest.) Indeed, the strips are so long that they can be carried only in the feathers of the lower back. These are the feathers erected when the strips are tucked in, and the feathers are compressed after each strip is inserted. The peach-faced lovebird loses about half of its cargo before it gets to its nest site; either pieces fall out while others are being cut or tucked in, or they fall out while the bird is flying. The lovebirds that use smaller bits of nest material are more successful in carrying them.

Carrying nest material in the feathers is unique to these birds and the related hanging parakeets. What is more, speculation about its origin must begin with the fact that no other parrots (with one unrelated exception) build nests at all. It is almost certain that this behavior arose from fortuitous occurrences associated with two characteristic parrot activities: chewing on bits of wood, bark and leaf to keep the bill sharp and properly worn down; and preening, which serves to keep the plumage clean and properly arranged. Some parrots that do not build nests will accidentally leave bits of the material in their feathers when they proceed directly from chewing to preening. Such oversights almost certainly initiated the evolution of the habit of carrying nest materials in the feathers.

The four white-eye-ringed forms are completely emancipated from this ancestral pattern. Fischer's lovebird, the black-masked lovebird, the Nyasaland lovebird and the black-checked lovebird all carry their nest materials as do most birds—in



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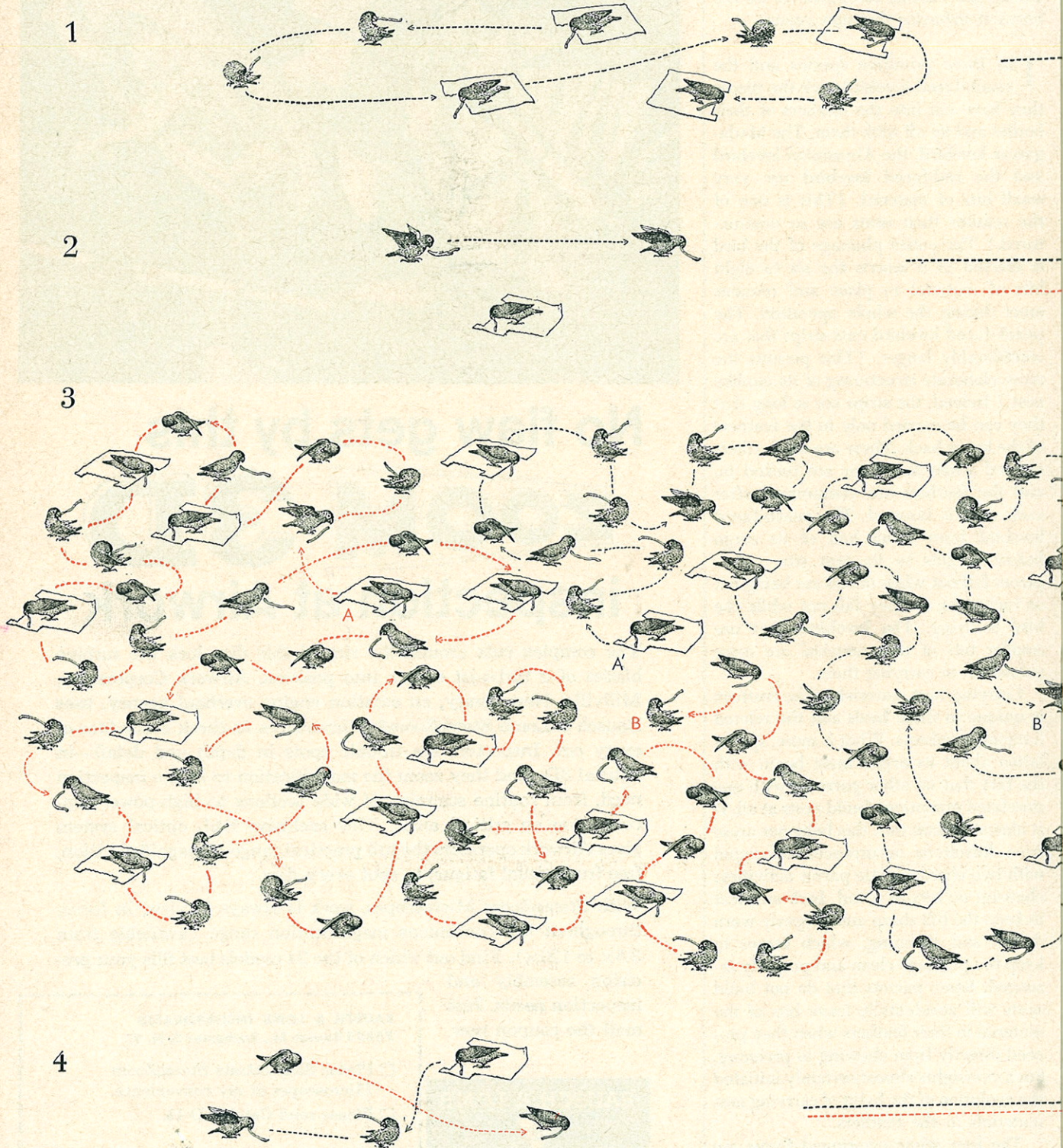
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their bills. They lose little material in the process of carrying, and they pick up twigs in addition to cutting strips of pliable material. With these materials, they can build their characteristically elaborate nests.

Although the peach-faced lovebird

normally carries its nest-building material in its feathers, on about 3 per cent of its trips it carries material in its bill. This peculiarity suggested an experiment. We mated the peach-faced lovebird with Fischer's lovebird (the birds hybridize readily in captivity) to see

what behavior would show up in the hybrids. In confirmation of the thesis that patterns of carrying nest materials are primarily innate, the hybrid displays a conflict in behavior between the tendency to carry material in its feathers (inherited from the peach-faced love-

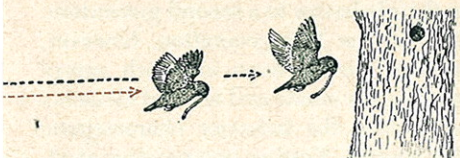
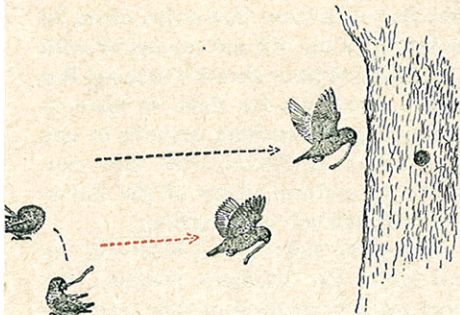
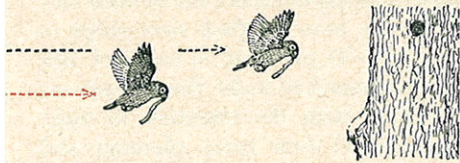
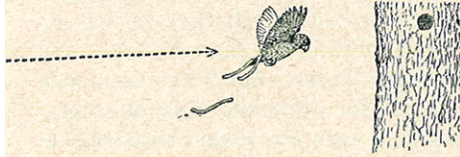


HYBRID LOVEBIRD inherits patterns for two different ways of carrying nest-building materials. From the peach-faced lovebird (1) it inherits patterns for carrying strips several at a time, in feathers. From Fischer's lovebird (2) it inherits patterns for carrying strips one at a time, in the bill. When the hybrid first begins

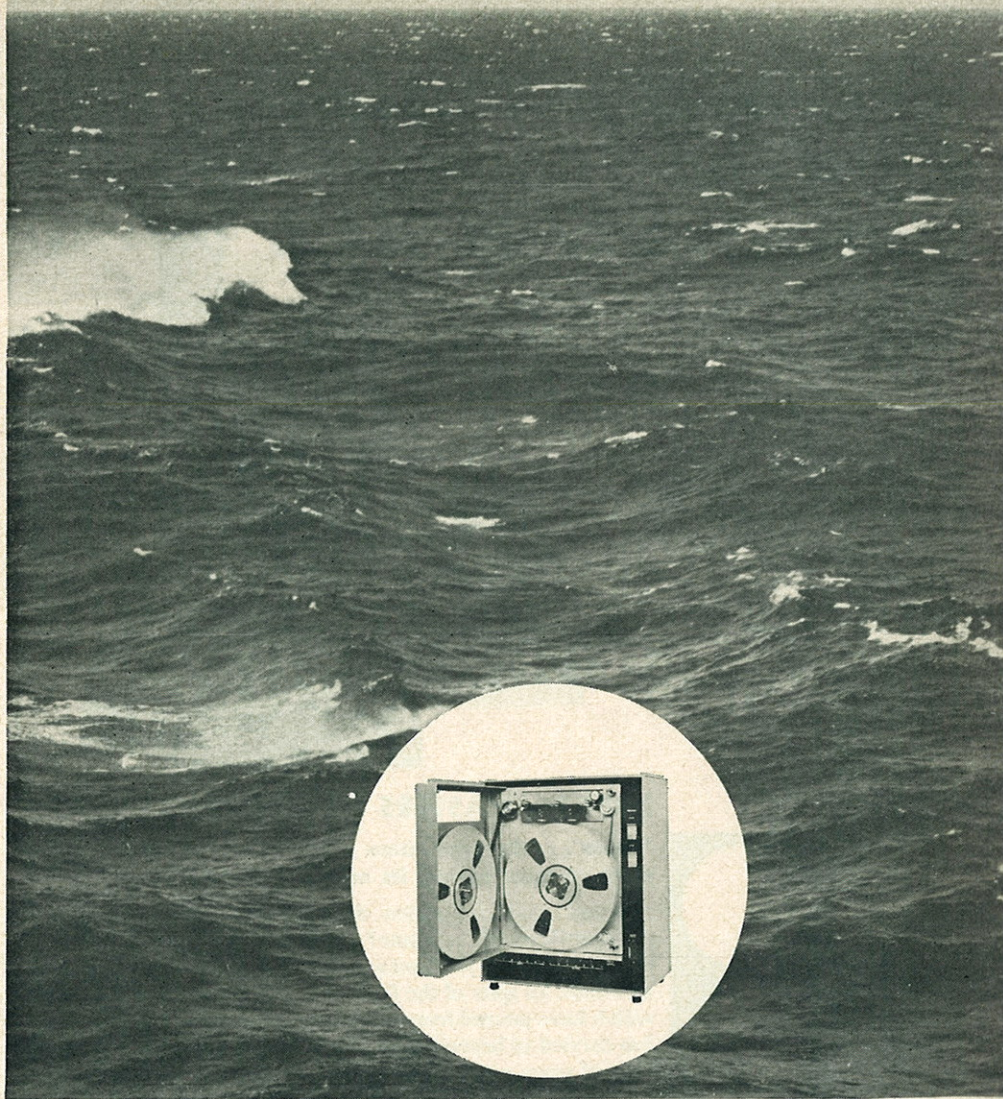
to build a nest (3), it acts completely confused. Colored lines from A to B and black lines from A' to B' indicate the number of activities necessary for it to get two strips to the nest site, a feat achieved only when the strips are carried singly, in the bill. It takes three years before the bird perfects its bill-carrying behavior (4),

bird) and the tendency to carry material in its bill (inherited from Fischer's love-bird).

When our hybrids first began to build their nests, they acted as though they were completely confused. They had no difficulty in cutting strips, but they could



and even then it makes efforts to tuck its nest materials in its feathers. As the bird gains experience it becomes more and more proficient in this activity, which, however, never results in successful carrying.



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