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Background-Color Acclimation of Brook Trout for Crypsis Reduces Risk of Predation by Hooded Mergansers *Lophodytes cucullatus*

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Abstract.—In a laboratory study, fry of brook trout *Salvelinus fontinalis* experienced less predation by hooded mergansers if they were previously acclimated for 11–12 weeks to tanks having the same background color as the predation arena. Color acclimation produced morphological color changes that rendered the fish more cryptic to the birds. Overall, cryptic brook trout accounted for 37% of predation, whereas unmatched fish experienced 63% of the total predation mortality. Implications of this study for salmonid management are that reduced predation of transplanted fish will occur if they are acclimated in hatcheries to backgrounds having similar coloration to the gravel in the habitat where they will be transplanted.

Natural selection has resulted in what has been described as an evolutionary arms race between predators and their prey (Edmunds 1974; Krebs and Davies 1981; Taylor 1984). Predators' adaptations increase their likelihood of successfully capturing prey and thereby enable them to forage optimally (Krebs 1978). Investigations have shown that a variety of characteristics, such as prey size and visibility (Brooks and Dodson 1968; Zaret and Kerfoot 1975), are used by predators to distinguish profitable from unprofitable prey. All predators are obligated to search for, attack, capture, and eat their prey (Holling 1959), and the length of time spent on each of these components of the predation process is important in determining prey profitability. Prey characteristics that reduce the efficiency of any of these foraging steps decrease profitability. Taylor (1984) suggested that, generally, prey will have an advantage in the evolutionary arms race because they have more at stake than do predators ("life–dinner principle").

Stocking salmonids is a common management tool, yet associated mortality can be high (Webster and Flick 1981) and inflates program costs. Few causes of stocking mortality have been identified (Webster and Flick 1981), and although predation has been mentioned (Schuck 1948), few authors have considered this as an explanation for transplant failure. Predator activity increases following stocking of juvenile Atlantic salmon *Salmo salar* (see Elson 1962; Mills 1964; Wood 1987). Predators may be able to recognize transplanted fish more easily than they can detect resident fish adapted to the color of the stream substrate.

Defenses from predation can be classified as primary, which interfere with the search time and make location of prey unlikely, or secondary, which operate during and following the attack (Edmunds 1974). Prey coloration may be important for predators that visually locate and track prey in the search and capture phases (Edmunds 1974). Palatable prey that contrast sharply with their backgrounds experience poorer survival than more cryptic morphs (Kettlewell 1955; Cott 1957; Edmunds 1974). Thus, prey color can be an important factor in primary defense, for which prey visibility determines the likelihood that an individual will be detected and captured (Brooks and Dodson 1968; Zaret and Kerfoot 1975). Sumner (1934, 1935a, 1935b) demonstrated that coloration influenced the probability of fish being captured by a variety of predators. He showed that mosquitofish *Gambusia affinis* were approximately twice as likely to be consumed by birds or fish if they contrasted with the background of the predation arena than if they were color-matched.

Donnelly and Dill (1984) regarded crypsis, the morphological and behavioral resemblance of organisms to their backgrounds, as the primary defense used by juvenile salmonids to avoid predator visual detection in their natal streams. Most salmonid populations exist as discrete stocks native to a particular stream or nursery lake (Ricker 1972; Riddell and Leggett 1981; Riddell et al. 1981). Species may migrate to the sea directly after hatching, rear in the natal stream for a time and then go to sea, or remain landlocked for life. Homing of spawning individuals to their natal stream limits gene flow between different stocks (Ricker 1972). Predatory pressure should result in selection toward cryptic color patterns that are more suitable for the natal stream than others (Donnelly and Dill 1984).

Several elements are involved in the stream coloration of juvenile salmonids (Nikolsky 1963). Countershading, coloration that is darker dorsally than ventrally, is important for crypsis (Thayer 1909). Parr marks differ sufficiently between species to be used for identification (Scott and Crossman 1973). Donnelly and Dill (1984) showed that the silvery sides of coho salmon *Oncorhynchus kisutch* reflect the coloration of the substrate in both wavelength and intensity, whereas the parr marks absorb light reflected from the substrate and break up the outline of the fish. The number and length of coho salmon parr marks vary among four different southwestern British Columbia streams (Donnelly 1985). Taylor and Larkin (1986) reported similar variability for chinook salmon *Oncorhynchus tshawytscha* in two southwestern British Columbia streams. Salmonid dorsal coloration was uniform for a given stream, but varied between streams. Donnelly and Dill (1984) predicted that variability in background coloration between streams and genetic color differences between stocks could result in increased predator detection if salmonids are transplanted.

Environmentally induced color changes occur if hatchery or wild fish are switched from one background color to another. Many fishes are capable of both physiological (short-term) and morphological (long-term) color changes (Fujii 1969). Salmonid juveniles placed on a white background lighten, whereas if transferred to a black background, they become uniformly darker. These physiological color changes begin almost immediately; the total response usually occurs in less than 30 min (Parker 1948; Fujii 1969). More long-term or morphological color changes occur as well (Neill 1940; Fujii 1969). Salmonids held for an extended period of time over a colored background color-acclimate due to changes in melanin production. Fading or intensification of other pigments also can occur depending on the background color. Juvenile Atlantic salmon held over blue backgrounds have enhanced blue coloration on the dorsum. Thus, expression of secondary pigments contained in xanthophores and erythrophores are influenced by the background color. When color-acclimated fish are transferred to a different background color, remnants of the previous color are retained for several days to weeks, so using a hatchery tank-truck for fish transport would not alter the color of color-acclimated fish permanently.

Our objective was to determine whether the color of current salmonid rearing facilities might contribute to fish vulnerability to predation. We tested this hypothesis by color-acclimating brook trout in either tan or brown tanks and then exposing them to predation by hooded mergansers in arenas where the color matched or differed from the acclimation tank.

Methods

Alevins of brook trout *Salvelinus fontinalis* were obtained from Baldwin Mills Fish Hatchery near Montreal. Brook trout are extensively stocked in the Province of Quebec, but because they are native and nonmigratory we predicted them to be less plastic in their capacity to change color than are anadromous species. The brook trout were kept in a blue-bottomed tank for 2 d with temperature controlled at 12°C, then randomly split into equal groups and transferred to four plastic 90-L tanks for color acclimation. They were fed Zeigler trout starter pellets. Fungal and bacterial infections were controlled by circulating water past germicidal (ultraviolet) lamps. Water flow was powered by Fluval 203 cannister-type filters.

The sides of two of the acclimation tanks were painted brown (Flecto CP 107; walnut) and had 5–30-mm brick (red-brown) fragments as substrate; the other two tanks were painted tan (Flecto CP 120; almond) and had 5–30-mm white marble chips as the substrate. Gravel substrate was used to mimic a natural habitat for brook trout as well as to give fish some experience with a natural substrate. Undergravel filters were used to keep the tanks clean of food and wastes. Gray fiberglass window screen was stretched over the tops of the tanks to prevent fish from leaping out. Overhead illumination of the tanks was provided by two single-tube 40-W fluorescent lights having 90% of the spectrum (color-rendering index) of natural sunlight (Chroma 50, General Electric).

Commercial refrigerated 900-L tanks for trout and lobster (C. English Co., Montreal) were used to provide cold water for fish in the plastic tanks. Cold water was supplied to the tanks through a Fluval 403 power filter and an overhead spraybar delivery system. The thermostat of the refrigerated tanks was set at 12°C. However, the water temperature rose as high as 18°C during extended periods of extremely hot summer weather. Fluval 203 filters and diatom filters were used for regular cleaning and maintenance of the refrigerated and plastic tanks.

The brook trout were acclimated to the colored backgrounds for 11–12 weeks; however, a power failure resulted in approximately 80% mortality of the acclimated fish. This left 90 brook trout that had been acclimated to each color for 11 weeks when the predation experiments began. Predation trials were carried out in two fiberglass stream channels with dimensions 308 × 64 cm and a depth of 38 cm. The stream channels were walled in on three sides by 240-cm-tall wooden panels covered by 0.15-mm-thick black polyethylene. The fourth side had hardware cloth to a height of 90 cm to leave viewing space through which the experiments were videotaped. Each channel was painted either brown or tan, and contained gravel substrate with either brick or marble chips, as in the acclimation tanks. Overhead illumination was provided by two double-tube fluorescent lights (Chroma 50) suspended at a height of 1.6 m over both ends of the channels. Water flow was generated in the channels by recirculating water with a 4,000-L/h sump pump. A 3.75-cm spraybar across the width of the head end of the experimental channel was used to distribute the flow. The two channels were joined at one end by a 7.5-cm-diameter ABS pipe. This allowed water to move from one channel to the other, but screens prevented the movement of fish from one channel to the other. Refrigerated water was provided to maintain the channels at 12°C during the experiments.

Mergansers are well-documented predators of salmonids (White 1936; Sayler and Lagler 1940; Huntsman 1941; Elson 1962; Wood 1987). We used hooded mergansers because of previous experience in using these birds as predators (Donnelly 1985) and their smaller appetites compared with those of other species. An unrelated pair of hooded mergansers was obtained from Kortwright Waterfowl Park in Guelph, Ontario, 1 week before the beginning of the experiments. The prey-naive birds were kept in an 8 × 8-m room having a sloped floor and overflow drains that allowed a portion of the floor to be flooded to a depth of 20 cm. The stream channels were housed in the same room with the mergansers. Water was supplied by drainage hoses from the channels to the sloped floor. The birds were fed live brook trout daily and high-protein dog food (Purina Puppy Chow) ad libitum.

Brook trout were given to the birds in the first week to accustom them to fish prey before the beginning of the experiments. At first the birds seemed disinterested in the fish that were released into the water of the sloped floor of the holding room. However, over a period of 3–4 d, they learned to catch and eat the fish. When the birds became adept at fish-catching, a practice trial was run to test the experimental protocol. In the practice trial, birds were deprived of food for 5 h before the start of the experiment. One-half of the 20 brook trout released into the brown stream channel were eaten within the first hour. Subsequently, the birds were deprived of food for a standard 5-h period before each 1-h predation trial. Fish used in predation experiments were pelvic fin-clipped to identify their color-acclimation group.

Ten brook trout acclimated to each color and of similar size were introduced into either the brown or tan channel predation arena. The pair of birds was then introduced into the channel and given 1 h to prey freely upon the fish. After 1 h, the birds were removed and the fish were counted and sorted according to their color-acclimation group. Eight trials were conducted: four in the tan channel, and four in the brown. Arena color was alternated between trials, and only predator-naive fish were used for all eight trials.

To determine if the acclimation color was affecting predation, we divided the total number of color-mismatched fish eaten by the total number of matched fish eaten in the experiment to yield a protection ratio similar to Sumner's. If predation on both groups was equal, the ratio calculated would be 1. Thus, any number greater than 1 indicates protection via crypsis. One-tailed chi-square tests were used to determine significant differences between numbers of matched and unmatched fish eaten.

Results

At the time of the predation experiments, the two groups of fish differed markedly in their coloration. The tan-acclimated trout had light dorsal coloration, nearly indistinguishable parr marks, and a few indistinct xanthophores and erythrophores. The dorsa of brown-acclimated trout were dark brown, and these fish had strong parr marks and highly visible erythrophores, with a few faded xanthophores.

The total number of fish eaten by the birds in the eight predation trials was not significantly different between the brown and tan channels (χ^2 = 1.2). An average of 8.38 fish was eaten per trial, and a total of 67 fish was eaten (Figure 1). Of the fish eaten in the four trials conducted in the brown channel (N = 29), 19 (66%) were tan-acclimated, and 10 (34%) were brown-acclimated (Table 1). This yielded a protection ratio of 1.9, almost 2:1. The ratio of color-mismatched fish to matching fish eaten in the tan channel was smaller. Of 38 fish eaten, 23 (62%) were brown-acclimated and 15 (38%) were tan-acclimated, yielding a protection ratio of 1.53. The chi-square value for the

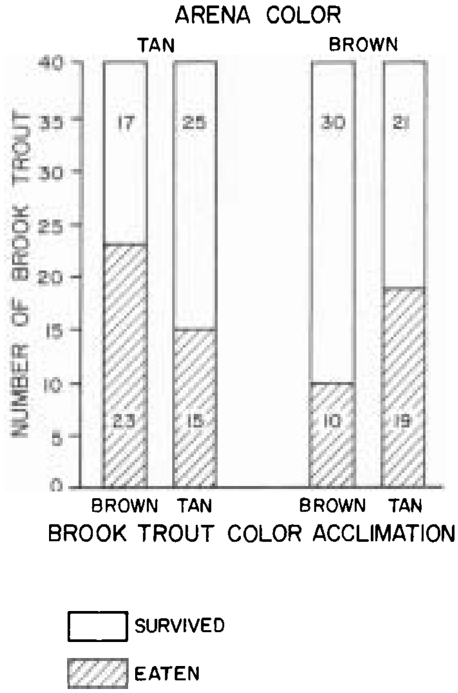

FIGURE 1.—Hooded merganser predation on brook trout in laboratory trials for different color backgrounds. Differences in survival were significant between tan- and brown-acclimated fish for either tan ($P < 0.10$), or brown ($P < 0.05$) backgrounds, and for both backgrounds pooled ($P < 0.025$).

predation trials in the brown channel was significant ($\chi^2 = 2.79$; $P < 0.05$, 1 df), indicating that color-acclimation reduces predation risk. For the tan-channel trials, the chi-square was marginally significant ($\chi^2 = 1.69$, $P < 0.10$, 1 df). Pooled data from both trials showed that color-acclimated fish have a clear survival advantage ($\chi^2 = 4.32$, $P < 0.025$, 1 df). Brook trout that were color-acclimated to match the background of the predation arena had a significantly decreased predation risk compared with that of fish that were not background-matched. Overall, there were 42 mismatched fish versus 25 color-matched fish eaten (protection ratio, 1.68). Overall, color acclimation reduced predation losses by 40%.

Discussion

Our findings are similar to those of Sumner (1934, 1935a, 1935b). His experiments were on a larger scale, but he found roughly a 2:1 survival advantage for background-matching fish. The results that we obtained are only slightly different from 2:1, the greatest deviation being for tan-acclimated fish preyed upon in the tan channel. The

TABLE 1.—Numbers of brook trout eaten by hooded mergansers in laboratory trials.

Acclimation background color	Total length (mm)	Number of brook trout eaten in the predation arena colored: Tan	Brown
Tan	70–75	2	4
	75–80	5	7
	75–85	4	4
	70–90	4	4
	All	15	19
Brown	70–75	5	3
	75–80	8	2
	75–85	6	1
	70–90	4	4
	All	23	10

pooled results suggest that there is a significant survival advantage to acclimating fish to a color background similar to that which they will be exposed to upon stocking. Conversely, a significantly higher predation risk resulted when fish were not acclimated to the arena background color.

Although Sumner's work led to the gradual acceptance of the concept of protective coloration (see Cott 1957), he used only a rough method of assigning survivors to acclimation groups (Sumner 1934). He placed survivors on a background opposite in color to the predation arena, and if they did not change color rapidly, they were identified as having been color-acclimated to the same color as the predation arena. If they did change rapidly, they were identified as fish that had been acclimated to the alternative-colored predation arena. Fish that could not be identified as to their acclimation color with this methodology were excluded from his analysis. Our method of identification, by pelvic fin-clipping, provided positive identification of acclimation group and also served to separate rapid physiological from slower morphological color changes.

Symons (1974) reported similar results by using brook trout to prey on Atlantic salmon. However, he reported that territorial behavior of the Atlantic salmon was a key factor in determining vulnerability to predation. In four trials, Symons demonstrated that fish acclimated to the predation arena for 15 d experienced only one-third the mortality of fish that had only 24 h to acclimate. The predation arena had boulders and gravel and a more natural brown color, whereas the acclimation tank used to hold Atlantic salmon before the experiment had no gravel or boulders and was blue in color. From our experiments and observations with both brook trout and Atlantic salmon, 24 h may be sufficient time for the physiological color change, but is insufficient for morphological color change. Thus, Symons' results could be reinterpreted as evidence for the survival advantage of color acclimation to the stream channel color by the territorial Atlantic salmon (acclimated for 15 d) and lack of color acclimation for the nonterritorial Atlantic salmon (acclimated for 24 h).

It seems unlikely that any territorial behavior developed in the hatchery would carry over to stocking or transplanting. On the other hand, primary defense and appropriate coloration can be developed in the hatchery and can result in lower vulnerability of fish to predators than for those with no color acclimation. Thus, color acclimation may be a worthwhile management technique for reducing poststocking mortality of salmonid species due to predation. Color acclimation may also have the additional benefit of minimizing losses to predators when hatchery fish are newly exposed to predators in outdoor rearing ponds.

Methods for matching fish to be transplanted to the recipient stream is a problem that we have been working on. Although spectrophotometric instruments that can be taken into the field can provide a spectral map of the background coloration of stream substrates, their purchase prices are a deterrent to widespread use. We have used a photometer (spotmeter) and colored filters (red, blue, and yellow) to measure and match substrate coloration. To use a photometer for this purpose, it is advisable to take readings of a white standard in addition to the averaged substrate or fish coloration so that readings can be compared under different light regimes. Photography can also be used to measure the coloration of the stream substrate or dorsal or lateral surfaces of fish. Photographic diapositives of the dorsa of several fish against a colored substrate may then be measured with a scanning spectrophotometer to indicate degree of cryptic coloration or degree of mismatch (see Donnelly and Dill 1984). Another alternative is to use paint samples and match these to the averaged color of the gravel substrate of the recipient stream. The color sample chosen determines the color that will be used for painting the acclimation tanks where the fish (for that stream) will be reared.

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