

TITLE: Trade-off between the risk of depredation and the risk of brood parasitism by brown-headed cowbirds (*Molothrus ater*) in red-winged blackbird (*Agelaius phoeniceus*) nests.

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## SUMMARY

Nest depredation is a major source of natural selection in passerine species. To avoid these events birds engage in more aggressive and intensive nest defence. However, species used as hosts by brood parasites might find that the more conspicuous their nest defence is, the easier it will be for parasites to detect their nests. Habitat effects also contribute to nest success, and often, nests closer to the edge of the nesting habitat are those most susceptible to nest depredation and parasitism. I quantified male nest defence by red-winged blackbirds (*Agelaius phoeniceus*), through experimental manipulations using alarm calling playbacks of different intensities, at nests parasitised and non-parasitised by brown-headed cowbirds (*Molothrus ater*), in two different habitats in Winnipeg, Canada. My results show that this species recognised high intensity alarm calls as a potential threat to nestlings. Males in marsh habitats responded quicker to playback presentations than males in ditch

habitats. Marshes, where there were no parasitised nests, had significantly more nest depredation events than ditches, where 33% of nests were parasitised by cowbirds. This suggests there is a trade-off between the risks of nest depredation and parasitism, and that cowbirds avoid habitats where male hosts defend their nests more conspicuously, as this would greatly limit brood parasites fitness.

Keywords: brood parasitism, brown-headed cowbird (*Molothrus ater*), habitat effects, nest defence, nest depredation, red-winged blackbird (*Agelaius phoeniceus*).

J. Nunes Trade-off between nest depredation and brood parasitism risks

1 1. INTRODUCTION

2 Nest depredation is a major source of nestling mortality in birds (Beletsky  
3 1996; Cresswell 1997; Burton & Yasukawa 2001; Avilés et al. 2006). Breeding-  
4 season decisions such as where and when to nest, and how to defend a nest,  
5 can influence species' reproductive success (Beletsky & Orians 1997). A  
6 potential response to a high risk of depredation is to reduce investment in any  
7 one breeding attempt. This can be achieved by reducing clutch size, which  
8 consequently reduces nest size, nest-building time, chick-rearing period and  
9 nest exposure to predators (Skutch 1949; Slagsvold 1989; Cresswell 1997;  
10 Tewksbury et al. 2002; Muchai & Plessis 2005). Another means by which to  
11 avoid nest depredation is to increase investment in nest protection, given that  
12 nest success has been positively correlated with increased nest defence (Knight  
13 & Temple 1986).

14 One of the most obvious anti-predator behaviours seen in bird species are  
15 alarm calls. Red-winged blackbird (*Agelaius phoeniceus*) males use at least ten  
16 different call types to signal the presence of potential predators to conspecifics  
17 (Beletsky et al. 1986; Beletsky 1996; Burton & Yasukawa 2001). Males with  
18 territories close to each other have been shown to use the same call type  
19 continuously, as part of a group display and interaction. However, when a  
20 predator is detected, males switch to a different type of call. Against the  
21 previous background noise, this change is easily detected by conspecifics  
22 (Beletsky 1996). This "anti-predator sentinel system" also signals the presence

23 of a predator to incubating females, who cannot easily detect predators while  
24 sitting on the concealed nest (Burton & Yasukawa 2001).

25 Nevertheless, nest protective behaviours are not always beneficial. Patterns  
26 of depredation can sometimes affect the arms race between avian brood  
27 parasites and their hosts (Martin et al. 2000; Garamszegi & Avilés 2005). For  
28 passerine species such as the red-winged blackbird, that often advertises and  
29 defends its territory acoustically (Catchpole & Slater 1995; Burton & Yasukawa  
30 2001; Garamszegi & Avilés 2005), alarm calls might represent a conspicuous  
31 behaviour that can enhance the chances of nests being detected and used by  
32 brood parasites (Gochfeld 1979; Uyehara & Narins 1995; Clotfelter 1998).  
33 Previous work has shown that the generalist brood parasite brown-headed  
34 cowbird (*Molothrus ater*) can more easily detect hosts that act conspicuously  
35 and aggressively towards predators than hosts that are not as effective nest  
36 defenders (nesting-cue hypothesis) (Burhans 2000). Brood parasitism is then a  
37 potential selection pressure that may provide a constraint on the effects of  
38 natural selection upon male nest defence and, therefore, select for less  
39 conspicuous parental activity (Garamszegi & Avilés 2005). Such an adaptation  
40 is particularly expected among individuals more susceptible to nest parasitism,  
41 but not those least vulnerable to this constraint to fitness. Ultimately, a trade-  
42 off between anti-predator behaviour and anti-parasite behaviour is likely to  
43 arise. On the one hand potential hosts of brood parasites can opt for intensive  
44 and aggressive nest defence, which deters predators but will probably attract  
45 parasites. On the other hand they can adopt more discrete nest defence

46 behaviours, which will not draw the attention of brood parasites, but will not  
47 be effective against nest predators (Krüger 2007).

48 Variation in nest site quality often also relates to nest success (Martin et al.  
49 2000). Nest search tactics used by both predators and brood parasites may be  
50 an expression of the role of different habitat and microhabitat characteristics  
51 (Clotfelter 1998). Recent studies have shown that nest depredation and  
52 parasitism are more frequent near the edge of the nesting habitat, where nests  
53 are less concealed (Moskát & Honza 2000; Hoover et al. 2006), as this increases  
54 the exposure of nests to potential parasites and visually hunting predators  
55 (Eggers et al. 2005). Thus, hosts whose nests are located on the edge of the  
56 nesting habitat, i.e. are more conspicuous and at higher risk of discovery,  
57 might have to invest more on nest defence to compensate for nest site effects  
58 than individuals with less conspicuous nests (Briskie et al. 1990; Cresswell  
59 1997; Muchai & Plessis 2005). Conversely, if there is a positive proximate  
60 relationship between nest depredation and parental activity, it has been  
61 proposed that environmental conditions might favour the evolution of reduced  
62 parental activity where nest depredation risk is greater (e.g. open nests)  
63 (Martin et al. 2000; Muchai & Plessis 2005). In this instance, the independent  
64 effects of habitat and nest defence on depredation rates could be easily  
65 confounded.

66

67 In the current study I quantified male nest defence in response to the  
68 presentation of alarm calling playbacks in a population of red-winged

69 blackbirds, at two different habitats with distinct edge effects: marsh habitats  
70 are characterised by extensive areas of open water (approximately 500 m<sup>2</sup>) and  
71 ditch habitats consisted on thin strips (approximately 6 m wide) of emergent  
72 vegetation along irrigation canals and represented an evidently linear and  
73 narrow habitat. Red-winged blackbirds are a passerine species that breeds in  
74 North America. Males of this species are highly territorial and defend nests  
75 from predators by adopting vigilant behaviours and using an alarm calling  
76 system (Beletsky et al. 1986; Burton & Yasukawa 2001). The red-winged  
77 blackbird is a common “acceptor” host (i.e. it does not usually remove eggs  
78 laid by parasites) of the brown-headed cowbird, an obligate, generalist brood  
79 parasite (Clotfelter 1998; Glassey & Forbes 2003). For this reason, these two  
80 species are likely to still be at an early stage of their co-evolutionary arms race  
81 (Stokke et al. 1999).

82 The aim of this study was to experimentally test whether the nest defence  
83 behaviour of male red-winged blackbirds with nests in habitats more exposed  
84 to predators was more conspicuous than that of male red-winged blackbirds at  
85 habitats less likely to be used by nest predators. At each experimental nest I  
86 examined the responses of territorial males to red-winged blackbird male  
87 alarm calling playbacks. Males were expected to respond to the presented  
88 alarm calls by calling more intensively, the higher the intensity of the  
89 respective playback (Beletsky 1996; Burton & Yasukawa 2001; Cramer & Price  
90 2007) and by setting off a group defence behaviour among their conspecifics  
91 (Arnold 2000; Krüger 2007). Consequently I verified if, as hypothesised above,

92 there was a trade-off between nest brood parasitism and nest depredation,  
93 linked through nest defence, i.e. if nests from males that defended their nests  
94 more intensively managed to be more successful, but were more susceptible to  
95 brood parasitism than nests from less defensive males. Thus, I assessed the  
96 effects of parasitism status and nesting habitat on parental nest defence, nest  
97 depredation rates and the direct effect of intensity of red-winged blackbird  
98 male defence on nest success.

99

## 100 2. STUDY AREA AND METHODS

### 101 General methods

102 The fieldwork took place at seven study sites established in Winnipeg,  
103 Manitoba, Canada (49° 54' N, 97° 14' W). These were occupied by breeding red-  
104 winged blackbirds and all nests of this species found at each site were  
105 monitored over five weeks from May to June 2008. The study sites represented  
106 two different habitats where red-winged blackbirds were the main nesting  
107 species: ditch and marsh habitats. In these different habitats the parasitism  
108 rates of red-winged blackbirds by brown-headed cowbirds were highly  
109 distinct: at marshes there were no parasitised red-winged blackbird nests; at  
110 ditches 33% of red-winged blackbird nests were parasitised by brown-headed  
111 cowbirds (n = 138).

112 Surveys took place daily, between 0900 and 1200 hours CST (Central  
113 Standard Time). All red-winged blackbird nests found were tagged, monitored  
114 and egg laying, egg hatching, fledging, parasitism and depredation events  
115 were recorded throughout building, egg-laying, incubation and nestling

116 phases. Fledging was assumed when a nest was found empty once the chicks  
117 had reached 10 days of age (Forbes & Glassey 2000) (field observations verified  
118 chicks were able to fly by this stage); nest parasitism occurred when brown-  
119 headed cowbird eggs were found in a red-winged blackbird nest; depredation  
120 was assumed when the entire contents of the nest disappeared (Martin et al.  
121 2000). I carried out experiments only on nests at the nestling stage (1-4 day old  
122 nestlings, hatch = day 0), when parental activity was greatest and red-winged  
123 blackbird males consequently showed more intense defence against predators  
124 (Knight & Temple 1986; Eggers et al. 2005; Muchai & Plessis 2005). I performed  
125 experiments at both parasitised and non-parasitised nests and in both habitats:  
126 14 parasitised nests in ditches, 14 non-parasitised nests in ditches and 9 non-  
127 parasitised nests in marshes. Nests included in the experiments were a  
128 minimal distance of 30 m from each other to guarantee they were from  
129 different territorial males (this was confirmed by behavioural observations).

130 I performed only one test at each nest. All tests were carried out in a  
131 random order and during the afternoon (between 1300 and 1800 hours CST),  
132 allowing at least one hour after the survey visit to the nest in order to minimise  
133 its impact on the birds' response (Cramer & Price 2007).

134

#### 135 Playback experiment

136 One of four different 7.5 minute long playbacks was used randomly at each  
137 study nest. Order and duration of each distinct portion of playback were  
138 standardised in this protocol: 90 seconds of control background marsh noise,

139 followed by 90 seconds of low intensity red-winged blackbird alarm calling (2  
140 calls per 10-second period), then 90 seconds of high intensity red-winged  
141 blackbird alarm calling (8 calls per 10-second period, Beletsky 1996) and finally  
142 an additional 3 minutes of control noise. Playbacks for both low and high  
143 intensity alarm calls were obtained from four different red-winged blackbird  
144 males to prevent pseudo-replication, using a Sony camera (model DCR-SR85)  
145 and a Gun Zoom Microphone (model ECM-HGZ1). These males were not used  
146 for playback presentation. Playbacks were broadcast at a constant volume of 30  
147 dB, using an iPod Nano (8GB) and a Centrios speaker (Centrios stereo iPod  
148 docking radio) mounted on a 0.70 m high tripod within 2 m of the focal nest  
149 (Arnold 2000). I videotaped responses to the playbacks from a minimum  
150 distance of 11 m from the focal nest (Tewksbury et al. 2002), using the camera  
151 and microphone mentioned above. Playback presentations started 5 minutes  
152 after set up of the equipment to control for any disturbance to the focal nest. At  
153 15 second intervals, I recorded both the number of red-winged blackbird males  
154 calling and the number of males seen within 5 m of the focal nest (Cramer &  
155 Price 2007) as measures of nest defence behaviour (Arnold 2000; Røskaft et al.  
156 2002a; Røskaft et al. 2002b).

157

## 158 Statistical analyses

159 The number of male red-winged blackbirds calling was qualitatively  
160 similar to the recruitment response (i.e. number of males recruited), so only the  
161 results from the latter analyses are presented.

162 I tested the following relationships.

163 (a) The effects of different playback types on male-red-winged blackbird  
164 recruitment were assessed using a general linear mixed effects model and  
165 including nest and site as random effects (Quasipoisson error structure).

166 (b) The effects of parasitism status and nesting habitat on speed and  
167 intensity of recruitment responses were assessed using general linear models  
168 (Poisson error structure).

169 (c) The effects of parasitism status, habitat, lag and amplitude of  
170 recruitment responses on red-winged blackbird nest survival were assessed  
171 using general linear models (Binomial error structure). A nest was considered  
172 successful when all nestlings fledged.

173 For (b) and (c) analyses the speed to reach the peak recruitment response  
174 was measured as the lag (s) between the start of the high intensity playback  
175 type and the point when maximum number of males was recruited; the  
176 intensity of recruitment responses was measured as the amplitude (i.e.  
177 difference) between the peak number of males responding and the number of  
178 males responding at the end of the low intensity alarm calling playback  
179 presentation.

180 Statistical analyses were performed using SPSS 15.0 and R 2.7.0 softwares. I  
181 obtained ANOVA reports from model simplifications and considered  
182 explanatory variables to have a significant effect at  $p < 0.05$ . Due to the error  
183 structures used in these analyses (either Poisson or Binomial) I simplified most

184 models using  $X^2$ -tests. If full models showed overdispersion, then I tested  
185 explanatory variables using F-tests (Crawley 2007).

186

### 187 3. RESULTS

#### 188 (a) Analysis of effect of playback type

189 Playback presentations revealed that significantly more male red-winged  
190 blackbirds responded to the high intensity alarm calling playback than to the  
191 other playback types ( $X^2 = 16.719$ ,  $p = 0.0008$ , d.f. = 3, figure 1). There was no  
192 difference in male response between the control and the low intensity alarm  
193 calling playbacks. For this reason, in further analyses the response used was  
194 the change from this baseline to the response to the high intensity alarm calling  
195 playback. Neither nest parasitism status nor habitat influenced the maximum  
196 number of red-winged blackbird males recruited at each nest (parasitism  
197 status:  $X^2 = 0.655$ ,  $p = 0.4181$ , d.f. = 1; habitat:  $X^2 = 0.304$ ,  $p = 0.5816$ , d.f. = 1).  
198 Moreover, chick age at the time of experiment was not included in any of the  
199 following statistical models as this variable did not have an effect on the  
200 number of males recruited during the high intensity alarm calling presentation  
201 ( $X^2 = 1.52$ ,  $p = 0.467$ , d.f. = 2).

202

#### 203 (b) Analysis of speed and intensity of defence responses

204 Red-winged blackbird males from marshes recruited conspecifics more  
205 than 4 times quicker than males with nests in ditch habitats ( $F = 95.57$ ,  $p =$   
206  $0.0067$ , d.f. = 31,32, figure 2). However, the intensity (i.e. amplitude) of  
207 recruitment responses of red-winged blackbird males did not differ between

208 different habitats ( $X^2 = 1.109$ ,  $p = 0.292$ , d.f. = 1). To clarify these results the  
209 effect of habitat on nest density (i.e. the number of active red-winged blackbird  
210 nests within a radius of 10 m from the focal nest) was tested, using a general  
211 linear model (Poisson error structure). This analysis showed nest density did  
212 not differ between ditch and marsh habitats ( $X^2 = 0.013$ ,  $p = 0.908$ , d.f. = 1).  
213 Similarly, nest parasitism status was not responsible for either differences in  
214 speed (i.e. lag) or amplitude of male recruitment response (lag:  $F = 0.001$ ,  $p =$   
215  $0.9918$ , d.f. = 30,31; amplitude:  $X^2 = 0.143$ ,  $p = 0.705$ , d.f. = 1).

216

#### 217 (c) Analysis of nest survival

218 Because the previous analyses showed that the amplitude of the  
219 recruitment response was not significantly different between males in different  
220 habitats, this variable was not included in the analysis of nest survival. Nest  
221 depredation at nests in ditches was significantly lower than in marsh habitats  
222 ( $X^2 = 9.582$ ,  $p = 0.003$ , d.f. = 1), so that nests in ditch habitats were more  
223 successful than nests in marsh habitats (figure 3). This result was verified more  
224 generally by using a general linear model (Binomial error structure) to  
225 compare nest success rates in ditch and marsh habitats for the full sample of  
226 the red-winged blackbirds nests surveyed in 2008 ( $n = 151$  nests in marsh  
227 habitats and 138 nests in ditches; abandoned nests were excluded from this  
228 analysis). Significantly less depredation events occurred in ditch habitats than  
229 in marshes ( $X^2 = 11.67$ ,  $p = 0.0006$ , d.f. = 1). Nest survival was not related to  
230 either nest parasitism status ( $X^2 = 0.005$ ,  $p = 0.9468$ , d.f. = 1) or the lag in

231 recruitment response ( $X^2 = 0.312$ ,  $p = 0.6044$ , d.f. = 1). Moreover, there was a  
232 marginally non-significant interaction between habitat and the lag of the  
233 recruitment response on red-winged blackbird nest survival ( $X^2 = 3.547$ ,  $p =$   
234  $0.0689$ , d.f. = 1). The lag of the defence response ( $\pm$  s.e.) of males in ditches was  
235 independent of nest survival ( $n = 23$  successful nests and 2 depredated nests),  
236 however in marsh habitats, males from successful nests ( $n = 3$ ) responded  
237 quicker than males from nests that were depredated ( $n = 5$ ) (figure 4).

238

#### 239 (d) Analysis of habitat quality

240 Analysis (c) showed habitat had a significant effect on nest success so  
241 further analyses were performed. General linear models were used to clarify  
242 the effect of habitat on different life-history response variables: lay date of first  
243 red-winged blackbird egg, clutch size, brood size (Poisson error structures),  
244 egg hatching success (i.e. proportion of hatched eggs per nest) and nest  
245 survival (Binomial error structures). Data from tested ( $n = 36$ ) and untested  
246 nests ( $n = 41$ ) were used and habitat was included in the models as a factor  
247 with three levels: ditch, marsh edge (nests within 3 m from the edge of  
248 marshland, which corresponds to the average ditch half width) and centre of  
249 marsh (nests more than 10 m from the edge of marshland).

250 It was found that red-winged blackbird egg hatching success was  
251 significantly higher in nests located in the centre of the marsh than in nests  
252 located in either ditches or marsh edge ( $X^2 = 10.139$ ,  $p = 0.006$ , d.f. = 2, figure 5).  
253 Nevertheless, ditches had significantly higher nest survival than either centre

254 or edge of marsh habitats ( $X^2 = 12.963$ ,  $p = 0.002$ , d.f. = 2, figure 6). However,  
255 there was no difference in lay date ( $F = 0.259$ ,  $p = 0.7727$ , d.f. = 62,64), clutch  
256 size ( $X^2 = 0.045$ ,  $p = 0.9775$ , d.f. = 2) or brood size ( $X^2 = 1.273$ ,  $p = 0.5292$ , d.f. =  
257 2) in relation to the habitat in which red-winged blackbirds were nesting.

258

#### 259 4. DISCUSSION

260 This study showed red-winged blackbird males recognised high intensity  
261 alarm calls as an indicative of potential threat to nestling survival and, as  
262 expected, responded more strongly to this playback type than to the other  
263 playback types presented. This supports previous suggestions that these  
264 passerines use alarm calls as an anti-predator response and are able to encode  
265 information about the level of danger in the calls used (Burton & Yasukawa  
266 2001). It has been previously shown that red-winged blackbird males have the  
267 ability to distinguish lesser or greater dangers and call accordingly (i.e. call at a  
268 higher rate the greater the risk) and in synchrony with their conspecifics  
269 (Beletsky 1996; Burton & Yasukawa 2001).

270 Male defence response following playback of the high intensity alarm  
271 calling was significantly quicker in marshes than in ditches. Considering the  
272 nature of these different habitats, marsh habitats as large areas of marshland  
273 with patches of open water and ditch habitats as thin strips of vegetation  
274 (Beletsky & Orians 1997), it seems logical to assume that in ditches it takes  
275 longer to reach the maximum number of red-winged blackbird males recruited  
276 than in marsh habitats because nests in such a habitat are usually more isolated

277 (Deng & Gao 2005). However, my results demonstrated that there was not a  
278 difference in nest density between the different habitats used in this study. A  
279 plausible reason for the relationship found between habitat and lag of male  
280 defence response might be that one of the marshlands used here was also  
281 breeding territory for a northern harrier (*Circus cyaneus*), a common predator  
282 of young and adult red-winged blackbirds (Sawin et al. 2003). For this reason,  
283 males with territories in this habitat might have been more alert to danger and  
284 able to respond to a threatening situation more readily than males in ditch  
285 habitats.

286       Moreover, it can be argued that the presence of a nesting predator in the  
287 same marshland as nesting red-winged blackbirds is likely to be the main  
288 reason for the different results in nest survival between ditches and marshes.  
289 The interaction between lag of recruitment response and habitat appears to act  
290 upon nest survival in this way: in ditches, speed of male defence response did  
291 not differ between depredated and successful nests, although in marshes, nests  
292 from males with slower nest defence responses tended to be later depredated.  
293 Nonetheless, the effect of this interaction was shown to be non-significant. It is  
294 likely that the difference in nest defence conspicuousness here shown might be  
295 ultimately responsible for the different nest depredation rates obtained at  
296 different habitats. Despite the fact that I did not find a significant effect of  
297 speed of nest defence on nest fate, these two variables can be indirectly linked  
298 by habitat. In my study both analyses of tested and non-tested nests indicated  
299 that nests in ditch habitats, where males from tested nests responded less

300 rapidly to the high intensity alarm calling playback, had greater survival than  
301 nests in marsh habitats. In fact, many studies have demonstrated that  
302 conspicuous parental activity is likely to attract nest predators that cue on  
303 these behaviours to detect available nests (e.g. Banks & Martin 2001;  
304 Tewksbury et al. 2002; Eggers et al. 2005). Besides, the fact that this interaction  
305 was found to be non-significant might be a consequence of low power. This  
306 could be improved with an increase in sample size and a carefully randomised  
307 experimental design in order to decrease extraneous sources of variation, such  
308 as differences in the prevalence of nesting predators between study sites.  
309 Another limitation of this study was that when testing the effects of ditch and  
310 marsh habitats in relation to nest survival by including all the nests surveyed,  
311 it was unknown how many clutches represented re-nesting following  
312 depredation of the first clutch. It is likely that red-winged blackbirds with nests  
313 that have been depredated early in the season will have re-nested (Tewksbury  
314 et al. 2002). In this instance habitat and male quality effects on nest survival  
315 might have been confounded.

316 It is possible that there is a link between the findings discussed above and  
317 the incidence of brood parasitism. My study demonstrated that the two  
318 different habitats assessed had completely distinct parasitism rates. It is  
319 possible that red-winged blackbirds at marshes are more exposed to nest  
320 depredation, through conspicuous male nest defence behaviour, and for this  
321 reason are not recognised by brown-headed cowbirds as suitable hosts (Avilés  
322 et al. 2006). Such hosts may indicate a lower chance of successfully rearing

323 viable offspring to brood parasites than hosts that are more capable of  
324 avoiding the attention of nest predators (Avilés et al. 2006). This possible  
325 negative effect of host nest defence on parasite fitness might clarify why no  
326 nests in marshes were parasitised and only nests in ditches were used by  
327 brown-headed cowbird females. Such a balance between costs and benefits  
328 surrounding behavioural responses to danger will vary temporally, as a  
329 function of red-winged blackbird life-histories and as a function of  
330 depredation frequency (Tewksbury et al. 2002).

331 My results from the analyses of habitat quality seem to clarify how this  
332 variable related to nest success. The highest hatching success was found in the  
333 centre of marshes. This indicates that nests located at the centre of a marsh  
334 survived through incubation stage better than nests on other locations.  
335 However, when analysing the relationship between nest location and nest  
336 success, nests in ditches were actually the most successful and there was no  
337 difference between nests at the edge of marsh and at the centre of marsh in  
338 terms of nest success. This suggests that nest defence behaviour is generally  
339 more intense at the nestling stage (Knight & Temple 1986; Eggers et al. 2005;  
340 Muchai & Plessis 2005). At this stage of the breeding season, the differences in  
341 nest defence found between males of different habitats might become even  
342 more evident, resulting in males from marsh habitats attracting more nest  
343 predators than males at ditch habitats. These analyses have also shown that  
344 ultimately there was no difference in nest survival between the tested marsh  
345 nests (at the edge of marsh habitat) and nests built in the centre of marshlands.

346 This indicates that in marsh habitats, the sub-sample tested was representative  
347 of the full sample of red-winged blackbird nests located in marshlands and  
348 that proximity to edge did not influence the success of these nests.

349 The results from my study indicate that at sites where red-winged  
350 blackbirds are under greater selection pressure from nest depredation (marsh  
351 habitats here) individuals have adopted quicker anti-predator responses when  
352 faced with threats to their offspring. Moreover, through experimental  
353 manipulation of red-winged male nest defence, this study indicates the  
354 presence of a clear trade-off between brood parasitism and nest depredation  
355 risks, however not in a direction that had been reported before: at marsh  
356 habitats, where nest defence is more conspicuous than at ditches, nests are  
357 more heavily depredated, but at the same time at a lesser risk of brood  
358 parasitism. From the rationale I have given above, nest depredation seems to  
359 have an evolutionary impact in shaping male nest defence, and consequently  
360 brown-headed cowbird female host choice, which modulates the incidence of  
361 brood parasitism and the co-evolution and life-history dynamics of brood  
362 parasites and their hosts. My findings here discussed are likely to represent a  
363 significant advance in our understanding of brood parasitism, nevertheless,  
364 measurement of nest depredation as a selective force acting on the co-  
365 evolution of host-parasite systems still deserves much consideration.

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368

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## FIGURES

Figure 1

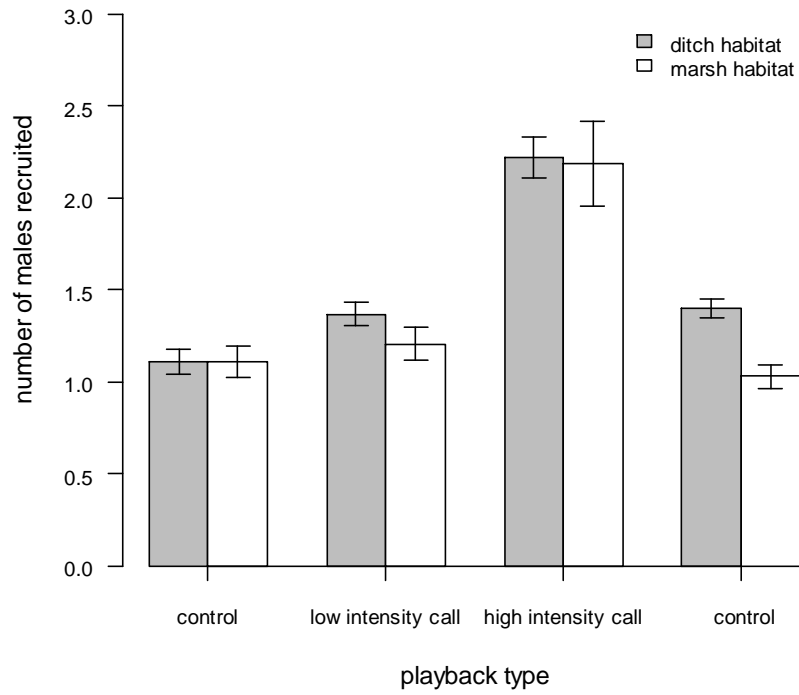


Figure 2

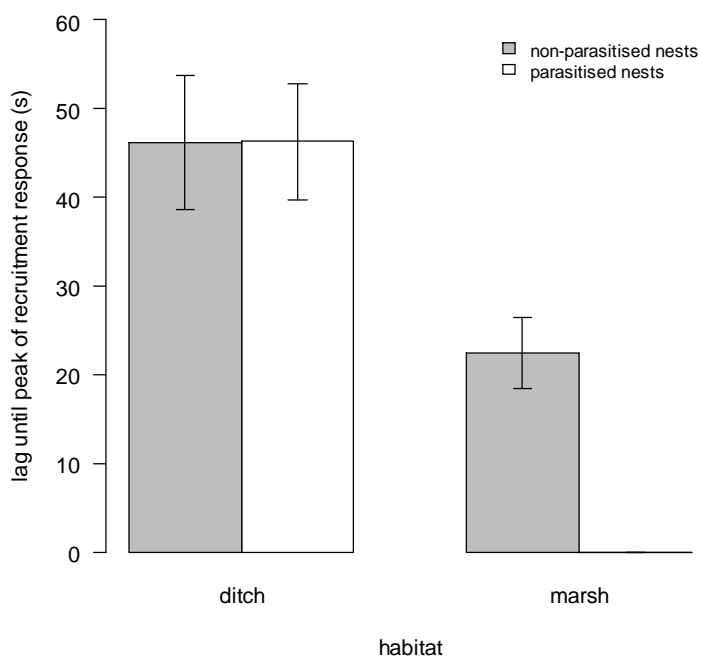


Figure 3

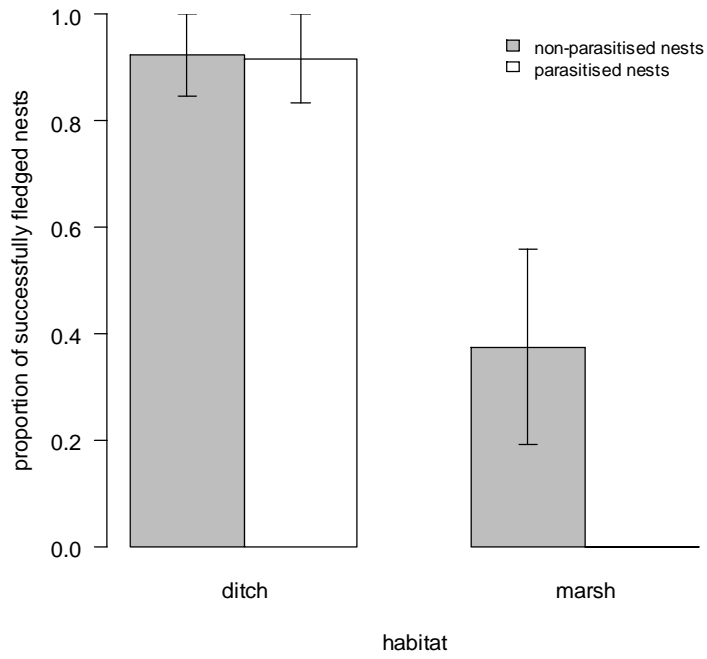


Figure 4

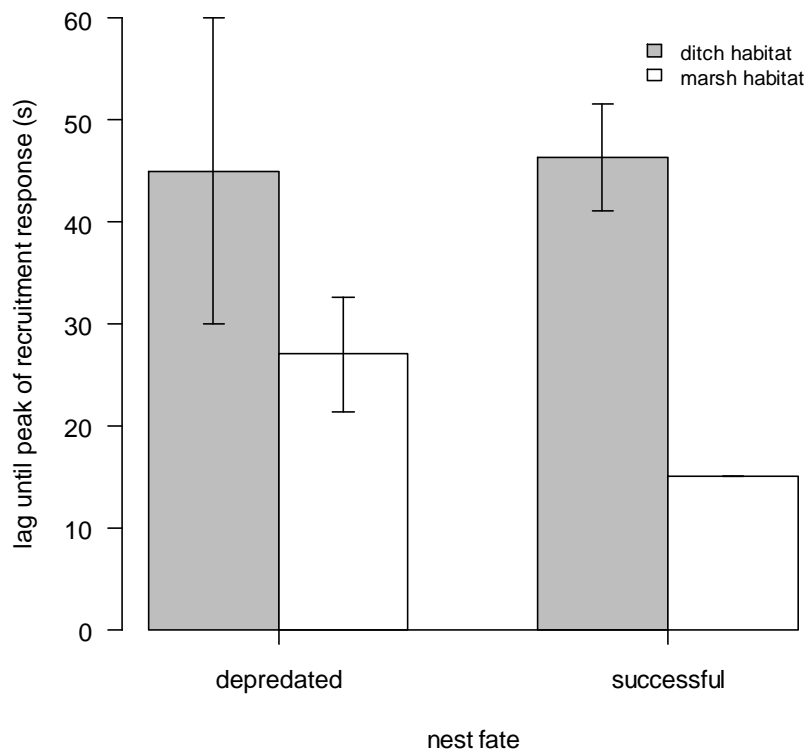


Figure 5

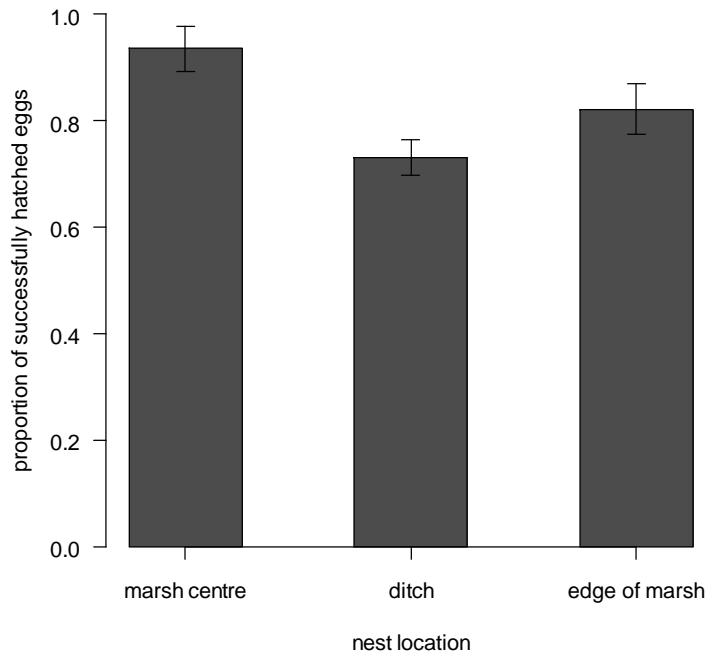
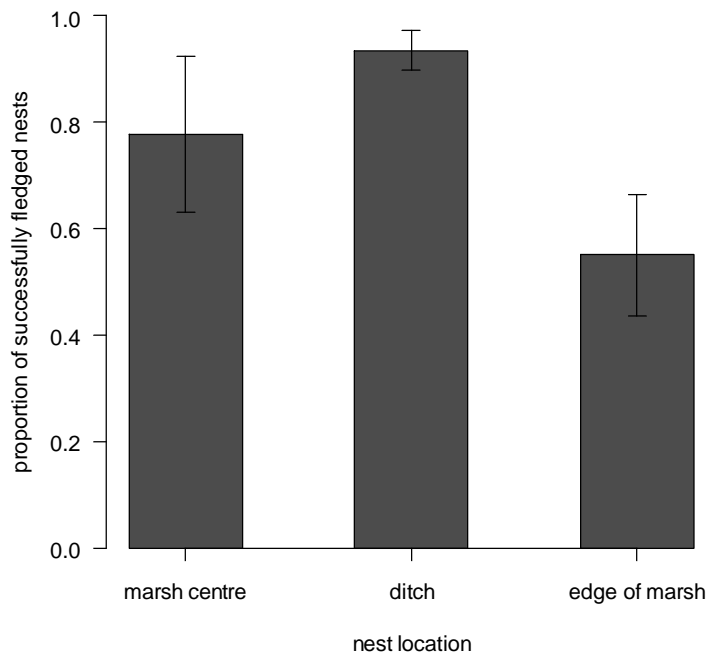


Figure 6



## FIGURE CAPTIONS

Figure 1. Number of red-winged blackbird males recruited during the playback presentation experiment. Bar plots represent the values of the means ( $\pm 1s.e.$ ) in relation to playback type presented and habitat where the nest was built.

Figure 2. Time until peak recruitment response in relation to habitat and nest parasitism status (mean  $\pm 1s.e.$ ).

Figure 3. Nest success in both habitats, at non-parasitised and parasitised nests (mean  $\pm 1s.e.$ ).

Figure 4. Time until peak recruitment response in relation to nest fate, in ditch and marsh habitats (mean  $\pm 1s.e.$ ). The bar representing successful nests in marshes has no s.e. bars because within these nests there was no variation in the speed of male response, i.e. at all these nests males took 15 seconds to recruit the maximum number of conspecifics.

Figure 5. Hatching success in relation to nest location (mean  $\pm 1s.e.$ ).

Figure 6. Nest success in relation to nest location (mean  $\pm 1s.e.$ ).