Effects of novelty and gregariousness in survival of aposematic prey

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We examined the reactions of captive wild great tits to novel unpalatable prey with (1) a traditional aposematic signal (black and yellow) (2) a novel signal (light pink), and (3) a control signal (brown). Prey were offered either singly or in groups to see whether novel signals with fewer possibilities for synergistic benefits are more dependent on grouping than are the traditional signals. Indeed, responses of birds toward unpalatable prey depended significantly on spatial distribution of prey (grouping versus solitary) and the type of the signal. Birds avoided more the traditional black and yellow signals than novel pink signals in both experimental set ups, but both of these prey items survived better in aggregation than solitarily. The success of traditional signals may demonstrate the importance of synergistic selection across species in the evolution of warning coloration (i.e., Müllerian mimicry). Unpalatable prey individuals benefit strongly from using similar color patterns. Our results suggest that aggregation may be important for the evolution of novel signals in particular, even if a synergistic selection component is also present. Key words: Aposematism, great tit, gregariousness, novel signal, Parus major, traditional signal. [Behav Ecol 8:174-177 (1997)]

Unpalatable or otherwise unprofitable prey species have often evolved a conspicuous warning coloration or exhibit special distinctive signals (Cott, 1940; Edmunds, 1974; Guilford et al., 1987). Such a combination of traits is called aposematism. Although the function of aposematism in allowing the predators to associate noxiousness with the signal is well tested (e.g., Gittleman and Harvey, 1986; Roper and Redston, 1987; Roper and Wistow, 1986; Tulltrot and Sundberg, 1991), evolutionary pathways from cryptic palatability to conspicuous unpalatability are more problematic to explore (Endler, 1991).

The relative role of individual benefits, kin benefits, and synergistic benefits in the evolution of conspicuously colored and unpalatable prey have been widely discussed (Endler, 1988; Guilford, 1988, 1990a; Leimar et al., 1986; Sillén-Tullberg and Leimar, 1988). It has been experimentally documented that gregariousness enhances discriminative aversion learning in aposematic prey (Gagliardo and Guilford, 1993), supporting the idea that kin selection might be essential in the origin of aposematism (Fisher, 1930; Guilford, 1988, 1988; Harvey and Paxton, 1981; Harvey et al., 1982). On the other hand, in many cases aposematic prey seem to also manage well solitarily; predators may leave the signaling prey unkillled after some initial handling, thus supporting straightforward individual selection (Edmunds, 1974; Järvi et al., 1982; Sillén-Tullberg, 1985a; Wiklund and Järvi, 1982).

The idea of synergistic selection is similar to the "green beard effect" (Dawkins, 1976). Unpalatable individuals may benefit by using similar warning colors, or any other signals, that other individuals of the same or other species have used (Guilford, 1990a,b; Maynard Smith, 1989). Then, prey individuals with traditional color patterns such as black and yellow or orange stripes should be more protected against predators than those exhibiting any new signals, which is to be expected from the traditional Müllerian mimicry operating across the species level.

To study the ancestral origin of warning signals, it would not suffice to use naive predators because avoidance of warning colors is also likely to have a genetic basis (Gehlbach, 1972; Rubinoff and Kropach, 1970; Schuler and Hesse, 1985; Smith, 1975, 1977). Thus, we did not use naive birds in this experiment, since we were tracking the situation when warning coloration appears in a new species in the world where many other unpalatable prey already have warning signals. This is the more common situation for most of the prey populations that have evolved warning signals, but obviously the situation would have been different in the ancestral history when warning coloration appeared for the first time. This paper examines the reactions of captive wild great tits to novel unpalatable prey with (1) a traditional signal (black/yellow), (2) a novel signal (light pink), and (3) a control signal (brown). The prey items were offered either in groups or solitarily to allow us to explore the benefits of signaling in relation to signal type and the spatial distribution of the prey.

METHODS

Adult great tits, Parus major, were used as predators, last-instar mealworm larvae, Tenebrio molitor, painted and artificially made distasteful, were chosen as prey. The experiments were done at Konnevesi research station in Central Finland. In this area meal worm larvae are not available in nature, and thus birds had no experience of the prey items, which are naturally tasteful to birds and not aposematic. We captured and ringed adult birds during the late nestling period in June 1994. After the approximate 2-h experimental trial, birds were released back to their nests. In each nest only one of the parents was used at a time, and the short absence of the parents had no effects on survival of the offspring.

Before the start of an experiment, we allowed a bird to use the experimental aviary (7.3 m²) for 90 min. Sunflower seeds were offered during the first 50 min of this habituation period, and only water was offered after that. Those that did not feed during the training phase were released before any experimentation. We used each bird only once. We made mealworm larvae unpalatable by injecting 0.03 ml Tabasco sauce inside them. We randomly divided the injected larvae into three groups and painted five dots on their backs with non-poisonous children's finger paints using either black and yel-
low (B/Y), light pink (P), or brown control (C). We checked in a blind taste test (n = 5 colleagues) that the colors were not separable according to their taste. Thus, B/Y represented novel prey that uses a commonly existing warning color combination, and P represented novel prey with a new or at least an uncommon signal for warning. There are many unprofitable prey types with black and yellow stripes in the habitats where the birds were captured (e.g., wasps, bees, bumblebees and caterpillars such as *Parnis brassicae*, *Phaleria bucephala*, *Lacanobia obtunguis*). C was novel prey that did not warn its unpalatability as brown is the original color of the larvae. To