PROTECTIVE COLORATION IN THE AMERICAN SPARROW HAWK

BY WILLIAM M. CLAY

THE adaptive features of the color pattern of the Sparrow Hawk (*Falco sparverius*) are remarkable enough to warrant discussion. Since captive individuals have commonly been available for close and prolonged observation, it is surprising that attention appears not to have been directed at least to the most notable feature, a pair of ocelli or "false eyes" on the back of the head and neck. In study skins, however, these ocelli often are obscured by increased overlap of the feathers in the straightened and somewhat shortened neck. Some well-known paintings show the ocelli and other color-pattern features described below (see Fuertes *in* Eaton, 1914, pl. 52; Brooks *in* Roberts, 1932, pl. 19, and *in* Dawson, 1923:1640).

The Sparrow Hawk plumage illustrates the principles of countershading, disruptive coloration, and deflective or parasematic coloration. Furthermore, there is the possibility, or even likelihood, that some of the markings may be useful in intraspecific or social control, as in sex recognition or in territorial defense.

Countershading (obliterative shading) is so common among birds that it merits but brief mention here. The principle was alluded to by Poulton (1890:37–38) in describing the resemblance between a butterfly (*Apatura iris*) pupa and a leaf, but the concept generally is associated with A. H. Thayer (1896a, 1896b, 1898) by whom it was more fully developed. Thayer's statement of the principle follows: "The newly-discovered law may be stated thus: Animals are painted by nature darkest on those parts which tend to be most lighted by the sky's light, and vice versa" (1896a:124 and 1898: 477). The principle is discussed further by G. H. Thayer (1909:25) and by Cott (1940:35–46). It is an optical or psychological law, that recognition of an object is hindered when the pigmentation of the more brightly illuminated (upper) surface is so intensified in relation to the shaded (lower) surface that the two appear of equal density to an observer. Thus the effect of relief is destroyed and the object appears as a single plane. When the Sparrow Hawk is observed from a moderate distance its lesser markings, such as the streaks of the lower side, are not discernible and the general effect is that described above.

The second principle, that of disruptive coloration, is also common among birds, fishes, insects, and various other animals. It is discussed by G. H. Thayer (*op. cit.*:77) under the terms "secant" and "ruptive," and by Cott (*op. cit.*:47) who used the term "disruptive." This principle, commonly employed in camouflage, is that perception of the true outline or form of an

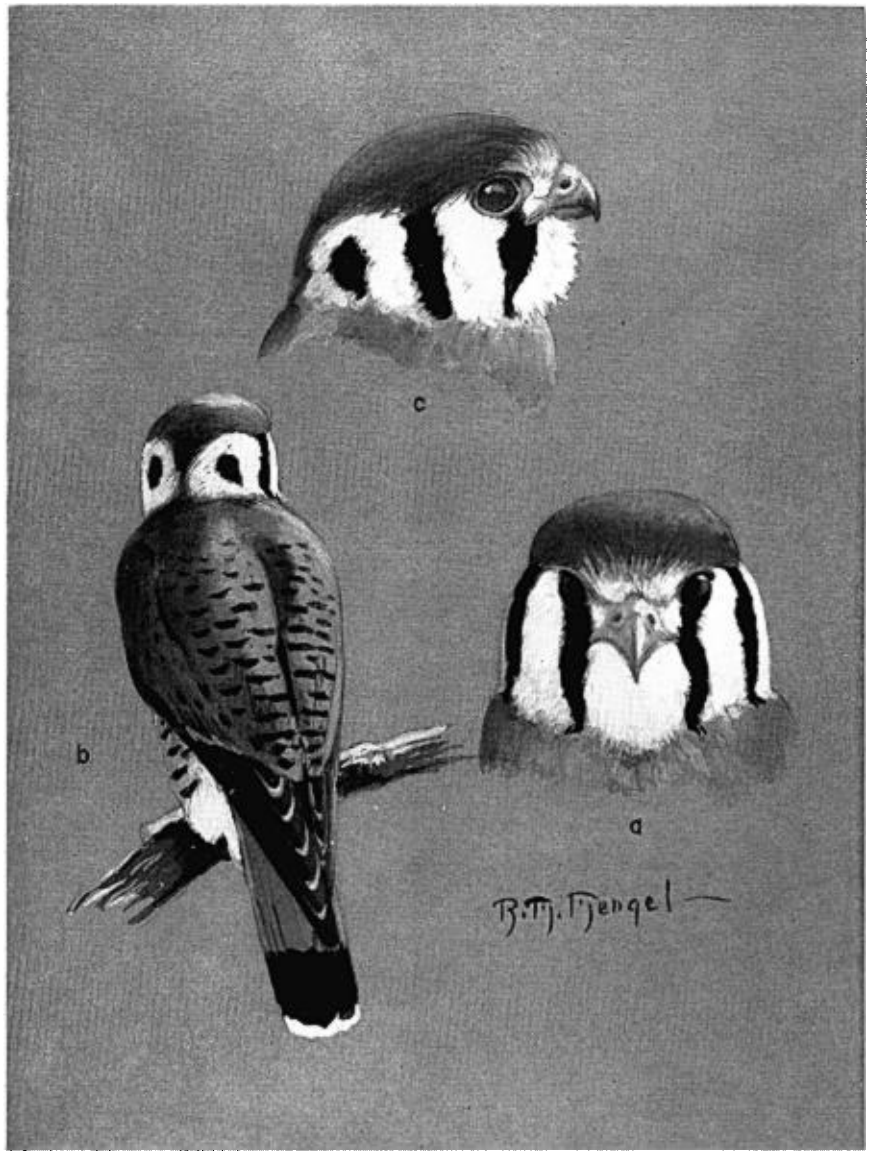

FIG. 1. Deflective and disruptive patterns in the American Sparrow Hawk (*Falco sparverius*). The features mentioned in text have been emphasized intentionally by the illustrator.

object is hindered by the presence of conspicuous markings which, although readily visible, bear no likeness to the true shape of the object. In some instances the eye may be concealed by a prominent stripe crossing it. One of the vertical bars on the Sparrow Hawk's head is effective in this way (Fig. 1a), illustrating disruptive coloration in the violent form designated by Cott (*op. cit.*: 51) as "maximum disruptive contrast." This type of concealment of the eye is common among predatory birds and mammals (G. H. Thayer, *op. cit.*: 81).

Deflective or parasematic coloration, the third and most remarkable type displayed by the Sparrow Hawk, was described by Poulton (*op. cit.*:207–208), who used as an example a hair-streak butterfly (*Thecla*) which misrepresents its posture by false eyes and antennae at the posterior end. Cott (*op. cit.*: 372) defined deflective coloration as "characters which misdirect the attack of enemies by misrepresenting the posture of their prey," and as patterns which "produce the impression of a head at the wrong end."

The orientation of the Sparrow Hawk's head is misrepresented by markings which produce the likeness of a face on the rear of the head, or upon each side of the head, according to the position of the observer, while the true face is obscured by the disruptive bars noted above. To the rear the bird presents an owlish "face" consisting of a pair of large "eyes" or ocelli with buffy-rufous irises and black pupils, between which is a slate-colored "beak" (Fig. 1b). In the first winter plumage the feathers comprising the "iris" are more nearly white than in the adult and the "eyes" are even more realistic, a condition which may be related to the greater incompetence during the youthful and inexperienced phase of life.

Fig. 1c shows the "eyes" of each lateral face to consist of one of the false "eyes" described above and the vertical bar which runs through one true eye. The bar, curiously, looks more eye-like from a lateral position than from the front. The "beak" of the lateral face consists of another black vertical bar in the auricular region. This "face" is highly deceptive from a postero-lateral point of observation and therefore to an observer located slightly behind the bird's field of sharp vision (*vide infra*). (Cover the true beak in Allan Brooks' painting in "The Birds of Minnesota," Roberts, *loc. cit.*, or that in Fig. 1c of the present paper, for the maximum deceptive effect.)

The position of the eyes in hawks is more frontal than in most other non-strigiform birds. This lessens the total field of vision but increases the area of binocularity. In accordance with this condition, the retina of hawks has developed a second point of acute vision, a temporal fovea (Walls, 1942: 308–309, Figs. 114 and 115), which serves the binocular or anterior field, while acute vision in the monocular or antero-lateral field is obtained by the central fovea. While binocularity doubtless is advantageous, it has been ob-

tained at the sacrifice of vision in postero-lateral directions. These are clearly the axes along which the deceptive faces are presented.

Mention may be made here of the possible effect of head-bobbing, a performance which the Sparrow Hawk frequently enacts, and which would seem to counteract the effects of concealing coloration. Grinnell (1921) pointed out that stationary objects, unlike those in motion, are more readily located by an actively-moving than by a passive searcher. Calling this mechanism "the principle of rapid peering," he divided birds into two groups according to the extent of their activity when seeking food. Head-bobbing, "teetering," or other movements which alter the location of the eyes, generally help to separate planes and to improve distance judgment, as may be readily tested for both monocular and binocular vision, and it is reasonable to assume that these properties are useful to the Sparrow Hawk. While motions of the body would appear to counteract the general effects of concealing coloration, it should be noted, firstly, that deflective coloration is not essentially cryptic in function, and, secondly, that head-bobbing by the Sparrow Hawk accentuates the conspicuousness of the ocelli and enhances their resemblance to the eyes of an actively peering owl.

The role of deflective coloration in the ecology of the Sparrow Hawk must remain largely speculative until more data are obtained. The presumed function is to "mislead" an observer with respect to the true orientation of the animal. It has been shown repeatedly that birds and many other animals respond to only one or a few attributes or "sign stimuli" in some other individual, with apparent disregard of all other attributes (Tinbergen, 1948). This is indicated in the case reported by Noble (1936) of a male Flicker (*Colaptes auratus*) attacking his own mate after an artificial male-resembling "moustache" of black feathers had been glued to her head, only to accept her again after its removal. We may postulate that the false eyes of the Sparrow Hawk may induce, in some animals, the reaction for which true eyes are the usual stimulus, while the true eyes of this bird, by their concealment, may fail to evoke a response.

It is conceivable that this stimulus-response could be of benefit in capturing food and escaping attack. With respect to the former, it should be noted that the food of the Sparrow Hawk consists partly of animals of poor visual acuity. Myopic grasshoppers and small rodents probably lack the ability and the opportunity to make discriminating observations upon a plunging Sparrow Hawk! However, this sort of deception may possibly be effective in the capture of small birds.

The Sparrow Hawk has not been reported as a major item in the diet of any predator. In fact, the predatory status of this bird so limits its own abundance that for any other animal to depend heavily upon it for food would

be ecologically unsound. However, some hawks and owls do take the Sparrow Hawk at least occasionally. Bent (as cited after each species following) lists the Sparrow Hawk in the food of the Duck Hawk, *Falco peregrinus* (1938:54, 60), Red-shouldered Hawk, *Buteo lineatus* (1937:191), and Screech Owl, *Otus asio* (1938:251). Cooper's (*Accipiter cooperii*) and Sharp-shinned (*A. striatus*) hawks are reported to include "small hawks" in their food (Bent, 1937:118, 133). The Great Horned Owl (*Bubo virginianus*) probably includes Sparrow Hawks in its varied diet. Thus the Sparrow Hawk is subject to predation which, in view of its own limited numbers, may be ecologically significant.

Persecution by non-predaceous birds may also be important to this small falcon. The entire tribe of raptorial birds is subject to such harrassment and, while it may be doubted that the larger hawks and owls are seriously menaced thereby, the small Sparrow Hawk may be more vulnerable. I have watched numerous diving attacks by Robins (*Turdus migratorius*) and Blue Jays (*Cyanocitta cristata*) upon a captive Sparrow Hawk perched on a low post. Not once have I been certain that contact actually occurred, although many times the swooping bird must have missed by less than an inch. Usually the hawk turned toward the attacker and ducked at the approach. It would seem possible that in a surprise approach from the rear the instinctive behavior of the attacker would not allow actual contact with what may appear to be an owl in defensive posture.

The Sparrow Hawk is most vulnerable when it has taken another bird and is having to cope with its struggles, particularly if the victim is a nestling whose parents are aroused to fury. If the victim is large, its struggles may force the hawk to the ground in order to make the kill, which it usually does by biting the occipital region. Perhaps it is significant that in the killing and feeding posture, with bowed head, the ocelli are brought into fullest display.

The evolution of such a complex pattern of coloration by chance alone, without recourse to utility, would appear to be highly improbable. The modern genetic interpretation of evolutionary process favors the assumption that either the color pattern, or some characteristic with which it is linked, confers upon its possessors a greater ability to leave reproducing descendants. Unfortunately, it is not easy to devise experiments to test theories on coloration as an ecological factor. We do know, however, that the average or ecological longevity of animals in the wild state is much less than their potential longevity. Most wild animals die young, from starvation, disease, predation, or other causes, and many that survive leave few or no reproducing offspring. While coloration is not a direct factor in life or death, it may have a bearing upon the possessor's ability to obtain food or to escape enemies, and it may be of service in intraspecific behavior. The very multiplicity of the factors

which affect the abundance of a vertebrate species increases the likelihood that coloration is important. To paraphrase a statement by Tinbergen (1952: 5), the duty of students of coloration is to attempt to explain coloration rather than to assume that it cannot be explained.

Summary

The color pattern of the Sparrow Hawk (*Falco sparverius*) embodies principles of countershading, disruptive coloration resulting in concealment of the eye, and deflective coloration, *i. e.*, presentation of a false "face" in the rear and another in a postero-lateral position. These "misrepresentations" cover the bird's blind area, which is greater in hawks than in most birds, and conceivably are of service in deceiving prey and/or enemies.

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