Apostatic selection by humans searching for computer-generated images on a colour monitor

G. M. Tucker* and
J. A. Allen

Department of Biology, University of Southampton, Southampton SO9 3TU, U.K.

A computer program was used to generate "populations" of dimorphic "prey" on the screen of a colour monitor. Different subjects were presented with the prey at seven different frequencies and were asked to use a light pen to remove each prey they detected. They all received the same two types of prey but 70 had them presented against a matching background and 49 had them against a background that made them conspicuous. The results showed that apostatic selection occurred when the prey were inconspicuous but not when they were conspicuous. There is evidence that the apostatic selection was caused by some effect of the difficulty in detecting the prey when they were cryptic.

INTRODUCTION

A preference for common prey—"apostatic selection" (Clarke, 1962) or "switching" (Murdoch, 1969)—has been demonstrated in several studies using artificial prey (*e.g.*, Allen and Clarke, 1968; Allen, 1972, 1974, 1976; Manly, Miller and Cook, 1972; Fullick and Greenwood, 1979; Raymond, 1984) and natural prey (Den Boer, 1971; Maskell *et al.*, 1977; Cornell and Pimentel, 1978; Akre and Johnson 1979; Bergelson, 1985). The magnitude of the response has been shown to be affected by the prey's density (Cook and Miller, 1977), palatability (Greenwood, Wood and Batchelor, 1981) and degree of crypsis (Cooper, 1984; Bond, 1983).

Theoretical work has demonstrated that apostatic selection has the potential to maintain colour polymorphisms in prey species (Haldane and Jayakar, 1963; Clarke and O'Donald, 1964; Cook, 1965), although its efficacy in nature has yet to be proven (Cain, 1983). Very little is understood of its behavioural basis. Clarke (1962) suggested that the development of specific search images (Tinbergen, 1960) is the primary cause but it is now clear that a wide range of behaviours can in theory give rise to frequency-dependent selection by predators (Murdoch, Avery and Smythe, 1975; Greenwood, 1984).

* *Present address*: British Trust for Ornithology, Beech Grove, Tring, Herts, HP23 5NR.

The experiments described in this paper were designed to test whether humans select in an apostatic manner when "killing" computer-generated dimorphic "prey" on the screen of a colour monitor. Despite the obvious pitfalls, the use of humans has given valuable insights into the development of predator–prey models (Holling, 1959; Gendron and Staddon, 1984). The computer-controlled technique has the advantage of giving the experimenter considerable control over important variables, as well as providing a means for the automatic and accurate recording of data. In the experiments the subjects simulated predation by using a light pen to remove prey from the screen until the trial was stopped automatically at the point when half the prey had been eliminated.

There is evidence from wild birds (Cooper, 1984) and captive pigeons (Bond, 1983) that a matching background increases the magnitude of the strength of apostatic selection. The behavioural basis of this effect is in doubt, but it could result from a greater ability of the predator to learn to distinguish prey from the background when they are common rather than rare (Bond, 1983; Cooper, 1984). Thus the experiments were designed to test whether humans select in a frequency-dependent manner when searching for prey distributed on backgrounds which made both morphs either conspicuous or inconspicuous.

MATERIALS AND METHODS

The program was written in Basic and run on a BBC Model B (32K) microcomputer linked to a Cub Microvitec Colour monitor. On the screen of the monitor (brightness set to maximum), each prey type consisted of a user-defined character in the form of a pattern of yellow pixels (dots) based on an 8×8 matrix of pixels approximately 7 mm square (fig. 1). Prey 1 was in the shape of an open circle and prey 2 was in the shape of a capital "T".

The background consisted of 800 copies of a third user-defined character randomly distributed over the dark screen. This character was again made from a predetermined random pattern of pixels within an 8×8 matrix. To avoid empty spaces around the prey, and to ensure that they appeared to be superimposed on the background, it was necessary to combine each prey type with a fixed set of additional pixels of a pattern similar to those in the background character. Fig. 1 shows prey 1 and 2 in isolation, the background character, and prey 1 and 2 combined with the additional "background" pixels.

The yellow prey were distributed randomly on the background in such a way that they did not overlap with one another (fig. 2). Yellow background characters were used for experiment 1, in which the prey were cryptic, and red characters were used for experiment 2, in which the prey were conspicuous. On the screen, the prey and background were displayed within a window 215 mm wide by 155 mm high, giving an effective density of 1200 prey m^{-2} in screen Mode 1.
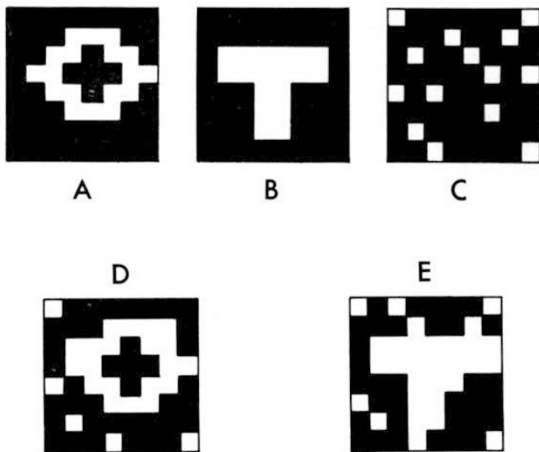

Figure 1 User-defined characters (approximate length of side of 8×8 pixel matrix in screen Mode 1 = 7 mm). A = prey 1, B = prey 2, C = background, D = prey 1 plus background pixels, E = prey 2 plus background pixels.

A limitation of the computer hardware was that the "background" pixels accompanying each user-defined prey character were unavoidably the same colour as the prey. Thus when the background characters were red, each yellow prey was immediately surrounded by a few yellow pixels. The alternative, of placing each prey in an area of blank screen, would have made both prey types more conspicuous irrespective of the background. In addition, the light pen recognised a prey on the basis of all the pixels within the defined character; the removal of pixels in the immediate background could have thus significantly altered the "handling" properties of the prey.

The subjects were 119 volunteers (58 female, 61 male) from the staff and students in the Medical and Biological Sciences Building, at the University of Southampton. Care was taken to ensure that each subject had no prior knowledge of the purpose of the experiment. Each subject was tested with the prey at a single frequency (either 0·05, 0·1, 0·25, 0·5, 0·75, 0·9, or 0·95). Each subject performed nine trials, all of which started with the presentation of a total of 40 prey. The first trial was for familiarisation with the use of the keyboard and light-pen, and the data were disregarded in subsequent analysis. Ten subjects were used for each frequency in experiment 1 and seven for each frequency in experiment 2. No subject was tested more than once. Subjects were randomly assigned to experiments and within each experiment the frequencies were presented in a random order.

Before the start of the first trial with a given subject the program displayed a set of written instructions stating that "an arena will be displayed on the screen consisting of a yellow background with scattered 'prey' of the same colour. These prey items are represented by two different shapes". The instructions also stated that the task was to locate and delete the prey as fast as possible and gave details of how the prey could be removed from the screen by touching them individually with the light-pen while pressing a particular key on the keyboard of the computer. To counteract the possible effects of novelty (*cf.* Lawrence and Allen, 1983) the subject was then shown an example of each prey simultaneously displayed against a blank (dark) screen for 10 seconds. The program then required the experimenter to enter a code for the prey frequencies that were to be presented. It then started to generate the prey and background, distributing the prey and background characters at random each time it was run. At this stage both elements were the same colour as the dark screen and were thus not detectable to the subject. When
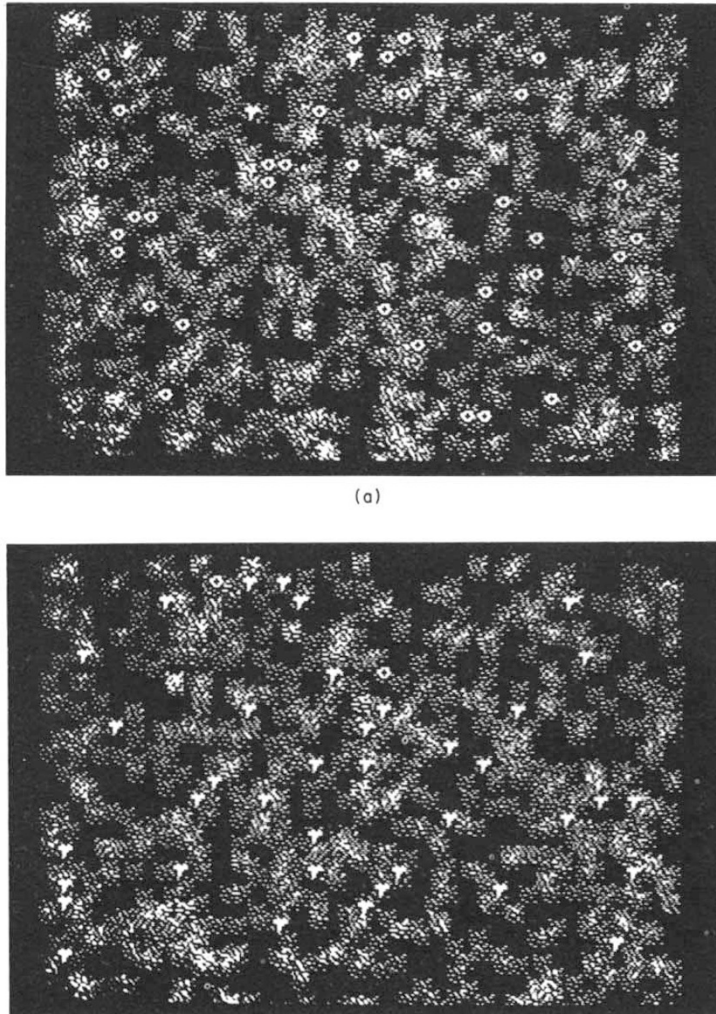
Figure 2 Black-and-white photographs of typical backgrounds with 40 cryptic prey. (a) Frequency of prey 1 (circles) = 0·95, frequency of prey 2 (T-shapes) = 0·05. (b) Frequency of prey 1 = 0·05, frequency of prey 2 = 0·95.

the distribution of the prey and the background had been completed (after 13 seconds), the program made them visible. The subject then started to eliminate the prey.

As each prey item was removed from the screen, the computer gave an audible "bleep", recorded the prey type, the time elapsed since the start of the trial and the time elapsed since the last prey elimination. These data were printed out automatically when the program terminated the trial as soon as half the prey (20) had been removed. At the same time, it cleared the screen. The time measurements will be used in analysis not reported here.

Analysis was by the method of Manly (1973). For each subject, a selection coefficient (β) against prey 1 was calculated from the mean number of each prey type remaining in the eight trials. The use of means avoided possible bias caused by the inflated variance when subjects did not select any individuals of the rarer prey in a trial. Frequency-dependence was tested by regression of arcsine transformed values of Manly's β selection coefficient on the frequency of prey 1. A transformed value of β of 45 indicates no selection; a value above 45 indicates selection against prey 1, and below 45 selection against prey 2. A positive slope suggests apostatic selection and its intercept with

the point where the prey are presented in equal frequencies gives an estimate of the frequency-independent preference for prey 1.

RESULTS

The results for the two experiments are summarised in figs 3 and 4. For the matching background (fig. 3), the positive slope of the regression of β on frequency is statistically significantly different from zero ($t = 3\cdot80$, df $= 68$, $p < 0\cdot001$), but no such difference was detected when the background made the prey conspicuous (fig. 4) ($t = 0\cdot828$, df $= 48$, $p > 0\cdot1$). Furthermore, the slopes of the two regression lines are significantly different from one another (standardised normal deviate $= 2\cdot835$, $p < 0\cdot005$). It is clear that selection occurred only when the prey were cryptic, and that this selection was apostatic.

The mean values of β when the prey were presented in equal numbers were $50\cdot2$ when the prey were cryptic and $44\cdot6$ when conspicuous, and this difference in selection is statistically significant ($t = 2\cdot241$, df $= 15$, $p < 0\cdot05$). The deviations from 45, the value expected assuming no selection, were significant when the prey were cryptic ($t = 2\cdot63$, df $= 9$, $p < 0\cdot005$) but not when conspicuous ($t =$
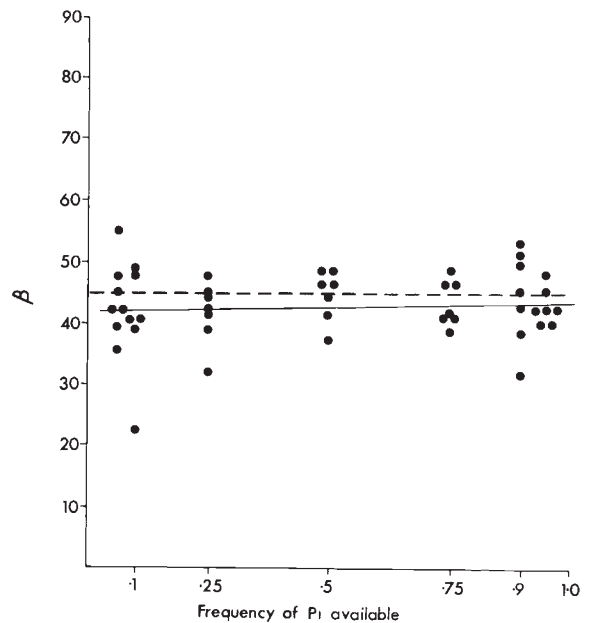

Figure 4 Selection against prey 2 in relation to frequency: both prey conspicuous. The broken line is the relationship expected in the absence of selection. Regression equation: $Y = 41\cdot94 + 1\cdot92x$; $r = 0\cdot119$, $p < 0\cdot1$.

$0\cdot253$, df $= 6$, $p > 0\cdot5$). There is thus some evidence that prey 1 was preferred when both prey were cryptic but not when they were conspicuous.

DISCUSSION

Murdoch *et al.* (1975) and Greenwood (1984) have listed the various mechanisms that can lead to frequency-dependent selection by predators. Assuming that our subjects behaved in a way that maximised their "feeding" efficiency, only two of these mechanisms could account for the apostatic selection observed when the prey images were cryptic. These mechanisms are: (a) some effect of handling experience or (b) some effect of searching (either minimisation of searching costs or optimisation of search rate). All the others depend on properties that our "prey" did not have, such as differences between the morphs in spatial distribution and profitability.

If predators have to learn to handle their prey, and if different types of prey require different handling techniques then it might pay the predator to concentrate on learning to handle the commoner form. Greater success in handling common prey through experience has been shown to produce frequency-dependent predation in real predators
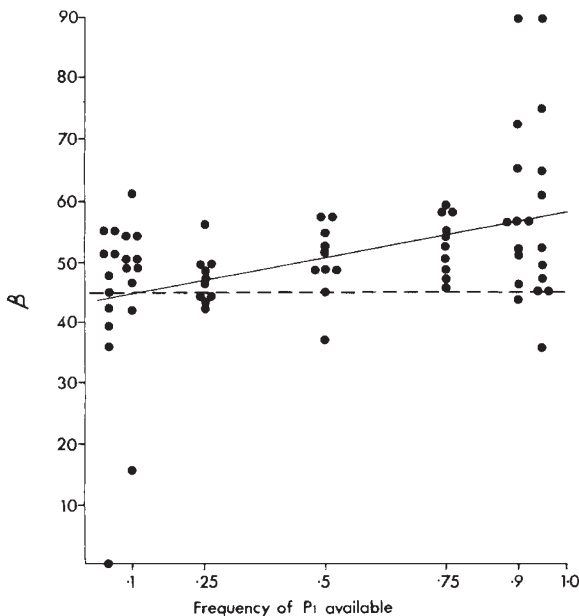

Figure 3 Selection against prey 1 in relation to frequency: both prey inconspicuous. The broken line is the relationship expected in the absence of selection. Regression equation: $Y = 43\cdot50 + 14\cdot77x$; $r = 0\cdot417$, $p < 0\cdot001$.

(Lawton, Beddington and Bonser, 1974; Bergelson, 1985). The same might apply in the present study if different techniques were required to use the light-pen on the two prey types. If this were the case, however, we would expect selection to have been apostatic even when the prey were conspicuous.

The most likely basis for the observed apostatic selection is that it was caused by some effect of searching for the prey on the matching background. Gendron and Staddon (1983) developed a model for predators searching for cryptic prey and demonstrated that the optimal rate of search "will reflect a trade-off between prey detection and frequency of encounter". When a predator is searching for two prey types that differ in their degree of conspicuousness the optimal rate of search increases with the frequency of the more conspicuous type and this may reduce considerably the chances of detecting the less conspicuous type. In this model the most conspicuous type would always be selected to excess and this preference would be greatest when it is common. This explanation does not appear to apply to our results. Although there is some evidence from the cryptic test that prey 1 (open circle) was more conspicuous ($\beta = 50 \cdot 2$ when the two forms were presented at a frequency of $0 \cdot 5$) it was not consistently preferred at all frequencies.

Alternatively, the subjects' perception of the prey might have altered when searching for them on a matching background (Endler, 1978; Bond, 1983; Cooper, 1984; Cook, 1986). For example, if there were a cost to searching for two inconspicuous images at the same time it might have paid to concentrate on the common form alone. On the other hand, when the prey were conspicuous it would probably have been more efficient for the subjects to attend to visual cues common to both types—the contrasting colour, for instance. Another possible cause of the apostatic selection on the matching background is that the subjects were more likely to acquire search images (in the sense of Dawkins (1971) and Lawrence and Allen (1983)) for the common prey because only this form was encountered sufficiently often for the subject to learn to distinguish it from the background (see also Staddon and Gendron (1983)). It is even conceivable that there was some interference between different search images, with the result that perception of the rare prey type was impeded.

Both Bond (1983) and Cooper (1984) detected increased apostatic selection in birds searching for cryptic artificial prey. They, too, believed that this result was caused by some effect of an increase in the difficulty of detecting the prey. We plan future work to investigate the behavioural basis of apostatic selection by humans hunting for images on a colour monitor.

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