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THE EVOLUTION OF BIRD COLORATION

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This paper is dedicated to the memory of
the late Professor H. E. Hinton, F.R.S.

CONTENTS

The aims in this paper are first to review theories of the evolution of bird coloration and, in some cases, partly revise and extend them, secondly to analyse the coloration of all the birds of a given geographical region using multiple regression, and thirdly on the basis of this analysis to evaluate the various theories.

Theories. There have been many discussions of the selective forces acting on the coloration of birds and we review the major proposals in some detail. The earliest suggestion (Darwin 1871) was that the bright coloration of many male birds originated through sexual selection by female choice of the most exotic variants in male plumage. A conflicting view (Hingston 1933) is that brightness has an intimidatory effect on opponents, and that bright male coloration arose through sexual selection but largely due to its advantages against other males in disputes concerning mating access to females. Bird coloration has also been considered in terms of predation (see, for example, Cott 1964*a*). Some birds with bright plumage patterns are known to be

unpalatable compared to cryptic species, and certain other patterns have been interpreted as adaptations to confuse predators. Bright colours may commonly be favoured when an individual is anyhow obvious (e.g. through activity) and where it represents an 'unprofitable' prey for a predator. This interpretation may be particularly relevant to lekking among polygamous males. A special case of unprofitable prey may be 'perception advertisement', where an animal signals (by flash patterns or alarm calls) that it has seen a predator (or opponent). It is also possible that bright coloration may serve to deflect predators away from the nest site; this requires in many ways conditions opposite to those for the unprofitable prey solution. Finally, bird colorations can act as a variety of social signals other than threat.

Analysis. The coloration of the 516 species of birds that breed and/or winter in the Western Palaearctic was analysed by multiple regression. Seven regions of a bird's body plus two areas of flash coloration were recognized and scored for colour on a cryptic/conspicuous scale. Five different age/sex/season categories were recognized and scored separately for each species. These dependent variables were each analysed with respect to 17 independent variables that reflect different aspects of the reproductive biology and ecology of the birds. The advantages and disadvantages of multiple regression as an analytical technique are discussed.

Results. The analysis identifies associations between the reproductive biology and ecology of the birds and the coloration of the different regions of the body of the different age/sex/season classes. Apparent exceptions to these associations are also identified and discussed. A relatively large proportion of the associations made sense in terms of the theories presented and usually there was a strong implication that for any specific association one theory was more relevant than any of the others. The results indicate that by far the most potent selective pressures to have shaped bird coloration are those related to predation risk. A number of the theories make use of predation risk, each in a different way, and for most of them some support can be gained for their involvement in the evolution of bird coloration. Of all the theories, however, it is the unprofitable prey model that seems to account for the major part of the variation in bird coloration. By contrast, no clear evidence for the involvement of sexual selection in the evolution of bird coloration could be found. Indeed, many associations, such as that between sexual dimorphism and polygamy, were more readily explicable in terms of selection pressures due to predation risk than of sexual pressures. The suggestion that bird coloration is shaped by predation rather than by sexual selection in no way prevents the coloration, as it evolves, being incorporated within the species and sex recognition system.

Conclusions. It is concluded that bird coloration has evolved almost entirely in response to predation-based selective pressures. Although plumage and coloration are involved in species and sex recognition systems, they have not evolved in response to sexual selection pressures. In species that are sexually dimorphic, the male is not brightly coloured as a result of female choice or male:male competition but because he represents a less profitable prey to a predator than the females and juveniles. We predict that brightly coloured birds will most often be found to suffer less from predation than will comparable more cryptic birds (though one of the predation-risk theories does allow the converse to be true).

1. PREFACE

This paper began as a result of a suggestion by the late Professor H. E. Hinton, F.R.S., early in 1974. Throughout its earlier stages he provided the impetus and stimulus for its development, and we shall never forget the inspiration he showed (so typically) in our meetings to discuss the work. Unfortunately, his untimely death (in August 1977) occurred before he had organized his notes into manuscript form and much has had to be omitted. We are certain that the loss of his final written contribution has affected the paper immeasurably.

We submitted the original version of the paper with Howard Hinton as senior author. Since then, and with reluctance, we have been persuaded against this, in response to the argument that authorship carries responsibility as well as credit. However, we feel we must stress that Howard Hinton alone deserves the credit for the (characteristically) controversial idea that the bright coloration of many male birds is an adaptation to the selective pressure of predation rather than to sexual selection. This idea was originally against our intuition, and we know it would have amused Howard that it took us much searching thought about plausible evolutionary mechanisms, and considerable time on the largest computer in Britain to approach the same conviction!

With emotion, we dedicate this paper to Howard's memory. It is also with some sadness that we express our gratitude to Mrs Hinton for kindly providing such convivial hospitality during our final and most lengthy discussion of this work with her husband. It was a delightful and memorable occasion, and very regrettably our last meeting with Howard.

2. Introduction

The coloration of birds has fascinated many biologists since Darwin (1871) suggested that there was an association between sexual selection and the bright colour patterns of many males (see, for example, Cott 1940, 1964*a*; Hamilton 1961; Lack 1968; Selander 1972). Over the years many hypotheses have been put forward to account for the evolution of bird coloration. The evidence advanced in their support, however, has always rested on a few specific examples. But bird coloration is so variable that it is nearly always possible to find both evidence for the rule being presented, and exceptions to it. This indicates that a realistic model of bird coloration must have many parameters and must allow for the existence of many, often conflicting, selective pressures.

Our aim in this paper is to review theories of the evolution of bird coloration and, in some cases, partly to revise and extend them. We make no attempt at a comprehensive review (this would be virtually impossible); our aim is to consider the major types of theories proposed. We then analyse the coloration of all birds from a given geographical region using as independent variables as many ecological, social, and sexual characteristics as possible that have some relevance to the theories. An attempt is then made to examine the plausibility of each type of theory in relation to the results of the analysis.

3. Theories of the evolution of bird coloration

(*a*) *Sexual selection theories*

The classical theory of sexual selection (Darwin 1871) involves two components. First, direct intra-male competition: a character spreads if it enables a male to outcompete other males in, say, combat for females; and secondly female choice: a character spreads if females mate more readily with males possessing the character.

That the first component accounts for much of male–male combat and eagerness to mate is generally accepted (although such behaviour was often interpreted in terms of group selection, see, for example, Wynne-Edwards, 1962). The second is more complex and has often been viewed more sceptically. Darwin argued that the bright colorations of many animals were sexually-selected adaptations arising through female choice. Evidence certainly exists that females in some species do exert a choice over males when mating (see, for example, Darwin

1871, Trivers 1972, 1976). There can be little doubt that selection will here cause the spread and fixation of the preferred male characteristic if it is heritable and has no other selective effects. Darwin thought that the advantages of bright coloration could be offset by the disadvantages of being more susceptible to predation (Darwin 1871, vol. 2, p. 97). Provided that mating advantage outweighs the predation disadvantage, then conspicuous coloration should evolve through female choice. The coloration should stabilize at an optimum where the two opposing forces are in balance (see Fisher 1930, O'Donald 1962).

Precisely *why* females exert a choice is a complex problem. Darwin's view was that exotic characteristics served 'to satify female whims and overcome female coyness'. However, this does little to explain the real origin of the choice. There are two possibilities. It could arise simply by some 'accident' of the physiological system for acceptance–rejection, so that occasionally male variants arise which do better than average in stimulating acceptance. Or, where females are attracted to males, the brighter the male the more females he attracts. The other possibility is that the choice *itself* is largely the product of selection (Fisher 1930).

Fisher (see also O'Donald 1962) argued that 'choice' genes would spread only if the preferred male type has some initial advantage. Suppose that a male shows a characteristic (e.g. bright coloration) that enhances its chances of mating. Females that exert a preference in favour of the brighter males will have more grandchildren, because of the activities of their sons. This may lead to an increase in the frequency of the choice genes, which will in turn increase the relative advantage of the brighter male type. Hence the selective advantage of the preferred characteristic and that of the preference trait will both initially accelerate as both increase in the population. Though the favoured male characteristic should fixate, it is less likely that the preference trait will. Once all males possess the characteristic, indiscriminate females do equally well as females that choose.

Trivers (1972) gives an extensive review of the sort of male characteristics over which females may be expected to show discrimination. Some elements of courtship behaviour may relate to the detection of future investment prospects of potential mates. A recent suggestion by Zahavi (1975) is that females may choose characteristics that confer a handicap on male survival. Zahavi argues as follows. A male with say, a huge tail and/or very bright coloration must sustain much higher predation risk than a cryptic, 'unhandicapped' male (following Darwin's argument). Hence a male carrying these handicaps which manages to survive to adulthood must, on average, be better able to avoid predators. A female choosing a handicapped male ensures that she obtains a male of 'high quality'. Zahavi interprets thus the striking sexual dimorphisms in bird plumage; he explains cryptic monomorphism as cases where predation risk is too great to allow dimorphism. With monomorphism, females are expected to take longer to 'assess' mate quality, and there is some evidence for this in warblers (Lein 1973).

Zahavi's theory is criticized by Davis & O'Donald (1976), who show analytically that it can work only with extremely high selection of handicapped males, and almost equally intense selection on the other (cryptic) males. Moreover, selection cannot continue to favour the handicap, and any initial advantage under intense selection is soon lost and turned to disadvantage. Maynard Smith (1976) also disputes Zahavi's theory, except for handicaps that are induced environmentally so that progeny inherit the 'good genes' without the handicap. Computer simulations with genetic handicaps failed to allow spread of a gene for choice of the handicapped males, for a wide range of conditions (but see Eshel 1978, Maynard Smith 1977). The handicap theory appears ingenious but implausible.

Finally, in many animals there is very little evidence that females choose mates. Indiscriminateness may here relate to (i) high costs of finding males (see Parker 1979) and/or (ii) when other females are also indiscriminate, a good way of ensuring a mating with a male of high competitive success is to mate with the first male that arrives.

(*b*) *Bright coloration and threat*

Darwin's idea that bright male coloration may have arisen via female choice has been criticized on several occasions. For instance, Hingston (1933, see also Huxley 1938*a*, *b*) saw bright male colours in terms of success in intraspecific threat. He outlined a theory of 'colour conflict' in which selection normally favours crypsis, but favours the display of conspicuous features during aggressive disputes. A conflict thus arises between the demands of concealment and of threat, and hence animals are expected to display bright colour patterns only agonistically. The evidence for this is often convincing. Also, there would be shifts in balance between the two opposing selective forces: when male competition is intense, colour dimorphism should intensify; females and young should be more cryptic; etc. Since Hingston's publication, an association between threat and bright coloration is often assumed (e.g. Hamilton 1961, Orenstein 1973, Norman 1977).

However, the major difficulty with Hingston's theory concerns *why* an opponent should be intimidated by bright coloration. He never really considered this, but assumed that bright colours automatically signify threat and consequently represent 'psychological weapons'. It is tempting to propose a modification of Zahavi's handicap theory here. An evolutionary stable strategy (ESS) can exist in which only the opponent with the greater strength or fighting ability is prepared to fight, whereas the one with less ability withdraws immediately without damage (Maynard Smith & Parker 1976). A more brightly-coloured male may have avoided predators under handicap and hence may also be stronger and more likely to win in a dispute against a more cryptic rival. Certainly, if relative brightness ever became involved in the settlement of intra-male disputes, then an evolutionary drive to exaggerate brightness seems likely. (Whether such a convention could spread would depend on how disputes were settled originally; for instance it is generally rather difficult for a convention, once fixed to be invaded by a different one. This is because a mutant that disobeys a convention – even assuming it always wins – must sustain the costs of fairly severe escalation each time it breaks the convention.) If the handicap conveys information to male rivals, and not (at least initially) to females, then the theoretical difficulties posed by the female choice aspects of Zahavi's theory can be shed. However, the other problems remain. For instance, it is still necessary that the initial, brightly-coloured, mutant male gained more than he lost by the coloration. Unfortunately, there seems to be little evidence that brightness is correlated with fighting ability. Also it is necessary that there be stability against a strategy that shows bright coloration when weak; i.e. that predation pressure acts against 'cheating'.

Hingston also stressed that colorations and displays associated with intra-male rivalry were inextricably linked with courtship and mating; this forms one of his main objections to the female choice theory. He envisaged that the female would be sensitive to the male's (aggressive) courtship display, since this conveys information about the male's competitive ability; and also there appeared to be evidence in some species that female acceptance is correlated with intensity of male aggression. Of man, (Major) Hingston wrote: 'Hence capacity to compete with the rival is what civilized man has to demonstrate to his lady, just as animals make similar demonstrations through the exhibition of battle array'.

(*c*) *Bird coloration and predation*

Few mammalian predators of birds have been proved to have colour vision. It is, however, logically impossible to prove that an animal is colour blind (Gruber 1979) and increasingly mammals thought to be so are being shown to have some colour sensitivity (DeValois & DeValois 1975). No aspect of predation-risk theories of bird coloration is entirely dependent on colour vision in mammalian rather than avian predators. Moreover, except for red, our scale (§4*b*) is of conspicuousness as well as colour.

(i) *Warning* (*aposematic*) *coloration associated with directly noxious characteristics*

Exotic colorations may serve as an anti-predator device, either directly (owing to noxious characteristics of the prey) or indirectly (e.g. via Batesian mimicry). Warning coloration as an anti-predator device in stinging, distasteful, or otherwise noxious insects has long been accepted, though the theory has been applied less intensively to other groups. The case for flowers in relation to warning coloration has been presented only recently (Hinton 1973). This theory is sometimes plausible for bird coloration (see Cott 1940, Van Tyne & Berger 1959), though it has attracted relatively little attention.

There is very good evidence that certain birds are distasteful, and that this is correlated with conspicuous coloration (Cott 1946, 1964*b*). Of two African bustards, *Afrotis afra* is brightly coloured and is claimed to be inedible to humans (Meinertzhagen 1951). *Eupodotis rupelli* is claimed to be not distasteful, and is cryptic (see Van Tyne & Berger 1959). Cott (1964*b*) found that distastefulness is commonest in relatively defenceless species, and is associated with a tendency for both sexes to become aposematic. Vulnerable species that are not exposed (have access to cover) may be cryptic. Warning coloration can occur in certain defenceless birds that nest in close association with some aggressive and aposematic genera of aculeate hymenoptera (e.g. *Polybia*, *Polistes*, *Apis*, *Azteca*, *Oecophylla*). These birds are tolerated by the insects, but (according to Cott 1964*a*) other intruders are attacked. Aposematic coloration can sometimes be linked with other noxious features. For example, the highly pugnacious drongos show exotic coloration and plumages and have elaborate tails. One Asiatic cuckoo is apparently a drongo mimic.

Aposematic coloration need not be associated directly with noxious characteristics to be effective. Owing to the tendency of predators to generalize cues linked with noxious stimuli, one might envisage a very loose Batesian effect in which some protection is conferred by having warning coloration even when other cues are widely different from those of noxious species. This protection may be mainly related to naive or semi-naive predators, although the possibility cannot be ruled out that predators have some innate recognition of warning coloration. However, if predators evolved an innate recognition of general warning coloration, then one must explain why it does not evolve in all defenceless species; put another way, an innate system may be unstable owing to evolutionary exploitation of the predator's response. Precise Batesian mimics are rare in birds, but do occur (e.g. *Oriolus* and *Philemon* in Indonesia; see Cott 1940, 1964*a*).

(ii) *Protean defence*, *flash coloration*, *etc.*

The term 'protean defence' has been used to describe adaptations which confuse a predator during its attack (Humphries & Driver 1970). The eyespots of peacocks and other phasianids, and extended plumes like those of birds of paradise (some of which also congregate in lek displays) could possibly serve to confuse predators at a time when the birds are otherwise preoccupied. Other aspects of plumage may act as flash patterns when the bird takes flight in response to a predatory attack. Many normally cryptic birds show flash colorations on taking flight, e.g. the underwing on waders (many of which are cryptic) consists of black–white bars. These flash colours may act both as protean defence and/or as 'perception advertisement' signals in which the prey communicate to the predator that the predator has been sighted (Hingston 1933, Smythe 1970, Alcock 1975; see also §3*c*(iv)).

There may be other subtle types of surprise coloration in birds. For instance, the striking pharyngeal coloration found in gaping nestlings is generally assumed solely to be a releaser for the parent to give food. Nestlings will also gape when a predator arrives at the nest. Even if the startling effect persists only a very short time, this may still confer a selective advantage if it occasionally enables a parent to return to and defend the nest before all the young are killed. Similar interpretations may apply to rare departures from extreme crypsis found in young birds. The young of the greater spotted woodpecker, *Dendrocops major*, has a scarlet cap far brighter than that of its parents, and the crown of the lesser spotted woodpecker, *D. minor*, is scarlet (and white in the adult female). A predator investigating a nest hole may be surprised by sudden appearance of such colours (Hingston 1933). The bright red beak of the nestling waterhen, the vermilion-red crown patch of the nestling red-crested grebe, and the vermilion wattles on the head of coot nestlings may have similar functions. They are certainly inexplicable in terms of sexual selection or intra-specific threat, being lost before maturity.

(iii) *Bright coloration and prey that are relatively difficult to catch: the 'unprofitable prey' theory*

There is another way in which conspicuous plumage may act in a sense as warning (aposematic) coloration to a predator. A predator is expected to learn the most efficient strategy of catching prey (maximum capture rate during hunting). Various mathematical models are available which discuss the optimum strategy to maximize net energy gain (through captures) with time (see review by Schoener 1971). Faced with a selection of possible prey types within its habitat, a predator may learn (or evolve) a strategy for concentrating effort on an optimal set of prey items; i.e. those that are more 'profitable' to the predator measured as the effect that expenditure on each type will have on Darwinian fitness. Obviously, the probability of eventual capture of a prey item will be a vital parameter determining the cost: benefit ratio to the predator of pursuit versus withdrawal. That effort wasted on prey that are very difficult to catch can lead to exactly parallel adaptations to distastefulness (e.g. aposematic coloration; Batesian mimicry) has been envisaged for some time (Jones 1932, Hingston 1933, Lindroth 1972, Thompson 1973, Gibson 1974).

Suppose that certain birds have generally such good vision and escape potentiality *as mature adults* that they rate as 'unprofitable' for many of the commoner predators. By 'unprofitable' we imply that for the decision (withdraw or continue) open to a predator on detecting a potential prey, the balance is that the probable future gain in fitness owing to continuing the predatory attack (further stalking; pursuit, etc.), should be less than the probable future gain in fitness owing to withdrawing in order to search for more 'profitable' prey, inclusive of search costs. We express this balance in the form

$$(A) < (B). \tag{1}$$

Learning processes should, by selection adjusting the reward values of positive reinforcements (captures and eating) and negative reinforcements (expenditure of effort in the absence of positive reinforcement), operate to maximize Darwinian fitness. This learning procedure will be facilitated by bright coloration and distinctiveness, provided that the benefits to the prey of a quick withdrawal of a non-naive predator outweigh the disadvantages of being more conspicuous to naive predators.

If $(A) < (B)$ for the predator, then we can explain its withdrawal without difficulty, and given that it learns to withdraw, we can also explain the increased conspicuousness. Provided that on rare occasions a naive predator does capture an 'unprofitable' prey, selection will act to enhance prey cues that facilitate learning and which reduce this probability to a minimum.

There are two important caveats. First, the enhanced cues must not significantly affect the prey's escape, otherwise the condition becomes $(A) > (B)$ and the predator learns to continue the attack. Second, bright coloration will evolve mainly where it makes the bird more distinctive and memorable, rather than where it increases the probability of being noticed in the first place. A male bird (such as polygamous, lek-displaying males common in gallinaceous groups) may be so conspicuous anyhow during the breeding season that bright colours and exotic plumage do little to increase this liability. The opposite is likely where the bird is normally not already vulnerably conspicuous, especially where conspicuousness may lead predators towards the nest. Here crypsis would seem the more likely adaptation. Hence where the female alone incubates the eggs, and the male practises lekking, the maximum degree of dimorphism may be anticipated.

Whether the relation $(A) < (B)$ holds for predators of adult birds is difficult to establish. It may be commoner for mammal predators than for hawks, because a mammal cannot continue pursuit if the prey takes to the air.

Obviously for colonial species living in exposed environments (many sea-birds, flamingoes, etc.) crypsis may again be an impractical solution for all but chicks. Adult sea birds often show white parts on the plumage, or may be totally white (or pink in flamingoes), and are hence very conspicuous against most land backgrounds. The chicks are invariably cryptic, however. Because of the chicks' negligible chances of escape after being perceived by the predator, the effect would undoubtedly be $(A) > (B)$, favouring crypsis. But because there are often several hundred pairs of vigilant eyes, then for adults it is likely that $(A) < (B)$, favouring conspicuousness.

In less social species the $(A) < (B)$ effect may be less pronounced. It is often just the breeding male that is aposematically coloured. These males are typically pugnacious and in peak condition with high escape abilities. In addition, their bright coloration often persists only during the breeding season – when a spate of young will be available – making it more likely that $(A) < (B)$ for mature adults.

In summary, this theory demands that brightly-coloured individuals (often males) are unprofitable relative to alternative prey. This strategy is unlikely to evolve where, as a result, it throws extra predation risk on to the eggs, mates and young of a given conspicuous male (cf. conditions necessary for the 'deflexion' theory, §3*c*(v)). It will often be associated with the following conditions:

(i) dispersal of the sexes after mating; parental care by one sex only;
(ii) adult males more difficult to catch than alternative prey;
(iii) most predators experienced, i.e. predator population fairly static;
(iv) tendencies towards lekking and gregariousness: this enhances the chances that a predator will be sighted early.

(iv) *Perception advertisement*

Features such as wing- and underside-flashing in many birds are often interpreted as warnings for nearby conspecifics (social signals, § 3*d*). The same applies to alarm calls. Kin selection (Maynard Smith 1965) or reciprocal altruism (Trivers 1971) are generally invoked to account for the evolution of such traits. A second interpretation is that the signaller itself benefits immediately by giving the signal, even though nearby individuals may also benefit incidentally. In the confusion following the signal, the signaller may run least risk of capture because it knows the whereabouts of the predator (Charnov & Krebs 1975).

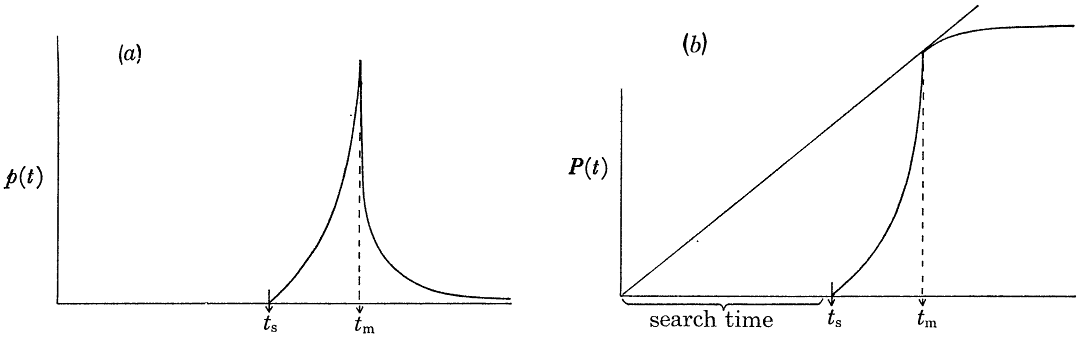

FIGURE 1. The predator takes a mean time cost t_s to search for and sight a prey individual that is unaware of the predator's presence. In (*a*) the probability $p(t)$ of eventual capture of the prey (within the predator's critical expenditure) increases as the predator gets closer. At t_m the prey sees the predator, and $p(t)$ may then decrease very rapidly (though not necessarily to zero), depending on how close the predator has managed to get before it is perceived at t_m. In (*b*), $P(t) = \int p(t)\,dt$ is plotted; it is optimal for the predator to give up the pursuit at the time cost given by the tangent (slope S_{max}) to $P(t)$ drawn from the origin. For the case given in (*b*), the predator should give up at the moment it is perceived (at t_m). Continuation of the predatory attack is favourable only when $S_{max} < dP(t_m)/dt$.

However, a variant of the 'unprofitable prey' theory may be the most plausible interpretation of alarm flashing and alarm calls. The prey may be unprofitable because it has perceived the predator and is therefore difficult to catch. This idea undoubtedly goes back to Hingston (1933; see also Smythe 1970); we attempt a more detailed and rigorous treatment.

Suppose that a predator sights a prey before the prey sights the predator. Let the instantaneous probability of capture of the prey through time that the predator approaches be $p(t)$. We shall define $p(t)$ as the expected probability that the predator will be successful in capturing a particular prey *within a certain critical expenditure of time and effort*, to be set by the 'value' of the prey to the predator and by the maximum benefit/cost obtainable from the system as a whole during a given (long) hunting time T. It seems likely that the mean form of $p(t)$ will be exponential-increasing, if the prey remains unaware (see figure 1*a*). At the moment t_m that the predator is perceived by the prey, the mean probability of capture of a prey with good escape possibilities will decline very steeply owing to the prey's avoidance reactions, or because the prey is ready to respond should this become necessary.

It is possible to deduce the optimal response for the predator as follows. Where t_s is the search time taken to find an unaware prey, then $p(t < t_s) = 0$. Selection will favour a predator response which maximizes the probable number of prey captures during time T, i.e. which maximizes its rate of captures. The optimal predator strategy can be deducted from optimal-foraging and resource-assessment theory (see Charnov 1976, Parker & Stuart 1976), which is stated verbally in equation (1). An approximate rule for the predation case is that (in the absence of prey capture) the predator should persist for an optimal time (t_o) derived as follows (see figure 1*b*). We define

$$P(t) = \int p(t)\,\mathrm{d}t,$$

and then the optimal persistence time is set by the tangent drawn to $P(t)$ from the origin (see figure 1*b*). This can favour continuation of the attack to time $t_o < t_m$, given by

$$\frac{P(t_o)}{t_o} = \frac{\mathrm{d}P(t_o)}{\mathrm{d}t}, \tag{2}$$

in the case where the gradient of $P(t)$ at the instant (t_m) after perception exceeds the tangent slope. Otherwise the attack should stop at t_m (i.e. $t_o = t_m$).

It is clear that owing to the abrupt reduction in $p(t)$ at t_m, there is a high probability that the tangent will touch $P(t)$ at the discontinuity at t_m. Thus selection will favour a predator's withdrawing at t_m (the moment of perception of the predator by the prey) provided that

$$\frac{P(t_m)}{t_m} > \frac{\mathrm{d}P(t > t_m)}{\mathrm{d}t}. \tag{3}$$

For the example illustrated in figure 1*b*, certainly t_m would be the optimal withdrawal or giving up point for the predator. However it must be noted that the most critical assessment to be made by the predator concerns the probability of capture at t_m. This decision is likely to be affected mainly by the closeness of predator and prey at the moment of perception and flight by the prey; where the predator gets very close, or strikes before the prey begins escape then clearly the inequality can be reversed and the predator will be under selection to show pursuit. Though the model so far is given mainly in relation to optimal predator strategy with only one prey type, it is not much altered by the inclusion of *n* prey types. The rule then becomes that where $S_{\max}$ is the maximum gain rate obtainable overall from the system during time T (equivalent to $P(t_o)/t_o$ for the single prey-type case), then

$$S_{\max} > \mathrm{d}P(t_m)/\mathrm{d}t \tag{4}$$

for withdrawal of the predator at t_m. When the sign is reversed (predator close enough) the predator should show pursuit. Thus again, the sudden decrease in $p(t)$ at t_m makes t_m the critical moment for a change in predator response to either pursuit or withdrawal.

When perception occurs early enough for (3) and (4) to be satisfied, then provided that $p(t > t_m) > 0$ (i.e. where there is at least a small chance that the prey may be caught during escape), then it is advantageous for the prey (as well as for the predator) that the interaction should cease and the predator withdraw as soon as it is seen by the prey. Even if $p(t > t_m)$ approaches 0, the time and effort wasted in the continual escapes would be costly for the prey as well as predator (Smythe 1970). Under such circumstances it is to the mutual (but not necessarily equal) benefit of both prey and predator that the perception should be advertised.

If signals advertising perception are obvious to the stalking predator, they are also likely to be evident to nearby prey. Selection is likely to favour altering or avoidance reactions by prey in response to such cues; this appears to have occurred in nature.

Perhaps one of the greatest problems in the evolution of innate communication mechanisms is that a rare mutant with a novel signal has no advantage when there are no respondents to the signal. Similarly, a rare potential respondent has no advantage when there are no individuals that give the signal. It is well known to ethologists that signals tend to be developed out of established behaviour that can induce at least a partial response of the appropriate nature. Thus many perception advertisement signals appear to accentuate the fact that the prey is about to flee, e.g. many mammals have white rump colorations that are most conspicuous during escape. In birds, the conspicuous flashings (particularly on the underside of the wings) are very likely to serve this function. Many birds, on sighting a ground predator, fly a small distance to a safer vantage point from where they view the predator. As a wader flock (especially of knot, *Calidris canuta*) is approached, some individuals often raise their wings (showing the conspicuous bars); as the observer approaches even closer, the flock takes flight. In addition to flash cues, many species also advertise their perception of a predator by alarm calls.

The above discussion assumes that the predator response must be related to the stage at which perception is advertised. Consider now a learned predator response. A mutant that advertises perception in an otherwise non-signalling population will always give negative reinforcement to local predators for as long as it is successful (i.e. alive), irrespective of distance between it and the predator at the moment of perception. Such a mutant may 'teach' local predators to avoid it by random chance. If the signalling mutant spreads, predators can learn the correct association between distance and optimal response.

It might be argued that when signallers are frequent, selection acts against them because although they teach predators to avoid them more quickly *outside* the threshold distance for pursuit, they also teach it more quickly to give chase when perception occurs *within* the threshold distance. There are several reasons why this may not be so:

(i) prey may sometimes be captured without having had chance to signal;
(ii) flash colours and other sudden noticeable stimuli will generally have a startling effect (protean defence) at very close range, especially with naive predators;
(iii) benefits (avoiding waste of time and energy) of having the predator withdraw quickly in the large number of cases where perception occurs outside the pursuit distance, may outweigh the disadvantage of the faster learning to pursue within the threshold distance. If the predator will not withdraw until a signal is given, signalling is always favoured even though the predator will not always withdraw.

We have assumed that the predator is stalking the prey before the prey sees the predator. Advertising perception to an unaware predator (the reverse case) may seem disadvantageous to the prey since it may attract an attack if the predator is naive. But if most predators are experienced, and usually withdraw, signalling to an unaware predator may be favoured because:

(i) the prey can resume its activities more quickly; also if eventual sighting is likely then the signal would have to be given anyway;
(ii) alerting nearby conspecifics is advantageous to the signaller because it helps to prevent the formation of search images (Trivers 1971);
(iii) it may prevent capture of close kin (see Hamilton 1964, Maynard Smith 1965).

Hence whether the prey animal should freeze or signal depends on the above factors, on the probability that the predator will withdraw in response to the signal, and on the probability of capture if it doesn't withdraw. Smythe (1970) observed that *Dolichotis patagonum* (Caviidae) signals ('stotts') when an observer is likely to walk into sensory contact with it; when this is unlikely, the rodent freezes.

'Indiscriminate signalling' (i.e. independent of predator awareness) occurs in many alarm calls and anti-predator displays. Mobbing behaviour may be an extension of this pattern. In a sense, brightly coloured 'unprofitable prey' (cf. § 3*c* (iii)) are indiscriminate signallers. A high probability that a given predatory episode will result in escape of the prey may favour general aposematic coloration, especially where prey are exposed and therefore already conspicuous (e.g. males of lekking species). If on the other hand the prey lives in cover, conspicuous coloration may be disadvantageous because predators may be attracted and can approach unnoticed. Nothing is lost, however, by displaying flash patterns once it has already been seen by the predator, and if the perception advertisement theory holds, much may be gained.

Selection will favour sensitivity to the perception advertisement signals of other nearby prey, whether conspecific or not, and this is a common adaptation. A second form of selection may also be expected: convergence in the signals. There are obvious parallels with Müllerian mimicry. Warning calls and flash colorations of many birds are often remarkably convergent, as are the rump patterns of many ungulates (Guthrie 1971). The possibilities for Batesian mimicry are also clear. Provided that a predator cannot discriminate at a given distance between two species, one 'profitable' and the other 'unprofitable', it would learn to withdraw if the mimic is relatively rare.

(v) *Conspicuousness as a means of deflecting predators from vulnerable young: the 'deflexion' theory*

Brooding parents of many ground-nesting birds show 'injury feigning' displays such as falling, lying on one side, leg-trailing, wing-dragging, etc. at some distance from the nest (Cott 1964*a*, Lack 1968). There is little doubt that these patterns evolved to lure the predator from the nest. This behaviour must involve at least some increased risk of predation to the parent.

Cott (1964*a*) has seen the conspicuous coloration of certain male anatids and phasianids as a means of deflecting 'the attention of enemies away from the more (incubating parent, or nestlings) to the less biologically valuable or vulnerable members of a social group'. We feel that this explanation is unlikely for those birds in which the sexes separate from each other after mating because there is here little chance that the deflexion will operate to the advantage of a given male's progeny. A more likely interpretation is that females disperse from the lek areas to breed because the male coloration and displays attract naive predators (Brown 1964, Crook 1965, Alexander 1975).

Although promiscuous birds appear to be poor contenders for the deflexion theory, it seems plausible for sexual dimorphism found in many monogamous birds, or polygynous birds where the sexes stay together after mating. The deflexion theory contrasts markedly with the 'unprofitable prey' hypothesis. With deflexion, the function is to attract predators so as to deflect them from one's mate and offspring; this implies increased risk to the parent at some (greater) reduction in risk to the young (see also Perrins 1968). With unprofitable prey, the function is to 'teach' predators to withdraw; partly at the expense of conspecific females and young. Which solution will be favourable will depend on the nature of the predation risks and on the mating system.

For the evolution of deflexion coloration, we predict the following conditions:

(i) males stay in close association with their families, probably vigilant at some distance from the nest site (i.e. guarding rather than rearing);

(ii) *either* most predators encountering the vigilant male are naive (here the profitability of pursuit can either be favourable or unfavourable to the predator), *or* most predators are experienced, and attack is favourable to the predator (it learns to continue attack);

(iii) Depending on the costs of moulting, bright coloration will be present mainly during the time that guarding is taking place, so that the disadvantage to the guarding male is restricted to the time it can confer an advantage on the offspring;

(iv) for a given predation risk (single visit of a predator to the locality in which the bird is breeding) there should be a high value of the ratio

$$k = \frac{\text{increase in probability of survival of the young}}{\text{decrease in probability of survival of the parent}};$$

the greater the number of broods that can be produced before age-dependent mortality becomes significant, the greater the necessary value of k;

(v) poor prospects of finding a second mate if a male deserts without guarding; the higher the benefit of promiscuity, the greater the necessary value of k as defined above; a high degree of synchrony of breeding and a short breeding season would act to reduce male search prospects (see also Maynard Smith 1977, Emlen & Oring 1977, Knowlton 1979).

(*d*) *Social signals other than threat*

There can be little doubt that however it initially arose, much of bird coloration is now used by conspecific individuals to convey information. For instance, individuals clearly show alerting and avoidance to nearby alarm calls and alarm flashing, though these may have arisen through perception advertisement.

Cott (1964*a*) believed that flashings on wings and rump may serve as social signals for flock cohesion, and that certain offspring features (e.g. the white nuchal band of plover chicks) may aid the parent to relocate and reassemble the brood. He argued that some specifically distinctive characters may serve 'to prevent confusion with other members of closely related species' (e.g. the speculum in ducks, and the head and neck features of penguins). Perhaps the best known colour signals that have a 'social' function in birds would be the feeding releasers in species with nidicolous young. The brilliant mouth colorations visible during gaping of nestlings release the parent's feeding responses (see, for example, Cott 1964*a*). (They may also relate to protean defence, see § 3*c* (ii).) When the young thrust their heads into the parent's mouth, it is then common for the parent to have a brightly-coloured mouth lining.

There is sometimes a conflict of interests between the individual that receives the information and that which gives it. Often both individuals gain (though not necessarily equally) and this will lead to specialization of the signal. But sometimes the response of the receiver will be against the best interests of the information-giver, favouring a reduction of the information given.

This can lead to various colour conflicts. In seabirds, for example, the best coloration for 'hunting camouflage' may be most conspicuous to competitors.

Phillips (1962) noted that white belly, front, and head coloration was more prevalent in seabirds that swim and dive, and related this to the fact that fish notice black more than white when viewing from below, against the water surface. The dark, dorsal plumage may help to reduce exposure to ultraviolet light. However, it may also be less likely to attract competitors to the same feeding area, since white is generally conspicuous in sea environments (Simmons 1972). The story is further complicated by the facts that it may sometimes be advantageous to attract conspecifics during feeding (e.g. pelicans cooperate to drive fish into shallow water), favouring whiteness; while dark coloration can also be effective as hunting camouflage for feeding at the water surface or for food-piracy (Simmons 1972).

Simmons stresses that because there is so little predation on adult seabirds, their coloration is determined entirely by considerations of feeding efficiency. Much remains controversial, however, even with respect to what is conspicuous. Ashmole & Ashmole (1967) note that the pure white coloration of the fairy tern, *Gygis alba*, a crepuscular feeder, makes it very cryptic against the sky in dim light (see also Cowan 1972, Phillips 1962).

4. Analysis of the coloration of the birds of Europe, North Africa and the Middle East by multiple regression

(*a*) *Introduction*

When the pages of any field guide to bird identification are examined, one finds that some correlations between coloration and other aspects of the general and breeding ecology of birds are immediately obvious and have been recognized previously on many occasions. For example, the correlation between polygamy and/or promiscuity and brightly coloured breeding males was pointed out long ago. In an attempt to obtain objective confirmation of the reality of these apparent relations and to identify other, less obvious, relations, an analysis by multiple regression was carried out on the coloration of birds that regularly breed and/or winter in the Western Palaearctic. More precisely, the area covered comprises Europe and the Mediterranean basin. It includes the Canary Islands, Madeira, and the Azores, and the North African region north of a line from these islands to the Gulf of Suez, the line extending eastwards to include the northern tip of the Persian Gulf. From here, the boundary runs northwards passing through Iran, the middle of the Caspian Sea to the Urals, and on to the Arctic. In its northern part it includes Novaya Zemblya, Spitsbergen and Iceland.

This area was chosen for three major reasons. First, it more or less coincides with, though it is slightly smaller than, the area covered in the book by Heinzel, Fitter & Parslow (1974) from which details of coloration were taken. Second, it seems to represent a reasonably naturally defined geographical area. Third, and perhaps most important, beyond the limits of this area the social and breeding ecology of the avifauna is much less well known, thus preventing inclusion in an analysis by multiple regression.

(*b*) *The dependent variables: the scoring of bird coloration*

Seven regions of a bird's body were recognized and scored for colour. These were: bill, crown, head, back, front, belly and legs (figure 2). In addition, two areas of flash coloration were recognized: (i) wing bars, rump and outer tail feathers, and (ii) underside of wings and underside of tail. The reason for lumping the 'flash' regions of the body in these particular combinations was that wing bars, rump, and outer tail feathers are visible from the side, rear and above as soon as the bird prepares for take-off. In contrast, the underside of the wings and tail are seen from beneath when the bird is already in the air, or perhaps from the front as the bird comes in to land. Thus (i) and (ii) may have rather different ecological implications.

Clearly bird coloration does not vary along a single spectrum. For example, a body region could be scored according to a light/dark scale, or a degree-of-redness scale, or a degree-of-mottling scale and so on. The main interest in this paper, however, is the cryptic/conspicuous (or degree of conspicuousness or brightness) scale. Degree of conspicuousness, however, cannot be divorced from the context of other variables such as the distance of perception, background colour, and degree of movement of the potential prey. Selection seems often to have favoured animal coloration that is cryptic when viewed from a distance but aposematic when viewed closely or that is cryptic when the animal is stationary and viewed against one background, but aposematic when the animal moves and/or is viewed against another background (see, for example, Baker 1970).

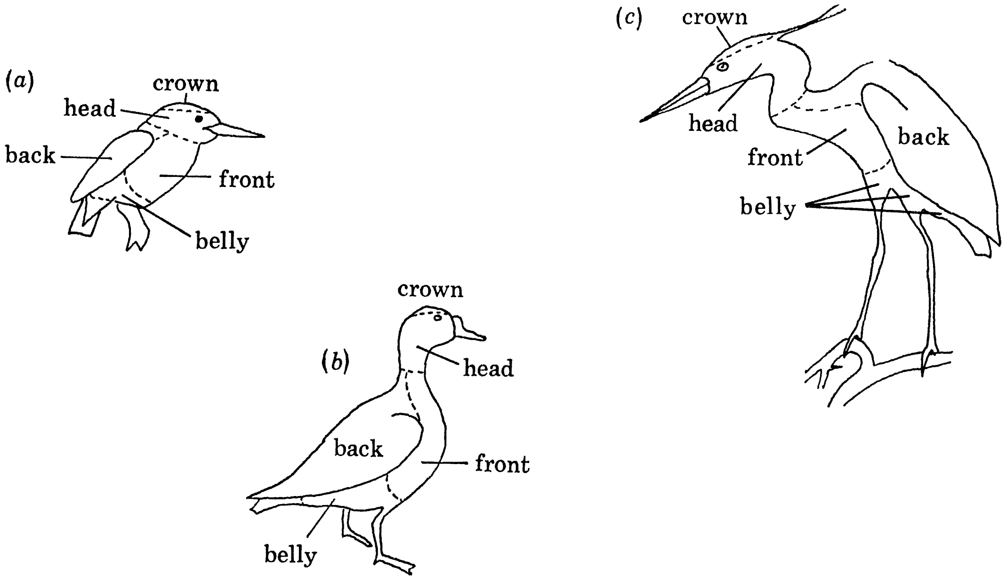

Figure 2. Three examples of the delimitation of plumage regions.

The three birds illustrated (*a*, *b* and *c*) each raise different problems in the delimitation of the various body regions when scoring for colour.

Crown is usually a relatively discrete, easily delimited region.

Head includes the crown and extends down to a position that varies from species to species. The criterion adopted was to include all parts that would move when the bird turned its head. The head of short-necked birds (*a*) was easier to delimit than that of long-necked birds (*b* and *c*). The colour of the iris was included in the head coloration as also was any extension of the base of the bill (as in *b*). The base of the bill was also scored in *bill* coloration. 'Collars' and other neck markings were excluded from the head region but were included in the *front* and/or *back* region.

Front was delimited as the region visible from the front and side as far dorsally as the lower edge of the wings and posteriorly nearly as far as the legs.

Back includes all parts (excluding head and crown) visible from above and from the side when the bird is sitting with wings folded as far ventrally as the lower edge of the wings. It includes any part of the upper surface of the tail that is exposed in such a position but excludes the rump and side tail feathers that only become visible when the bird takes flight. These features, along with wing bars, are scored as *upper surface flash* coloration. Any part of the wing bar feathers that remain visible while the bird is at rest, however, also contribute to the score for *back* coloration.

Belly extends from just anterior to the legs back as far as the base of the tail. It was conceived as the area that would be concealed if the bird were to 'sit' on the ground. Feathers covering the tops of the legs were scored as *belly* rather than *legs*. Body feathers, as opposed to tail feathers, that extend posteriorly from about the cloacal opening (see *a*) were scored (along with the under surface of the wings and any side tail feathers that are visible from below as well as from above) as *under surface flash* coloration rather than as belly.

In order to produce a single scale for degree of conspicuousness, therefore, it is necessary to view the bird in a single environmental context. In the present case, degree of conspicuousness has been scored as we consider it would appear at close quarters to a potential predator once the latter had either distinguished the bird from its surroundings or had accidentally arrived so close to the bird that the latter was at risk of immediate capture once noticed. With these predator–prey situations in mind, the following scoring system was developed and applied to the bird illustrations in Heinzel *et al.* (1974).

Each of the nine regions of the body was coded for each age/sex/season category for each species or race on a scale for 'conspicuousness' from 0 to 5 (0 = minimum conspicuousness, 5 = maximum). A uniform neutral colour (brown or brown-grey) was given a zero rating. Increase in darkness or lightness of a uniform colour displaced the rating towards a maximum of 3, which was scored when the body region concerned is uniformly white or black. Decrease in uniformity displaces the rating towards a maximum of 4 which was given regions with marked black/white, black/pale blue, white/dark blue, etc. contrast. Increased red content of a general brown coloration displaced the rating towards a maximum of 4 for a uniform bright chestnut coloration. Pink or dullish-yellow coloration was also rated at 4. A rating of 5 was reserved for bright red or yellow coloration or even less bright red or yellow if in association with black or some other bright colour such as blue or green. As far as the general body plumage was concerned, each region (i.e. crown, head, back, front and belly) was viewed in isolation from the adjacent regions. The bill and legs, on the other hand, and the wing bars/rump and underwing/undertail regions were weighted in addition according to the degree of contrast with the relevant part of the body. Hence, a black bill was given a 3 rating if attached to a neutral head but a 2 rating if attached to a black head and a 4 rating if attached to a white head.

Five different age/sex/season categories were recognized and scored separately for each species. These were: (i) juveniles, (ii) adult females in the breeding season, (iii) adult females in the non-breeding season, (iv) adult males in the breeding season, and (v) adult males in the non-breeding season. In addition age and sex differences were obtained by subtracting, for each region of the body, the score for one age/sex/season category from another. Six such categories were analysed: (i) adult male–female differences in the breeding season, (ii) adult male–female differences in the non-breeding season, (iii) adult male breeding/non-breeding differences, (iv) adult female breeding/non-breeding differences, (v) adult breeding male/juvenile, and (vi) adult breeding female/juvenile.

Given nine regions of the body for each of five age/sex/season categories and six categories of age/sex/season differences, it was necessary to obtain 99 codings for each species. A total of 516 species were scored thus giving 51084 separate codings for conspicuousness and differences in conspicuousness available for entry as dependent variables into a multiple regression analysis.

(c) *The independent variables: the scoring of aspects of the feeding and breeding ecology of birds*

Many different aspects of the breeding and feeding ecology of birds seem likely to be associated with different degrees of conspicuousness of different regions of the body. In order to employ multiple regression analysis as a tool to identify such associations it is necessary not only to score conspicuousness along a linear spectrum but also to produce a linear scale for the different ecological aspects.

Some variables, e.g. body length, can be entered into the regression according to their numerical value and no interpretation is necessary. The majority, however, require coding in much the same way as coloration. The following list describes briefly each of the independent variables entered into the analysis, the coding scheme used to attempt to generate a linear scale, and the mean, maximum and minimum values. The variables have been grouped according to the ecological category that they describe. Each variable is introduced by the name given to it for computer analysis and which is used later for shorthand in the presentation of the calculated regression equations.

(i) *Morphological*

Only one morphological variable was used.

LENGTH: the length (centimetres) of the bird from the tip of the bill to the tip of the tail. Data were obtained from Heinzel *et al.* (1974). The extreme values of this variable were 170 for the Dalmatian pelican, *Pelecanus crispus*, and 9 for the goldcrest, *Regulus regulus* and firecrest, *R. ignicapillus*. (Mean value = 35.3.)

(ii) *Latitudinal*

Four latitudinal variables were entered into the analysis, two relating to the breeding range and two relating to the non-breeding range. In all cases the numerical value of the relevant latitude was used without transformation. Data were obtained from Baker (1978), Heinzel *et al.* (1974), Moreau (1972), Voous (1960) and Vaurie (1959, 1965).

NBREED: the northernmost point of the breeding range within the study area. The minimum value was therefore fixed at 28. The maximum value of 85 was given to various Arctic-breeding sea birds, e.g. Ivory gull, *Pagophila eburnea*. The mean value was 58.2.

SBREED: the southernmost point of the breeding range. The maximum value (80) was scored by Ross's gull, *Rhodestethia rosea*. As far as the minimum value was concerned, however, it was thought that although the scale may be linear as far south as the equator, the use of negative values for species of which the breeding range extended into the southern hemisphere may produce a non-linear scale. For example, conditions experienced by birds breeding in the southern summer at latitude 35° S may be more similar to conditions experienced by birds breeding in the northern summer at middle latitudes than to conditions experienced by birds breeding near the equator. Species like the kestrel, *Falco tinnunculus*, that extend their breeding range into the southern hemisphere, therefore, were nevertheless given a minimum value of 0. Measured in this way, NBREED and SBREED together were assumed to reflect the climatic extremes to which the species is subjected during the breeding season. Mean values for SBREED was 34.9.

NWINTER: the northernmost point of the non-breeding range during winter in the northern hemisphere. Again the maximum value was scored by some Arctic sea birds. The minimum value was scored by those species for which the entire population consists of transequatorial migrants. In this case negative values were considered to be justified. The mean value was 44.4.

SWINTER: the southernmost point of the non-breeding range during winter in the Northern Hemisphere. The maximum value (70) was still scored by some Arctic sea birds. The minimum value (−60) was scored by the Arctic tern, *Sterna paradisaea*, with many land birds scoring −35. The mean value was 12.9.

(iii) *General feeding ecology*

Three variables were entered into the analysis on data obtained from Heinzel *et al.* (1974).

DAYNIGHT: indicated whether feeding occurred chiefly by night or by day. It was scored on a binary system. Nocturnal feeders such as the night heron, *Nycticorax nycticorax*, all owls (Tytonidae, Strigidae) and nightjars (Caprimulgidae) were coded 0 and all other species, which are primarily diurnal feeders, were coded 1. Mean score was 0.96.

DIET: indicated whether the species fed chiefly on seeds, fruit, or leaves (0 scored) other animals either vertebrate or invertebrate (2 scored), or a more or less equal mixture of both (1 scored). Mean score was 1.47.

HEIGHTAG: the relative mean height above ground level that the species occurs while searching for, obtaining, and handling its food. It was scored on a 0 to 5 scale. A score of 0 was given to divers (Gaviidae), grebes (Podicipitidae), ducks, geese and swans (Anatidae), etc. whereas a score of 5 was reserved for most birds of prey (Accipitridae, Falconidae), swifts (Apodidae), and swallows and martins (Hirundinidae). Mean score was 1.83.

(iv) *Degree of gregariousness*

Two variables were entered into the analysis.

BRGREG: the degree of gregariousness during incubation. A scale of 1 to 5 was used. The scale was not, however, a simple reflexion of the degree of clumping of the species during incubation. Instead the scale was intended to represent gregariousness of incubating birds as monitored by the visual sense and is therefore a measure of how many incubating birds are visible at the same time to an incoming predator and how many other incubating conspecifics are visible to each incubating bird. A maximum score of 5 was given therefore to colonial sea birds such as the kittiwake, *Rissa tridactyla*, and gannet, *Sula bassana*. A minimum score of 1, however, was given not only to solitary nesters in the visual sense but also to all hole-nesters, whether or not large numbers of birds nested in close proximity. Data were obtained from Harrison (1975). Mean score was 1.51.

FDGREG: the degree of gregariousness while feeding, as opposed to roosting, during the non-breeding season. A scale of 1 to 5 was used; a score of 1 being given to all solitary feeders, such as most birds of prey, and a score of 5 to those such as the flamingo, *Phoenicopterus ruber*, and many ducks and geese that feed in large flocks outside the breeding season. Data were obtained from Heinzel *et al.* (1974), Vaurie (1959, 1965) and Voous (1960). Mean score was 2.26.

(v) *Breeding season* (*non-social*)

Three variables were entered into the analysis, two of which were concerned with degree of exposure during incubation. Data were obtained from Harrison (1975).

FEXINC: indicated the degree of exposure of the female while in an incubation position. A scale of 0 to 5 was used. A score of 0 was given to females that either do not incubate or that nest in holes or domed nests. A score of 5 was given to females that incubate completely exposed on the ground. Mean score was 2.67.

MEXINC: indicated the degree of exposure of the male while in an incubation position. The scale was the same as for the female. MEXINC and FEXINC only differed, therefore, in species in which only one sex incubates. Even then they were the same (i.e. zero) for hole-nesting species. Scored in this way, MEXINC monitors the influence of having one or both sexes incubate for species that are exposed while incubating. Mean score was 1.69.

NOBROODS: indicated the usual number of broods per breeding season. A scale of 1 to 5 was used; 1 being scored for single-brooded species, 3 for double-brooded species and 5 for treble-brooded species. Scores of 2 and 4 were used when the number of broods varied between 1 and 2 and 2 and 3 respectively. Mean score was 1.64.

(vi) *Male parental care*

Before beginning the analysis it was anticipated that the different phases of male parental care would influence coloration in different ways. If this were so, a single estimate of male parental investment would be a poor indicator of the way that selection has operated on the male parental care/coloration association. Eventually it was decided to recognize four different aspects of male parental care. Data were obtained from Harrison (1975).

POLYGAMY: indicated the number of females likely to be inseminated by a successful male. Scored in this way it was assumed that POLYGAMY was a measure both of the intensity of male: male competition and of the variance of male reproductive success. A scale of from 1 to 5 was used, being applied as follows: 1 = monogamous pair bonding; 2 = occasional or frequent bigamous pair bonding (e.g. pied flycatcher, *Ficedula hypoleuca*); 3 = sequential polygamy (e.g. wren, *Troglodytes troglodytes*); 4 = harem polygamy (e.g. pheasant, *Phasianus colchicus*); 5 = promiscuity, both when the male displays gregariously on a lek (e.g. ruff, *Philomachus pugnax* and when it displays solitarily (e.g. golden pheasant *Chrysolophys pictus*). A similar scale for polyandry was not entered into the analysis because few species were involved and because even where polyandry is suspected, there is a shortage of information. Mean score was 1.09.

MINC: indicated how much time the male spent incubating the eggs. A scale of from 0 to 5 was used which was applied as follows: 0 = only female incubates; 1 = incubation almost entirely by female; 2 = incubation mainly by female; 3 = both sexes incubate; 4 = incubation mainly by male; 5 = only male incubates. Mean score was 1.52.

MGUARD: indicated how much time the male spent guarding the nest from a distance, i.e. away from the nest but within the breeding territory. It is therefore a measure of the amount of time and effort the male is likely to invest in distracting or diverting potential predators away from the nest. A scale of 0 to 5 was used. A zero score was given for two types of male, those that are promiscuous and those that take sole charge of incubation. In both cases the male serves a minimal distractive function. A score of 5 was given for those species in which only the female incubates but in which the male stays near the female throughout the stages of egg-laying, incubation, feeding and caring for the young. Those ducks in which the male finally leaves the female sometime during the incubation phase of this process were given a score of 3. A score of 2 was given when both sexes incubate equally. Mean score was 3.27.

MFEDYONG: indicated how much time is invested by the male in the care and/or feeding of the young. A scale of 0 to 6 was used; a zero score being given for promiscuous species and for those polygamous and monogamous species such as some ducks in which the male has no contact with the young. A score of 6 was given to those species, such as the phalaropes, *Phalaropus fulicarius* and *P. lobatus*, painted snipe *Rostratula benghalensis*, dotterel, *Eudromias morinellus*, and Andalusion hemipode, *Turnix sylvatica* in which only the male cares for the young. Those many species for which male and female feed and care for the young equally were given a score of 4. Mean score was 3.60.

(*d*) *The analysis: advantages and limitations of stepwise multiple regression as an analytical technique*

Multiple regression analysis is a statistical technique whereby, given a dependent variable, Y, and a set of independent variables X_i, $i = 1, \ldots, n$, where, in this case, $n = 17$), the best prediction equation for Y may be calculated from the n independent variables. In the present case, the analysis was carried out on the ICL 1906A/CDC 7600 joint computer system at the University of Manchester Regional Computer Centre (UMRCC), with the regression procedures of the Statistical Package for the Social Sciences (SPSS). These procedures allow multiple regression to be carried out using either a fixed or a stepwise mode or a combination of the two.

In fixed mode, all 17 of the independent variables are entered at one step, thereby giving directly the best predictive equation for Y from X_1 to X_{17}. However, with so many independent variables a great deal of information is lost by entering all of the independent variables at one step. First, the resultant equation is less likely to be a significant ($P < 0.05$) linear fit to the data than an equation containing fewer independent variables. Secondly, fewer of the independent variables show a significant relation with the dependent variable (see § 4*d* (iii)) than would be the case if only the more significant independent variables has been used.

The use of the stepwise mode resolves these problems, though it does raise other, mainly interpretative, problems. In stepwise regression the variables are entered into the regression one at a time. In the first step, the dependent variable is regressed on only one of the independent variables. The independent variable chosen is the one which gives the best prediction equation when it alone is in the regression. In the second step another independent variable is added to the regression. This variable is the one which gives the best two-term prediction equation in conjunction with the first variable. Other steps then follow, each one adding one independent variable to the regression. As each new variable is added, the significance of variables already in the regression changes. By monitoring these changes it is possible to reach far more conclusions concerning the way that the dependent variable relates to each of the independent variables than would be possible if a fixed mode had been used.

In the present case, each of the 99 dependent variables in turn was analysed with respect to the 17 independent variables. As a result of this analysis, the following statistics are available for consideration:

(i) *A predictive equation*

The dependent variable, Y, is related to the independent variables X_i (where, in this analysis, the maximum value for n is 17) by the equation:

$$Y = a + \sum_{i=1}^{n} b_i X_i,$$

where a (the intercept) is a constant and b_i are the regression coefficients, respectively, for the independent variables X_i. This multiple regression equation can then be used to predict the expected value of the dependent variable (in this case the degree of conspicuousness of a given body region) for any given Western Palaearctic bird species.

Equations should only be used if they are a significant linear fit with the data. All equations presented here show no significant ($P = 0.001$) departure from linearity. In each case the equation given is that which contains the maximum number of independent variables for which computation is possible without departing from linearity.

(ii) *The degree of explanation of the variation of the dependent variable*

Before analysis begins, all of the variation of the dependent variable is unexplained. Usually, each time an additional independent variable is entered into the multiple regression equation, the sums of squares are reduced, thus increasing the coefficient of multiple determination (R^2)

for the regression. In other words, the unexplained variation of the dependent variable is reduced. Ideally, all of the variation of the dependent variable should be explicable. This is only possible, however, if (i) the dependent and independent variables can be quantified accurately, (ii) the dependent variable is continuous, without restraint on limits, (iii) the relation between dependent and independent variables is *perfectly* linear. None of these situations obtains in the present case. The subjective nature of the quantification process and the use of integer scales restrained between narrow limits (i.e. usually between 0 and 5) all automatically limit the amount of variation that can be explained. In the present analysis, therefore, even if the variation in the dependent variable is solely a function of the independent variables being considered, a full explanation is impossible. This problem is considered further in the results section.

(iii) *Multiple regression coefficients significantly different from zero*

The dependent variable can be considered to be a significant function of a given independent variable only if the multiple regression coefficient b_i by which the two are related is significantly different from zero. Although the necessary statistics are given by the SPSS regression procedure used here, problems of interpretation arise on account of the stepwise mode of the analysis. These problems arise because although the multiple regression coefficient for an independent variable may be significant at one step, it may no longer be significant at a later step, and vice versa. The conclusions concerning bird coloration that are presented later, therefore, are the result of an *interpretation* of the stepwise multiple regression output. In order to obtain uniformity of interpretation for each analysis the following set of 'rules for interpretation' was developed.

The level of probability that the regression coefficient for any given independent variable was different from zero by chance was taken to be the minimum (= maximum significance) level achieved by that regression coefficient at any step during the stepwise procedure, as long, that is, as the overall multiple regression at that step did not depart significantly (at the 5% level) from linearity. For example, if the multiple regression coefficient for *bill* colour on LENGTH was significantly different from zero at the 2% level at step 6, but significant only at the 5% level at steps 1 to 5 and 7 to 13, and not significant even at the 10% level from steps 14 to 17, it would nevertheless be considered that *bill* colour was a significant function of LENGTH at the 2% level (given that at step 6 the overall multiple regression, containing six independent variables, did not depart significantly from linearity). There was, however, one situation in which this rule was not followed. If, at some step, entry of the independent variable D (say) causes an independent variable A that previously was significant ($P < 0.05$) to be no longer significant, then the conclusion reached depends on the fate of variable D in later steps. If D never achieves significance ($P > 0.05$), then the previous rule still applies. If on the other hand D achieves significance, but A never regains significance, then the dependent variable is considered to be a significant function of D but not of A. This last rule is based on the assumption that A was therefore selected before D only because of spurious assistance A received in explaining the variation in the dependent variable from other variables (B, C, etc.). When the masking effect of these other variables is removed by their entry into the equation, D can be seen to be more significant than A. These interpretative rules would seem to allow for the maximum advantage to be gained from the stepwise mode for multiple regression yet at the same time to reduce to a minimum the dangers of misinterpretation.

It should be noted that all of the problems inherent in the application of multiple regression analysis to variation in bird coloration that were discussed in the previous section in relation to proportion of unexplained variance are also relevant here. On account of the problems of quantification, the lack of continuously distributed dependent variables, etc. the estimates of the significance of relations are also influenced. The nature of this influence, however, is uniform and conservative, in that it always acts to reduce calculated significance levels. We may reasonably assume that any relation demonstrated between any independent variable (as scored here) and the degree of conspicuousness of a given region of a bird's body (as scored here) is a real one, and in reality is even more significant than stated. On the other hand, it follows that some relations that in our analysis do not achieve significance (at the 5% level) may in nature be significant.

(iv) *The identification of exceptional species*

The SPSS regression procedure contains options whereby, a multiple regression equation having been calculated that relates the dependent variable to the 17 independent variables, an expected value can be calculated for each case of the dependent variable. The residual (i.e. the difference between the observed and expected values of the dependent variable) is then calculated and expressed in standard deviation units. Any residual that is more than 2 standard deviations from the expected value is outside the 95% confidence limits of the calculated multiple regression equation, and can therefore be considered to be exceptional. For each region of the body for each age/sex/season group, therefore, the possibility presents itself of identifying which of the 516 species studied have a coloration that is exceptional. For such species there is the implication that some aspect of their ecology not entered into the analysis has had an overriding selective influence on their coloration during its evolution.

(v) *Variation within and between families: the problem of independence*

One of the major problems encountered in applying multiple regression techniques to biological situations is that of deciding the extent to which variables are really independent of one another. In the present case, this problem arises primarily because species are grouped into families. Within a family, species are often similarly coloured and have similar patterns of ecology and behaviour. The presence of large numbers of species within few families at the ends of a (statistical) distribution may produce significant results due to differences between families and not to differences in behaviour or ecology. By analysing all the species of a given region (516 species spread over 66 families), we have assumed that differences in coloration between families are governed by the same selective pressures as the differences in coloration between species within each family. Clearly our results could be influenced unduly by the response of certain large taxa, such as the superfamily Muscicapidae (warblers, thrushes, chats, flycatchers: 60 species in our analysis) and the family Anatidae (ducks, geese, swans: 44 species in our analysis). In order to justify our analysis, therefore, it would seem necessary first to show that the same colour responses are shown within families as between them.

This would be a very stringent and conservative test of the analysis. Part of the reason for using so many species is that in order for the independent influence of 17 variables to be unravelled by multiple regression a large number of cases (e.g. 516 as here) is desirable. To attempt the same analysis on a single group, even when it contains 60 cases as in the muscicapids, provides far less material for the independent effects to be isolated. The situation is aggravated by the fact that each group, whether taxonomic or ecological, shows relatively little variation in many of the behavioural and ecological characteristics that have been scored here as independent variables. Without such variation, of course, multiple regression analysis cannot operate. Coloration, the dependent variable, may also show little variation within taxa (e.g. gulls, birds of prey). Finally, some colour responses to ecological/behavioural variables may well vary from family to family without in any way contradicting the generality of a thesis. For example, it is argued later that the association between increased conspicuousness in the colour of the bill and increased body size may well be the result of the advantage of drawing the attention of a potential predator to the possession by the bird of a weapon. Such an effect, however, could well only apply to birds above a certain body size. A positive association between bill conspicuousness and body size in a family of large-bodied birds but not in a family of small-bodied birds, far from contradicting the generality of the thesis for bill coloration, could in fact be taken to support it.

On the one hand, therefore, there is the need to validate our analysis by showing that the coloration of birds within taxa is influenced by behaviour and ecology in the same way as between taxa. On the other hand, it can be seen that failure to find such a similarity of response does not necessarily invalidate the analysis. In the latter event, there would be a real problem in assessing the meaning of the results presented in the next section. As it happens, this problem does not arise.

A separate analysis was carried out for each taxonomic or ecological group that contained more than 25 species, this being the minimum number for which there would be any point at all in attempting a multiple regression analysis with 17 independent variables. Seven groups were analysed. These were: anatids (44 species); diurnal birds of prey (45 species); game birds (tetraonids and phasianids: 28 species); waders (56 species); larids (30 species); muscicapids (warblers, thrushes, chats, flycatchers: 60 species); and finches and buntings (30 species). For each group, 45 separate multiple regression equations were calculated corresponding to the headings given in tables 26–30 (appendix). The sign (+ or −) of each multiple regression coefficient indicated as significant ($P < 0.05$) in tables 26–30 was then entered into a 2×2 contingency table with the sign of the corresponding coefficient for the group under consideration. If the coloration of this group was influenced in the same sense as western palaearctic birds in general, a positive association should be evident. Degree of association was assessed by a χ^2 test, with Yate's correction for continuity.

Six of the seven groups showed a significant positive association between the signs of the regression coefficients and the signs of the same coefficients calculated for all 516 species. These groups were: anatids ($\chi^2 = 38.95$, $P < 0.001$); diurnal birds of prey ($\chi^2 = 4.15$, $P < 0.05$); game birds ($\chi^2 = 18.74$, $P < 0.001$); waders ($\chi^2 = 30.55$, $P < 0.001$); finches and buntings ($\chi^2 = 4.86$, $P < 0.05$); and muscicapids ($\chi^2 = 37.17$, $P < 0.001$). The only group that failed to show a significant positive association was the family Laridae ($\chi^2 = 0.00$). Whether this lack of association indicates that the relatively slight and subtle variation in the conspicuousness of gulls and terns is associated with factors different from those for other birds, or whether it simply indicates that our scoring system was relatively too crude and/or subjective to cope with such little variation cannot easily be decided. By and large, however, this analysis suggests that variation in coloration within families is associated in the same way with the same behavioural and ecological factors as variation between families.

5. Results

The information obtained from this analysis of bird coloration has been collected into a number of tables, some of which are presented in this section and some (tables 17–30) in an appendix. An attempt has been made to present the results in such a way that, although most of the interpretation has already been done, it is still possible for the raw output to be examined if necessary.

The procedure adopted from § 4*d* onwards is first to consider the factors that affect the coloration of adult males and females. The coloration of juveniles is considered only when it aids interpretation of the coloration of adults. Next, factors that affect the degree of sexual dimorphism are discussed, followed by a similar discussion of the coloration of juveniles and adult/juvenile dimorphism. Finally, there is a discussion of seasonal change in coloration.

In the discussions that follow, the terms 'cryptic' and 'conspicuous' are used in a relative way. In a sense they are used to indicate the distance from which a bird becomes discernible to a predator. This distance is obviously greater for a 'conspicuous' bird than a 'cryptic' bird, but it is also, whatever the bird's coloration, greater for a specialized than for a casual predator and greater for an experienced predator (that has formed a search image) than for a naive predator.

Table 1. Mean conspicuousness† of nine body regions for five age/sex/season classes and mean difference in conspicuousness for four age/sex/season comparisons as calculated for 516 species of Western Palaearctic birds

	body region								
	bill	legs	crown	head	back	front	belly	wing bars and rump	underside of wing and tail
mean conspicuousness of:									
breeding ♂	2.58	2.45	2.13	3.18	2.10	2.71	2.78	1.74	1.59
breeding ♀	2.37	2.38	1.69	2.73	1.76	2.35	2.52	1.61	1.53
juvenile	1.98	2.05	1.17	2.17	1.45	1.92	2.24	1.56	1.50
'winter' ♂	2.53	2.40	1.96	2.99	2.01	2.54	2.71	1.70	1.56
'winter' ♀	2.34	2.34	1.59	2.61	1.69	2.23	2.49	1.57	1.50
mean difference in conspicuousness between:									
breeding ♂–♀	0.21	0.07	0.44	0.45	0.34	0.36	0.26	0.13	0.06
breeding ♂–juv.	0.60	0.40	0.96	1.01	0.65	0.79	0.54	0.18	0.09
breeding ♀–juv.	0.39	0.33	0.52	0.56	0.31	0.43	0.28	0.06	0.03
'winter' ♂–♀	0.19	0.06	0.37	0.38	0.32	0.31	0.22	0.13	0.06

† Conspicuousness for each body region was scored on a subjective scale from 0 (maximum crypsis) to 5 (maximum conspicuousness).

(*a*) *Mean conspicuousness of the different body regions in different age/sex classes*

Table 1 shows the mean conspicuousness for each of the nine body regions considered in this paper for five different age/sex/season classes and four comparisons between classes. There are no surprises in this table. For all regions of the body the order of conspicuousness is: (i) breeding season males, (ii) non-breeding season males, (iii) breeding season females, (iv) non-breeding season females, and (v) juveniles. The greatest sexual and adult/juvenile dimorphism is found with respect to the head region, followed in decreasing order of dimorphism by the crown and front. After these, the greatest sexual dimorphism involves the remaining major plumage regions (back and belly) but the greatest adult/juvenile dimorphism involves the bill and legs.

(*b*) *The predictive equations and the significance levels of the regression coefficients for each of the independent variables*

Predictive equations for each of nine body regions for five different age/sex/season classes are given in the appendix (tables 26–30). These equations represent the best predictive equation for the dependent variable from the 17 independent variables entered into the regression. All are a significant ($P < 0.001$) linear fit to the observed variation in the dependent variable.

Tables 26–30 can be used in a number of ways. First, as predictive equations in their own right they can be used to calculate the expected conspicuousness of a part of the body of any Western Palaearctic bird, given that the value of each of the independent variables entered into the equation have been coded according to the scales presented earlier. They can also be used, of course, to calculate differences between age or sex classes etc. Their major use for this paper, however, is that the signs of the regression coefficients indicate the sense in which conspicuousness is influenced by that particular independent variable, given that the influence of all the other independent variables remains constant. However, the confidence that can be placed in the signs of the regression coefficients depends on the probability that the absolute value of the regression coefficient could differ from zero by chance by the calculated amount. These probabilities are also indicated in tables 26–30. Note that these probabilities do not refer specifically to the regression coefficients presented but are derived according to the convention described earlier (§4*d*(iii)).

TABLE 2. PERCENTAGE EXPLANATION OF THE VARIANCE OF CONSPICUOUSNESS (AS SCORED HERE) FOR 9 BODY REGIONS OF 11 DIFFERENT AGE/SEX/SEASON CLASSES AND COMPARISONS

age/sex classes	bill	legs	crown	head	back	front	belly	wing bars and rump	underside of wing and tail
breeding ♂	22	17	19	9	19	17	17	20	13
breeding ♀	31	18	24	17	21	26	20	17	13
juvenile	16	10	17	16	19	18	20	21	13
'winter' ♂	23	17	21	11	21	18	14	21	13
'winter' ♀	30	18	24	17	21	26	19	17	13
age/sex differences									
breeding ♂–♀	14	12	26	27	34	37	27	14	5
breeding ♂–juv.	8	10	13	14	18	18	14	13	9
breeding ♀–juv.	10	12	16	22	18	22	18	15	8
'winter' ♂–♀	14	11	23	25	35	35	26	15	6
seasonal differences									
♂	6	2	8	13	12	13	5	1	8
♀	5	2	10	16	15	16	5	2	9

(*c*) *The extent to which bird coloration is influenced by the variables*

Table 2 shows what proportion of the variance in conspicuousness of the different body regions of the different age/sex/season classes can be explained by the socio-ecological independent variables entered into this analysis. As noted earlier, however, although this explained variance is expressed as a percentage, the degree of explanation in the present case cannot be judged against a ceiling of 100. Yet it is clearly greater than 37, which is the maximum explanation achieved in any of these analyses. Doubtless, experimentation with different transformations could have increased the calculated explanation considerably. With such a subjective scoring system for coloration, however, it would not have been possible to raise the level of the explained variance to a much higher level, even if virtually all of the variation in bird coloration is governed by the variables considered here.

TABLE 3. MAJOR EXCEPTIONS TO THE PREDICTIVE EQUATIONS GIVEN IN TABLES 26–30 (APPENDIX)

(B), breeding season only; (W), non-breeding season only.

(i) *Species that have a part of the body much brighter than expected*

	bill	legs	crow	head	back	front	belly	wing bars and rump	underside of wing and tail
males	Blackbird	Red-crested pochard (B)	Golden oriole Purple gallinule		Golden oriole			Greater flamingo Wall creeper	Ruddy shelduck Dotterel (B) Whiskered tern (B)
females	Moorhen Water rail	Velvet scoter	Purple gallinule Crested coot Firecrest Goldcrest Goldfinch Hoopoe					Greater flamingo Wall creeper	Ruddy shelduck Whiskered tern (B)
juveniles	Water rail	Arabian bustard Velvet scoter Senegal thick-knee White-tailed plover	Purple gallinule Hoopoe	Bald ibis Red wattled plover				Wall creeper	Ruddy shelduck Collared pratincole

(ii) *Species that have a part of the body much less bright than expected*

	bill	legs	crown	head	back	front	belly	wing bars and rump	underside of wing and tail
males	Demoiselle crane	Cormorant Shag (B)		Plain sand martin		Willow grouse (W) Ptarmigan (W)	Willow grouse (W) Ptarmigan (W)	Common scoter	
females		Cormorant Shag (B)		Plain sand martin			Willow grouse (W) Ptarmigan (W)	Common scoter	
juveniles						Plain sand martin	Starling	Common scoter Long-tailed duck	

(*d*) *Apparently exceptional species*

Table 3 lists those species of birds that, as explained earlier, fall well outside of the multiple regression equations calculated in this analysis. In compiling this table, the following procedure has been adopted. The starting point was the 5% of birds (i.e. approximately 25 species) that were identified by the computer as falling outside of the 95% confidence limits for the relevant predictive equation. Of these, all species were entered into the table for which observed and predicted scores for conspicuousness differed by three units or more on the scale adopted here. Many of these apparent major exceptions can be explained, or at least explained away, and the following few observations indicate the types of considerations that could be involved.

The firecrest, *Regulus ignicapillus*, and goldcrest, *R. regulus*, for example, are the two smallest birds of the region, and the fact that the crown of the females appears exceptionally bright could be due to the fact that the influence of body size on crown conspicuousness is non-linear. The bald ibis, *Geronticus eremita*, is rapidly decreasing in numbers and its geographical distribution is now very restricted. The latitudinal data entered into the regression for this species do not really indicate, therefore, those relevant to the bird during the evolution of its coloration. This may explain the apparently exceptional brightness of the head of the juvenile. The inclusion of other exceptional species in the list presumably indicates that during the evolution of these species factors not included in this analysis acted with sufficient force to displace them from the level of conspicuousness that, in the present context, might be expected. The hoopoe, *Upupa epops*, for example, is known to be a distasteful species (§3*c*(i)), and, in the females and juveniles, has a head brighter than expected. Most other regions of the body plumage of this species also came close to being exceptionally bright, as also did the bill and legs of the kingfisher, *Alcedo atthis*, and Smyrna kingfisher, *Halcyon smyrnensis*, two other distasteful species. The exceptionally conspicuous red-flashing of the upper surface of the wall creeper, *Tichodroma muraria*, may well serve a function in this species that is additional to the function of upper-surface flashing in other species. The wall creeper is noted for its habit of continual flicking of its wings.

All of the above 'explanations' are species-specific and perhaps, given sufficient insight to the socio-ecology of the other species listed in table 3, most of these apparent exceptions could be explained. In the case of the rallids and hirundines, however, there is an indication of something unusual about the group as a whole rather than as isolated species. Among the rallids, the moorhen, *Gallinula chloropus*, water rail, *Rallus aquaticus*, purple gallinule, *Porphyrio porphyrio*, and crested coot, *Fulica cristata*, are all brighter than expected with respect to their bills, crowns or legs. Among the hirundines, although only the plain sand martin, *Riparia paludicola*, appears in the list for the head and front, other parts of the plumage of this and other martins nearly qualified for inclusion, their plumage being less bright than expected. No reason is offered here for the apparently exceptional nature of these two groups.

Attempts to explain the exceptions, of course, presuppose that the results of the multiple regression analysis are meaningful. Three of the apparent exceptions would seem to increase confidence that this is so. The crown and back of the male golden oriole, *Oriolus oriolus*, are both included in table 3. In addition, the head, front and belly of the male of this species came extremely close to inclusion level. It would seem, therefore, that from its social behaviour and ecology, the golden oriole male might be expected to be on the cryptic side of average conspicuousness. Yet, being a bright yellow bird, it was coded in this analysis as being of maximum conspicuousness. Interestingly, the male golden oriole is notorious among ornithologists as being, despite its bright plumage, extremely difficult to see in its natural habitat even from close range (Heinzel *et al.* 1974).

The willow grouse, *Lagopus lagopus lagopus*, and ptarmigan, *L. mutus*, both become white in colour during the Arctic winter. As these species are found on snow-covered ground, most parts of their body were coded as highly cryptic (zero) in winter during this analysis. The front and belly of the males and females, however, when thus coded are less bright than expected. Indeed the calculated value was between 2 and 3 which was only slightly less than the value accorded to white plumage for other species. Perhaps, then, whereas the back, crown and head coloration is cryptic at all distances, the front and belly coloration is cryptic only from long distances. In front to front confrontation with a predator at a short distance perhaps the white coloration serves the same function in these as in other, non-Arctic, species as discussed later (§5*e*).

TABLE 4. DIEL INCIDENCE OF FEEDING ACTIVITY

(Restriction of feeding activity to daylight hours has (0) no consistent influence, or favours (+) an increase, or (–) a decrease.)

	level of conspicuousness of:	*dimorphism*		*seasonal change*
body regions	all age/sex classes	sexual	adult/juvenile	
head	0			
underside flashing	–			
all other parts	+			
bill and legs		0	+	
flashing		–	–	
all other plumage		+	+	
all parts				0

(*e*) *Some associations between the coloration of adults and social, reproductive and ecological variables*

(i) *Diel incidence of feeding activity*

Restriction of feeding activity to the hours of daylight has a clear effect on coloration (table 4); for all age and sex classes there is an increase in conspicuousness of all parts of the body except the head, which is unaffected, and underside flashing, which decreases in intensity. These effects are greater in males than in females and greater in adults than in juveniles. The nett result is that birds that feed at night but rest by day are less conspicuous (except for the head) but have more intense undersurface flashing than birds that feed by day.

This association between nocturnal activity and cryptic coloration with flashing has parallels elsewhere among metazoans, most noticeably with Lepidoptera in which day-flying species are more conspicuously coloured than night-flying species, though the latter make more use of flash coloration. The implications of this association are perhaps more profound than they might first appear. If we accept that the major difference between nocturnal and diurnal species of birds, as far as selection on coloration is concerned, is that the former are immobile during daylight hours whereas the latter are mobile, then an important principle emerges: if a bird moves during daylight, selection favours conspicuous coloration; if it does not move during daylight, selection favours cryptic coloration. The same principle could be applied to Lepidoptera.

Perhaps this principle can be pushed even further and used to account for the head and flash coloration of diurnally immobile birds. The only part of a roosting owl or caprimulgid that is likely to be moved much is the head. At close range the red eye and black and white head of the night heron, *Nycticorax nycticorax*, the red or yellow eyes and striking face patterns of many owls, and the throat and collar patches of caprimulgids, are most conspicuous in contrast with the rest of the body. Similarly, the underside flash colorations are only exposed when the animal moves.

TABLE 5. TIME SPENT ON GROUND/WATER

(Increase in the time spent on the ground or water has (0) no consistent influence, or favours (+) an increase, or (−) a decrease.)

body region	*level of conspicuousness of:*		
	males	females	juveniles
bill, legs, crown and head	−	−	−
back and front	0	−	−
belly and upper surface flashing	+	+	+
underside flashing	0	0	0

	dimorphism	
	sexual	adult/juvenile
legs	−	−
head, back, front, and belly	+	+
upper surface flashing	0	+
other parts	0	0

	seasonal change
flashing	−
all other parts	+

It would seem, therefore, that there is an association between movement in daylight and conspicuous coloration. Conversely, if there is no need for a bird (or part of a bird) to move in daylight, maximum advantage is gained through crypsis, thereby avoiding detection in the first place. Presumably the selective pressures involved are those that result from predation risk rather than from sexual or other social selection pressures. As far as underside flash coloration of diurnally immobile birds is concerned, it seems likely that the surprise effect is the most important. The relatively conspicuous head coloration could also function in the same way insofar as the sudden movement of a conspicuous head at close range could well surprise a potential predator that had not previously noticed the bird and delay attack long enough for the bird to escape. The brightly coloured gape of many caprimulgids may well function similarly as suggested earlier for nestlings. The exposure of underside flash colour and in particular the movement of the head could also function as an indication that the bird has perceived a potential predator (i.e. perception advertisement).

Other selective pressures, this time associated with the unprofitable prey model could also perhaps be invoked to account for the generally greater level of conspicuousness of day-active species. If on average a bird that is moving when first seen by a predator is less likely to be caught (and therefore less likely to be chased by an experienced predator), then there can be an advantage in making movement more conspicuous through brighter coloration, provided this does not attract predators to the prey when immobile. Such an explanation could perhaps also be advanced for the relative conspicuousness of butterflies and moths during the day. When active, butterflies and day-flying moths are more or less conspicuously coloured and in general are ignored by avian predators (except for a few specialists such as flycatchers). When at rest, however, with wings folded, butterflies, like moths, are generally cryptic and are often preyed upon by birds.

TABLE 6. BODY LENGTH

(Increase in body size has (0) no consistent influence, or favours (+) an increase or (−) a decrease.)

	level of conspicuousness of:		
body region	males	females	juveniles
bill and legs	+	+	+
crown	+	+	+
back	+	+	−
head and front	+ (winter only)	+	−
belly and all flashing	−	−	−

	dimorphism	
	sexual	adult/juvenile
all parts	−	+

	seasonal change
crown, head and front	−
all other parts	0

(ii) *Amount of time spent at ground or water level*

Ground-living and water birds of all age and sex classes have a belly that is more conspicuous than that of birds that spend less time at ground level (table 5). Upper surface flash coloration (wing-bars, rump, and/or outer tail feathers) is also more pronounced. The rest of the body, except for the back and front of males, is more cryptic than that of other birds. The general indication, therefore, is that ground-living birds gain an advantage from crypsis and escaping detection. They show surprise flash coloration once they have been detected, the belly contributing to the flash effect. Birds that are in the air or flying from branch to branch are continually opening their wings during movement. In such species flash coloration has less surprise value. The fact that it is the belly and upper surface flash coloration that is more pronounced in ground birds (variation in under surface flashing being unrelated to time spent on the ground) suggests that these flashings function mainly during an attack from above and behind, either from an aerial predator or, perhaps more likely, during the running or early take-off stages in escape from a mammalian predator.

(iii) *Body length*

All flash coloration of larger birds is reduced in conspicuousness relative to that of smaller birds (table 6). This is consistent with the surprise function proposed for flash coloration. This effect is probably of only split-second duration. As larger birds require longer to take-off than smaller birds, potential predators have more opportunity to recover from temporary surprise. Flash coloration is therefore reduced in advantage in larger birds and may even be a disadvantage if the early stages of take-off are more likely to be noticed by distant predators which then have time to reach the bird before take-off is achieved. Belly coloration, which may well function in this instance as flash coloration, is also less conspicuous in larger birds.

All other parts of the body of the adults of larger birds are more conspicuous than the same parts of the adults of smaller birds, particularly in females. This can perhaps be interpreted as aposematic coloration, the warning being that the bird is capable of inflicting injury. Such a warning may be most effective against casual or naive predators if aposematic colours are generalized (§ 3*c* (i)), but may also be effective against experienced predators if the latter have learned that larger prey items are unprofitable (§ 3*c* (iii)) through the time taken to catch and handle them and through the greater risk of injury. In order to appreciate this effect as a human predator it is necessary to envisage the problems and dangers of handling, say, an ostrich or perhaps a swan, compared with a duck. Smaller predators, however, presumably experience the same range of difficulty with proportionately smaller prey.

Juveniles of large birds are more cryptically coloured than the juveniles of smaller birds in all regions of the body except the bill, legs and crown which are more conspicuous than those of smaller birds. This implies that juveniles gain maximum advantage through escaping detection and that if they are larger, and therefore potentially more conspicuous, selection for crypsis is more intense. Upon discovery, however, the juvenile's weapons, the bill and legs, are more conspicuous than the same parts of smaller birds, again perhaps as a warning that the bird is capable of inflicting injury. The fact that the bill and legs are less conspicuous than those of the adult (e.g. black or pink rather than red) can be attributed to the conflicting pressures on juveniles for crypsis at a distance but conspicuousness at close range.

Table 7. Gregariousness while nesting

(Increased gregariousness while nesting has (0) no consistent influence, or favours (+) an increase or (−) decrease.)

	level of conspicuousness of:		
body region	males	females	juveniles
bill and legs	+	+	+
all flashing	−	−	−
crown, head and front	+	+	0
back and belly	+	0	0
		dimorphism	
	sexual		adult/ juvenile
bill and legs	0		+
crown and head	+		+
back, front, and belly	+		0
upper surface flashing	+		−
under surface flashing	+		0
		seasonal change	
bill, legs, and all flashing		+	
back, front and belly		−	
crown and head		0	

(iv) *Gregariousness*

The major effect of gregariousness is to increase the conspicuousness of all parts of the body of all age and sex classes (tables 7 and 8). Again the principle seems to emerge, therefore, that if a bird is going to attract attention to itself anyway, in this case through being gregarious, then there is an advantage in being even more conspicuous by virtue of brighter coloration. Possible advantages with respect to gregariousness are: (i) advertisement to a predator that the prey is unprofitable because there is an increased chance of (the predator) being detected in advance, (ii) advertisement of injury risk through being attacked by many birds rather than one, and (iii) protean defence, the predator being confused by large numbers of conspicuous birds.

Table 8. Gregariousness while feeding during non-breeding season

(Increased flock size while feeding during non-breeding season has (0) no consistent influence, or favours (+) an increase or (−) a decrease.)

body region	*level of conspicuousness of:* all age/sex classes	
all parts	+	
	dimorphism	
	sexual	adult/ juvenile
bill and legs	+	0
crown and head	−	+
back, front, and belly	−	0
upper surface flashing	+	−
under surface flashing	−	+
	seasonal change	
back	0	
all other parts	+	

The exceptions to the general trend toward increased conspicuousness with increased gregariousness, are particularly instructive. Flash coloration can be an effective form of protean defence because as a bird flies its flashes are alternately exposed and concealed. A predator among a flock of birds therefore has its attention attracted by first one individual, then another. It many be significant that during the non-breeding season (table 6), gregarious birds have flash coloration that is more pronounced than more solitary birds, whereas during the breeding season gregarious nesters tend not to have flashing. Possible explanations could include: (i) In the non-breeding season there is abundant food for individual maintenance, but not for reproduction. Hence there is little intra-specific competition, and (in addition to the immediate advantages of perception advertisement) it is advantageous to warn conspecifics about predators so that the predator does not form a search image (see Trivers 1971). In the breeding season, food is commonly a limiting factor and thus intra-specific competition intense. Here the benefits of having a nearby competitor predated outweigh the drawback that the predator may become a greater risk. (ii) Overwintering individuals can afford to take off and use confusion tactics and perception advertisement. Adults in breeding aggregations can not take off either singly or as a group for predator confusion, since there is a major risk of the predator stumbling across the young. Thus a naive predator attracted to a breeding flock by underside flashing could be positively reinforced.

As with flashing, the other exceptions to generally greater level of conspicuousness of gregarious birds also occur during the breeding season and are the back and belly of females and all non-flashing plumage of juveniles. All of these effects can be related to the disadvantage of betraying the precise location of the nest, even though the colony as a whole is readily detected.

(v) *Degree of concealment of incubation site*

The general result of an increase in concealment of the incubation site is an increase in conspicuousness of all parts of the body of all age and sex classes (table 9). The only exception is under surface flash coloration, which is reduced in conspicuousness, and the bill, legs and upper surface flashing of juveniles whch are unaffected.

Table 9. Degree of concealment of incubation site

(Increase in the concealment of the incubation site shows (0) no consistent influence, or favours (+) an increase, or (−) decrease.)

	level of conspicuousness of:		
body region	males	females	juveniles
bill, legs and upper-surface flashing	+	+	0
under surface flashing	−	−	−
all other plumage	+	+	+
		dimorphism	
	sexual		adult/ juvenile
bill and legs	−		0
belly and flashing	−		+
back	+		+
front	0		+
crown and head	0		0
		seasonal change	
bill and under surface flashing		+	
belly and legs		−	
all other parts		0	

The increase in conspicuousness associated with adoption of a concealed incubation site once again emphasizes the apparent advantages (§ 5*e* (i)) of being conspicuously coloured, whether male, female or juvenile, except when immobile and exposed. Because birds with a concealed incubation site cannot be seen during the major period of diurnal immobility, selection for bright coloration when mobile can have a more pronounced effect without being opposed by the need to be cryptic when immobile.

The fact that upper-surface flashing of adults, but not juveniles, increases in conspicuousness with adoption of a concealed incubation site whereas under surface flashing decreases in conspicuousness may also be instructive. It implies that there is an advantage in flashing at predators that are above the bird but a disadvantage in flashing at predators that are below. Perhaps the critical factor is differential predation risk from aerial and ground predators. Birds with a concealed incubation site, whether it is at ground level (e.g. in a hole or under vegetation) or above (e.g. a hole in a tree) probably experience little risk of predation of the incubating bird, eggs or nestlings, from aerial predators. Parent birds flying toward or, particularly, just leaving the incubation site, on the other hand, are at risk to such predators. Concealed nests, even those in holes, are nevertheless at risk to ground predators, many of which can climb. Selection is likely, therefore, to favour coloration that avoids attracting the attention of predators to an otherwise concealed incubation site. Birds that nest in holes in the ground or under grass often either return to the nest site at night or land some distance away and walk to the nest under cover. Reduced under surface flashing, particularly in birds that nest above the ground, could reduce the risk of attracting the attention of a ground-based predator to the location of the nest site. In the absence of flash coloration, the general level of conspicuousness of under surface coloration is probably less critical as a bird in the air will often appear as a silhouette to ground-based predators. Enhanced upper-surface flash coloration can then be interpreted as surprise coloration, with respect to aerial predators, particularly as the bird emerges from concealment.

Converse pressures are likely to act on birds with exposed incubation sites. Here, upper surface coloration would be a disadvantage in that from time to time it may betray the presence of an incubating bird through accidental exposure during preening, wing-stretching, or other movements. Under surface flashing on the other hand can be advantageous through its surprise effect on ground predators upon sudden take-off.

Table 10. Incubation by both sexes (when the incubation site is at all exposed)

(Incubation by both sexes when the incubation site is exposed has (0) no consistent influence, or favours (+) an increase, or (−) a decrease.)

	level of conspicuousness of:		
body region	males	females	juveniles
bill and legs	+	+	0
head (in breeding season)	+	+	0
front and belly	+	+	+
crown and back	−	−	−
underside flashing	−	−	−
upperside flashing	−	+	−
		dimorphism	
	sexual		adult/ juvenile
bill, belly and all flashing	−		+
all other parts	0		+
		seasonal change	
legs and upper surface flashing		0	
all other parts		+	

(vi) *Incubation by both sexes*

We assume that during the breeding season in species where the male contributes to incubation: (i) the male experiences longer periods of diurnal immobility, (ii) the female experiences longer periods of diurnal mobility, (iii) there is more movement of adult birds to and from the nest, and (iv) the eggs and nestlings are left unattended for shorter periods.

The effect of incubation by both sexes on coloration depends on whether or not the incubation site is concealed (tables 10 and 11). When it is exposed, there is an increase in conspicuousness of the bill, head and front and the belly and legs of both males and females. As the front, belly and legs are hidden while on the nest they may function as surprise coloration or, in the case of the bill, to exaggerate or draw attention to a weapon. Increased conspicuousness resulting from incubation by both sexes can then be attributed to the almost continuous presence of an adult at the nest site. The message conveyed to a predator, therefore, may be that investigation of the nest site is unprofitable because it is almost continuously defended. As expected, however, the crown and back of both sexes becomes more cryptic when the incubation site is exposed to any degree. The most vulnerable time for a bird using such a nest site is probably during the time that the bird is just about to enter the nest. Increased traffic to and from such a nest site due to incubation by both sexes could well elicit selection for more cryptic coloration of crown and back than when the female alone incubates in such a site, even though the male may often visit to feed the female.

Table 11. Contribution to incubation by male (when the incubation site is concealed)

(Increased contribution to incubation by the male when the incubation site is concealed has (0) no consistent influence, or favours (+) an increase, or (−) a decrease.)

	level of conspicuousness of:		
body region	males	females	juveniles
front, belly and legs	−	−	−
underside flashing	+	+	+
crown, head and back	0	0	+
bill and upper-surface flashing	0	0	0

	dimorphism		
	sexual		adult/juvenile
all flashing	+		+
front	−		−
head	−	(in breeding season)	−
all other parts	0		0

	seasonal change
back	+ (♀ only)
head	−
all other parts	0

When the incubation site is concealed, the front, belly and legs of all age and sex classes become more cryptic if both sexes incubate whereas the underside flashing becomes more pronounced. The implication is, therefore, that the coloration of birds that nest in concealed sites has been shaped by selection resulting from predators approaching the nest site at the same height or from beneath rather than from above. Given this, an explanation might be that under surface flashing has a surprise function during the vulnerable moment of emergence from a hole or domed nest whereas front, belly and legs are more cryptically coloured so as not to attract attention during the final approach to the incubation site. This can also apply to birds with concealed incubation sites when only one sex incubates. The evolutionary optimum is simply shifted slightly further in the crypsis-plus-flashing direction on account of the greater traffic to and from the nest when both sexes incubate.

(vii) *Time spent by the male guarding the nest site*

We assume that in species in which the male spends a lot of time guarding the nest site, as opposed either to deserting, incubating, or travelling long distances for food: (i) the female spends *less* time in diurnal activity, (ii) the male may or may not spend *more* time in diurnal activity, and (iii) aerial predators, but perhaps not smaller ground-dwelling predators, are far less likely to be able to approach the nest site unobserved.

The most noticeable effect of males increasing the time they spend guarding the nest site is that it is associated with an increased crypsis of almost all body regions of the females and juveniles but has no effect on the conspicuousness of the males (table 12). Given the above assumptions, this again is in accord with the general principle that diurnally immobile birds tend toward crypsis whereas diurnally mobile birds tend toward conspicuousness. Explanations derived from either the unprofitable prey (§3*c* (iii)) or the deflexion (§3*c* (v)) models would seem to be equally applicable.

Table 12. Time spent by the male guarding the nest site

(Increase in the time spent by the male guarding the nest site shows (0) no consistent influence, or favours (+) an increase or (–) a decrease.)

	level of conspicuousness of:		
body region	males	females	juveniles
back	+	+	+
under surface flashing	–	– (in winter)	–
all other parts	0	–	–

	dimorphism		
		adult/juvenile	
	sexual	♂/juv.	♀/juv.
flashing	+	+	+
all other parts	+	+	0

	seasonal change
under surface flashing	+
all other parts	0

The exception to the general effect of guarding by the male concerns the back region which becomes more conspicuous in all age and sex classes, though particularly in the male. It seems likely that this effect is the result of pressures generated by aerial predators, given that when a male 'stands guard' an aerial predator is unlikely to approach without being seen. In this particular case we can perhaps rule out the possibility that the male's back is conspicuously coloured to attract avian predators away from the females and young otherwise it would be expected that the back coloration of the females and young would be less conspicuous when the male guards rather than more conspicuous. It seems likely, therefore, that the message conveyed by the male's relatively conspicuous back is that he is unprofitable prey and that the predator would gain greater advantage through searching for a more profitable prey. In which case the increased back conspicuousness of the females and young could be a form of Batesian mimicry, the females and juveniles also having the appearance of unprofitable prey. Alternatively, because of the assumed greater vigilance in such species, it is possible that the females and juveniles really are unprofitable prey. In which case the situation is a form of Mullerian mimicry, females and juveniles having less bright backs than males as the result of compromise with the advantage of crypsis when immobile in a nest.

(viii) *Degree of care of the post-hatching young by the male*

On account of the relative numbers of the species showing different levels of this variable (§4*c* (vi)), table 13 reflects principally the variation in coloration between species with no male parental care and species in which male and female share parental care more or less equally. Species that show reversal of the sex role, such as the phalaropes, can be discussed after this main part of the ground has been considered.

We assume that, on average, when both male and female feed and care for the post-hatching young: (i) there will be *greater* vigilance (owing to the presence of the male) for predators likely to attack the females and young, (ii) there will be *less* vigilance for predators likely to attack the male because the male has a greater pre-occupation with collecting food, and (iii) there will be more traffic to and from the location of the young, at least while they are in the nest. Given this greater traffic, the reduction in all flash coloration can be attributed to increased selection against attracting attention to the location of the young.

TABLE 13. DEGREE OF CARE OF THE POST-HATCHING YOUNG BY THE MALE

(Increased care of the post-hatching young by the male (and decreased care by the female) shows (0) no consistent influence, or favours (+) an increase, or (−) a decrease.)

level of conspicuousness of:

body region	males	females	juveniles
bill and legs	+	+	+
crown and head	−	+	+
back and front	−	+	+
belly	+	+	+
upper and under-surface flashing	−	−	−

dimorphism

	sexual	adult/juvenile	
		♂/juv.	♀/juv.
bill and legs	−	0	+
head and body plumage	−	−	+
upper surface flashing	−	−	+
under surface flashing	−	−	−

	seasonal change
all parts of body except flashing	+
upper surface flashing	+
under surface flashing	−

It seems clear from table 13 that, irrespective of sex, increased contact with the post-hatching young is associated with a general decrease in conspicuousness of body plumage (except the belly) or, conversely, decreased contact leads to increased conspicuousness. The fact that juveniles just before and after leaving the nest are also more conspicuous also seems instructive in that, given the above assumptions, a relation emerges for the different age and sex classes between conspicuousness and vigilance for predators.

There remains the problem of accounting for an increase in conspicuousness of the bill and legs of the male with increased association with the post-hatching young. It could be argued that the bill coloration serves as some form of social releaser for the young birds. However, if this were the function it is difficult to see why the bill coloration of the female (and also of the juvenile) also increases in conspicuousness with increased attention by the male. It is also difficult to explain why the increased conspicuousness of the legs (and perhaps belly) are involved if a social releaser mechanism is the main function. Of course, having evolved for some other function, there is then no reason why bill, or even leg and belly coloration, should not serve as social signals of some form. Perhaps the most likely explanation is that when two adults are present to care for the young, attack is more often an efficient form of defence against predators than when only one adult cares for the young. Also involved may be the element that when both parents care for the young, if one is injured or killed through attacking a potential predator, one is still left to raise some or all of the young through to fledging. Perhaps, then, when both parents care for the young the brighter coloration of bill and legs in both sexes exaggerates or draws attention to the birds' weapons of attack or defence and perhaps also warns a predator of the greater probability of being attacked. A bright belly may also be part of such a system when attacking a predator from above.

When we consider the other half of the range of male parental care, that from both parents to the male alone caring for the post-hatching young, certain of the trends already identified are seen to continue. In the painted snipe, *Rostratula benghalensis*, and to a lesser extent the phalaropes, the male has a crown, head, back and front that is less conspicuous than the same parts of the female. There is little, if any, sexual dimorphism of the bill, legs and belly but then these parts of the male do not seem more conspicuous than the same parts of males that receive assistance from the female. Flash coloration, on the other hand, particularly on the upper surface, is of above average conspicuousness. This suggests that, as the female decreases her contribution to parental care, resulting once more in a one-parent system, the trend noted above is reversed. This reversal is entirely expected if the argument concerning rate of visit to the nest site is correct.

(ix) *Polygamy*

It should be noted that because our analysis has been made by multiple regression, the effects of polygamy demonstrated in table 14 can be divorced from correlated behaviour taken into account by other independent variables (except perhaps where there has been a marked but unknown departure from a linear relation). The reduced contribution by the male to guarding, incubation, or care for the post-hatching young normally associated with polygamy can therefore be disregarded in interpreting table 14. We assume, therefore, that the calculated effects can be attributed either to: (i) the increase in the number of females inseminated in a single breeding season by the most sexually successful males, or (ii) the fact that the majority of species scored as polygamous display or lek in exposed areas. For present purposes, promiscuity is part of the spectrum of polygamy (§4*c*(vi)).

Increased polygamy, as measured in this analysis, is associated with: (i) males which, particularly during the breeding season, have an increased conspicuousness of all non-flashing body plumage but a less conspicuous bill, (ii) females with a decreased conspicuousness of flashing and bill coloration, and (iii) juveniles that are generally less conspicuous than those of other birds. Although (i) seems compatible with predictions of Darwin's female choice theory, it can also be used in support of the unprofitable prey theory (see below). One problem with the female-choice interpretation is that there is little evidence that females are reluctant to mate with males that are less brightly coloured. The most plausible possibility would seem to be that the more noticeable the male, the more extensive the range of its attraction of females. Provided that drive to increase male conspicuousness occurs by gradual (rather than sudden) change, there is little chance that females would fail to recognize brighter males as conspecifics.

Adjustments to the female recognition system could thus occur gradually and simultaneously as a result of Fisher's advantage-via-sons effect.

TABLE 14. POLYGAMY

(Increase in the number of females inseminated in a single breeding season by the most successful (in this respect) males shows (0) no consistent influence, or favours (+) an increase, or (−) a decrease.)

	level of conspicuousness of:		
body region	males	females	juveniles
bill	−	−	−
all flashing	0	−	−
all other parts	+	0	−
		dimorphism	
	sexual		adult/ juvenile
all parts	+		+
		seasonal change	
upper surface flashing		0	
all other parts		+	

It must be noted that although female-choice theory alone could explain enhanced male coloration, it does not explain the dimorphism. Most of the differences between the plumages of the two sexes are likely to be the products of sex-limitation rather than sex-linkage. Selection for sex-limitation requires that selection for a given characteristic is positive in one sex and negative in the other; not merely that there is strong positive selection in one sex alone, with the other approaching neutrality. Though he knew nothing of the genetic mechanisms, it is clear that Darwin envisaged that selection must act in opposite directions on the two sexes to favour sexual dimorphism of brightness versus crypsis. It was for this reason he suggested that males alone would benefit by brightness (through female choice) but that brightness carried an enhanced predation risk (favouring crypsis in females).

Another facet of sexual selection that could be involved in the evolution of the bright coloration of the males of polygamous species is male:male threat (§ 3*b*). It is perhaps worth noting, however, that the bill coloration of polygamous males is less bright than that of the males of monogamous species. Such a response to the adoption of polygamy would perhaps not be expected if male:male threat were an important function of the coloration.

An alternative to male:male competition or female choice as the chief selective force leading to the enhanced coloration of polygamous males is that of advertisement of unprofitability. Zahavi (1975) notes that males commonly display or lek in exposed areas in what appear to be dangerous places and envisaged that this behaviour would constitute a handicap. However, an open locality renders the predator exposed as well as the prey (see Lack 1968). Such areas would seem excellent (and safe) 'training grounds' for naive predators, from the viewpoint of the prey. That many species lek in the open in the same place every day and from year to year can be interpreted as the safest strategy, rather than the most hazardous. Support for the view that it is lekking behaviour, rather than female choice, that generates the enhanced conspicuousness of the males of polygamous birds can be derived from the fact that where polygamy does not involve lekking, sexual dimorphism is often reduced or absent and the males are more or less cryptic (e.g. the bittern, *Botaurus stellaris*, pectoral sandpiper, *Erolia melanotos*, and wren, *Troglodytes troglodytes*). Furthermore, when lekking occurs in sites where, on account of relatively dense vegetation, the birds are at a seemingly greater risk to predation than in more open sites, there is again an absence of sexual dimorphism and an emphasis on crypsis (e.g. great snipe, *Capella media*).

Care has to be taken in extending this consideration of the association between polygamy and sexually dimorphic coloration beyond the geographical area studied here. In the absence of multiple regression analysis it is not possible to be confident that given examples of sexual dimorphism are associated with, or enhanced by, polygamy *per se* rather than by associated behaviour. Bearing this in mind, however, extension of this consideration to tropical birds (see Lack 1968) seems to support our assertion that the critical factor in the evolution of brightly coloured polygamous males is their unprofitability as prey rather than any element of female choice. Thus polygamous tropical birds that lek in the open, either on the ground or on the tops of trees, are strongly sexually dimorphic (e.g. cotingids, various manakins, and at least two species of birds of paradise). Males of other polygamous species that live in tropical forests often display in dispersed leks in which the males are aggregated and within earshot but cannot see each other. Nevertheless, these males presumably gain some extra warning about approaching predators as a result of this behaviour. Such males may or may not constitute unprofitable prey as a result of this behaviour and it is instructive that whereas various cotingids and most birds of paradise are strongly sexually dimorphic, the forest hummingbirds, Trochilidae, are dull-coloured and monomorphic. The buff-breasted sandpiper, *Tryngites subruficollis*, the males of which also display in dispersed leks, is also monomorphic and not very conspicuous.

Among the polygamous phasianids, many dimorphic species have males that display in open leks. In contrast, the argus pheasants, *Argusianus argus*, and *Rheinardia ocellata*, which are also strongly sexually dimorphic, display solitarily in forests but in open clearings the floors of which are cleared by the birds thus removing ground cover for predators (Lack 1968). In assessing the degree of association between polygamy and sexual dimorphism in phasianids, however, it has to be noted that even monogamous species can be sexually dimorphic, either strongly (*Tragopan* and *Ithaginis*) or slightly (*Catreus*). When monogamous phasianids are monomorphic (*Crossoptilon*), it is as a result of the female being brightly coloured rather than the male being cryptic.

(*f*) *Sexual dimorphism*

In the previous section, the conspicuousness of males and females was discussed as if selection acted on the two sexes independently. Reference was made to their relative conspicuousness only when this aided an understanding of the selective forces involved on each sex separately. In this section we review briefly the variation in sexual dimorphism irrespective of absolute level of conspicuousness.

Examination of tables 4 to 14 shows that four factors are strongly associated with variation in sexual dimorphism. For all regions of the body, sexual dimorphism is increased by: (i) small body size, (ii) increased guarding of the incubating female by the male, (iii) only one sex caring for the post-hatching young, and (iv) polygamy. Diurnal feeding, increased time spent at ground or water level, and gregarious nesting (as defined in §4*c*(iv)) also increased sexual dimorphism with respect to most regions of the body.

Further examination of the tables reveals that, with some simplification, sexual dimorphism may be said to result from: (i) greater *crypsis* of females with respect to increase in guarding by the male, (ii) greater *conspicuousness* of males with respect to increase in polygamy and (iii) greater conspicuousness of the sex showing least care of the post-hatching young. The response to variation in body size, diurnal mobility, amount of time spent on the ground or water, and the degree of gregariousness during nesting, is for the coloration of both sexes to respond in the same sense but for one sex to respond more than the other, thereby increasing or decreasing the degree of dimorphism.

These responses of sexual dimorphism raise no new problems and are all consistent with the detailed interpretations presented above. A consideration of the relevance of these results to theories of the evolution of sexual dimorphism in the coloration of birds is given in the general discussion.

(*g*) *Adult: juvenile dimorphism*

Nestlings and young precocial birds before they are able to fly seem universally to be cryptically coloured with occasional possible examples of surprise flash coloration (§ 3*c* (ii)). Such coloration is consistent with the rule developed in relation to adults that birds with enforced diurnal immobility gain maximum advantage from crypsis. Once out of the nest and up to the time of the post-juvenal moult the young birds, now juveniles, are at a stage characterized by marked differences in ability, experience and behaviour from those they will have when adult. We assume that juveniles: (i) are less able to distinguish predators from non-predators and experienced predators from naive predators, (ii) are less able to escape when attacked by a predator, (iii) spend some time, albeit often brief, in the company of their parents or other experienced adults, and (iv) spend much of their time in exploratory migration through an unfamiliar area (Baker 1978). This last point may be of particular importance since the juveniles may spend a relatively large part of their time in areas not normally frequented by adults of their species and in which, therefore, the predators may be largely naive. Even if adults of the same species represent unprofitable prey, or even if the juvenile is noxious or distasteful, the local predators may not have learned that this is so. In that case, given the relative inability of a juvenile to escape attempts at predation, any coloration that draws attention to itself may be disadvantageous.

As a result of the time spent in exploratory migration, juvenile birds spend more time moving than adults (Baker 1978). Remembering the rule for adults (that greater mobility was associated with increased conspicuousness), it might have been expected that juveniles should be more conspicuous than their parents. This, of course, is not the case. Wherever adult:juvenile dimorphism occurs, except for scattered instances of possible flash coloration that would be inappropriate to an adult (§ 3*c* (ii)), the juvenile is more cryptic than the adult. This fact can be taken as support for the suggestion that the advantage of increased conspicuousness in more mobile adults concerns advertisement that they represent unprofitable prey. Juveniles, on the other hand, are highly profitable prey for the reasons given above. Even Batesian mimicry of the adults is not often advantageous to the juveniles, especially once they have fledged. This is partly because, as a result of exploration of areas not occupied by adults, juveniles spend a relatively large amount of time in areas where the predators are naive, and partly because the time of year that juveniles are active is the time of year of maximum abundance of the naive young of their predators. The only strategy generally open to juveniles, therefore, is that of crypsis and avoidance of detection. The fact that post-fledging juveniles are so mobile and active and yet are profitable prey probably generates selection, in contrast to that on adults, for a greater level of crypsis than if they were less active.

So far, most attention has been given to the post-fledging stage. A number of factors that influence the colour of juveniles, which have already been discussed, indicate that selection also acts on the stage during which the juvenile is still associated with its nest site. Thus, as far as general body plumage is concerned, more cryptic juveniles are favoured by an exposed nest site and by pre- and post-hatching parental care by only one parent if the nest site is exposed. Presumably in the latter case the nestling, while it is growing juvenile plumage, is left exposed and unguarded for longer periods than when both parents care for the young.

Table 15. Number of broods per breeding season

(Increase in the number of broods per breeding season shows (0) no consistent influence or favours (+) an increase or (–) a decrease.)

	level of conspicuousness of:		
body region	males	females	juveniles
bill and legs	–	–	–
crown and head	0	+	–
back and belly	–	–	–
front	+	+	+
all flashing	–	–	–

	dimorphism	
	sexual	adult/ juvenile
bill	+	+
legs and head and body plumage	0	0
upper surface flashing	+	0
under surface flashing	0	0

	seasonal change
all parts	0

When a male bird is brightly coloured for unprofitable-prey reasons, it is implicit that potential predators will increase their predation on the young of the same species. Thus, in species in which the male guards his own nest site from a distance, juveniles are more cryptically coloured (except for the back) (see § 5*e* (vii)), especially when there is more than one brood per breeding season (table 15) so that post-fledging juveniles are active while males are still showing nest-guarding behaviour. Also, in polygamous species with males that we suggest are brightly coloured to advertise their unprofitability as prey, the juveniles are more cryptically coloured (table 14). Both of these effects are also consistent with the deflexion model (§ 3*c* (v)).

An increase in post-fledging association with other individuals, particularly parents and other adults, leads to decrease in crypsis of juveniles. Thus increased gregariousness after fledging, post-hatching care by both parents, and being a member of the only brood produced by the parents in a breeding season, are all associated with increased conspicuousness of juvenile coloration. An element of Batesian mimicry may be involved in such a situation, the juveniles spending less time on their own at risk to naive predators, but it seems more likely that Müllerian mimicry is the system involved. When in company with other individuals, particularly adults, the juveniles probably do represent less profitable prey to potential predators. The eventual need (Baker 1978) for a juvenile to perform some solitary exploratory migration, however, in most cases leads optimum coloration for juveniles to be more cryptic than that for adults. Finally, greater crypsis for juveniles is favoured by large size. An increased amount of animal food in the diet, however, which is likely to be associated with increased movement or increased conspicuousness while moving, seems to favour less cryptic coloration of juveniles (table 16).

TABLE 16. DIET

(Increase in the animal content of the diet has: (0) no consistent influence on, or favours: (+) an increase; or (–) a decrease.)

	level of conspicuousness of:		
body region	males	females	juveniles
bill and legs	0	0	0
crown, head and back	0	+	+
front	–	0	+
belly	0	0	+
all flashing	+	+	+

	dimorphism		
		adult/juvenile	
	sexual	♂/juv.	♀/juv.
bill, belly and all flashing	0	–	–
all other parts	–	–	0

	seasonal change
bill and all flashing	0
all other parts	+

The coloration of the bill and legs of juveniles seems to show a fairly consistent trend in that increased association with other individuals, particularly adults, leads to more conspicuous coloration. Thus gregariousness of the adults during nesting and gregariousness of adults and post-fledging young, monogamy by the parents, care of the post-hatching young by both parents, and only one brood per breeding season, all lead to increased bill and leg conspicuousness of the juveniles. To this list can be added large body size. The implication is, therefore, that the juveniles are either mimicing the coloration of adult weapons, warning a predator of the likely presence of adults with such weapons (see § 5*e* (iii)), or perhaps warning that because of the presence of such adults, the juvenile is more likely to attack the predator. Brightly coloured bill and legs may either exaggerate, or draw attention to, the effectiveness or existence of such weapons. In addition, bright bills and legs among gregarious birds may serve as protean defence to confuse a predator. The increased conspicuousness of flash coloration, again presumably for protean defence, in juveniles that are gregarious after fledging has already been noted.

Species that do not reproduce until they are several years of age often only gradually undergo the transition from juvenile to adult plumage throughout their extended period of immaturity. Adult–immature dimorphism after the post-juvenal moult has not been analysed in this work. The impression gained, however, from sea birds and other large land and water birds is that the optimum compromise between crypsis and conspicuousness gradually shifts toward greater conspicuousness as the bird matures. This would be consistent with the former arguments if individuals of such species did not become fully experienced until the age of maturity in their avoidance of predators, particularly of naive predators that may attack and occasionally catch essentially unprofitable prey. Direct evidence for this cannot be presented. It has been suggested

(Baker 1978), however, that the advantage of extending immaturity in birds and other vertebrates is to allow them to establish a familiar area large enough to support them when reproductive. The larger the optimum familiar area for an adult, the longer the required period of exploratory migration, and consequently the longer the period that the young bird is likely to encounter unfamiliar and naive predators. Once a bird confines its activity to its familiar area it probably becomes familiar with its potential predators, and *vice versa*, perhaps even at the individual level. It is this state of familiarity that would seem to generate maximum advantage for strategies such as unprofitable prey advertisement and perception advertisement.

Evidence that crypsis of immatures is due ultimately to a high predation risk through inexperience and lack of familiarity with their environment rather than to sexual or epigamic recognition may be derived from those species (e.g. scarlet grosbeak, *Carpodacus erythrinus*; various sea-birds) that often breed for the first time while still in immature plumage. Male scarlet grosbeaks often first breed while in plumage that is very similar to that of the adult female.

(*h*) *Seasonal change*

Seasonal change in coloration is of relatively infrequent occurrence amongst birds. Where it occurs in adults it seems always to be toward greater crypsis when not breeding, greater conspicuousness when breeding. In young birds, however, it seems always to be toward greater crypsis during the breeding season (of the adults), greater conspicuousness in the non-breeding season. This seasonal change of juvenile coloration, however, is probably associated more with ageing than with the seasons (§ 5*e* (vii)).

Most birds show a post-nuptial moult, whether or not they show a seasonal colour change. There is, therefore, little if any extra cost in changing from one colour pattern or plumage in the breeding season to another in the non-breeding season. Not all birds, however, show a pre-nuptial moult. Species that do not need to moult for any reason other than colour change incur some cost, therefore, from the necessity for a pre-nuptial moult (unless some other mechanism, such as abrasion, can be employed) to regain their breeding plumage. Any extra cost that may thus be incurred through seasonal plumage changes could well have counteracted selection for such changes. However, the fact that many species show both post- and pre-nuptial moults without seasonal change in coloration suggests that the main reason for the relative infrequency of such colour change is the lack of positive selection for change rather than the counteractive selection that results from the cost of moulting.

Some of the seasonal factors that influence the coloration of birds that breed in temperate regions seem likely to depend on whether or not the species performs long-distance seasonal return migration. If the species occupies its breeding range all year, the more polar its distribution the more likely it is when not breeding to be exposed to snow cover, reduced ground cover, and, in deciduous forest regions, reduced tree cover. If the species migrates toward or across the equator, these factors may cease to be important, though obviously the details of the environment will change.

The influence of breeding and non-breeding latitude on seasonal change in coloration is indicated in the appendix in tables 17–25. Only the bill and crown seem to show increased seasonal change if the species migrates long distances. The back, front, belly and legs show greater seasonal change if the species does not migrate, particularly (in the case of the front and back) if the breeding range is at relatively high latitudes.

The other major category of selective pressures to be considered derives from seasonal breeding. Breeding season effects apply in most tropical as well as temperate regions. Selective pressures associated with behaviour during courtship, incubation and the care of the young may well favour coloration during the breeding season that is disadvantageous when not breeding. When both sexes incubate and care for the post-hatching young, particularly when the incubation site is exposed, there is an increase in seasonal colour change. The adults of polygamous species (table 14), particularly males, also tend to show a greater reduction in conspicuousness during the non-breeding season than other species.

The fact that seasonal colour change of adults, where this occurs, is always toward greater crypsis in the non-breeding season could be argued to support the importance of sexual selection in the evolution of the enhanced brightness of males during the breeding season. Further support could be claimed from the observation that polygamy, more than any other factor, increases the extent of seasonal change in coloration of the male. The suggestion is that as soon as breeding finishes the advantage of bright coloration in attracting females disappears thus leaving only the disadvantage of bright coloration in attracting predators (Lack 1968).

A number of factors, however, make this explanation of seasonal change unconvincing. First, on average females decrease in conspicuousness almost as much as males (table 1). Second, birds that perform long-distance seasonal migrations show less seasonal change than birds that do not. Finally, birds both sexes of which incubate and show parental care (tables 10 and 13) show greater change than those for which only one does so (except for polygamous males). All of these factors, on the other hand, are consistent with the suggestion, derived from the unprofitable-prey model, that seasonal change in coloration is related to seasonal change in predation risk. In temperate regions all adult birds are more profitable as prey in winter than in summer. There are several reasons for this. First, the birds have to spend more time searching for food and consequently less time in vigilance for predators. Second, there is less cover in the environment into which the birds can escape from predators, though the predators themselves are also more exposed and more easily detected. Third, if prey items are more scarce, a predator is more likely to attempt to catch relatively difficult prey. Finally, as young birds become reduced in number and more experienced at escaping predation and as incubation ceases, there are fewer profitable prey items available, with a consequent reduction in the unprofitability index of birds that were previously relatively unprofitable. This reduction in unprofitability should be less in birds that migrate toward or across the equator when not breeding than in birds that remain at their breeding latitude all year.

One category of seasonal colour change that deserves special mention is that of the eclipse plumage of many male ducks. Here, after copulating, the males aggregate, lose their flight feathers (to the extent that in many species they are unable to fly), and adopt for a brief period a cryptic coloration very similar to that of the females. This again is consistent with the unprofitable prey model. Conspicuous coloration, in the breeding or non-breeding season, is an advantage only if the bird is mobile and difficult to catch.

It seems, therefore, that the unprofitable prey model fits well most aspects of the seasonal change of coloration of adult birds. The deflexion model is also consistent with many of the observed effects though it seems unable to account for either the eclipse plumage of male ducks or the association of degree of colour change with migration distance.

6. General discussion

In previous sections the results of the multiple regression analysis have been considered and an attempt has been made to interpret them in the light of the theories presented at the beginning of this paper. A relatively large proportion of the results made sense in terms of these theories and usually there was a strong implication that in any specific case one theory was more relevant than any of the others. It should be noted, however, that many of the results of the analysis have not been interpreted. Often this was for the sake of brevity but often also it was because we could offer no immediate explanation for the result in question. We feel, however, that none of these unexplained results contradict our main conclusions, which can now be considered.

We suggest that by far the most potent selective pressures that have shaped bird coloration are those related to risk of predation. A number of theories have been proposed that make use of risk of predation, and for most of them some support for their involvement in the evolution of bird coloration can be gained from our analysis.

The use of bright aposematic coloration to warn predators that the bird is dangerous or has some noxious characteristic can be derived particularly from variation in bill and leg coloration. These often seem to be brightly coloured when their use as weapons is in some way enhanced, either through large body size, gregariousness, or the presence of both parents. Support is also derived for Cott's (1964*a*) suggestion that bright plumage sometimes signifies distastefulness (§ 4*d* (iv)).

The enhanced flash coloration and perhaps bright bill of birds that are gregarious during the non-breeding season supports the suggestion that bird coloration may often involve an element of protean defence, serving to confuse a predator. Most of the variation in the occurrence of flash coloration on upper and under surfaces, however, suggests that the main functions of flash patterns are either to surprise a nearby predator or to attract the attention of a more distant predator away from the location of the nest site or young.

Some of the variation in under surface flash coloration suggests that it is involved in perception advertisement but the major example of bright coloration to advertise perception of a predator seems to concern the head (cf. § 3*c* (iv) for mammals). Head movement, exaggerated by bright coloration, is an obvious signal to a relatively near predator that it has been perceived and that subsequent attack will be unlikely to succeed. This could be the major reason why the head of all age and sex classes is, on average, the most conspicuous part of the body (table 1).

Perception advertisement is essentially a part of the unprofitable prey model in that the bird is advertising that it is unlikely to be caught. Of all the theories, it is the unprofitable prey model that seems to account for the major part of the variation in bird coloration, at least with respect to general body plumage. Most facets of bird ecology and social behaviour interact with coloration in a way that is consistent with the unprofitable prey model. There seem to be several causes of unprofitability, though always it is related to the bird being able to move without inevitably sacrificing its own offspring. Usually, also, it is related in some way to improved vigilance for predators.

So far, little has been said concerning the remaining predation-based theory which suggests that males are brightly coloured in order to deflect predatory attacks away from females and young. Yet, as will become apparent below, the applicability of this theory becomes of crucial importance in determining the relative extent to which sexual and predation-based selection have acted on bird coloration. Before discussing the deflexion theory in relation to our analysis, however, it is important to distinguish between the deflexion of naive and experienced predators. Where bright coloration may deflect naive predators away from the females and young, it is doing so essentially as part of an unprofitable prey situation. After all, the mechanism whereby naive predators are transformed into experienced predators (as far as the unprofitable prey theory is concerned) is chiefly through an initial series of relatively unsuccessful attacks during which, presumably, the naive predator is deflected away from the females and young (see § 3*c* (iii) for formal presentation). At the end of this 'training' period, assuming that in the meantime the predator has also encountered more 'profitable' prey, such as the females and young of the same or other species, attempts to catch the conspicuous prey are no longer made and the unprofitable prey system has begun to operate. For this training period to be successful, capture of the conspicuous bird must occur less frequently than the capture of other, less conspicuous, birds. Where the deflexion system operates as part of the unprofitable prey system, therefore, predation risk on the conspicuous bird is probably always less than that on less conspicuous birds, such as the females and young. When the deflexion system is aimed at experienced predators, however, it must result in greater predation risk on the conspicuous bird than on less conspicuous birds. It is for this reason that the applicability of the deflexion theory becomes important. Sexual selection theories also all argue that predation risk is greater on conspicuous than cryptic birds. All other predation risk theories require the converse to be true, that predation is less on conspicuous than cryptic birds.

The general indication of our analysis is that the deflexion model is less often applicable to bird coloration than the unprofitable prey model. Several examples of colour dimorphism have been demonstrated: (i) diurnally active birds are more conspicuous than diurnally inactive birds, (ii) large birds are more conspicuous than small birds, (iii) gregarious birds are more conspicuous than solitary birds, (iv) concealed nesters are more conspicuous than exposed nesters, (v) males are more conspicuous than females, (vi) adults that do not care for the young are more conspicuous than adults that do, (vii) adults are more conspicuous than juveniles, and (viii) adults in the breeding season are more conspicuous than adults in the non-breeding season. If we search for an explanation that is applicable to all of these dimorphisms, we conclude that in every case the more colourful category is likely to be a less profitable prey to a predator than the more cryptic category. Furthermore, only for (v)–(vii), and to some extent (viii), can the deflexion model also apply. Even in these cases, however, detailed consideration tends to favour the unprofitable prey model rather than the deflexion model. We are not suggesting, however, that the deflexion of experienced predators has never been a factor in the evolution of bird coloration.

Our major conclusion, therefore, is that it is possible to explain variation in the coloration of adult birds largely in terms of the selective pressures generated through predation risk. As far as sexual dimorphism is concerned, variation in the relative predation risk on the two sexes has been argued (§ 5*e*) to be the sole determinant of their relative conspicuousness. In this respect it is perhaps significant that in some sexually dimorphic species (e.g. greenfinch, *Carduelis chloris*), as the female ages and (presumably) becomes more experienced at escaping predation (i.e. less 'profitable' to predators) her plumage becomes more and more like that of the male.

In many instances, of course, the predictions from sexual selection theory and from predation theories are identical. Thus, polygamous species that do not lek and inhabit dense vegetation are not sexually dimorphic for colour (e.g. bittern, *Botaurus stellaris*, and wren, *Troglodytes troglodytes*) nor is the great snipe, *Gallinago media*, that does lek but again in dense vegetation.

Predation theory would argue that dense vegetation conceals predators as well as prey and that either such birds are profitable rather than unprofitable as prey or perhaps that they cannot advertise unprofitability from a safe distance using visual cues. Sexual selection theory would argue that where visibility is reduced there is less likelihood of sexual selection on visual cues. The situation appears to be stalemate. Further consideration, however, still seems to support the predation theory rather than sexual selection theory.

Polygamous species are characterized by a lack of guarding behaviour and other parental care by the male. In the western palaearctic they are also, by and large, ground-dwelling species with precocial young. Their nearest monogamous equivalents in these respects are most ducks and a few phasianids (§5*e*(ix)) which are themselves notably sexually dimorphic. It follows, therefore, that sexual dimorphism cannot be attributed to polygamy. Nevertheless, we have shown (§5*e*(ix)) that when polygamy or promiscuity is associated with display behaviour by the males, either communally or solitarily, in an open area where predators cannot approach unseen, sexual dimorphism is exaggerated still further. When polygamy or promiscuity is associated with display behaviour, either communally or solitarily, in dense vegetation, however, sexual dimorphism for colour is reduced or disappears. Again if we search for an explanation that is applicable to all these effects, including the marked dimorphism in the monogamous ducks, we conclude that the degree of sexual dimorphism for colour is a direct function of the difference between the sexes in their profitability as prey to a predator.

Sexual selection theory, on the other hand, cannot accommodate these phenomena so neatly. Ducks may be monogamous but perhaps they also indulge in male–male competition and rape to an extent greater than that of other monogamous birds. Female choice is perhaps less but male–male competition is perhaps greater than in other monogamous birds. Given an albeit unidentified role for bright coloration in influencing the outcome of male–male contests, therefore, sexual selection theory can accommodate the sexual dimorphism of ducks by postulating male–male competition. The sexual dimorphism of polygamous and promiscuous species, however, can only easily be accommodated by relying largely on female choice. Only in this way can the absence of dimorphism in polygamous species that live in dense vegetation be explained. If females cannot compare the visual attributes of several males at one time, the advantage of such attributes declines. But if this argument is used for the polygamous inhabitants of dense vegetation, how can sexual selection theory account for the striking dimorphism of those phasianids that display solitarily? Solitary display prevents females from making immediate comparisons just as much as dense vegetation. Here, sexual selection theory has to use male–male competition for display sites as the critical factor. Clearly sexual selection theory can be used to interpret all of these phenomena, but in its usual form it cannot be used as neatly or as consistently as the predation theory. On the other hand, it could be argued that, given good visibility, an incoming female searching for a mate is more likely to see a male that is more rather than less conspicuously coloured. Such a sexual selection advantage could perhaps account for the variations described above as consistently as a predation-based advantage.

When some feature of male plumage is used during solitary courtship display to a female and is concealed or less conspicuous at other times (e.g. in some ducks, many phasianids, birds of paradise), the possibility that the feature evolved through sexual selection might seem greater than when a feature is continuously visible. Even here, however, the possibility that the feature evolved initially in response to predation-risk pressures requires consideration. When the same plumage features are used in aggressive encounters with predators, this possibility seems high.

Even when not, the absence of predation-risk selection cannot be assumed. The critical factor seems likely to be whether a displaying male represents a profitable or unprofitable prey to a predator. The male's vigilance may or may not be reduced during display, but as he is in the company of a presumably relatively vigilant female, a displaying male may well be a less profitable prey than a non-displaying male. In which case, enhanced conspicuousness during display will be an advantage both to the male and to the female. This advantage in turn might well favour males that, in the absence of a female, direct courtship displays at an intruder or predator, thereby training the predator to ignore the bird during courtship. Alternatively, a displaying male could be more vigilant than the observing female. In which case bright display coloration could announce that the male is a less profitable prey than the nearby female.

Finally, some exotic plumage, such as long feathers, may well also serve to deflect the attack of a naive predator away from a vulnerable part of the body. If easily broken or detached they may also function in the same way as the deciduous tails of many reptiles.

Field evidence that could support the involvement of sexual selection in the evolution of bird coloration is scarce. Perhaps the best known is that of O'Donald and his co-workers (O'Donald, Wedd & Davis 1974; O'Donald 1976) on female choice of colour morphs in the Arctic skua, *Stercorarius parasiticus*. It was demonstrated that perhaps 40% of female skuas show a 'mating preference' for dark morph males during their first breeding season and that dark males were more successful than pale males at fledging young, though again the effect was only detectable during the males' first breeding season. The 'mating preference' by females for reproductively more successful males could be taken as evidence that sexual selection is operating. The mechanism of 'mating preference' was not identified and O'Donald points out that perhaps dark males are more successful than pale males at obtaining territories early on in their first breeding season. Females that pair off first are therefore more-likely to pair with dark males. Furthermore, early-formed pairs have a higher fledging success rate. The only difference between dark and pale males, therefore, seems to be that dark males are better at obtaining territories during their first breeding season than pale males. It now seems, however, that pale males start to breed at an earlier age than dark males (O'Donald 1976). The real difference, therefore, could be simply that younger birds are less successful than older birds at obtaining their first territories. There is no evidence that females exert a direct choice on male coloration.

Smith (1972) observed the consequence in the field of painting out or dying the red epaulets of the American red-winged blackbird, *Agelaius phoeniceus*. He found that such males were still accepted by females and allowed to mate. There was no evidence, therefore, that female choice in this polygamous species was influenced by the most conspicuous feature of male coloration. As discussed later, however, the red coloration may be involved in male–male interactions, though not necessarily in the sense required by sexual selection theory.

Unequivocal field evidence in support of the sexual selection theory seems, therefore, not to exist. Equally, unequivocal field evidence in support of predation theory does not exist. If sexual selection has not acted in a direct sense on bird coloration, and if the deflexion model is usually less applicable than the unprofitable prey model, it follows that field observation and experiment should show that predation is less intense on conspicuously coloured birds when compared with predation on cryptically coloured birds. Most authors have assumed that brightness is associated with increased predation risk, but this requires substantiation. Selander (1958, 1965) found a significant differential mortality between the sexes (higher in males) in winter flocks of grackle, *Quiscalus mexicanus*, which he suggests is due to the fact that males are less cryptic and have long tails. In particular, there was evidence that the male tail-plumage was disadvantageous in strong winds. However, it is not certain that the increased mortality arose from differential predation. Indeed, unequivocal evidence on this point does not seem to exist (Lack 1968).

Increased predation risk on conspicuously coloured birds has classically been argued to be the factor that opposes the drive for ever brighter coloration that results from sexual selection. If bright coloration evolves in birds that are at a reduced predation risk, it is necessary to consider what factors oppose selection for increased brightness, thus producing the (presumably) relatively stable evolutionary state observed at the present time.

No bird is 'unprofitable' continuously. Diurnal birds are also inactive part of the time (while resting, preening, or incubating). Vigilant birds are pre-occupied while feeding. Gregarious birds may need or may be forced to be solitary for brief periods. Birds incubating in concealed sites have to emerge for shorter or longer periods. Finally, there is always the problem of being pursued by a naive predator and the possibility that just occasionally such pursuit may end in capture. There may well, therefore, be an advantage in being as conspicuous as possible while unprofitable, but at other times there is an advantage in being cryptic. The coloration that results may be either a 'compromise' between these forces or a maximum or minimum. At what point on the conspicuous: cryptic scale (i.e. the distance from which the bird can be identified by a predator; see §5) is optimum for any particular part of the body will depend on the relative frequency with which the bird is profitable or unprofitable to a predator.

It is clear from tables 4 to 14 and from the detailed discussion in §5 that selection acts in a different way and with different intensity on the different parts of a bird's body. Consequently, optimum colour and conspicuousness varies from body region to body region. This presumably is the explanation for the mosaic or patchwork form that is such a feature of bird coloration.

The suggestion that bird coloration is shaped by predation rather than by sexual selection in no way prevents the coloration, as it evolves, being incorporated within the species and sex recognition system (see §3*d*). This is true, however, whether the coloration that evolves is sexually dimorphic or not. The involvement of coloration in species or sex recognition behaviour may well oppose further selection (through predation) to change the coloration. It seems likely, however, that as long as change in coloration occurs gradually (§5*e* (ix)), this resistance will rarely if ever be great enough to prevent the eventual evolution of coloration that is as near the optimum adaptation to predation pressures as is possible.

The involvement of coloration in species/sex recognition systems has been used in the past to explain aspects of bird coloration that cannot otherwise be accommodated by sexual selection theory. One of these is that birds on small oceanic islands tend to be reduced in conspicuousness and sexual dimorphism when compared with their mainland relatives. The argument usually advanced (Moreau 1966) is that because there are fewer species on islands, the problems of inter-sexual recognition are reduced with a resultant decrease in conspicuousness and sexual dimorphism. Whether species and sex recognition is a real problem when closely related species are similarly coloured and sexually monomorphic cannot easily be answered. However, the observation (Lack 1968) that hybrids are more frequent in families of sexually dimorphic birds (e.g. Paradisaeidae, Phasianidae, Anatidae) than in any others suggests that such dimorphism is relatively unimportant in such recognition. In any case, the observation (Lack 1968) that reduced conspicuousness and dimorphism occurs even when an island group of birds supports more closely related species than the mainland, argues against the importance of species or sex recognition in the evolution of this situation. The effect can, however, be accommodated within the unprofitable prey model. The avian fauna of small, oceanic islands is usually characterized by small numbers, both of individuals and species. If choice of prey items is restricted, any one category is less likely to be unprofitable. In addition, ground predators are often absent and aerial predators may be less likely to take incubating birds and nestlings than to take adult, non-incubating birds. Post-fledging juveniles, on small islands at least, have much less opportunity for exploratory migration than the juveniles of mainland species. In consequence, they should more rapidly establish a familiar area (§5*g*) and become experienced at avoiding predators (which themselves are likely in any case to be less varied than on the mainland). Small oceanic islands, therefore, are probably characterized by relatively few profitable prey items and in consequence there is relatively less evolutionary advantage in being conspicuous to advertise unprofitability.

Hamilton (1961) used the involvement of colour in sex and species recognition in an attempt to explain an apparent latitudinal gradient of sexual dimorphism in the New World Parulidae and Icteridae. In these families, tropical species tend to be sexually monomorphic and conspicuous whereas north temperate species tend to be sexually dimorphic. Hamilton attributes the gradient to the fact that the tropical species are non-migratory and form relatively permanent pair-bonds. North temperate species, on the other hand, are migratory and each spring need to find a mate. Sexual dimorphism facilitates sex recognition and reduces the time spent in courtship, time that would be important to a migratory species. Again, however, in view of the many cues other than colour by which sex recognition can be achieved, it seems doubtful that this time waste exists and acts as a selective pressure against monomorphism. This is especially so in view of the likelihood that many males and females of even long-distance migrants return to breed with the same individual, often in the same place, as the previous year (Baker 1978). In the absence of multiple regression analysis of the North American situation the reality of an association between migration and dimorphism cannot be assessed. In our analysis there is an association for western palaearctic birds between the southern limit of the breeding range and conspicuousness, species breeding further north being less conspicuous (SBREED, in tables 26 and 27). However, this decreased conspicuousness affects both sexes more or less equally, not only the females as suggested by Hamilton for New World species. Whether there is a real difference between the two areas cannot be assessed until an equivalent analysis for New World species has been carried out. Perhaps the critical factor is the same as for the island situation. Because there are more species at lower latitudes there is an opportunity for more categories to become relatively unprofitable and to announce the fact, and perhaps also more opportunity for Batesian and Mullerian mimicry of males by females (§3*c*(iii)).

We are not suggesting, of course, that sexual selection does not act on birds, only that it has not acted on coloration. After all, the evolution of reproductive behaviour itself is undoubtedly in large part the result of sexual selection pressures (Trivers 1972). As reproductive behaviour evolves, partly through the action of sexual selection, those predation-risk selective pressures are generated that we argue have shaped the coloration of the birds. We assume that this relation is more likely than the admittedly possible alternative that as sexual selection shapes the coloration of birds, incipient sexual dimorphism generates selection on reproductive behaviour, etc. It seems clear, also, that sexual dimorphism with respect to body size and loudness/depth of voice can also be the result of sexual selection (both female choice and male–male competition).

There would seem, however, to be a good reason why these characteristics, but not colour, should respond to sexual selection.

While acknowledging the theoretical possibility that an otherwise 'neutral' character can spread through a male population as a result of female choice, it seems clear that such spread is far more likely, and faster, if the character confers some other advantage on the male and hence on the female through her sons. Body size and depth or loudness of voice of a male are all likely to show good correlation with resource holding power (Parker 1974, Morton 1977, Davies & Halliday 1978, Clutton-Brock & Albon 1979). In particular, they are relatively difficult to fake and hence provide a more or less reliable cue, both to another male or a female for which it is important accurately to assess resource holding power of that male. There would seem, however, to be no inevitable reason for colour to correlate with resource holding power. It would seem, intuitively, to be a cue relatively easy to fake and therefore unlikely to be adopted evolutionarily within a resource holding power assessment system. Hence our argument that sexual selection has acted on birds with respect to body size and voice dimorphism but not with respect to colour dimorphism. It should be noted, however, that field evidence exists that at first sight seems to indicate a correlation between male coloration and resource holding power. When the red epaulets of male red-winged blackbirds, *Agelaius phoeniceus*, were painted or dyed black, such males were significantly less likely than control males to retain their territories (Smith 1972). Further consideration, however, raises doubts that this experiment provides unequivocal evidence for the involvement of sexual selection in the evolution of colour dimorphism.

The reason for dyed males being more likely to lose their territories was not identified with certainty but seemed to be because intruding males were more persistent in staying within the territory of an all-black male than in that of a control. It does not inevitably follow, however, that assessment of resource holding power based on red coloration was involved. One chance observation (Smith 1972) was of a male that, having lost his territory, eventually managed to chip off a thin layer of (in his case) paint to reveal a thin strip of *white*. Having done so, this male successfully regained his territory and was the only male to do so. It would seem, therefore, that the critical factor was that experimental males were all-black, not that they had lost their red coloration. It was interesting also that dyed males invariably lost their territories to immigrant males, not to those neighbouring males that were familiar with the bird as an individual (see Baker 1978). Quite possibly, therefore, although females accepted the dyed male as conspecific (perhaps because they were the same mate as in the previous year), intruding males considered the territory as empty, perhaps occupied by an all-black blackbird of the genus *Euphagus*, and persisted in the area as a result. In consequence, the territorial male either had to escalate the territorial interaction or leave. Whatever the real explanation, the evidence cannot be taken as unequivocal support for sexual selection for sexual dimorphism. A more critical test for the involvement of sexual selection in the red-winged blackbird situation would, as suggested by Smith (1972), be experimentally to vary the size of the red patch, rather than obscure it altogether.

In conclusion we make several suggestions concerning the evolution of bird coloration: (i) colour is far less likely than body size or voice to be acted upon by sexual selection, (ii) unequivocal field evidence for the direct involvement of sexual selection in coloration is lacking, and (iii) predation-based theories provide a much neater and more consistent explanation than sexual selection theories of virtually all aspects of bird coloration, not only those aspects associated with polygamy and other relatively infrequent reproductive systems. There is, however, one way in which predation and sexual selection theories can be reconciled. If, during the evolution of sexual dimorphism in a particular lineage, more-conspicuous males are at an advantage relative to less-conspicuous males owing to reduced predation risk, selection would favour those females that mated preferentially with the more-conspicuous males. The converse would also be true, of course, in lineages for which less-conspicuous males experience reduced predation risk. Such sexual selection could act in monogamous (O'Donald *et al* 1974) as well as in polygamous situations, albeit less intensely in the former. Sexual selection, acting through female choice, could conceivably, therefore, speed up the evolution of colour patterns. The final coloration, however, is still determined by predation. Furthermore, sexual selection, on this argument, could equally well act to reduce as to accentuate conspicuousness. We suggest, therefore, that if sexual selection is involved at all in the evolution of bird coloration it acts simply to speed up changes that would have occurred in any case through the selective agency of predation.

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APPENDIX. TABLES 17–30

The appendix contains the following tables.

Coloration: tables 17–25.

Table 17.	Bill	Table 22.	Front
Table 18.	Leg	Table 23.	Belly
Table 19.	Crown	Table 24.	Upper surface flash
Table 20.	Head	Table 25.	Under surface flash
Table 21.	Back		

Predictive equations for conspicuousness of each of the nine body regions: tables 26–30.

Table 26.	Breeding males
Table 27.	Breeding females
Table 28.	Juveniles
Table 29.	Non-breeding season adult males
Table 30.	Non-breeding season adult females

TABLE 17. BILL COLORATION

Increased conspicuousness favoured mainly by:

in adults	*in juveniles*
(*a*) large body size	
(*b*) diurnal feeding activity	(*b*) diurnal feeding activity
(*c*) less time on ground/water	(*c*) less time on ground/water
(*d*) more southerly breeding range	(*d*) more southerly breeding range
(*e*) more northerly northern edge to winter range	(*e*) more northerly northern edge to winter range
(*f*) more southerly southern edge to winter range	(*f*) more southerly southern edge to winter range
(*g*) gregariousness	(*g*) gregariousness
(*h*) concealed incubation site	
(*i*) incubation by both sexes when the incubation site is exposed	
(*j*) single brood/breeding season	(*j*) single brood/breeding season
(*k*) monogamy	(*k*) monogamy
(*l*) care of post-hatching young mainly or solely by male	(*l*) care of post-hatching young mainly or solely by male

Increased sexual dimorphism favoured mainly by:	*Increased adult/juvenile dimorphism favoured mainly by:*
(*a*) *small* body size	(*a*) *large* body size
	(*b*) diurnal feeding activity
(*c*) incubation by female alone when incubation site concealed	(*c*) incubation by both sexes when incubation site exposed
(*d*) several broods/breeding season	
(*e*) polygamy	
(*f*) care of the post-hatching young by female alone	

Increased seasonal change in bill coloration favoured mainly by:

(*a*) increased distance between southern edges of breeding and winter ranges
(*b*) gregariousness
(*c*) concealed incubation site
(*d*) incubation by both sexes when the incubation site is exposed

TABLE 18. LEG COLORATION

Increased conspicuousness favoured mainly by:

in adults	*in juveniles*
(*a*) large body size	
(*b*) diurnal feeding activity	(*b*) diurnal feeding activity
(*c*) less time on ground/water	(*c*) less time on ground/water
(*d*) a more southerly southern edge to the breeding range	
	(*e*) a more northerly northern edge to the winter range
	(*f*) a more southerly southern edge to the winter range
(*g*) gregariousness	(*g*) gregariousness
(*h*) incubation by both sexes when the incubation site is exposed	
(*i*) single brood/breeding season	(*i*) single brood/breeding season
(*j*) incubation mainly or solely by the female when the incubation site is concealed	
(*k*) care of post-hatching young mainly or solely by male	(*k*) care of post-hatching young mainly or solely by male

Increased sexual dimorphism favoured mainly by:	*Increased adult/juvenile dimorphism favoured mainly by:*
	(*a*) large body size
(*b*) a vegetarian diet	(*b*) a vegetarian diet
	(*c*) less time on ground/water
	(*d*) more southerly northern edge to the breeding range
	(*e*) more northerly southern edge to the winter range
	(*f*) incubation by both sexes when the incubation site is exposed
(*g*) polygamy	
(*h*) care of post-hatching young mainly or solely by female	(*h*) care of post-hatching young mainly or solely by male

Increased seasonal change in leg coloration favoured mainly by:

(*a*) more time on ground/water
(*b*) decreased distance between northern edges of breeding and winter ranges
(*c*) gregariousness

TABLE 19. CROWN COLORATION

Increased conspicuousness favoured mainly by:

in adults	*in juveniles*
(*a*) large body size	
(*b*) an animal diet (females only)	(*b*) an animal diet
(*c*) diurnal feeding activity	(*c*) diurnal feeding activity
(*d*) less time on ground/water	(*d*) less time on ground/water
(*e*) more northerly southern edge to the winter range	(*e*) more northerly southern edge to the winter range
(*f*) gregariousness	(*f*) gregariousness
(*g*) concealed incubation site	(*g*) concealed incubation site
(*h*) monogamy (females only)	(*h*) monogamy
(*i*) lack of guarding of nest site by male	(*i*) lack of guarding of nest site by male
(*j*) decrease in time invested by either sex in the feeding and/or care of the post-hatching young increases the conspicuousness of that sex	

Increased sexual dimorphism favoured mainly by:	*Increased adult/juvenile dimorphism favoured mainly by:*
(*a*) *small* body size	(*a*) *large* body size
(*b*) a vegetarian diet	(*b*) a vegetarian diet (male/juvenile dimorphism only)
	(*c*) diurnal feeding activity
(*d*) a more northerly northern edge to the breeding range	(*d*) a more northerly northern edge to the breeding range
	(*e*) a more southerly northern edge to the winter range
	(*f*) gregariousness
	(*g*) incubation by both sexes when the incubation site is exposed
(*h*) polygamy	
(*i*) increase in guarding of nest site by male	(*i*) increase in guarding of nest site by male (male/juvenile dimorphism only)
(*j*) care of the post-hatching young by one sex only (the sex showing no care being the more conspicuous)	(*j*) care of the post-hatching young by one sex only (the sex showing no care having the greater adult/juvenile dimorphism)

Increased seasonal change in crown coloration favoured mainly by:

(*a*) small body size
(*b*) an animal diet
(*c*) more time on ground/water
(*d*) increased distance between southern edges of breeding and winter ranges
(*e*) incubation by both sexes when the incubation site is exposed

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Table 20. Head coloration

Increased conspicuousness favoured mainly by:

in adults	*in juveniles*
(*a*) large body size (except breeding males)	
(*b*) an animal diet (females only)	(*b*) an animal diet
(*c*) less time on ground/water	(*c*) less time on ground/water
(*d*) more southerly southern edge to breeding range	
(*e*) more northerly southern edge to winter range	(*e*) more northerly southern edge to winter range
(*f*) gregariousness	
(*g*) concealed incubation site	(*g*) concealed incubation site
(*h*) polygamy (males only)	
	(*i*) increased contribution to incubation by the male
(*j*) decrease in time invested by either sex in the feeding and/or care of the post-hatching young increases the conspicuousness of that sex	

Increased sexual dimorphism favoured mainly by:	*Increased adult/juvenile dimorphism favoured mainly by:*
(*a*) *small* body size	(*a*) *large* body size
(*b*) a vegetarian diet	(*b*) a vegetarian diet (male/juvenile dimorphism only)
	(*c*) diurnal feeding activity
	(*d*) more time on ground/water
	(*e*) more southerly southern edge to breeding range
	(*f*) more southerly northern edge to winter range
	(*g*) gregariousness
	(*h*) incubation by both sexes when incubation site exposed
(*i*) polygamy	(*i*) polygamy
(*j*) incubation mainly by female when incubation site concealed (breeding season only)	(*j*) incubation mainly or solely by female when incubation site concealed
(*k*) care of the post-hatching young by one sex only (the sex showing no care being the more conspicuous)	(*k*) care of the post-hatching young by one sex only (the sex showing no care having the greater adult/juvenile dimorphism)

Increased seasonal change in head coloration favoured mainly by:

(*a*) small body size
(*b*) an animal diet
(*c*) more time on ground/water
(*d*) gregariousness
(*e*) incubation by both sexes when the incubation site is exposed
(*f*) polygamy
(*g*) incubation mainly by female when incubation site concealed

TABLE 21. BACK COLORATION

Increased conspicuousness favoured mainly by:

in adults	*in juveniles*
(*a*) *large* body size	(*a*) *small* body size
(*b*) an animal diet	(*b*) an animal diet
(*c*) diurnal feeding activity	(*c*) diurnal feeding activity
(*d*) a more southerly southern edge to the breeding range	(*d*) a more southerly southern edge to the breeding range
(*e*) a more northerly southern edge to the winter range	(*e*) a more northerly southern edge to the winter range
(*f*) gregariousness while nesting (males only)	
(*g*) gregariousness while feeding during non-breeding season	(*g*) gregariousness while feeding during non-breeding season
(*h*) concealed incubation site	(*h*) concealed incubation site
	(*i*) incubation only by female if incubation site exposed
(*j*) single brood/breeding season	
(*k*) increased guarding of the nest site by the male	
(*l*) decrease in time invested by either sex in the feeding and/or care of the post-hatching young increases the conspicuousness of that sex	(*l*) increased care of the post-hatching young by the male

Increased sexual dimorphism favoured mainly by:	*Increased adult/juvenile dimorphism favoured mainly by:*
(*a*) *small* body size	(*a*) *large* body size
	(*b*) diurnal feeding activity
(*c*) a more northerly southern edge to the breeding range	(*c*) a more northerly southern edge to the breeding range
	(*d*) a more southerly southern edge to the winter range
(*e*) gregariousness while nesting	
	(*f*) concealed incubation site
	(*g*) incubation by both sexes if the incubation site is exposed
(*h*) polygamy	(*h*) polygamy
(*i*) incubation mainly or solely by one sex when the incubation site is concealed (the sex that does not incubate being the more conspicuous)	
(*j*) increased guarding of the nest site by the male	(*j*) increased guarding of the nest site by the male (male/juvenile dimorphism only)
(*k*) care of the post-hatching young by one sex only (the sex showing no care being the more conspicuous)	(*k*) care of the post-hatching young by one sex only (the sex showing no care having the greater adult/juvenile dimorphism)

Increased seasonal change in back coloration favoured mainly by:

(*a*) an animal diet
(*b*) more time on ground/water
(*c*) a more northerly breeding range
(*d*) solitary nesting
(*e*) incubation by both sexes when the incubation site is exposed
(*f*) polygamy
(*g*) incubation mainly or solely by the male (female change only)
(*h*) care of the post-hatching young mainly or solely by the male

Table 22. Front coloration

Increased conspicuousness favoured mainly by:

in adults	*in juveniles*
(*a*) *large* body size (♀ only)	(*a*) *small* body size
(*b*) a *vegetarian* diet (♂ only)	(*b*) an *animal* diet
(*c*) diurnal feeding activity	(*c*) diurnal feeding activity
(*d*) less time on ground/water (♀ only)	(*d*) less time on ground/water
(*e*) more southerly southern edge to breeding range	(*e*) more southerly southern edge to breeding range
(*f*) more northerly southern edge to winter range	(*f*) more northerly southern edge to winter range
(*g*) gregariousness	(*g*) gregariousness
(*h*) concealed incubation site	(*h*) concealed incubation site
(*i*) incubation mainly, though not solely, by the female if the bird is concealed while incubating	
(*j*) several broods/breeding season	
(*k*) polygamy	
(*l*) decrease in time invested by either sex in the feeding and/or care of the post-hatching young increases the conspicuousness of that sex	(*l*) increased care of the post-hatching young by the male

Increased sexual dimorphism favoured mainly by:	*Increased adult/juvenile dimorphism favoured mainly by:*
(*a*) *small* body size	(*a*) *large* body size
(*b*) a vegetarian diet	(*b*) a vegetarian diet
(*c*) more time on ground/water	(*c*) more time on ground/water
	(*d*) a more northerly northern edge to the breeding range
	(*e*) a more southerly southern edge to the breeding range
	(*f*) concealed incubation site
	(*g*) incubation by both sexes when the incubation site is exposed
	(*h*) polygamy
(*i*) incubation mainly or solely by the female	
	(*j*) guarding of the nest site by the male if the incubation site is exposed
(*k*) care of the post-hatching young by one sex only with the sex showing no care being the more conspicuous	(*k*) care of the post-hatching young by one sex only with the sex showing no care having the greater adult/juvenile dimorphism

Increased seasonal change in front coloration favoured mainly by:

(*a*) small body size
(*b*) an animal diet
(*c*) more time on ground/water
(*d*) more northerly breeding range
(*e*) solitary nesting
(*f*) incubation by both sexes if the birds are exposed while incubating
(*g*) care of the post-hatching young mainly or solely by the male

TABLE 23. BELLY COLORATION

Increased conspicuousness favoured mainly by:

in adults	*in juveniles*
(*a*) small body size	(*a*) small body size
	(*b*) an animal diet
(*c*) diurnal feeding activity	(*c*) diurnal feeding activity
(*d*) more time on ground/water	
(*e*) a more northerly southern edge to winter range	
(*f*) gregariousness during non-breeding season	(*f*) gregariousness during non-breeding season
(*g*) concealed incubation site	
(*h*) incubation by both sexes if the incubation site is exposed	
(*i*) care of the post-hatching young mainly or solely by the male	

Increased sexual dimorphism favoured mainly by:	*Increased adult/juvenile dimorphism favoured mainly by:*
(*a*) *small* body size	(*a*) *large* body size
	(*b*) a vegetarian diet
(*c*) more time on ground/water	(*c*) more time on ground/water
(*d*) an exposed incubation site when incubation is by the female alone	(*d*) a concealed incubation site and incubation by both sexes
(*e*) polygamy	(*e*) polygamy
(*f*) increased guarding of the nest site by the male	
(*g*) care of the post-hatching young mainly or solely by the *female*	(*g*) care of the post-hatching young mainly or solely by the *male* (female/juvenile dimorphism only)

Increased seasonal change in belly coloration favoured mainly by:

(*a*) more time on ground/water
(*b*) more northerly breeding range
(*c*) solitary nesting
(*d*) exposed incubation site
(*e*) incubation by both sexes if the incubation site is exposed

Table 24. Upper surface flash coloration: wing-bars, rump and outer tail feathers

Increased conspicuousness favoured mainly by:

in adults	*in juveniles*
(*a*) small body size	(*a*) small body size
	(*b*) an animal diet
(*c*) more time on ground/water	(*c*) more time on ground/water
(*d*) more northerly northern edge to the winter range	(*d*) more northerly northern edge to the winter range
(*e*) more southerly southern edge to the winter range	(*e*) more southerly southern edge to the winter range
(*f*) solitary nesting	
(*g*) gregarious feeding during non-breeding season	(*g*) gregarious feeding during non-breeding season
(*h*) several broods/breeding season	
	(*i*) monogamy
(*j*) care of the post-hatching young mainly or solely by female	(*j*) care of the post-hatching young mainly or solely by female

Increased sexual dimorphism favoured mainly by:	*Increased adult/juvenile dimorphism favoured mainly by:*
	(*a*) large body size
	(*b*) a vegetarian diet
	(*c*) more time on ground/water
(*d*) a more northerly northern edge to breeding range	
	(*e*) more southerly southern edge to winter range
	(*f*) solitary nesting
(*g*) an exposed incubation site when incubation is by the female alone	(*g*) concealed incubation site
(*h*) several broods/breeding season	
	(*i*) polygamy
	(*j*) increased contribution to incubation by male
(*k*) increased guarding of nest site by male	(*k*) increased guarding of nest site by male
(*l*) care of the post-hatching young mainly or solely by female	(*l*) care of the post-hatching young mainly or solely by female (male/juvenile dimorphism) or male (female/juvenile dimorphism)

Increased seasonal change in upper-surface flash coloration favoured mainly by:

(a) gregariousness

TABLE 25. UNDER-SURFACE FLASH COLORATION: UNDERSIDE OF WINGS AND TAIL

Increased conspicuousness favoured mainly by:

in adults	*in juveniles*
(*a*) an animal diet	(*a*) an animal diet
(*b*) nocturnal feeding activity	
(*c*) more southerly northern edge to breeding range	(*c*) more southerly northern edge to breeding range
(*d*) more northerly northern edge to winter range	(*d*) more northerly northern edge to winter range
(*e*) more southerly southern edge to winter range	
(*f*) solitary nesting	(*f*) solitary nesting
(*g*) gregarious feeding during non-breeding season	(*g*) gregarious feeding during non-breeding season
(*h*) exposed incubation site	(*h*) exposed incubation site
	(*i*) incubation by female alone when incubation site exposed
(*j*) single brood/breeding season	(*j*) single brood/breeding season
(*k*) monogamy (females only)	(*k*) monogamy
(*l*) increased contribution to incubation by male	
(*m*) lack of guarding of nest site by male (except breeding female)	(*m*) lack of guarding of nest by male

Increased sexual dimorphism favoured mainly by:	*Increased adult/juvenile dimorphism favoured mainly by:*
	(*a*) large body size
(*b*) more southerly northern edge to winter range	(*b*) more southerly northern edge to winter range
	(*c*) concealed incubation site
	(*d*) incubation by both sexes when incubation site exposed
(*e*) polygamy	(*e*) polygamy
	(*f*) increased contribution to incubation by male
	(*g*) guarding of nest site by male
(*h*) care of post-hatching young mainly or solely by female	(*h*) care of post-hatching young mainly or solely by female

Increased seasonal change in under-surface flash coloration favoured mainly by:

(*a*) more northerly southern edge to winter range
(*b*) gregariousness
(*c*) concealed incubation site
(*d*) incubation by both sexes when incubation site exposed (male coloration only)
(*e*) polygamy
(*f*) guarding of nest site by male

Table 26. Predictive equations for the conspicuousness of each of nine body regions for breeding males in the Western Palaearctic

ndependent variables (see § 4*c*)	bill	crown	head	back	front	belly	legs	wing bars and rump	underside of wing and tail
LENGTH	$+0.016^4$	$+0.006^3$	-0.001	$+0.005^4$	0.000	-0.007^4	$+0.007^4$	-0.014^4	-0.002
DIET	-0.058	-0.100	$+0.050$	$+0.157$	-0.052	0.000	-0.129	$+0.064$	$+0.241^4$
DAYNIGHT	$+1.090^4$	$+1.954^4$	0.000	$+1.703^4$	$+1.563^4$	$+1.093^4$	$+1.332^4$	$+0.281$	-0.697^1
HEIGHTAG	$+0.070^3$	$+0.081^3$	$+0.005$	-0.016	-0.024	-0.095^4	$+0.166^4$	-0.214^4	$+0.013$
NBREED	-0.007	$+0.005$	$+0.004$	$+0.007$	$+0.006$	$+0.006$	$+0.003$	-0.005	-0.192^3
SBREED	-0.010^4	-0.005	-0.010^2	-0.001	-0.005	-0.005	-0.013^1	$+0.008$	$+0.004$
NWINTER	$+0.011^1$	0.000	-0.006	-0.004	-0.005	-0.005	$+0.005$	$+0.014^3$	$+0.010^1$
SWINTER	-0.007	$+0.010^4$	$+0.010^4$	$+0.007^4$	$+0.007^4$	$+0.005^2$	-0.003	-0.013^4	-0.010^3
BRGREG	$+0.082$	$+0.123^3$	$+0.085$	$+0.042$	$+0.086$	$+0.024$	$+0.065$	-0.155^3	-0.294^4
FDGREG	$+0.184^4$	$+0.158^4$	$+0.120^3$	$+0.063$	$+0.130^4$	$+0.099^3$	$+0.085^1$	$+0.208^4$	$+0.211^4$
FEXINC	-0.069	-0.096^3	-0.111	-0.184^4	-0.159^3	-0.040	-0.026	-0.026	$+0.165^4$
MEXINC	$+0.104^4$	-0.009	$+0.057$	-0.035	$+0.163^4$	$+0.032$	$+0.156^4$	-0.021	-0.070
NOBROODS	-0.144^1	-0.047	-0.019	-0.104^1	$+0.109^2$	-0.064	-0.196^3	-0.076	-0.128
POLYGAMY	-0.214^1	$+0.133$	$+0.289^3$	$+0.233$	$+0.186^1$	$+0.055$	$+0.029$	-0.121	$+0.052$
MINC	$+0.021$	-0.046	-0.027	$+0.163$	-0.139^2	-0.086	-0.213^1	$+0.150$	$+0.217$
MGUARD	0.000	-0.031	$+0.045$	$+0.193^1$	-0.011	-0.018	-0.122	$+0.076$	$+0.064^4$
MFEDYONG	$+0.073$	-0.072^3	-0.066	-0.131	0.000	$+0.023$	$+0.238^2$	-0.276^4	-0.158
ntercept	$+0.884$	-0.555	$+3.009$	-0.038	$+0.825$	$+2.09$	$+0.566$	$+2.424$	$+2.421$

Superior figures indicate the probability that the calculated regression coefficients differ from zero by chance: 1, $P < 0.05$; 2, $P < 0.02$; 3, $P < 0.01$; 4, $P < 0.001$.

Table 27. Predictive equations for the conspicuousness of each of nine body regions for breeding females in the Western Palaearctic

ndependent variables	bill	crown	head	back	front	belly	legs	wing bars and rump	underside of wing and tail
LENGTH	$+0.018^4$	$+0.013^4$	$+0.006^3$	$+0.008^4$	$+0.005^1$	-0.004^3	$+0.008^4$	-0.012^4	-0.002
DIET	-0.084	$+0.380^4$	$+0.369^4$	$+0.233^3$	$+0.089$	0.000	-0.063	$+0.081$	$+0.204$
DAYNIGHT	$+0.961^4$	$+1.772^4$	-0.229	$+1.488^4$	$+1.375^4$	$+0.902^4$	$+1.341^4$	$+0.349$	-0.607
HEIGHTAG	$+0.078^1$	$+0.085^2$	$+0.039$	$+0.008$	$+0.019$	-0.058^1	$+0.150^4$	-0.217^4	0.000
NBREED	-0.011	-0.001	$+0.001$	$+0.006$	$+0.006$	$+0.008$	$+0.003$	-0.008	-0.018^3
BREED	-0.011^4	-0.004	-0.008^3	-0.005	-0.005	-0.006	-0.012^2	$+0.006$	$+0.004$
NWINTER	$+0.014^3$	-0.001	-0.007^1	-0.004	-0.007	-0.005	$+0.006$	$+0.014^3$	$+0.011^1$
WINTER	-0.008^1	$+0.011^4$	$+0.010^4$	$+0.009^4$	$+0.008^4$	$+0.005^1$	-0.003	-0.013^4	-0.009^2
BRGREG	$+0.084$	$+0.086$	$+0.079$	-0.026	$+0.080^1$	0.000	$+0.064$	-0.189^4	-0.322^4
FDGREG	$+0.167^4$	$+0.206^4$	$+0.171^4$	$+0.110^3$	$+0.156^4$	$+0.130^4$	$+0.072$	$+0.188^4$	$+0.220^4$
FEXINC	-0.104	-0.089^4	-0.122^3	-0.145^4	-0.169^4	-0.083^3	-0.035	-0.046	$+0.146^4$
MEXINC	$+0.145^4$	-0.020	$+0.058$	-0.059	$+0.155^4$	$+0.077^3$	$+0.146^4$	$+0.014$	-0.053
NOBROODS	-0.197^4	$+0.045$	$+0.036$	-0.070	$+0.135^3$	-0.019	-0.203^3	-0.115^1	-0.129^1
POLYGAMY	-0.367^3	-0.237	$+0.053$	-0.060	$+0.091$	-0.140	-0.134	-0.224	-0.144
MINC	-0.058	-0.123	-0.061	$+0.095$	-0.063	-0.070	-0.220	0.000	$+0.162^1$
MGUARD	-0.080	-0.180^1	-0.060	$+0.014$	-0.044	-0.061	-0.143	-0.051	$+0.016$
MFEDYONG	$+0.268^4$	$+0.272^4$	$+0.232^4$	$+0.234^4$	$+0.324^4$	$+0.231^4$	$+0.307^4$	-0.061	-0.102
ntercept	$+0.911$	-1.416	$+1.536$	-1.010	-0.783	$+1.281$	$+0.421$	$+2.506$	$+2.560$

Superior figures indicate the probability that the calculated regression coefficients differ from zero by chance: 1, $P < 0.05$; 2, $P < 0.02$; 3, $P < 0.01$; 4, $P < 0.001$.

Table 28. Predictive equations for the conspicuousness of each of nine body regions for juveniles in the Western Palaearctic

independent variables	bill	crown	head	back	front	belly	legs	wing bars and rump	underside of wing and tail
LENGTH	$+0.005$	$+0.002$	-0.003	-0.006^{2}	-0.008^{4}	-0.016^{4}	$+0.002$	-0.017^{4}	-0.004
DIET	$+0.026$	$+0.281^{4}$	$+0.341^{4}$	$+0.301^{4}$	$+0.129^{1}$	$+0.123^{1}$	-0.017	$+0.350^{4}$	$+0.257^{4}$
DAYNIGHT	$+0.713^{1}$	$+1.280^{4}$	-0.484	$+1.112^{4}$	$+1.136^{4}$	$+0.791^{4}$	$+1.089^{4}$	$+0.435$	-0.432
HEIGHTAG	$+0.084^{1}$	$+0.123^{4}$	$+0.083^{3}$	$+0.014$	$+0.086^{4}$	-0.020	$+0.117^{4}$	-0.177^{4}	$+0.008$
NBREED	-0.013^{1}	-0.006	$+0.001$	$+0.003$	-0.002	$+0.003$	$+0.008$	-0.008	-0.017^{3}
SBREED	-0.009	-0.003	-0.002	-0.008^{1}	-0.006^{3}	-0.004	-0.010	$+0.009$	$+0.003$
NWINTER	$+0.015^{4}$	$+0.006$	0.000	-0.002	$+0.001$	-0.002	$+0.004^{1}$	$+0.014^{3}$	$+0.014^{3}$
SWINTER	-0.008^{2}	$+0.008^{4}$	$+0.012^{4}$	$+0.013^{4}$	$+0.006^{4}$	$+0.004$	-0.005^{2}	-0.009^{2}	-0.007
BRGREG	$+0.069^{4}$	$+0.082$	-0.026	$+0.033$	$+0.078$	-0.016	$+0.056^{4}$	-0.118	-0.294^{4}
FDGREG	$+0.154^{4}$	$+0.082^{3}$	$+0.064$	$+0.091^{3}$	$+0.165^{4}$	$+0.124^{4}$	$+0.082$	$+0.223^{4}$	$+0.185^{4}$
FEXINC	$+0.005$	-0.095^{4}	-0.085^{4}	-0.075^{4}	-0.086^{3}	-0.012	-0.044	$+0.022$	$+0.217^{4}$
MEXINC	0.000	-0.087	-0.091	-0.107^{2}	$+0.018$	$+0.005$	$+0.074$	-0.018	-0.119^{2}
NOBROODS	-0.220^{4}	-0.043	-0.036	-0.082	$+0.072$	-0.010	-0.151^{2}	-0.094	-0.133^{1}
POLYGAMY	-0.315^{4}	-0.271^{3}	-0.098	-0.135	-0.052	-0.166	-0.133	-0.314^{1}	-0.284^{2}
MINC	0.000	$+0.011$	$+0.052^{1}$	$+0.120$	-0.055	-0.109	-0.218	-0.037	$+0.042$
MGUARD	-0.021	-0.084^{1}	-0.075	$+0.040$	-0.054	-0.101	-0.133	-0.089	-0.122^{4}
MFEDYONG	$+0.130^{3}$	$+0.045$	$+0.024$	$+0.054^{4}$	$+0.141^{4}$	$+0.107$	$+0.214^{2}$	-0.186^{4}	-0.051
intercept	$+1.229$	-0.135	$+2.415$	$+0.035$	$+0.396$	$+1.960$	$+0.616$	$+2.330$	$+2.722$

Superior figures indicate the probability that the calculated regression coefficients differ from zero by chance: 1, $P < 0.05$; 2, $P < 0.02$; 3, $P < 0.01$; 4, $P < 0.001$.

Table 29. Predictive equations for the conspicuousness of each of nine body regions for non-breeding season adult males that breed in the Western Palaearctic

independent variables	bill	crown	head	back	front	belly	legs	wing bars and rump	underside of wing and tail
LENGTH	$+0.015^{4}$	$+0.011^{4}$	$+0.005^{4}$	$+0.004^{4}$	$+0.003$	-0.006^{4}	$+0.007^{4}$	-0.013^{4}	0.000
DIET	-0.031	$+0.053$	-0.044	$+0.138$	-0.169^{3}	-0.023	-0.149	$+0.082$	$+0.220^{3}$
DAYNIGHT	$+1.109^{4}$	$+1.939^{4}$	0.000	$+1.645^{4}$	$+1.464^{4}$	$+1.059^{4}$	$+1.292^{4}$	$+0.328$	-0.661^{1}
HEIGHTAG	$+0.079^{1}$	$+0.143^{4}$	$+0.064$	$+0.022$	$+0.042$	-0.073^{3}	$+0.187^{4}$	-0.218^{4}	$+0.004$
NBREED	-0.005	-0.002	0.000	$+0.004$	$+0.001$	$+0.003$	$+0.004$	-0.006	-0.019^{3}
SBREED	-0.013^{4}	-0.003	-0.007^{1}	-0.005	-0.006^{2}	-0.005	-0.011^{1}	$+0.008$	$+0.003$
NWINTER	$+0.011^{1}$	$+0.002$	-0.004	-0.004	-0.004	-0.004	$+0.003$	$+0.015^{3}$	$+0.010^{1}$
SWINTER	-0.004	$+0.010^{4}$	$+0.011^{4}$	$+0.011^{4}$	$+0.005^{2}$	$+0.005^{1}$	-0.002	-0.014^{4}	-0.008^{1}
BRGREG	$+0.039$	$+0.149^{2}$	$+0.072$	$+0.090^{1}$	$+0.151^{2}$	$+0.053$	$+0.048$	-0.171^{3}	-0.323^{4}
FDGREG	$+0.181^{4}$	$+0.108^{3}$	$+0.025$	$+0.069$	$+0.111^{4}$	$+0.083^{4}$	$+0.070$	$+0.189^{3}$	$+0.175^{4}$
FEXINC	-0.017	-0.011^{4}	-0.103^{4}	-0.162^{4}	-0.192^{4}	-0.055^{1}	-0.029	-0.021	$+0.190^{4}$
MEXINC	$+0.066^{4}$	-0.044	-0.019	-0.070	$+0.107$	$+0.018$	$+0.163^{4}$	-0.029	-0.113
NOBROODS	-0.180^{3}	$+0.093$	-0.017	-0.096	$+0.088$	-0.053	-0.200^{2}	-0.059	-0.132^{1}
POLYGAMY	-0.296^{3}	-0.022	$+0.174$	$+0.130$	$+0.135$	$+0.037$	-0.030	-0.132	-0.049
MINC	$+0.048$	-0.024	$+0.060$	$+0.164$	-0.067^{1}	-0.092	-0.239^{1}	$+0.162$	$+0.182$
MGUARD	0.000	-0.038	$+0.059$	$+0.192^{1}$	$+0.038$	-0.039	-0.147	$+0.076$	$+0.014^{3}$
MFEDYONG	$+0.059$	-0.100^{3}	-0.105^{2}	-0.200^{3}	-0.056	$+0.017$	$+0.231^{1}$	-0.291^{4}	-0.128
intercept	$+0.896$	-0.327	$+3.139$	$+0.141$	$+1.161$	$+2.303$	$+0.763$	$+2.404$	$+2.723$

Superior figures indicate the probability that the calculated regression coefficients differ from zero by chance: 1, $P < 0.05$; 2, $P < 0.02$; 3, $P < 0.01$; 4, $P < 0.001$.

Table 30. Predictive equations for the conspicuousness of each of nine body regions for non-breeding season adult females that breed in the Western Palaearctic

dependent variables	bill	crown	head	back	front	belly	legs	wing bars and rump	underside of wing and tail
NGTH	$+0.017^{4}$	$+0.016^{4}$	$+0.011^{4}$	$+0.007^{4}$	$+0.007^{3}$	-0.004^{3}	$+0.009^{4}$	-0.011^{4}	0.000
ET	−0.057	$+0.274^{4}$	$+0.246^{3}$	$+0.189^{2}$	−0.058	−0.033	−0.090	+0.102	+0.184
YNIGHT	$+0.993^{3}$	$+1.759^{4}$	−0.194	$+1.466^{4}$	$+1.307^{4}$	$+0.881^{4}$	$+1.302^{4}$	+0.394	−0.568
IGHTAG	$+0.081^{1}$	$+0.126^{4}$	$+0.080^{4}$	+0.040	$+0.082^{3}$	−0.042	$+0.168^{4}$	-0.218^{4}	−0.016
BREED	−0.007	−0.003	+0.002	+0.004	+0.003	+0.007	+0.005	−0.009	-0.018^{3}
REED	-0.014^{4}	−0.004	−0.006	-0.010^{1}	−0.007	−0.007	-0.010^{1}	+0.007	+0.002
VINTER	$+0.014^{3}$	−0.001	-0.008^{2}	−0.005	-0.008^{1}	−0.006	+0.004	$+0.015^{3}$	$+0.011^{2}$
INTER	−0.005	$+0.011^{4}$	$+0.012^{4}$	$+0.010^{3}$	$+0.007^{4}$	$+0.005^{1}$	−0.002	-0.013^{4}	-0.008^{1}
GREG	+0.045	$+0.107^{1}$	+0.061	+0.025	$+0.137^{4}$	+0.017	+0.053	-0.201^{4}	-0.349^{4}
GREG	$+0.158^{4}$	$+0.155^{4}$	$+0.075^{1}$	$+0.108^{3}$	$+0.131^{4}$	$+0.117^{4}$	+0.052	$+0.176^{4}$	$+0.179^{4}$
XINC	−0.059	-0.116^{4}	-0.132^{4}	-0.134^{4}	-0.190^{4}	-0.085^{3}	−0.044	−0.053	$+0.169^{4}$
EXINC	$+0.110^{4}$	−0.034	0.000	−0.075	$+0.113^{3}$	+0.059	$+0.154^{4}$	+0.019	−0.099
BROODS	-0.217^{4}	+0.067	+0.045	−0.051	$+0.138^{3}$	−0.014	-0.190^{3}	−0.094	−0.122
LYGAMY	-0.396^{3}	-0.280^{1}	−0.014	−0.127	+0.046	-0.184^{1}	−0.170	−0.219	-0.223^{1}
NC	−0.026	−0.119	0.000	+0.058	−0.059	−0.096	−0.241	0.000	+0.129
UARD	−0.072	−0.157	−0.037	+0.018	−0.026	−0.093	−0.171	−0.045	-0.035^{3}
EDYONG	$+0.254^{4}$	$+0.238^{4}$	$+0.197^{4}$	$+0.187^{4}$	$+0.275^{4}$	$+0.232^{4}$	$+0.298^{4}$	−0.076	−0.072
tercept	+0.791	−1.200	+1.607	−0.547	−0.271	+1.577	+0.572	+2.452	+2.819

Superior figures indicate the probability that the calculated regression coefficients differ from zero by chance: 1, $P < 0.05$; 2, < 0.02; 3, $P < 0.01$; 4, $P < 0.001$.

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