Do predation rates on artificial nests accurately predict predation rates on natural nests? The effects of nest type, egg type and nest-site characteristics

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Abstract. We compared the predation rate on natural nests of the Eastern Yellow Robin, *Eopsaltria australis*, with the predation rates on four types of artificial nests in a woodland remnant in southern Victoria. The aims of this study were: to compare the overall rates of predation on artificial and natural nests; to determine whether artificial nests accurately reflect the effects of nest-site characteristics on the predation rate of natural nests; and to examine the effects of using different nest types and egg types for artificial nests. The predation rates on artificial nests were significantly greater than those on natural nests. The predation rate was significantly greater on artificially constructed nests than on real, disused Eastern Yellow Robin nests, but there was no difference in the predation rates on artificial nests of nest-site characteristics on the predation rates are no effects of nest-site characteristics on the predation rates are no effects of nest-site characteristics on the predation rate was significantly greater on artificially constructed nests than on real, disused Eastern Yellow Robin nests, but there was no difference in the predation rates on artificial nests containing plasticine or Canary, *Serinus canarius*, eggs. There were no effects of nest-site characteristics on the predation rates on either artificial or natural nests. These results showed that the method of construction of artificial nests can affect the rate of nest predation, and suggest that artificial nests should be made as realistic as possible in order to gain more accurate information on the predation rates on the natural nests they are meant to represent.

Introduction

The factors that influence the predation rate on bird nests are of much interest to researchers from both theoretical and conservation perspectives. These factors can include nestsite characteristics and landscape features such as habitat patch size and distance to habitat edge. It is often difficult, however, to find and monitor an adequate number of natural bird nests to make a meaningful assessment of the effects of such factors on the rate of nest predation. Consequently, artificial nests are frequently used as a substitute for natural ones, as they offer researchers control over sample sizes and the type, distribution, timing and treatment of nests, while controlling for confounding effects (Mankin and Warner 1992; Whelan *et al.* 1994; Wilson *et al.* 1998).

There are a number of important differences between artificial and natural nests that may affect the usefulness of artificial nests in estimating predation rates on natural nests. The absence of attending adults or nestlings at artificial nests (Angelstam 1986; Major and Kendal 1996; Vander Haegen *et al.* 2002) or a difference in the egg size (Roper 1992; Haskell 1995*a*, 1995*b*; Maier and DeGraaf 2000, 2001) or colour (Fleming and Giuliano 2001) may affect the relative rates of predation on artificial and natural nests. Plasticine eggs can be made to match natural eggs in size and colour; however, their distinctive odour and malleability may dis-

proportionately influence predation by small mammals (Yahner and DeLong 1992; Keyser *et al.* 1998; Rangen *et al.* 2000; Maier and DeGraaf 2001). The unnatural appearance or odour of artificially constructed nests may also dissuade or attract certain types of predator (Martin 1987; Davison and Bollinger 2000). Artificial nests are often positioned at regular intervals and usually at higher than natural densities, which may cause a density-dependent increase in the rate of nest predation (Bergin *et al.* 1997). Researchers may inadvertently place artificial nests in positions that are more accessible and make them more conspicuous and thus more vulnerable to predation than natural nests (Andrén and Angelstam 1988; Martin 1993; Luck *et al.* 1999).

As a result of these differences, artificial nests may suffer an overall predation rate that is not equal to that of natural nests in the same habitat. Although most researchers acknowledge that the predation rate on artificial nests is likely to be different to that on natural nests in absolute terms, it is still commonly believed that artificial nests can provide an accurate index of predation relative to the factors under investigation (Paton 1994; Andrén 1995; Reitsma and Whelan 2000). This belief is based on the assumption that the relative effects on the rate of predation of the factors being tested are similar for artificial and natural nests. However, biases in the types of predators of artificial nests, due to the inherent differences between artificial and natural nests, may invalidate this assumption. This could mean that conclusions about the factors affecting nest predation drawn from studies of artificial-nest predation are misleading (Martin 1987).

Many authors have stressed the need for direct, comparative studies to test whether predation rates on artificial nests accurately reflect those on natural nests in the same habitat (Martin 1987; Major and Kendal 1996; Wilson *et al.* 1998; Davison and Bollinger 2000). There is a particular need to determine whether the effects of factors such as nest-site characteristics on the rate of predation are similar for artificial and natural nests (King *et al.* 1999). In addition, the type of egg and/or materials used to construct artificial nests may affect both the overall rate of predation and the effects of particular nest-site characteristics on predation (Martin 1987; DeGraaf and Maier 1996; Bayne *et al.* 1997; Maier and DeGraaf 2000, 2001).

This study compares the predation rate on artificial nests with that on natural nests of the Eastern Yellow Robin, Eopsaltria australis, in a woodland remnant in southern Australia. The Eastern Yellow Robin is a small (20 g: Yom-Tov et al. 1992) member of the Pachycephalidae that builds an open-cup nest. We compared the actual rate of predation on artificial and natural nests, as well as the predation rate relative to a number of nest-site characteristics (nest height and density of vegetation surrounding the nest). The aims of this study were to determine (a) whether the predation rate on artificial nests accurately predicted that on natural nests and (b) whether nest-site characteristics influenced the predation rate on artificial and natural nests similarly. We also examined the effects of egg type (plasticine or Canary, Serinus canarius, eggs) and nest type (artificially constructed or real disused) on the predation rate of artificial nests.

Methods

Study site

We conducted this study at Langwarrin Flora and Fauna Reserve, a 214-ha woodland and heathland remnant 44 km south-south-east of Melbourne, Victoria, Australia (38°10'S, 145°11'E). The reserve is surrounded by paddocks that are used primarily for grazing. The climate is temperate, with cool winters and warm summers, and the average annual rainfall is 790 mm (National Parks Service 1986). Known nestpredator species that occur in the reserve include the Grey Shrikethrush, Colluricincla harmonica, Little Raven, Corvus mellori, and a number of snakes, small rodents and marsupials (Berry 2002 and unpublished). Twelve areas within the reserve, covering a total of 11.2 ha (5% of the reserve), were selected for their high density of disused bird nests. These areas were located in dense thickets of scrub, dominated primarily by Prickly Tea-tree, Leptospermum continentale, with some Coast Tea-tree, L. laevigatum, Scented Paperbark, Melaleuca squarrosa, and Swamp Paperbark, M. ericifolia. These study areas were marked with numbered flagging tape in a 10×10 -m grid pattern.

Field methods

The study areas were searched regularly for new Eastern Yellow Robin nests from the beginning of August 1999 until the end of February 2000, the main breeding season of this species in the study site. Each

time a natural nest was located, we placed four artificial nests, one of each of four types (see below), in the remnant. The location of each artificial nest was determined by randomly selecting, for each of the four nests, one of the twelve study areas, and then selecting at random a location within that study area. In this way, the locations of each of the five nests (four artificial and the one corresponding natural nest) were independent from one another. However, we placed the four artificial nests at the same height, in the same plant species and in a position with a similar density of surrounding vegetation as the corresponding natural nest. We recorded the location of artificial and natural nests relative to the nearest grid marker. The four artificial-nest treatments were: (a) artificially constructed nest with plasticine eggs; (b) artificially constructed nest with Canary eggs; (c) disused robin nest with plasticine eggs; and (d) disused robin nest with Canary eggs. Artificial nests were constructed from halved tennis balls covered in leaves, bark and lichen taken from species in the study area and attached with construction adhesive (Major et al. 1994). They were 'aired' outdoors for four weeks to reduce odour. We collected disused robin nests from previous breeding seasons from the study area and surrounding areas and stored them in plastic bags outdoors prior to use to avoid transferring human scent to the nest. We made the plasticine eggs out of creamcoloured Pro Art Plastalina[™] modelling clay moulded into an egg shape 22 mm \times 15 mm, the same size as Eastern Yellow Robin eggs. Canary eggs were used in treatments (b) and (d) because they are the same size as, and of similar colour and markings to, Eastern Yellow Robin eggs. The number of eggs placed in artificial nests matched the number of eggs in the corresponding natural nest. Rubber gloves were worn when handling the eggs and nests to minimise transference of human odours to the artificial nests.

We inspected natural nests every 2-3 days. Such frequent checks were necessary in order to accurately determine the initiation dates, hatch dates and subsequent outcome of the natural nests. Artificial nests were also checked every 2-3 days to keep the level of impact due to visitation on natural and artificial nests equal. Natural nests were considered to have been depredated if the eggs or nestlings were damaged or removed between inspections and the nestlings were not due to fledge. For breeding attempts in natural nests that ended in any way other than successful fledging, we arbitrarily assumed that the attempt ended midway between the last known active day and the day that failure was detected. For comparison with artificial nests, natural nests that ended in any other way than by predation were classed as 'successful'. This included abandoned nests and nests containing eggs that did not hatch due to infertility. This was done because artificial nests could not fail due to these causes, and natural nests were 'successful' up until this point.

To overcome the problem of comparing predation rates on artificial and natural nests that had been monitored for different periods, we ensured that the maximum exposure periods of each of the four artificial nests equalled that of the corresponding natural nest. The maximum exposure period of an artificial nest equalled the number of days that elapsed between finding the corresponding natural nest and either the end of its associated breeding attempt (nests that were not depredated) or the estimated day of fledging had it been successful (depredated nests). If an artificial nest remained untouched by predators for this period, it was deemed successful; if the eggs were damaged or removed during this exposure period, it was classed as depredated. This meant that the overall predation rates on artificial and natural nests could be compared directly without using Mayfield's (1975) method of calculating daily predation rates.

The characteristics of each artificial and natural nest site were recorded after the exposure period of each nest was finished. Nest height was measured from the ground to the rim of the nest. The number of woody plant stems at nest height within a 2×2 -m quadrat centred on the nest was counted to obtain an index of the vegetation density

surrounding the nest. We did not measure these characteristics at all nests because a fire late in the season destroyed some of the nest sites before measurements could be were taken. The number of nests (artificial and natural) that were destroyed before measurements could be taken was 69 (15.3% of nests).

A list of known or suspected nest-predator species present in the reserve was compiled from evidence in the literature and personal observation. A reference set of tooth and beak markings in plasticine eggs was then made by offering plasticine eggs to live individuals of these species, either captive or from the wild. The marks on plasticine eggs recovered from depredated artificial nests were compared with those made by live animals to identify the predator species as either avian or mammalian.

Statistical analysis

Breeding attempts in natural nests had two main stages: egg and nestling. The egg stage was defined as beginning when the eggs were first observed and ending when the last egg hatched. The nestling stage began when the last egg hatched and ended when the last nestling fledged (i.e. had left the nest: Middleton and Prigoda 2001). We calculated the daily predation rate on natural nests during the egg and nestling periods using Mayfield's (1975) equation, with the standard error calculated following Johnson (1979), and we used the CONTRAST software program to compare these daily predation rates with a χ^2 test (Hines and Sauer 1989; Sauer and Williams 1989).

We constructed a 5×2 contingency table showing the number of artificial (treatments a-d) and natural nests that were successful and depredated. We then used a χ^2 test to compare the overall predation rate on artificial (a-d) and natural nests. We constructed a $2 \times 2 \times 2$ contingency table showing the number of successful and depredated constructed and disused artificial nests containing plasticine and Canary eggs. We then tested for the significance of interactions between these factors (nest outcome, nest type and egg type) using log-linear modelling (Agresti 1990). The terms included in the initial log-linear model were the main effects of the three factors and the three two-way interactions between the factors. We used hierarchical modelling, which meant that models containing two-way interactions also included all main effects of the factors that comprised the interactions (Agresti 1990). We sought the model with the fewest number of terms that still adequately fitted the data (Noon and Block 1990). A non-significant likelihood-ratio χ^2 value indicated that the model fitted the observed data (Wilkinson 1998). Terms were therefore removed one at a time from the model, in order of least change to the model, to increase the goodness-of-fit of the new model, as long as the χ^2 value for the removal of the interaction from the model was not significant (Wilkinson 1998). The model from which no more terms could be removed without causing significant change was designated the model with the best fit. Inclusion of interactions in this model indicated that these interactions were significant (Noon and Block 1990).

We transformed the values for the vegetation density around nests to natural logarithms to obtain a more normal distribution. We used a two-factor MANOVA to test for differences in the variables nest height and vegetation density among the factors nest category (artificial a–d or natural) and nest outcome (success or predation) of artificial and natural nests (excluding those nest sites destroyed by fire before measurements could be taken). A three-factor MANOVA was performed to compare the variables nest height and vegetation density among the factors nest type (constructed or disused), egg type (plasticine or Canary) and nest outcome (success or predation) of artificial nests. The Pillai trace statistic (Pillai 1967) was used to test for the significance of multivariate effects. A significant multivariate effect indicated that there were significant differences between treatments for at least some of the variables (Johnson 1998). If the multivariate test was not significant, then the significance level for the univariate tests was reduced to $P < \alpha/p$, where α = the initial

significance level (0.05) and P = the number of variables (in this case two) (Johnson 1998). This meant that the significance level for univariate effects in the absence of a significant multivariate effect was P < 0.025. We performed all statistical analyses using SYSTAT Version 9.0. Except for the case described above, the significance level was set at P < 0.05 in all statistical tests.

Results

In total, 90 Eastern Yellow Robin nests were found and monitored; 50% of these were depredated. The daily predation rates during the egg period (0.0299 ± 0.00304 s.e., n = 85) and nestling period (0.0293 ± 0.00745 s.e., n = 49) were not significantly different ($\chi^2_1 = 0.0030$, P = 0.96). The predation rates during the two stages were therefore combined for comparison with artificial nests.

Overall predation rates on artificial and natural nests

There was a significant difference in the overall predation rate on artificial and natural Eastern Yellow Robin nests ($\chi^2_4 = 21.8$, P = 0.0002). The overall predation rate on natural nests was much lower than that on any of the four types of artificial nests (Table 1).

Effects of nest-site characteristics on predation rates on artificial and natural nests

A two-factor MANOVA showed there were no significant differences in the heights of, or vegetation densities surrounding, successful and depredated nests or nests of the five different types, and there was no significant interaction between nest type and outcome and nest height and vegetation density (Table 2). Although the *P*-value for the univariate effect of vegetation density on nest outcome was 0.039, this was not considered significant, as the *P*-value for the multivariate effect was >0.05 (see Methods). The mean heights and vegetation densities of successful and depredated artificial and natural nests are shown in Table 3.

Effects of nest type and egg type on predation of artificial nests

Log-linear modelling was used to test for the effects of egg type and nest type on the overall predation rate on artificial nests (Table 4). There was no significant interaction between egg type and nest outcome ($\chi^2_1 = 0.2$, P = 0.67 to remove the

Table 1. Ove	rall predation rate (percentage of nests that were
depredated) of	artificial and natural Eastern Yellow Robin nests
	n = 90 for all nest types

Nest type	Overall predation rate (%)
Artificially constructed nest with plasticine eggs	76
Artificially constructed nest with canary eggs	78
Real disused robin nest with plasticine eggs	68
Real disused robin nest with canary eggs	68
Natural	50

Effect	Variable	d.f.	F	Р
Туре	Nest height	4	0.1	0.98
	Vegetation density	tt 4 0.1 a density 4 0.4 a statistic $8,742$ 0.3 at 1 0.6 a density 1 4.3 a statistic $2,370$ 2.4 at 4 1.0 a density 4 2.0	0.4	0.80
	Pillai trace statistic	8,742	0.3	0.98
Outcome	Nest height	1	0.6	0.45
	Vegetation density	1	4.3	0.039
Pillai trace sta	Pillai trace statistic	2,370	2.4	0.089
Type \times outcome	Nest height	4	1.0	0.39
	Vegetation density	4	2.0	0.093
	Pillai trace statistic	8,742	1.5	0.15

 Table 2. Results of two-factor MANOVA testing for effects of the factors 'nest type'

 (artificial and natural Eastern Yellow Robin nests) and 'nest outcome' (success or predation)

 on the nest-site characteristic variables 'nest height' and 'vegetation density'

interaction from the model) and so this interaction was removed. The final model indicated that there was a significant effect of nest type on nest outcome ($\chi^2_1 = 4.5$, P = 0.034 to remove the interaction from the model); the model including this interaction fitted the data (Table 4). Artificially constructed nests had a higher overall predation rate (78%) than natural disused nests (68%).

A three-factor MANOVA revealed no significant differences in the height and vegetation density of artificial nests of different nest types, egg types and nest outcomes, and no interactions between these factors (Table 5). The mean heights of, and vegetation densities around, artificial nests are shown in Table 6.

Identifying predators of artificial nests containing plasticine eggs

Of the 180 artificial nests that contained plasticine eggs, 129 (71.7%) were depredated. Of these nests, 15 contained eggs marked by mammals, and 56 contained eggs marked by birds. For the remaining 58 depredated nests, eggs were

either not found (47 nests) or the markings present could not be identified as being made by birds or mammals (11 nests). Three of the nests depredated by mammals contained eggs marked by an antechinus species, most likely the Agile Antechinus, *Antechinus agilis*, on the basis of its known presence in the reserve. Other mammalian marks were possibly made by the Black Rat, *Rattus rattus*, Swamp Rat, *R. lutreolus*, House Mouse, *Mus musculus*, Common Brushtail Possum, *Trichosurus vulpecula*, or Common Ringtail Possum, *Pseudocheirus peregrinus*. However, we could not confidently identify which of these species depredated the nests, as the marks made by the teeth of these species were too similar to one another. Similarly, we could not reliably identify marks made by birds to species level.

Discussion

The predation rate on artificial nests was significantly greater than that on natural nests in the same habitat. Some other studies have reported similar findings (MacIvor *et al.* 1990; Sloan *et al.* 1998; Wilson *et al.* 1998; King *et al.* 1999), but

Table 3. Mean height and vegetation density of successful or depredated artificial and natural Eastern Yellow Robin, Eopsaltria australis, nests

The 69 nest sites that were destroyed by fire before measurements were taken were not included

Nest category	Mean \pm s.e. (<i>n</i>) of nests ending in			
	Predation	Success	All	
Nest height (cm)				
Artificially constructed nest with plasticine eggs	$217.6 \pm 7.2 (57)$	203.7 ± 11.4 (19)	214.1 ± 6.1 (76)	
Artificially constructed nest with canary eggs	221.3 ± 6.8 (67)	203.6 ± 12.6 (15)	218.1 ± 6.0 (82)	
Real disused nest with plasticine eggs	206.0 ± 6.5 (53)	216.4 ± 13.1 (22)	209.1 ± 6.0 (75)	
Real disused nest with canary eggs	221.1 ± 7.2 (47)	207.8 ± 12.1 (26)	216.3 ± 6.3 (73)	
Natural nest	210.5 ± 9.7 (38)	221.2 ± 10.1 (37)	215.8 ± 7.0 (75)	
All	215.8 ± 3.3 (262)	212.4 ± 5.3 (119)		
Vegetation density (no. of stems per 4 m ²)				
Artificially constructed nest with plasticine eggs	$59.0 \pm 5.0 (57)$	$63.9 \pm 8.2 (19)$	60.3 ± 4.2 (76)	
Artificially constructed nest with canary eggs	67.7 ± 4.5 (67)	$69.2 \pm 10.1 (15)$	68.0 ± 4.1 (82)	
Real disused nest with plasticine eggs	$55.9 \pm 3.6 (53)$	59.6 ± 5.1 (22)	57.0 ± 2.9 (75)	
Real disused nest with canary eggs	67.5 ± 8.3 (47)	62.0 ± 7.2 (26)	65.5 ± 5.9 (73)	
Natural nest	$49.8 \pm 4.6 (38)$	82.1 ± 8.8 (37)	65.7 ± 5.3 (75)	
All	60.8 ± 2.4 (262)	69.0 ± 3.8 (119)		

Table 4. Results of log-linear modelling examining the significance of interactions between the factors 'nest type' (artificially constructed or real disused), 'egg type' (plasticine or canary) and 'nest outcome' (success or predation) of 360 artificial nests

Model column shows the terms included in the model. The likelihoodratio χ^2 value, degrees of freedom and *P*-value for each model are given. The model from which no more terms can be removed without significant change to the model is that which best fits the data. The asterisk indicates the model with the best fit. Inclusion of interactions in this model indicates that the interactions are significant

Model ^A	χ^2	d.f.	Р
NO, EO, NE	0.3	1	0.60
NO, EO NO*	0.3	3	0.95
NO*	0.5	4	0.97
N, O	5.0	5	0.42

^AKey to variables in model terms: N = nest type, E = egg type, O = nest outcome. Single terms denote main effects of factors, double terms denote interactions between factors. Models are hierarchical; thus models including interactions between factors also include main effects of factors.

conversely some have shown that predation was greater on natural nests (Martin 1987; Roper 1992; Davison and Bollinger 2000) and one study found no difference (Butler and Rotella 1998). In general, however, predation rates appear to be greater for artificial nests than natural ones (Major and Kendal 1996).

Differences in the predation rates on artificial and natural nests could be due to different probabilities of predators finding the two types of nest, a difference in the types of predators involved, or both (Martin 1987; Willebrand and Marcström 1988; Major and Kendal 1996). Higher rates of predation on artificial nests may have been due to the absence of parental defence (Götmark *et al.* 1990; MacIvor *et al.* 1990; King *et al.* 1999). In addition, the exposed eggs in artificial nests may be more visible to predators than the eggs or nestlings concealed by an incubating or brooding

eggs or nestlings concealed by an incubating or brooding adult in natural nests (Angelstam 1986). Together, these factors could have accounted for the greater rate of predation on artificial nests in this study. Artificial nests may also be placed by experimenters in positions that make them more susceptible to predation than natural nests (Andrén and Angelstam 1988; Reitsma *et al.*

natural nests (Andrén and Angelstam 1988; Reitsma *et al.* 1990; Martin 1993; Luck *et al.* 1999). In the current study, however, the heights and vegetation densities of artificial and natural nest sites were not significantly different. Marks left in plasticine eggs from depredated artificial nests revealed predation by mammals (Agile Antechinus, as well as possum and/or rodent species) and birds (most likely Grey Shrikethrush and Little Raven: Berry 2002). It was not possible, however, to compare the relative rates of predation by different types of predators on artificial and natural nests, as we could not identify predators of artificial nests containing Canary eggs, nor of natural nests.

One criticism of the use of artificial nests is that the appearance of the nest or the type of egg used may not closely match those of the natural nest being modelled (Major and Kendal 1996). The type of egg and nest can potentially affect the rate of nest predation, and thus the usefulness of the arti-

 Table 5. Three-factor MANOVA testing for differences in nest height and vegetation density of artificial nests

 The factors being compared are 'nest type' (constructed or disused), 'egg type' (plasticine or canary) and 'outcome' (success or predation)

Effect	Variable	d.f.	F	Р
Nest type	Nest height	1	0.03	0.86
	Vegetation density	1	0.2	0.63
	Pillai trace statistic	2,297	0.1	0.87
Egg type	Nest height	1	0.1	0.72
	Vegetation density	1	1.0	0.32
	Pillai trace statistic	2,297	0.6	0.58
Outcome	Nest height	1	1.5	0.22
	Vegetation density	1	0.5	0.49
	Pillai trace statistic	2,297	1.0	0.36
Nest type × egg type	Nest height	1	0.01	0.92
	Vegetation density	1	0.5	0.49
	Pillai trace statistic	2,297	0.3	0.78
Nest type \times outcome	Nest height	1	1.0	0.31
••	Vegetation density	1	0.4	0.85
	Pillai trace statistic	2,297	0.5	0.58
Egg type \times outcome	Nest height	1	1.0	0.33
	Vegetation density	1	0.2	0.68
	Pillai trace statistic	2,297	0.6	0.57
Nest type \times egg type \times outcome	Nest height	1	0.5	0.48
	Vegetation density	1	0.2	0.70
	Pillai trace statistic	2,297	0.3	0.73

ficial nest in predicting the predation rate on natural nests (Martin 1987). We found that the predation rate on real, disused nests was significantly lower than that on truly artificial nests, and was closer to the predation rate on natural nests. Davison and Bollinger (2000) found that predation on artificial nests made from wicker baskets was significantly greater than that on artificial nests made from grass. In contrast, Martin (1987) found that artificial wicker nests had a much lower predation rate than those made of moss, and that the predation rates on the moss-covered nests were more like those on natural nests. However, Rangen et al. (2000) found that nest appearance did not affect the predation rate on artificial nests. We also found that the predation rate on artificial nests containing Canary eggs was no different to that on nests containing plasticine eggs. In contrast, Rangen et al. (2000) found that artificial nests containing plasticine eggs suffered a heavier predation rate than artificial nests containing finch eggs. These authors suggested that plasticine eggs are comparatively more vulnerable to predation by small mammals that use olfaction to find nests than are real eggs. Maier and DeGraaf (2001) found that captive White-footed Mice, Peromyscus leucopus, depredated plasticine eggs more frequently than real eggs of a similar size, and concluded that this was because they were easier to penetrate than shelled eggs. Collectively, these variable findings highlight the importance of understanding how the egg and nest type used can influence predation rates on artificial nests and thus the usefulness of artificial nests in predicting predation rates on natural nests.

Most researchers acknowledge that the overall absolute predation rate on artificial nests does not necessarily reflect that on natural nests in the same habitat (Haskell 1995b; Davison and Bollinger 2000). However, it is still believed that they can be used to study the effects of nest-site characteristics and other factors on the rate of predation on the assumption that patterns observed in artificial nests will also apply to natural nests in the same habitat (Andrén and Angelstam 1988; Esler and Grand 1993; Arango-Vélez and Kattan 1997). For example, artificial nests are often used to examine the effects of proximity to habitat edges on predation rates, and it is assumed that whatever patterns are found for artificial nests will be the same as that found for natural nests (Andren 1995; Arango-Vélez and Kattan 1997; Degraaf et al. 1999; Vander Haegan et al. 2002). It is therefore essential to determine whether this is true: whether the effects of nest-site characteristics on nest predation are the same for both artificial and natural nests within the same habitat. In our study, there was no difference in the effects of nest-site characteristics on the predation rate on artificial and natural nests; neither nest height nor vegetation density surrounding the nest appeared to affect the risk of predation of either artificial or natural nests. Likewise, the type of nest and egg used did not influence the effects of nest-site characteristics on predation of artificial nests. In contrast, Martin (1987) found that whilst artificial nests made from wicker baskets indicated that predation was greater on ground than arboreal nests, the opposite pattern was shown for both more realistic-looking artificial nests and natural nests. Similarly, Davison and Bollinger (2000) found that realistic-looking grass nests were better than wicker nests at predicting the effects of nest-site characteristics on predation of natural nests. These studies suggest that artificial nests should be

Nest type	Egg type	Mean \pm s.e. (<i>n</i>) of nests ending in		
		Predation	Success	All
Nest height (cm)				
Constructed	Plasticine	$217.6 \pm 7.2 (57)$	203.7 ± 11.4 (19)	214.1 ± 6.1 (76)
	Canary	221.3 ± 6.8 (67)	203.6 ± 12.6 (15)	218.1 ± 6.0 (82)
	All	219.6 ± 4.9 (124)	203.7 ± 8.3 (34)	$216.2 \pm 4.3 (158)$
Real	Plasticine	206.0 ± 6.5 (53)	216.4 ± 13.1 (22)	209.1 ± 6.0 (75)
	Canary	221.1 ± 7.2 (47)	207.8 ± 12.1 (26)	216.3 ± 6.3 (73)
	All	$213.1 \pm 4.9 (100)$	$211.7 \pm 6.8 (48)$	$212.7 \pm 4.3 (148)$
All	Plasticine	212.0 ± 4.9 (110)	210.5 ± 8.8 (41)	$211.6 \pm 4.3 (151)$
	Canary	$221.2 \pm 4.9 (114)$	206.2 ± 8.9 (41)	$217.3 \pm 4.3 (155)$
	All	216.7 ± 3.5 (224)	208.4 ± 6.2 (82)	
Vegetation density (no.	of stems per 4 m ²)			
Constructed	Plasticine	59.0 ± 5.0 (57)	63.9 ± 8.2 (19)	60.3 ± 4.2 (76)
	Canary	67.7 ± 4.5 (67)	$69.2 \pm 10.1 (15)$	68.0 ± 4.1 (82)
	All	63.7 ± 3.4 (124)	$66.2 \pm 6.3 (34)$	$64.3 \pm 3.0 (158)$
Real	Plasticine	55.9 ± 3.6 (53)	59.6 ± 5.1 (22)	57.0 ± 2.9 (75)
	Canary	67.5 ± 8.3 (47)	62.0 ± 7.2 (26)	65.5 ± 5.9 (73)
	All	61.4 ± 4.3 (100)	60.9 ± 4.5 (48)	$61.2 \pm 3.3 (148)$
All	Plasticine	$57.5 \pm 3.1 (110)$	61.6 ± 4.6 (41)	$66.8 \pm 3.5 (151)$
	Canary	$67.6 \pm 4.3 (114)$	64.6 ± 5.8 (41)	58.6 ± 2.6 (155)
	All	62.7 ± 2.7 (224)	63.1 ± 3.7 (82)	

Table 6. Mean height and vegetation density of successful and depredated artificial nests of different nest type and egg type

made as realistic as possible in order to give more reliable results on the effects of nest-site characteristics on the predation rates on natural nests.

Another important point concerns the way in which artificial nests are distributed in space and time. In this study, although artificial nests were at higher than natural densities, they were deliberately distributed in space and time so as to mimic the spatio-temporal distribution of natural nests. In many studies, however, artificial nests have been set out in a non-random pattern on one day and exposed over the same interval of time. This, of course, is vastly different to how most natural nests are distributed, and potentially leads to lack of independence among nests and a density-dependant increase in predation (Picman 1988; Major and Kendal 1996; Bergin *et al.* 1997). The effects of spatial and temporal distribution on the relative predation rates of artificial and natural nests need to be further investigated.

In conclusion, we found that the predation rates on artificial nests were significantly greater than those on natural nests in the same habitat. Artificial nests constructed from tennis balls covered in plant material suffered significantly greater rates of predation than did artificial nests made with real disused robin nests. There was no significant difference, however, in the predation rate on artificial nests containing plasticine or Canary eggs. Neither nest height nor vegetation density surrounding the nest appeared to affect the rate of predation of artificial or natural nests. It is recommended that artificial nests be made as realistic as possible in order to gain more accurate information on the predation rates of the natural nests they are meant to represent.

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