Table I. Between-strain and within-strain courtship and orientation

Male	Female	$(CI-COPI)/$ $(1-COPI)^*$	$OI/(1-COPI)^*$
T†	T	0·70	0·37
T	E	0·70	0·49
E†	T	0·71	0·37
E	E	0·77	0·41

* CI, COPI, and OI from Collins & Hewitt (1985).
† T = Texas 1, E = Edinburgh.

calculate the time spent courting as the CI minus the time spent copulating (CI − COPI). However, since copulating flies do not perform courtship, a fly that begins to copulate within 10 min has less time to court than a fly which does not mate during the observation period; hence, the former will have a lower CI − COPI value than the latter if the two males spend the same proportion of the time that they do not copulate, courting.

To calculate a courtship index that takes into account the time that males can perform courtship activities, it is necessary to divide CI − COPI by the fraction of the observation period that elapses before copulation begins (1 − COPI). Similarly, a valid orientation index (OI) can be calculated by dividing Collins & Hewitt's OI by (1 − COPI).

When one performs these calculations, it is evident that all of the courtship indices are similar except for the relatively high CI of Edinburgh males courting Edinburgh females, a within-strain combination (Table I). With respect to orientation, the highest values are for Texas 1 males courting Edinburgh females and Edinburgh males courting Edinburgh females. In this case, the two between-strain values are almost certainly significantly different from each other and the two within-strain values may also be different, so it would not be valid to compare the two within-strain orientation indices to the two between-strain OIs.

Tompkins & Hall's (1984) Oregon-R and Canton-S males do consistently perform more courtship between strains than within strains. It will be of interest to determine whether these males also orient and follow more when they are courting females from strains other than their own.

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Conspicuous Plumage of Birds: Sexual Selection or Unprofitable Prey?

Baker & Hounsome (1983) recently attempted to test whether the conspicuous bright plumage of males in sexually dimorphic birds is a product of sexual selection or a signal to predators of their unprofitability. They claim that their evidence 'tips the balance in favour' of the unprofitable prey hypothesis of Baker & Parker (1979) which states that conspicuous male plumage signals a potential predator that the bearer would not be a profitable prey item. Their conclusion has already been criticized because their analysis was based on questionable predation rates (Reid 1984). In this note we discuss a more fundamental problem concerning the kinds of tests that can be used to reject the sexual selection hypothesis. We show that Baker & Hounsome's statement, that 'Classical sexual selection models predict a positive correlation between conspicuousness and probability of predation whereas the unprofitable prey model predicts a negative correlation' is incorrect and we suggest that interspecific comparisons of the kind used by Baker & Hounsome are inappropriate tests of sexual selection theory.

It has long been assumed that predation balances the sexual selection advantages of bright male plumage (Darwin 1871; Krebs 1979). Thus, brighter individuals within species should be subject to a higher risk of predation. But sexual selection theory makes no particular prediction about the relation between predation rate and conspicuousness among species. If the relation between the costs of predation and conspicuousness were constant across a group of species, then different intensities of sexual selection (due to different mating systems, sex ratios, etc.) would result in a positive correlation between observed predation rate and conspicuousness (Fig. 1a). Conversely, if the relation between costs of predation and conspicuousness varied among species with the same intensity of sexual selection, then a negative correlation might be expected (Fig. 1b).
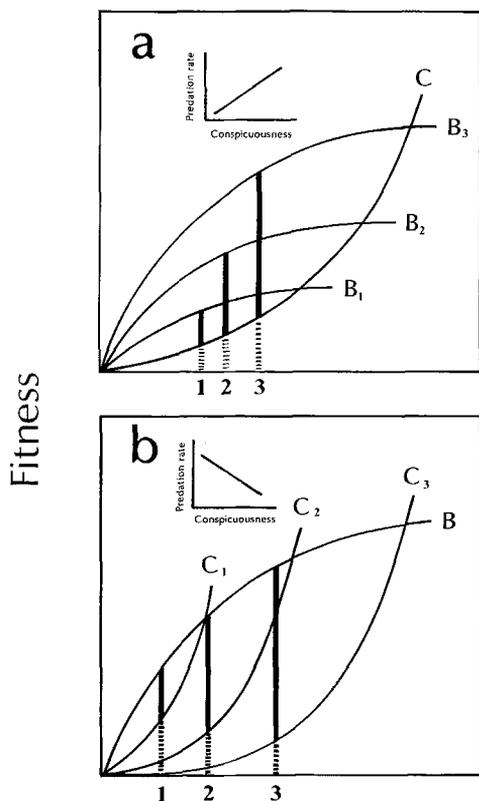
Figure 1. Simple models of the fitness costs (C; predation risk) and benefits (B; mating success) of conspicuous plumage as predicted by sexual selection theory. Optimal conspicuousness is achieved when the difference between benefit and cost is maximized. Interspecific differences in the optimal conspicuousness of males (indicated by the numbers along the abscissae) may be due to differences in either benefits (1a) or costs (1b) or both. The resulting relations between conspicuousness and predation rate are shown as insets.

As Krebs (1979) has already suggested, predation risk may determine how far sexual selection can push the degree of conspicuousness within species. As a result, males of species under high risk of predation may be dull-coloured because the cost of being more conspicuous outweighs any sexual selection advantages. In contrast, species under low risk of predation can evolve by sexual selection to be brighter and more conspicuous. The mortality rate due to predation will determine the limits to conspicuousness that result from sexual selection (Fig. 1b). Thus the negative correlation between predation rate and conspicuousness found by Baker & Hounsome is consistent with both the sexual selection and the unprofitable prey hypotheses. Moreover, the birds chosen for their analysis

are mainly monogamous passerines in which the intensity of sexual selection might be expected to be relatively low compared with polygynous species. In these species variation in the risk of predation would probably have a much greater impact on male coloration than would variation in the intensity of sexual selection. A negative correlation between predation rate and conspicuousness is therefore expected among the species analysed by Baker & Hounsome.

Baker & Hounsome argued that a negative relation between predation risk and conspicuousness (as in Fig. 1b) could not result from sexual selection as suggested by Krebs (1979). To formulate this argument they used results from a simulation model (Parker 1982) showing that selection should stabilize within species when all individuals experience equal predation risk. They extrapolated this intraspecific model to predict the pattern among species. This implies that all species within the prey species pool (i.e. community) should experience the same risk of predation. We know, however, that many factors unrelated to an animal's conspicuousness, such as habitat (Kaufmann 1974), abundance (Murdoch et al. 1975) and body size (Parker 1971), influence predation rate in different species. Thus the assumption that all species in a community experience similar predation risk is not supported by any empirical evidence. Most important, in a world where all species experience similar risk of predation, all would be equally profitable and therefore signals of unprofitability could not evolve in the manner suggested by Baker & Parker (1979).

Since sexual selection theory makes no particular prediction about the relation between predation rate and conspicuousness across randomly chosen species, it is more appropriate to test the critical predictions of the models of sexual selection and unprofitable prey. The critical prediction of sexual selection theory here is that bright colour provides a mating advantage (either increasing the probability of obtaining a mate, or increasing mate quality). Unprofitable prey theory predicts no relation between conspicuousness and mating advantage. Variation in male plumage found in many passerine birds provides an opportunity to test this prediction. Bright males had a higher probability of attracting a mate in northern orioles (*Icterus galbula*; Flood 1984), American redstarts (*Setophaga ruticilla*; Procter-Gray & Holmes 1981) and indigo buntings (*Passerina cyanea*; Payne 1982). Thus, the empirical evidence available to date appears to favour the sexual selection hypothesis.

The unprofitable prey hypothesis predicts that predators should prefer dull individuals over bright individuals whenever given a choice and this

preference should obtain both within and among species in a given community. Studies of predation within species of fish (Endler 1980), moths (Sargent 1969) and mammals (Kaufmann 1974) have all shown that more conspicuous individuals suffer increased predation risk. Similarly, conspicuous white male ptarmigan (*Lagopus mutus*) apparently suffer heavier predation from gyrfalcons (*Falco rusticolus*) than do cryptic brown females (Gardarsson 1971). In contrast there is no evidence whatever that predators prefer cryptic individuals as prey, but an experimental evaluation of this critical prediction would be the most appropriate method of testing the unprofitable prey hypothesis.

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