Antipredation role of clumped nesting by marsh-nesting red-winged blackbirds

J. Picman[1], M. Leonard[1] *, and A. Horn[2]

[1] Department of Biology, University of Ottawa, Ottawa, Ont. K1N 6N5, Canada
[2] Department of Zoology, University of Toronto, Toronto, Ont., Canada

Summary. Red-winged blackbirds, *Agelaius phoeniceus*, breed in marshes in high densities and their nests are frequently clumped. Because predation is consistently the most important cause of redwing nesting mortality, high densities of breeding individuals could be an anti-predation adaptation. In our study site predation by marsh wrens, *Cistothorus palustris*, was the main cause of redwing nesting losses. In situations when marsh wrens were near, predation rates on redwing nests decreased with increasing female density. Group life could reduce predation because of improved nest defense, selfish herd effects, or predator dilution effects. We differentiated between these possibilities by introducing experimental colonies consisting of 3, 6, and 9 artificial nests near and away from active redwing nests. The experimental colonies near active nests suffered less predation, but predation rates were not correlated with colony size or a nest's location within the colony. Therefore, the advantage of group life in this population is probably mutual nest protection.

Introduction

Marsh-nesting birds generally suffer the highest nesting losses of all temperate zone passerines. These losses are due to predation (Ricklefs 1969). In spite of this, passerines such as the red-winged blackbird, *Agelaius phoeniceus*, and yellow-headed blackbird, *Xanthocephalus xanthocephalus*, occur in marshes in high densities (e.g. Orians 1961, 1980). One explanation for the high densities is that predation patterns are predictable in marshes (i.e. a small number of predators are involved and

their activities are temporally and spatially predictable). The predictable predation patterns may in turn favour specific adaptations allowing prey to reduce more effectively the impact of predators. This is supported by the fact that in red-winged blackbirds some marsh-nesting populations have lower nesting losses than populations nesting in adjacent uplands (e.g. Case and Hewitt 1963; Robertson 1972; but see Howard 1977; Goddard and Board 1967).

The red-winged blackbird is a polygynous icterid breeding in high numbers in North American marshes. Marsh-nesting redwings have frequently been considered colonial (e.g. Mayr 1941; Wittenberger 1979). However, the great variability in territory sizes between marshes suggests that a system of grouped territories (Lack 1968) or neighborhoods (Crook 1964) better describes the spatial arrangement of breeding populations. Data on the distribution of nests within marshes suggest that, on a population level (i.e. within a marsh), female redwings clump (Mayr 1941; Caccamise 1976; Picman 1980a, b; Ritschel 1985). Although the redwing has been the subject of numerous investigations that concentrated mostly on its polygynous mating pattern, the adaptive value of its spacing strategies has rarely been addressed (but see Smith 1943; Robertson 1972).

Increased density of breeding individuals could result in lower predation because of three consequences of group life. First, by breeding close to each other, females could improve antipredator defense through cooperation with their neighbors in detection and mobbing of predators (Kruuk 1964; Pulliam 1973; Curio 1978). Benefits of increased density could result either from true active cooperation implying altruistic behavior, or from passive mutualism when the mutual benefits are shared more or less equally between members of a group.

* *Present address:* Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK

Second, colonial nesting may lower the impact of predators through predator satiation and dilution effects (Holling 1959; Pulliam and Caraco 1984). Third, by breeding in the centre of a colony females may increase their success through geometric (i.e. selfish herd) effects (Hamilton 1971). These hypotheses could be tested by introducing clumps of nests of three sizes near and away from active redwing nests. If active nest defense reduces predation, then artificial nests near redwing nests should be more successful than nests away from breeding redwings. A positive correlation between success of artificial nests and colony size would suggest that predator dilution and satiation affect success. Finally, if selfish herd effects are important, then peripherally located nests should suffer more predation than centrally located nests.

In this study, we examined the importance of nest predation as a selective force acting on redwing spacing tactics. The questions that we address are: (1) How important is predation relative to other causes of nesting mortality? (2) Which predators operate in our study area and what is their relative importance? (3) Is group living adaptive with respect to predation? And (4) if group living does lower predation, does this happen because of mutual nest defense (i.e. active cooperation or passive mutualism), predator dilution, or geometric effects?

Methods

This study was conducted in a brackish water marsh at George C. Reifel Migratory Bird Sanctuary in Delta, British Columbia. The higher grounds of this brackish water marsh are covered by relatively uniform cattail, *Typha latipholia*, vegetation where almost all redwing nests are built. A detailed description of this area can be found in Picman (1980a). The common passerines breeding in this area are the red-winged blackbird and the marsh wren, *Cistothorus palustris*. These species exhibit complex behavioral interactions which have been described by Picman (1977, 1980a, b, 1983, 1984). Descriptive data on redwing reproductive success, mortality factors, and the effects of female density on nesting success were collected between April and July 1976–1982. A description of general methods can be found in Picman (1980a).

Identification of predators

Three lines of evidence were used to identify nest predators and establish their relative importance. First, ten cameras were set up at artificial nests between 8 May and 15 June, 1986. The artificial nests were constructed of dry grass and resembled redwing nests in size and material. Blue-breasted quail, *Coturnix coturnix*, eggs were used as bait. Manipulation of the egg laid on a trigger mechanism by a predator set off the camera, which took a picture of a predator (see Picman 1987). The artificial nests were checked every 24 h for predation and cameras were reset after predation events. The nests with cameras

were placed at least 10 m apart along a transect, and the camera transect was moved every 5 days to sample predation over a larger area.

The relative importance of marsh wren predation was also examined in May 1984. Forty-three redwing nests were distributed along two parallel transects (nests 10 m apart; transects 100 m apart). We placed one redwing and one blue-breasted quail egg (wrens can break redwing eggs but not quail eggs; Picman 1977) in each nest. The nests with eggs were introduced on May 10 and examined for predation 1, 3, 6, and 9 days after placement.

Finally, we examined the appearance of depredated quail eggs that we offered predators in 1986 during a study of the antipredation value of redwing group life (see below). During this study we used quail eggs treated with acetic acid (after this treatment marsh wren can break quail eggs). Marsh wren attacks on these eggs were indicated by the presence of small punctures.

The antipredation function of increased female density

Because all evidence presented below on predation implicated marsh wrens as the most important nest predators, we examined the effect of female density on nest predation rates in relation to wren predation. We divided all redwing nests into categories according to the number of conspecific nests present within 30 m of a focal nest and according to their proximity to the nearest marsh wren nest. A nest whose distance from the nearest marsh wren nest was equal to or less than the distance at which 50% of nests were depredated was classified as "near" wrens. A nest whose distance from the nearest marsh wren nest exceeded the distance at which 50% of redwing nests were depredated was classified as "far" from wrens. The distance at which 50% of nests were successful was found from the regression between redwing success and distance from the nearest wren nest (redwing success is positively correlated with distance from marsh wren nests; Picman 1980a). Spearman rank correlation coefficients were then computed between the number of conspecifics within 30 m and success of redwings with marsh wrens nearby and farther away for each year.

Test of hypotheses on antipredation benefits of group life

The experimental test of predictions from hypotheses proposing an antipredation function of increased female density was conducted between 5 and 22 May 1986. We constructed a total of 229 artificial nests of dry grass by pressing three layers of grass into plastic bowls the size of redwing nests. The three layers of grass were glued together by pouring strips of apparently odorless transparent glue (LePage Multi-Usage Bond Fast) between these layers. We placed three blue-breasted quail eggs in each nest. However, because marsh wrens cannot break these eggs (Picman 1977), we reduced the thickness of the egg shells by placing the eggs in a 20% solution of acetic acid for 20 min. The eggs treated in this way were then washed thoroughly under running water for approximately 10 min. Preliminary trials conducted with these eggs in 1985 showed that, following this treatment, marsh wrens could puncture the quail eggs, and a variety of avian and mammalian predators consumed the quail eggs (Picman, unpublished data).

Artificial nests were placed in groups ("colonies") of 3, 6, and 9 nests. Each experimental colony was placed around an active redwing nest (the redwing nests were chosen at ran-

dom with respect to colony size). A control colony of equal size was placed at least 20 m away. In selecting locations for control colonies, we tried to choose an area that had similar vegetation density to the experimental situation but lacked an active redwing nest. We also placed the control colonies as far away from marsh wren nests as the experimental nests were.

Nests were attached to the supporting cattail vegetation 50–70 cm high with a piece of twine. Groups of 3 nests ($N = 22$) were placed in the corners of a triangle, and groups of 6 nests ($N = 12$) were distributed uniformly in a circle. In the largest experimental groups ($N = 9$), three nests were placed in the corners of a triangle (central positions) and the remaining six nests were distributed uniformly in a circle surrounding the triangle (peripheral positions). Inter-nest distances within groups of different sizes were approximately 5 m, depending on the availability of suitable vegetation for nest support. Although this distance was less than the average inter-nest distance in this area (around 20 m; Picman 1980a), it is still well within the range of recorded distances (the minimum distance between two simultaneously active nests was 1 m; Picman, unpublished data).

The location of groups of different sizes was random. Thirty-two groups were introduced initially and 14 groups five days later. Situations in which the active redwing nest was depredated were excluded from our analyses.

Results

Nest predation as a selective agent

In seven years between 19 and 45% of all nests fledged at least one young (Table 1). Thirty-seven to 52% of all nests in different years were depredated and predation was consistently the most important nest mortality factor (Table 1). Furthermore, the importance of predation is likely to be underestimated because some of the cases of nesting failure in the category of undetermined causes of nesting failure probably failed due to predation. Therefore, throughout our study predation was the most important source of mortality in this marsh.

The relative importance of various predators

The potential nest predators that we observed during this study inlcude, in decreasing order of abundance, marsh wrens, crows, *Corvus brachyrhynchos*, marsh hawks, *Circus cyaneus*, and racoons, *Procyon lotor*. During the camera study conducted in 1986 a total of 47 photographs where nest visitors could be identified were obtained. These pho-

Table 2. The effect of distance from the nearest marsh wren nest on survival of experimental redwing nests containing redwing eggs

Distance from wren nest (m)	Number (%) eggs		Total
	Depredated	Intact	
1–10	20 (100)	0	20
11–20	12 (92)	1	13
21–30	2 (40)	3	5
31–40	1 (20)	4	5

$\chi^2 = 23.7$; d.f. $= 3$; $P < 0.0005$

tographs revealed only three animals, marsh wrens (36 cases), redwings (6 males and 4 females) and a crow (1 case). However, because redwings in this marsh do not peck eggs (Picman, unpublished data), the marsh wren predation is the most important egg mortality factor. The importance of marsh wrens this year is also evident from data on appearance of depredated quail eggs obtained during the study of the adaptive value of group living in redwings. In 71 of 76 (93%) cases of predation quail eggs had one to several small punctures, eggs were not removed from the nests and the egg contents were not consumed by predators. In 3 cases eggs were gone from the nests and were not found in the nest area and in 2 cases punctured eggs were found below the nests. Nests were never damaged, although the linings were frequently disarranged. These signs of predation are consistent with nest attacks by marsh wrens (e.g. Picman 1977).

Of a total of 86 redwing and quail eggs placed in 43 redwing nests in 1984, 36 (42%) were destroyed over a nine-day study period. The four consecutive nest checks suggested that predators in this marsh are very efficient as most (64%) of the depredated eggs were destroyed in the first 24 hours. However, predators were destroying almost exclusively redwing eggs (35 out of 36 cases). The damage to the eggs ranged from small punctures in the shells to a complete removal of an egg. Nests were left intact, although in a few cases linings were disarranged. Finally, the predation rates on experimental eggs were higher in situations in which marsh wrens were close (Table 2).

Table 1. Nesting success and causes of nesting mortality of redwings in Delta, BC, in 1976–1982

Nesting history	1976	1977	1978	1979	1980	1981	1982	Combined 1976–1982
% nests successful	18.9	28.7	38.0	45.1	35.7	45.0	38.2	35.1
% nests depredated	40.8	50.5	42.9	36.9	51.7	43.7	45.8	44.2
% destroyed by high tides	18.5	0.0	3.1	1.0	2.1	4.0	2.1	4.8
% failed for unknown reason	21.8	20.8	16.0	17.0	10.5	7.3	13.9	15.9
Total no. nests	211	188	163	206	143	151	144	1206

Table 3. Spearman rank correlations r_s between redwing nesting success and the number of conspecific neighbors breeding simultaneously within 30 m of a focal nest for situations with marsh wrens nearby and farther away (see text for definition of the two redwing – marsh wren distance categories)

Year	Marsh wrens close			Marsh wrens far		
	r_s	N	P	r_s	N	P
1976	0.38	107	<0.0002	0.24	14	>0.4
1977	0.42	120	<0.0005	0.33	29	>0.05
1978	0.27	94	<0.01	0.09	38	>0.5
1979	0.35	78	<0.005	0.42	90	<0.0005
1980	0.33	83	<0.005	0.14	42	>0.3
1981	0.40	81	<0.001	0.18	23	>0.4
1982	0.24	91	<0.05	0.36	27	>0.05

Table 4. Predation on experimental nests from artificial colonies with and without redwing nests over a four-day study period. The sample size was 102 and 117 nests for colonies with and without the active redwing nest, respectively

Day	Cumulative number of depredated nests (% of total) for artificial colonies		χ^2	d.f.	P
	with redwings	without redwings			
1	11 (10.8)	31 (26.5)	9.51	1	<0.005
2	14 (13.7)	45 (38.5)	16.26	1	<0.001
3	18 (17.7)	52 (44.4)	16.44	1	<0.001
4	20 (19.6)	56 (47.9)	17.05	1	<0.001

The above evidence, thus, suggests that marsh wrens were the most important predators of redwing nests in our study area.

The antipredation function of increased female density

Nesting success of redwings with marsh wrens nearby was statistically significantly positively cor-

related with the number of conspecific nests within 30 m of a focal nest in every year (Table 3). However, for redwing nests with marsh wrens farther away the correlations between nesting success and the female density were lower and statistically not significant in all but one year (Table 3). This suggests that, with respect to marsh wren predation, female redwings benefit from the presence of other conspecifics.

Test of hypotheses on antipredation benefits of group life

Seventy-six (34.7%) of 229 experimental nests were depredated within 4 days. However, for both types of colonies (with and without the redwing nest) over 50% of all depredated nests were attacked in the first 24 h of the experiment. Predation rates during the following three days were generally low (Table 4).

On all 4 days, predation rates on control nests were more than twice as high as on experimental nests (Table 4). Redwings thus provided protection to the experimental nests with quail eggs.

The number of nests in colonies did not significantly affect the survival of nests over the 4-day study period, regardless of the presence or absence of the active redwing nests (Table 5).

Centrally and peripherally located nests in large experimental colonies suffered similar predation losses (Table 6). Therefore, position within a colony did not influence success of the experimental nests.

Discussion

Data on redwing nesting collected over 7 years suggest that in our marsh predation is consistently the most important mortality factor reducing

Table 5. Effect of colony size on success of artificial nests on day 4 in situations with and without the active redwing nest. Proportion of depredated nests in colonies of different size on days 1–4 were compared by Chi-square; probabilities shown are for 2-tailed tests with 2 degrees of freedom

Redwing nest	Colony size	Percent depredated nests (total no. nests) on day			
		1	2	3	4
Present	3	6.7 (30)	13.3 (30)	20 (30)	26.7 (30)
	6	5.6 (34)	5.6 (34)	8.3 (33)	8.3 (33)
	9	19.4 (29)	22.2 (28)	25 (27)	25 (27)
	χ^2; P	4.36; >0.1	4.23; >0.1	3.6; >0.1	4.52; >0.1
Absent	3	38.9 (36)	47.2 (36)	47.2 (36)	52.8 (36)
	6	19.4 (36)	25 (36)	33.3 (36)	36.1 (36)
	9	32.3 (45)	42.2 (45)	51.1 (45)	53.3 (45)
	χ^2; P	4.18; >0.1	4.19; >0.1	2.72; >0.25	2.88; >0.1

Table 6. The effect of location within a colony on predation losses from artificial nests on day 4. Only large colonies (9 nests) without redwing nests were included. The sample size for the centrally and peripherally located nests is 15 and 30, respectively

Day	Percent (no.) depredated nests in		χ^2	d.f.	P (1-tail)
	Colony center	Colony edge			
1	26.7 (4)	16.7 (5)	0.63	1	>0.15
2	46.7 (7)	40.0 (12)	0.18	1	>0.25
3	66.7 (10)	43.3 (13)	2.18	1	>0.05
4	66.7 (10)	46.7 (14)	1.61	1	>0.1

redwing reproductive success. Because other studies on marsh-nesting redwings conducted in different areas reported high nesting losses due to predation (e.g. Orians 1961, 1980; Holm 1973; Robertson 1972; Caccamise 1976; Weatherhead and Robertson 1977; Runyan 1979; Searcy 1979; Lenington 1980), predation should be an important selective force influencing redwing reproductive strategies.

Our studies of predators operating in the study marsh strongly suggest that the marsh wren was by far the most important nest predator in 1984 and 1986. The evidence from 1976–1982, which indicated that redwing nesting success increased with increasing distance from marsh wrens (Picman 1980a, b; unpublished data), and the finding that the higher local female density increased female success when marsh wrens were close, demonstrate that in this marsh, marsh wrens are consistently important nest predators. The simple and relatively predictable pattern of nest predation should, therefore, favor specific anti-predation adaptations such as an increased female density which may lower the impact of marsh wrens through one or more benefits of group life.

The correlative study of the effect of increasing female density on nesting success supported the idea that grouping by female redwings lowers the impact of marsh wrens. However, another explanation is that this relationship could result from a positive correlation between the quality of the breeding area and female density. For example, females might breed preferentially in areas without marsh wrens or in areas with more suitable vegetation. This latter explanation is not, however, supported by results of the experimental study during which artificial colonies were introduced around and away from the active redwing nests. This test of various consequences of group life for female fitness showed that the artificial nests with red-

wings nearby suffered lower predation than those away from redwings. Therefore, active nest defense by redwings (redwings of both sexes are known to aggressively exclude marsh wrens from the vicinity of their nests; e.g. Picman 1983) provided protection to artificial nests placed nearby. This suggests that a female defending her own nest could also have an effect on her neighbour's nest. Hence, in our population there should be strong selection on females to breed close to other conspecifics which should result in mutual protection of nests against predators. The positive correlations between density and nesting success of female redwings breeding near marsh wrens could, thus, be best explained by mutual nest defense. In contrast, we failed to obtain any evidence for geometric effects or predator dilution and satiation. These findings are consistent with the fact that (1) redwings can aggressively exclude wrens from the vicinity of their nests (Nero 1956; Orians and Willson 1964; Burt 1970; Verner 1975; Picman 1983; Ritschel 1985), and (2) marsh wrens usually do not consume contents of eggs they break (Picman 1977; but see Bump 1983; Ritschel 1985). Hence, when given the opportunity, marsh wrens should be able to destroy a large number of eggs in a small amount of time.

Our findings are similar to those of Ritschel (1985), who studied a similar marsh-nesting population of redwings in California. In Ritschel's study, redwings could also reduce the impact of marsh wrens by breeding close to other conspecifics. In contrast to our study, however, redwings in Ritschel's (1985) population benefited not only from improved nest defense but also from predator satiation and geometric effects. These differences could be explained by the fact that in Ritschel's study marsh wrens were real predators that consumed eggs. In our marsh, destruction of eggs by marsh wrens was not usually followed by consumption of egg contents, which suggests that this behavior may function as a mechanism of interference competition (Picman 1977, 1980a).

The apparently strong selection for increased female density raises the question: why don't female redwings breed closer to one another? Dispersion camouflages nesting activities, and so may reduce predation by mammals. In 1986 we found two active redwing nests where the resident females were killed and eaten at the nest, probably by raccoons. Such predation, though infrequent, destroys a female's lifetime reproductive output and may select for dispersion. Redwings in this marsh are exposed to two different predation pressures; marsh wrens favoring high female density and ter-

restrial predators presumably favoring spacing out. Female redwings in this marsh nest in relatively low densities (Picman 1980a, b), although they are clumped on a population level. This suggests a compromise in nesting patterns based on the different predation pressures. Different degrees of coloniality and polygyny of redwings in different marshes might, thus, reflect various predation pressures in different areas. To test these ideas, we need data on the type of predators operating in different marshes and the anti-predation role of redwing spacing strategies.

Our results have implications for the theory on the evolution of polygyny in the red-winged blackbird. Four hypotheses have been proposed by previous workers: (1) a high degree of heterogeneity in food distribution within marshes may favour resource defence polygyny (Verner and Willson 1966; Orians 1969); (2) higher predation rates in upland habitats may favour polygyny in better quality marsh territories (Wittenberger 1976); (3) female redwings may increase their fitness by mating with "sexy" males and thus producing sons attractive to females (Weatherhead and Robertson 1979); and (4) some form of cooperation between females may favour the cooperative type of (or harem) polygyny (Altmann et al. 1977). Our results suggest that female redwings can actively defend their nests against predators (marsh wrens). In addition, by reducing inter-nest distances female redwings can make the nest defence more effective, thereby further increasing their chances of success. Clumping by females should result in intense competition among males for monopolization of the female clumps. Our present results and the work conducted by Ritschel (1985) in California thus support the hypothesis that, at least in some redwing populations, high predation caused by marsh wrens may have favored high degrees of polygyny. Conversely, this hypothesis would predict that redwings from marshes where marsh wrens are relatively unimportant should not exhibit a clumped nesting dispersion. In such a situation redwings should exhibit lower degrees of polygyny. These predictions remain to be tested.

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