Articles

Ringing or colour-banding does not increase predation mortality in redshanks *Tringa totanus*

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The use of metal and colour-rings or bands as a means of measuring survival, movements and behaviour in birds is universal and fundamental to testing ecological and evolutionary theories. The practice rests on the largely untested assumption that the rings do not affect survival. However this assumption may not hold for several reasons, for example because the 'oddity effect' predicts predators select prey that appear different to their neighbours in order to avoid the 'confusion effect'. We compared the foraging behaviour and the death rates of redshanks *Tringa totanus* conspicuously marked with six colour rings and one metal ring each to unmarked birds in a study system, where routinely up to 50% of the total population are killed by avian predators during a winter. If avian predators selectively target and/or have a higher capture success of ringed birds then we would predict the proportion of colour-ringed birds in the population to decline through a winter. The proportion of colour-ringed birds in the population did not change over the course of three separate winters, and in one winter the ratio of marked:unmarked birds found killed by sparrowhawks *Accipiter nisus* was the same as the ratio of marked birds alive in the population. In the year with largest sample size, power was sufficient to detect a greater than 2.2% difference in predation rate between ringed and unringed groups. The average kill rate difference between ringed and unringed birds across the three winters was less than 1% ($0.73 \pm 2.2\%$) suggesting that even if there were differences in predation rate that were not detected because of low statistical power they were extremely small. There were no differences in any foraging measures comparing ringed and unringed birds, suggesting that the rings did not affect the ability of birds to meet their daily energy budgets. The results showed that colour-ringed birds were not preferentially targeted or killed by avian predators, and suggest that the presence of a metal and even several large colour-rings is unlikely to affect behaviour and predation mortality even under extreme selection.

The use of metal and colour-rings or bands as a means of measuring movements (Berthold 2001), survival (Brownie et al. 1985), and behaviour (Sutherland et al. 2004) in birds is universal, forming the basis of ornithology and of much evidence used to test ecological and evolutionary theory (Dobson 1990). The validity of this approach, however, rests on the assumption that the rings do not affect survival. This assumption is largely untested because it is almost impossible to monitor the survival of birds without marking them in some way. Usually it is only possible to monitor how marks that vary in degree of disturbance to the bird vary in their effect, for example the

difference in survival in birds marked with one or two bands (Froget et al. 1998), and with neck collars or leg bands (Castelli and Trost 1996). Recently it has become possible to monitor the survival of birds marked with external tags relative to those with internal tags (Jackson and Wilson 2002, Gautier-Clerc et al. 2004): in general, larger or heavier tags lead to lower survival, but these studies did not address whether leg rings alone affect survival. One study, however, compared the effects of zero to three colour-rings on chick survival within broods of semi-palmated sandpipers *Calidris pusilla* and found no effects of leg rings on survival or mass gain (Bart et al. 2001). Similarly, another study

put variable numbers of plastic rings on white-breasted nuthatches *Sitta carolinensis* and concluded that rings had no effects on time budgets and foraging behaviour (Weiss and Cristol 1999), although the value of this result is limited because the study was done on a captive population.

To date no study had tested specifically whether metal or plastic leg rings affect the probability of predation, one of the most important components of mortality for many populations. Metal and plastic rings may affect predator attack rate because the presence of metal catching the light or conspicuous colours may attract the attention of predators (Froget et al. 1998), or may lead to marked individuals being selected because of the oddity effect (Götmark and Olsson 1997) in an attempt to overcome confusion (Mueller 1971, 1975). Conversely it may actually deter predators because of their novelty (Götmark 1994, 1996). The presence of rings may affect escape probability on attack because rings may physically damage the birds (Sedgwick and Klus 1997, Amat 1999, Berggren and Low 2004). Alternatively the rings may impair foraging performance or time budgets so birds spend longer exposed to predation risk (Culik et al. 1993). Theoretically and empirically the presence of rings may also affect escape probability on attack because increased mass may decrease escape acceleration (Witter and Cuthill 1993, Kullberg et al. 1996), although in most cases rings are considered to be of negligible mass.

Here we compare foraging behaviour and predation rates on redshanks *Tringa totanus* ringed or banded with metal and several plastic colour-rings with un-ringed birds in a population under predation pressure from sparrowhawks *Accipiter nisus* at the Tyninghame Estuary, south-east Scotland. The "experiment" we report here, where we compare the survival rates of birds marked with several rings with unmarked birds was an opportunistic by-product of an officially sanctioned international colour-ringing scheme that we use as part of a long-term study of the dynamics of individual predation risk management.

Sparrowhawks in our system make attack decisions based on the relative vulnerability of the redshanks (Cresswell and Quinn 2004, Quinn and Cresswell 2004) and speed of escape after detection of an attacking sparrowhawk is an important component to the escape probability for redshank (Cresswell 1993, 1994b). Therefore, given that the rings could increase redshank vulnerability through effects on foraging or escape behaviour, predation risk may be higher among ringed redshanks. On average 86% of juveniles in our system may be captured by sparrowhawks during a winter (Cresswell and Whitfield 1994) so allowing a reasonable power to detect any selection effects due to rings. We predicted that if rings affect the risk of attack and capture of a ringed bird by an avian predator then relatively more ringed birds would be killed than occur in the population, leading to a higher proportion of ringed bird kills, and a lower proportion of live ringed birds than the initial starting proportion. We also tested whether any potential increased mortality could have been caused by increased vulnerability due to reduced foraging rate or success. If this were the case we would predict differences in foraging measures between ringed and unringed birds.

Methods

The study was carried out at the Tyninghame Estuary, on the Firth of Forth, Scotland (56°0′N 2°35′W). The estuary is the site of a long-term study of anti-predation behaviour in redshanks (Cresswell 1993, 1994b, Hilton et al. 1999b, Yasué et al. 2003, Quinn and Cresswell 2004). Tyninghame is characterised by a very high death rate because of raptor predation, mainly from sparrowhawks and to a lesser extent from peregrines *Falco peregrinus* (Cresswell and Whitfield 1994). Over three winters (1989−90, 90−91 and 91−92) when kill rate was intensively monitored $86 \pm 15\%$ (mean $\pm$ SE) of juveniles and $14 \pm 8\%$ of adults were recovered dead, 98.8% (n $=587$) of which were killed by raptors and 81% by sparrowhawks alone (Cresswell and Whitfield 1994). Sparrowhawks in the study system attack redshanks on the ground (97.3% of attacks n $=$ 477), predominantly from low flights (<1 m above the ground) from cover (88.9%, n $=517$ attacks), and chase birds in flight that they get very close to before the redshank starts to escape (71.5% of chases <1 s, 23.1% of chases $2-5$ s, n $=438$ attacks; Cresswell 1996). Therefore rings could potentially influence sparrowhawk attack rates through their conspicuousness and sparrowhawk capture rates through their effects on escape flights.

Colour-ringing

Redshanks were caught by cannon-netting or by whoosh-netting under British Trust for Ornithology (BTO) licence. Cannon-netting occurred in October 1990 and in March 1991 when 12 and 35 redshanks were captured respectively: 36 of these individuals returned (all as adults i.e. birds in at least their second winter) to the study site for the winter following capture (1992−1993-winter 1). Whoosh netting occurred in November-early December 2004 (winter 2) and 2005 (winter 3), when 30 and 32 juvenile (i.e. birds in their first winter) redshanks were captured respectively: these individuals were then monitored through the rest of the winter in which they were captured.

On capture redshanks were aged according to criteria in Hayman et al. (1986). Each redshank was fitted with six DARVIC colour-rings of spiral design according to an international scheme coordinated by the Wader Study Group (BTO, Thetford, Norfolk, UK). A "tall" blue ring was put on each leg on the tarsus (12 mm high × 6.8 mm external diameter; 0.24 ± 0.01 g, n = 10), and two "short" rings of white, red, black, green, blue or yellow were put on each leg on the tibia (6.8 mm high × 6.8 mm external diameter; 0.15 ± 0.02 g, n = 10). Finally a standard BTO metal "D" ring was attached to either the right or left leg on the tarsus and below the colour-rings (7.3 mm high × 6.9 mm external diameter; 0.60 ± 0.01 g, n = 10). Each redshank therefore had 6 conspicuous colour-rings and a metal ring (Fig. 1a), with a total mass of 1.7 g. It is important to note that colour-ring combinations were variable (each bird had a unique combination) and some colours and combinations were more conspicuous than others (although combinations were selected for maximum conspicuousness). Therefore the study can only look at the influence of a range of colour-ring
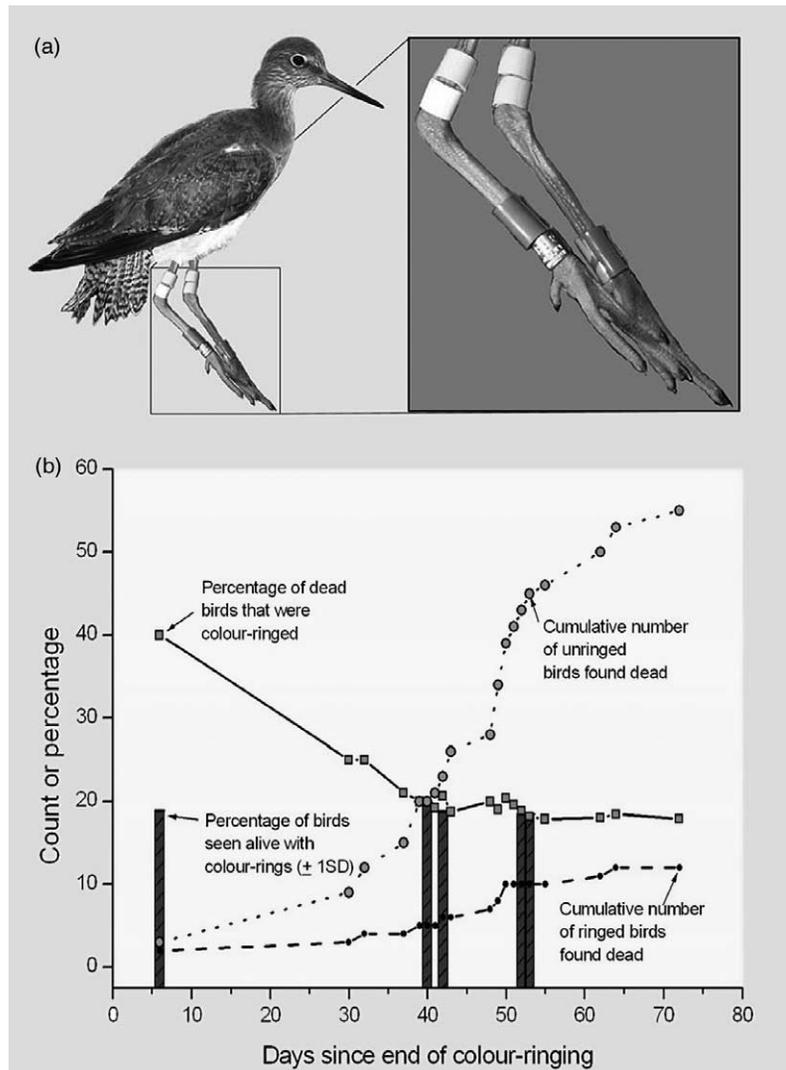

Fig. 1. (a) Numbers and types of metal rings and colour-rings attached to the legs of the redshank. (b) Changes in the number of colour-ringed birds observed alive in the population and recovered dead after capture by sparrowhawks with days since the end of colour-ringing for winter 3 (7th December 2005, e.g. day 75 is 21st February 2006). Note that the bars represent the mean count of the percentage of birds seen alive with colour-rings for a particular day with 1 SD plotted: variation is relatively small in these percentages so the standard deviations are barely visible. Note also that although the proportion of colour-ringed birds found dead is initially high this is not significant (see text) because sample sizes were initially very small.

combinations that might be typically used in a ringing study, rather than a test of a particular level of conspicuousness.

Monitoring mortality of colour-ringed birds

The total number of redshanks present on the estuary and the proportion of adults and juveniles were estimated by systematic high tide counts at the end of October and during late February or early March (Cresswell and Whitfield 1994). The decline in the population due to predation was estimated as the difference in the mean late October count minus the mean late winter count: few redshanks starve at Tyninghame (1.0%, 6/587 kills recovered 1989–92, Cresswell and Whitfield 1994). Previous studies have shown through resightings of colour-ringed birds that all of the redshank population on the Tyninghame estuary probably visits the counting area at high tide; recoveries of both ringed and unringed birds have also shown that the population is closed during the midwinter period in the sense that emigration or immigration is undetectable between November and early March, and that declines in the number of birds alive through the winter are matched by the number of dead birds found in both number and time (Cresswell and Whitfield 1994).

The occurrence of marked redshanks in the population was monitored after colour-ringing had ceased at the start of the winter period and again at the end of the winter period. Scan samples were carried out regularly during a sampling day, recording the percentage of birds at the study site that were colour-ringed: these scan samples were highly repeatable (see Fig. 1). The significance of any change in winter 1 was determined by comparing the ratio of ringed to unringed birds in the population at the beginning and end of the winter with a chi-square test, and in winters 2 and 3 by comparing the proportion of colour-ringed individuals in a sample within and between sampling days (three days in winter 2 and four in winter 3 including the start and finish of the period) across the whole winter period with a one-way ANOVA.

In winter 3, raptor kills of redshanks were recovered by systematic and opportunistic searching to locate the plucked primary feathers (Cresswell and Whitfield 1994). Sparrowhawks and peregrines almost always pluck the flight feathers near to the killing site (Whitfield 1985, Cresswell and Whitfield 1994), but may eat or carry the legs well away from the estuary search area, so we also marked primary tips of ringed birds to ensure that we could identify ringed birds from plucked remains that did not include legs. Each redshank was marked by cutting less than 0.5 mm from the tip of both outer primaries resulting in a clearly blunt ended primary shape that allowed us to identify whether a kill in the absence of legs, and therefore rings, was of a colour-ringed individual. A single kill was counted only if both outer primaries were recovered to prevent double counting (Cresswell and Whitfield 1994). We did not expect this treatment to affect the birds in any way as our cuts deliberately replicated the pattern of wear that most juvenile redshank outer primary feathers show through the winter, although in a more systematic way. We could however assess the effect of this further treatment on predation rates by examining whether there were any differences in the ratio of colour-ringed birds observed that were killed and the expected number of kills (the ratio of birds colour-ringed × total number of kills) between the first two winters of the study when feathers were not marked and the third winter when the feathers were marked. There was no significant difference in the ratio of observed and expected kills comparing any winter pair, e.g. across the three years: $\chi^2_2 = 0.04$, P = 0.98, mean difference -0.03 ± 0.06 SE kills, n = 3 winters (data from Table 1 used to calculate expected values). In winter 3, the significance of any difference between the ratio of ringed:unringed killed birds to that occurring alive in the population at the start of the winter, and the significance of any change in the ratio of colour-ringed to unringed redshanks killed over the winter was determined by chi-square tests.

Table 1. Numbers of birds colour-ringed and their occurrence in the population through three winters.

Start Period Date	No. of colour-ringed initially	Start pop. (A)	Percent of pop. ringed	Finish period Date	No. of ringed left alive	Finish pop. (B)	Percent of pop. ringed	Population decline during period (A−B)	No. of actually found killed	Test Comparing the proportion of ringed birds at the start and the end of the winter
1. Oct 1991	36 adults	237	15.2	Mar 1992	28	180	15.6	57	30	$\chi^2_1 = 0.01$, P = 0.92
2. Dec 2003	30 juv.	277	10.8	Febr 2004	6	51	11.8	226	38	$\chi^2_1 = 0.04$, P = 0.84
3. Dec 2004	32 juv.	169	18.9	Febr 2005	10	54	18.5	115	67	$\chi^2_1 = 0.02$, P = 0.89

Foraging behaviour

Foraging rates (swallow rate as a measure of foraging intake, peck rate as a measure of foraging effort, proportion of pecks that resulted in swallows as a measure of success rate of foraging and step rate as a measure of effort expended in foraging) and behaviour that may be affected by foraging ability (distance to predator concealing cover, flock spacing and flock size) of both ringed and unringed redshanks was observed on 16 days between 14 January and 2 February 2005. Focal observations of foraging redshanks ($n = 513$) lasted for 30 seconds and were made using a telescope ($30 \times$ magnification) at distances of $10-75$ m. The distance between the focal bird and the closest predator-concealing cover (the edge of the salt marsh, metres to cover), the distance between the focal bird and its nearest neighbour (nearest-neighbour distance) and the number of birds in the flock (flock size) were recorded for each focal bird. The number of swallows (swallow rate), the number of pecks or probes at the ground (peck rate) and the success rate of pecks (swallows/pecks) were recorded using tally counters for each 30 s focal sample, although in some samples, unintentionally, only swallows or pecks were recorded. A smaller number of 30 s focal samples ($n = 60$) were carried out where only the number of steps taken (step rate) was recorded (for logistical reasons it was difficult for an observer to record swallows, pecks and steps simultaneously).

Foraging and flock variables were compared between ringed and unringed birds using t tests. Mean values were calculated for all ringed birds and compared to all of the individual focals collected from unringed birds: because one half of the sample consisted of unringed birds it was impossible to fully control for the effects of repeated sampling (i.e. pseudo-replication) so the degrees of freedom were the total number of focal samples from unringed birds plus the number of ringed birds sampled minus two. Nevertheless the effects of pseudo-replication within the unringed birds was unlikely to be a problem because samples were taken from a pool of about 80 different unringed birds throughout the 16 day period ($n = 448$ focal samples), so that the probability of collecting many cases from the same unringed bird was likely to be very low.

Power analyses determined the size of the mortality needed to detect a significant effect of rings on mortality at the 5% level of significance.

Results

The ratio of killed to surviving ringed birds was the same as the ratio of killed to surviving unringed birds in all three winters (Table 1) with between $50-222$ individuals being killed during a winter. In winters 2 and 3, a greater than 2.2% and a 5.2% difference in kill rate due to ringing respectively would have been detectable (e.g. if a further 5 and 6 ringed birds instead of unringed birds had been killed in winters 2 and 3 respectively then we would have detected a significant increase in kill rate due to ringing). In winter 1, however, only a greater than 21.0% difference in kill rate would have been detectable If a further 12 ringed birds instead of unringed birds had been killed then we would have detected a significant increase in kill rate due to ringing. In winters 2 and 3, at least, there is therefore reasonable power in the system to detect differences in kill rate because significant differences could arise by relatively small changes in the kill ratio. The average kill rate difference between ringed and unringed birds across the three winters was $0.73 \pm 2.2\%$ suggesting that even if there were differences in survival rate that were not detected because of low power, they were extremely small.

The ratio of colour-ringed birds alive in the population did not change significantly with time during each of the two winters that live colour-ring ratios were monitored ($n = 21$ daily samples compared across three months in winter 2, $F_{2,18} = 0.06$, $P = 0.95$, monthly means varying from $10.8 \pm 0.03\%$ to $13.6 \pm 0.07\%$; $n = 12$ samples on 4 separate days winter 3, $F_{3,8} = 0.2$, $P = 0.90$, daily means varying from $18.5 \pm 0.02\%$ to $19.8 \pm 0.04\%$; see Fig. 1). In winters 2 and 3 respectively, 98.8% and 98.6% of the variance in observed colour-ringed ratios was within days or months rather than between months: therefore despite variation in any one estimate of the percentage of colour-ringed birds in the population, the percentages were very evenly distributed around the mean over a winter.

In winter 3, the ratio of ringed to unringed birds found killed by sparrowhawks was very similar throughout the winter ($\chi^2_1 = 0.03$, $P = 0.86$ comparing ratios from the first to the second half of the winter; or $\chi^2_1 = 0.5$, $P = 0.77$ comparing ratios from the first, second and third 30 day period from colour-ringing): Also the proportion of ringed birds found killed by sparrowhawks was the same as the proportion of birds initially colour-ringed in the population ($\chi^2_1 = 0.05$, $P = 0.81$; Fig. 1). A greater than 7.0% difference in kill rate due to ringing would have been detectable (e.g. if a further 8 ringed birds instead of unringed birds had been killed then we would have detected a significant increase in kill rate due to ringing; Fig. 1a). Therefore there is reasonable power in the system to detect differences in kill rate because significant differences could arise by relatively small changes in the kill ratio.

There were no differences in foraging and flock variables between ringed and unringed birds: swallows

$t_{459} = 0.4$, P = 0.68 (n = 15 means from ringed birds, n = 446 focal samples from unringed birds); pecks $t_{409} = 1.0$, P = 0.31 (n = 15 ringed means, n = 396 unringed focals); steps $t_{56} = -1.0$, P = 0.34 (n = 6 ringed means, n = 52 unringed focals); success rate of pecks $t_{458} = 0.9$, P = 0.36 (n = 15 ringed means, n = 445 unringed focals); flock size $t_{455} = -1.0$, P = 0.33 (n = 15 ringed means, n = 442 unringed focals); nearest neighbour distance $t_{382} = 1.1$, P = 0.27 (n = 14 ringed means, n = 370 unringed focals); and distance to predator concealing cover $t_{460} = -0.7$, P = 0.50 (n = 15 ringed means, n = 447 unringed focals).

Discussion

The results suggest that the presence of multiple colour-rings or bands on the legs of redshanks is unlikely to affect their probability of predation by avian predators in any biologically significant way. This study can only draw conclusion on differences in survival between ringed and unringed birds in terms of predation rate, and not in terms of other sources of mortality such as starvation. However, very few birds at Tyninghame die of starvation (Cresswell and Whitfield 1994). Moreover, if colour ringing affected starvation rate it is likely that this would be through effects on foraging behaviour, and we have shown that there are no such effects present.

Our conclusions are, however, somewhat limited because of the statistical power of the study: our sample sizes at best were only sufficient to pick up effects that would change predation rates by at least 2.2%. Nevertheless, our results are important because the effects of other marking techniques have been shown to result in survival decreases at a similar or much higher rate (Culik et al. 1993). Furthermore the hypothesis that leg rings affect the probability of predation specifically has never been tested directly.

One potential confounding effect in our study was any bias introduced by our catching methods. Samples of birds obtained by any catching method can potentially be biased, most often towards individuals of poor quality (Gosler 2004). Our conclusions are unlikely to be affected if this did occur during our study because, if anything, this would most probably have led to an overestimate of predation among ringed birds, since poor quality birds are likely to suffer higher predation. Similarly our sample could have been biased towards' bolder' individuals on the front edges of the flocks from where birds were most likely to have been caught by whoosh nets. Other studies have shown bolder fish occupy front positions (Ward et al. 2004), which are attacked more often by predators, and that bolder birds

may be less effective at managing predation risk (Quinn and Cresswell 2005). But again this would have overestimated the effect of ringing on predation rate.

Assuming that our results are true, why do metal and colour-rings have no effect on targeting and capture rates of sparrowhawks? Rings are thought to have the potential to affect predation rates in four ways. Firstly, addition of rings may increase the mass of the bird compromising escape acceleration on attack. However, even in our extreme case of seven rings the mass increase for a redshank was only approximately 1.7 g or 1.2% of its mean body weight (145.0 ± 2.3 g, n = 25 birds from this study). In general it is thought that artificial increases of body mass of less than 5% have negligible effects (Kenward 2000), but this has rarely been tested and a 7% increase in body mass in starlings reduced their escape take-off angle by 30% (Lee et al. 1996).

Second, addition of marks to a bird may reduce the aerodynamic or hydrodynamic performance and so compromise foraging or escape performance (Kinkell 1989, Culik et al. 1993). However, legs are usually tucked tightly under the body in the vast majority of flying birds, and often covered with feathers (pers. obs.) so that flight performance is unlikely to be compromised by leg rings, though it is possible that it is more difficult to completely cover ringed legs with feathers. We also found no evidence for any foraging or flock effects that might arise if leg rings interfered with walking: other species with more variable foraging locomotion methods may be more susceptible however (Berggren and Low 2004).

Third, addition of rings may result in injury to a bird resulting in reduced foraging performance (Sedgwick and Klus 1997, Amat 1999), increased exposure time and therefore more risks being taken by the damaged individual to compensate. However, we detected no adverse effects of the rings on foraging performance or three measures (distance to cover, flock size and nearest neighbour distance) that are important in determining the risk of capture on attack by sparrowhawks (Cresswell 1994a, b, Hilton et al. 1999a, Quinn and Cresswell 2004). Rings may also result in reduced foraging performance because birds may spend time investigating their new rings and attempting to remove them: we however did not see redshanks ever investigating their rings even immediately after capture and as above, found no effects of rings on foraging time budgets. Rings may also potentially affect foraging performance and the predation-starvation risk trade-off within groups if they affect the social dominance of the bird (Burley et al. 1982) although this has shown not to be the case for colour-ringed dark−eyed juncos (Cristol et al. 1992).

Fourth, addition of colour-rings may change the appearance of prey either making them more conspic-

uous to predators (Götmark and Olsson 1997), or unattractive to predators (Götmark 1994). Although it is clear that avian predators do select or avoid avian prey according to visual cues it is likely that prey vulnerability, which is a function of many factors such as position, potential for escape, behaviour and sociality, is the main determinant of attack rate in our system (Cresswell et al. 2003, Cresswell and Quinn 2004, Quinn and Cresswell 2004).

Our system provided an ideal opportunity to conduct a post hoc study of the effect of leg rings on predation risk because the predation risk from sparrowhawks and the number/size of rings used were both very high. Even in the presence of such extreme conditions we recorded no effects of leg rings on predation mortality. In most study systems where a single inconspicuous metal ring is attached to a leg and where predation rates are much lower, it seems even more likely that leg rings do not influence predation mortality.

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