Effects of bill pigmentation and UV reflectance during territory establishment in blackbirds

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During intrasexual interactions, the visual properties of conspicuous male sexually selected traits may be important in social signalling. We used intruder models to examine the effect of pigmentation and ultraviolet (UV) reflectance of a single male trait on the responses of male blackbirds, *Turdus merula*. Stuffed models of male blackbirds with brown, yellow or orange bills were presented to residents in their natural habitat; we altered UV reflectance from the bills by applying nail varnish. This UV reflectance did not appear to affect the response of resident males during simulated territorial intrusions under natural signal and viewing conditions. However, models with brown bills received less attention from resident males than models displaying yellow or orange pigmentation. Brown bills are typical of first-year males and may be an effective signal of subordinate status, reducing aggression from adult males. Furthermore, resident males came closer, and initiated aggressive displays more quickly, in the presence of orange-versus yellow-billed models, suggesting that orange-billed models may be perceived as more of a threat to territory ownership. In 44% of presentations, females also responded to models (a response rate half that of males). Females spent more time more than 10 m from models when they lacked UV, suggesting that UV may be more important during intersexual interactions. However, bill pigmentation did not affect female responses to the models. Males and females may be attentive to different properties of bill appearance when establishing the territory.

Many diurnal birds are known to be sensitive to ultraviolet (UV) light (Chen et al. 1984; Chen & Goldsmith 1986; reviewed in Vorobeyev et al. 1998). Because UV vision and sexually selected traits are so prevalent in birds, there has been increasing interest in the function(s) that UV reflectance might serve (Bennett & Cuthill 1994; Vorobeyev et al. 1998). For example, studies on Pekin robins, *Leiothrix lutea* (Maier 1993), zebra finches, *Taeniopygia guttata* (Bennett et al. 1996; Hunt et al. 1997), blue tits, *Parus caeruleus* (Andersson & Amundsen 1997; Hunt et al. 1999) and European starlings, *Sturnus vulgaris* (Bennett et al. 1997), indicate that UV reflectance is used as an important cue during mate choice. However, the majority of studies of UV-based signals have been carried out in simulated natural light environments, which enhance UV emission, potentially affecting the perception of and response to signals (Endler 1993). In addition, experiments usually involve placing screens, which filter UV, between the signalling animal and the respondent (but see Andersson & Amundsen 1997). Such screens influence not only the UV reflectance of the trait being examined, but also the whole light environment (e.g. entire plumage reflectance and background appearance). The influence of UV reflectance from specific traits cannot be examined independently with these techniques.

The existing UV literature has focused on intersexual interactions even though UV-based signals may also play an important role in intrasexual encounters. We investigated the influence that UV wavelengths from a single conspicuous sexually selected trait (the bill) have on the intrasexual interactions of male blackbirds, *Turdus merula*, under natural signal and viewing conditions. We measured the effect of eliminating UV reflectance by recording the responses of wild territory owners to simulated intruders (stuffed models). To our knowledge, this is the first time a study has investigated the influence of UV reflectance from conspicuous sexually selected traits on male–male interactions in a natural setting; we also investigated the reactions of female residents whenever they responded to the models.

The blackbird is a common and easily observed monogamous passerine that defends well-defined territories and forms long-term (possibly life-long) pair bonds (Snow 1958). Blackbirds show marked sexual dimorphism: adult males have black, and females brown,

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plumage. In addition, bills are yellow to bright orange in males and brown to dark brown in females (Snow 1958). Male bill pigmentation varies considerably within a population (A. Bright, J. R. Waas, C. M. King & P. D. Cuming, unpublished data) and is the only conspicuous sexually selected trait. Finally, the blackbirds in this study lived in woodland, a shortwave-biased light environment, suitable for UV signals (Endler 1993).

A second aim of our research was to examine how bill pigmentation in general influenced the responses of territory owners to simulated intruders. Conspicuous and highly pigmented bird plumages are thought to have evolved because of the mating advantage they provide their bearers (Darwin 1871). Conspicuous pigmentation may reveal aspects of male quality such as parasite resistance, physical condition, or parental ability, which may be used in female mate choice (e.g. Hamilton & Zuk 1982; Hill 1991; Burley et al. 1992; Sundberg & Larsson 1994). Alternatively, selection for male competitive ability and aggression might favour the evolution of conspicuous signals or 'badges' of status in intrasexual interactions (Rohwer 1982; Butcher & Rohwer 1989). If conspicuously pigmented individuals are better at defending resources (e.g. food, territories), their plumage might act as a signal of good fighting ability (Rohwer 1982) or aggressive motivation (Studd & Robertson 1985).

First-year male blackbirds initially have a brown bill, but this changes to yellow/orange during the bird's first winter/spring when it is attempting to establish a territory and find a mate (Snow 1956, 1958). The time of this change varies considerably between individuals, and flecks of brown usually remain on the bills of first-year males until the next autumn moult (Snow 1958). There is little variation in plumage between or within first-year and adult categories of blackbirds (Snow 1958; A. Bright, personal observation). We predicted that models with brown bills (first-year males) would pose less of a threat and elicit a less aggressive response from territory owners than models with yellow or orange bills (adult males). We also predicted that yellow-billed models would elicit less aggression than orange-billed models.

We examined the responses of male blackbirds to bill pigmentation and UV reflectance during territory establishment when male–male competition is intense (Snow 1958). Territories are essential for pair formation and successful breeding (Snow 1958), and males may be selected for their competitive ability in the acquisition and defence of these territories. Territory establishment during the 2–3 months prior to nesting is a critical time of year for a male blackbird (Snow 1958). At this time, territorial boundaries and neighbours may change swiftly, with rival males attempting to expand their territories or occupy part of a vacant territory (Gurr 1954; Snow 1956, 1958). Territorial fighting is common only during the territory establishment period (Snow 1956, 1958), and Gurr (1954) showed that blackbirds will respond promptly and aggressively to a stuffed model during this time. Once the territorial boundaries are defined, they are maintained mainly by threat from a distance as territory owners have only to deal with trespassers and not rivals (Gurr 1954; Snow 1956, 1958).
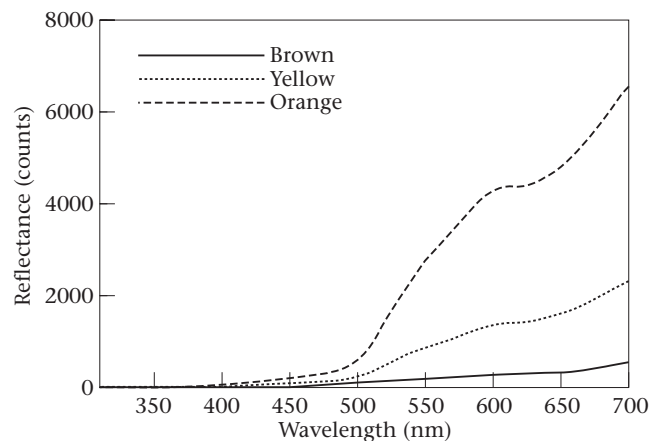

Figure 1. Reflectance measured at 15 ms for brown, yellow and orange bills of models used in the experiment.

METHODS

Our experiment was conducted, with approval of the University's Animal Ethics Committee, in woodland areas of the University of Waikato campus (Hamilton, New Zealand) from 20 May to 31 July 2000 (the time of territory establishment for this species in New Zealand; Gurr 1954). Over 9 months before the experiment, we determined the territories of resident males from observations of song posts, feeding sites and border disputes between males.

We presented stuffed male blackbird models with brown (first-year male), yellow or orange bills, with (+UV) and without (−UV) UV reflectance on 33 territories. The models were blackbirds that we found dead on the side of local roads (presumably killed by cars) and were similar in size, plumage condition and plumage colour. They were mounted in a neutral posture (i.e. the head was horizontal, the tail was depressed, the wings were held to the body and the feathers were sleeked; Snow 1958) and fastened on to small pieces of wood.

A.B. measured the bills of the models with a Zeiss spectrometer MMS (Carl Zeiss Corporation, Jena, Germany) with an Ocean Optics LS1 10-W halogen lamp (Ocean Optics, Dunedin, Florida, U.S.A) at HortResearch, Hamilton, New Zealand. A fibreoptic interactance probe (Ocean Optics, Florida, U.S.A) positioned at a 45° angle to the bill (middle of the upper left mandible) was used to direct the illumination and collect the light scattered by the samples. Measurements were taken at 15-ms integration time (309–700 nm); the reflectance spectra are shown in Fig. 1. Dark current measures were taken before each sample to minimize error associated with drift of the light source and sensor. For practical reasons, bill samples could not be measured against a white reflectance standard and we present reflectance spectra as raw counts. All bill samples were measured twice. Reflectance spectra were averaged from 20 scans and recorded in 3.3-nm wavelength bands, which were later reduced to 7-nm wavelength bands because of software and memory limitations. We applied clear nail enamel (Sally Hansen Colour Fast, No. 01, Dell Laboratories, New York, U.S.A)

to the bill of each model to eliminate UV reflectance without altering reflectance in the visible wavelengths (determined from visual inspection of spectra). We removed it with Manicare Extra Gentle Nail Enamel Remover (Impco International, Victoria, Australia).

We kept the background conditions of presentations as consistent as possible to avoid confounding influences of habitat variation on signal reception (Endler 1993). Presentations were made from 0730 to 1000 hours, a period when the blackbirds were most active, on days when there was no wind, rain or fog. We presented models to resident males in a random order, and successive presentations to the same individual were separated by at least 7 days to avoid habituation. The models were placed near the approximate centre of a blackbird's territory (so as to simulate an intrusion), in a grassy area with trees/ shrubs in the background, never in direct sunlight. We observed responses from 20–30 m away for 600 s. This observation period began as soon as the male territory owner responded to the model (i.e. by flying towards or vocalizing at the model). We expected to obtain few (if any) responses from females to our male model intruders. Males are most active in territory defence and will drive out intruders of both sexes whereas females are usually aggressive only towards same-sex intruders, where the motive appears to be intrasexual competition for a mate rather than defence of a territory (Snow 1956). However, in several territories, the female also responded. We recorded male and female responses separately.

During model presentations we measured (1) the time (s) an owner spent <2, 2–10 and >10 m from the model (all distances were measured and marked with bamboo poles) and (2) the intensity of display of the owner clearly directed towards the model. Four levels of intensity for aggressive displays were defined from Snow (1958): (a) the owner advanced towards the model in an aggressive posture (neck stretched upwards, beak pointing above horizontal and tail fanned; Snow 1958); (b) the owner ran 1–2 m up and down beside the model (the run began with the head and tail lowered and ended with the head and tail pointing upwards); (c) the owner flew steeply down towards the model before veering sharply upwards ('dive bomb'); and (d) the owner advanced towards the model emitting an 'alarm rattle', then with the breast displayed and the wings outstretched flew 1–2 m up and down in front of the model. We also recorded (3) the time during the 600-s presentation at which a display was first performed. Our inclusion of 'time to display' as a variable in our analysis was based on detailed observations by Snow (1956, 1958) who found that blackbirds would adopt ritualized display postures more quickly in response to individuals that represented a greater threat to territory defence.

We did not use song to attract the resident male to our models because most blackbird song begins in early spring and is mostly sung by first-year males (Snow 1956, 1958). Older males do not begin song until the female of the pair has started to nest (August/September in the southern hemisphere); song probably serves as a signal of continuing ownership and as a way of threatening potential intruders (Snow 1958; Dabelsteen 1988). We presented each resident male with two versions of each brown-, yellow- and orange-billed model (one +UV and the other −UV). Each model was also presented in a slightly different spatial context (i.e. the exact site and direction of placement varied between presentations) owing to simple environmental heterogeneity. As a result, no two presentations of a given treatment were completely identical, allowing us to be confident that any responses observed were due to the bill manipulations, not minor differences in the way models were presented.

Statistical Methods

We converted the time recorded at each distance category to the percentage of the total time spent responding. The resulting responses were analysed with the residual maximum likelihood (REML) procedure in the Genstat 5.3 statistical package. The correlations arising from the repeated measurement nature of the data were modelled by incorporating random sources of variation for resident male (territory) and its interaction with pigmentation and UV reflectance factors. Presentation order was included with pigmentation and UV reflectance (plus their interactions) as fixed effects. The statistical results we present for a given effect incorporate adjustments for imbalances detected in the other effects that were included in the model. The test for the territory by reflectance error component was never statistically significant and was omitted from the random models. Order of presentation was also nonsignificant (<2 m: $F_{5,164}=1.12$, $P=0.35$; 2–10 m: $F_{5,58}=1.26$, $P=0.29$; >10 m: $F_{5,78}=0.90$, $P=0.49$) but we retained it as a fixed effect as the distribution of bird models across presentation order was uneven. An initial analysis showed considerable residual heteroscedasticity, inadequately controlled by arcsine transformation. We therefore used the full model, weighting each observation inversely according to the smoothed residual variance associated with its fitted value and recycling until no further change occurred. The weights from the final run were then retained for statistical tests and means estimation. Based on our a priori expectations, pigmentation effects were split into the components brown versus the average of yellow and orange, and yellow versus orange. The Wald chi-square statistics for fixed-effect tests obtained from the REML analysis were converted to approximate F tests using the relevant error component degrees of freedom in the denominator.

Distance data for females were converted to percentage of time spent responding and were analysed for a posteriori comparisons of UV and bill pigmentation effects using a two-way repeated measures ANOVA.

Few resident males (and no females) directed aggressive displays towards model intruders. Owing to the low number of responses (and high error), we could not analyse the intensity and timing of aggressive displays by resident males statistically. However, we present means ± SE to identify the major trends in the display data.
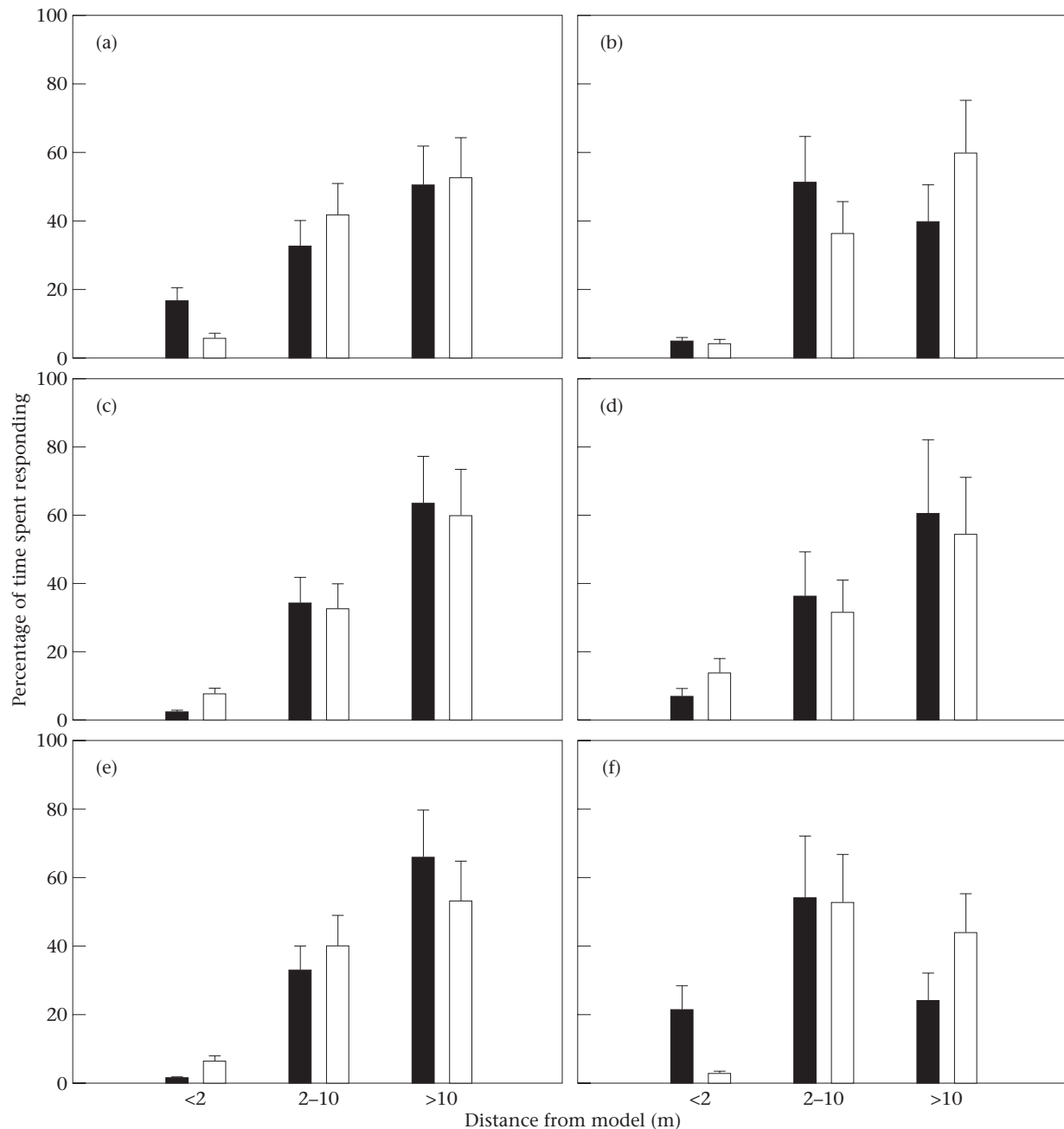
Figure 2. Percentage of time spent by males (a, c, e) and females (b, d, f) at each distance category and for each type of model presented. (a, b) Orange-billed model, (c, d) yellow-billed model and (e, f) brown-billed model. ■: Bill with UV reflectance; □: bill without UV reflectance.

RESULTS

Males

Of the 198 presentations, 25 (13%) failed to elicit any discernible response from the resident male within 600 s. There was no difference in the percentage of males that did not respond to a presentation (range 2–7%) across treatments. Presentations that did not elicit a response were excluded from all analyses.

UV reflectance

Approach distance. There were no significant differences in the percentage of time spent by resident males during presentations <2, 2–10 or >10 m from models with and without UV reflectance (<2 m: $F_{1,164}=1.4$, $P=0.24$; 2–10 m: $F_{1,58}=2.6$, $P=0.11$; >10 m: $F_{1,78}=0.1$, $P=0.75$; Fig. 2).

Display. The percentage of males that displayed towards models was slightly higher for orange- and yellow-billed models presented without UV (this was not

Table 1. Intensity of aggressive display (average response of the 33 residents), time taken to display during the 600-s presentation and percentage of males that responded to each model

Model	Display intensity	Time to display (s)	Percentage displaying
Brown UV	1.8±0.49	302±66.57	2.5 (5)
Brown No UV	2.2±0.49	323±66.23	2.5 (5)
Yellow UV	4.0	60	0.5 (1)
Yellow No UV	2.3±0.47	209±84.08	3.5 (7)
Orange UV	2.0±1.00	35±9.50	1.0 (2)
Orange No UV	2.0±0.37	118±25.14	3.0 (6)

Means are given±SE. The number of responses observed is given in parentheses.

the case for brown-billed models; Table 1). However, response rates were too low for statistical analyses (Table 1). The time elapsed before displaying during presentations was longer on average for models presented without UV (Table 1). There was no obvious difference in the intensity of aggressive displays directed towards models presented with or without UV (Table 1).

Bill pigmentation
Approach distance. Resident males who responded to models spent a significantly greater proportion of time >10 m from the model during presentations with brown bills than during presentations with yellow and orange bills ($F_{1,87}=4.6$, $P=0.04$; Fig. 2). There was no significant difference in the amount of time males spent >10 m from yellow- and orange-billed models ($F_{1,87}=0.2$, $P=0.65$; Fig. 2). However, resident males spent a greater proportion of time <2 m from orange-billed than yellow-billed models ($F_{1,164}=4.2$, $P=0.04$; Fig. 2). There was no significant difference in the proportion of time that males spent <2 m from models with brown bills and yellow or orange bills ($F_{1,164}=2.2$, $P=0.14$; Fig. 2). Bill colour did not influence the proportion of time resident males spent 2–10 m from the model (orange versus yellow: $F_{1,65}=0.1$, $P=0.75$; brown versus yellow/orange: $F_{1,65}=3.1$, $P=0.08$). There were no significant UV–bill pigment interactions for any distance category (<2 m: $F_{2,162}=0.9$, $P=0.41$; 2–10 m: $F_{2,56}=0.35$, $P=0.21$; >10 m: $F_{2,75}=0.65$, $P=0.52$).

Display. There was no apparent difference between the percentage of males that directed displays towards differently pigmented models (Table 1). The mean intensity of display was slightly higher for yellow-billed than brown- or orange-billed models (Table 1). Males responded with an aggressive display towards orange-billed models earlier in the presentation than to yellow-billed models, and earlier to yellow-billed than brown-billed models (Table 1). However, display response rates were too low for statistical analyses.

Females

In 44% of presentations, females also responded to models (a response rate half that of males). The percentage of females that responded to each model was similar (range 6–10%) across presentations.

There was no difference between the amount of time females spent <2 m from models presented with and without UV reflectance ($F_{1,34}=0.83$, $P=0.68$; Fig. 2), but they spent more time 2–10 m from models with UV, although not significantly so ($F_{1,34}=5.91$, $P=0.06$; Fig. 2). Females also spent more time >10 m from models presented without than with UV ($F_{1,34}=7.07$, $P=0.04$; Fig. 2). There was no difference in the amount of time females spent <2, 2–10 or >10 m from models with brown, yellow or orange bills (<2 m: $F_{2,34}=1.01$, $P=0.39$; 2–10 m: $F_{2,34}=0.04$, $P=0.96$; >10 m: $F_{2,34}=0.86$, $P=0.16$; Fig. 2). No females were observed directing aggressive displays towards the model intruders.

DISCUSSION

UV reflectance from the bills of male blackbirds did not affect the response of resident males to a simulated territory intruder; however, the bill pigmentation of intruders did. Models presented with brown bills received less attention from resident males than models displaying carotenoid-based pigmentation (yellow and orange). Furthermore, resident males came closer, and displayed more quickly, to orange-billed than yellow-billed models during presentations. Bill pigmentation did not affect female responses to the models; females tended to ignore (i.e. stay >10 m from) models without UV.

Males

UV reflectance
Under natural signal and viewing conditions, UV reflectance from a blackbird's bill did not appear to be important during male–male interactions. Since woodland is a shortwave-biased light environment (Endler 1993), it is unlikely that UV reflectance was undetectable, contributing to the lack of significant UV effects. Resident males were on average more likely to respond with an aggressive display towards models without UV reflectance (but took longer to do so; Table 1). However, responses involving displays were so rare that statistical comparisons were not possible. Overall, we conclude that UV reflectance from the bills of male blackbirds is not particularly important for social signalling during territory establishment and defence prior to the breeding season.

Bill pigmentation
Resident males spent significantly more time more than 10 m from model intruders with brown than yellow or orange bills. They also spent more time close to (<2 m) orange-billed than yellow-billed models. Other authors have also found the distance from the model to be an important indicator of aggressiveness by resident males to intruders (Studd & Robertson 1985; Hill 1989). Resident blackbirds may have identified the brown-billed models as subordinate birds posing little threat and therefore did not approach more closely during the

presentations. First-year males have brown bills that gradually become yellow during winter/spring (Gurr 1954; Snow 1958). Older blackbirds (2 years and over) dominate 1-year-old blackbirds when foraging for prey (Desrochers 1992). First-year males will also be less experienced than older males in territory acquisition and defence or in acquiring mates (Snow 1958). The brown bills of first-year males may signal their lower competitive ability, reducing aggression from adult birds and thus avoiding risky and unnecessary confrontations (Lyon & Montgomerie 1986).

Display is the main means of settling territorial disputes in blackbirds (Snow 1956, 1958). However, when driving out submissive intruders, males do not adopt a particular display posture (Snow 1958). If the intruder stands its ground during territorial disputes, attempted evictions may take on a more ritualized form (Snow 1958; see also Methods). In this study, resident males that did display during model presentations took longer to display to brown-billed than orange- or yellow-billed models (Table 1). Residents may have decided to approach the brown-billed models only after they failed to leave the territory on their own. Studd & Robertson (1985) and Hill (1989) demonstrated lower levels of aggression towards intruders with dull pigments. However, owing to the low level of display response by male blackbirds, our data on aggressive displays must be treated cautiously.

The yellow/orange bills of blackbirds are probably produced by the deposition of carotenoid-based pigments (Brush 1978). Carotenoids cannot be synthesized by birds and must be obtained from the diet (Goodwin 1984). Thus, the degree of carotenoid-based bill pigmentation in the blackbird is probably a consequence of a male's ability both to acquire and to use food for carotenoid accumulation (see review by Hill 1999). Hatchwell et al. (2001) showed that the bills of male blackbirds infected with the blood parasite *Plasmodium* tended to be duller than that of uninfected males. Faivre et al. (2001) also showed that male blackbirds with bright orange bills tend to be mated with females in better condition that make more breeding attempts per season and fledge more offspring than females mated to duller-billed males. Because producing carotenoid-based pigments is costly (Hill 1996; Olson & Owens 1998), and bill pigmentation may be related to male quality (Faivre et al. 2001; Hatchwell et al. 2001), bill pigmentation may be a reliable signal used by rival males when contesting limited resources (i.e. food, territories, mates; Rohwer 1982).

Blackbirds will single out and actively drive off individuals that represent a potential threat to the owner's territory, while ignoring less threatening birds (Snow 1958). In this study, resident males spent more time close to (<2 m), and appeared to respond with an aggressive display more quickly to, orange-billed than yellow-billed models. Orange-billed models might have been regarded as more of a threat to territory ownership than yellow-billed models and prompted resident males to respond in a more aggressive manner.

Females

Female blackbirds are usually active in territory defence only against other females; the motivation for such interactions seems to relate to intrasexual competition (Snow 1956, 1958). Females responded to only 44% of our model presentations. They spent more time >10 m and marginally less time 2–10 m from models presented without UV reflectance suggesting UV plays a role in attracting females (e.g. Bennett et al. 1996, 1997; Hunt et al. 1997, 1999). However, there was no difference between the time females spent <2 m from models presented with or without UV reflectance, or from models with brown, yellow or orange bills. Furthermore, females did not display towards the models. At the time of this study, pair bonding and pair formation activity was common; however, it is normally the male that initiates pair formation activities with persistent chasing and posturing towards the female (Snow 1958). Females will solicit males for only a short period prior to nesting (Snow 1958). The responses to the models by the females might have been due largely to 'curiosity' (Lack & Light 1941), or alternatively, a simple consequence of their reacting to their own partner's movements.

Conclusions

We found little evidence to suggest that UV reflectance from the bill of male blackbirds is used during male–male interactions under natural signal and viewing conditions. UV reflectance may not be important for social signalling during male–male territory disputes before nesting commences but may be used for social signalling closer to clutch initiation. We found evidence that the brown bills of first-year male blackbirds were an effective signal of subordinate status and may reduce aggression from adult males. Thus resident males spent significantly more time >10 m from models with brown bills and came closer to orange-billed intruders. Orange-billed models might have been perceived as higher quality individuals and thus as a greater threat to territory ownership than yellow-billed intruders. In contrast, female blackbirds appeared unaffected by the pigmentation of the model's bill while showing some attentiveness to UV reflectance. Male and female blackbirds may therefore be attentive to different properties of bill appearance, at least during the period of territory establishment.

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