



Rival imprinting: interspecifically cross-fostered tits defend their territories against heterospecific intruders

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Failure to recognize conspecifics in social interactions such as mate choice and aggressive encounters will often result in reduced fitness. Studies on mate choice show that the ability to recognize conspecifics as mates is not universally present at birth, but often needs to be learned. In contrast, little is known about the ontogeny of intrasexual species recognition. To test whether learning influences the recognition of sexual rivals, we compared the aggressive response towards intruders of interspecifically cross-fostered individuals and controls reared by conspecific parents. We simulated territorial intrusion by presenting either a caged individual or playback song near the nest of breeding pairs of great tits, *Parus major*, and blue tits, *P. caeruleus*. Great tits reared by blue tit parents responded much more to blue tit stimuli than did great tit controls, and furthermore showed stronger responses to blue tit stimuli than to those of their own species. Blue tits reared by great tits responded much more to great tit stimuli than did blue tit controls. In contrast, blue tits cross-fostered to coal tits, *P. ater*, did not respond more to coal tits than did blue tit controls. There was a species difference in the response to conspecifics: blue tits cross-fostered to great tits responded more to conspecifics than did cross-fostered great tits. The results were similar for males and females. We conclude that learning influences intrasexual species recognition in these tits.

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The ability to discriminate between conspecifics and heterospecifics is crucial in social interactions and may be important for the establishment and maintenance of premating isolation between species (Ratcliffe & Grant 1983; Price 1998; Irwin & Price 1999). In particular, correct species recognition is important when choosing a mate and when defending a resource such as a territory. Choosing a heterospecific mate is disadvantageous because hybrid offspring generally have low fitness (Arnold 1997), and heterospecific aggression may be a waste of time and energy (Lynch & Baker 1990). Important species recognition cues in birds may include vocalizations (Grant & Grant 1996), plumage (Kroodsma 1974), morphology (Ratcliffe & Grant 1983) and display behaviour (Crook 1963).

Young individuals may learn to recognize their own species by imprinting on parents or siblings. Filial imprinting refers to the acquisition of social preferences expressed early in life, notably the 'following response' of precocial birds (reviewed by Bateson 1966; Bolhuis 1991). Sexual imprinting is the process by which young individuals learn species-specific cues that enable them to find a conspecific mate when adult. Mate choice has long

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been considered a largely innate process (Lande 1981; Andersson 1986), but there has been a growing awareness that learning may be involved (Laland 1994; Grant & Grant 1997; Price 1998; ten Cate & Vos 1999; Slagsvold & Hansen 2001). In birds, both sexes seem to be affected by sexual imprinting, and the initial sexual imprinting is consolidated during courtship (Bischof & Clayton 1991; Immelmann et al. 1991; Kruijt & Meeuwissen 1993). Sexual imprinting has been documented in some mammal species (Kendrick et al. 1998; Penn & Potts 1998), and in more than 100 bird species (reviewed by ten Cate & Vos 1999), including great tits, *Parus major*, and blue tits, *P. caeruleus* (Slagsvold et al. 2002).

Intrasexual competition for breeding resources such as mates and territories is widespread (e.g. Andersson 1994; Brandtman et al. 1999; Kemp & Wiklund 2001). Possible evolutionary advantages of intrasexual aggression during the breeding season include defence of territory, monopolization of mate and protection of parentage. Intrasexual aggression primarily takes place between individuals of the same species since they compete for the same resources.

Few studies on imprinting concern intrasexual interactions. Vos (1994) showed that cross-fostered zebra finch, *Taeniopygia guttata*, males were more aggressive to males than to females of the familiar morph, but not the

novel morph. In addition, we have shown that great tit females cross-fostered to blue tits respond more aggressively to blue tit females than do conspecifically reared controls (Slagsvold & Hansen 2001). Furthermore, males of congeneric species may show different aggressive responses in sympatric and allopatric populations (Emlen et al. 1975; Lynch & Baker 1990).

Visual and vocal stimuli are both important in avian species recognition (Gottlieb 1971; Catchpole & Slater 1995). In this study, we investigated the intrasexual aggressive response to these stimuli in separate experiments by simulating territorial intrusions through presentations of a caged bird or song playback. The respondents were breeding great tits and blue tits that had been reared by conspecifics or heterospecifics. We compared the responses to conspecific and heterospecific stimuli of controls and cross-fostered individuals, hence testing to what extent species recognition in intrasexual interactions is learned in both species and both sexes.

METHODS

Study Area and Species

We conducted the fieldwork in a nestbox plot at Dæli, near Oslo, Norway in 1998–2001. Each year, about 70 great tit, 80 blue tit and up to six coal tit, *P. ater*, pairs breed in the 400 or so nestboxes provided. Great tits and blue tits are closely related, and form a clade that is the sister group to the rest of *Parus* (including the coal tit; Sheldon et al. 1992). No hybridization occurs between great tits, blue tits and coal tits. Their dietary and habitat preferences overlap to some extent (Perrins 1979). During winter, they may form mixed-species flocks. The great tit is socially dominant to the blue tit, and the blue tit is dominant to the coal tit (Haftorn 1993; approximate adult weights: coal tit: 9 g; blue tit: 11 g; great tit: 18 g). Great tits and blue tits are in general socially monogamous with moderate levels of extrapair paternity (Krokene et al. 1998), although some blue tits (<10% of the males in our population) are polygynous. Both species and sexes defend a resource territory throughout the breeding season.

Experimental Treatments

We exchanged eggs between nests during egg laying or incubation. In some nests we replaced all host eggs with heterospecific eggs ('pure broods'; all young of a brood were conspecific to each other and heterospecific to their foster parents), and in others we replaced just one or a few host eggs ('mixed broods'; cross-fostered individuals were heterospecific to siblings and foster parents). We distinguish between cross-fostered individuals from pure and mixed broods only in the analyses of sibling effects. We created the following groups: (1) great tits cross-fostered in blue tit nests (pure and mixed broods); (2) blue tits cross-fostered in great tit nests (pure and mixed broods); (3) blue tits cross-fostered in coal tit nests (only pure broods); (4) great tit controls (unmanipulated); and (5) blue tit controls (unmanipulated).

All young were banded with a numbered metal ring and a coloured plastic ring when the eldest brood member was 15 days old. Birds were recaptured by mist netting in August–May and given a unique combination of colour rings for subsequent identification in the field.

Experiments

Only mated birds participated, and the experiments were done during nest building and egg laying, between 27 April and 26 May 1999–2001, and between 0600 and 1700 hours. In general, aggression in territorial birds is strongest before and during the fertile period (reviewed for females by Slagsvold & Lifjeld 1994). Experiments were done mainly with yearlings. For each respondent, we presented a conspecific and a heterospecific stimulus (either a caged bird or song playback) in separate trials lasting 5 min each. For cross-fostered birds, the heterospecific stimulus was always of the species of the foster parents. In reference to the experiments, the term 'heterospecific' refers to blue tits for great tits, and great tits or coal tits for blue tits. We randomized the order of presentation of the two stimuli (conspecific and heterospecific) between response individuals. At least 1 h passed between the two trials. We recorded only the response of the individual of the same sex as the stimulus bird. Caged stimulus birds did not sing, giving no stimulus overlap between the cage and playback experiments.

We tested the following maximum number of subjects in the two experiments: cross-fostered great tits: eight males, six females; control great tits: 14 males, 15 females; blue tits cross-fostered to great tits: 10 males, 10 females; blue tits cross-fostered to coal tits: four males; blue tit controls exposed to great tits as heterospecific intruders: 18 males, 16 females; blue tit controls exposed to coal tits as heterospecific intruders: five males. Blue tits cross-fostered to coal tits produced only one female recruit which is not included here. Not all subjects participated in both experiments, hence the sample sizes in individual tests may be lower than is indicated above.

Exposure to Caged Birds

All stimulus birds were reared under normal conditions, and the majority were caught outside the study area. Stimulus birds caught in the study area were not tested near their territory.

We placed the cage containing the stimulus bird within 5 m of the nestbox of the response individual and played ca. 30 s of song to attract it. The song was always by a male conspecific to the response bird, recorded outside the study area. When the response bird arrived, the observer withdrew to record its response towards the stimulus bird. Response behaviour was recorded continuously as the time the response bird kept within 2 m of the cage.

Exposure to Playback Song

Stimulus songs were recorded outside the study area at dawn and edited to last approximately 5.5 min. Songs of

10 males of each species were used as stimulus songs in the experiment. The song of the same individual was used no more than twice within the same treatment group. We played the stimulus song from a portable audiocassette player placed within 5 m of the nestbox of the response male and recorded inspection behaviour every 30 s as the distance the male kept from the cassette player. The playback stimulus elicited a weaker positive response than a caged intruder. To register a potentially more finely graded response, we recorded five distance categories: 0–2, 2–5, 5–10, 10–20 and >20 m. However, frequency distributions of the collected data revealed that in 76% of cases the response bird was either <5 m or >20 m from the stimulus, indicating a dichotomous response. We thus interpreted only registrations <5 m from the stimulus as a response. We also noted whether the response male vocalized during each 30-s period. The results obtained with these two response types were similar. We report results only in terms of proximity to the stimulus because this response is most comparable to that in the cage experiment. The experiment was conducted only with male respondents, and blue tits cross-fostered to coal tits did not participate in the playback experiment.

Ethical Note

The study was conducted under licenses from the Directorate for Nature Management and the National Animal Research Authority in Norway. The cross-fostering was done so that the demands of cross-fostered broods should not exceed those of the natural broods of foster parents. Because blue tits are smaller than great tits, blue tit hosts received four to six great tit eggs, which is about half their natural brood size, and great tit hosts generally received whole blue tit clutches. Mixed cross-fostering treatments were analogously conducted. Cross-fostered individuals of both species thrived in the nests of their heterospecific foster parents and their recruitment did not differ from that of unmanipulated controls (Slagsvold et al. 2002). Survival beyond the first year also seemed to be high for cross-fostered birds. The oldest tit in our study area is a 5-year-old cross-fostered great tit. Furthermore the mating success of cross-fostered birds seemed to increase after their first breeding season. Pairings between blue tits and great tits, occurring at a low frequency as a result of cross-fostering, do not result in hybrid offspring (Slagsvold et al. 2002). Hence, the cross-fostering treatment does not seem to compromise animal welfare in the long term.

Stimulus birds in the cage experiment were caught in mist nets or while roosting in nestboxes, and kept in individual cages (40 × 24 cm and 40 cm high). When kept overnight, birds were housed indoors with natural lighting. When not participating in experiments, their cages were covered with cloth to minimize stress. For ethical and practical reasons, each stimulus bird was used in experiments once or twice within each treatment group (except in three cases where it was used three or four times). We monitored the body mass of caged birds, supplied them with meal worms and water ad libitum,

and released them at the site of capture after use. Two stimulus birds were released immediately; one sustained a minor cut on one toe and the other did not feed properly. None of the stimulus birds died in captivity. We always minimized time in captivity for stimulus birds, but in a few cases our schedule was delayed by response birds that were absent from their nest or by unfavourable weather (trials were not conducted during rainfall). Hence, most stimulus birds were released on the day of capture or the following day, but a few were kept for up to 5 days. Several stimulus birds were observed breeding after testing.

Statistics

Response ratios are expressed as the response to a heterospecific stimulus (R_h) relative to the response to a conspecific stimulus (R_c), calculated as:

$$[R_h/(R_c+R_h)].$$

Thus, a response ratio of 50% indicates identical responses to conspecific and heterospecific stimuli.

Forward stepwise regressions showed that the variables year of trial, date of trial and time of day of trial sometimes explained a significant amount of variation in the response variables, but the variables breeding stage (day of trial relative to the laying of the first egg) and age of response bird did not (we analysed great tit and blue tit respondents from both treatments separately, both with heterospecific and conspecific stimuli). The effects of the covariates year, date and time of trial were not consistent across samples, and proved to be nonsignificant in the vast majority of cases when included in ANCOVAs (analyses not shown). In addition, the effects of these covariates never influenced the results qualitatively, and therefore did not affect our conclusions regarding the response variables under study. Hence, we did not include them in the analyses.

Proportional variables were arcsine square-root transformed to meet the assumptions of parametric procedures. To facilitate interpretability, we report effects as percentages. For the cage experiment, we report ANOVAs controlling for sex in cases where sex or its interaction with experimental treatment explained a significant amount of variation in the dependent variable. In most cases, sex was unimportant, and we then report *t* tests. All tests are two tailed and were done with Statview 5.0 for Macintosh.

RESULTS

Cage Experiment

Great tit controls responded more to the presentation of a great tit than to the presentation of a blue tit. Cross-fostered great tits, in contrast, responded more to blue tits than to great tits (Table 1). The response ratios of controls and cross-fostered individuals were significantly different ($F_{1,39}=117.38$, $P<0.0001$; Fig. 1), showing that

Table 1. The aggressive response ($\bar{x}\pm\text{SD}$) of cross-fostered and control great tits and blue tits to caged conspecific and heterospecific intruders placed near their nests

Response bird	Social parents	N	Conspecific intruder	Heterospecific intruder	Paired <i>t</i> test	
					t_{N-1}	<i>P</i>
Great tit	Great tit	29	76±30	12±22	11.46	<0.0001
Great tit	Blue tit	14	30±38	63±34	3.66	0.003
Blue tit*	Blue tit	31	94± 8	19±32	13.14	<0.0001
Blue tit	Great tit	20	83±35	90±18	0.60	0.56
Blue tit†	Blue tit	5	93±13	20±26	6.75	0.003
Blue tit	Coal tit	4	93± 9	13±17	9.85	0.002

Response was measured as % time spent close to a conspecific or a heterospecific intruder in 5 min. Subjects included both males and females, and their response to same-sex intruders was similar.

*Controls exposed to great tits as heterospecific intruders.

†Controls exposed to coal tits as heterospecific intruders.

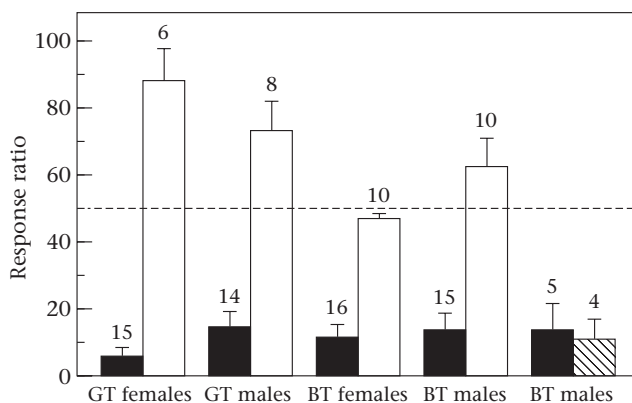


Figure 1. The relative response (response ratio) of great tits (GT) and blue tits (BT) to heterospecific and conspecific caged intruders near their nests. Blue tits were cross-fostered to coal tits (▨), great tits and blue tits were reciprocally cross-fostered (□) and controls (■) were unmanipulated. Response ratio is the response to the heterospecific divided by the sum of the responses to the heterospecific and conspecific intruders. A response ratio of 50% represents identical responses to the two stimuli (---). Bars indicate mean±SE values. Sample sizes for each group are given above the bars.

great tit intrasexual species recognition is highly affected by learning. Females had a stronger relative response to conspecifics than did males in the control group, but not in the cross-fostered group (treatment × sex interaction: $F_{1,39}=4.74$, $P=0.036$).

Blue tit controls also responded mostly to conspecific intruders, as did blue tits cross-fostered to coal tits, but blue tits cross-fostered to great tits responded to conspecifics and heterospecifics (Table 1). The response ratios of controls and blue tits cross-fostered to great tits were significantly different ($t_{49}=7.65$, $P<0.0001$; Fig. 1), and controls and blue tits cross-fostered to coal tits had similar response ratios ($t_7=0.04$, $P=0.97$).

The absolute response levels of controls and cross-fostered birds towards caged intruders perceived as rivals were similar (Table 1). The response to the species of the social parents did not differ between controls and individuals cross-fostered to great tits or blue tits (great tits: $t_{41}=1.20$, $P=0.24$; blue tits: $t_{49}=0.37$, $P=0.72$), but blue

tits cross-fostered to coal tits and blue tit controls differed in this respect ($t_7=6.40$, $P<0.001$). Blue tits cross-fostered to great tits and great tits cross-fostered to blue tits responded more to conspecifics than controls of either species responded to heterospecifics (great tits: $t_{41}=2.0$, $P=0.052$; blue tits: $t_{49}=6.61$, $P<0.0001$). The response ratio of controls was similar for great tits and blue tits ($t_{58}=0.97$, $P=0.33$). In contrast, blue tits cross-fostered to great tits responded relatively more to conspecifics, and relatively less to heterospecifics, than did cross-fostered great tits ($F_{1,30}=12.53$, $P=0.001$; treatment × sex interaction: $F_{1,30}=5.06$, $P=0.032$). Blue tits cross-fostered to coal tits responded mostly to conspecifics, in contrast to cross-fostered great tits ($t_{10}=4.36$, $P=0.001$) and blue tits cross-fostered to great tits ($t_{12}=3.55$, $P=0.004$).

Cross-fostered individuals reared in mixed broods with siblings heterospecific to themselves responded relatively less to conspecifics, and relatively more to heterospecifics than did cross-fostered individuals reared in pure broods with conspecific siblings only (ANOVA controlling for species, nonsignificant interaction removed: $F_{1,31}=7.84$, $P=0.009$). We also tested whether an increasing number of conspecific siblings led to a stronger relative response to conspecifics, but found no significant effect when controlling for species (ANCOVA for birds originating from cross-fostered pure broods only, nonsignificant interaction removed: $F_{1,24}=2.23$, $P=0.15$). We did not have sufficient data to test potential sibling effects for each species separately. Blue tits cross-fostered to coal tits were excluded from the analyses of sibling effects.

Playback Experiment

Great tit controls responded more to conspecific song than to blue tit song, but cross-fostered great tits did not respond significantly more to blue tit than to great tit song (Table 2). The response ratios of controls and cross-fostered great tits differed significantly ($t_{16}=2.32$, $P=0.034$; Fig. 2). Blue tit controls responded more to conspecific song, but blue tits cross-fostered to great tits responded similarly to great tit and blue tit song (Table 2). The response ratios of controls and cross-fostered blue tits differed significantly ($t_{25}=2.37$, $P=0.026$; Fig. 2).

Table 2. The response ($\bar{X} \pm SD$) of cross-fostered and control great tits and blue tits to conspecific and heterospecific song played near their nests

Response bird	Social parents	N	Conspecific intruder	Heterospecific intruder	Paired <i>t</i> test	
					<i>t</i>	<i>P</i>
Great tit	Great tit	12	65±32	27±24	3.62	0.004
Great tit	Blue tit	6	38±31	70±26	1.66	0.16
Blue tit	Blue tit	18	64±36	17±24	4.58	<0.001
Blue tit	Great tit	9	54±31	63±34	0.49	0.64

Response was measured as % time spent close to the audiocassette player, recorded every 30 s. Trials lasted 5 min. Only males participated in the experiment.

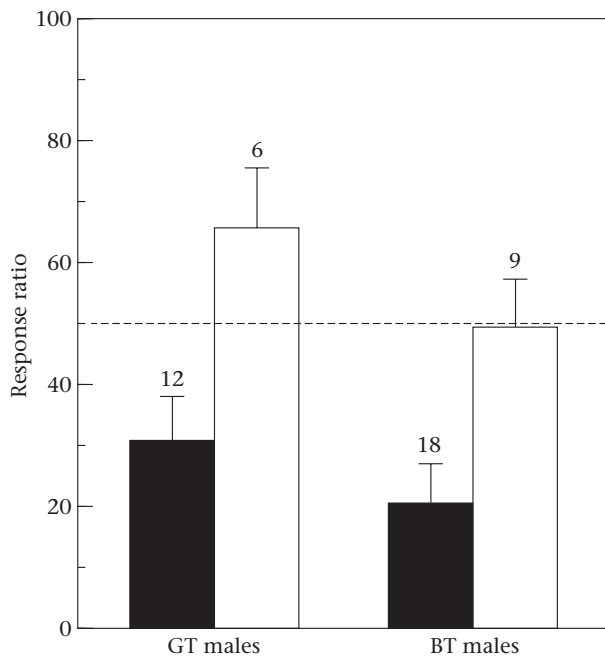


Figure 2. The relative response (response ratio) of control (■) and reciprocally cross-fostered (□) great tits (GT) and blue tits (BT) to heterospecific and conspecific playback stimuli. Response ratio is the response to the heterospecific divided by the sum of the responses to the heterospecific and conspecific intruders. A response ratio of 50% represents identical responses to the two stimuli (---). Bars indicate mean±SE values. Sample sizes for each group are given above the bars.

The absolute response levels of controls and cross-fostered birds towards playback song of perceived rivals were similar (Table 2). The response to the species of the social parents did not differ between controls and individuals cross-fostered to great tits or blue tits (great tits: $t_{16}=0.28$, $P=0.78$; blue tits: $t_{25}=0.22$, $P=0.83$). Cross-fostered blue tits responded more to conspecifics than did controls to heterospecifics ($t_{25}=3.74$, $P=0.001$), but great tits did not differ in this respect ($t_{16}=0.73$, $P=0.48$). The response ratios of great tits and blue tits were similar for controls ($t_{28}=1.28$, $P=0.21$) and cross-fostered individuals ($t_{13}=1.39$, $P=0.19$).

Low sample sizes prevented analyses of potential sibling effects.

DISCUSSION

We have shown that great tits and blue tits of both sexes may learn species characteristics of sexual rivals from their parents. The recognition of both visual and vocal cues was affected by learning. Controls responded to conspecific intruders but showed little interest in heterospecifics. In contrast, great tits cross-fostered to blue tits and blue tits cross-fostered to great tits seemed to perceive heterospecifics of the foster species as rivals. Cross-fostered blue tits also responded aggressively to conspecifics, but cross-fostered great tits did not.

Controls responded to conspecifics in the same way as blue tits cross-fostered to great tits and cross-fostered great tits responded to their foster species. Learning alone hence seemed to be sufficient to acquire rival recognition. However, cross-fostered birds responded more to conspecifics than controls responded to heterospecifics. This may indicate that some aspects of rival recognition are inherited. On the other hand, it may be an effect of learning through more interactions initiated at cross-fostered individuals by conspecifics than at controls by heterospecifics (Kruijt et al. 1982), or through the impact of siblings (Slagsvold & Hansen 2001).

Unlike the subjects of the many laboratory studies on imprinting, the cross-fostered birds of this study had been exposed to social interactions with both heterospecifics and conspecifics throughout their lives, and the effects of imprinting were still evident. Both great tits and blue tits are highly social species. They live in groups throughout the nonbreeding season, typically composed of members of both species and occasionally of additional species. Learning processes may be of particular importance in social systems, in which frequent interactions with other group members require individuals to possess a host of social skills. A group of individuals represents a variable environment, and changing group size and composition adds to this variation. The principal advantage of imprinting and learning in general is that it enables the individual to adapt quickly to a changing environment (Immelmann 1972; Bolles & Beecher 1988). Sociality may also facilitate consolidation of initial imprinting.

The relative abundance of the host species may be important for the degree of imprinting of the cross-fostered birds. In our study area, great tits and blue tits are both abundant but coal tits are not. This may have resulted in different opportunities for consolidation of

the initial imprinting for blue tits cross-fostered to great tits and blue tits cross-fostered to coal tits. Blue tits cross-fostered to coal tits may have encountered relatively few coal tits while blue tits cross-fostered to great tits probably interacted with great tits much more frequently. Blue tits cross-fostered to great tits might also have been courted by cross-fostered great tits, but blue tits cross-fostered to coal tits were probably not courted by coal tits because no coal tits were cross-fostered. Such factors may affect sexual imprinting in captive birds (Kruijt et al. 1982; Kruijt & Meeuwissen 1991). Furthermore, blue tits are more distantly related to coal tits than to great tits, and coal tits may hence represent a less suitable role model for imprinting than great tits.

Cross-fostered blue tits responded to conspecific intruders to a greater extent than did cross-fostered great tits. This suggests that the ontogeny of species recognition may differ even between closely related species. A similar difference exists in sexual imprinting: cross-fostered blue tits, although clearly sexually misimprinted, tend to mate conspecifically, but cross-fostered great tits generally fail to mate or mate heterospecifically (Slagsvold et al. 2002).

Cross-fostered great tits had fewer conspecific siblings than cross-fostered blue tits ($\bar{X} \pm \text{SE}$ fledging brood size for pure broods from which breeding cross-fostered birds originated: great tits: 4.11 ± 0.31 ; blue tits: 7.17 ± 0.32 ; $t_{25} = 6.12$, $P < 0.0001$). Kruijt et al. (1983) suggested that brood size may influence imprinting directly, because social interactions between siblings will increase with brood size, or indirectly through parental care which, per chick, may decrease with brood size, for example because of lower heat loss in larger broods. A modest effect of the number of conspecific siblings on the degree of sexual imprinting has been shown in zebra finches (Kruijt et al. 1983), but other studies on species with biparental care have failed to document a clear effect of siblings (Immelmann 1969; ten Cate 1984; ten Cate et al. 1984, 1992). We found no significant effect of brood size on the relative response to conspecifics, but more data are needed to test this. The presence of heterospecific broodmates influenced the response, in concordance with previously reported effects on sexual imprinting (Slagsvold & Hansen 2001). Siblings are thus not unimportant for the learning of species-specific cues in tits.

The two experiments gave similar results, indicating that both visual and vocal species recognition cues are learned. The results were less pronounced in the playback experiment, and fell short of significance in some instances. This may, at least in part, be explained by lower sample sizes in the playback experiment. In addition, the playback stimulus elicited a weaker positive response than did live birds, which may have reduced effect sizes in the playback experiment.

If the primary function of the response to territorial intrusion was mate defence, one would expect different responses for males and females in systems where only males may be cuckolded. In this study, males and females responded similarly to birds of the foster species of the same sex as themselves, indicating that a key function of the response recorded is defence of the territory per se.

The potential cost of relying on imprinting in species recognition is that it might lead to mistakes if the wrong characteristics are learned, as shown in the present study. This might be a problem if individuals are exposed to heterospecific stimuli during the sensitive period for learning, for instance as the result of interspecific egg dumping, nest take-over or close heterospecific neighbours that are particularly dominant (Grant & Grant 1996). The extent of this problem is likely to depend on the particular habits of the species in question. In spite of extensive studies on blue tits and great tits, there are to our knowledge no reports of natural misimprinting in these species. The prevalence of sexual imprinting across taxa and the few reports of natural misimprinting suggest that the selection pressure against an imprinting mechanism of species recognition may be low in species with parental care.

Studies of filial and sexual imprinting illustrate the importance of the ability to identify conspecifics in certain social situations (reviews in Bolhuis 1991; ten Cate & Vos 1999). The learning of species characteristics used in intrasexual competition does not fall into either of these two imprinting categories as they have been defined in the literature. We suggest the term 'rival imprinting' to describe learning to recognize potential sexual rivals. We do not know whether rival imprinting is a separate process or a consequence of a more general species imprinting which functions both inter- and intrasexually. Knowing who really represents a sexual competitor is no doubt advantageous, because erroneous responses in this respect are at best wasteful.

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