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The Evolution of Aggression: Can Selection Generate Variability? [and Discussion]

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The evolution of aggression: can selection generate variability?

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Three models – the war of attrition, the size game and the badges of dominance game – are described, in which natural selection can maintain genetic variability for aggression. The models differ in whether or not the traits that settle contests are costly in contexts other than fighting, and also in whether signals are used. It is concluded that contests will be settled by non-costly traits only if the value of the contested resource is small relative to the cost of fighting, and that 'honest' signalling of aggressiveness is stable only if individuals giving signals that are inconsistent with their behaviour suffer costs. The literature on 'badges of dominance' in birds is reviewed. New data on great tits, greenfinches and corn buntings show that there is plumage variability within age and sex that sometimes serves to settle contests, and that, in the first two species but not the third, the badges are uncorrelated with size, and settle contests only over trivial resources.

Introduction

This investigation was stimulated by two sets of observations. The first (Barlow *et al.* 1986) concerns Midas cichlids. These fish can be ranked in aggressiveness by the vigour with which they attack a dummy. If two fish were placed in a tank, but separated by an opaque barrier, they fought when the barrier was removed. If the barrier was removed after 1–2 h, the more aggressive fish won after a brief fight, involving little injury. But if the barrier was removed after 24 h, there was a prolonged and injurious fight. The winner was usually the heavier fish, although mass differences were slight: aggressiveness towards a dummy did not predict the outcome.

The second set of observations concerns 'status signals' in birds (for reviews, see Roper (1986) and Whitfield (1987)). These observations are discussed later in the paper. However, the essential point is that, in many bird species, plumage is variable within age and sex classes, and in at least some cases it does play a role in settling contests.

What these observations suggest is that natural selection can cause genetic variability for aggressiveness, which may not be closely correlated with size and strength, and that signals may indicate an individual's level of aggression. This at once raises a number of questions. For example, why is there not an optimum level of aggression? If aggression is variable, can signals accurately convey the level in an individual? Will there not be selection for lying? This paper describes various models of how frequency-dependent selection can maintain variability for aggression, and for signals indicating aggression, and it reviews some data relevant to the models.

The hawk–dove game: problems and limitations

The simplest model of contest behaviour is shown in table 1. Given the assumptions of the model, we can expect individuals to behave in a variable manner. The variability may be

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genetic (genetic polymorphism), or individuals may adopt sometimes one strategy and sometimes the other (mixed Evolutionarily Stable Strategy (ESS)). In the rest of this paper we shall assume that if selection favours variability, it will be achieved by genetic polymorphism, but the alternative of a mixed ESS should be borne in mind. In either case, the payoffs (changes in fitness) to an individual adopting one or other strategy will be equal. In applying the model to real situations, a number of points should be remembered.

Table 1. Payoffs in the hawk–dove game

(Payoffs are changes in fitness arising from the contest. The entries in the matrix are payoffs to an individual adopting the strategy on the left, if its opponent adopts the strategy above. V, value of resource; C, cost of injury; h, hawk; d, dove. The matrix on the right gives the payoffs if $V = 2$ and $C = 4$.)

	h	d		h	d
h	$(V-C)/2$	V	h	-1	2
d	0	$V/2$	d	0	1

1. The existence of a stable polymorphism, or of a mixed ESS, depends on $C > V$. If $V > C$, we expect all individuals to be hawks: qualitatively, we expect polymorphism only if the costs of fighting are high relative to the rewards.

2. The hawk–dove game predicts polymorphism or a mixed ESS, but not all cases of variable behaviour are mixed ESSs. An equally plausible explanation for variable behaviour is that individuals vary, perhaps for environmental reasons, in size and strength, and that their behaviour is adjusted to their size. If so, all individuals adopt the pure strategy 'if large, do A; if small, do B'. The crucial test is that in a stable polymorphism the payoffs to the alternative strategies should be equal.

3. The hawk–dove game is 'symmetrical'. Most actual contests are asymmetric, because one of the contestants is already in possession of the resource, or because there is a perceivable difference in resource holding power (RHP) (e.g. size or weapons) between the contestants, or both. If so, the contest is likely to be settled, more or less conventionally, by the asymmetry. It can be evolutionarily stable for there to be an initial 'assessment' phase that makes differences in size or strength apparent. There has been some debate about whether the asymmetries that settle contests must be correlated with RHP, or with the value of the resource to the individual. In brief, if the strategies available to an individual are continuously distributed, then the asymmetry must be correlated. But if the strategies (or, what amounts to the same thing, the risks associated with different acts) are discontinuous, then an uncorrelated asymmetry can settle the contest. Ownership may be uncorrelated with payoff. If ownership does settle contests, the proximate mechanism will be that the vigour with which an individual defends a resource will increase with the length of time for which it has been in possession of it, as illustrated by the cichlids described above.

Because of the role of asymmetries, of RHP or ownership, in settling pairwise contests, mixed ESSs are most commonly met with when an individual is competing, not against a single opponent, but against the whole population, or some section of it. However, we are now asking, not only whether natural selection can generate variability in behaviour, but also whether it can generate differences that can be used to settle contests conventionally.

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SOME TERMINOLOGY: MOTIVATION, RHP AND CONVENTIONAL SIGNALS

We can imagine three ways in which a contest might be settled.

1. By an all-out fight. Parker (1974) defined the characteristics determining the outcome of such a fight as RHP: colloquially, we can refer to fighting ability, or even to 'size', so long as we remember that traits other than mere size will be relevant. For modelling, the essential point is that an increase in RHP, or size, reduces fitness in other contexts: for example an increase in size might require a delay in reproduction.

2. By a limited fight. The winner will be the individual willing to fight harder, or continue for longer. We will refer to this willingness as 'aggressiveness'. From a modelling point of view, high aggressiveness may be costly in the context of a fight (e.g. an aggressive animal may get involved in more fights), but not at other times.

3. By signals. The contest is settled without cost. We distinguish between 'assessment signals' and 'conventional signals'. The former are necessarily connected with RHP, and cannot be faked. For example, the spider *Agelenopsis aperta* can assess the mass of an opponent by signals that vibrate the web on which they are standing (Riechert 1978). In contrast, conventional signals may or may not be correlated with RHP, but there is no physical or physiological reason why they must be so: examples are plumage patterns in birds, or verbal abuse in our own species.

These distinctions are necessary if models are to be developed. In particular, one must distinguish between traits that are costly in contexts other than fighting, and those that are not. In practice, the distinction may not be easy to make. Thus greater size is likely to be costly, but what of willingness to fight hard? Such willingness may be caused by a high level of testosterone, and this may raise the metabolic rate, and so be costly, as size is costly, even if the animal does not fight (Silverin 1980). In describing the models, we will use the phrase 'costly trait' for traits that are costly in contexts other than fighting, and 'aggressiveness' for traits that are not. Thus a costly trait might be size, or weapons, or a motivational state involving a high and costly metabolic rate. It is then an empirical question which model best fits any particular case.

THREE MODELS

We now describe three models that can lead to genetic polymorphism for aggression.

1. The war of attrition game (Maynard Smith 1974). Contests settled by aggressiveness. No signals.

2. The size game (Parker 1983; Maynard Smith & Brown 1986). Contests settled by a costly trait.

3. The badges of dominance game. Contests settled by aggressiveness. Signals used.

The war of attrition

Each individual is characterized by a level, m, to which it is prepared to escalate: m measures the loss of fitness it is prepared to suffer. Thus m could be a function of the time for which an individual was prepared to continue, or of the injury it was prepared to undergo. The winner is the individual with the larger value of m; for example, it is the individual willing to go on for longer. Both contestants suffer a loss of fitness equal to the loser's value of m, because that is the time for which the fight actually continues. The payoffs are given in table 2.

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Table 2. Payoffs in the war of attrition game

(V is the value of the resource. m_A and m_B are the 'motivations' of A and B, measured by the cost each is prepared to pay to acquire the resource.)

	player A	player B
$m_A > m_B$	$V - m_B$	$-m_B$
$m_A = m_B$	$V/2 - m_B$	$V/2 - m_B$
$m_A < m_B$	$-m_A$	$V - m_A$

The stable distribution of motivation in the population is

$$p(m) = \frac{1}{V} e^{-m/V}, \tag{1}$$

where $p(m)$ is the probability density of individuals of measure m, and V is the value of the resource.

The weakness of the model is that it ignores possible differences in RHP that could be detected, and it ignores signals. Perhaps the observations that most nearly fit the model are Parker's (1970) on dungflies, in which the length of time males stay at cowpats varies so as to equalize mating success: note that these males are engaged, not in a pairwise contest, but in a 'game against the field'. However, the model may apply more widely than is realized. For example, the brief contests in Midas cichlids may best be thought of as a war of attrition.

The size game

Each individual is characterized by a size, m. Fights are won by the larger individual. In one version, fights occur only between individuals of roughly equal size: appreciable size differences are perceived through assessment signals, and the larger wins without cost. The fitness of an individual of size m is

$$W(m) = S(m) \cdot B(m), \tag{2}$$

where $S(m)$ is the probability of surviving to size m, and $B(m)$ is the breeding success of individuals that do survive to size m.

$B(m)$ is supposed to depend on an individual's size relative to that of the rest of the population. If $p(x)$ is the probability density of size in the population, then $z = \int_0^m p(x)\,dx$ is the fraction of the population smaller than m. $B(m)$ is assumed to be an increasing function of z.

The model analysed by Maynard Smith & Brown (1986) assumed

$$W(m) = e^{-\alpha m}(a + bz - C(m)). \tag{3}$$

In this equation the cost of size is represented by the term $e^{-\alpha m}$, the advantage of size in fighting by the term bz, and the cost of fighting by the term $C(m)$.

A stable size distribution requires that $W(m)$ be constant, or $dW(m)/dm = 0$. The conclusions are as follows.

1. Cost of fighting constant: $C(m)$ = constant.

No stable polymorphism is possible. If m is genetically determined, then the mean size of the population would increase without limit. If, however, some variance of size is environmental, and if mortality increases more rapidly with size than exponentially – for example, as $e^{-\alpha m^2}$ – then the population reaches a stable size. At this equilibrium, all variance of size is environmental (or, in practice, maintained by recurrent mutation), and the mean size would

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be substantially greater than that favoured by selection in the absence of contests: intraspecific competition lowers mean fitness, but does not maintain variability.

2. Fights occur only with opponents of similar size.

Given that fights are costly, it is reasonable that there should be an assessment phase, so that fights occur only between individuals that are similar in size. The cost of fighting to an individual is $C(m) = c \cdot p(m)$.

A stable genetic polymorphism is possible. Essentially, this is because it pays an individual to be different in size from others, because it is less likely to be involved in fights.

The badges of dominance game

Suppose that contests are settled by aggressiveness, but that this is signalled, and that the opponent with the lower value backs down. Prolonged contests would only take place between individuals of similar aggressiveness. This situation will be analysed in two stages. We first ask whether, if signalling is honest, a stable polymorphism is possible. Then we ask whether such a polymorphism would be stable against invasion by a mutant giving a dishonest signal: that is, a signal that does not correspond to its aggressiveness.

The fitness of an individual of aggressiveness m is

$$W(m) = a + bz - kC(m) \cdot p(m), \tag{4}$$

where, as before, $z = \int_0^m p(x)\,\mathrm{d}x$ is the fraction of the population less aggressive than m, and $C(m)$ is the cost of a fight between individuals of value m.

Note that (4) differs from (2) in two significant ways: there is no cost of large m except in the context of fighting, and the cost of a fight inreases with m. We seek a distribution $p(m)$ such that $W(m)$ is constant. The solution is given in the appendix. It is assumed that there is an upper limit, M, to the value of aggressiveness, corresponding to a willingness to engage in an all-out fight. Some solutions are shown in figure 1. In looking at these distributions, it should be remembered that they are the ideal distributions that give all phenotypes the same fitness: in practice, the genetic system would be unable to generate precisely these distributions.

If the cost of a fight increases steeply, relative to the value of winning, then a stable polymorphism is likely. If cost is independent of m, or increases only slowly, then most members of the population will have a motivation close to the maximum, M: in practice, contests would be settled by RHP.

The answer to our first question, then, is that there can be a stable polymorphism provided that the cost of a fight rises sufficiently steeply with m, relative to the value of winning: this is in line with the conclusions from the much simpler hawk–dove game. But is honest signalling of aggressiveness stable? First, we must explain why we introduce the concept of signalling at all. We do so because a contest between individuals of different aggressiveness can only be settled either by paying the full m value of the less aggressive contestant, or by signals. Thus if there are no signals we are back with the war of attrition. We are also assuming that the contest is settled by aggressiveness, and not by RHP: hence we are concerned with conventional signals, and not with assessment.

Can honest conventional signals be evolutionarily stable? This depends on what happens when an individual of low aggressiveness, but giving a dishonestly high signal, encounters an opponent that gives an honestly high signal. There are two possibilities:

1. The dishonest signaller can escape from the contest without cost. If so, such a mutant

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could invade the population because it would be fitter than an honest signaller of equal aggressiveness: it would win some contests that the honest signaller would lose, and would pay no costs not paid by the honest signaller.

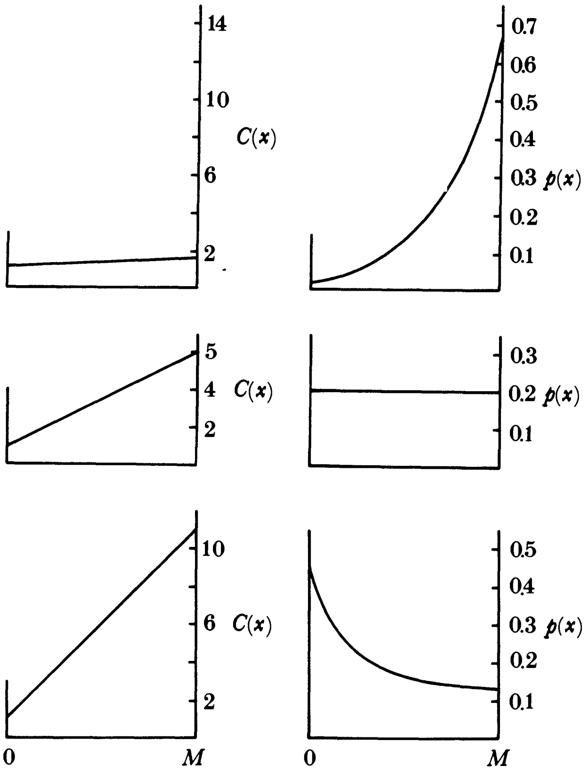

FIGURE 1. Frequency distribution $p(x)$ of aggressiveness in the population, for various cost functions $C(x)$, in the badges of dominance game. M is the maximum possible value of aggressiveness, corresponding to commitment to an all-out fight. The value of k in (4) has been chosen to make the probability that an individual, matched against a random opponent, will be involved in a fight equal to $\frac{1}{5}$ when $p(x)$ is constant.

2. The dishonest signaller pays the full cost of the contest: that is, it pays the cost appropriate to the level it is signalling. If so, the mutant could not invade, because it is less fit than an opponent that actually has the m-value being signalled: thus it loses contests against such an opponent, but otherwise gets the same payoffs.

It follows, then, that honest signalling of motivation can be stable, but only if a dishonest individual, with a low m-value but signalling a high one, pays a high cost against a highly aggressive opponent. This has sometimes been expressed by saying that a dishonest signaller must be 'punished'. As discussed later, there is some evidence in Harris's sparrows (*Zonotrichia querula*) (Rohwer & Rohwer 1978) and in house sparrows (*Passer domesticus*) (Møller 1987*b*) that this is so. What is less clear is why such punishment takes place. One possibility is that the winner is provoked into punishing by the discordance between the actual and the expected behaviour of its opponent. The snag with this is that, although it may correspond to the way we expect humans to behave, it does not explain why punishment behaviour should be selected. A more plausible alternative is that a highly aggressive individual fights vigorously against any opponent signalling an equally high value, both because vigour is usually needed to win the fight and because it pays to drive a potentially threatening opponent away. Whatever the explanation of punishment behaviour may be, it is clear that the stability of honest signalling in the badges of dominance game does depend on it.

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A summary of models

The following patterns of behaviour are possible.

1. *War of attrition*. Genetic variability of aggression maintained by frequency-dependent selection. No correlation between winning and RHP. Contests not settled by conventional signals. A contest between an individual of medium and of high aggressiveness will have the same expected cost as one between two individuals of medium aggressiveness (in contrast to the badges of dominance game, in which the latter type of contest would be more costly).

2. *Size game* 1. No genetic variance for aggressiveness or RHP, except that maintained by recurrent mutation or migration. Assessment signals may or may not be used. Larger individuals win fights. Mean size of population larger than it would be if contests were not important: this could be recognized by high sexual dimorphism in size, if contests are mainly between members of one sex.

3. *Size game* 2. Genetic variance of size maintained by frequency-dependent selection. Contests between individuals of different size settled by assessment signals. Total fitness not correlated with size.

4. *Badges of dominance game*. Genetic variance of aggression maintained by frequency-dependent selection. Conventional signals indicate level of aggressiveness. Fights occur between individuals of equal aggressiveness, and are more costly if the value is high. Cost of fights high relative to value of resource. Individuals giving dishonest signals are 'punished': this can be demonstrated by experimental manipulation.

BADGES OF DOMINANCE IN BIRDS

Introduction

Rohwer (1975) suggested that many birds have variable plumage so that individuals can signal their social status. Age and sex differences in plumage are best excluded from discussions of such 'badges of dominance' because they may well have evolved for different reasons (Balph *et al.* 1979; Whitfield 1987). Attempts to detect plumage features that correlate with dominance rank within an age and sex produced equivocal results for Harris's sparrows (Rohwer 1985; Watt 1986*a*, *b*) and dark-eyed Juncos (*Junco hyemalis*) (Balph *et al.* 1979) and failed for at least four species: white-throated sparrow (*Zonotrichia albicollis*) (Watt *et al.* 1984), white-crowned sparrow (*Z. leucophrys*) (Fugle *et al.* 1984), oystercatcher (*Haematopus ostralegus*) (Ens & Goss-Custard 1986) and turnstone (*Arenaria interpres*) (Whitfield 1986). Positive results have been obtained for at least six species (table 3) and suggestive data are available for others (Studd & Robertson 1985*a*, *b*; Roper 1986). The entries in table 3 show that dominants can have badges that are larger, smaller or more brightly coloured than subordinates, depending on the species. We will refer to 'badge size' when describing the nature of badges and to dominants as having 'large badges', regardless of the observed variation.

Badges in different contexts

There is evidence that badges are only relevant in certain contexts, as predicted by our badges game. Rohwer *et al.* (1981) found that the darker of two Harris's sparrows (of the same age and sex) was more likely to win contests over dispersed food (our analysis: 18 of 23, $p < 0.05$), but not when food was clumped (63 of 125). Avoidance reactions – interactions

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TABLE 3. BADGES OF DOMINANCE IN BIRDS

(In the second column + and − indicate the direction of the correlation between badge and dominance rank.)

species	badge	age and sex differences in badge size	reference
great tit (*Parus major*)	width of black belly stripe (+)	between sexes large, between ages small	Jarvi & Bakken (1984); A. Porter (personal communication)
red-winged blackbird (*Agelaius phoeniceus*)	length of red shoulder patch (+)	only present in males	Eckert & Weatherhead (1987)
house sparrow (*Passer domesticus*)	area of black bib on throat (+)	only present in males	Moller (1987*a*, *b*); J. Maynard Smith & D. G. C. Harper, personal observations
pine siskin (*Carduelis pinus*)	length of yellow wing bar (−)	very small	Balph & Balph (1979)
greenfinch (*Carduelis chloris*)	yellowness of plumage (+)	moderate	C. Eley (personal communication)
corn bunting (*Emberiza calandra*)	size of black bib on throat (+)	moderate	J. Maynard Smith & D. G. C. Harper, personal observations

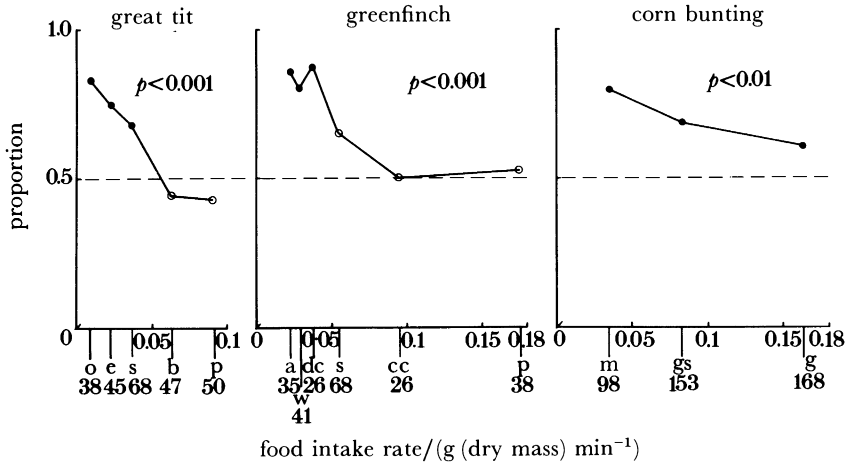

FIGURE 2. Proportion of dyads of birds (of the same age and sex in free-living winter flocks) in which the dominant (winning the majority of contests) had the larger badge. Nature of badges and sources is given in tables 3 and 4. Data are plotted for feeding sites with different rates of food intake. Site abbreviations (food, seeds unless stated): o, oak (invertebrates); e, elder (berries); s, sunflower (seeds); b, beechmast; p, peanuts; a, arable; w, woodland; dc and cc, dispersed and clumped cereals; m, marsh meadows; gs, gorse scrub; g, grain store. Sample sizes are given under site abbreviations. Solid symbols indicate results differing from the random prediction of 0.5 at the $p = 0.05$ level. Results of G tests for differences between sites are indicated after the species name.

not including displays or chases – 'almost never' involved the darker bird losing (Rohwer 1975), suggesting that badges are more likely to be respected in less intense contests. Our observations of three other species show that badges were better predictors of the outcome of interactions at sites where food intake rates were low than at higher quality sites (figure 2), whereas tarsal length showed the opposite trend (figure 3). The proportion of interactions involving chases or physical contact tended to increase with food intake rate (figure 4 and table 5). These data are consistent with the hypothesis that badges are only important when

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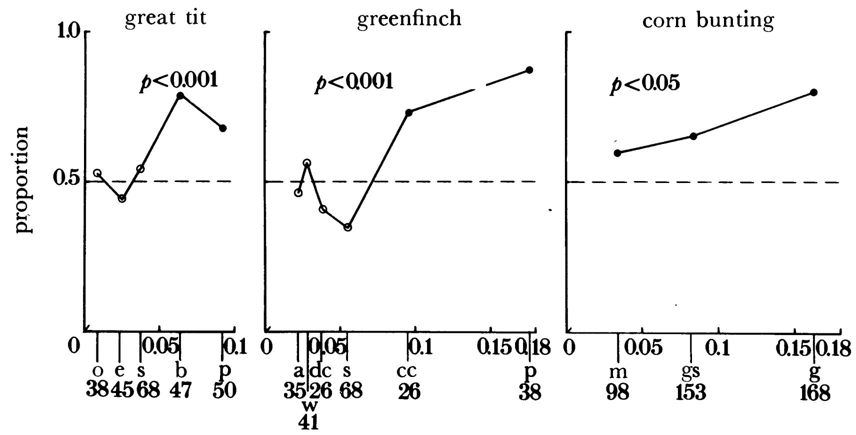

FIGURE 3. Proportion of dyads in which the dominant had the larger tarsus. Abbreviations as in figure 2.

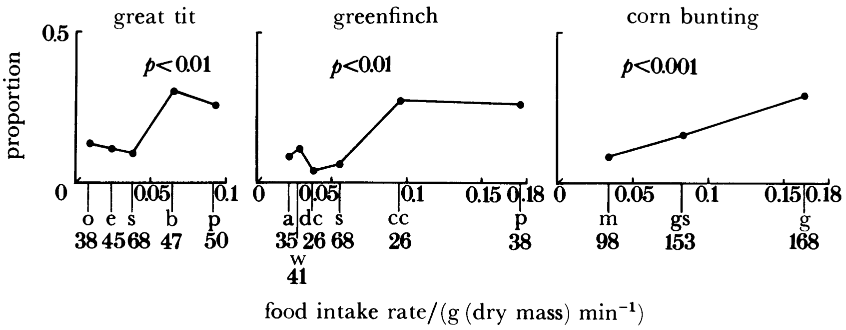

FIGURE 4. Proportion of dyads whose interactions ever involved chasing or physical contact. Conventions as in figure 2, except that there is no random prediction.

the disputed resources are of low value and that costly traits such as body size become important when resources are valuable. However, the feeding sites differed in many respects other than food intake rate. The most profitable feeding sites tended to have the highest density of food items, which may have increased the rate of fighting due to encroachment of individual space. Body size may be more important than aggressiveness in determining the outcome of fights in this context.

Badges and costly traits

There is evidence that badges are correlated with costly traits. Most of the examples known to us involve body size. In dark-eyed juncos, the whiteness of the outer tail feathers is a good predictor of dominance, but is confounded by winglength which correlates with fighting ability (Balph *et al.* 1979). Badge size and tarsus length (figures 2 and 3) were not significantly correlated for great tits and greenfinches of the same age and sex, but large corn buntings tended to have large badges (table 4). There is one example involving a costly trait other than body size: male great tits with large badges have heavier hearts relative to body mass than average (Roskaft *et al.* (1986); their correlation between badge size and metabolic rate appears to us to be confounded by sex). If badges were independent of RHP, we might expect that territory quality (presumably a valuable resource) would not be correlated with the size of the owner's badge. However in yellow warblers (*Dendroica petechia*) (Studd & Robertson 1985*a*, *b*)

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TABLE 4. PEARSON CORRELATION COEFFICIENTS FOR RELATION BETWEEN TARSAL LENGTH AND BADGE SIZE FOR DIFFERENT AGE AND SEX CLASSES OF THREE SPECIES OF PASSERINE

(For nature of badge see table 3. Sample sizes in parentheses. Significance levels given where appropriate: ** $p < 0.01$; *** $p < 0.001$.)

		first winter		older	
species	measure of badge	females	males	females	males
great tit	mean of widths at five positions	+0.153 (69)	−0.042 (56)	−0.095 (30)	+0.118 (36)
greenfinch	mean score of five observers viewing photographs of bird in hand	−0.086 (34)	+0.127 (37)	+0.173 (21)	+0.083 (19)
corn bunting	product of length and width	+0.228 (41)	+0.473 (38) **	+0.414 (82) ***	+0.483 (68) ***

TABLE 5. PROPORTION OF DYADS WHOSE INTERACTIONS EVER INVOLVED CHASING OR PHYSICAL CONTACT (SAMPLE SIZES IN PARENTHESES)

(For details of badges see tables 3 and 4. Sites in figure 2 are divided according to whether or not the badge was a better predictor of outcome than tarsal length. Similarity in badge size expressed relative to median at that site; dyads that were more similar than average are further divided according to the mean size of their badges (compared to population median). Results of G tests are presented at the base of the table. n.s., not significant.)

badge as predictor of outcome compared with tarsus size	similarity of badges	badge size	great tit	greenfinch	corn bunting
better	low	all	0.07 (75)	0.03 (65)	0.08 (125)
	high	small	0.13 (38)	0.06 (32)	0.15 (55)
	high	large	0.18 (38)	0.19 (36)	0.23 (71)
worse	low	all	0.21 (48)	0.22 (32)	0.17 (84)
	high	small	0.33 (27)	0.18 (17)	0.29 (41)
	high	large	0.36 (22)	0.47 (15)	0.53 (43)
G tests	predictive value of badge		$p < 0.001$	$p < 0.001$	$p < 0.001$
	similarity of badges		$p < 0.05$	$p < 0.05$	$p < 0.01$
	badge size if similar		n.s.	$p < 0.01$	$p < 0.01$

and corn buntings (A. Moller, personal communication; J. Maynard Smith & D. G. C. Harper, personal observations) males with large badges appeared to have the best territories. The limited data therefore suggest that badges are at least sometimes correlated with costly traits such as body size, heart size and fighting ability. So far, the amount of variance in badge size explained by these traits has been small (Roskaft *et al.* 1986) (table 4).

Cheating

Dark-eyed juncos (Balph *et al.* 1979), house sparrows (Møller 1987*b*), great tits, greenfinches and corn buntings were more likely to fight with birds with a badge similar to their own. In the last three species this result holds among birds of the same age and sex, and in the last two fights were more frequent if both individuals had large badges (table 5). When fights are commoner between birds with similar badges, cheats with enlarged badges will suffer from increased aggression from individuals with high aggressiveness. In cases in which badges are correlated with costly traits which are components of RHP (e.g. body size), the costs of cheating will be even higher.

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We are aware of only two experiments testing the hypothesis that cheats are punished and one of these is flawed (Watt *et al.* 1984; Fugle *et al.* 1984; Rohwer 1985). Rohwer & Rohwer (1978) created cheats by painting larger bibs on the throats of Harris's sparrows and found that they were attacked by their cage mates and failed to rise in status. Subordinates injected with testosterone behaved more aggressively than controls, but did not become dominant because opponents failed to retreat. Only subordinates that were both painted and injected rose in status, suggesting that discordance between signal and behaviour is punished. Why don't subordinates increase their androgen levels? Experiments with pied flycatchers (*Ficedula hypoleuca*) suggest that testosterone injections can push some individuals beyond their capabilities and reduce their fitness (Silverin 1980). If a high level of testosterone is a costly trait, our badge of dominance game is inappropriate. In fact, the black feathering involved in this experiment may not be a badge of individual status at all (Shields 1977; Watt 1986*a*, *b*; Whitfield 1987), although it settles the outcome of some contests between birds of different ages (Watt 1986*a*, *b*; Rohwer 1985). Painted birds may have been regarded as unfamiliar individuals, and injecting testosterone without painting may not alter status if the other birds continue to recognize an individual they have previously dominated.

The size of the black bib on the throats of male house sparrows is a better predictor of dominance rank than age (Møller 1987*a*) or body size (J. Maynard Smith & D. G. C. Harper, personal observations). In experiments, a dyed bird with an enlarged bib, and a control, were introduced into captive flocks. Dyed birds did not achieve higher rank than controls and received more aggression from large bibbed (dominant) birds, suggesting that cheats are punished. House-sparrow flocks tend to be small and very stable in membership during the winter and it is unlikely that individuals meet many unfamiliar conspecifics at any one time (Møller 1987*b*). This is not true for the other species in table 3; the birds in figure 2 met hundreds of unfamiliar conspecifics during a few months. It remains to be seen how effective social probing of the kind described by Møller (1987*b*) is in these cases.

Other hypotheses

Plumage variability among birds of the same age and sex may have evolved for reasons completely unrelated to status signalling. Few studies have evaluated competing hypotheses, but Jarvi *et al.* (1987) examine eight relating to the pied flycatcher. One popular hypothesis is that plumage variation facilitates individual recognition (Watt 1986*a*; Whitfield 1986, 1987). When territorial turnstones were replaced by models, neighbours were much less likely to attack if a model resembled the former owner than if it was darker or lighter (Whitfield 1986). Although these data support the recognition hypothesis, the fact that attack intensity was not related to the colour of the model is not good evidence against the status signalling hypothesis because territories may be too valuable a resource for badges to be respected (but see Studd & Robertson 1985*a*, *b*). It is hard to see how the individual recognition hypothesis could apply to most of the species in table 3, which (with the exception of house sparrows) winter in large unstable flocks, unless the relevant selection occurs in the breeding season.

Future work

The hypothesis that badges signal aggressiveness rather than fighting ability has been discussed verbally by Rohwer (1982) and Studd & Robertson (1985*a*, *b*). Our badges game assumed (*inter alia*) that badges signal an aggressiveness which is costly only in the context of

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fights. It predicted that badges would be relevant only in certain contexts and that the costs of an interaction would be higher if both opponents had large badges. So far, the data support the predictions rather better than the central assumption! Future models need to examine the case where badge size is correlated with components of RHP, like body size or hormone levels, which are costly when the animal is not fighting.

Empirical studies need to address a variety of issues. Are badges relevant only in certain contexts and if so, which? Is badge size correlated with costly traits? Hormones seem particularly interesting in this context. Is badge size heritable? There seem to be considerable differences between species in the amount of plumage variability and in some species there are differences in badge size between sexes, ages, seasons and/or populations (all four in corn bunting, J. Maynard Smith & D. G. C. Harper, personal observations). It would be interesting to know why. Most studies have been of birds in wintering flocks. Other seasons and species with different natural histories require attention. The work on Midas cichlids (Barlow *et al.* 1986) described earlier will probably encourage work on aggressiveness and fighting ability in other taxa.

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APPENDIX. THE BADGES OF DOMINANCE GAME

Let x be aggressiveness level of an individual, $p(x)$ be probability density of x, M be maximum possible aggressiveness, b be pay-off for winning a contest, $C(x)$ be cost of a fight between individuals of aggressiveness x and $W(m)$ the fitness of an individual of aggressiveness m. Then

$$W(m) = L + b\int_0^m p(x)\,\mathrm{d}x - kp(m)\,C(m), \qquad \text{(A 1)}$$

where k and L are constants. $kp(m)$ is the probability that an individual of aggressiveness m is involved in a fight.

If $p(x)$ is evolutionarily stable, then $W(m)$ must be independent of m. That is, $\mathrm{d}W(m)/\mathrm{d}m = 0$, or

$$bp(m) - kC'(m)\,p(m) - kC(m)\,p'(m),$$

or

$$p'(m) + \frac{kC'(m) - b}{kC(m)} \cdot p(m) = 0. \qquad \text{(A 2)}$$

It is also required that

$$\int_0^m p(x)\,\mathrm{d}x = 1. \qquad \text{(A 3)}$$

Equation (A 2) has the solution $p(m) = D\,\mathrm{e}^{-A(x)}$,

where

$$A(x) = \int_0^x \frac{kC'(m) - b}{kC(m)}\,\mathrm{d}m, \qquad \text{(A 4)}$$

and D is a constant determined by (A 3).

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If $C(x) = \alpha+\beta x$,

$$p(x) = D\left(\frac{\alpha}{\beta}+x\right)^{(b/k\beta)-1} \tag{A 5}$$

The critical parameter in determining the shape of the distribution is $b/k\beta$: that is, the ratio of the value of winning, b, to the rate at which fight costs increase with m. The form of the distribution also depends on the ratio of the maximum value of the aggressiveness, M, to the constant k. If we consider the case where $p(x)$ is constant, then (A 3) gives $p(x) = 1/M$, and hence the probability that an individual in a random encounter will be involved in a fight is $kp(x) = k/M$. In practice, this probability would depend on the accuracy with which signals are given and perceived. Figure 1 is based on the assumption that $k/M = \frac{1}{5}$, which seems plausible.

If there is no upper limit, M, then there is no stable distribution of x for a linear cost function $\alpha+\beta x$. Motivation would increase indefinitely. If costs increase more steeply with increasing x, there can be a stable distribution. For example, if $C(x) = \alpha+\beta x^2$, then

$$p(x) = \frac{D}{\alpha+\beta x^2}\exp\left(\frac{b}{k\surd(\alpha\beta)}\tan^{-1}\sqrt{\frac{\beta}{\alpha}}x\right). \tag{A 6}$$

However, it is more plausible biologically to assume that there is an upper limit.

Discussion

J. F. Y. **Brookfield** (*Department of Genetics, University of Nottingham, U.K.*). The model for the badges of dominance game is haploid and differing genotypes differ in their levels of aggression and, correspondingly, in their levels of expression of their badges of dominance. However, one would not expect the same genes to determine plumage and aggression in these birds, and in a sexual species with recombination, one would expect the genetic variation in the two characters to become uncoupled. Dr Harper says that in simple models an allele for ‘cheating’, which causes the state of the badge to inaccurately reflect the aggression level of the animal bearing it, will spread. However, in a sexual species decoupling of the badges from the behaviours will occur spontaneously through recombination, and without any special genetic mechanism. Why, therefore, should plumage ever come to reflect aggression accurately and thereby constitute a badge?

D. G. C. **Harper**. We do not assume that the same genes determine plumage and aggression. Instead, we accept that the two traits can evolve independently. In the simplest case, in which an individual can ‘cheat’ without cost, alleles for cheating will indeed spread, and we do not expect plumage to reflect aggression accurately. However, we argue that if individuals whose signals do not reflect their level of aggression are punished, it will be evolutionarily stable for signal and aggression to coincide. When they do coincide, a cheating mutant will not spread, even though, genetically, the two traits are independent. Introducing sex would make no difference to this conclusion. It is selection, and not the asexual nature of the model, that can cause plumage to reflect aggression accurately.