Behav. Ecol. Sociobiol. 5, 359–371 (1979)

Behavioral Ecology and Sociobiology

Spatial and Temporal Multi-Species Nesting Aggregations in Birds as Anti-Parasite and Anti-Predator Defenses

Karen L. Clark and Raleigh J. Robertson

Department of Biology, Queen's University, Kingston, Ontario Canada K7L 3N6

Received July 31, 1978

Summary. 1. The purpose of this study was to determine whether the yellow warbler (*Dendroica petechia*) derives any benefits from nesting in close proximity to its own and other species in reducing predator pressure or the incidence of brood parasitism by the brown-headed cowbird (*Molothrus ater*).

2. Yellow warblers nesting synchronously with their own and with neighbouring species resulted in a proportionate reduction in the number of nests preyed upon, suggesting a 'swamping effect' of the local predators. A significantly lower incidence of predation occurred at yellow warbler nests which were inside a gray catbird (*Dumetella carolinensis*) response range. This was thought to be the result of yellow warblers taking advantage of the catbird's nest-guarding behaviour and aggressive responses to predators.

3. Yellow warblers nesting synchronously with other yellow warblers were subject to a proportionately lower incidence of brood parasitism than asynchronous nests, suggesting a 'swamping effect' on the cowbird. A significantly lower incidence of brood parasitism occurred at yellow warbler nests which were in a red-winged blackbird (*Agelaius phoeniceus*) response range. The yellow warbler was thought to be taking advantage of the aggressive response of red-winged blackbirds to cowbirds.

4. Overall, yellow warblers which nested within the response range of red-winged blackbirds or gray catbirds had significantly higher nest success than other yellow warblers. This suggests that selection for defence against predators and cowbirds may lead to multi-species aggregations.

Introduction

The dispersion pattern of nesting birds is subject mainly to selection forces of (1) food availability and exploitation (Crook, 1965; Horn, 1968; Krebs, 1974), (2) nest site availability (Lack, 1968), and (3) predator pressure (Kruuk, 1964; Patterson, 1965; Lack, 1968; Robertson, 1973). All of these selective

0340-5443/79/0005/0359/$02.60

forces have been discussed with respect to the colonial nesting of individual species (Alexander, 1974), but little is known of how these forces have resulted in multi-species aggregations of nesting birds.

Although patterns of food availability and exploitation and nest site availability can explain many multi-species aggregations of nesting birds, there are many instances where neither of these appear to apply. In passerines, there is often suitable nesting habitat available (with sufficient nest sites and food resources) where no birds can be found, and then in a similar adjacent area, there is a large aggregation of nesting birds (Lack, 1968; Ward and Zahavi, 1973). Predation pressure might be an important selection pressure influencing the nesting pattern of these birds.

Although predation pressure may increase with nest density due to functional and numerical responses by predators (Holling, 1959), this may be outweighed by the advantages of group defence to the extent that predation is lower in aggregations than at solitary nests. There are basically two means of group defence afforded by aggregations of nesting birds.

Aggregations can allow the simultaneous occurrence of a large number of birds which can result in either a 'swamping effect' or the 'selfish herd effect' on predators (Hamilton, 1971; Robertson, 1973), and/or large behavioural group responses to predators (Kruuk, 1964; Hoogland and Sherman, 1976). Also some species are more effective than others in driving away predators due to physical attributes such as large body size, flying agility, and the ability to inflict injury on the predator. Weaker species less effective in deterring predators have been shown to capitalize on the protection afforded by the Arctic tern (Evans, 1970) and the lapwing (Kvaerne, 1973) by nesting close by.

Brood parasitism by the brown-headed cowbird (*Molothrus ater*) can be considered a kind of predation, since cowbirds remove host eggs and reduce nest success (Friedmann, 1963). The advantages of nesting in aggregations to reduce predation could also apply to reduce the incidence of parasitism. Aggressive responses to cowbirds can reduce the incidence of parasitism (Robertson and Norman, 1977), and although cowbirds do adjust their territories to host availability, female cowbirds could be 'swamped' if all the potential host species in a territory are available simultaneously.

The objective of this study was to determine whether the yellow warbler (*Dendroica petechia*), a species which commonly nests in loose multi-species aggregations (Schrantz, 1943), derives any benefits from nesting in close proximity to members of its own and other species in reducing the incidence of predation or brood parasitism.

Materials and Methods

The study was conducted in two large study areas of 10 ha and 15 ha and five small study areas each between 1–2 ha near Queen's University Biological Station, Chaffey's Lock, Ontario. All of the areas were wet lowlands along streams. The predominate vegetation was *Spirea latifolia*, *Myrica gale*, *Alnus rugosa*, sedges, and grasses. Most of the areas included a marsh of *Typha latifolia*.

Nests records were kept for all bird species that nested within the study areas. The study areas were completely searched for new nests every 2 or 3 days, from early May to mid-July in 1975–1977. Nests that had been damaged, and/or eggs or young that were missing before their expected fledging time, were assumed to have been preyed upon. Those nests in which the contents remained intact, but were no longer tended by the parents, were considered deserted.

At the end of the nesting season the locations of all nests were mapped by using a tape measure and compass. Nesting density was determined by measuring the distance to neighbouring nests from a yellow warbler nest.

Using playback recordings, it was found that red-winged blackbirds would participate in group responses which were initiated up to 57 m from their own nests. This distance also often coincided with the responding bird's territorial boundary. If yellow warblers were to derive any benefit from red-winged blackbirds' or catbirds' responses to predators or cowbirds it would be necessary to nest within this range. For this reason, nests that fell within a radius of 57 m of a yellow warbler nest were counted to give a measure of the number of nests per hectare at a given yellow warbler nest. Only those nests were counted that were active at the same time as was the yellow warbler nest. Nesting success, calculated as the number of young fledged per egg laid, was determined for each yellow warbler nest.

Results

Although a large area of apparently suitable habitat for yellow warbler nesting was searched, nests were found in loose aggregations. Gray catbirds, red-winged blackbirds, and 13 other species in fewer numbers (Table 1) were found nesting near yellow warblers. A complete knowledge of the territory and nest site requirements of all species would be necessary to determine whether yellow warblers were choosing to nest in close proximity to other species and that this association was not the result of some characteristic of the habitat. The median nearest

Table 1. Total size of the study areas and the number of nests found of each species[a]

Species	1975 (18 ha)	1976 (15 ha)	1977 (30 ha)
American robin (*Turdus migratorius*)	7	7	11
Black-capped chickadee (*Parus atricapillus*)[b]	1	1	1
Chipping sparrow (*Spizella passerina*)	1	1	2
Eastern kingbird (*Tyrannus tyrannus*)	0	0	1
Field sparrow (*Spizella pusilla*)	2	1	1
Gray catbird (*Dumetella carolinensis*)	8	4	9
Least flycatcher (*Empidonax minimus*)[b]	1	1	1
Northern oriole (*Icterus galbula*)	3	2	4
Red-eyed vireo (*Vireo olivaceus*)[b]	4	3	2
Red-winged blackbird (*Agelaius phoeniceus*)	16	10	19
Rufous-sided towhee (*Pipilo erythrophthalmus*)[b]	1	1	1
Rose-breasted grosbeak (*Pheucticus ludovicianus*)	1	1	2
Song sparrow (*Melospiza melodia*)	2	1	2
Virginia rail (*Rallus limicola*)	1	0	0
Wood thrush (*Hylocichla mustelina*)[b]	1	2	2
Yellow-throat (*Geothlypis trichas*)[b]	2	0	3
Yellow warbler (*Dendroica petechia*)	34	26	49

[a] Includes only nests found within 57 m of a yellow warbler nest

[b] Nests not found in all cases. Singing male also used as evidence for nest

Table 2. General breeding data for yellow warblers in all study areas

	1975	1976	1977	1975–77
Total number of active nests	34	26	49	109
Number of successful nests[a] (%)	18 (53)	19 (73)	18 (37)	55 (50)
Number of eggs	129	109	143	381
Mean clutch size	3.8	4.2	3.8	3.9
Number of eggs hatched (%)	74 (57)	64 (59)	80 (56)	218 (57)
Number of young fledged (% of eggs)	62 (49)	64 (59)	67 (47)	193 (51)
Number fledged per active nest	1.8	2.5	1.4	1.8
Number fledged per successful nest	3.4	3.4	3.7	3.5
Number of nests deserted (% of nests)	4 (12)	3 (12)	5 (10)	12 (11)
Number of nests preyed upon (% of nests)	12 (35)	4 (15)	24 (49)	40 (37)
Number of successful nests preyed upon	1	0	0	1
Number of nests parasitized (% of nests)	12 (35)	13 (50)	20 (41)	45 (41)
Mean nest success[b]	0.43	0.50	0.29	0.38
Mean nest success of parasitized nests	0.26	0.40	0.26	0.30
Mean nest success of nests not parasitized	0.52	0.60	0.31	0.41

[a] Fledged at least one nestling
[b] Nestlings fledged per egg laid

neighbour distance for yellow warblers to any other species was 29 m and the median nest density was five nests of any species per nectare.

Nest success of yellow warblers ranged from 0.29 to 0.50 in the three seasons of the study (Table 2). The incidence of predation was 37% of all nests, which is within the range found in nesting studies of other passerines (Nice, 1937; Weatherhead and Robertson, 1977). The majority of predation in the wet lowland habitats was likely by black rat snakes (*Elaphe obsoleta obsoleta*), common crows (*corvus brachyrhynchos*), blue jays (*Cyanocitta cristata*), and chipmunks (*Tamias striatus*). Predation in the marsh habitats was likely by racoons (*Procyon lotor*) and water snakes (*Natrix sipedon sipedon*).

Nesting Synchrony and Predation

Nests which were earlier or later than the majority of birds nesting in the area were subject to higher predation than those nests which were synchronous

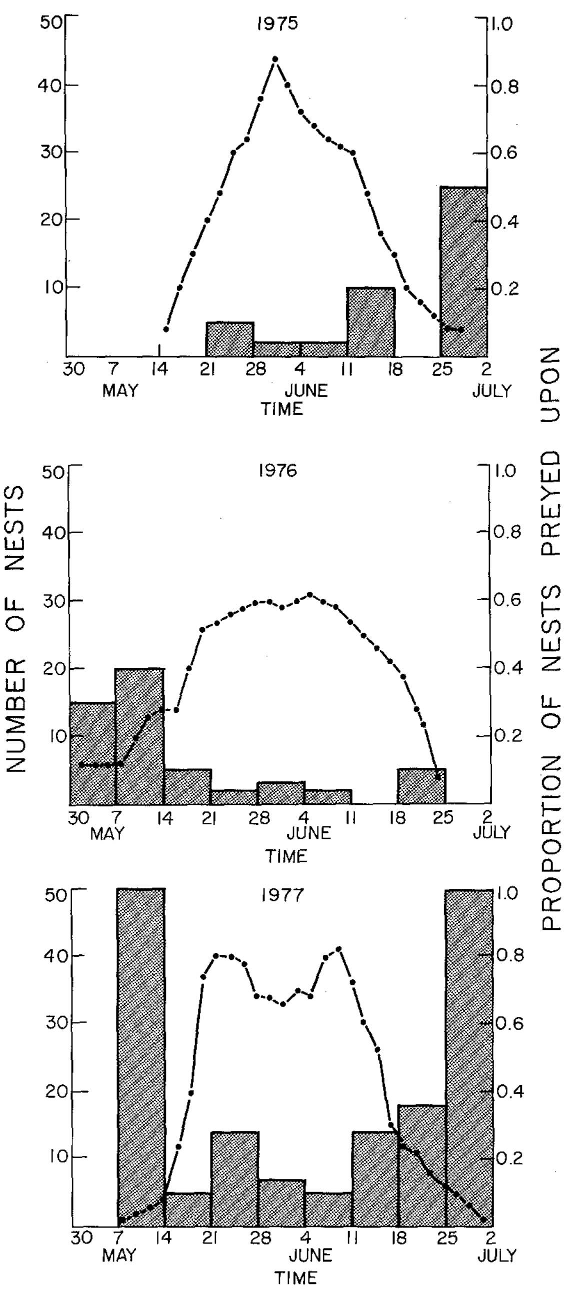

Fig. 1. Number of nests of all species available to predators and the proportion of nests preyed upon over time for the three breeding seasons. The area searched in each season was 18 ha in 1975, 15 ha in 1976, and 30 ha in 1977

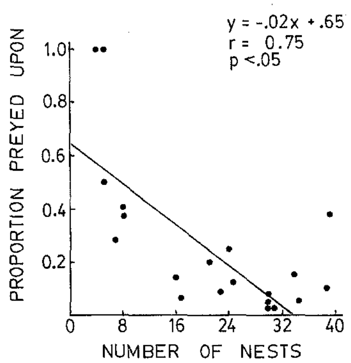

Fig. 2. Proportion of yellow warbler nests preyed upon versus the number of nests of all species within the study areas available to be preyed upon (1975–1977 seasons combined)

with the majority of other nests (Fig. 1). Overall, the proportion of nests preyed upon was negatively correlated with the number of active nests (Fig. 2).

All species nests, with the exception of the northern oriole, black-capped chickadee, eastern kingbird, and ruffed grouse, were found in similar vegetation types within the height range of 0–1.5 m, and were of similar open-cup construction. Consequently, when nest synchrony was related to predation, all except the species nests mentioned above were included because they were expected to be of equal effectiveness in swamping predators.

High nest densities were expected to complement the swamping effect of synchronous nesting in reducing predation. Alternatively, if nest densities were not high enough to result in the predators in the area being swamped, there was expected to be a functional and/or numerical response by the predators in the area, resulting in higher predation pressure in higher nest densities. There was, however, no association between nest density and the incidence of predation. In nest densities of 1–4 nests per hectare, 21 out of 58 were preyed upon, whereas nests in densities of five nests or more per hectare, 14 out of 38 nests were preyed upon ($\chi^2 = 0.026$, $P > 0.50$).

There was no correlation between the number of days from the peak in nesting and the mean nest density of all active nests each day (1975 $r = 0.23$, $n = 24$, $P < 0.05$; 1976 $r = 0.22$, $n = 23$, $P < 0.05$; 1977 $r = 0.10$, $n = 19$, $P < 0.05$), indicating that the 'swamping effect' for yellow warblers is a temporal phenomena independent of the fine detailed pattern of nests.

Nesting Synchrony and Parasitism

The yellow warbler was heavily parasitized by the cowbird, resulting in significantly lower nest success at parasitized nests (Mann-Whitney U test, statistics for large samples $P < 0.05$) (Table 2).

In determining the importance of synchrony in reducing brood parasitism, not all species nests were of equal value in their effect in swamping the cowbird. The common species in the areas other than yellow warblers were red-winged blackbirds, catbirds, and northern orioles, none of which are subject to a high incidence of parasitism (Berger, 1951; Young, 1963). The selective advantage

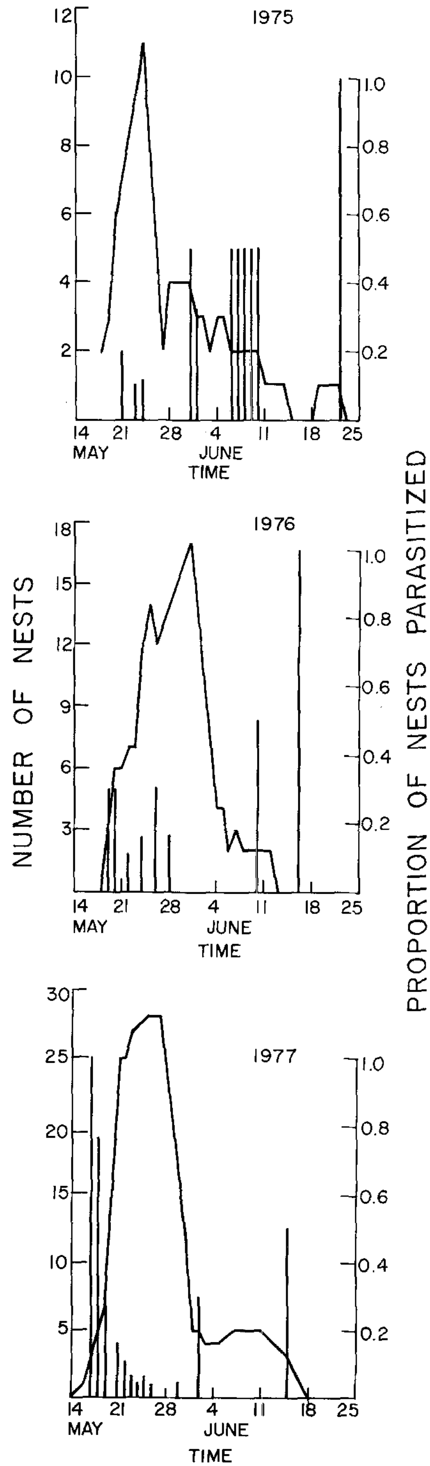

Fig. 3. Number of yellow warbler nests available for parasitism (nests during and 1 day after egg laying) and the proportion of those nests parasitized over time for the three breeding seasons. The area searched in each season was the same as in Fig. 1

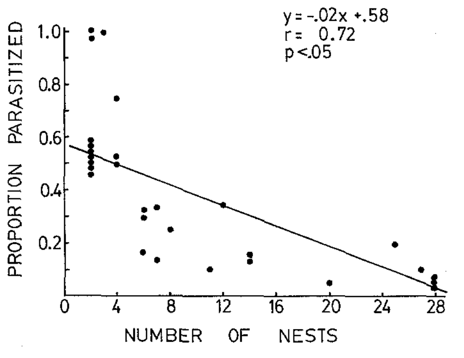

Fig. 4. Proportion of yellow warbler nests parasitized versus the number of yellow warbler nests available to cowbirds for parasitism (nests during and 1 day after egg laying) (1975–1977 seasons combined)

of nesting synchronously with these species would not be that great since the yellow warblers are the cowbird's preferred hosts. It would be more important for yellow warblers to nest synchronously with other yellow warblers. Consequently, when determining the importance of nest synchrony in reducing brood parasitism, only yellow warbler nests were used.

When the number of yellow warbler nests available to a brood parasite (nests during and 1 day after egg laying) was plotted against time, and the proportion of the available nests that were parasitized on each day was plotted against time, it appeared that the cowbirds were being 'swamped' by the synchronous laying of the yellow warblers (Fig. 3). The importance of swamping of cowbirds to reduce parasitism was also shown by the significant negative correlation between the proportion of nests parasitized and the number of available nests (Fig. 4). When there were few available nests for parasitism the proportion of nests that were parasitized was high. When there was a large number of available yellow warbler nests the proportion of nests that were parasitized was low.

Since nest synchrony was effective in 'swamping' cowbirds it was expected that high nest densities might also have a similar effect, especially because nest density of yellow warbler nests susceptible to parasitism was significantly negatively correlated with the number of days from the peak in nesting (1975 $r=0.57$, $n=18$, $P<0.05$; 1976 $r=0.49$, $n=16$, $P<0.05$; 1977 $r=0.49$, $n=18$, $P<0.01$).

Parasitism, however, was not significantly different at high nest densities (5 or more nests/ha) where 15 out of 38 yellow warbler nests were parasitized, than at low nest densities (1–4 nests/ha) where 26 out of 58 yellow warbler nests were parasitized ($\chi^2=0.27$, $P<0.50$).

Aggressive Neighbours and Predation

The two species which were expected to be most effective in driving off predators and cowbirds were the red-winged blackbird and the catbird. Both species are known to respond aggressively to cowbirds (Sutton, 1928; Selander and Larue,

Table 3. Predation on yellow warbler nests inside and outside red-winged blackbird and catbird territories

	Number (proportion) of nests	
	preyed upon	not preyed upon
Redwing territories		
Nests inside	10 (0.36)	18 (0.64)
Nests outside	17 (0.19)	62 (0.81)
	$\chi^2=2.21$, $P>0.10$	
Catbird territories		
Nests inside	7 (0.22)	25 (0.78)
Nests outside	33 (0.43)	43 (0.47)
	$\chi^2=4.52$, $P<0.05$	

Table 4. Parasitism by cowbirds of yellow warbler nests inside and outside red-winged blackbird and catbird territories

	Number (proportion) of nests	
	parasitized	not parasitized
Redwing territories		
Nests inside	7 (0.25)	21 (0.75)
Nests outside	39 (0.49)	40 (0.51)
	$\chi^2=4.31$, $P<0.05$	
Catbird territories		
Nests inside	14 (0.40)	21 (0.60)
Nests outside	24 (0.44)	30 (0.56)
	$\chi^2=0.09$, $P>0.90$	

1961; Robertson and Norman, 1976; Scott, 1977) and because of the loudness of their call and larger body size than the yellow warbler and most of the other species which nested in the area, they were expected to pose a greater threat to predators.

Yellow warblers nesting within the response range (57 m) of catbirds were subject to lower predation than nests outside (Table 3). Nests which were inside or outside the response range of red-winged blackbirds showed no difference in the incidence of predation (Table 3).

Although parasitism was not significantly lower at yellow warbler nests within the response range of catbirds, it was lower within the response range of red-winged blackbirds (Table 4).

Overall, the median nest success of yellow warblers in either red-winged blackbird or catbird response ranges was 0.60 and was significantly higher than the median of 0.25 of nests outside their response range (Mann-Whitney U test, statistics for large samples$=2.34$, $P<0.05$). Only three yellow warblers nested within both a red-winged blackbird and a catbird territory and so it was not possible to determine whether the advantages were compounded by nesting within both these species territories.

To determine whether the higher nest success in red-winged blackbird and catbird territories could in part be attributed to better quality habitat associated with the territories of these species, nest success of nests not parasitized or preyed upon was compared for nests inside and outside catbird territories. The median nest success for nests in each of red-winged blackbird territories, catbird territories, and nests outside these species territories was 0.80 and was not significantly different (Mann-Whitney U test $P < 0.98$). The differences between nest success of nests within the response ranges of red-winged blackbirds or catbirds and nests outside their territories can be considered independent of differences of habitat quality.

Discussion

The yellow warblers were flexible in nest site requirements, nesting in a variety of shrubs and trees at varying heights. There were many areas where there were no nests found but that was similar nesting habitat, suggesting that nest sites were not limiting.

There was evidence that neither food nor nest site limitations were influencing the nest success of the yellow warbler. Starvation of nestlings never occurred and dead nestlings were found only in nests where they had been trampled by a cowbird. Nest desertion occurred only at parasitized nests, so it is unlikely that adults were forced to desert their nests because of insufficient food.

The most common causes of a reduction in nest success for the yellow warbler were predation and brood parasitism. Because of the large losses in nest success caused by these factors, selection should favour any means of reducing their occurrence.

Nest Synchrony

The reduced incidence of predation at synchronous yellow warbler nests indicates a swamping effect on the local predators. These results are similar to those found by Caccamise (1976) in a study of red-winged blackbirds, in which predation pressure was independent of nest density or spatial arrangement of nests, but colony size or prey abundance was the most important factor influencing predation pressure. He concluded selection to maintain a high prey abundance to reduce predation pressure should lead to nesting synchrony. For yellow warblers, selection should favour nesting synchrony with their own and other species with similar open-cup nests. To reduce predation pressure, it would also have been useful to assess predation pressure in solitary and aggregated nests, but our sample of nests did not include any truly solitary nests far removed from other nesting birds, so this comparison could not be made.

Synchrony was also effective in causing a swamping effect on the cowbird, reducing the incidence of parasitism at synchronous nests. The swamping effect could only occur when hosts are concentrated in aggregations. Female cowbirds adjust territory size to the number of available hosts, so high nest density alone would not be effective in swamping cowbirds. If nests are highly synchronized, the cowbird may not be able to parasitize them all, since one egg can be laid per day and the cowbird clutch size is only 4–5 eggs (Friedmann, 1963; Payne, 1965). More dispersed host nests would be more likely to be in a female cowbird's territory which has fewer hosts than the cowbird could potentially parasitize. This will occur because of the female cowbird's ability to defend a limited area. Yellow warblers, therefore, should nest either in high nest densities and in synchrony with other suitable cowbird hosts or at low nest densities to reduce parasitism pressure.

Aggressive Neighbours

The red-winged blackbird and the catbird gave some protection to the yellow warbler against cowbirds and predators, respectively.

Catbirds are larger than the yellow warbler and issue a relatively loud alarm call similar to the meow of a cat. They also show nest-guarding behaviour resulting in an almost continuous presence of the male or female near the nest. Slack (1976) has suggested that nest guarding may be an important factor in prevention of predation and can account for the high nesting success of the species. A yellow warbler nesting in a catbird response range could take advantage of the relatively loud aggressive response to deter predators, and the guarding behaviour of the catbird to alert the yellow warbler of the approach of a predator. This nest-guarding behaviour of the catbird likely resulted in the lower incidence of predation at yellow warbler nests in the response range of catbirds.

Catbirds, although physically larger and potentially a greater threat to a cowbird than a yellow warbler, did not afford any protection to the yellow warblers nesting within their response range. Robertson and Norman (1977) showed that catbirds exhibit a much lower aggressive response to a cowbird than either a red-winged blackbird or a yellow warbler. Catbirds are rejector species (Rothstein, 1975), so parasitism by the cowbird does not usually result in significant losses of nest success as occur in the red-winged blackbird and yellow warbler because the cowbird egg can be easily ejected. Since the cowbird sometimes ejects a host egg before laying its own, selection would favour catbirds exhibiting some aggressive response to cowbirds.

Red-winged blackbirds exhibit aggressive response to predators and commonly actively mob predators and have the potential for inflicting greater injury on a predator than a yellow warbler, yet yellow warblers in red-winged blackbird territories suffered the same predation pressure as those outside. All of the red-winged blackbirds which the yellow warblers nested near, except one upland nest, were in marshes.

In 1974 in the marsh habitats, 49% of the red-winged blackbird nests were preyed upon (Weatherhead and Robertson, 1977) and yet in the surrounding area only 35% of all yellow warbler nests were preyed upon. Yellow warblers may be subject to increased predation pressure when nesting in marsh habitats but may benefit from the aggressive group responses of the red-winged blackbirds to maintain the predation pressure at the same level as outside red-winged blackbird territories. Alternatively, yellow warblers do not benefit from the aggressive responses of red-winged blackbirds. Regardless, there would be no benefit of nesting in a red-winged blackbird territory to reduce predation.

The red-winged blackbird was one of the species studied by Robertson and Norman (1976) which would physically attack the model of a female cowbird. It also was much higher in its aggression score to a cowbird than the yellow warbler (Robertson and Norman, 1977). The redwing is an acceptor species (Rothstein, 1975) but is subject to a very low incidence of parasitism. Of 381 red-winged blackbirds nests found in the marshes adjacent to our study areas in 1974–1975, only one was found with a cowbird egg in it (Weatherhead, personal communication). Roberson and Norman (1977) were able to rule out any differences in the difficulty of nest searching in the marsh habitat and attributed the low incidence of parasitism to aggressive responses of the red-winged blackbirds to cowbirds.

The only factor which could account for the reduced parasitism of yellow warblers in red-winged blackbird territories is the aggressive response of the red-winged blackbirds and their ability to impose a greater threat to a cowbird.

Overall, it is beneficial for yellow warblers to nest within the response ranges of red-winged blackbirds and catbirds to capitalize on their aggressive responses to cowbirds and predators. The increase in nest success as a result of yellow warblers being able to capitalize on aggressive responses of red-winged blackbirds to cowbirds and catbirds to predators is likely the main selective force which has led the yellow warbler to nest in close proximity to these species.

Acknowledgements. This study benefited greatly from the use of the facilities of Queen's University Biological Station, the assistance of Dave Cameron, Richard Norman, and Pat Weatherhead, and the financial support of Queen's University and the National Research Council of Canada. To each we express our thanks.

References

Alexander, R.D.: The evolution of social behaviour. Ann. Rev. Ecol. Syst. **5**, 325–384 (1974)

Berger, A.J.: The cowbird and certain host species in Michigan. Wilson Bull. **63**, 26–34 (1951)

Caccamise, D.F.: Nesting mortality in the red-winged blackbird. Auk **93**, 517–534 (1976)

Crook, J.H.: The adaptive significance of avian social organizations. Symp. Zool. Soc. Lond. **14**, 181–218 (1965)

Evans, R.M.: Oldsquaws nesting in association with Arctic terns at Churchill, Manitoba. Wilson Bull. **82**, 383–390 (1970)

Friedmann, H.: Host relations of the parasitic cowbirds. Washington, DC: Smithsonian Inst. 1963

Hamilton, W.D.: Geometry for the selfish herd. J. Theor. Biol. **31**, 295–311 (1971)

Holling, C.S.: The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can. Entomol. **91**, 293–320 (1959)

Hoogland, J.L., Sherman, P.W.: Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. Ecol. Monogr. **46**, 33–58 (1976)

Horn, H.S.: The adaptive significance of colonial nesting in the Brewer's blackbird (*Euphagus cyanocephalus*). Ecology **49**, 682–694 (1968)

Krebs, J.R.: Colonial nesting and social feeding as strategies for exploiting food resources in the great blue heron (*Ardea herodias*). Behaviour **51**, 99–131 (1974)

Kruuk, H.: Predators and anti-predator behaviour of the black-headed gull (*Larus ridibundus*). Behaviour [Suppl.] 11, 129p (1964)

Kvaerne, J.: Kan vipa vaere vaktful for andre fuglearter? Is the Lapwing a 'watchdog' for other wader species? Sterna **12**, 85–90 (1973)

Lack, O.: Ecological adaptations for breeding in birds. London: Methuen 1968

Nice, M.: Studies in the life history of the song sparrow. Trans. Linn. Soc. NY (1937)

Patterson, I.: Timing and spacing of broods in the black-headed gull (*Larus ridibundus*). Ibis **107**, 433–459 (1965)

Payne, R.B.: Clutch size and numbers of eggs laid by brown-headed cowbirds. Condor **67**, 44–60 (1965)

Robertson, R.J.: Optimal niche space of the red-winged blackbird: Spatial and temporal patterns of nesting activity and success. Ecology **54**, 1085–1093 (1973)

Robertson, R.J., Norman, R.F.: Behavioural defenses to brood parasitism by potential hosts of the brown-headed cowbird. Condor **78**, 166–173 (1976)

Robertson, R.J., Norman, R.F.: The function and evolution of aggressive host behaviour towards the brown-headed cowbird (*Molothrus ater*). Can. J. Zool. **55**, 508–518 (1977)

Rothstein, S.I.: Evolutionary rates and host defenses against avian brood parasitism. Am. Nat. **109**, 161–176 (1975)

Schrantz, F.G.: Nest life of the eastern yellow warbler. Auk **60**, 367–387 (1943)

Scott, D.M.: Cowbird parasitism on the gray catbird at London, Ontario. Auk **94**, 18–27 (1977)

Selander, R.K., Larue, C.J.: Interspecific preening invitation display of parasitic cowbirds. Auk **78**, 473–504 (1961)

Slack, R.D.: Nest guarding behaviour by male catbirds. Auk **93**, 292–300 (1976)

Sutton, G.M.: The birds of Pymating Swamp and Commeaut Lake, Crawford County, Pennsylvania. Ann. Carnegie Mus. **18**, 19–239 (1928)

Ward, P., Zahavi, A.: The importance of certain assemblages of birds as information centres for food-finding. Ibis **115**, 517–534 (1973)

Weatherhead, P.J., Robertson, R.J.: Harem size, territory quality and reproductive success in the redwinged blackbird (*Agelaius phoeniceus*). Can. J. Zool. **55**, 1261–1267 (1977)

Young, H.: Breeding success of the cowbird. Wilson Bull. **75**, 115–122 (1963)