Is fitness affected by ring colour?

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Many ecologists mark their free living study animals with the aim to collect knowledge on individual life histories. Yet, marking animals may affect life histories and it is important to quantify such effects. Literature on this subject is relatively rare, especially when it concerns the effect of bird rings. This is partly because control groups are often missing, since the rings were not applied with the goal to measure their effect on life histories. From studies in captivity there is evidence that the colour of rings may affect partner choice and in the field certain outstanding colours of rings may affect predation risk. Here we use data of an ongoing study of Great Tits *Parus major* to analyse whether the colour of rings fitted in different combinations to nestling Great Tits (day 14, $n = 9818$) affected their life histories in terms of natal dispersal, first year local recapture rate, breeding performance and second year local recapture rate. We measured reflectance spectra to quantify the brightness of the colour rings, and we used a human panel to judge the conspicuousness of the rings against a grey background. We found support for a positive effect of the conspicuousness, as judged by human observers, of the colour ring combination on local recapture rate, but not on natal dispersal suggesting that survival was affected. No effect was detected on breeding performance. The brightness of the rings did not explain variation in life history components. Although the effect of conspicuousness was statistically weak, the effect size is of potential biological importance. Life expectancy of individuals without conspicuous rings is estimated to be 28% shorter than for individuals with three conspicuous rings. Our result could have a considerable impact on life history studies where fitness measures are based on colour-marked bird populations. Colour of the colour rings will affect the variance of fitness estimates and may even bias the mean of fitness estimates when specific colours are used in specific periods, in specific environments or to mark particular categories of birds like year classes.

Key words: colour rings, local recapture rate, dispersal, local survival rate, reproduction, expected number of breeding seasons, life history, bias

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Knowledge on the ecology and evolution of avian life history traits has increased dramatically through the use of data on individually marked birds. Recaptures and resightings of marked individuals not only allow estimates of survival rates, but also enable us to study within and between individual variation in ecologically relevant traits. Originally, only metal rings with unique inscriptions were used, but over time more advanced marking methods have been used, ranging from relatively cheap individual colour ring combinations (Nice 1937, 1943), via wing or leg flaps (Kinkel 1989), to transponders (Nicolaus *et al.* 2008), geolocators (Elliott *et al.* 2012, Tottrup *et al.* 2012), transmitters (Robert *et al.* 2006) or satellite transmitters (Phillips *et al.* 2003, Gill *et al.* 2009) where the location and behaviours of individuals can be monitored sometimes in real time and in fascinating detail. All these methods have greatly enhanced our knowledge (Drent *et al.* 2003), yet there may be a downside. The marks themselves may affect the birds in various aspects of their life histories, and hence may bias our findings. Therefore, it is of great importance that we study the effects of marking.

The biological processes responsible for the effect of colour rings on life history parameters can be divided into broadly three, nonexclusive, classes: social effects, predation effects and other performance effects. In addition, when the experimenter relies on observations it is possible that the detection of a colour ringed bird depends on the colours it wears, potentially biasing estimates of life history parameters. We are not aware of a study that systematically tests this. With regard to the social effects, we know from studies in captivity that colour rings may affect partner choice in the Zebra Finch *Poephila guttata* (Burley 1981, Burley *et al.* 1982, but see Ratcliffe & Boag 1987), reproductive success and sex ratio of surviving offspring (Burley 1981, 1986a, 1986b) and longevity (Burley 1985). Also in the lab, Hunt *et al.* (1997) and Cuthill *et al.* (1997) detected effects of colour rings on dominance in Zebra Finches. Such effects may enhance fitness for some birds in a population (having the attractive or impressive colours) and thereby subsequently reduce fitness for the others due to competition. The findings of Burley triggered field studies on effects of colour rings as secondary sexual traits (effect of red rings on territory retainment in Red-winged Blackbirds *Agelaius phoeniceus*, Metz & Weatherhead 1991, Weatherhead *et al.* 1991 , but this was not found by Beletsky & Orians (1989)). Mating success was positively affected by colour rings that resembled comb colour in Rock Ptarmigans *Lagopus mutus* (Brodsky 1988). Cristol *et al.* (1992) found no effect of ring colour on dominance in captive flocks of Dark-eyed Juncos *Junco hyemalis*. Breeding success was negatively affected by red colour rings in the Red-cockaded Woodpecker *Picoides borealis* (Hagan & Reed 1988) but the results were questioned by Hill & Carr (1989). In conclusion, social effects of colour rings have been detected mainly in lab studies, less often in field studies perhaps because it is technically more difficult to show such effects in field studies.

Colour rings may affect predation mortality because detectability is enhanced by outstanding colours ('oddity effect': Cresswell *et al.* 2007), or alternatively colour rings may negatively affect predation rate through camouflage (Hagan & Reed 1988) or distractive or unusual colour patterns ('confusion effect': Cresswell *et al.* 2007). Experimental work of Götmark (1994) revealed a lower attack risk by predators of stuffed Blackbirds T*urdus merula* with bright spots. The predation risk for young tits painted red tended to be higher due to Sparrowhawks *Accipiter nisus* (Götmark & Olsson 1997). No knowledge is available on the effect of metal rings alone, the standard marking method for most birds, on predation rate. The difficulty is to get good data on the unmarked group. The only method that we know of is to compare the proportion of ringed versus non-ringed birds in a closed population as used by Cresswell *et al.* (2007) for colour ringed birds. In their elegant study they found no indications that rings (a combination of colour and metal rings) affected predation mortality in their closed Redshank *Tringa totanus* population. Regrettably, most populations are not closed, preventing the differentiation of any predation and dispersal effects of rings. Verner *et al.* (2000) found no difference in return rates in relation to the number and the colour of the rings in four species of granivores (Spotted Towhee *Pipilo maculatus*, Golden-crowned Sparrow *Zonotrichia atricapilla*, White-crowned Sparrow *Z. leucophrys*, and Dark-Eyed Junco), nor did Watt (2001) in the American Goldfinch *Carduelis tristis*. Castelli & Trost (1996) and Caswell *et al.* (2012) compared a sample of birds that had leg rings versus a sample with neck collars and leg rings, and found a negative effect of neck collars in geese relative to rings on recapture rate, perhaps related to hunting. Thus, although there is evidence that bright colour spots affect predation risk both negatively and positively, there is apparently no direct evidence for effects of colour rings on predation risk.

As a last possibility, colour rings may affect a bird in performing during tasks such as foraging. The colours may influence the behaviour of conspecifics or heterospecifics, for instance affect social behaviour, affect the behaviour of kleptoparasites or attract or scare off prey. Such effects may be found back in all life history parameters. There is, as far as we know, no evidence that such effects occur. Cresswell *et al.* (2007) found no difference in foraging behaviour between Redshanks ringed with both metal and colour rings and un-ringed birds.

In this paper we test whether the colour of colour rings, that were applied to nestlings of a small passerine bird, the Great Tit, affected their life history. We used physical measures of colour as well as human judgement of the conspicuousness of colour rings to quantify colour differences between birds. We analysed whether different aspects of colour affected the nestlings local recapture rate in a statistical model including known effects of body mass, sex, birth date, nesting plot, year and the relevant interactions. The life history parameters studied were: first year local recapture rate, natal dispersal, breeding performance and second year local recapture rate in a large sample (n = 9818 individuals) during six years (2005–2010).

We also analysed natal dispersal probability within the study area, and breeding performance of the survivors, as well as their second year local recapture rate, to estimate life time effects of colour ring colour.

METHODS

Study population and selection of the data

We studied life history variation in a population of Great Tits living in 600 nestboxes in 12 plots with 50 nestboxes each in the Lauwersmeer, The Netherlands (1993–2012, 53°20'N, 06°12'E). In the period 2005–2010 we ringed all juveniles with a metal ring when they were six days old (hatching date of the first chick = day 0) and with three additional colour rings (supplied by A.C. Hughes, Middlesex, UK) when they were 14 days old. At this age body mass (0.1 g), tarsus (0.1 mm) and third primary length (0.5 mm) were also measured. All chicks were sexed using molecular techniques when they were 2–3 days old resulting in a sample of 9818 14-day-old individuals with all data available over six years. We captured all breeding birds in the nestbox using spring traps (2006–2011) to estimate local recapture rates (for details on the study site and measurements see Tinbergen & Sanz 2004, Nicolaus *et al.* 2009).

Colour rings

We used nine types of colour rings with plain colours and five striped rings with two colours (see Table 1). We planned the colour combinations to be used before the start of the season and made sure that we randomized the order of the colour ring combination list, thereby ensuring random allotment of colour combinations to chicks. Because we ran out of combinations we included new colours in 2007 (black–white) and 2009 (yellow–mauve). We did not keep track of the different batches we obtained, so that it is not possible to control for differences between them.

Brightness

Reflectance spectra of the colour rings were measured with an Avaspec 2048-2 CCD detector array spectrometer using a bifurcated probe (Avantes FCR-7 UV200; Avantes, Eerbeek, The Netherlands). The light source was a deuterium/halogen lamp. The reference was a diffuse white reflectance tile (Avantes WS-2).

We classified the colour rings in terms of reflectance over the spectrum from 360–680 nm using measurements of reflectance starting at 360 nm at each 40 nm interval till 680 nm resulting in 9 measurements per ring. Little reflectance in the UV part of the spectrum was detectable (360–400 nm). From these 9 reflectance measures we extracted a brightness measure (*i.e.* mean reflectance over the 9 measurements, 0–100%) per ring. For each bird this single mean reflectance measure per ring was used to calculate a number of brightness parameters for its colour combination. We calculated the mean brightness values (the mean of the brightness of the three colour rings on the bird), the maximum brightness (based on the colour ring with the highest brightness), and the standard deviation of the brightness of the three colour rings on the focal individual. These values were used as explanatory variables in the regression explaining offspring local recapture rates.

Great Tit colours versus non Great Tit colours

We selected the colours that were similar to Great Tit colours based on our human judgment. These colours were: yellow, black, white, green, yellow–black and black–white. The Great Tit own colour score summed the number of rings the bird had of this collection (ranging from 0–3).

Human judgment of conspicuousness

We asked 20 human subjects to arrange 16 colour rings from conspicuous to dull for the combinations used in this study plus a grey and a purple ring (colours used in recent years not included in the recapture analysis). The human subjects were chosen as an approximate

Table 1. Colour rings ranked on the basis of their brightness (%) and on the basis of human judgement of conspicuousness (14 levels) from most to least conspicuous on a grey background. Double colours refer to striped rings.

Colour	Brightness %	Rank brightness	Rank conspicuousness
White	45.48	1	6
Yellow	28.08	2	2
Pink	27.73	3	1
Red–White	26.27	4	5
Blue–White	24.85	5	9
Black–White	23.73	6	13
Yellow–Mauve	22.18	7	10
Yellow–Black	15.03	8	7
Pink–Black	14.86	9	3
Orange	8.70	10	4
Green	7.41	11	11
Red	7.06	12	8
Blue	4.22	13	12
Black	1.98	14	14

animal model for the conspicuousness judgment of birds since birds were expected to be involved in either selective predation or social interactions affecting recapture or survival. Since our colour rings did hardly reflect UV, we expected that this approximation was reasonable (Vorobyev & Osorio 1998). The subjects were offered the colour rings on a grey background under good light conditions. Per colour a number of colour rings were offered on a black plastic stick as they were supplied by the manufacturer. Subjects were asked to arrange the sticks in order of the conspicuousness of the colour rings. From these measurements we calculated the mean order in conspicuousness per ring. On the basis of this mean order the high ranking 50% of the colour rings was considered conspicuous. The parameter used as an explanatory variable in the analysis was the number of conspicuous rings per bird (ranging from 0 to 3).

Human judgment vs. brightness measurements

Ranks of colour rings from high brightness to low brightness did not correspond very well to the ranks based on the judgment of the human observers (Figure 1, Table 1, $r = 0.57$) leading us to include both in the analysis to explain local recapture rates. We included two rings (grey and purple) that were not yet used on the birds in the years discussed here. The grey ring was included because it closely resembled the background colour used in human judgment tests. Consistent with this, the grey colour was judged as not conspicuous by the human observers. Interesting in itself, the conspicuousness of white rings was judged very variable by different observers (Figure 1).

Natal dispersal, local recapture rate and next year performance

We define local recapture rate (R_{loc}) as the fraction of birds recaptured in year n+1 that were known to be alive in year n. We recorded 871 young of the 9818 fledglings (2006–2012) as locally recaptured to the next breeding season by resighting or recapturing them, for simplicity all called recapture here. We used this data set for the analysis. Of these a subset of 817 birds were actually caught in their first breeding season. Another 38 females were identified by reading their colour rings while they were incubating the eggs, while 16 males were identified by colour ring reading in the surroundings of the nest all in their first breeding season. Birds that were not seen in their first season but were seen in their second season were not included, enabling us to correct the local recapture rate estimate to local survival estimates using the detection probability. For 818 birds we have records on both lay date and clutch size of their first clutch in their first breeding year (no second clutches and repeat clutches included). Natal dispersal was quantified, as whether or not the birds dispersed to breed to another study plot within the study area in their first breeding year (dispersal = 1, no dispersal = 0; distances between study plots ranged from 0.4 to 5.2 km). Yet, differences in recapture rate in the first breeding season could be caused by colour ring related large scale dispersal. Because it is known that Great Tits tend to be resident after their first breeding season, we also measured local recapture rate of the breeding birds from the first to their second breeding year (measured as the proportion of birds recorded breeding the next year either recaptured or

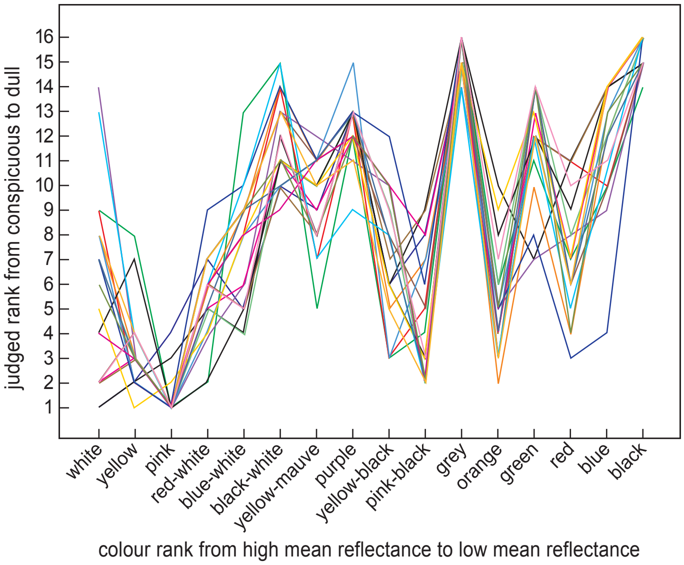

Figure 1. Plot of the rank of colours of colour rings from conspicuous to dull as judged by twenty human observers plotted against the rank in mean brightness of those rings. Humans apparently do not rank the colour rings on basis of brightness per se. NB the humans ranked 2 extra colours (grey and purple) that were not applied to the birds. The rank of the grey ring is interesting because grey was used as a background colour.

resighted in our study plot). The high detection probability (0.897, Tinbergen & Sanz 2004) leaves relatively little scope for effects of colour on detection probability.

Calculation of the expected number of reproductive seasons

To judge the effect of colour rings we calculated the expected lifetime number of reproductive seasons for young wearing no conspicuous rings and for young wearing 3 conspicuous rings separately as judged from the model fit. We assumed that half of the young emigrated from the area in their first winter, and that when breeding next year in the study area their resighting probability was 0.897 (Tinbergen & Sanz 2004). We assumed that adult dispersal was non-existing. We also assumed that adult survival after the first breeding season was constant and that the effect of wearing no or at least one colour ring existed throughout life. Based on these assumptions we calculated the expected number of reproductive seasons (E(r)) as:

$$\mathrm{E(r)} = 2 * S_{locy} + 2 * S_{locy} * \sum_{k=2}^{n} (k) * (S_{loca})^{k-1} \quad (1)$$

Where

$\mathrm{D_{prob}}$ = detection probability when alive in the study area
$\mathrm{R_{locy}}$ = local recapture rate young
$\mathrm{S_{locy}} = \mathrm{R_{locy}}/\mathrm{D_{prob}}$ = local survival rate young
$\mathrm{R_{loca}}$ = local recapture rate adult
$\mathrm{S_{loca}} = \mathrm{R_{loca}}/\mathrm{D_{prob}}$ = local survival rate adult

The factor 2 accounts for the dispersal of the offspring out of the study area. For these emigrants we assume the same survival rates as the local birds.

Statistical analysis

We analysed the recapture rate of the nestlings as local breeding birds using logistic regression. Local recapture rate was first modelled as the best model explaining variation in recapture rate without information on the colour rings (base model). This base model was selected from a number of candidate models including the explanatory variables body mass, body mass squared, sex, plot (as a factor, 12 levels), lay date of the clutch the chick was born in, year (as a factor, 6 levels) and all two-way interactions between year, sex, lay date and mass. The model with the lowest AIC value included mass, mass^2, sex, lay date, plot, year and lay date × year and was 0.517 AIC better than the next best model. We used this model to subsequently include the explanatory parameters characterizing the colour combination of the individual birds.

In a first attempt to estimate the effect of colour rings on local recapture rate in the next year we included 14 variables each for a colour, and coded the variable (for instance yellow) 0 if the colour (yellow) was not on the bird and a 1, 2 or 3 if it had one, two or three yellow colour rings. The value of this variable thus contained the number of rings of that particular colour on the bird. We included these 14 colour variables in a logistic regression to explain variation in local recapture on top of the base model. This led to an overfit, as judged from the large confidence intervals around unrealistic estimates for each colour. To solve this problem we needed to characterize the colours of the colour rings with the aim to reduce the number of parameters needed to describe the colour combination. For this we a) measured brightness of the colour rings, b) scored the number of colours rings that were 'natural' when compared to Great Tit feather colours, and c) used human judgment of colour ring conspicuousness.

We tested the effect of different colour parameters (brightness, maximum brightness and the standard deviation of the brightness as well as the number of natural Great Tit colour, and the number of conspicuous colour rings per bird and, to allow for nonlinearity, their squares) as explanatory variables in addition to the base model. The inclusion of year in the analysis also controlled for usage of new colours (Black-White from 2007 and Yellow-Mauve from 2009 onwards, see above) and birth plot to allow for systematic recapture differences between plots. We used AIC to select the best models.

RESULTS

Effects of colour on local recapture rate

Our best model showed that individual nestlings with no conspicuous rings survived worse than individuals with conspicuous rings (Figure 2, Table 2). For this we tested 10 candidate models, each including the base model and in addition one colour parameter and its square (Table 2). The model including the human conspicuousness estimate was the best supported model and differed by 2.114 AIC units from the base model without colour information. Parameter estimates (Table 3) show that the model including colour information (conspicuousness) reduces the deviance significantly as compared to the base model. The raw recapture rates as well as the fit of this model are presented in Figure 2. To study whether conspicuousness effects were sex specific we included the interaction sex×conspicuousness in the model. This reduced the AIC value of the model only slightly (by 0.412). The parameter estimates from this model suggest that the

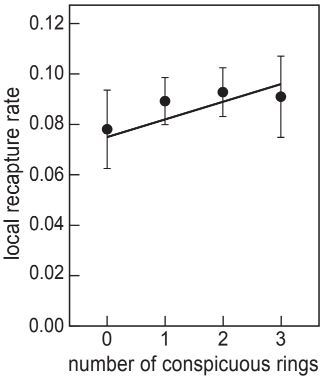

Figure 2. Raw mean values (±SE) of the local recapture rate of the young for different numbers of conspicuous rings. The line represents model fit (based on Table 3) for a 16.5 g nestling, lay date April 28 and averaged between the sexes.

effect of colour was more pronounced in males (beta = 0.148 (SE 0.083)) than in females (beta = 0.019 (SE 0.060)). Although biologically interesting, the support for this sex specific model is almost non-existing.

Effect size

The odds ratio related to one extra conspicuous ring was 1.092 meaning that one extra conspicuous ring increases the odds of recapture by 9.2%.

Natal dispersal, recapture rate and performance in the next year

Natal dispersal between the different plots within the study area was not affected by conspicuousness (Figure 3A, controlled for year and sex, $\chi^2_1 = 0.4$, $P > 0.5$, $n = 818$) suggesting that local dispersal was not an important cause for the colour ring effect on the recapture rate. First year lay date and clutch size were also not affected by the number of conspicuous rings (Figure 3B, C, females only, controlled for year, respectively $\chi^2_1 = 0.2$, $P = 0.64$ and 2.13, $P > 0.14$, $n = 413$), nor was the hatching success (not shown). Thus, we found no evidence for breeding success being affected by ring colour.

Recapture after first reproduction in the next breeding season was not affected by conspicuousness (controlled for year and sex, $\chi^2_1 = 0.3$, $P = 0.59$, $n = 818$, odds ratio = 1.046). Yet, recapture after first reproduction in the next breeding season tended to be lower for the group without conspicuous rings than for the other three groups (Figure 3D, controlled for year and sex, $\chi^2_3 = 5.336$, $P = 0.15$). Local recapture rate for the group with 0 conspicuous colour rings was 0.222, while from the other three groups it amounted to 0.362, a difference of 39%, a big biological difference, yet non-significant.

Table 2. Model comparison (on basis of AIC) to detect whether colour of rings explained additional variance in local recapture rate of nestling Great Tits as compared to the base model. The base model included mass, mass-squared, lay date, year, lay date×year, sex and plot. Ten additional models were run, each attempting to quantify the colour combination of the focal bird using the colour trait and its square. Consp = conspicuousness, Brightmax = ring with maximum brightness, Brightmean = mean brightness of the colour rings, Brightsd = standard deviation of the brightness of the colour rings on the focal bird. Own colours=number of rings with colours similar to the colours of the body of the Great Tits (= 3 minus number of rings with colours *dissimilar* to the colours of the body of the birds).

Model	**Extra explanatory variables**	**AIC**	**Δ AIC**	***df***
Base+	Consp	5550.18	–2.11	27
Base+	Consp Consp^2	5550.71	–1.58	28
Base+	Brightmax	5551.53	–0.74	27
Base+	Own colours	5552.16	–0.14	27
Base		5552.29	0	26
Base+	Bright mean	5552.62	0.33	27
Base+	Brightmax Brightmax^2	5553.04	0.75	28
Base+	Own colours Own colours^2	5553.05	0.76	28
Base+	Brightmean Brightmean^2	5553.74	1.45	28
Base+	Brightsd	5553.93	1.64	27
Base+	Brightsd Brightsd^2	5555.61	3.32	28

Table 3. Coefficients of the most supported (Table 2) logistic regression explaining variation in local recapture rate of Great Tit nestlings. Explanatory variables are body mass (g), body mass squared, plot, year and year specific lay dates (date from 1 April, April 1 = 1) and conspicuousness of colour rings (coded as 0–3).

Coefficients	**Estimate**	**SE**	***df***	**Delta Deviance**	***P***
(Intercept)	–13.9	2.59	1		
Body mass	1.247	0.314	1	138.5	<0.0001
Body mass^2	–0.0311	0.0096	1	–12.1	0.0005
Sex	–0.188	0.075	1	6.3	0.0122
Plot			11	48.8	<0.0001
Conspicuousness	0.0881	0.0435	1	4.1	0.043
Year			5	150.3	<0.0001
Lay date	–0.018	0.0026	1	53.3	<0.0001
Year×lay date			5	10.9	0.053
Residual			9791	5496.2	

Rejected terms:
year×conspicuousness, year×mass, year×sex, mass×sex, sex×date, date×mass.

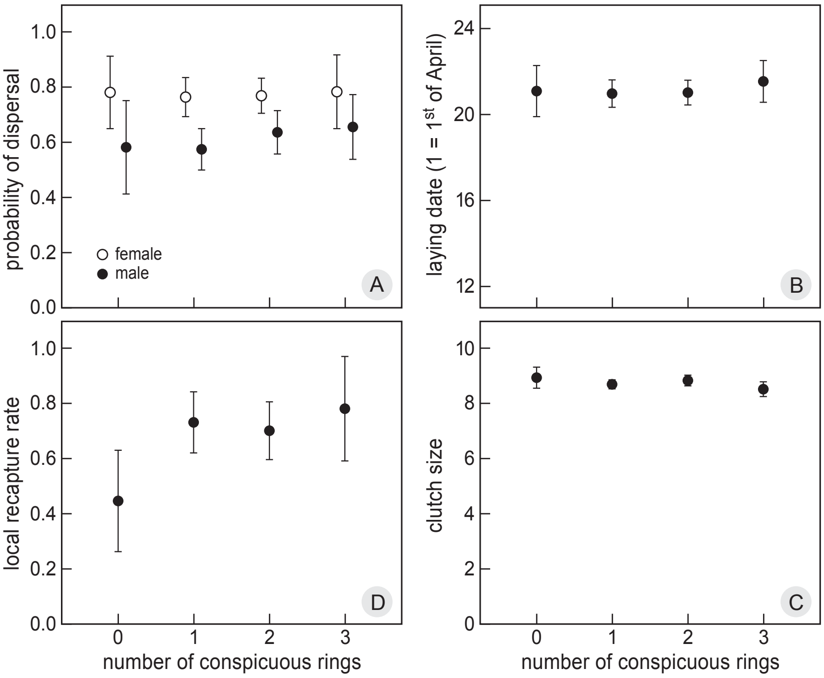

Figure 3. Natal dispersal (A), lay date (B), clutch size (C) and local recapture rate from first breeding to the next breeding season (D) in relation to the number of conspicuous colour rings.

Life time breeding seasons

We calculated the expected local recapture rates for a bird with no versus a bird with 3 conspicuous rings on basis of models predicting recapture from a continuous variable conspicuousness and controlled for year and sex. The expected life time number of breeding seasons for a nestling of 14 days old as calculated from formula (1) was 0.371 for the group without conspicuous rings and 0.519 for the group with 3 conspicuous rings. Wearing 3 conspicuous rings would increase the number of expected breeding seasons by 28%. Because we did not detect colour ring effects on annual reproduction, this means that, assuming a stable population, the fitness of the group wearing three conspicuous colour rings was 28% higher than the group wearing non-conspicuous rings.

Table 4. Mean local recapture rates and detection probabilities(D_{prob}) for young (R_{locy}) and adult (R_{loca}) Great Tits wearing no or three conspicuous colour rings (calculated from the regression with conspicuousness as continuous variable) used as the basis to calculate life time number of breeding seasons. Detection probability was assumed to be independent of ring colour. First year dispersal of the young was assumed to be 50% and independent of ring colour. For further explanation see text.

	number of conspicuous rings	
	0	**3**
R_{locy}	0.0696	0.0876
R_{loca}	0.317	0.347
D_{prob}	0.897	
Dispersal in first year	50%	

DISCUSSION

We provide evidence that, in a population of nestling Great Tits all wearing three colour rings and one metal ring, local recapture rate was positively affected by the number of conspicuous colour rings (as judged by human observers) they were wearing. First year breeding performance was not affected by conspicuousness. Why human judged conspicuousness and not physical measures of ring colour, such as brightness, did affect local tit recapture rates remains unexplained.

In the second winter of these birds, local recapture rate tended to be lower for birds without conspicuous rings. Because first year birds are known to disperse a lot, but second year birds are known to be resident, the similarity of the positive colour ring effect between the age categories is in favour of the interpretation that the effect of ring conspicuousness on recapture rate is caused by variation in survival rather than dispersal. While statistically the evidence for an effect of conspicuousness on local survival is not very strong, the effect size on expected life time as based on the estimates was considerable and suggests a potential bias in studies on life history parameters through the use of colour rings, especially when different categories of birds are given different colour rings.

There are a number of hypotheses that may explain the pattern found. They may be generated by 1) observer effects of the researchers, by 2) colour effects on dispersal or 3) colour effects on survival. With regard to the mechanism involved we could imagine social effects (mostly within, but perhaps also between species), predation and performance effects. We will discuss them in turn.

Detection probability by the observer

Recapture rate estimates, based partly on resightings, are potentially affected by the conspicuousness of the rings because conspicuous rings may be easier to read by the observers. Our recapture estimates were to some extent based on colour ring readings (54 of the 871 birds; see methods). We checked for a potential bias by repeating the analysis of recapture rate for the subset of recruits based on actual recaptures, excluding the colour ring readings (n = 817). The results were consistent with the main analysis, disproving detectability effects as a cause for the observed pattern.

Dispersal or survival effects?

We measured recapture rate of our birds locally. It is known that in our Great Tit population natal dispersal from the place of birth could be considerable (Tinbergen 2005), meaning that recapture rate cannot be equated to survival. Therefore, effects of colour rings on recapture rate may be caused by differential dispersal of the fledglings. With respect to the distinction between real survival and dispersal effects on colour ring related recapture rate, it is interesting that we did not find an effect of ring colour on natal dispersal probability within our study site. This suggests that the effect of colour rings on local recapture rate is likely to be caused by differences in survival, unless large scale dispersal of the juveniles (outside the study area) is at stake. In this light, the adult (second year birds) local survival data are of interest. Adult Great Tits seldom disperse out of their breeding plot, suggesting that differences in recapture rate for them do reflect differences in real survival (when corrected for the detection probability). Because adult birds with more than one conspicuous colour ring tended to survive better locally (Figure 3D), we judge it more likely that we are dealing with a real survival effect of ring conspicuousness than with a dispersal effect.

Effect size on life expectancy

If the reduction in local recapture rate is indeed due to survival effects of colour rings, the expected number of reproductive seasons was reduced by 28% (assuming that 50% of the fledglings disperse out of the breeding area but have similar survival), and so was individual fitness, since reproduction was not affected by the colour of the rings.

Do colour rings enhance survival?

Since we have no adequate control group we do not know whether conspicuous rings enhance survival or dull rings reduce survival, relative to birds that would not wear colour rings at all. This makes it harder to detect the mechanism responsible for the effects found. And to make it even more complicated, reduction of survival of one subgroup may enhance the survival of the others, because competition may be affected. Thus, the colour ring effect does increase the overall variance in the recapture rate. If the effect of colour rings additionally depended on biological parameters of interest, like for instance body mass, results would be biased. However, we have no indications that the latter was the case, because neither interactions between the number of conspicuous rings and the body mass of the fledgling, nor an interaction with year improved the fit of the model (Table 3).

Mechanism

The different colour measurements taken show that brightness and human judged conspicuousness ranked the colours differently (Figure 1). It is interesting that human judged conspicuousness rather than physically measured brightness had some power to predict local recruitment rate while brightness did not. Human judgment apparently catches an aspect of the biological mechanism involved. Perhaps social effects as visual attraction or predator detection by eye play a role.

Social effects

As mentioned, the fact that we do not know the direction of the recruitment effect relative to birds wearing no colour rings makes it harder to pinpoint potential mechanisms causing the effects. Yet the difference between the conspicuous and the dull rings may be explained by the colour ringed birds being sexually more attractive. In this light it is worth mentioning that there is a weak suggestion that the effect was more pronounced for the males than for the females, consistent with the idea that males may indeed be more attractive when wearing more conspicuous colour rings (Burley *et al.* 1982), and may survive better (Burley 1985) perhaps due to effects on dominance (Cuthill *et al.* 1997).

Predation

The hypothesis that the main effect of colour rings is that conspicuous rings suffer more predation than dull rings can be rejected. Yet, the positive effect of conspicuousness on survival may, apart from social effects as partner choice and dominance also be due to reduced attractiveness for the predator, a confusion effect or a novelty effect (Lindström *et al.* 2001) or even decreased detectability (increased camouflage). Alternatively, predation risk of birds with dull rings may have increased. Perhaps the predator switched to taking birds with dull rings because of negative effects of conspicuous rings on attractiveness as a prey.

Performance of the bird

Moreover, as suggested in the introduction but perhaps unlikely, the colour could handicap a bird in performing, or the colours may attract or scare off its prey.

In conclusion, we can say that there are many potential mechanisms involved. The fact that birds with conspicuous colour rings survived relatively better only narrows down the potential biological hypotheses explaining the mechanism to some extent. The results suggest that the main effect is not that conspicuous rings positively affected predation risk. Perhaps, a social explanation of the effect is more likely.

Can we circumvent the effects of colour rings?

We have strong indications that the colour of rings, what we might think of as a small handicap to the birds, did affect survival rate in a small passerine, the Great Tit, substantially. We therefore do not recommend using a particular colour ring to recognize a cohort because a difference between cohorts in survival may then be affected by the colour chosen.

The fact that we found an effect of conspicuousness of colour rings also raises the question how other, perhaps heavier, bulkier, handicapping devices such as neck rings, transmitters or geolocators might affect life history parameters. We would advise everybody using devices to mark or follow individual birds to strive to have a control group, so that we at least have the probability to detect the biases that these devices may cause in our estimates of life history parameters.

If there is no detectable effect of tags we can use them. However, when an effect is detected, unbiased estimates of the magnitude of the effect on life history parameters is difficult because competition between individuals of a population with different marks precludes an unbiased estimate of the effect of a single type of mark within one population. We would have to compare many different study populations where the different marking methods of interest were used. This would involve an enormous project, because between study-site variation in life history parameters has to be estimated adequately for each marking method, and a problem remains that no data can be gathered on a non-marked population except when the populations are completely closed.

Perhaps one alternative, for small passerine birds, is implanted pit tags. Until now, we could not show survival effects of pit tags (Nicolaus *et al.* 2008, Nicolaus *et al.* 2009, Schroeder *et al.* 2011). Yet, pit tags cannot be detected at a distance as colour rings can. So we are afraid that for some research questions we will have to accept the colour ring effects on survival until smarter and smaller devices are available that do not affect our study species.

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SAMENVATTING

Bij ornithologisch onderzoek worden vaak kleurringen gebruikt om individuele vogels in het veld te herkennen. Het is daardoor mogelijk individuele levensverhalen (*life histories*) te verzamelen en na te gaan welke factoren bepalend zijn voor het gevonden patroon en voor individuele verschillen daarin. Een nadeel van deze techniek is dat het merken van individuen zelf een effect kan hebben op het verdere verloop van hun leven. Zo is uit de literatuur bekend dat kleurringen bij vogels in gevangenschap effect kunnen hebben op levensduur, dominantie, partnerkeus, voortplantingssucces, en sekseverhouding bij de nakomelingen. In het vrije veld zijn er aanwijzingen dat dergelijke effecten ook kunnen optreden (zoals effecten van ringen met een kleur die overeenkomt met een seksueel signaal). Maar er zijn ook studies die geen effect van kleurringen vinden. In dit artikel gaan we na of de kleuren die we gebruikten om jonge Koolmezen *Parus major* te ringen, meetbare effecten op hun verdere levensloop hadden. Bij elk jong werden drie kleurringen en een metalen ring aangelegd. In totaal hebben we in 2005–2010 in ons studiegebied (600 kasten verdeeld over 12 plots met ieder 50 nestkasten) alle Koolmezen (n = 9.818) van 14 dagen oud van kleurringen voorzien en gewogen. Gedurende deze periode werden alle broedvogels in het jaar daarop gevangen, zodat hun overleving geschat kon worden. Om het effect van kleurringen te bekijken hebben we verschillende kleurmaten gebruikt. We maten 1) de helderheid van de ringen met een spectrofotometer, 2) in hoeverre de kleuren overeenkwamen met de kleuren van de Koolmees en 3) de opvallendheid van de ringen voor menselijke waarnemers (tegen een grijze achtergrond, gebaseerd op de mening van 20 proefpersonen). Het bleek dat de overleving van de mezen vooral samenhing met de opvallendheid van de ringen zoals die door de proefpersonen werd ervaren. Koolmezen zonder opvallende ringen overleefden het eerste jaar slechter dan Koolmezen met opvallende ringen. Er was eenzelfde trend in de overleving van het eerste naar het tweede jaar. We vonden geen verschillen in dispersie binnen het studiegebied (doorsnee 5 km) in de eerste winter noch in het broedsucces (legdatum, legselgrootte, uitkomstsucces) die samen hingen met de kleuren van de ringen. Hoewel de gevonden verschillen statistisch zwak zijn, is het effect biologisch zeer relevant. Al met al bleek de levensduur voor Koolmezen zonder opvallende ringen 28% korter te zijn dan van de groep met drie opvallende kleurringen! Zowel een sociaal effect (bijvoorbeeld voordeel door opvallende ringen) als een predatie-effect (voorkeur van predator voor niet opvallende ringen) zou het effect kunnen verklaren. Maar waardoor dit verschil echt ontstaat, blijft onduidelijk.

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