A COMPARATIVE APPROACH TO THE STUDY OF AVIAN NEST DEFENCE: EXPERIENCE AND ADAPTIVE SIGNIFICANCE

BY

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A Thesis
Submitted to the Faculty of Graduate Studies
in Partial Fulfillment of the Requirements
for the Degree of

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THE UNIVERSITY OF MANITOBA

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Of

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ABSTRACT

This study focused on nest defence of two passerine species whose reproductive success is decreased by acts of brood parasitism and nest predation. My objectives were two-fold. First, I determined whether a threatening experience at the nest triggered a modification in the expression of nest defence, and, secondly, whether intensely defensive individuals benefited by achieving higher nest survival compared with less responsive individuals.

The species studied were the Yellow Warbler (*Dendroica petechia*) and Reed Warbler (*Acrocephalus scirpaceus*) parasitized by the Brown-headed Cowbird (*Molothus ater*) and Common Cuckoo (*Cuculus canorus*), respectively. There is considerable literature that reveals the ability of Yellow Warblers to discriminate its enemies, but there is less evidence that the same ability exists in the Reed Warbler. In Chapter, I fill this gap by testing whether Reed Warblers discriminated among a brood parasite, a nest predator and an non-threatening species. Results revealed that Reed Warbler not only discriminated among threats, but it also adjusted its defensive behaviour relative the risk each species poses at different nesting stages. The type of threat and the nesting stage thus influenced most Reed Warbler defensive responses whose modulation was not, however, influenced by the reproductive value of the nest content (e.g., number and age of offspring). The only exception was one type of alarm call that was influenced by the offspring age but not by the threat type.

In the second and third chapters, I tested whether defensive intensities of both species were shaped by individual or social learning. With mounted specimens, clutch manipulations and playbacks, I simulated events of parasitism, egg removal and conspecifics responding to the visit of a parasite at their nest. Defence by Yellow Warblers changed slightly after an event of parasitism, and significantly after egg removal, but remained unchanged after individuals had observed conspecifics uttering the alarm call specific to brood parasites. For Reed Warblers, results were the opposite, as individuals increased the intensity of their nest defence after the social experience but their responses did not change after a direct experience of parasitism or egg removal at their nest. The occurrence of individual versus social learning is explained in terms of the stability of the environmental pressure (i.e., parasitism and nest predation frequencies) that selects for the behaviour of interest (i.e. nest defence).

The focus of the final part of this dissertation was the adaptive significance of nest defence. I first quantified the frequency of parasitism and nest predation as a function of the time a nest survived to these events. Yellow Warblers were parasitized at similar rates each year, whereas the nest predation rate was higher in the second year. The Reed Warbler population was exposed to similar levels of parasitism and nest predation rates. The frequency fluctuations in the nest failure were consistent with the conditions suggested to favour the selection of one learning mechanism over another. Thus, relatively stable environmental pressures select for social learning, whereas sudden changes select for individual learning. Social learning is the least expensive way to acquire an already-optimal behaviour, as individuals do not incur the costs involved in trial-and-error learning. However, as environmental pressure is not constant, social learners would acquire a behaviour that may be suboptimal because it is based on outdated information. This hypothesis is consistent with the form of learning found in both species. Yellow Warblers, living under fluctuating nest threat pressure, did not adopt

information from conspecifics for refining their nest defence, whereas Reed Warblers, living under a more stable pressure, capitalized on this experience and intensified their defence.

The second aim of Chapter V was to test whether specific defensive expressions, their intensity, or their flexibility were associated with nest survival. In Yellow Warblers, there was no defensive response associated with parasitism events, which indicates that no behaviour prevented or facilitated parasitism. Several responses, however, were associated with a low risk of nest predation when expressed with high intensities. These responses were part of different defensive strategies. The small number of nests tested before parasitism prevented determination of whether individuals that were more plastic after a threatening event enjoyed higher nest survival. Reed Warblers that uttered a specific alarm call and changed perches frequently had higher nest survival to parasitism and to predation compared to those that were more silent and moved less. The number of other birds attracted to the nest site during the defence of the breeding pair was associated with a high predation rate, which suggests that their presence was exploited by predators to better locate their nest target.

In the last part of Chapter V, I determined the extent to which optimal defensive responses were adopted in the populations. By comparing the survival rates obtained across all individuals tested and those obtained with the lowest and highest response intensities, I obtained a common result in both species, thus the behaviours resulted as predictors of nest survival were adopted in the populations with high intensities, suggesting an adaptive advantage. The only exception was the aggressive response by Yellow Warblers that was instead expressed with low intensity in most individuals. In

both species, although intense defensive responses were adopted by a majority of individuals in the population, the highest intensities associated with the highest nest survival were not. In Reed Warblers, two survival predictors were inversely associated to nest survival. The number of other birds was associated negatively with nest survival whereas the alarm calls were positively associated with it. At the same time these two survival predictors were correlated positively to each other, thus individuals that uttered a high number of alarm calls received the highest number of visits of other birds at their nest. This indicated a possible constraint for Reed Warblers to adopt the highest intensity of this alarm call. I could not find an equivalent constraint for Yellow Warblers and further investigations are warranted to test the ability of their calls used to recruit nesting neighbours during defence and whether additional activity of other birds at the nest is exploited by parasites and predators to better locate their target.

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CHAPTER 1

GENERAL INTRODUCTION

Nest defence is a component of parental investment that affords protection against potential threats to eggs and young (Knapton 1984, Montgomerie and Weatherhead 1988, Redondo and Carranza 1989). Nest predators and avian brood parasites cause most of the reproductive failures in many species of birds. Depredation generally destroys the eggs or nestlings, whereas the offspring of brood parasites often outcompete host nestlings or eject host eggs and young from the nest (Ricklefs 1969, Rothstein 1975a, Martin 1995, Lorenzana and Sealy 1999, Davies 2000). The behaviours of adults defending themselves and their offspring are sometimes considered collectively as antipredator responses when, in fact, each imposes different fitness consequences on the individual (Andersson et al. 1980, Redondo and Carranza 1989). If the first fails, the individual can lose its life, whereas ineffective nest defence can lower current reproductive outcome or jeopardize future reproductive performance (Montgomerie and Weatherhead 1988, Griffin 2004). For this reason, responses triggered by predators on adults should be more hard-wired and selection should favour phenotypes that respond optimally to the threat because the first dangerous encounter may be the last (Lima and Dill 1990, Griffin 2004). Nest defence, which is triggered by a less urgent threat, on the other hand, would require that individuals be more flexible and adjust their reactions according to the level of danger (Montgomerie and Weatherhead 1988, Griffin 2004).

Flexibility of antipredator behaviours is widespread phylogenetically, with different animals responding to different threats, which implies their ability to discriminate among risks posed by each species (Seyfarth et al. 1980, McLean and Rhodes 1991, Chivers and Smith 1994, Caro 2005). For example, Bonnet Macaques (*Macaca radiata*) climb up into trees when under attack by a terrestrial predator, but the same response is not triggered by an aerial predator (Coss et al. 2007). Flexible defences are also those acquired through time, following direct or indirect experiences. For example, Fathead Minnows (*Pimephales promelas*) do not flee when confronted with a novel predator but they acquire this response when the novel threat is associated with conspecific alarm substances (Chivers and Smith 1994).

Adjustable versus rigid behaviours have been indicated to be both beneficial, and then selected under different contexts (Laland et al. 1993). In particular, discriminatory ability and specific responses that follow previous experiences may be favoured when predation pressure and type of predation risk change over time (Berejiakian et al. 2003, Lind and Cresswell 2005, Griffin 2004, Fendt 2006). Because of opportunistic foraging or environmental fluctuations, predator communities can change in composition over time, and thus, prey that are readily able to adjust their responses to new predators are favoured (Stephens and Krebs 1986, Shettleworth 1998). Moreover, rare predators impose too a relaxed pressure to select for specific responses, whereas common predators select for prey with more refined defences against them (Martin 1993, 1995). Recently, however, it has been pointed out that the adaptiveness of acquired antipredator responses is difficult to measure for two reasons (Lind and Cresswell 2005). First, when prey are exposed to different predators, they may adopt an optimal response toward one predator type and simultaneously, but maladaptively, draw the attention of another predator (Sih et al. 1998). This makes it problematic to assess whether a species has adopted a repertoire of antipredator defences that are optimal in all situations. Secondly, it becomes difficult to quantify predator-prey encounters when wild species are investigated and, therefore, to assess whether the pressure that each potential predator exerts is sufficient to select for specific antipredator responses (Picman and Schriml 1994, Sealy 1994).

Studies of nest defence have advantages over those of antipredator behaviour because the pressure of predation and brood parasitism, as well as fitness in the form of nest success, may be directly quantified by monitoring nest contents (Davies and Brooke 1989a, Redondo 1989, Lorenzana and Sealy 1999). Visits by predators to nests may be less urgent because the nest owner's life is not imminently threatened (Montgomerie and Weatherhead 1989, Redondo 1989). Moreover, birds might experience variable nest predation and parasitism pressure in space and time as well. In fact, opportunistic nest predators can switch their target depending on the most profitable nests whose availability depends, in turn, on the local and temporal composition of the community, a factor that may also influence the parasitism frequency on single host species (Stephens and Krebs 1986, Martin 1993, 1995, Stokke et al. 2007). These two aspects of nest predation, less urgency (Griffin 2004) and environmental variability (Boyd and Richerson 1988), should favour more plastic responses shaped by experience but, surprisingly, few proximate and ultimate hypotheses have been advanced on the importance of learning and the role it plays in shaping responses of parents to threats at their nests (Wiebe 2004, Duckworth 2006).

I studied defensive responses elicited primarily by avian brood parasites and secondarily by predators to unravel the role played by discriminatory abilities and threatening experiences in the modulation of nest defence. I also quantified the fitness advantages conferred by different levels of intensity and flexibility of defence responses when threats were encountered at the nest. The species studied were the Yellow Warbler (*Dendroica petechia*) and Reed Warbler (*Acrocephalus scirpaceus*), two passerine birds that nest in the Nearctic (Lowther et al. 1999) and Western Palearctic (Cramp 1992), respectively. These species are parasitized by the Brown-headed Cowbird (*Molothrus ater*) and Common Cuckoo (*Cuculus canorus*), respectively (Friedmann et al. 1977, Davies 2000). The study of populations affected by both parasitism and nest predation provides a broader basis for examining the pressure exerted by each potential source of mortality and, therefore, a better evaluation of the adaptive basis underlying the evolution of specific defensive responses.

Results are presented in the four chapters that follow. The sections below provide details of the species studied. These details are especially useful for the Reed Warbler population which, in contrast to Yellow Warblers, have been little studied (Giannella and Gemmato 2003). Nest defence responses of Yellow Warblers have been extensively studied and it has been shown that these warblers discriminate between nest predators and brood parasites (Tab. 1.1). Reed Warblers have been tested for their ability to recognize different species but the results are contradictory. In an English population, this species' responses toward cuckoos differed from those directed to predators (Lindholm and Thomas 2000), whereas, in the Czech Republic, cuckoos and non-threatening species elicited a similar defence (Honza et al. 2004; Tab. 1.2). As the main questions of this study were derived from the Yellow Warbler's ability to recognize different species at the nest, in Chapter II, I tested the enemy discrimination of Reed Warblers and their ability to adjust their responses according to the level of threat encountered at their nest (i.e.,

Table 1.1. Literature review of the recognition ability of Yellow Warblers and their defensive responses toward cowbirds, predators, and non-threatening control species.

Study site (years, sample size)	Defensive responses of Yellow Warblers	Source
Chaffey's Locks, Ontario (1973-74, 5)	Similar aggression index toward cowbird and control[1] models at the egg stage.	Robertson and Norman 1976
Chaffey's Locks, Ontario, and Delta Marsh, Manitoba (1972-75, 12)	Higher aggression index toward cowbird than control[1] models in Ontario and Manitoba populations.	Robertson and Norman 1977
Dickinson County, IA, USA (1983, 8)	Higher aggression index toward cowbird than control[2] models.	Folkers and Lowther 1985
	Toward cowbird, lower aggression index during the "later" of the nesting cycle.	
Delta Marsh, Manitoba (1986-87, 18-22)	Toward novel predator[3], no responses correlated with nesting stage, age, nest success, brood size. Distraction displays depended on nest concealment.	Hobson et al. 1988
Mer Bleue Bog, Ontario (1984, 8)	At egg laying and incubation stages, higher aggression index toward female cowbird than male cowbird, predator[4] and control[5] models, but at nestling stage, lower aggression index.	Burgham and Picman 1989
	At nestling stage, higher aggression index toward predator models.	
Delta Marsh, Manitoba (1986-87, 18-47)	At all nesting stages, more *seet* calls toward cowbird than control[6] models.	Hobson and Sealy 1989
	Unparasitized yearlings uttered more *seet* calls toward cowbird models than unparasitized older females.	
	Unparasitized yearlings uttered more *chip* calls and perch changes, fewer sat in the nest and struck cowbird models than unparasitized older females and parasitized females of various ages.	

Tab. 1.1. Continued.

Study site (years, sample size)	Defensive responses of Yellow Warblers	Source
Delta Marsh and Churchill, Manitoba (1987-89, 15)	Toward cowbird models, fewer *seet* calls, fewer females sat in the nest and no strikes in allopatric population (Churchill) compared with population sympatric (Delta Marsh) with cowbirds.	Briskie et al. 1992
Delta Marsh, Manitoba (1974-87, 25)	In nests at the first egg-laying day, cowbird model in laying position on the nest and addition of a cowbird egg model did not elicit the same desertion and burial rates observed in naturally parasitized nests.	Sealy 1995
Delta Marsh, Manitoba (1993, 35)	More *seet* calls and strikes toward cowbird than predator[7] and control[6] models at all nestling stages, whereas longer "nest-protection" behaviour toward cowbird at the egg stage only. *Seet* calls and nest-protection decreased from egg to nestling stage toward cowbird models.	Gill and Sealy 1996
	More *chip* calls and longer distraction displays toward predator than toward cowbird and control[6] models, at all nesting stages. *Chip,* metallic *chip* and *warbler* calls increased from egg to nestling stages toward the predator[7] models.	
	At all nesting stages, values intermediate between responses to cowbird and predator[7] toward the sparrow[6] models.	
Delta Marsh, Manitoba (1994-95, 12-22)	More *seet* calls, longer nest-protection and time at < 2m toward cowbird than cowbird with experimental enlarged by bill models. Longer distraction displays to model of cowbird with experimentally enlarged bill.	Gill et al. 1997a
	Longer latency in response to sparrow than female and male cowbird playbacks. More *seet* calls and longer nest-protection behaviours in response to female cowbird playbacks.	
Delta Marsh, Manitoba (1993-94, 32)	No significantly different responses between parasitized and unparasitized females toward cowbird models placed at short, medium, and long distances from the nest.	Gill et al. 1997b

Tab. 1.1. Continued.

Study site (years, sample size)	Defensive responses of Yellow Warblers	Source
Delta Marsh, Manitoba (1993-95, 9-26)	No significantly different responses between parasitized and unparasitized females toward cowbird, predator[7] and control[6] models.	Sealy et al. 1998
Bitterroot Valley, MT, USA (1999, 17)	At incubation, longer nest attentiveness after cowbird than control[8] playbacks.	Tewksbury et al. 2002
Delta Marsh, Manitoba (1993-94, 12)	Shorter latency in response to *seet* than *chip* playbacks. Similar number of *seet* and *chip* calls elicited by *seet* playbacks at laying and nestling stages.	Gill and Sealy 2003
	Longer inactivity of nestlings during *chip* vs. *seet* playbacks.	
Delta Marsh, Manitoba (1993-94, 15)	More *seet* calls and longer nest-protection behaviour in response to *seet* vs. *chip* playbacks.	Gill and Sealy 2004
	Longer nest-protection at short than medium and long distances toward cowbird models	
Churchill, Manitoba (1994, 15)	Similar alarm calls and nest-protection toward cowbird, predator[9] and control[6] models.	
	No *seet* calls or nest-protection behaviour in response to *seet* playbacks.	

[1] Song Sparrow (*Melospiza melodia*), Savannah Sparrow (*Passerculus sandwichensis*), or House Sparrow (*Passer domesticus*); [2] Song Sparrow; [3] Gray Squirrel (*Sciurus carolinensis*); [4] American Crow (*Corvus brachyrhynchos*); [5] House Sparrow; [6] Fox Sparrow (*Passerella iliaca*); [7] Common Grackle (*Quiscalus quiscula*); [8] Gray Catbird (*Dumetella carolinensis*); [9] Gray Jay (*Perisoreus canadensis*).

Table 1.2. Literature review of the discrimination ability of Reed Warblers and their defensive responses toward cuckoos, predators, and non-threatening control species.

Study site (years, sample size)	Defensive responses of Reed Warblers	Source
Wicken Fen, UK (1985-86, 9-42)	Response toward cuckoo models described qualitatively as a close mobbing with many billsnaps, *churr* calls and attraction of neighbouring conspecifics and Sedge Warblers (*Acrocephalus schoenobaenus*). Responses toward nest predator[1] models described as vigorous mobbing toward the cuckoo.	Davies and Brooke 1988
	The sight of cuckoo models before the addition of a cuckoo egg model elicited higher rejection rates than the sight of nest predator models[1].	
Wicken Fen, UK (1989, 18-54)	*Churr* calls were elicited in more nests by nest predator[2] than by adult predator[3] and cuckoo models. Songs were elicited in more nests by adult predator models. *Rasp* calls elicited in a similar number of nests by the three models. Responses from laying to nestling stage were analyzed together.	Duckworth 1991
	Songs were elicited in more nests during laying. No significant difference between incubation and nesting stages for other behavioural variables. Responses elicited from the three models were analyzed together.	
	Songs, *rasp* calls and the presence of a second bird were elicited in more nests when the models were presented on the nest than at 3 m. Responses to the three models during all nesting stages were analyzed together.	

Table 1.2. Continued.

Study site (years, sample size)	Defensive responses of Reed Warblers	Source
Llangorse Lake, Pannel Valley, Wicken Fen , UK (1993-95, 8-42)	Shorter latency and higher number of trials with billsnaps in sympatric than in allopatric and recently sympatric populations when responding to cuckoo models. More birds responding in the recently sympatric populations. Similar number of trials with alarm calls, attacks and closest approach in all three populations.	Lindholm and Thomas 2000
	In the allopatric population, PCA scores indicated the strongest response to nest predator[2], the lowest to adult predator[3], and intermediate to cuckoo models. No differences at univariate level of analysis.	
Southern Moravia, Czech Republic (1995-1996, 14)	Video recordings of natural parasitism. Higher rejection rate of cuckoo eggs when host present than when host absent during parasitism events.	Moksnes et al. 2000
	During 28% of parasitism events, cuckoos chased hosts off nest.	
	Hosts mobbed cuckoos but close-ups of videorecordings did not allow for a description of their reactions.	
Norway, Sweden, Denmark, Czech Republic, Hungary (1986-2000, 1-47)	In a study of 14 species, aggression toward a cuckoo model assessed by an ordinal scale 1-4. Higher aggressiveness in sympatric (included Reed Warblers) than allopatric species, in species nesting close to trees than in open areas, and among species suitable for being parasitized (host nestling diet compatible with cuckoo's).	Røskaft et al. 2002a
Southern Moravia, Czech Republic (1992-98, 20-37)	At the laying stage, aggression assessed by 5-category ordinal scale higher when cuckoo models presented close than distant from the nest.	Røskaft et al. 2002b
	Partial egg losses (as a measure of egg recognition errors) similar in nests with and without model presentations.	

Table 1.2. Continued.

Study site (years, sample size)	Defensive responses of Reed Warblers	Source
Wicken Fen, UK (2000-01, 8-12)	When a cuckoo model was presented at the prelaying stage and on the day the first egg was laid, hosts increased nest attendance during the days on which the first and second eggs were laid in comparison to the presentation of a nest predator[2] model that elicited a lower nest attendance. Later presentations did not result in an increase of nest attendance.	Davies et al. 2003
Southern Moravia, Czech Republic (1997-98, 11-30)	At laying, similar aggression index when cuckoo and control[4] model presented. At laying, no differences in the responses during 30 min after presentation of cuckoo model, cuckoo model and addition of a cuckoo egg model, control model[4], and visits by experimenters.	Honza et al. 2004
Wrøclaw, Poland (2004-05, 24-34)	More distress and "excitement" calls, more attacks and closer distance by Great Reed Warblers (*Acrocephalus arundinaceus*) than by Reed Warblers when a cuckoo model was presented at the laying stage.	Dyrcz and Halupka 2006

[1] Jackdaw (*Corvus monedula*); [2] Jay (*Garrulus glandarius*); [3] Sparrowhawk (*Accipiter nisus*); [4] Rock Pigeon (*Columba livia*).

defence modulation). In the third and fourth chapters, I tested whether the two warblers changed their defensive responses after experiencing the simulated threat of parasitism and after observing conspecifics defending their nests from brood parasites, respectively. These events were staged using taxidermic prepared models, playbacks and clutch manipulations. In Chapter V, I determined whether nest defence, and learned components of that defence, conferred fitness benefits. First, parasitism and nest predation pressures exerted on the warbler populations were determined by survival analyses, utilizing functions that quantified seasonal rates of nest survival to parasitism and predation during the time nests were susceptible to these two events (Muenchow 1986). Secondly, I tested whether the intensity of defensive responses and their modulation following threatening experiences were associated with lower probabilities of parasitism or depredation. Finally, I determined to what extent adaptive defensive responses were adopted by the warblers in the populations.

I used a comparative approach in Chapters 3-5. Yellow Warblers and Reed Warblers are placed in different families of the order Passeriformes (Parulidae and Sylviidae, respectively), but have similar life history traits, such as body mass, lifespan, age of sexual maturity, clutch size, mating system, and parental care (Cramp 1992, Lowther et al. 1999). Common life history traits have been shown to promote convergence in the expression of nest defence (Ghalambor and Martin 2000). Nest defence has been suggested to be an antiparasite response that involves less cost than other antiparasite responses (i.e., nest desertion, burial and ejection of parasitic eggs), if it effectively prevents parasitism events in the first place (Sealy et al. 1998). There were indications that Reed Warblers were exposed to a higher parasitism frequency than

Yellow Warblers (Woolfenden et al. 2004, L. Bonetti, C. Giannella pers. comm.), so that a stronger selection would have operated on this species for nest defence to deter parasitism or reduce its impact. A comparative approach allowed me to reveal divergence or convergence of defensive traits and their adaptiveness with respect to particular sets of environmental factors (Shettleworth 1993), such as the frequencies of parasitism and nest predation.

STUDY SPECIES AND AREAS

Yellow Warbler

Yellow Warblers were studied in 2002 and 2003 at Delta Marsh (Manitoba, Canada; 50°11'N, 98°19'W) on a 5-km portion of the forested dune ridge that separates Lake Manitoba and Delta Marsh (MacKenzie 1982, MacKenzie et al. 1982). The main tree species on the study site are Manitoba Maple (*Acer negundo*), Green Ash (*Fraxinus pennsylvanica*), and Peach-leaved Willow (*Salix amygdaloides*); the main shrubs are Red-berried Elder (*Sambucus pubens*) and Sandbar Willow (*Salix interior*), all of which are used by Yellow Warblers for nesting (MacKenzie et al. 1982).

The Yellow Warbler is a migratory species that nests throughout North America in wet, deciduous thickets (Lowther et al. 1999). On the study area, its breeding biology and foraging ecology were extensively studied from the mid-1970s to the early 1990s (e.g., Busby and Sealy 1979, Biermann and Sealy 1982, Goossen and Sealy 1982, MacKenzie et al. 1982, Sutherland 1987, Hébert 1991) and, throughout this period, this species has been reported as one of several host species parasitized by the Brown-headed Cowbird studied at this site (Sealy 1992, 1995; Woolfenden et al. 2004).

The Brown-headed Cowbird is a generalist brood parasite that parasitizes more than 200 species of passerines (Friedmann et al. 1977). Depending on the species parasitized, cowbird parasitism may result in a partial or total failure of host reproduction (Lorenzana and Sealy 1999), because cowbird eggs interfere with host incubation (McMaster and Sealy 1999, Sealy et al. 2002) and cowbirds manipulate clutches (Sealy 1992), outcompete host nestlings (Clark and Robertson 1981, Dearborn et al. 1998), and compromise their fledging survival (Payne and Payne 1998, Rasmussen and Sealy 2006). At Delta Marsh, the cowbird's main hosts are, in addition to the Yellow Warbler, the Red-winged Blackbird (*Agelaius phoeniceus*) and Song Sparrow (*Melospiza melodia*) (Woolfenden et al. 2003, 2004, McLaren and Sealy 2003, Underwood et al. 2004a, Underwood and Sealy 2006a). Parasitism frequency and its variation on this Yellow Warbler population has been recorded over many years (Sealy 1995, Woolfenden et al. 2004, Tab. 1.3). Parasitism frequency of Yellow Warblers is affected by the overall abundance of the three major hosts (Woolfenden et al. 2004), an influence also shown in other host communities parasitized by cowbirds (Clark and Robertson 1979, Freeman et al. 1990, Barber and Martin 1997).

Nest predation rates at Delta Marsh have been reported to be as high as 63% of Yellow Warbler nests (Goossen and Sealy 1982, Tab 1.3). However, there are no similar data to compare variation in nest predation among years. Nest predators on Yellow Warbler nests at Delta Marsh include the Red-winged Blackbird, Brown-headed Cowbird (but see McLaren and Sealy 2000), Common Grackle (*Quiscalus quiscula*), American Red Squirrel (*Tamiasciurus hudsonicus*), whereas the Gapper's Red-backed Vole (*Clethrionomys gapperi*) and White-tailed Deer (*Odocoileus virginianus*) are reported as

Table 1.3. Frequencies of parasitism (%) and nest predation (%) and their change (%) between years in Yellow Warblers at Delta Marsh (Manitoba).

Study period (number of nests)	Parasitism frequency[1]	Parasitism change[2]	Nest predation frequency[1]	Nest predation change[2]	Source
1974-76 (227)	9.0[3]	---	63.0[3]	---	Goossen and Sealy 1982
1983-84 (310)	30.0	+6.6	---	---	Weatherhead 1989
1983-86 (578)			24.3	-6.1 / +11.0	Sutherland 1987
1984-86 (682)	17.8	-4.3 / +6.2	---	---	Briskie et al. 1990
1974-87 (1,885)	21.0	+0.7 / -14.4	29.6[4]	---	Sealy 1992, 1995
1994-98 (447)	16.7	-0.6 / -22.9	---	---	Woolfenden 2000
2002-03 (120-338)	17.0	+4.0	71.0[5]	-25.0	This study

[1] Relative to the entire period of study.

[2] Between years. When more than two years were studied, minimum and maximum differences between successive years are reported.

[3] Frequency determined on nests found before the last egg was laid.

[4] Frequency of egg losses during laying stage as a measure of egg removal by cowbirds.

[5] Sum of frequencies of egg and nestling predation.

incidental predators (Sealy 1994). The species above are generalist predators observed depredating eggs and nestlings of other nesting species (Sealy 1994).

To determine to what extent Yellow Warblers were affected by cowbird parasitism and by nest predation, I quantified nest abundance, nest success, and frequency of parasitism and nest predation, at egg and nestling stages where possible. I searched for Yellow Warbler nests and tagged them with numbered tape for reference on successive visits every 1-3 days until clutch completion and until nestlings were 4-5-days of age. Monitoring effort was not consistent for all nests as the priority of this study was to determine the effect of learning on nest defence responses. Therefore, it was not possible to determine the fate for all nests that were not sampled for behavioural data (53%). During the two years of the study at Delta Marsh, the temporal window used by cowbirds to parasitize Yellow Warbler nests was from the clutch initiation day to two days after clutch completion (see Sealy 1995). For those nests found with complete clutches, laying dates were back-dated from hatching assuming that one egg was laid per day and the incubation period was 11 days. For those nests found parasitized, laying dates were back-dated assuming an incubation period of 10 days and a nestling stage of 11 days for the cowbird eggs and nestlings, respectively (Goossen and Sealy 1982, Briskie and Sealy 1990). Field work was conducted under Canadian Wildlife Service Permit (CWS03-M013) and the protocol was approved by the Animal Care Committee at the University of Manitoba (protocol no. F02-008/1).

Reed Warbler

Reed Warblers were studied in 2004 and 2005 at the Natural Reserve of the Valli di Mortizzuolo (Modena, Italy, 44°52'N, 11°7'E) and surrounding area (hereafter Tomina). This lowland area is composed of 200 ha covered primarily by marsh with *Phragmites australis*, *Typha latifolia*, and *Typha angustifolia* (Ferrari et al. 1995). Reed beds occupy about 30% of the area, whereas about 40% of the area consists of freshwater ponds and irrigation canals. The rest of the area is occupied by service roads and cultivated fields (Comune di Mirandola 2001). This area is part of the largest Italian lowland, the Pianura Padana, an alluvial plain historically prone to frequent flooding due to the hydrodynamics of its freshwater (Pellegrini and Tellini 2000). A banding station has been operated at Tomina since 1995, targeting both migratory and nesting birds (Gemmato et al. 1997, Giannella and Gemmato 2002).

The Reed Warbler is one of the favoured cuckoo hosts in northern Europe, although there are concerns that this assessment is biased on unsystematic studies based on nest cards (Glue and Morgan 1972, Davies and Brooke 1989b, Schulze-Hagen 1992, Soler et al. 1999). Cuckoos are specialist parasites and, recently, the abundance of host species has been reported to be one factor that determines their preference for a single species (Stokke et al. 2007). Cuckoo parasitism is extremely costly because the cuckoo nestlings evict all host eggs and/or nestlings (Davies 2000). There is little information on the frequency of parasitism on Mediterranean populations, where community structures differ considerably in the composition of species and their abundance from those nesting in Northern Europe (Cramp 1992, Hagemeijer and Blair 1997). In Italy, Truffi (1986, 1987) considered the Reed Warbler one of the most frequently parasitized species, although no frequencies were reported. The only systematic study of a marsh avian community that involved *Acrocephalus* spp. in Tuscany revealed that 9% of Reed Warbler nests were parasitized (Quaglierini 2006). Before the beginning of the present study, the population of Reed Warblers at Tomina was reported to be nesting at a density of 10 pairs/ha of reed beds and "frequently" parasitized by cuckoos (Bonetti L. and Giannella C. pers. comm.). In this study, each year, 16% of the total nests were parasitized, 21%-22% (2004 and 2005, respectively) depredated of eggs, and 7% depredated of nestlings.

To determine to what extent Reed Warbler nests were affected by cuckoo parasitism and by depredation at Tomina, I quantified nest abundance and success, and frequency of parasitism and nest predation, at the egg and nestling stages where possible. I tagged Reed Warbler nests with numbered tape for reference on visits every 1-3 days until clutch completion and nestlings were 5-6-days old. At this time, most nestlings were banded by personnel of the banding station, then visits stopped to avoid premature fledging. As with Yellow Warblers, monitoring effort was not constant for all nests as the priority of this study was to determine the effect of learning on nest defence responses and, therefore, it was not possible to determine the fate of all nests not sampled for behavioural data (34%).

At Tomina, the temporal window used by cuckoos to parasitize Reed Warbler nests was between the day of clutch initiation to three days after clutch completion. For nests found with completed clutches, laying dates were back-dated from hatching day assuming that one egg was laid per day and the incubation period lasted 12 days (Cramp 1992). For those nests found parasitized, laying dates were back-dated assuming an incubation period of 12 days and a nestling stage of 19 days for the cuckoo eggs and nestlings, respectively (Cramp 1992). Field work was conducted under the Istituto Nazionale per la Fauna Selvatica Permit (reference # 001658) and the protocol was approved by the Animal Care Committee at the University of Manitoba (protocol no. F04-044/45).

CHAPTER 2

ENEMY RECOGNITION IN REED WARBLERS

INTRODUCTION

Many animal species discriminate among different predators and, after assessing the threat each poses, respond accordingly (Cheney and Seyfarth 1988; Hauser and Caffrey 1994; Mark and Stutchbury 1994; Tewksbury et al. 2002; Gill and Sealy 2003, 2004; Sloan et al. 2005). The adaptive value of such discrimination has been discussed in terms of the high costs of responding to predators and selection against wasting energy responding to nonthreatening species (Patterson et al. 1980, Montgomerie and Weatherhead 1988). Discrimination among threats is also expressed by breeding birds at their nests when they attempt to drive threats away or silence the offspring (Montgomerie and Weatherhead 1988, McLean and Rhodes 1991). One prediction of adaptive nest defence is that an individual should behave more aggressively toward species that are perceived to pose a greater danger to their eggs or nestlings compared with a nonthreatening species (Curio 1975, Greig-Smith 1980, Gochfeld 1984, Briskie and Sealy 1989, Dale et al. 1996, Briskie et al. 1992, Gill and Sealy 1996). Moreover, a predator may represent a different level of threat to the nest contents at different stages of the nesting cycle and, therefore, parents are expected to react with different intensities at different stages of the nesting period (Patterson et al. 1980, Montgomerie and Weatherhead 1988, Burgham and Picman 1989). Stimulus-specific responses are supported by studies that find a waning of the intensity of defence exhibited toward egg predators or brood parasites at the nestling stage, whereas reactions are more aggressive at that stage toward predators of nestlings (Patterson et al.1980, Burgham and Picman 1989, Gill and Sealy 1996, Pavel and Bureš 2001; but see Knight and Temple 1986a).

Patterson et al. (1980) defined this differential response in terms of the type of stimulus and the amount of reproductive success gained by defending the current offspring against a particular threat at a given time of the breeding cycle. The intensity of nest defence, however, also seems to be influenced by the value of the current offspring and the value of future reproductive opportunities (Montgomerie and Weatherhead 1988, Burgham and Picman 1989, Sandercock 1994). Reviewers of nest defence behaviour in birds have pointed out that life history traits, value of the brood, renesting potential, and even experimental conditions may influence the defensive responses elicited by different threats and the modulation of their intensity across the breeding cycle (Montgomerie and Weatherhead 1988, Burgham and Picman 1989, McLean and Rhodes 1991, Caro 2005), all of which potentially confound the interpretation of the results. For example, high aggressiveness toward a predator during the nestling stage might be due to the parent's ability to assess a threat, but could also to be attributable to an increased value of the brood versus the clutch (Andersson et al. 1980, Winkler 1987), or to a decreased opportunity for renesting (Redondo 1989; but see Weatherhead 1989). On the other hand, less aggressive defence at the nestling stage may reflect habituation toward visits by researchers and not an inability to discriminate (Knight and Temple 1986b). Although results of theoretical studies have revealed the reproductive and experimental factors that may affect the modulation of nest defence, relatively few analyses have considered both of these simultaneously when quantifying enemy discrimination in birds (Patterson et al. 1980, Regelmann and Curio 1983, Burgham and Picman 1989, Grim 2005).

In this chapter, I quantified the ability of Reed Warblers at different stages of the breeding cycle to discriminate among a brood parasite (Common Cuckoo [hereafter cuckoo]), nestling predator (European Magpie [*Pica pica*, hereafter magpie]), and a species that does not threaten the nest or clutch (Rock Pigeon [*Columba livia*, hereafter pigeon]). I also determined whether the variables that influence the value of offspring, such as time of season, size and age of clutch/brood, and experimental conditions, such as time of day and number of visits to the nest, explained the variability in the changes in intensity of defence recorded during two different nesting stages.

The ability of Reed Warblers to recognize cuckoos has been studied previously, but most workers have not tested the warblers' responses to a nonthreatening species (Tab. 1.2); when a control group was tested, warblers responded equally intensively to cuckoo models and controls (Honza et al. 2004). In one study, the model of a nest predator elicited more *churr* calls than a cuckoo model, which suggests an active discrimination between threats (Duckworth 1991). Contradictory results may be due to the use of behavioural scores or ranks to quantify the responses. Although these methods have often been used in studies of nest defence (Biermann and Robertson 1981, Pavel and Bureš 2001), the best approach is still to quantify each variable separately to avoid overestimating frequent behaviours or underestimating rare ones (Curio 1980, Knight and Temple 1986b, Breitwisch 1988, Sealy et al. 1998, Caro 2005). To quantify a behaviour merely as present or absent in the entire trial may lead to erroneous conclusions (Martin and Bateson 1986), especially when different vocalizations are elicited by different threats (Hobson and Sealy 1989), but recorded as general alarm calls (Honza et al. 2004). In some species, different functions have been ascribed to alarm or defence calls (East

1981, Knight and Temple 1988, Gill and Sealy 2003), from attracting other conspecifics or heterospecifics and group-harassment of a predator (Elliot 1985), to confounding or intimidating the predator (Curio and Regelmann 1985), and to silencing the young in the nest (Haskell 1999, Gill and Sealy 2004). I quantified Reed Warbler behaviours separately to identify potential nuances in the defences elicited by different threats.

As in many migratory passerine birds, Reed Warblers have limited time each year to nest and raise their young before migrating again (Cramp 1992). Late nesting attempts are more valuable because if they fail there may not be opportunities for renesting (Montgomerie and Weatherhead 1988). The intensity of nest defence, therefore, is predicted to be higher later in the nesting season (Patterson et al. 1980). Moreover, more effort should be expended to protect nests that are more valuable when larger clutches or broods are at stake (Lambrechts et al. 2000), as well as when older clutches or broods have a greater expectation of survival (Andersson et al. 1980, Patterson et al. 1980, Winkler 1987). Individuals with larger and older broods, therefore, should be more aggressive (Patterson et al. 1980, Montgomerie and Weatherhead 1988).

Considering all the above-mentioned reproductive value variables, I attempted to tease apart each one's effect on the expression of defence toward different threats by using univariate and multivariate analyses to test their importance in variation of nest defence shown by Reed Warblers across the nesting season. Exposing Reed Warblers to different stimuli, I predicted that nest defence would be more intense when warblers were confronted by cuckoos and magpies than by pigeons and, with respect to the first two species, I also predicted an inverse pattern in defence intensity across the breeding cycle because cuckoos are a threat only during laying and early incubation (Davies 2000), whereas magpies depredate eggs and young (Birkhead 1991, Cramp 1992). Given the higher survival potential of young, I predicted a more aggressive defence toward magpies during the nestling stage. Finally, I predicted that both the threat type and the reproductive value of the nest being tested would have an interactive effect on the defence intensity. Reed Warblers are expected to discriminate between threats posed by each model but the intensity of defence is expected to be higher among individuals with a diminished renesting potential and with larger and older clutches or broods.

MATERIALS AND METHODS

The study was conducted at Tomina (Modena, Italy) from April through July 2004 and 2005. Details of the study area and the methods of nest searching and monitoring are given in Chapter 1.

Model Presentations

Reed Warblers were presented with models of a cuckoo, pigeon, and magpie, at the laying, incubation, and nestling stages. To minimize pseudoreplication (Hurlbert 1984), I had two models of each type and the one to present was chosen randomly via coin toss. Trials were performed between 0600 and 1900 Central European Time (CET). Twenty minutes before presenting the first model, I set up a blind 2-5 m from the nest from which I recorded the warblers' responses. The blind was made of a folding wooden trestle covered by burlap that formed the four walls and the ceiling of the structure (about 80 x 80 x 140 cm). Burlap was attached to the trestle so that one side allowed access. On the opposite side, a window of about 20 x 10 cm was cut from the burlap to allow for viewing outside. Each nest was tested only once for 5 min, with the three models on the same day. The presentation order of model species was randomly determined by drawing sticks of different lengths. I presented models 20 minutes apart to avoid the potential problem of habituation or carry-over aggression (Knight and Temple 1986a, b; Neudorf and Sealy 1992). Because of inclement weather, some nests were exposed to one or more models on different days; however, this lag among presentations did not affect the results (Root 1 of Canonical Analysis with Factor Structure value 0.26). Models were taxidermic mounts in perched positions attached to wooden poles (painted to match the vegetation) of different lengths. They were placed within 0.5 m of and faced the nest rim. None of the nests tested had been parasitized or partially depredated.

I chose the pigeon as a control because this species does not threaten Reed Warblers or their eggs or young (Goodwin 1983) and they are similar to cuckoos in length (31-34 cm versus 32-34 cm, respectively, Cramp 1992), plumage colouration (medium grey), although pigeons are heavier than cuckoos (200-302 g versus 106-133 g, respectively, Cramp 1992). At Tomina, pigeons are also present and, therefore, warblers may have had prior opportunities to encounter them and to assess them as nonthreatening. Although sympatric with Reed Warblers, pigeons forage on agricultural fields surrounding reed beds and roost on roofs of the numerous rural buildings in the area, some of which were located near the reed beds. Magpies were chosen because they threaten nest contents as they feed opportunistically, often depredating passerine young, occasionally adults and rarely eggs (Holyoak 1968, Birkhead 1991, Cramp 1992). At Tomina, they nest abundantly despite being frequently trapped by the local Wildlife Service during pest-control activities (pers. obs.).

Behavioural Analyses

In the first three days of the nesting season of 2004, I presented cuckoo, magpie and pigeon models at Reed Warbler nests with the purpose of establishing a detailed list of behavioural categories to be recorded during the successive model presentations. During these presentations, I also recorded warbler calls using a Sony TMC 5000 EV tape recorder and a Sennheiser K3-U directional microphone placed about 1 m from four focal nests. Nests used in this preliminary survey were not included in the statistical analyses. The variables recorded during these presentations are given in Table 2.1. I classified Reed Warbler behaviours on the basis of motor patterns and vocalizations (Curio 1980, Smith et al. 1984, Breitwisch 1988, Hobson and Sealy 1989). Behaviours 1-8 were quantified as the number of times they occurred in the trial, whereas behaviours 9-11 were recorded as the number of 10-s intervals in which the behaviour occurred (Tab. 2.1). Perch changes, Strikes, Bill snaps, and Close flights are measures of frequency of individual approach to the model, whereas Out of sight quantifies the time spent away from the model. Displacement activities, including preening and eating, were expressed only sporadically, and could not be analyzed statistically. Distances from the model were also recorded, but were not analyzed statistically because they were not mutually exclusive of the other behaviours. Moreover, the thick vegetation around Reed Warbler nests usually precluded precise estimation of distances. Behavioural observations were spoken into a cassette recorder and transcribed later.

In previous behavioural studies of Reed Warblers (Duckworth 1991, Lindholm and Thomas 2000, Røskaft et al. 2002a, Honza et al. 2004), the behaviour of only the first individual that approached closely to the nest was recorded. Given the differential

Table 2.1. Behaviours of Reed Warblers at Tomina (Italy) elicited by models and used as variables for statistical analyses.

Behaviour	Reed Warbler behaviour
1. Perch change	Hopping or flight from one reed to another
2. Strike	Physical contact of the bill on model
3. Bill snap	Sound produced by quickly closing mandibles with a simultaneous movement of the head toward the model
4. Close flights	Hovering flight ≤ 0.20 m over the model or warbler approaches the model at a distance of ≤ 0.20 m but there is no physical contact
5. *Churr* call	Harsh call (spectrograph in Fig. 2.1A)
6. *Huit* call	High-pitched piping call uttered by males as a prelude to song
7. Song	Melodious vocalization given by males
8. Other bird	Other birds ≤ 5 m from focal nest, in addition to the breeding pairs
9. *Zirr* call	Continuous rasping call (spectrograph in Fig. 2.1B)
10. Silent watching	Stares at model with no other activities and no calls uttered
11. Out of sight	Flies outside visual field or disappears into vegetation

investment in reproductive effort (Knapton 1984), however, both males and females may have different optimal defensive intensities (Montgomerie and Weatherhead 1988, McLean and Rhodes 1991, Leisler and Catchpole 1992, Pavel and Bureš 2001) and, therefore, analyzing either male or female responses as equivalent reactions may bias the results. The Reed Warbler is monomorphic, though the sexes can be distinguished in captured individuals by noting brood patches in females and cloacal protuberances in males (Brown and Davies 1949, Cramp 1992) and by colour banding them for future identification. I attempted this in 2004, but pre-trial observations revealed that the likelihood of finding marked individuals was low, probably because many banded individuals had only stopped over at Tomina while migrating (Giannella and Gemmato 2003).

Another way to distinguish males from females is to observe them during courtship or copulation or to identify the singing member of the pair. Only males sing an advertising call and utter the *huit* call, described as a prelude to song (Impekoven 1962, Catchpole 1980, Cramp 1992). *A posteriori* coding of the 2004 responses revealed that both adults responded in more than 90% of the presentations; males sang or uttered *huit* calls in 95% of cases, which allowed the sexes to be recorded separately. The same criteria for including trial responses were followed in 2005. It was possible to distinguish between sexes in trials where females arrived at the nest after a singing individual or where females arrived at the nest first followed by a singing male. All the instances that did not allow sex discrimination were discarded and not included in the analyses (see Results). The trial started when the female arrived within at least 5 m from the nest.

Female responses were recorded for variables 1-5 and 8-11, whereas male responses only for variables 6 and 7 (see Table 2.1).

Statistical Analyses

Preliminary Analyses

I analyzed responses toward models during 5-min trials. However, as the model presentations were part of a broader experimental design (Chapters 3-4), preliminary analyses established whether these data were suitable to be analyzed to test and quantify the warblers' ability to discriminate among different threats.

First, the nests tested for 5 min with all model presentations had also been tested for 2 min with cuckoo and pigeon models 1-3 days earlier as controls for the learning experiments described in Chapters 3 and 4. As the first exposure to the same stimuli could have influenced defensive behaviours of Reed Warblers through habituation and sensitization (Knight and Temple 1986a, b), I tested whether the responses to each model during the first presentations differed from the responses during the first 2 min of the second presentations using a factorial ANOVA (Underwood 1997). The factors were model species (cuckoo versus pigeon), order of presentation (first versus second), and year (2004 versus 2005), whereas the behavioural responses were treated as dependent variables. Variable values were treated with a square-root transformation and their homogeneity of variance was tested using Cochran's C test. Despite the transformation, some variables (strike, close flight, *huit* call, song, and silent watching) still had a heterogeneous variance (Cochran's C test, $P < 0.05$). Parametric tests in these cases increase the probability of a Type I error in the results (Underwood 1997), thus comparisons of data with a heterogeneous variance might result in a significant difference when in fact there is none. However, as none of the test results were significantly different (see below), my interpretation of the results were not affected by such a bias. The interaction among all factors was not statistically significant for all variables (ANOVA, $P > 0.05$; Tab. 2.2 and 2.3), which indicates that not only did the responses toward each model did not change between the first and second presentations, but also, they were not different between years.

Second, as habituation or carry-over aggression might have waned or increased over the 5-min presentation, I also correlated responses elicited during the first 2 min with those given during the entire 5-min trials with a Spearman Rank Correlation test (Zar 1999). The two data sets were significantly correlated ($n = 180$, $P < 0.05$; Tab. 2.4), which indicates that the responses elicited over 5 min were similar to those recorded during the first 2 min of the same trials. The only exception was the variable out of sight, which will be discussed separately.

Finally, as there are indications that hosts respond similarly during laying and incubation (Gill and Sealy 1996), I also tested for differences between the responses at these two stages with separate ANOVAs (Underwood 1997), treating the model (cuckoo, pigeon, and magpie) and stage (laying versus incubation) as factors, and all behaviours as dependant variables. Responses elicited by each model did not differ significantly during the two stages for all variables (ANOVA, $p > 0.05$; Tab. 2.5 and 2.6), which allowed me to pool these data under the egg stage for successive comparisons with the nestling stage. As a result of the previous statistical tests, for the subsequent analyses, I considered a data set that included the responses of Reed Warblers elicited by cuckoo, pigeon, and

Table 2.2. Sample sizes (n) of nests of Reed Warblers tested in 2004 and 2005 at Tomina (Italy) with cuckoo and pigeon models during two presentations.

Model	Presentation	Year	n
Cuckoo	First	2004	17
Cuckoo	First	2005	15
Cuckoo	Second	2004	16
Cuckoo	Second	2005	14
Pigeon	First	2004	17
Pigeon	First	2005	16
Pigeon	Second	2004	16
Pigeon	Second	2005	14

Table 2.3. Results of ANOVA testing differences in the responses of Reed Warblers at Tomina (Italy) toward cuckoo and pigeon models between the first and second presentations, and between 2004 and 2005. The sample size for each group tested is given in Table 2.2.

Behavioural variable	Species x Presentation x Year effect	
	$F_{1, 124}$	P
Perch change	3.3	0.07
Strike	0.35	0.55
Bill snap	0.02	0.88
Close flights	0.01	0.94
Churr call	0.01	0.93
Huit call	0.81	0.37
Song	0.04	0.84
Other birds	0.01	0.92
Zirr call	0.87	0.35
Silent watching	1.19	0.66
Out of sight	0.56	0.45

Table 2.4. Results of Spearman Rank Correlation test between the responses of Reed Warblers at Tomina (Italy) recorded in the first 2 min and 5 min of the same trials (n = 180).

Behavioural variable	Spearman R	P
Perch change	0.46	< 0.001
Strike	0.68	< 0.001
Bill snap	0.58	< 0.001
Close flights	0.53	< 0.001
Churr call	0.33	< 0.001
Huit call	0.29	0.0001
Song	0.28	0.0001
Other birds	0.39	0.0002
Zirr call	0.64	< 0.001
Silent watching	0.25	0.0008
Out of sight	0.12	0.1019

Table 2.5. Sample sizes of nests of Reed Warblers at Tomina (Italy) exposed in 2004 and 2005 to cuckoo, pigeon and magpie models during laying and incubation stages.

Model	Nesting Stage	n
Cuckoo	Laying	10
Cuckoo	Incubation	22
Pigeon	Laying	11
Pigeon	Incubation	22
Magpie	Laying	11
Magpie	Incubation	22

Table 2.6. Results of ANOVA testing differences in responses of Reed Warblers at Tomina (Italy) toward cuckoo, pigeon and magpie models in the laying and incubation stages. Sample size for each group tested is listed in Table 2.5.

Behavioural variables	Species x Stage effect	
	$F_{1,97}$	P
Perch change	0.26	0.768
Strike	0.25	0.782
Bill snap	1.5	0.229
Close flights	0.62	0.542
Churr call	0.36	0.7
Huit call	1.09	0.342
Song	0.36	0.696
Other birds	0.57	0.568
Zirr call	0.27	0.766
Silent watching	0.15	0.863
Out of sight	0.3	0.744

magpie models during 5-min trials and during both the egg and nestling stages (Table 2.7).

Enemy Recognition

Having established the data set to be used for the analysis of enemy recognition in the Reed Warbler (Table 2.7), I tested for differences among the responses elicited by the cuckoo, pigeon, and magpie model within each nesting stage with Friedman ANOVA tests (Zar 1999). To compare the responses between egg and nestling stages for each model species, I used the Mann-Whitney U-test (Zar 1999). To analyze the overall complexity of nest defence, I used Principal Component Analysis (PCA, Digby and Kempton 1987) on the responses elicited by the three models at each nesting stage after a square-root transformation of the variables (Zar 1999). I also ran separate PCAs on the responses elicited by each model in each nesting stage.

To test the potential effect of reproductive variables and experimental conditions on the responses, I used a Canonical Analysis (Digby and Kempton 1987) where the two data sets were represented by the behavioural variables reported in Table 2.1 and by the following reproductive and experimental variables: (1) number of eggs/nestlings, (2) age of clutch/brood, (3) time of season, (4) time of day, (5) number of visits by the investigator, and (6) presentation lag. Values analyzed were those relative to the time the models were presented. Variables 1 and 4 were recorded prior to each model presentation, variables 2, 3, 5, and 6 were calculated *a posteriori* from field notes of nest inspections (Chapter 1). Age of clutch/brood was the day after the clutch initiation, time of season was the day after the first egg was laid in the population of Reed Warbler

Table 2.7. Sample sizes of nests of Reed Warblers at Tomina (Italy) exposed to cuckoo, pigeon and magpie models during egg and nestling stages. Responses obtained from these nests were analyzed to test the ability of Reed Warblers to discriminate among threats each species posed at each stage.

Model	Nesting Stage	n
Cuckoo	Egg	30
Cuckoo	Nestling	30
Pigeon	Egg	30
Pigeon	Nestling	28
Magpie	Egg	31
Magpie	Nestling	31

as a whole, and presentation lag was the number of hours since the last model was presented.

RESULTS

I presented models of cuckoo, pigeon and magpie at 65 nests, but two were depredated before the end of the experiment. The responses to models during 10 presentations in 2004 and four in 2005 could not be analysed because I could not identify the focal female. Sample sizes in the analyses are given in Table 2.7.

Recognition of Threat

The main vocalizations of Reed Warblers were the *churr* call, characterized by lower pitch and longer duration, and the *zirr* call (Fig. 2.1). Moreover, *churr* was uttered at a lower rate than the *zirr* call. In fact, during model presentations, I could count the number of *churr* calls, whereas quantifying the *zirr* call was based on the total time it was uttered during the trial.

Responses to the cuckoo, pigeon, and magpie models differed significantly (Fig. 2.2 and 2.3). Reed Warblers uttered more *zirr* calls toward the cuckoo (Friedman ANOVA, $P < 0.001$, $n = 30$) and bill snapped more ($P < 0.001$) during both egg and nestling stages. They also struck the cuckoo model more ($P < 0.001$) and flew close to it more often ($P = 0.0012$) during the egg stage, but this difference with the other models disappeared at the nestling stage. In the egg stage, the number of other birds attracted to the focal nest was significantly higher when the cuckoo model was presented ($P < 0.001$), whereas in

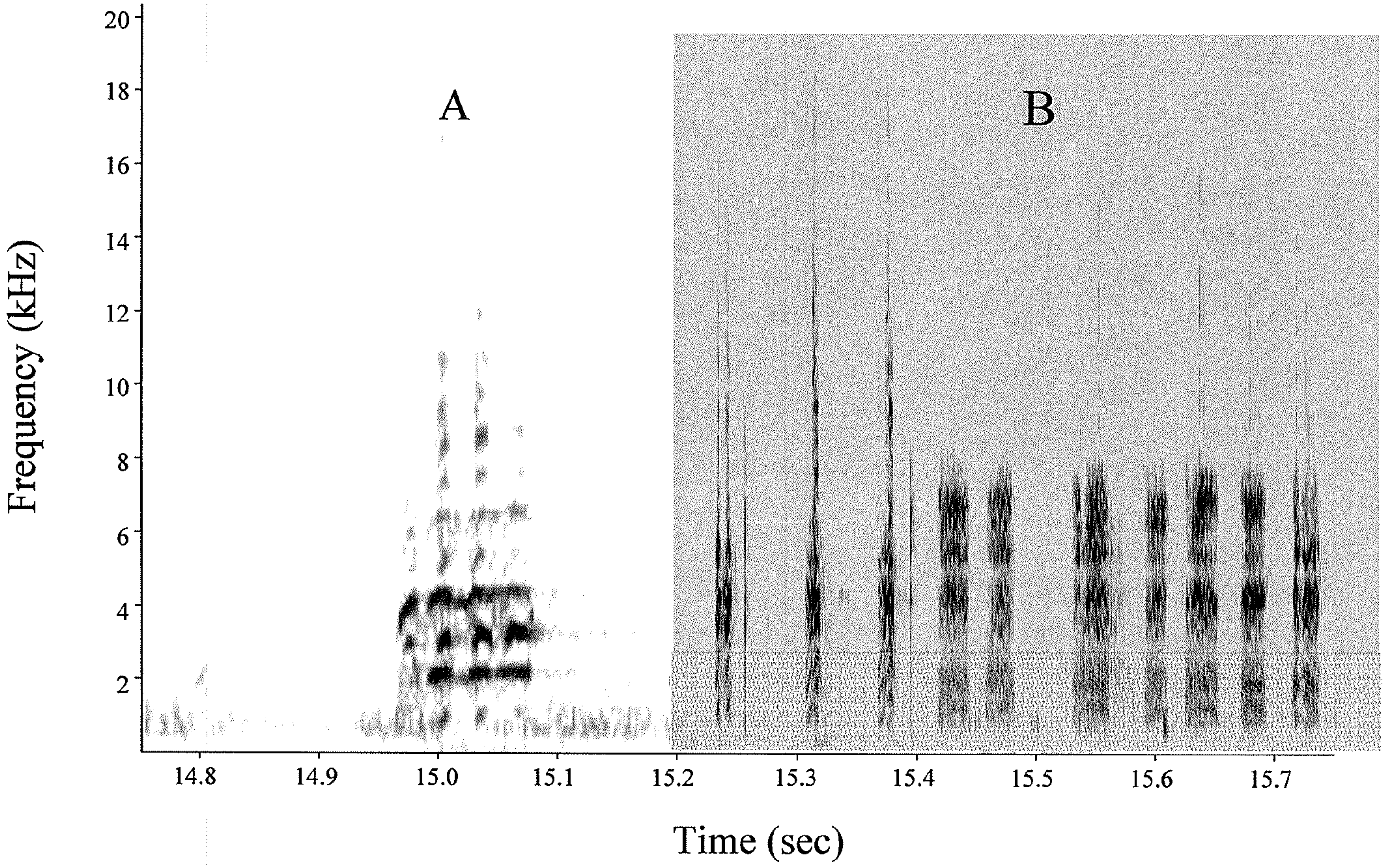


Figure 2.1. Spectrographs of *churr* (A) and *zirr* (B) calls uttered by Reed Warblers at Tomina (Italy) during presentations of cuckoo, pigeon and magpie models. The vocalizations were recorded by using a Sony TMC 5000 EV tape recorder and a Sennheiser K3-U directional microphone placed about 1 m from four focal nests.

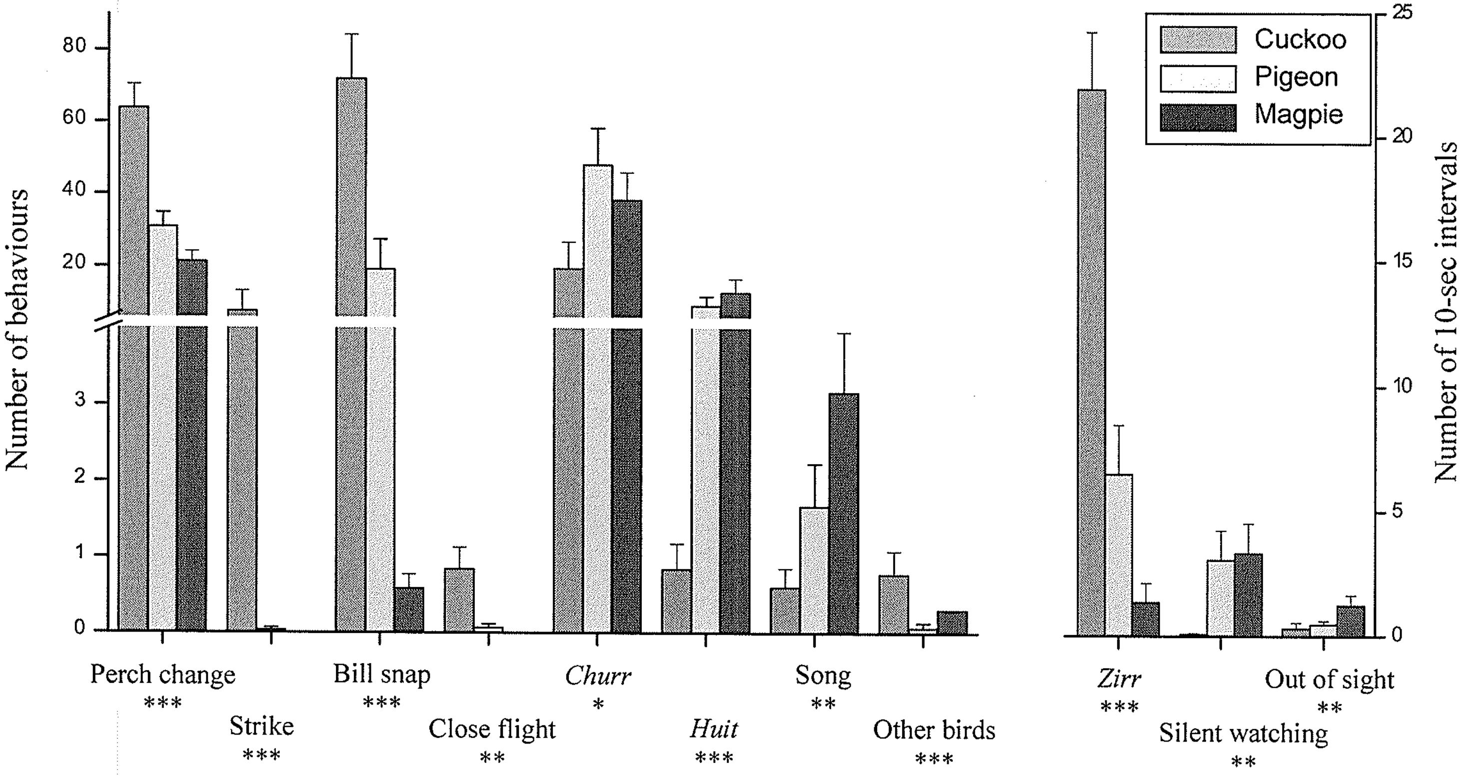


Figure 2.2. Nest defence responses (mean + SE) of Reed Warblers at Tomina (Italy) during the presentation of cuckoo (n = 30), pigeon (n = 28), and magpie (n = 31) models at the egg stage. Results of Friedman ANOVAs show the differences in defence intensities elicited by the three model species: ns = $P > 0.05$, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

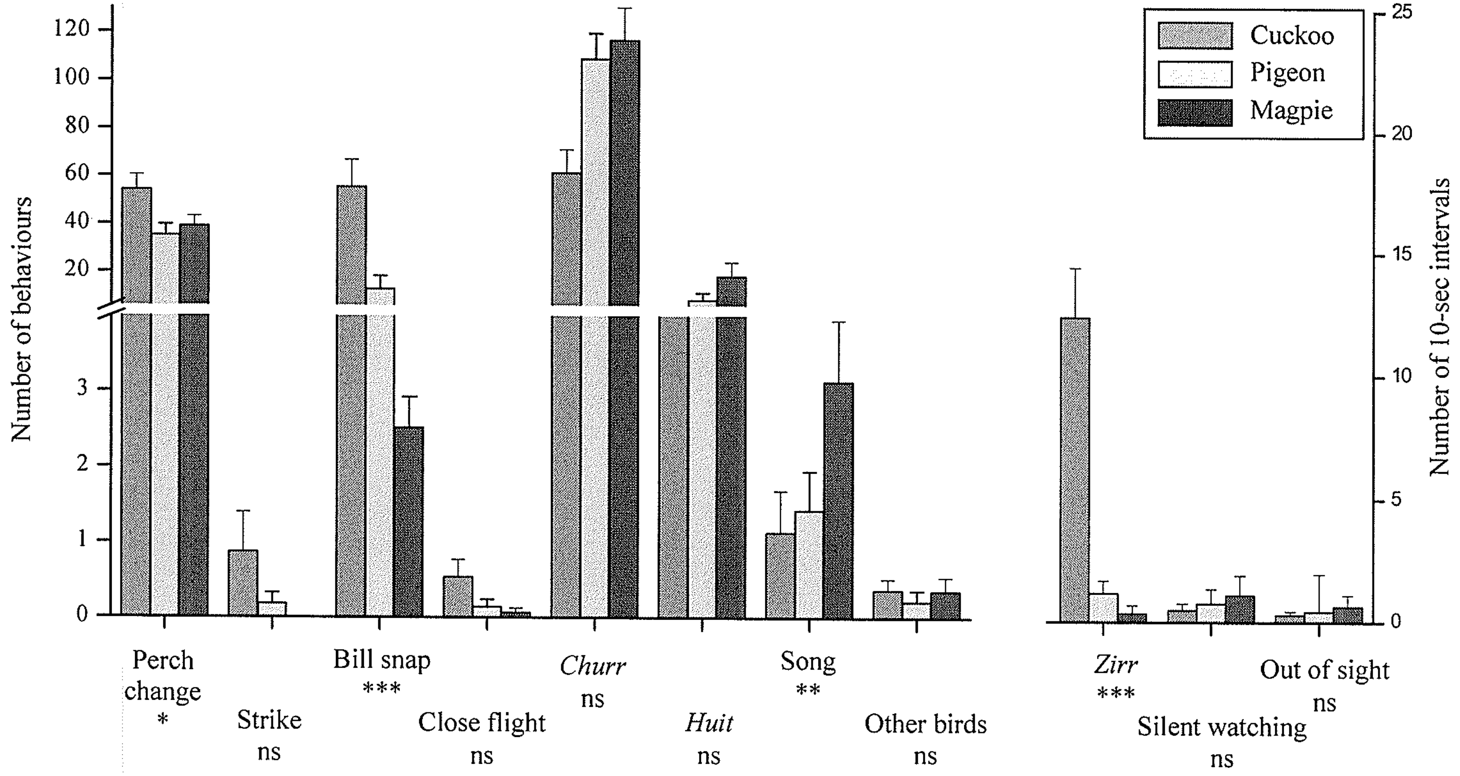


Figure 2.3. Nest defence responses (mean + SE) of Reed Warblers at Tomina (Italy) during the presentation of cuckoo (n = 30), pigeon (n = 28), and magpie (n = 31) models at the nestling stage. Results of Friedman ANOVAs show the differences in defence intensities elicited by the three model species: ns = $P > 0.05$, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

the nestling stage, their number was similar regardless of which model was presented ($P = 0.59$). Reed Warblers sang more in response to magpie models at the egg ($P = 0.0014$, $n = 31$) and nestling ($P = 0.0011$) stages, but uttered significantly more *huit* calls ($P < 0.001$) and spent more time silently watching ($P = 0.0011$) and out of sight ($P = 0.003$) at the egg stage. When presented with the pigeon, Reed Warblers uttered the most *churr* calls ($P = 0.018$, $n = 30$) and attracted the fewest other birds ($P < 0.001$, $n = 28$) during the egg stage. For all other behaviours, Reed Warblers responded to pigeons with intensities intermediate between the cuckoo and magpie models.

When I compared responses between the egg and nestling stages within each model species (Fig. 2.4), I found that Reed Warblers uttered fewer *zirr* calls (Mann-Whitney U-test, $Z = 3.23$, $P = 0.0012$, $n = 30$) and struck the cuckoo model less often ($Z = 1.41$, $P = 0.068$) in the nestling than in the egg stage, although the second comparison only approached significance. In the nestling stage, warblers significantly increased the number of perch changes ($Z = -2.99$, $P = 0.003$, $n = 31$) and decreased significantly the time spent silently watching ($Z = 2.55$, $P = 0.011$) and out of sight ($Z = 1.96$, $P = 0.050$) in response to the magpie model. Finally, Reed Warblers increased significantly the number of *churr* calls toward all three models during the nestling stage (cuckoo: $Z = -3.34$, $p < 0.001$, $n = 30$; pigeon: $Z = -3.87$, $P < 0.001$, $n = 30$ at egg and 28 at nestling stage; magpie: $Z = - 4.12$, $P < 0.001$, $n = 31$). Except for this variable, Reed Warblers did not change any nest defence response between egg and nestling stages when presented with the pigeons.

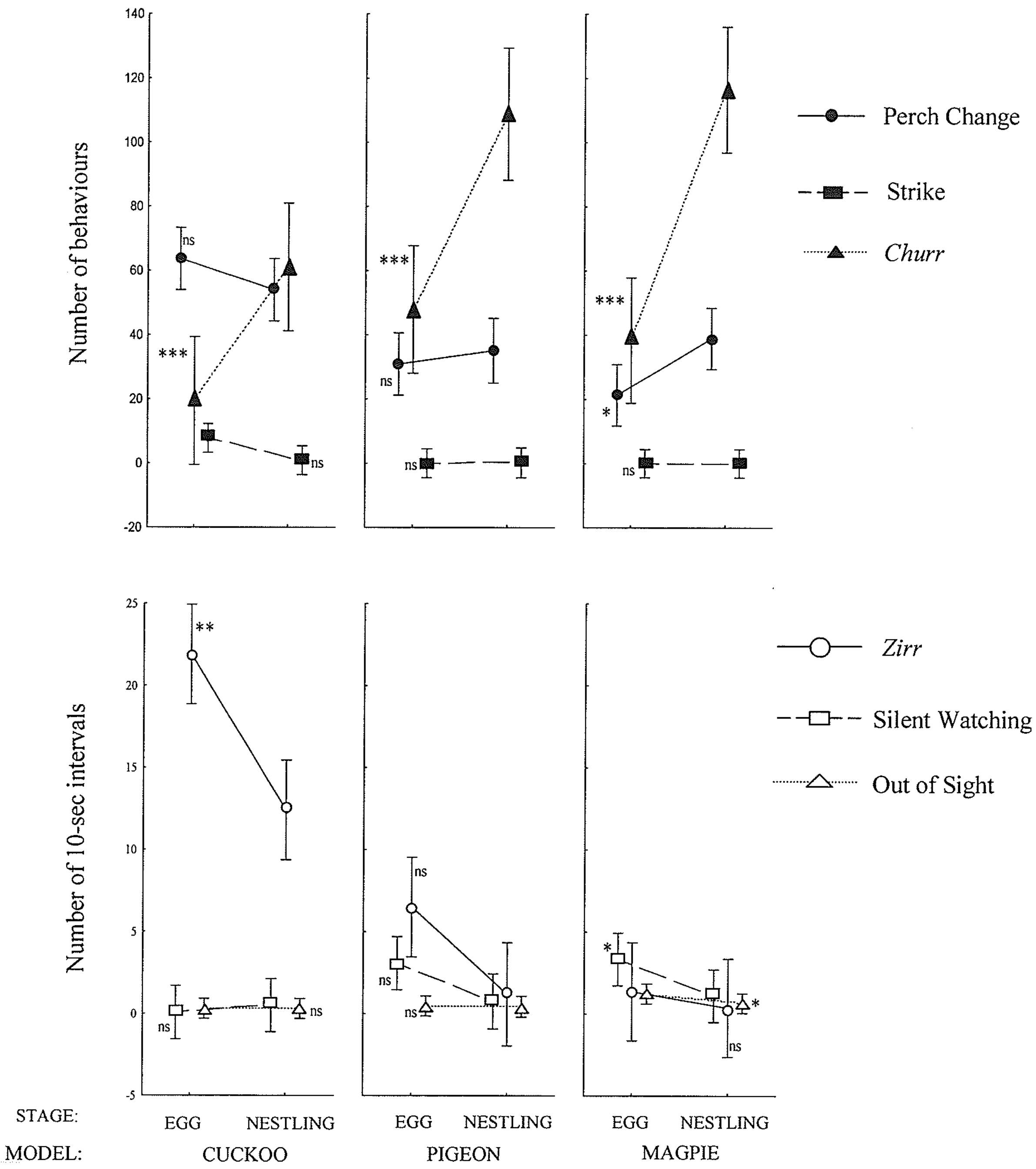


Figure 2.4. Defence responses (mean + SE) recorded at Reed Warbler nests (Tomina, Italy) during egg and nestling stages and elicited by the presentation of cuckoo, pigeon, and magpie models. Results of Mann-Whitney U-tests show the differences in intensity of defence between egg and nestling stages within each model species: ns = $P > 0.05$, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

The first two components of the PCA on the responses toward the three model species explained 74% and 79% of the variance in nest defensive responses recorded during the egg and nestling stages, respectively (Fig. 2.5 and 2.6). The greatest weight of the first component was attributed mostly to bill snaps (Eigenvectors: egg stage 0.71, nestling stage 0.66), whereas the highest value for the second component was the *churr* call (egg stage -0.88, nestling stage 0.76). Separate PCAs on the responses to each model showed that most variation in defence toward the cuckoo explained by the first two components changed from mostly bill snaps and strikes during the egg stage to bill snaps and *churr* calls during the nestling stage (Tab. 2.8). Variation in defence toward pigeons was mostly explained by bill snaps and *churr* calls and toward magpies by *churr* and *huit* calls, uttered with equal frequency at both egg and nestling stages (Tab. 2.8).

Effects of Reproductive Variables and Experimental Condition

The mean (± SE) number of eggs and nestlings contained in nests tested was 3.9 (± 0.05, n = 31) and 3.4 (± 0.10, n = 31), respectively. The mean age of clutches when models were presented was 6.2 days (± 0.23) after clutch initiation, whereas the mean age of the brood was of 21.9 days (± 0.29). Mean time of the season when tests were conducted during the egg stage was 29.7 days (± 1.19) after the first egg was laid in the population, whereas it was 40.5 days (± 0.83) for those tested during the nestling stage. Mean time of day of model presentations in the morning was 1001 hr (± 0.009, n = 96), whereas it was 1813 hr (± 0.010, n = 88) in the afternoon. Nests were visited on average 3.4 times (± 0.13, n = 184) before being exposed to the models. There was a lag of 2 hours (± 0.48) between presentation of successive models.

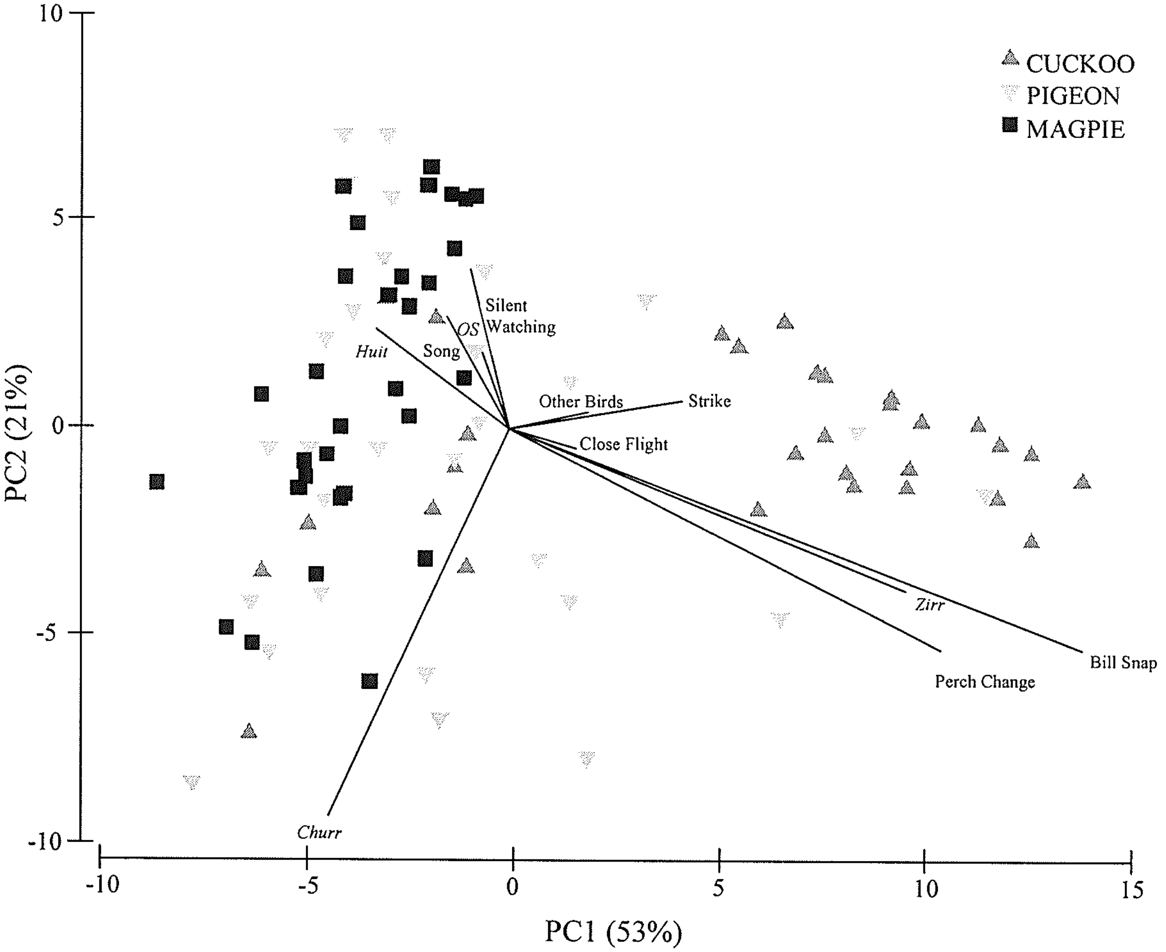


Figure 2.5. Results of Principal Component Analysis of the defensive responses of Reed Warblers at Tomina (Italy) when presented with cuckoo, pigeon, and magpie models during the egg stage. Single behaviours are represented by vectors whose length is proportional to the weight assigned by the analysis on the first (PC1) and second (PC2) components (OS = out of sight).

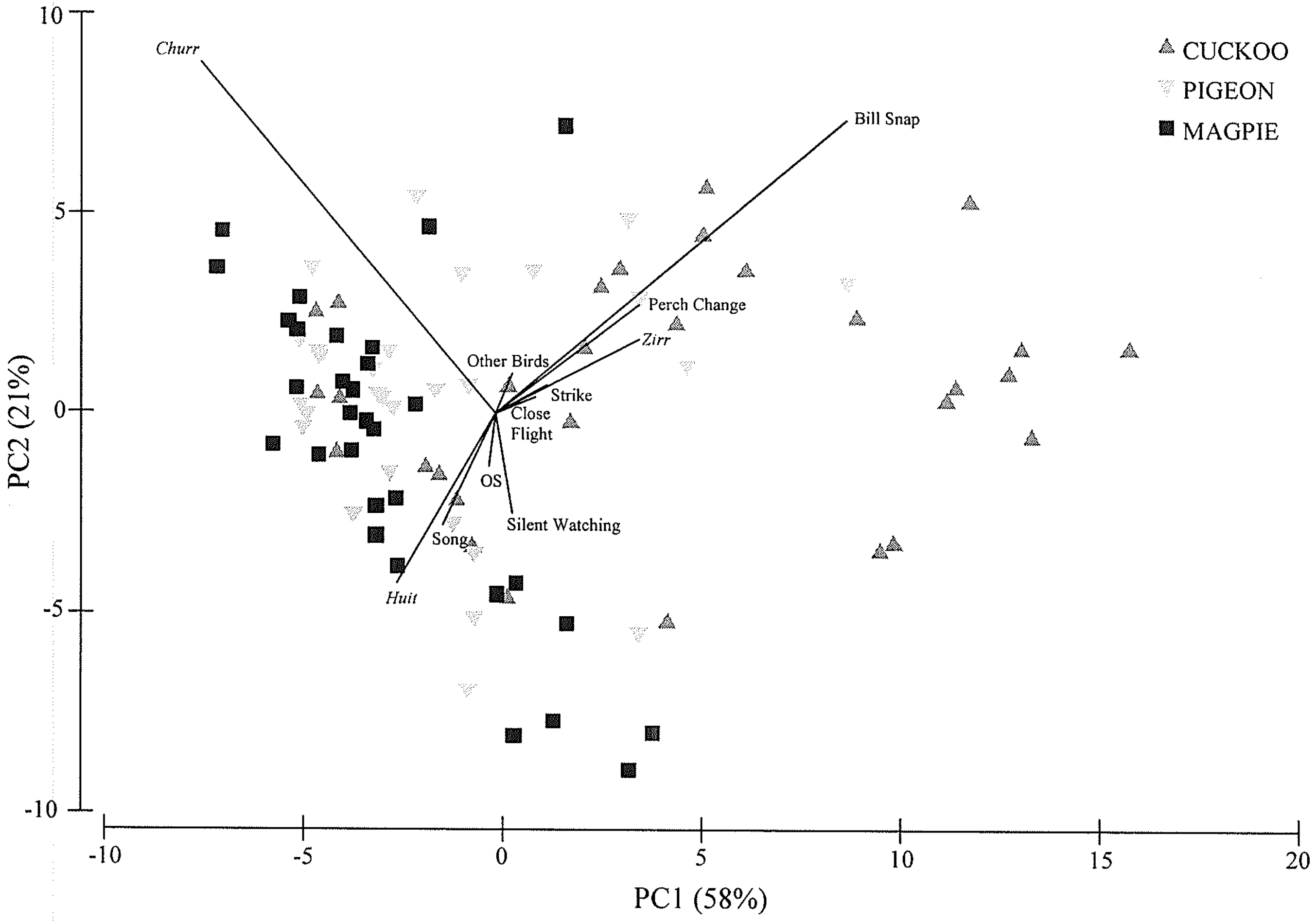


Figure 2.6. Results of Principal Component Analysis (PCA) of the defensive responses of Reed Warblers at Tomina (Italy) when presented with cuckoo, pigeon, and magpie models during the nestling stage. Single behaviours are represented by vectors whose length is proportional to the weight assigned by the analysis on the first (PC1) and second (PC2) components (OS = out of sight).

Table 2.8. Highest Eigenvector values relative to the first (PC1) and second (PC2) components from separate PCAs on the responses of Reed Warblers at Tomina (Italy) to cuckoo, pigeon, and magpie models during the egg and nestling stages. In the last column the percentages of variation of defence explained by the first two components of the responses recorded during 5-min trials are presented.

Model	Stage	PC1		PC2		% Variation (PC1+PC2)
Cuckoo	Egg	Bill Snap	0.71	Strike	-0.86	83
Cuckoo	Nestling	Bill Snap	0.71	*Churr* Call	-0.79	84
Pigeon	Egg	Bill Snap	0.75	*Churr* Call	0.94	78
Pigeon	Nestling	Bill Snap	0.77	*Churr* Call	-0.88	69
Magpie	Egg	*Churr* Call	0.96	*Huit* Call	-0.92	72
Magpie	Nestling	*Churr* Call	0.98	*Huit* Call	0.95	78

Canonical Analysis was performed on the behavioural responses of the first data set, and on reproductive variables (i.e., number and age of eggs and nestlings and time of season) and experimental conditions (i.e., time of day and number of visits) of the second data set. The second data set explained 6.7% of the variation of the nest defence elicited by the three models during egg and nestling stages (Canonical Analysis, $R = 0.64$, $\chi^2 = 161$, $P < 0.001$). Root 1 was the only root that significantly explained this variation ($R = 0.36$, $P = 0.051$, when Root 1 was removed) and was represented mostly by the *churr* call (Factor Structure value -0.89) in the first data set, and the age of clutch or brood (- 0.95) in the second, which indicated that the explained variation in the nest defence was represented mostly by more *churr* calls as clutches or broods became older (Fig. 2.7).

DISCUSSION

Discrimination of Threats

Reed Warblers responded differently toward the models of the cuckoo, pigeon, and magpie. The cuckoo elicited more bill snaps and attacks, long repetitions of *zirr* calls and close mobbing. As shown by the PCAs, bill snaps were more important than other variables in explaining the variance in the expressions of nest defence in the three model species and specifically toward cuckoos. Bill snaps are defined as mechanical sounds and have been recorded in storks and owls (Manson-Barr and Pye 1985). Bill snaps directed toward more specific threats were found among Least Flycatchers (*Empidonax minimus*) that preferentially produced them when confronted with parasitic Brown-headed Cowbird models than with the non-threatening Fox Sparrow (*Passerella iliaca*); however, no predator models were presented so that it is unknown whether the snaps are used only

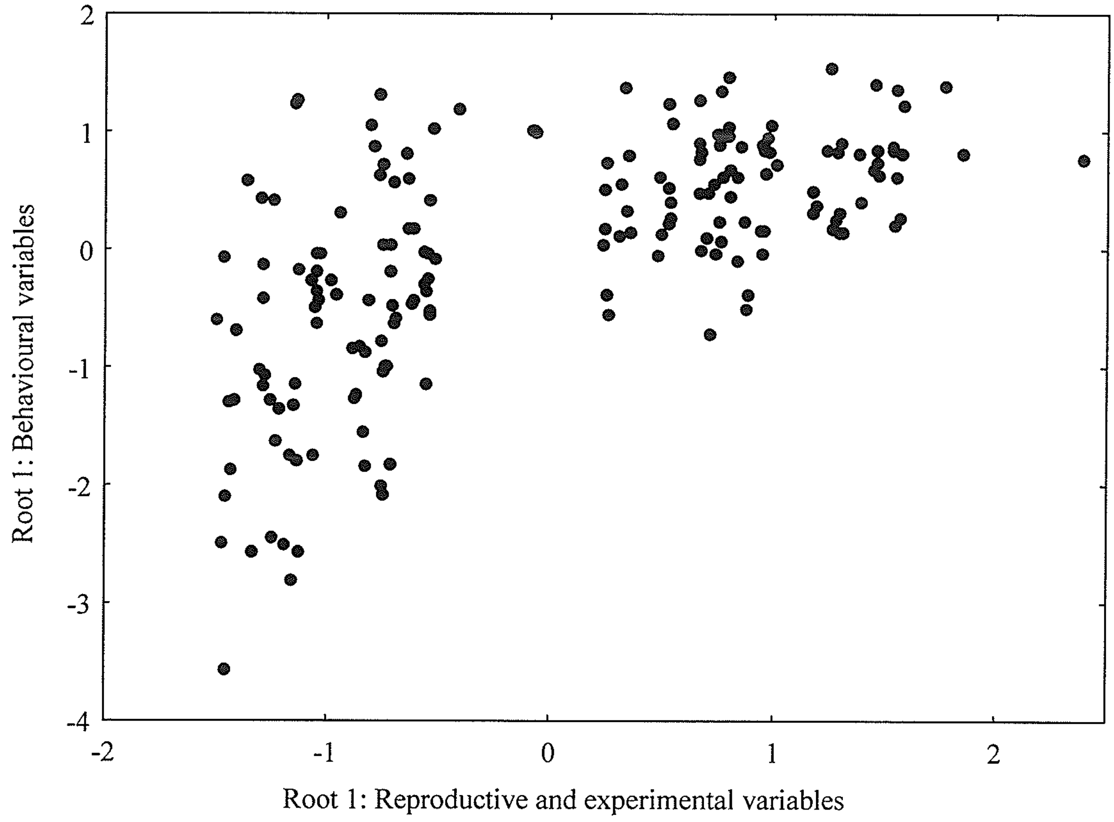


Figure 2.7. Factor Structure values in the Root 1 of the Canonical Analysis conducted on behavioural variables of Reed Warblers at Tomina (Italy) and reproductive/experimental variables (see text for the list of variables). Age of clutch/brood in the x-axis and *churr* call in the y-axis were the variables that most represented each data set in explaining the variation of nest defence.

toward parasites (Briskie and Sealy 1989). Lindholm and Thomas (2000) also reported that parasitized Reed Warblers responded to cuckoos with more bill snaps than birds in unparasitized populations, but they did not use controls. If bill snaps are part of mobbing to force a threatening species to leave the nest, it is puzzling that at Tomina, Reed Warblers rarely used them when threatened by a magpie, but preferentially used them in response to a cuckoo. Bill snaps in Reed Warblers are usually produced simultaneously with a forward movement so that the defending individual gets closer to the source of threat. As discussed below for other specific responses, the larger magpies might have been perceived as a greater risk by adults, reducing the likelihood of warblers performing this behaviour, an explanation also consistent with the fewer attacks elicited by this predator model.

Duckworth (1991) analyzed two alarm calls separately, *churr* and *rasp*, given by Reed Warblers toward cuckoos and toward predators of nestlings and adults. What I denoted as the *zirr* call probably was equivalent to Duckworth's *rasp* call, but this cannot be confirmed because spectrographs of the call were not published and Duckworth did not identify significant differences in frequencies of *rasp* calls elicited by the three models. Most alarm calls warn conspecifics of the presence of predators and, in fact, their monotonic sounds may promote reception of sound by conspecifics (Sloan and Hare 2004) and reduce their detectability by predators (Klump et al. 1986). The structure of the *zirr* call is a broadband sound characterized by loud noises with a wide frequency range and repeated in long bouts (cf. Aubin and Brémond 1989, Neudorf and Sealy 2002, Gill and Sealy 2004). Such characteristics are common in mobbing or assembly calls and in distress calls (Marler 1955, Klump and Shalter 1984, Neudorf and Sealy 1992); however, they function quite differently. Distress calls seem to be directed to predators to startle them into releasing their prey (Driver and Humphries 1969, Neudorf and Sealy 2002), whereas assembly calls are directed toward conspecifics that would be recruited to mob the predator and force it to leave the area (Inglis et al. 1982, Bradbury and Vehrecamp 1998). Examples are provided in Blackbirds (*Turdus merula*), Mistle Thrushes (*T. viscivorus*), Stonechats (*Saxicola torquata*), but also Forest Guenons (*Cercopithecus cephus*), which, with their broadband calls, recruit other animals (Marler 1959). Support for this function comes from this study where significantly more other individuals were attracted to the focal nest when Reed Warblers defended it against the cuckoo, when mostly *zirr* calls were uttered. Moreover, this difference disappeared during the nestling stage when the frequency of *zirr* calls significantly decreased. Most individuals recruited were conspecifics but during nine of the 30 cuckoo presentations Great Reed Warblers (*A. arundinaceus*) also arrived vocalizing loudly and struck the model so hard that feathers were dislodged from the crown and nape (such damage was never observed during Reed Warbler attacks).

As well as physical injuries, mobbing may confuse the threatening individual (Curio 1978) and there are indications that the larger the mobbing group the greater the likelihood the predator will retreat (Robinson 1985), which would reduce the impact of predation (Pavey and Smyth 1998). The benefits of coloniality in marsh-nesting birds have been explained by mutual nest defence and not by predator satiation or selfish-herd effects (Picman et al. 1988, 2002). Moreover, recruitment of other mobbing individuals has been correlated with a reduced probability that the same predator would revisit the area (Lima 2002). Mobbing group size might have been influenced by the local nesting density (Andersson 1976, Robinson 1985), and thus by the number of individuals, conspecific and heterospecific, close to the “attacked” nest. However, if nesting density were important solely in forming mob, I would have recorded birds attracted at the nest when all three model species were presented. Instead, only cuckoo presentations resulted with significantly more birds attracted by the defending pair, which, in turn, uttered significantly more *zirr* calls than they did when confronted with predators or non-threatening species. My findings strongly suggest that Reed Warblers recognize cuckoos near their nests and they modulate their defensive responses relative to the level of threat they pose across the nesting cycle. In fact, results of univariate analyses and the single PCAs revealed a significant decrease in aggressive behaviours toward cuckoos during the nestling stage so that the overall variance in the nestling stage was similar to that in response to the nonthreatening pigeon.

Reed Warblers responded to magpies by singing much of the time and frequently uttering *huit* calls. Apart from these vocalizations, during laying/incubation stages, their defence did not involve conspicuous behaviours as they were away from the model most of the time but, when visible, watched it silently. However, during the nestling stage, they changed perches around the model and the nest more often, but rarely attacked or mobbed closely. Reed Warblers do not perform “true” distraction displays (Impevoken 1962, Wyllie 1975, Duckworth 1991, Lindholm and Thomas 2000, Honza et al. 2004, Dyrcz and Halupka 2006); however, “zigzagging” around a predator has been suggested to serve the same function, thus attracting attention to themselves and drawing the predator away from the nest (Greig-Smith 1980). The univariate analyses revealed these differences, but the PCAs did not identify differential defence toward magpie models between egg and nestling stages. An optimal defence is probably a compromise between its efficacy in thwarting the predator and the level of risk assumed in the attack (Montgomerie and Weatherhead 1988, Burgham and Picman 1989). In contrast to cuckoos, magpies also kill adult passerines (Holyoak 1968, Birkhead 1991) and they are larger (Cramp 1992), so defence at close quarters would impose a risk of death or severe injury (Gochfeld 1984). Moreover, although Reed Warblers were parasitized at a frequency of 16%, depredation on their nestlings was 7% (Tab. 2.2), which suggests lower selection pressure for a high-intensity defence toward nestling predators.

Consistent nest defence over the entire nesting cycle was recorded in the responses elicited by the pigeon models. Intensities of most behaviours were intermediate between those recorded in response to the cuckoo and magpie. During both nesting stages, the behaviours that best described Reed Warbler responses to pigeons were indicated by the single PCAs as bill snaps and *churr* calls, the same behaviours that characterized defence against cuckoos during the nestling stage only. Pigeons did not elicit significantly different responses between incubation and nestling stages, except for an increase in *churr* calls. Such a significant increase involved the responses to all three model species, which indicates that, contrary to the *zirr* call and the other defensive behaviours, the *churr* call was elicited by any model in the presence of young in the nest. Some calls elicited during nest defence by other avian species silence the offspring (Greig-Smith 1980, McLean and Rhodes 1991, Haskell 1999, Gill and Sealy 2003). Begging and large broods increase the predation rate (Leech and Leonard 1997) and parental calls that elicit crouching and silencing seem to increase the survival of young (Haskell 1994). Whether the structure of the *churr* call contains information used by young to become less active and vocal should be tested with a functional reference study. With the use of playbacks it would be possible, in fact, to determine whether a call conveys signals that trigger in call recipients a consistent response to specific threatening contexts (Seyfarth et al. 1980, Gill and Sealy 2003, Sloan et al. 2005).

Reed Warblers responded differently to cuckoos and nonthreatening species. Honza et al. (2004), on the other hand, reported that Reed Warblers responded similarly to cuckoo and pigeon models. The differences in these results may reflect different methodological approaches, because in the present study, responses to pigeons were also generally similar to those elicited by cuckoos, i.e., Reed Warblers bill snapped and alarm called to both species. However, upon analyzing alarm calls separately and quantifying the frequency of these and the other behaviours, I identified different responses toward the two species. The general consensus for an optimal defence is that its intensity is shaped by the efficacy of the parent to deter predation but also by the threat the predator poses to the adults (Greig-Smith 1980, Montgomerie and Weatherhead 1988, Burgham and Picman 1989). Stonechats (*Saxicola torquata*) call from exposed perches more often and loudly when nest predators are nearby but hide and call quietly when threatened by species that may capture them (Greig-Smith 1980). Results from the present study provided the basis for suggesting that Reed Warblers adhere to this general scheme.

Reed Warblers responded more aggressively to cuckoos, which do not prey on adults, but responded less aggressively to species that might prey on them (Holyoak 1968, Birkhead 1991, Cramp 1992). Similar results were found among Yellow Warblers, which provide the best documented case of threat recognition between brood parasites and nest predators (Hobson et al. 1988; Hobson and Sealy 1989; Briskie et al. 1990, 1992; Gill and Sealy 1996, 2003, 2004; Gill et al. 1997a; Sealy et al. 1998). Yellow Warblers in the first trials with the brood parasites preferentially elicited *seet* calls, nest-protection behaviour and close attacks, which have been suggested to deter cowbirds more effectively, whereas the larger nest predators were rarely attacked and warblers remained at 2-5 m away performing distraction displays, which suggests they were perceived as a greater risk for adults (Gill and Sealy 1996). In parallel with the present results, mobbing at close quarters, attacking with loud *zirr* calls, and bill snaps might have been responses that posed too much risk when facing a potential adult predator but not toward a parasite, whereas frequent perch changes might serve as distraction displays, thus luring nest predators away. Efficiency of recruiting and, therefore, of *zirr* calls, in deterring parasitism events and of perch changes in deterring nest predation are questions that will be addressed in Chapter 5.

Effects of Reproductive Variables and Experimental Conditions

The Canonical Analysis showed that the number of researcher visits and time of day nests were tested did not affect the level of responsiveness of Reed Warblers. Although others have indicated that defence wanes or increases following multiple exposure (Knight and Temple 1986b), I did not detect this. The nesting avifauna at Tomina is habituated to humans due to the activity of the banding station operating among the same reed beds. Exposing Reed Warblers to models throughout the day also did not affect the intensity of their response, despite indications that warblers are more likely to encounter cuckoos in the afternoon (Davies 2000). However, I recorded parasitism events during the morning, as did Honza et al. (2002), which suggests encounters occur all day and explains the lack of effect of time of day on defence.

Most Reed Warbler responses apparently were independent of the number and age of eggs/nestlings, as well as of the time of season the models were presented. In other words, the numbers of *zirr* calls, bill snaps and strikes specifically in response to the cuckoo models were similar regardless of clutch size, stage of incubation or hatching, and despite the cuckoo "visits" in May or July. The only exception to this scenario was that Reed Warblers uttered more *churr* calls as their offspring matured. This is in accordance with numerous researcher who have shown that defence increases as offspring age (Andersson et al. 1980, Winkler 1987, Burgham and Picman 1989). The same analysis did not point to the time of the season as an explanation for this increase, which suggests that the increased frequency of *churr* calls depended on the higher expected survival of older offspring rather than the diminished renesting potential later in the season. The *churr* call was the only variable that significantly increased through the nesting cycle independently of the species confronted.

Patterson et al. (1980) suggested that an optimal nest defence is shaped by the interaction between stimulus and reproductive values. They revealed that nest defence of White-crowned Sparrows (*Zonotrichia leucophrys*) was influenced by the level of threat posed by a species (i.e., stimulus value). Moreover, future reproductive opportunities and size/age of the clutch/brood being defended (i.e., reproductive value) interacted with the stimulus factor resulting in differently modulated nest defence expressions (Patterson et al. 1980). Operating in tandem, these two components influence the intensity of defence: the discriminatory ability allowed an individual to invest its defensive effort in species that were a real danger, whereas the size and age of the clutch/brood elicited an adjustment in the intensity of defence when confronted with the same threat. Nest defence modulation in Reed Warblers apparently was not influenced by the interaction of these two components, but each of them seemed to control defence intensity independently. Reed Warbler responses were influenced mostly by the threat posed to the nest or to the adults. At the same time, nest defence intensity was independent of the reproductive value of the defending individuals. In one exception, the *churr* call was indiscriminately uttered toward all threats and dependent only on offspring age.

In conclusion, I described Reed Warbler nest defence in the presence of different threats. Individuals modulated the intensity of their defence according to the threat posed but generally not according to their reproductive potential. The different strategies adopted toward the different threats might have been selected on the basis of their efficacy to deter parasitism and predation events, but only further studies investigating the fitness outcome of the defending individuals can address the ultimate causes of this differential nest defence.

CHAPTER 3

ROLE OF EXPERIENCE IN NEST DEFENCE

INTRODUCTION

Responses to predators involve trade-offs between the costs of time and energy necessary to perform the behaviours and the benefits derived from possibly evading or deterring the predators (Lima and Dill 1990, Caro 2005). Among these behaviours are defences performed by parents to protect their offspring (Montgomerie and Weatherhead 1988). Responding ineffectively to nest predators may lower the individual's fitness through loss of offspring or injury to itself, which compromises future reproductive attempts (Patterson et al. 1980, Montgomerie and Weatherhead 1988). Conversely, to assess a threat specifically and respond with an intensity in accord with the risk posed would enhance fitness (Patterson et al. 1980, Ferrari et al. 2006). In fact, enemy discrimination allows several species to respond specifically to different threats and, in some cases, this ability is genetically determined (McLean and Rhodes 1991, Hawkins et al. 2004). Acquisition and maintenance of fine-tuned antipredator behaviour can also result from the ability of an animal to perceive a causal relationship between predators and the aversive events following their encounter (Conover 1987, Curio 1988, Shriner 1999, Reudink et al. 2007). Flexibility gained through experience may be advantageous for populations living in conditions where predation pressure fluctuates (Johnston 1982, Heyes 1994, Laland et al. 1996, Shettleworth 1998).

Under natural conditions, learning is considered to be represented by the ability of an animal to adjust its behaviour to specific demands (Johnston 1982, Shettleworth

1998). Plasticity in behaviour, facilitated by individual experiences, is adaptive because organisms can exploit their environmental resources more efficiently, an important determinant of longevity, especially in so-called K-selected species (Johnston 1982). As with any other trait, behavioural plasticity includes costly components. Incompetence and greater vulnerability during the learning period are some of the costs implicit in experience-dependent behaviour, along with much more complex neural structures necessary for processing, storing and retrieving information (Shettleworth 1993, 1998). These costs seem to be outweighed, however, by the benefits accrued when environmental pressures change frequently (Johnston 1982, Laland et al. 1996). For example, the ability to adopt different foraging strategies seems to have evolved in species that inhabit low-competition, temperate zones and occupy wider ecological niches. All of these factors determine the temporal and spatial fluctuations of trophic availabilities and, therefore, promote the exploitation of diverse resources via learned adjustments (Klopfer 1959, Lefebvre and Giraldeau 1996).

Most studies of adaptive advantages of learning new strategies in changing ecological contexts have focused on foraging (Giraldeau et al. 1994), song learning (West and King 1988), or alarm communication (Coss and Owings 1985). Under fluctuating conditions, comparative studies have shown that individuals changed their responses after learning from individual experiences (Giraldeau et al. 1994) and that the learned behaviour was adaptively advantageous (Williams et al. 1993). In contrast, in more stable environments, behavioural flexibility was not favoured instead (Greenberg 1989, Dukas and Real 1991). Antipredator behaviour is also shaped by experience (Curio 1978, Curio et al. 1983, Caro 2005).

A comprehensive ecological study of the role of experience in the acquisition of adaptive antipredator responses is constrained by the difficulty in rigorously assessing predation pressure and identifying fitness consequences of specific antipredator behaviours (Lind and Cresswell 2005). Varying predation pressure and threat characteristics may selectively determine whether an individual benefits from adjustable antipredator responses (Coss and Owing 1985). We often rely on indirect measures of predation pressure and these uncertain assessments may lead to misinterpretation (Urton and Hobson 2005, Murray and Patterson 2006, Souttou et al. 2006). Further, it has been recently pointed out that there are significant difficulties in determining the fitness consequences of antipredator responses because individual optimal responses might depend, for example, on the habitat where the predator is encountered (Lind and Cresswell 2005). This limitation would preclude assessment of whether a changed response following a predation attempt results in a higher fitness (Lima 1998).

In this study, I overcame these constraints and investigated nest defence responses toward a specific threat, an avian brood parasite. Defence of the nest occurs in one spot which removes spatial variables that may influence individual responses (Martin 1993). While it is difficult to assess the pressure exerted by one predator as the cues left on a depredated nest rarely identify the predator, parasitism frequency is more easily estimated, especially when only one parasite is involved (Rothstein 1975a; Sealy 1994, 1995; Davies 1999).

Whenever an adaptive specialization is suspected, other species that are subjected to similar ecological pressures should be tested (Shettleworth 1993, Lefebvre and Giraldeau 1996). A comparative approach is based on evidence of evolutionary divergence or convergence of the trait of interest tested across phyletic groups and with respect to particular sets of environmental conditions (Shettleworth 1993). Ecological factors that vary over a long period or that present fixed patterns in an individual lifetime are not considered biologically relevant agents for the selection of behavioural plasticity (Johnston 1982). As an example, Coss and Owings (1985) compared the ability of refining anti-snake responses among different species of ground squirrels living in different habitats (from Alaska to California) and exposed to different species of snakes. The differential learning ability has been explained by selection resulting from the different rate of snake predation to which each species of ground squirrel were exposed to (Coss and Owings 1985).

In a similar vein, I investigated two species of passeriformes, Yellow Warbler and Reed Warbler, hosts of the brood-parasitic Brown-headed Cowbird (hereafter "cowbird") and Common Cuckoo (hereafter "cuckoo"), respectively. These hosts may experience parasitism pressure that varies among years (Goossen and Sealy 1982, Weatherhead 1989, Brooke et al. 1998, Woolfenden et al. 2004). Like nest predation, brood parasitism lowers the reproductive performance of hosts (Payne 1977, Davies and Brooke 1988, Sealy 1992, Lorenzana and Sealy 1999), and specific nest defence responses that can reduce the probability of a parasitism event in the first place have been suggested to enhance fitness (Molnár 1944, Dawkins and Krebs 1979, Davies and Brooke 1988, Sealy et al. 1998). These species are both able to discriminate between the parasite and other threatening or non-threatening species by responding with specific defensive behaviours (Burgham and Picman 1989; Gill and Sealy 1996, 2003; Chapter 2). There is indirect evidence that defensive responses of Yellow and Reed warblers are shaped by experience

(Smith et al. 1984, McLean and Maloney 1998, Briskie et al. 1992, Lindholm and Thomas 2000, Gill and Sealy 2004); however, this hypothesis has not been tested.

In this study, I tested whether Yellow Warblers and Reed Warblers modify their defensive responses toward the parasite species after I provided them experimental experiences simulating events of parasitism. I also discuss their behavioural changes in relation to the parasitism pressure suffered by each species during the investigation period.

MATERIALS AND METHODS

Yellow Warblers were studied at the Delta Marsh, Manitoba, from May through July 2002 and 2003, and Reed Warblers were tested at Tomina (Modena, Italy) from April through July 2004 and 2005. Details of the study areas and monitoring of nests were given in Chapter 1.

Model Presentations and Clutch Manipulations

Yellow Warblers and Reed Warblers were exposed to models that simulated parasitism events. Unparasitized and not-depredated nests were presented with models of brood parasites and non-threatening species at the laying or incubation stage. Twenty minutes before presenting a model, I set up a blind (see description in Chapter 2) 2-5 m from the nest at which I recorded the adult warblers' responses. Trials on Yellow Warblers were performed between 0500 and 1930 Central Standard Time (CST), and those on Reed Warblers between 0600 and 1900 Central European Time (CET).

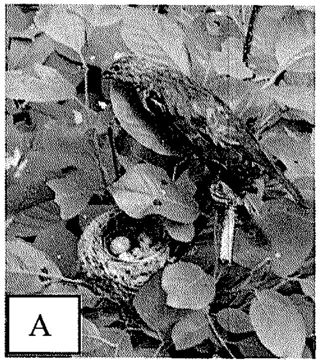
Because I predicted a change in the nest defensive responses (see Behavioural Analyses) after a simulated event of parasitism, to verify that this change was not due to my experimental protocol *per se* (*i.e.*, sensitization, *sensu* Mackintosh 1983), I tested a control group by presenting a model of the brood parasite and a non-threatening species one day, and I repeated the same two presentations another day. Exposed to these multiple presentations, this group of nests was a double control for the entire experiment. Although it was exposed to the same number of presentations of the treatment groups, this was a group exposed to no training, and, secondly, it was exposed to differently threatening species, whose different perception was an important element to validate the potential training effects. Presentations lasted two 2 and 5 min on the first and second days, respectively. As the first presentations were reduced to 2 min to avoid problems of habituation with repeated exposures (Knight and Temple 1986a, b), only the first 2 minutes of the second presentations were analyzed to allow statistical comparisons. Yellow Warblers were tested with models of a female cowbird and Fox Sparrow (hereafter "sparrow"); the sparrow served as a control because it is similar in size (32g, Dunning 1984) and shape to the female cowbird (39 g) and it does not threaten Yellow Warblers.

Reed Warblers were tested with models of a cuckoo and Rock Pigeon (hereafter "pigeon"); the pigeon served as a control because this species is similar to cuckoos in length (31-34 cm versus 32-34 cm, respectively), plumage colouration (medium gray), but pigeons are heavier than cuckoos (200-302 g versus 106-133 g, respectively, Cramp 1992), and they pose no threat to Reed Warblers (Goodwin 1983). Models were taxidermic mounts perched or clipped to vegetation or attached to wooden poles (painted to match the vegetation) of different lengths and placed within 0.5 m facing the nest rim. Each nest in the control group was, therefore, exposed on one day to the parasite and control models, and the next day to the same two stimuli (Tab. 3.1 and 3.2). Inclement weather forced some nests to be tested with the models over more than two days, but this difference did not affect the results (see Results) and, therefore, these nests were included in the analyses. To minimize pseudoreplication (Hurlbert 1984), I had two models of each type and the one used for a given trial was chosen randomly via coin toss. The presentation order of model species was randomly determined via coin toss in Yellow Warblers and by drawing sticks of different lengths in Reed Warblers because, for the purpose of the experiment described in Chapter 2, the choice was among three models.

To assess whether experience modified the intensity of the specific responses toward brood parasites, I simulated visits by parasites to host nests using repeated model presentations. Cowbirds and cuckoos frequently remove one egg from host nests as well as parasitize them. Cowbird parasitism and egg removal are usually separate events (Neudorf and Sealy 1994, Sealy 1992, Sealy et al. 2000, Granfors et al. 2001), whereas cuckoos usually remove one host egg seconds before laying their eggs (Wyllie 1981). For this reason, I conducted two separate treatments on Yellow Warblers and one treatment on Reed Warblers. Each treatment was performed on different groups of nests, thus each nest was tested with only one treatment. Each treatment consisted of three trial periods: BEFORE, TRAINING, and AFTER (Tab. 3.1 and 3.2). During the BEFORE and AFTER trials, I presented the cowbird or cuckoo model following the same protocol used in the control group, thus with the parasite perched near the nest. The goal of the TRAINING

Table 3.1. Experimental and control treatments to which four groups of Yellow Warblers were exposed in 2002 and 2003 at Delta Marsh (Manitoba).

Day	Trial	Parasitism	Egg Removal	Social Interaction	Control
1	BEFORE	Perched cowbird [A]	Perched cowbird [A]	Perched cowbird [A]	Perched cowbird [A] Perched sparrow [B]
2-3	TRAINING	Parasitizing cowbird [C] + 1 cowbird egg model	Egg removing cowbird [D] - 1 warbler egg	Warblers defending from cowbird [E] + *seet* call playback	No trials
4	AFTER	Perched cowbird [A]	Perched cowbird [A]	Perched cowbird [A]	Perched cowbird [A] Perched sparrow [B]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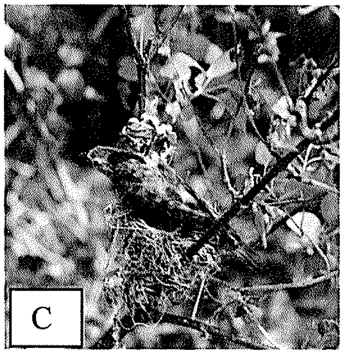
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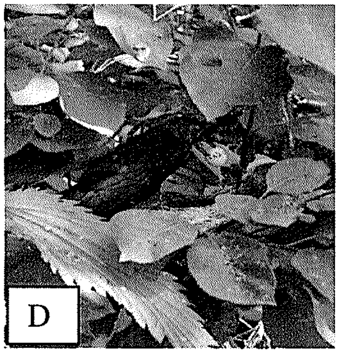
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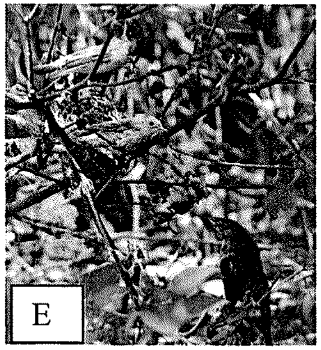
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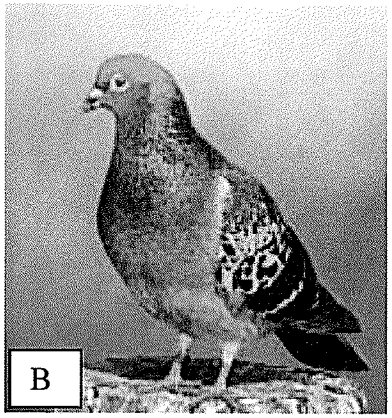
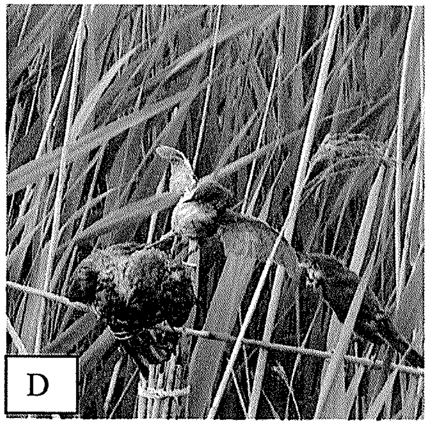
Table 3.2. Experimental and control treatments to which three groups of Reed Warblers were exposed in 2004 and 2005 at the Tomina, (Italy).

Day	Trial	Parasitism	Social Interaction	Control
1	BEFORE	Perched cuckoo[A]	Perched cuckoo[A]	Perched cuckoo[A]
				Perched pigeon[B]
2-3	TRAINING	Parasitizing cuckoo[C] + 1 cuckoo egg model - 1 warbler egg	Warblers defending from cuckoo[D] + *zirr* call playback	No trials
4	AFTER	Perched cuckoo[A]	Perched cuckoo[A]	Perched cuckoo[A]
				Perched pigeon[B]





period was to expose hosts to repeated experiences, specific for each treatment. To minimize habituation (Knight and Temple 1986a, b), I performed only two days of training and reduced the duration of each trial to 1 minute. One group of Yellow Warbler nests was provided with an experimental parasitism experience, i.e., a cowbird placed on the nest in laying position (Tab. 3.1). After the first training presentation, I inserted a cowbird egg model into the nest and removed it at the end of the AFTER presentation. Another group of Yellow Warbler nests was provided with an experimental egg removal experience where a cowbird model was placed on the nest rim with a warbler egg model affixed on the tip of its bill (Tab. 3.1). After the initial training, I removed a warbler egg from the nest and put it in another warbler nest at a similar nesting stage, and retuned it at the end of the experiment. The Reed Warblers were provided with an experimental parasitism where the cuckoo model in laying position was placed on the nest with a warbler egg model affixed on the tip of its bill (Tab.3.2). After the initial training, a cuckoo egg model was added to the clutches and one warbler egg was removed and put in another warbler nest at a similar nesting stage. At the end of the experiment, the cuckoo egg model was removed and the warbler egg was returned to its own nest.

I followed the protocol suggested by Rothstein (1975b) to make the parasite egg models with plaster-of-Paris and I painted them with non-toxic acrylic paints to match the appearance of the parasite eggs (Underwood et al. 2004b, Underwood and Sealy 2006b). Egg models were similar in size to cowbird eggs at Delta Marsh (mean ± SE, 21.1 x 16.4 ± 0.1 x 0.1 mm, n = 73; Sealy 1992) and to cuckoo eggs recorded mostly in Northern Italy (21.9 x 16.4 ± 0.14 x 0.11 mm, n = 73; A. Pazzuconi, pers. comm.).

Behavioural Analyses

During model presentations, the birds' responses were spoken into a cassette recorder and transcribed later. The testing interval began when the female warbler arrived within 5 m of the focal nest. Male and female Yellow Warblers are readily distinguished on the basis of the plumage coloration and pattern (Lowther et al. 1999), whereas female Reed Warblers were identified because they did not sing (see Chapter 2 for additional details on identification of Reed Warbler females).

To quantify nest defence in Yellow Warblers, I recorded the following categories of behaviour (Hobson and Sealy 1989, Gill and Sealy 1996): (1) *chip* calls; (2) perch changes; (3) *seet* calls; (4) strikes; (5) close flights; (6) displacement activities; (7) silent watching; (8) nest-protection behaviour; (9) distraction displays; and (10) out of sight. Categories 1-5 were quantified as the number of times they occurred in the trial, whereas categories 6-10 were recorded as the number of 10-s intervals in which they occurred. Previous studies have shown that Yellow Warblers respond differentially to cowbirds and sparrows, the first preferentially eliciting *seet* calls, attacks at the model and nest-protection behaviour (Gill and Sealy 1996, 2003, 2004; Tab. 1.1). Accordingly, my predictions were that, if such defensive behaviours were experience-based, Yellow Warblers would have increased these behaviours after the simulated events of parasitism, whereas they would not change their defensive intensities when not exposed to training (control group). Moreover, according to my hypothesis, *seet* calls, attacks at the models and nest-protection behaviour were expected to be significantly less frequent when sparrow models were presented.

To quantify nest defence in Reed Warblers, I recorded the behavioural categories listed in the Table 2.1. Reed Warblers respond to cuckoos mostly with *zirr* calls, bill snaps and attacks at the models, whereas *churr* calls were more frequently uttered toward pigeons (Chapter 2). As with Yellow Warblers, I predicted an increased number of these behaviours after a simulated event of parasitism, and unchanged defensive expression among the Reed Warblers not exposed to training (control group). Finally, I predicted that these behaviours would be expressed less intensely when pigeons were presented.

Statistical Analyses

To test whether responses elicited by the two models differed between the first and second presentations in the control group, I performed a factorial ANOVA (Underwood 1997), treating the model type (parasite versus nonthreatening species) and the presentation (first versus second) as factors, whereas each behaviour was treated as a dependent variable. Variables were square-root transformed and their variance was tested using Cochran's C test. Despite the transformation, some variables still had a heterogeneous variance (Cochran's C test, $P < 0.05$); however, as no significant differences were detected (see Results), they could not represent Type I errors (Underwood 1997). To test whether over two presentations the two warblers still responded differently to the two species, I used the Wilcoxon Matched-Pairs test (Zar 1999).

As a further control, to test whether the responses recorded in the first presentation of the control group and the BEFORE trials of the experimental treatments were similar, I performed a one-way ANOVA (Underwood 1997), which considered the treatments (controls versus experiences) as factors and the behaviours as dependent variables. To test the effect of the experimental experience provided to each warbler group, I compared the responses recorded in the BEFORE trials with those recorded in the AFTER trials using a Mann-Whitney U-test. I used this test because the responses given during the BEFORE trials recorded in all the nest groups were not significantly different (see Results) and, therefore I pooled them. Once pooled, the comparison of the responses between BEFORE and AFTER trials were not from the same individuals, and, therefore, this led me to use the Mann-Whitney U-test (Zar 1999).

Finally, to analyze the changes in nest defence that took into account all of the behavioural variables, I performed a Principal Component Analysis (PCA, Digby and Kempton 1987) on the responses recorded in the first presentations and those recorded after the experimental experiences provided to warblers.

RESULTS

Yellow Warblers

I initiated tests on 146 Yellow Warbler nests, but 24 nests were depredated and two were parasitized before results could be obtained; therefore, they were not included in the analyses. The following analysis therefore involved 40 nests tested with the control treatment, another 40 with the parasitism treatment, and 40 with the egg removal treatment.

Responses obtained in the control group were not significantly different between the first and second model presentations of cowbird and sparrow models (ANOVA, all $P > 0.05$, Tab. 3.3). Nonsignificant differences persisted when the nests tested over more than two days were removed from the analyses. Over the entire period of exposure,

Table 3.3. Results of ANOVA comparing responses recorded in the first and second exposures to cowbird and sparrow models in the control group of 40 Yellow Warbler nests at Delta Marsh (Manitoba).

Nest defence behaviours	Model Presentation	Cowbird	Sparrow	Species x Presentation Effect	
		mean ± SE	mean ± SE	F	P
Chip call	First	6.05 ± 1.70	10.50 ± 2.84	0.763	0.384
	Second	8.53 ± 2.62	6.93 ± 2.05		
Perch change	First	4.85 ± 0.73	8.28 ± 0.97	0.002	0.967
	Second	5.95 ± 1.11	9.40 ± 1.38		
Seet call	First	22.35 ± 4.35	8.08 ± 2.97	0.080	0.777
	Second	21.78 ± 4.69	8.70 ± 3.04		
Strike	First	1.80 ± 0.59	0.10 ± 0.07	1.204	0.274
	Second	1.40 ± 0.63	0.35 ± 0.18		
Close flight	First	0.35 ± 0.21	0.25 ± 0.12	0.182	0.670
	Second	0.28 ± 0.18	0.10 ± 0.06		
Displacement activities	First	0.30 ± 0.17	0.73 ± 0.26	0.037	0.848
	Second	0.23 ± 0.11	0.65 ± 0.16		
Silent Watching	First	0.05 ± 0.05	0.10 ± 0.07	0.705	0.403
	Second	0.23 ± 0.20	0.08 ± 0.08		
Nest-protection	First	5.18 ± 0.76	1.65 ± 0.59	2.633	0.107
	Second	4.20 ± 0.81	2.68 ± 0.71		
Distraction displays	First	0.93 ± 0.27	0.43 ± 0.19	0.078	0.780
	Second	1.05 ± 0.35	0.43 ± 0.18		
Out of sight	First	1.70 ± 0.41	2.65 ± 0.54	0.022	0.883
	Second	1.13 ± 0.38	1.98 ± 0.43		

Yellow Warblers responded differently to cowbirds and sparrows for seven out of 10 variables analyzed (Tab. 3.4).

Responses recorded in the first cowbird presentations of the control group and in the BEFORE trials were not significantly different for all the variables analyzed (ANOVA, all $P > 0.05$, Tab. 3.5), thus they were pooled and compared with the responses in the AFTER trials. Before the treatments, 89% of the variation in Yellow Warbler responses to cowbird models were explained by the first (PC1) and second (PC2) components of PCA, where the highest weights of the PC1 fell on *seet* and *chip* calls, strike, and perch changes (Tab. 3.6).

After being presented with the female cowbird on their nest, Yellow Warblers significantly increased the number of *seet* calls and spent less time out of sight (Tab. 3.7, Fig. 3.1). They also struck the model more frequently (BEFORE [mean ± SE] = 3.0 ± 0.6, AFTER = 6.1 ± 1.7), spent more time on the nest (BEFORE = 3.9 ± 0.4, AFTER = 4.65 ± 0.7) and performed more distraction displays (BEFORE = 1.1 ± 0.2, AFTER = 1.8 ± 0.4), but these differences were not statistically significant (Tab. 3.7). None of the other behavioural categories changed significantly after the parasitism experience was provided ($P > 0.05$, Tab. 3.7). Multivariate analysis explained 86% of the defence variation as PC1 and PC2, and the behaviours most representative of the PC1 were the same recorded for defence expressed during the first model presentations (Tab. 3.6).

After encountering a cowbird model with an egg model affixed on its bill, Yellow Warblers significantly increased the number of *seet* calls and struck and mobbed the model more frequently (BEFORE = 0.3 ± 0.1, AFTER = 0.5 ± 0.2, Tab. 3.7, Fig. 3.2). They also spent more time performing distraction displays but less time out of sight (Tab.

Table 3.4. Results of Wilcoxon Matched-Pairs tests comparing responses recorded in the control group of Yellow Warblers at Delta Marsh (Manitoba) and elicited by cowbird and sparrow models.

	Cowbird	Sparrow	Z	P
n	80	80		
Chip call	7.29 ± 1.56	8.71 ± 1.75	1.654	0.098
Perch change	5.40 ± 0.66	8.84 ± 0.84	3.982	< 0.001
Seet call	22.06 ± 3.18	8.39 ± 2.11	5.245	< 0.001
Strike	1.60 ± 0.43	0.23 ± 0.10	3.557	< 0.001
Close flight	0.31 ± 0.14	0.18 ± 0.07	1.156	0.248
Displacement activities	0.26 ± 0.10	0.69 ± 0.15	2.895	0.004
Silent watching	0.14 ± 0.10	0.09 ± 0.05	0.105	0.917
Nest-protection	4.69 ± 0.55	2.16 ± 0.46	4.497	< 0.001
Distraction display	0.99 ± 0.22	0.43 ± 0.13	2.165	0.030
Out of sight	1.41 ± 0.28	2.31 ± 0.35	2.901	0.004

Table 3.5. ANOVA results relative to the Yellow Warbler responses elicited by perched cowbird models during the BEFORE trials in the Parasitism, Egg Removal, and Control treatments, at Delta Marsh (Manitoba).

		Chip call			Perch change			*Seet* call		
Source	df	MS	F	P	MS	F	P	MS	F	P
Treatment	2	544.01	2.02	0.14	57.81	2.01	0.14	488.81	0.87	0.42
Error	117	269.39			28.75			564.08		
		Strike			Close flights			Displacement activities		
		MS	F	P	MS	F	P	MS	F	P
Treatment	2	44.31	0.94	0.39	0.47	0.39	0.68	0.21	0.19	0.83
Error	117	47.32			1.22			1.08		
		Silent watching			Nest-protection behaviour			Distraction display		
		MS	F	P	MS	F	P	MS	F	P
Treatment	2	0.10	1.02	0.36	55.36	2.57	0.08	0.76	0.16	0.85
Error	117	0.10			21.55			4.61		
		Out of sight								
		MS	F	P						
Treatment	2	1.23	0.21	0.81						
Error	117	6.01								

Table 3.6. The first four behaviours of the PC1 and PC2 in the Principal Component Analysis that explained most of the variation in defence responses of Yellow Warblers at Delta Marsh (Manitoba) toward a perched cowbird model presented before and after simulations of a cowbird parasitizing their nests or removing an egg (AFTER PARASITISM). Eigenvector values are given for each variable.

	BEFORE		AFTER PARASITISM		AFTER EGG REMOVAL	
PC1	*Seet* call	0.92	*Seet* call	0.95	*Seet* call	-0.96
	Chip call	-0.37	*Chip* call	-0.26	*Chip* call	0.24
	Strike	0.07	Strike	0.16	Strike	-0.13
	Perch change	-0.07	Perch change	-0.11	Distraction display	-0.04
PC2	*Chip* call	-0.92	*Chip* call	0.94	*Chip* call	-0.83
	Seet call	-0.37	*Seet* call	0.28	Strike	0.44
	Nest protection	0.08	Perch change	0.11	*Seet* call	-0.26
	Strike	0.02	Nest protection	-0.10	Perch change	-0.16

Table 3.7. Results of Mann-Whitney U-test comparing responses of Yellow Warblers at Delta Marsh (Manitoba) to perched cowbird models before (n = 120) and after simulations of parasitism (n = 40) and egg removal (n = 40) events.

	BEFORE versus Parasitism AFTER		BEFORE versus Egg Removal AFTER	
	Z	P	Z	P
Chip call	1.500	0.134	0.594	0.552
Perch Change	0.732	0.464	-0.182	0.855
Seet call	-2.157	0.031	-2.627	0.009
Strike	-1.828	0.068	-2.958	0.003
Close flight	-0.954	0.340	-2.739	0.006
Displacement activities	1.554	0.120	1.091	0.275
Silent Watching	1.006	0.314	1.006	0.314
Nest protection	-0.864	0.387	-0.142	0.887
Distraction display	-1.464	0.143	-2.460	0.014
Out of sight	2.467	0.014	2.536	0.011

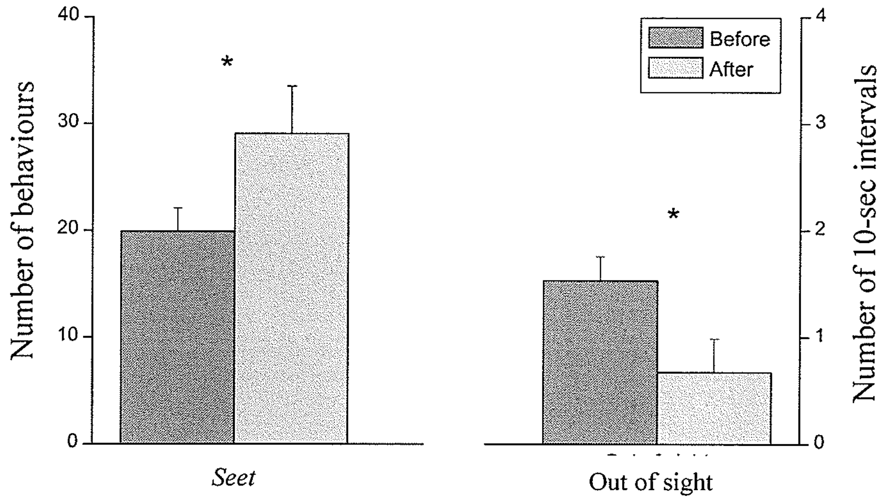


Figure 3.1. Significant differences in the responses (mean + SE) recorded before and after the experimental parasitism at 40 Yellow Warbler nests at Delta Marsh (Manitoba). Mann-Whitney U-test, * $P \leq 0.05$.

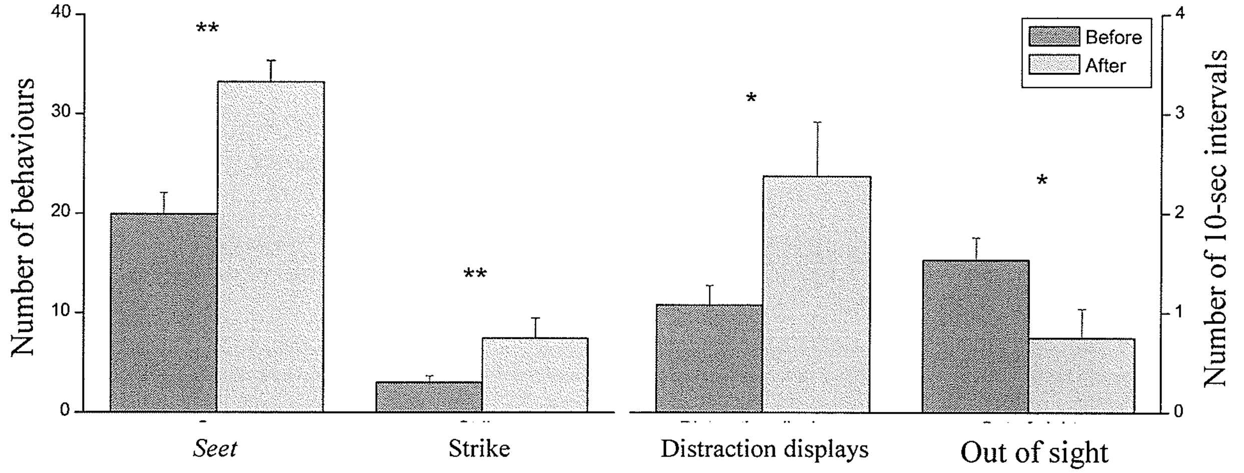


Figure 3.2. Significant differences in the responses (mean + SE) recorded before and after the egg removal experience provided at Yellow Warbler nests at Delta Marsh (Manitoba). Mann-Whitney U-test, * $P \leq 0.05$, ** $P \leq 0.01$.

3.7, Fig. 3.2). No other significant changes in the other variables were detected (all $P > 0.05$, Tab. 3.7). PC1 and PC2 explained 86% of the defence variation when Yellow Warblers were exposed to the egg removal treatment. In comparison with the results obtained on the responses recorded before providing experiences, distraction displays replaced perch changes among the behaviours most representative of the PC1 (Tab. 3.6). Moreover, in PC2, attacking the model replaced *seet* calls recorded before the training as the behaviour with the second highest Eigenvectors (Tab. 3.6).

Reed Warblers

I initiated tests on 84 Reed Warbler nests, but nine nests were depredated, one was parasitized, one was deserted, and one was destroyed by inclement weather, and thus were not included in the analyses. Moreover, during 14 model presentations, I could not identify the focal female, and thus, those responses were not included in the analyses. Responses of the control group therefore consisted of 33 and 30 trials for the first and second exposures to pigeon models, respectively, and 32 and 30 trials for the first and second exposures to cuckoo models, respectively. The analyses pertaining to the group tested with the parasitism experience included the responses recorded during 39 and 32 trials BEFORE and AFTER model presentations, respectively.

There were no significant differences between the first and second model presentations of cuckoo and pigeon models in the control group (ANOVA, $P > 0.05$, Tab. 3.8). Non-significant differences persisted when the nests tested over more than two days were removed from the analyses. Over the entire period of exposure, Reed Warblers responded differently to cuckoos and pigeons for nine out of 11 variables analyzed (Tab. 3.9).

Table 3.8. Results of ANOVA comparisons between the responses recorded in the first and second exposures to cuckoo and pigeon models in the control group of Reed Warbler nests at Tomina (Italy). For each model, sample sizes of first and second presentations are in parentheses.

Nest defence behaviours	Model Presentation	Cuckoo (32, 30) mean ± SE	Pigeon (33, 30) mean ± SE	Species x Presentation Effect F	P
Perch change	First	22.38 ± 2.54	13.91 ± 1.99	0.106	0.745
	Second	27.07 ± 2.91	14.90 ± 2.08		
Strike	First	0.78 ± 0.72	0.00 ± 0.00	2.092	0.151
	Second	3.57 ± 2.52	0.03 ± 0.03		
Bill snap	First	23.44 ± 4.91	5.55 ± 2.44	0.220	0.640
	Second	35.97 ± 5.92	9.90 ± 3.95		
Close flight	First	0.38 ± 0.18	0.09 ± 0.07	0.424	0.516
	Second	0.53 ± 0.22	0.03 ± 0.03		
Churr call	First	5.78 ± 1.85	9.06 ± 1.99	2.009	0.159
	Second	6.53 ± 2.53	18.23 ± 4.29		
Huit call	First	1.94 ± 0.56	4.45 ± 1.25	1.248	0.266
	Second	0.37 ± 0.20	4.50 ± 1.42		
Song	First	0.72 ± 0.26	1.36 ± 0.33	0.017	0.897
	Second	0.40 ± 0.17	1.00 ± 0.29		
Other birds	First	0.50 ± 0.19	0.15 ± 0.08	0.349	0.556
	Second	0.47 ± 0.17	0.03 ± 0.03		
Zirr call	First	6.63 ± 0.94	2.12 ± 0.71	1.671	0.199
	Second	8.90 ± 0.88	2.43 ± 0.81		
Silent watching	First	0.13 ± 0.10	1.21 ± 0.41	1.057	0.306
	Second	0.07 ± 0.05	0.60 ± 0.26		
Out of sight	First	0.09 ± 0.05	0.27 ± 0.13	0.135	0.714
	Second	0.07 ± 0.05	0.30 ± 0.15		

Table 3.9. Results of Wilcoxon Matched-Pairs tests comparing the responses recorded in the control group of Reed Warblers at Tomina (Italy) and elicited by cuckoo and pigeon models.

	Cuckoo	Pigeon	Z	P
n	62	63		
Perch change	24.65 ± 1.93	14.38 ± 1.43	5.276	< 0.001
Strike	2.13 ± 1.28	0.02 ± 0.02	3.059	0.002
Bill snap	29.50 ± 3.88	7.62 ± 2.27	5.900	< 0.001
Close flight	0.45 ± 0.14	0.06 ± 0.04	2.794	0.005
Churr call	6.15 ± 1.54	13.43 ± 2.34	3.134	0.002
Huit call	1.18 ± 0.32	4.48 ± 0.93	3.212	0.001
Song	0.56 ± 0.16	1.19 ± 0.22	2.459	0.014
Other birds	0.48 ± 0.13	0.10 ± 0.04	2.840	0.005
Zirr call	7.73 ± 0.66	2.27 ± 0.53	5.304	< 0.001
Silent watching	0.10 ± 0.05	0.92 ± 0.25	2.987	0.003
Out of sight	0.08 ± 0.03	0.29 ± 0.10	2.192	0.028

Responses recorded in the first cuckoo presentation of the control group and in the BEFORE trials did not differ significantly in all the variables analyzed (ANOVA, all P > 0.05, Tab. 3.10), except for perch change, which differed between the number recorded in the first presentation of the control group (22.4 ± 2.5) and that of the BEFORE trials (14.0 ± 1.6, Mann-Whitney U-test, Z = -2.6, P = 0.010). Consequently, all variables, except the number of perch changes, were pooled and compared with the responses recorded in the AFTER trials. PCA run with perch changes excluded (given the significant difference reported above) explained 94% of the variation recorded during the first exposure to cuckoo models with bill snaps, *churr, zirr* and *huit* calls representing mostly the PC1 (Tab. 3.11).

After being subjected to the parasitism experience, Reed Warblers increased the number of strikes, bill snaps, and *churr* calls (Fig. 3.3), but these, along with all the other variables, were not significantly different from the responses before the parasitism experience was provided (Tab. 3.12). PC1 and PC2 explained 97% of the variation of the responses of Reed Warblers exposed to experimental parasitism. In comparison with the results obtained on the responses recorded before the experimental experiences, the number of strikes replaced *huit* calls among the behaviours most representative of the PC1 (Tab. 3.11).

DISCUSSION

Defensive Responses Affected by Experience

Yellow Warblers modified their nest defence after a threatening experience, in this case either a simulated parasitism or an egg removal event at their nest. They

Table 3.10. ANOVA results relative to the Reed Warbler responses elicited by perched cuckoo models during the BEFORE trials in the Parasitism and Control treatments at Tomina (Italy).

		Perch Change			Strike			Bill snap		
Source	df	MS	F	P	MS	F	P	MS	F	P
Treatment	1	1240.46	8.29	0.01	2.77	0.28	0.60	1749.31	2.80	0.10
Error	69	149.63			9.81			623.67		
		Close flight			*Churr* call			*Huit* call		
		MS	F	P	MS	F	P	MS	F	P
Treatment	1	1.07	1.76	0.19	385.04	1.71	0.20	1.82	0.11	0.74
Error	69	0.61			225.64			16.31		
		Song			Other birds			*Zirr* call		
		MS	F	P	MS	F	P	MS	F	P
Treatment	1	0.56	0.26	0.61	0.23	0.26	0.61	0.33	0.01	0.91
Error	69	2.17			0.89			25.82		
		Silent Watching			Out of sight					
		MS	F	P	MS	F	P			
Treatment	1	0.01	0.05	0.83	9.28	2.44	0.12			
Error	69	0.19			3.80					

Table 3.11. The first four behaviours of the PC1 and PC2 in the Principal Component Analysis that explained most of the variation in defence responses of Reed Warblers at Tomina (Italy) toward a perched cuckoo model presented before and after simulations of cuckoo parasitism and egg removal (AFTER PARASITISM). Eigenvectors values are given for each variable.

	BEFORE		AFTER PARASITISM	
PC1	Bill snap	-0.97	Bill snap	0.97
	Churr call	0.21	*Churr* call	-0.23
	Zirr call	-0.09	*Zirr* call	0.09
	Huit call	0.03	Strike	0.03
PC2	*Churr* call	0.97	*Churr* call	-0.97
	Bill snap	0.22	Bill snap	-0.24
	Zirr call	-0.07	*Zirr* call	0.08
	Out of sight	0.07	*Huit* call	0.04

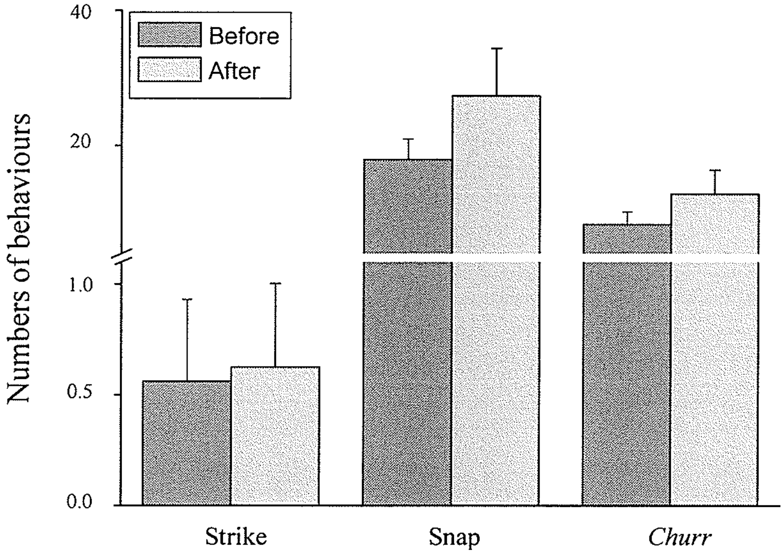


Figure 3.3. Comparisons of some responses (mean + SE) recorded before and after experimental parasitism provided to a group of Reed Warblers at Tomina (Italy) (n BEFORE = 39, n AFTER = 32). Mann-Whitney U-test, non significant differences ($P > 0.05$) for all the variables analyzed.

Table 3.12. Results of Mann-Whitney U-test comparing responses of Reed Warblers at Tomina (Italy) to perched cuckoo models before (n = 71) and after simulations of parasitism (n = 32) events.

	Z	P
Strike	-0.694	0.488
Bill snap	-0.142	0.887
Close flight	-0.049	0.961
Churr call	-0.251	0.801
Huit call	0.946	0.344
Song	0.500	0.617
Other birds	-1.158	0.247
Zirr call	-0.499	0.618
Silent watching	0.353	0.724
Out of sight	-0.814	0.415

significantly increased the number of *seet* calls, attacks on the models, and distraction displays, all of which have been reported as the responses directed specifically toward cowbirds (Hobson and Sealy 1989; Briskie et al. 1990, 1992; Gill and Sealy 1996, 2003, 2004). The different behaviours elicited by cowbirds and sparrows, consistent with previous studies (Tab. 1.1), and the unchanged responses in the untrained control group eliminated the likelihood of any possible artefact due to the multiple-exposure protocol used in this study. In a past investigation, yearlings Yellow Warblers responded to cowbirds with fewer *seet* calls, perch changes and attacks on the models, and they spent less time on the nest than older females (Hobson and Sealy 1989). Moreover, a similar low intensity was recorded among Yellow Warbler females in an unparasitized population compared with females sympatric with cowbirds (Briskie et al. 1992). In these earlier studies, it was suggested that learning shaped the recognition ability of Yellow Warblers, although this hypothesis was not tested specifically. In my study, I found that a threatening experience primes Yellow Warblers to react more aggressively during successive encounters with the threat.

While personal experience has been shown to play a fundamental role in the adjustment of several behaviours (e.g., foraging: Giraldeau et al. 1994, mate choice: Dugatkin 1996, habitat selection: Doligez et al. 2002), testing whether this also applies to defensive behaviours has proven problematic in natural settings. Captive Tammar Wallabies (*Macropus eugenii*) increased their responsiveness toward a Fox (*Vulpes vulpes*) model after this had been associated with the risk of a human capture (Griffin et al. 2001). Moreover, Fathead Minnows (*Pimephales promelas*, Chivers and Smith 1994), New Zealand Robins (*Petroica australis*, Maloney and McLean 1995), and Houbara

Bustards (*Chlamydotis macqueenii*, van Heezik et al. 1999) increased the intensity of their defensive responses toward novel predators only after they had observed tutors responding defensively or had been exposed to conspecific alarm signals. These investigators, however, tested the role of observing conspecifics, and not personal experience, in shaping defensive responses. The paucity of these specific studies is due to logistic difficulties in designing repeated predator-prey encounters and to ethical concerns in staging experiments that would require exposing animals to dangerous conditions (Griffin 2004). In this investigation, I overcame these difficulties by simulating events of parasitism that do not impose life-threatening events and I also showed that defensive responses and their intensities are shaped by information specifically acquired during personal experiences.

Yellow Warblers, reacted much less aggressively to a perched cowbird when they had been "trained" with a female cowbird in laying position than when they had encountered a cowbird carrying an egg in its bill. In fact, after they had encountered a female cowbird sitting on their nest on each of two days, Yellow Warblers significantly increased the number of *seet* calls to a perched cowbird, but their overall response did not change, as is evident from the results of the multivariate analysis. On the contrary, after the egg removal experience, when a perched model of a cowbird was close to their nests, Yellow Warblers increased not only the number of *seet* calls but also strikes and distraction displays, a change in the overall nest defence detected by the multivariate analysis. As defensive responses are costly and indicated to be adjusted accordingly to the risk each threat poses (Montgomerie and Weatherhead 1988, Redondo 1989), the greater use of them after an experience of egg removal indicates that Yellow Warblers perceived the egg removal event as a greater risk for their clutch.

Differential learning that resulted from the two different experiences can be explained considering both the nature of the learning mechanisms involved in the two treatments provided to warblers and their contextual significance. The parasitism treatment required Yellow Warblers to learn via association. Since the first controlled scientific studies of learning (Thorndike 1898, Pavlov 1927), animals have shown the ability to associate species and aversive events, to store these relationships and to modify their behaviour accordingly in successive similar contexts. A specific tone did not elicit antipredator responses in Golden-mantled Squirrels (*Spermophilus lateralis*) until it was paired with a predator (Shriner 1999). Thus, individuals made an association between an event (i.e., the tone) and a threat (i.e., the predator) so that the first predicted the occurrence of the second. This information was remembered and squirrels altered their vigilance accordingly when the tone was played again (Shriner 1999). For this association to occur, it was necessary that squirrels could distinguish among different tones and the species presented. After a cowbird was presented in laying position and a cowbird egg model was placed inside their nest, Yellow Warblers should have made an association between the presence of the cowbird and its egg, remembered this relationship the next time they encountered a perched cowbird at their nest, and responded more aggressively. Although Yellow Warblers possess a sophisticated ability to discriminate among species (Burgham and Picman 1989; Hobson and Sealy 1989; Gill and Sealy 1996, 2003, 2004), there are indications that they cannot make a visual association where a foreign egg is involved. In fact, they are not able to recognize their own eggs (Sealy and Lorenzana 1998), which suggests that they cannot visually recognize cowbird eggs in their clutch, although a recent finding indicates that they reject non-egg-shaped objects possibly as a manifestation of nest sanitation (Guigueno 2007). Moreover, while Yellow Warblers often desert parasitized nests or bury the parasite's eggs under new nest material (Sealy 1995, Mico 1998), the presence of a laying cowbird model and the introduction of a real cowbird egg in their nest elicited a significantly lower rate of desertion and burial than in naturally parasitized nests (Sealy 1995), which is consistent with the inability to make this association. Unable to recognize cowbird eggs, a threat for their clutch, the association needed to trigger a behavioural change cannot occur (Heyes 1994, Shettleworth 1998). The more intense reaction shown after the egg removal event can be explained by the operation of another learning mechanism not independent of associative abilities but more easily triggered by perceptual features of the stimulus. While associative learning requires individuals to relate two different stimuli in a cause-effect relationship, perceptual learning occurs when these two stimuli occur simultaneously during the individual experience (Heyes 1994, Shettleworth 1998). For example, in an investigation of the "dear enemy phenomenon" (Wilson 1975), perceptual learning was deemed to be responsible for a decline in aggressiveness of Bullfrogs (*Rana catesbeiana*) toward conspecifics when they were exposed to the same calls coming from the same locations (Bee and Gerhardt 2001). Same calls-same locations were both necessary to represent the stimulus that triggered the observed behavioural change. The treatment of egg removal provided Yellow Warblers with a cue that contained information of threat *per se* (cowbird on the nest rim with an egg in its bill), and thus they could distinguish a threat at a perceptual level (Reed 1985, Heyes 1994).

But why do Yellow Warblers modify their defences on perceptual and not on associative bases? Learning triggered by association is more expensive than that based on perception (Shettleworth 1993, 1998) and, as such, it will only be selected when the costs outweigh the benefits. During this investigation, parasitism was the second major cause of reduced reproductive success in Yellow Warblers (17%), followed by egg predation that accounted for 55% of all nests that failed (Tab. 1.3). Learning abilities are selected on the basis of biological relevance, which in turn, depends on the relationship between the nature of the threat and the likelihood of encountering it in the environment (Shettleworth 1998). Rare events may have exceptional relevance in changing individual responses (Heyes 1994). When survival is not urgently threatened, however, the more frequently a threat is encountered, the more biologically relevant the event, and the more immediate the behavioural change (Shettleworth 1998). For example, within the same population of California Ground Squirrels, Coss and Owings (1985) found a diminished learning ability toward the Pacific Gopher Snake (*Pituophis melanoleucus catenifer*) that rarely preys upon adults, whereas the more dangerous Northern Pacific Rattlesnake (*Crotalus viridis oreganus*) elicited rapidly learned antipredator behaviours. In Yellow Warblers, nest predation was more frequent than parasitism, which suggests that its greater prevalence may promote behavioural adjustments toward this threat (i.e., egg removal) and explains the milder effect of the parasitism experience on the refinement of defence. In other words, results indicated that learning abilities of Yellow Warblers are more fine-tuned toward egg depredation than parasitism events.

Defensive Responses not Affected by Experience

Reed Warblers did not change their nest defence behaviours after they were provided with a parasitism experience and there was a minimum change in the variables that explained the overall nest defence variance. The lack of learning by Reed Warblers after the parasitism experience is puzzling, because results from past studies were consistent with a learned component in their ability to discriminate enemies (Tab. 1.2). Individuals in populations sympatric with cuckoos reacted to parasite models more intensely than those in allopatric populations (Lindholm and Thomas 2000); females tended to abandon their experimentally parasitized nests (Davies and Brooke 1988) and males increased their nest guarding (Davies et al. 2003) if both were presented with a cuckoo model. Moreover, the consistent response of Reed Warblers after experimental parasitism is even more puzzling because this treatment included an egg removal experience so that the overall experiment provided perceptual cues conveying the danger of the situation (i.e., cuckoo with an egg affixed on its bill), which did not require an associative ability. Moreover, Reed Warblers were exposed to a frequency of parasitism of 16% and of nest predation of 22%, pressures more than sufficient to trigger specific defensive behaviour (Rothstein 1990, Martin 1995).

The ecological significance of learning is not only that organisms adjust quickly to environmental variability but also that their behavioural plasticity nets them fitness benefits (Johnston 1982, Boyd and Richerson 1996). One of the greatest costs of learned behaviours is the incompetence to respond to specific stimuli during the learning period (Shettleworth 1993, 1998). During this time, organisms may respond suboptimally or even maladaptively during trial-and-error attempts to cope with a specific stimulus (Boyd and Richerson 1985, Laland 2004). However, animals may reduce their period of personal learning and, in turn, the trial-and-error costs by relying on public information, provided via experience acquired in observing conspecifics (Heyes 1994). Individuals should ignore personal information, thus knowledge acquired during personal experiences, when its use becomes more costly and error prone and, instead, they should rely on social information to cope with varying ecological demands (Boyd and Richerson 1985, 1988, Laland et al. 1996, Doligez et al. 2003, Reader 2004, Campobello and Hare 2007). Social learning has been indicated to be beneficial when social information is easily accessible, when social sources are reliable, and, finally, when the rate of environmental change is relatively low so that the social information does not become quickly outdated (Heyes 1994). Most support for these theoretical analyses comes from studies on the acquisition of foraging skills where, for example, European Starlings (*Sturnus vulgaris*) copied their tutors rather than sampling the environment by themselves when the first choice was more accessible (Templeton and Giraldeau 1996). Moreover, Giraldeau et al. (2002) suggested that when an individual observes several conspecifics responding consistently to an environmental stimulus, it would use this social information and ignore its own. In relatively predictable environments, similar results are shown for learning mate choices in Quail (*Coturnix japonica*, White and Galef 2000) and food preferences in Norway Rats (*Rattus norvegicus*, Galef and Whiskin 2004), but there are no specific investigations that have tested whether environmental conditions are factors promoting the preferential selection of social over individual learning for the refinement of defensive behaviours.

The pressures selecting for defensive responses in the Reed Warbler environment are consistent with the lack of individual learning detected in this study, as they appeared to be under consistent parasitism and nest predation across nesting years (Chapter 1). Moreover, Reed Warblers seem to match all of the above parameters that promote learning based on social rather than personal cues. When they encountered a parasite at their nest, they responded consistently with the *zirr* call (Chapter 2), which is emitted specifically toward the cuckoo especially during the laying/incubation stages; thus conspecifics receive a reliable cue of the threat represented by the cuckoo. Secondly, the nesting density and variation in the frequency range of this alarm call allow easy localization of the signaler by other nesting individuals as shown by other birds recruited when model cuckoos were presented (Chapter 2). Although Reed Warblers seem to be subject to an ecological context that would not favour individual learning (Boyd and Richerson 1985, 1988, Laland 2004), little investigation of the effect of personal information on the acquisition of antipredator responses does not allow a comparison. Most reserchers have focused on socially acquired defensive responses and on their proximate causes, but little attention has been paid to the role of the environmental fluctuations as selective agents favouring individual or social learning of defensive responses (Curio et al. 1978, Curio 1988, McLean et al. 1999, van Heezik et al. 1999). In his review, Griffin (2004) challenged the assumption that fearful events, such as an imminent predator attack, should always result in a rapid acquisition of efficient and fixed antipredator responses. He further argued that it might be disadvantageous to incorporate mobbing responses in permanently fixed patterns because the stimuli for mobbing may change over time. This suggests indirectly, once again, that in nest defence, asocial learning would be advantageous under a relatively stable threat frequency.

In conclusions, although suggested by previous studies (Tab. 1.1 and 1.2), the occurrence of a learned component in the discrimination ability of Yellow Warblers and Reed Warblers has never been tested. I provided the first results that Yellow Warblers learned from their experiences and identified the threat of egg removal as the experience that most effectively triggered high-intensity responses towards cowbirds. On the contrary, Reed Warblers did not rely on personal information to refine their defensive reactions toward cuckoos. Moreover, there is little evidence of individual learning as a mechanism to induce behavioural changes in defensive behaviours among wild organisms and no one has focused on nest defence in particular. These results represent some of the few empirical results that support the theoretical predictions of an ecological approach for the selection of individual learning applied to defensive behaviours (Boyd and Richerson 1985, Heyes 1994, Laland 2004). In fact, differential temporal variation of parasitism and predation in two populations, fluctuations in Yellow Warblers and stability in Reed Warblers (Chapter 1), are consistent with those factors suggested to favour individual learning and to select against it, respectively. However, further tests on socially acquired nest defence are necessary and, in fact, they will be presented in the next chapter.

CHAPTER 4

SOCIAL LEARNING IN NEST DEFENCE

INTRODUCTION

Social learning modifies behavioural repertoires of animals after they have observed other individuals (usually conspecifics) or interacted with products emanating from those individuals (e.g., alarm substances). Behaviours acquired via this process are called socially induced (Heyes 1994). Many studies have shed light on the mechanisms and adaptive advantages of social learning in comparison with individual or asocial learning (Boyd and Richerson 1985, Laland et al. 1993, Giraldeau et al. 1994, Galef 1995, Danchin et al. 2004).

Individual learners acquire or refine their behaviours after successive trial-and-error attempts. This learning phase is a vulnerable period because it involves suboptimal or even maladaptive behaviours before competence is attained, i.e., "practice makes perfect" (Johnston 1982, Shettleworth 1998). Animals that instead process information by observing conspecifics may acquire already honed behaviours, thus, they may reduce the number of mistakes and shorten their vulnerable period and, as such, they may be more advantaged than individual learners (Galef and Whiskin 1997). From an ecological perspective, social learning requires specific contexts to provide such advantages (Boyd and Richerson 1988). Interactions with more experienced individuals should be readily accessible, thus, population density should allow frequent intraspecific interactions (Laland et al. 1996), and environmental pressures should be moderately stable (Boyd and Richerson 1988). If the environment is unstable, social learners risk acquiring a less-optimal behaviour because the information may be outdated (Giraldeau et al. 2002, Lefebvre and Giraldeau 1996).

In recent studies, the role of environmental fluctuation has been confirmed as the main selective agent for socially induced food preferences (Laland and Williams 1998), habitat selection (Doligez et al. 2004), and mate choice (Freeberg et al. 1999). The study of socially acquired antipredator behaviour has not benefited from the numerous empirical results and theoretical models that have greatly advanced our understanding of the dynamics of social learning as it refines other behaviours (Galef and Allen 1995, Reader 2004, Galef and Laland 2005). As most studies of social learning have been conducted in laboratory settings, there has been an increasing interest in validating results on socially induced behaviours among individuals exposed to stimuli in natural contexts (Conover 1987, Shettleworth 1993, Carlier and Lefebvre 1997, Annett and Pierotti 1999, Griffin 2004).

Socially transmitted antipredator behaviour, in the form of mobbing behaviour, was first investigated by Curio et al. (1978) who showed that European Blackbirds (*Turdus merula*) could be induced to mob an object or a species that was previously perceived as a neutral stimulus. Especially for fish and mammals, social learning studies have progressed in asking not only whether these species acquire socially induced behaviours (Chivers and Smith 1994, Griffin and Evans 2003), but also whether socially induced avoidance responses can be "unlearned" (Ferrari and Chivers 2006) or increase survival during predator encounters (Mirza and Chivers 2002). In birds, no other investigations on social learning have been conducted since the pioneering investigations of Curio and his colleagues (Vieth et al. 1980, Curio 1988) and no studies specifically address social learning in nest defence. Most recent studies on birds have instead been designed to mediate problems of conservation concern and, therefore, as Griffin (2004) has pointed out, the focus has been to maximize the likelihood of learning using both individual and social training regimes rather than identifying and understanding mechanisms that underlie the processing of behavioural information (Maloney and McLean 1995, van Heezik et al. 1999).

In the present investigation, I tested whether two wild populations of passerine birds modified their nest defence by letting them observe simulations of conspecifics defending their nest from intruding brood parasites. Using groups not exposed to training regimes as controls, I teased apart the effects of observing other individuals from the potential effects of the experimental treatments *per se* and the effects of individual learning on changes in nest defence. The species studied were the Yellow Warbler, host of the socially parasitic Brown-headed Cowbird, and Reed Warbler, host of the Common Cuckoo.

Yellow Warblers and Reed Warblers are frequently parasitized (Lowther et al. 1999, Davies 2000) and both species recognize their respective brood parasite with specific behavioural responses and alarm calls (Gill and Sealy 2004, Chapter 2). There are indications that the acquisition of these responses involves learning (Briskie et al. 1992, Lindholm and Thomas 2000), but whether the refinement of their defence is attained via social interactions has not been tested. Both species nest at high density (Woolfenden et al. 2003, pers. obs.), which allows them to observe conspecifics when they are visited by the parasites and, therefore, to learn by observing them. I predicted that Yellow Warblers and Reed Warblers would refine their nest defence, quantified as a higher level of aggressiveness, after observing other individuals responding to cowbirds and cuckoos, respectively.

MATERIALS AND METHODS

Yellow Warblers were studied at the Delta Marsh Field Station (Portage la Prairie, Manitoba, Canada) from May through July 2002 and 2003, whereas Reed Warblers were tested at Tomina (Modena, Italy) from April through July 2004 and 2005. Details of the study areas and methods used for searching and monitoring nests are given in Chapter 1.

Model Presentations and Playbacks

Yellow Warblers and Reed Warblers were presented models following the general protocol outlined in Chapter 3. The control group used in Chapter 3 also served as a control for this experiment, as it involved the presentation of a parasite and nonthreatening species model for two days without being exposed to any training (Tab. 3.1 and 3.2). Details of the protocol used for this group are given in Chapter 3 (pp. 62-65).

To determine whether observing conspecifics responding to a brood parasite at their nest triggers a different defensive behaviour, I simulated parasite visits to host nests using repeated model presentations. The social interaction treatment involved three trial periods: BEFORE, TRAINING, and AFTER. During the BEFORE and AFTER trials, I presented the parasite model following the same protocol used in the control group (Tab. 3.1 and 3.2). The goal of the TRAINING period was to allow Yellow Warblers and Reed Warblers to observe conspecifics responding to a parasite at their nest. To provide this experience, 20 minutes before presentation, I placed an experimental nest in a bush or among reeds about 3-5 m from the focal nest. The experimental nest was chosen randomly, via coin toss or draw of sticks of different lengths, among 2-3 natural warbler nests found abandoned during the same nesting season as the experimental trials. For Yellow Warblers, I used a Sony TMC 5000 EV tape recorder/player and, for Reed Warblers, a Sony MZ-N710 Mini Disk (MD) recorder/player for the following steps. Concealed in the vegetation, I placed Koss SA/35 loudspeakers connected to the Sony player about 0.5 m from the experimental nest. The blind from which I recorded the warbler response was placed about 2-5 m from the focal nest and 3-5 m from the experimental nest, so that I could see both nests. The pre-presentation set up lasted around 3 min from the time I arrived in the nest area. Once at least 20 min elapsed, I placed one parasite and two warbler models about 0.5 m from the experimental nest and I broadcast *seet* (Fig. 4.1) and *zirr* (Fig. 2.1b) calls to Yellow and Reed warblers, respectively, during the 2-min trial. I chose these vocalizations because they were preferentially uttered toward cowbirds (Gill and Sealy 2003, 2004) and cuckoos (see Chapter 2), respectively. The perched parasite was mounted in the same fashion as in the control presentations. The two warblers were mounted in aggressive posture with their wings and bills open, feathers on the crown ruffed, and one model was placed on the back of the parasite model to simulate natural attacks as photographed by Smith and Hosking (1955; Tab. 3.1 and 3.2). Playbacks of alarm calls were recorded at the beginning of 2002 and 2004 seasons during presentations of parasite models at nests not included in the subsequent experiments. Vocalizations were recorded with the Sony recorder and

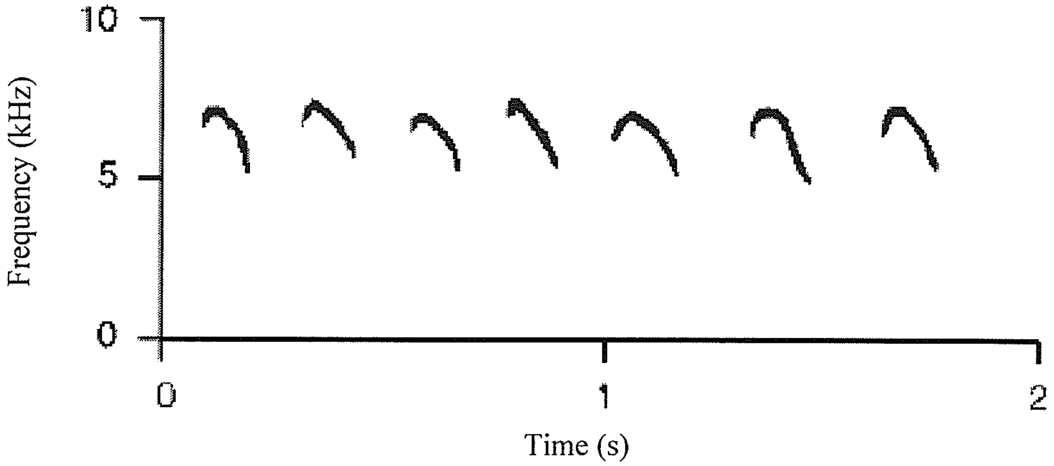


Figure 4.1. Spectrograph of the *seet* call of Yellow Warblers uttered when confronted with cowbird models at Delta Marsh, Manitoba (from Gill and Sealy 2003, Fig. 1A).

Sennheiser K3-U directional microphone placed about 1 m from the focal nest. I chose *seet* and *zirr* call recordings from among those with minimal background noise and reverberation to make two 5-min tracks. The tracks were transferred to 90-min TDK Type I audio cassettes and Sony premium 80 MDs using their respective Sony recorder/players and played back during the 2-min training trials. S*eet* and *zirr* calls were broadcast at amplitudes of 70 dB and 60 dB SPL (Sound Pressure Level), respectively, at 3-5 m from the focal nest, calibrated from about 10 calls/nest measured at 2-5 m from the warblers by a Realistic 33-2050 sound level meter (weighting C, response slow; n = number of nests, *seet* calls: mean ± sd = 68 ± 5 dB, n = 5 ; *zirr* calls: 59 ± 6 dB, n = 4).

The training trials were conducted over two consecutive days, therefore, each nest was exposed the first day to the BEFORE, the second and the third days to the TRAINING, and on the fourth day to the AFTER trials (Tab. 3.1 and 3.2). Due to inclement weather, a few nests did not receive the four trials on consecutive days; however, in the analyses, I tested whether this change affected the results (see Results).

Behavioural Analyses

During model presentations, observations were spoken into a cassette recorder and transcribed later. The testing interval began when the female arrived within 5 m from the focal nest. Female Yellow Warblers are easily distinguished from males on the basis of the plumage colouration (Lowther et al. 1999), whereas Reed Warbler females were identified by their lack of song among their vocalizations (see Chapter 2 for additional details on identification of Reed Warbler females). To quantify nest defence in Yellow and Reed warblers, I recorded the behavioural categories described in Chapter 3.

Statistical Analyses

The responses recorded in the control group were analyzed using the tests described in Chapter 3. To test whether the responses recorded in the first presentation of the control group and the BEFORE trials were similar, I performed a one-way ANOVA (Underwood 1997), considering the treatments (control versus social experience) as factors and the behaviours as dependant variables. To test for effect of the social interaction treatment, I compared the responses recorded in the BEFORE trials with those recorded in the AFTER trials using a Mann-Whitney U-test (Zar 1999). Finally, to analyze the changes in nest defence taking into account all behavioural variables, I performed Principal Component Analysis (PCA, Digby and Kempton 1987) on the responses recorded in the first presentations and those recorded after the social experience provided to warblers.

RESULTS

Yellow Warblers

I tested 98 Yellow Warbler nests, 14 of which were depredated and four which were parasitized before the end of the treatment; these nests were not included in the analyses. The analyses therefore included data from 40 nests tested with the control treatment and 40 with the social interaction treatment.

Responses obtained in the control group were not significantly different between the first and second model presentations of cowbird and sparrow models (ANOVA, P

> 0.05, Tab. 3.3). Over the entire period of exposure, Yellow Warblers responded differently to cowbirds and sparrows for seven out of 10 variables analyzed (Tab. 3.4).

Responses recorded in the first cowbird presentations of the control group and in the BEFORE trials were not significantly different for all the variables analyzed (ANOVA, all $P > 0.05$, Tab. 4.1); therefore, they were pooled and compared with the responses recorded in the AFTER trials. Before the social interaction treatment, PCA explained 91% (PC1 and PC2) of the total variation of defence observed in Yellow Warblers. *Seet* and *chip* calls, strikes and perch changes were those that accounted for the majority of the variation in the first component (Tab. 4.2).

After the social interaction treatment, Yellow Warblers significantly increased their mobbing of the model (BEFORE [mean ± SE] = 0.19 ± 0.1; AFTER = 0.25 ± 0.1, Tab. 4.3). They also uttered more *seet* calls (BEFORE = 21.6 ± 2.9; AFTER = 24.2 ± 3.4), spent more time on the nest (BEFORE = 4.7 ± 0.4, AFTER = 5.1 ± 0.7), and performed longer distraction displays (BEFORE = 1.0 ± 0.2, AFTER = 1.4 ± 0.4). These differences, however, were not statistically significant (Tab. 4.3). None of the other behaviours changed significantly after the social interaction treatment (all $P > 0.05$, Tab. 4.3). Multivariate analysis explained 92% of the variance in defensive behaviours along two PC axes, where the behaviours most representative of the PC1 were the same as those recorded for the defence expressed during the first model presentations, except that distraction displays replaced perch changes (Tab. 4.2).

Table 4.1. ANOVA results relative to the Yellow Warbler responses elicited by perched cowbird models during the BEFORE trials in the Social Interaction and Control treatments at Delta Marsh (Manitoba).

		Chip call			Perch change			*Seet* call		
Source	df	MS	F	P	MS	F	P	MS	F	P
Treatment	1	4.51	0.03	0.85	19.01	0.86	0.36	46.51	0.07	0.79
Error	78	133.61			22.04			681.63		
		Strike			Close flights			Displacement activities		
		MS	F	P	MS	F	P	MS	F	P
Treatment	1	59.51	1.72	0.19	2.11	2.35	0.13	1.51	1.13	0.29
Error	78	34.67			0.90			1.34		
		Silent watching			Nest-protection behaviour			Distraction display		
		MS	F	P	MS	F	P	MS	F	P
Treatment	1	0.11	0.71	0.40	15.31	0.68	0.41	0.20	0.06	0.80
Error	78	0.16			22.39			3.23		
		Out of sight								
		MS	F	P						
Treatment	1	3.61	0.45	0.51						
Error	78	8.11								

Table 4.2. The first four behaviours in the PC1 and PC2 of the Principal Component Analysis that explained most of the variation in defence responses of Yellow Warblers at Delta Marsh (Manitoba) toward a perched cowbird model presented before and after simulation of conspecifics defending their nest from a cowbird. Eigenvector values are given for each variable.

	BEFORE		AFTER	
PC1	*Seet* call	-0.97	*Seet* call	0.98
	Chip call	0.20	*Chip* call	-0.17
	Strike	-0.08	Strike	0.07
	Perch change	0.06	Distraction displays	0.06
PC2	*Chip* call	0.94	*Chip* call	0.92
	Seet call	0.22	Perch change	0.25
	Nest protection	-0.19	Nest protection	-0.24
	Perch change	0.15	*Seet* call	0.15

Table 4.3. Results of Mann-Whitney U-test comparing responses of Yellow Warblers at Delta Marsh (Manitoba) to perched cowbird models before (n = 80) and after simulations of conspecifics defending their nest from cowbird models (n = 40).

	Z	P
Chip call	0.474	0.635
Perch Change	0.714	0.475
Seet call	-1.502	0.133
Strike	-0.725	0.469
Close flight	-2.220	0.026
Displacement activities	0.974	0.330
Silent Watching	0.667	0.505
Nest protection	-0.370	0.711
Distraction display	-0.605	0.545
Out of sight	2.118	0.074

Reed Warblers

I tested 73 Reed Warbler nests, but three nests were depredated and three were parasitized before the treatments ended, and hence, they were not included in the analyses. During 13 model presentations I was unable to identify the focal female and data from these were not included in my analyses. Responses of the control group involved 33 and 30 trials for the first and second exposures to pigeon models, respectively, and 32 and 30 trials for the first and second exposures to cuckoo models, respectively. The analyses of nests tested with the social interaction treatment included the responses recorded during 34 and 28 trials of the BEFORE and AFTER model presentations, respectively.

Results from the control group showed no significant differences between the first and second model presentations of cuckoo and pigeon models (ANOVA, $P > 0.05$, Tab. 3.8). Over the entire period of exposure, Reed Warblers responded differently to cuckoos and pigeons for nine out of 11 variables analyzed (Tab. 3.9).

Responses recorded in the first cuckoo presentation of the control group and in the BEFORE trials did not differ significantly for the variables analyzed (ANOVA, all $P > 0.05$, Tab. 4.4); consequently, I pooled and compared them with the responses recorded in the AFTER trials. PCA explained 80% of the variation recorded during the first exposure to cuckoo models, which was mostly represented by bill snaps, *churr* calls, perch changes, and *zirr* calls in PC1 (Tab. 4.5).

After exposure to the social interaction treatment, Reed Warblers significantly changed more perches, bill snapped more, uttered more *zirr* calls, and significantly

Table 4.4. ANOVA results relative to the Reed Warbler responses elicited by perched cuckoo models during the BEFORE trials in the Parasitism and Social Interaction treatments at Tomina (Italy).

		Perch Change			Strike			Bill snap		
Source	df	MS	F	P	MS	F	P	MS	F	P
Treatment	1	294.67	1.60	0.21	269.36	1.18	0.28	198.98	0.20	0.66
Error	64	184.31			228.66			988.17		
		Close flight			*Churr* call			*Huit* call		
		MS	F	P	MS	F	P	MS	F	P
Treatment	1	1.09	1.89	0.17	1295.75	2.56	0.11	1.69	0.10	0.75
Error	64	0.58			505.27			16.59		
		Song			Other birds			*Zirr* call		
		MS	F	P	MS	F	P	MS	F	P
Treatment	1	2.21	1.41	0.24	0.13	0.10	0.75	0.86	0.03	0.86
Error	64	1.57			1.28			26.72		
		Silent Watching			Out of sight					
		MS	F	P	MS	F	P			
Treatment	1	0.07	0.41	0.53	1.11	1.84	0.18			
Error	64	0.18			0.60					

Table 4.5. The first four behaviours in the PC1 and PC2 of the Principal Component Analysis that explained most of the variation in defence responses of Reed Warblers at Tomina (Italy) toward a perched cowbird model presented before and after simulation of conspecifics defending their nest from a cuckoo. Eigenvector values are given for each variable.

	BEFORE		AFTER	
PC1	Bill snap	0.89	Bill snap	-0.94
	Churr call	-0.36	Strike	0.23
	Perch change	0.24	Perch change	-0.18
	Zirr call	0.08	*Churr* call	0.17
PC2	*Churr* call	-0.92	Strike	0.94
	Bill snap	-0.38	Bill snap	0.24
	Strike	0.12	Perch change	-0.18
	Perch change	0.33	*Churr* call	-0.15

decreased the number of *churr*, *huit* calls, and songs (Tab. 4.6, Fig. 4.2). PC1 and PC2 explained 83% of the total variation of defence in the Reed Warblers exposed to the social interaction treatment. The behaviours with the highest Eigenvectors of PC1 are shown in Table 4.5. Moreover, after training, strikes replaced *churr* calls as the primary behaviour explaining defence variation in the PC2 (Table 4.5).

DISCUSSION

Yellow Warblers were only weakly influenced by social experiences, whereas Reed Warblers significantly modified their responses toward a parasite after seeing conspecifics interacting with a cuckoo. Results on Reed Warblers are not surprising as social learning has been reported across several vertebrate taxa and suggested to confer fitness advantages (Chivers and Smith 1995, Griffin 2004). Fatheaded Minnows (*Pimephales promelas*) increased predator avoidance (i.e., spent more time under cover) when presented with a Pike (*Esox lucius*) if they had been previously exposed to this predator paired with minnow alarm substances (Chivers and Smith 1994). Birds are also able to acquire antipredator behaviours socially, but investigations have been limited to socially acquired mobbing in captive European Blackbirds (Curio et al. 1978) and in Ring-billed Gull (*Larus delawarensis*) colonies (Conover 1987), and investigations of learned nest defence did not differentiate between social and individual mechanisms of behavioural acquisition (Maloney and McLean 1995, van Heezik et al. 1999). The puzzling result of this investigation was that Yellow Warblers seemed little influenced by conspecifics to incorporate more intense responses in their defence.

Table 4.6. Results of Mann-Whitney U-test comparing responses of Reed Warblers at Tomina (Italy) to perched cuckoo models before (n = 66) and after simulations of conspecifics defending their nest from cuckoo models (n = 28).

	Z	P
Perch change	-2.796	0.005
Strike	-1.202	0.230
Bill snap	-1.995	0.046
Close flight	-0.416	0.678
Churr call	2.337	0.019
Huit call	2.698	0.007
Song	2.325	0.020
Other birds	1.005	0.315
Zirr call	-3.121	0.002
Silent watching	-0.781	0.435
Out of sight	0.185	0.853

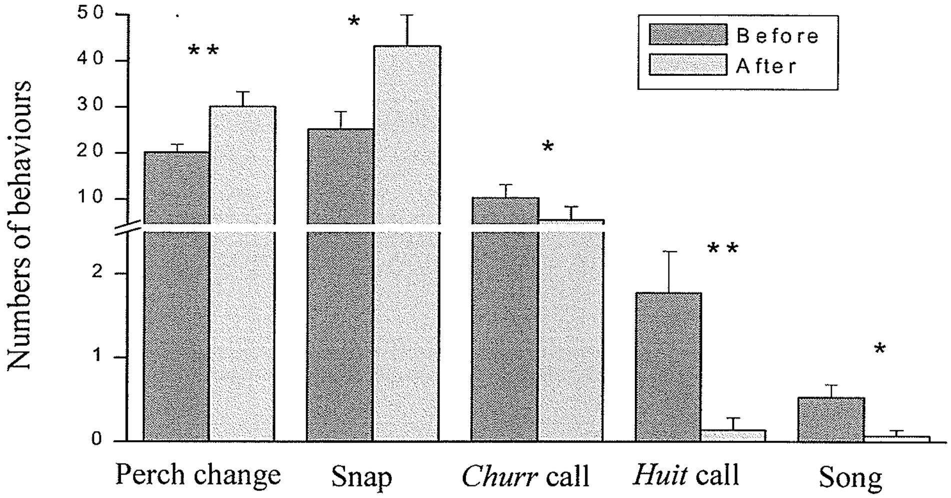


Figure 4.2. Comparisons between responses (mean + SE) recorded before and after the social experience provided to Reed Warblers at Tomina (Italy) (n BEFORE = 66, n AFTER = 28). Mann-Whitney U-test, * $P \leq 0.05$, ** $P \leq 0.01$.

Comparatively speaking, the differential use of social and personal information can be explained by examining ecologically relevant factors suggested to select for one form of learning over the other (Laland et al. 1993). In fact, social learning is considered adaptive only within particular ecological contexts (Shettleworth 1998, Lefebvre and Giraldeau 1996, DeWitt and Scheiner 2004). Galef (1995) and Galef and Whiskin (1997) have suggested that social learning can be approached as any other meme, the unit described by Dawkins (1976) as the behavioural equivalent of a gene. As such, three elements promote social learning: fidelity, fecundity and longevity. Fidelity indicates how reliably socially transmitted cues convey information content. Fecundity depends on the opportunities individuals have to interact with each other, implying that individuals in populations with low densities observe conspecifics less frequently and, therefore, have few opportunities to learn from them. Longevity depends on the use frequency of a socially acquired behaviour and on the benefits accrued by the individual using it (Boyd and Richerson 1988). This last element refers to the pressure exerted temporally and spatially for the maintenance of a socially acquired behaviour. For example, if a foraging technique is optimal to consume specific prey but if this prey rarely occurs in the foraging range during the life of an individual, then, the use of the acquired foraging technique would be rarely expressed and would accrue little benefit. Consistency in the transmission of information, high densities of populations, frequent use of socially acquired behaviour, and some fitness advantages, are all necessary for a socially learned trait to spread through a population (Klopfer 1959, Boyd and Richerson 1988, Heyes 1994, Galef 1995, 1996, Laland 1996, Laland et al. 1996).

Nest defence in Yellow and Reed warblers seems to possess the requisites of fidelity and fecundity that promote social learning. They may acquire elements of nest defence toward parasites from conspecifics because they transmit signals of threat presence with high consistency (i.e., high fidelity, Gill and Sealy 1996, Chapter 2). Both warblers live in a context that allows frequent interaction with conspecifics (i.e., high fecundity). Individuals nest within a short distance to each other (Woolfenden et al. 2003), which allows them to observe movements and hear vocalizations, including those performed during visits by a parasite, from their neighbours.

If Yellow and Reed warblers adhere to the requisites of high fidelity and fecundity that promote optimal social learning, their differential use of social information might rely on factors that promote a different longevity of socially acquired behaviours, and thus on the factors that influence the use rate of socially acquired behaviours (Galef and Whiskin 1998). As indicated above, the more a socially acquired behaviour is used, the higher the probability is that it will become permanently integrated in the individual's repertoire (Shettleworth 1998, Heyes 1994, Galef 1996, Laland 1996). Considered in the context of nest defence, parasitism frequency might be one measure that can be used to quantify how many opportunities hosts have to use their socially acquired antiparasite nest defence. Overall prevalence of parasitism frequency suffered by Yellow Warblers and Reed Warblers was 17% and 16%, respectively (Chapter 1), frequencies considered more than sufficient to select for efficient antiparasite defences (Rothstein and Robinson 1998, Davies 2000). It is the fluctuation of parasitism pressure, however, that would select for individual or social learning. Such variation occurred for the Yellow Warbler population but did not for the Reed Warblers in the two years of the investigation

(Chapter 1, Table 1.3). Variation in parasitism frequencies are partially confirmed by previous studies that recorded both stable and different parasitism pressures on Yellow Warbler nests between successive years (Tab. 1.3). There are no long-term data on parasitism rate for Reed Warblers at Tomina; however, the closest populations recorded stable parasitism frequencies for up to 14 years (Czech Republic: Øien et al. 1996; Tuscany, Italy: Quaglierini 2006).

In addition to parasitism frequency, in Yellow and Reed warbler populations, predation pressure was characterized by fluctuations in the first species and by stability in the second, in the two years of study (Chapter 1, Tab. 1.3). The variability of these ecological conditions in the Yellow Warbler population is consistent with factors that promote individual use of information and the occurrence of individually acquired defensive responses (see Chapter 3), whereas the stability recorded in this study in the Reed Warbler population is consistent with the conditions promoting social use of the information (Boyd and Richerson 1988, Laland et al. 1993, 1996, Kendal et al. 2004).

All of the theoretical predictions reported above were supported in the study of other behaviours and increasing evidence showed that, when consistent information is accessible, individuals tend to rely upon social cues to enhance their efficiency in responding to environmental conditions (Boyd and Richerson 1988, Laland et al. 1996, Templeton and Giraldeau 1996, Galef and Whiskin 1997, 2001, Kendal et al. 2005). Red Crossbills (*Loxia curvirostra*) more efficiently assess food patch quality, not by sampling information themselves, but vicariously sampling the availability of resources by observing conspecifics. Thus, when other individuals are experimentally provided, crossbills acquire cues of food patch quality by observing conspecific foraging success

(Smith et al. 1999). Terns capture fish more when they forage in mixed-species flocks rather than solitarily (Brenninkmeijer et al. 2002). However, when social cues become rapidly outdated because of a changing environment, adoption of conspecific behaviours would not prove optimal under the current ecological context (Boyd and Richerson 1988, Laland et al. 1993, 1996, Kendal et al. 2004). Nine-spined Sticklebacks (*Pungitius pungitius*) adjusted their food choices by switching between social and individual learning when the former was based on unreliable social information (van Bergen et al. 2004). Similarly, when breeding patch quality (depending on the ectoparasite intensity) was consistent between years, Black-legged Kittiwakes (*Rissa tridactyla*) and Cliff Swallows (*Petrochelidon pyrrhonota*) chose the same nesting sites, despite previous unsuccessful nesting attempts, because they used the information based upon conspecific success as a measure to assess their patch as a good quality breeding site (Danchin et al. 1998, Brown et al. 2000). On the contrary, when breeding patch quality was not consistent among years, unsuccessful Gull-billed Terns (*Sterna nilotica*) nesting in good quality patches (i.e., their conspecifics nesting in the same patches were mostly successful) chose another breeding site the next year, indicating their failure to use public (i.e., social) information (Erwin et al. 1998). As is evident from the cases outlined above, learned nest defence is also expected to be influenced by environmental conditions that would preferentially select one form of learning over another. However, past investigations of socially acquired nest defence did not quantify frequencies of predation or parasitism in relation to the intensity of defensive responses (Curio et al. 1978, Conover 1987).

Another explanation for the differential use of individual and social learning in Yellow and Reed warblers would be the different fitness advantages accrued by individual and social learners (Heyes 1994). Social learning is maintained in a population when behavioural flexibility enhances fitness, whereas individually learned behaviours are favoured if socially acquired alternatives are suboptimal or selectively neutral (Johnston 1982, Laland et al. 1993, 1996, Laland 1996, Rafacz and Templeton 2003). Young Oystercatchers (*Haematopus ostralegus*) that foraged by observing parents were as efficient as those that foraged by trial-and-error attempts and, therefore, both learning strategies occurred within the same population (Norton-Griffith 1967, Goss-Custard and Sutherland 1984). On the contrary, European Starlings relied on personal information regarding food patch quality and discarded social cues when these were made experimentally difficult to access or when demonstrators provided little information (Templeton and Giraldeau 1996). There are no data that directly quantify fitness benefits of individual and social learners, as it applies to the acquisition of antipredator/parasite behaviours. At least in Yellow Warblers, there is some indirect and contrasting evidence as to whether intense defensive responses toward parasites deter parasitism, perhaps even reducing nest success. Cowbirds may exploit defensive intensity of hosts to locate their nests or to assess their quality (Robertson and Norman 1977, Smith 1981), but this does not appear to be the case in Yellow Warblers (Gill et al. 1997b). In some studies, however, more aggressive hosts benefited in terms of higher nesting success (Blancher and Robertson 1982), whereas in other cases the opposite has been recorded (Robertson and Norman 1976), indicating that increased activity at the nest may increase nest predation (Tewksbury et al. 2002, Martin 1995). Such contrasting evidence also occurs in relation to the benefits obtained by aggressive Yellow Warblers in terms of nest survival in the face of parasitism or predation events (Folkers and Lowther 1985, Tewksbury et al. 2002, Gill and Sealy 1997b, Sealy et al. 1998). These studies predicted that parasitized individuals would be more aggressive than unparasitized individuals if the hypothesis of defence exploitation by cowbirds applied. However, it was assumed that parasitized individuals used the same defence intensity before and after the parasitism event, so that their responses recorded after parasitism were compared with those of the unparasitized individuals. In Chapter 3, Yellow Warblers modified their response toward a perched cowbird after a parasitism or an egg removal event. Therefore, analyzing the responses after, and not before, the parasitism event could have resulted in these contrasting results. Increased nest defence associated with decreased nest survival would explain the lack of social learning among Yellow Warblers, indicating that defensive responses facilitate parasitism or nest predation and, therefore, to acquire such defence from conspecifics would be selected against (Galef 1995). In the next chapter, I will analyze the fitness advantages in terms of nest survival correlating that with behaviours elicited before and after parasitism and nest predation events. The results will also promote a better understanding of the differential use of the social information in Yellow and Reed warbler populations.

Results from this study provided evidence that in the refinement of nest defence behaviours, social learning comes into play in at least one of the species studied. To explain the lack of social learning in Yellow Warblers, variation in the frequency of parasitism and nest predation recorded during this study are consistent with the factors proposed to promote selection favouring individual over social learning in other behaviours. Given the limited period of study for each species, my results also offer a new avenue for further investigations documenting parasitism frequencies as well as nest defence over the long term, providing results to address this hypothesis.

CHAPTER 5

ADAPTIVE SIGNIFICANCE OF NEST DEFENCE

INTRODUCTION

Several examples of behavioural adaptiveness are apparent among animals, such as nest-site selection, optimal foraging, mate choice, and territoriality (Goss-Custard et al. 1998, Adams 2001, Thünken et al. 2007). Behaviour that allows individuals to escape predation is implicitly adaptive because the surviving individuals may continue to produce offspring; individuals that die obviously have reduced lifetime reproductive output (Lind and Cresswell 2005).

Animals face not only imminent dangers, such as close encounters with predators, but they also find themselves in situations where their own survival may not be at stake but, nevertheless, their fitness is still threatened (Ajie et al. 2007). Visits to nests by predators and avian brood parasites are such situations because they may considerably decrease the number of offspring produced in a given breeding attempt and, consequently, affect population abundance and dynamics (Petit 1991, Martin 1995, Takasu 1998, Zanette et al. 2005, Anderies et al. 2007). Birds incorporate different behavioural traits in their nest defence (Caro 2005), and there is contrasting evidence suggesting that nest defence can either deter or facilitate parasitism. For example, the stealthy habit of cowbirds of parasitizing only in a narrow temporal window around sunrise seems to exploit the absence of hosts that do not roost at the nest before clutch completion (Sealy et al. 1995). The specialization of cowbirds and cuckoos to lay their eggs in a few seconds suggests an advantage for the parasites to avoid encounters with hosts while they are parasitizing their nests (Sealy et al. 2000). Moreover, there are reports of parasites laying their eggs despite the intense attacks of hosts (Sealy et al. 1995), but others reported that parasites were thwarted by defensive hosts (Molnár 1944, Ellison and Sealy 2007). Whether these traits deter brood parasitism and thus enhance host fitness has seldom been addressed in specific studies (Blancher and Robertson 1982, Duckworth 2006, Sealy et al. 1998).

Under less threatening circumstances, flexibility in defensive behaviour should enhance an individual's fitness as it adjusts to spatial and temporal variability both in the nature of threats and their intensity, and thus to environmental demands (Lind and Cresswell 2005). Adaptiveness of behavioural plasticity in defensive behaviour has been assumed implicitly when animals react specifically to a particular threat (McLean and Rhodes 1991, Griffin 2004); learned enemy recognition, therefore, often has been considered synonymous with increased fitness (Curio 1978, Vieth et al. 1980). Species that react differently to different threats have been suggested to accrue some form of benefit (Seyfarth et al. 1980, Chivers and Smith 1994, Sealy et al. 1998); however, quantifications of fitness advantages gained by the adoption of specific antipredator strategies and their contextual adjustments are scarce in literature. The absence of specific tests for the adaptive role of nest defence and its plasticity can be explained, first, by the few opportunities to witness acts of predation or brood parasitism at bird nests (Wilson and Cooper 1998, Rader et al. 2007) and, second, by the absence of behavioural data recorded before the threat was encountered (Blancher and Robertson 1982, Gill et al. 1997b). Adaptiveness of a behavioural trait, or plasticity therein, should be assessed by testing not only its use in appropriate contexts but also its modulation in accordance with the environmental pressure that selects for it (Lima 2002). When a behavioural trait is costly, presumably it evolves and spreads in populations only if selective pressure is strong enough to balance the benefits accrued by the individual (Lefebvre and Giraldeau 1996). During nest defence, individuals may be injured and thus lower their ability to reproduce now or in the future. Therefore, specific responses able to reduce the likelihood of a threat at their nests are supposed to evolve when the threat occurrence is relatively frequent (Montgomerie and Weatherhead 1988).

In this chapter, I studied two species of passerine birds and tested whether their nest defensive traits and the flexibility of their responses influenced the survival of nests, the immediate fitness currency hypothesized to be affected by nest defence. First, I quantified the environmental pressure potentially selecting for threat-specific responses by measuring frequencies of predation and parasitism, both major causes of decreased nest success. Predation and parasitism traditionally were quantified as the number of nests depredated or parasitized out of the total nests in a sample (Rothstein and Robinson 1998, Davies 2000, Yeh et al. 2007). However, such rates might be an artefact of the actual ecological pressure because they do not account for the temporal sequence of nest failures and the daily number of nests potentially available to nest predators and parasites (Mayfield 1961, 1975). I circumvented this bias by using a statistical model that generated survival functions, and daily as well as seasonal rates of nest survival to parasitism and predation during the time that nests were susceptible to brood parasitism and predation (Muenchow 1986, Woodworth 1999). To determine whether defensive responses, their intensity and/or flexibility, predicted nest survival as a measure of individual fitness, I correlated behavioural data recorded before and after simulated parasitism and egg removal events (Chapters 3-4) with nest survival data. If a behavioural variable predicted nest survival, to quantify its effect on fitness, I modeled the relative rate of nest survival if all individuals adopted the lowest and the highest response intensity recorded in the population (Cox 1972, Cox and Oakes 1984).

Behavioural syndromes are defined as linkages that occur among particular behavioural traits that result in the expression of different animal personalities (Sih et al. 2004). The adoption of a behavioural trait may not be independent of others, similar to allometric relationships that limit or favour morphological changes in body size and shape (Gould and Lewontin 1979, Duckworth 2006). Analysis of the adaptive significance of traits, therefore, should consider correlations among behaviours (Riechert and Hedrick 1993, Sih et al. 2003). Accordingly, once I determined the behavioural predictors of nest survival, I verified whether they were positively or negatively associated with each other, indicating, in the former case, that they constitute part of the same defensive strategy or, in the latter, they exist as mutually exclusive strategies.

When a behaviour appears to confer fitness advantages, it does not necessarily spread through a population (Stamps 2003). In addition to behavioural syndromes potentially limiting plasticity, environmental contexts within populations also select for a mixture of behavioural traits, of which the optimum for any given context is not necessarily the most common, and the others might appear maladaptive (Arnold 1992, Sih et al. 2003, Loyd and Martin 2004, Dochtermann and Jenkins 2007, Igual et al. 2007). For example, despite increased nest success gained by access to a diet rich in fish, most individuals in a Western Gull (*Larus occidentalis*) population foraged at the local dump (Annett and Pierotti 1999). Such apparent maladaptive foraging was explained by limited access to the sea resources by most young individuals (Annett and Pierotti 1999). After I identified nest defence strategies associated with the highest rates of nest survival, I tested whether they were adopted in the population more frequently than the alternative strategies associated with lower nest survival rates.

I studied the Yellow Warbler and Reed Warbler, in North America and Europe, respectively (Cramp 1992, Lowther et al. 1999). Although these species are spatially and phylogenetically distant, their reproductive success is reduced by nest predation and brood parasitism, the latter perpetrated by the Brown-headed Cowbird and Common Cuckoo, respectively (Lowther et al. 1999, Davies 2000). Both species are ideal subjects for this research as they differentially recognize parasites and nest predators and respond to them differently (Gill and Sealy 1996, 2004; Chapter 2). Both modify their responses after individual or social interactions with threats at their nests (Chapters 3-4). There are also indications that such a plastic defence is adaptive. Yellow Warblers induce specific defensive responses in mates and young by issuing vocalizations (Gill and Sealy 2003, Tab. 1.1) and defensive activities do not seem to be exploited by parasites to better locate nests (Gill and Sealy 1997b). Unparasitized populations of Reed Warblers respond less toward cuckoos than parasitized populations (Lindholm and Thomas 2000), which indicates that the presence of a threat selects for more aggressive responses.

My objectives were to: (1) quantify the parasitism and predation frequencies suffered by the two populations, each over two years, by measuring nest survival rates, (2) determine whether one or more defensive responses and/or their changes in intensity predicted nest survival and their effect on nest survival, and, (3) determine to what extent behavioural predictors of nest survival were adopted by the populations.

MATERIALS AND METHODS

Yellow Warblers were studied at Delta Marsh (Portage la Prairie, MB, Canada) from May trough July 2002 and 2003, whereas Reed Warblers were studied at Tomina (Modena, Italy) from April through July 2004 and 2005. Details of the study areas and the methods used for nest monitoring are given in Chapter 1 (pp. 12-18).

Survival Analyses of Warbler Populations

To determine the proportion of warbler nests that were not parasitized or depredated, I performed a series of Survival Analyses commonly used to analyze ecological data in the form “time until an event occurs” (Muenchow 1986). Survival Analysis accommodates censored data points; the cases where the event has not occurred during the observation period. These cases are described as the survived cases to the specific event of interest. Accordingly, in this study, the nests that were unparasitized or did not suffer predation are said to have survived to parasitism and predation, respectively. Rather than a mere proportion of nests that survived out of the total number nests in the sample, this method estimates the distribution of survival times, thus determining the survival function, day by day, using the Kaplan-Meier procedure (Fox 2001).

To quantify nest survival to parasitism, I used all nests that were inspected in 2002 and 2003 for Yellow Warblers and in 2004 and 2005 for Reed Warblers, and for which I determined the date of clutch initiation by nest inspection or by backdating from the hatching date (Chapter 1). The latter procedure probably underestimated survival to parasitism for Reed Warblers because it did not account for the cases of possible cuckoo egg ejection that were not observed during the first days of laying (12% is the frequency of ejection of mimetic egg models recorded in Britain; Davies and Brooke 1988). The observation period spanned the day of clutch initiation to two days after clutch completion, for Yellow Warblers, whereas for Reed Warblers it spanned from clutch initiation to three days after clutch completion. These windows of parasitism were determined using the dates parasitism was observed in these two populations (Chapter 1). All nests not parasitized at the end of the observation period were recorded as censored, whereas those parasitized nests were considered uncensored with the date of parasitism as the time of the occurrence of parasitism.

To determine nest survival to egg predation, in addition to the above nests, I also included all the nests found with eggs and for which clutch initiation could not be determined. In fact, while it is necessary to know the clutch-initiation date to be able to determine whether a nest is susceptible to parasitism (i.e., two or three days after clutch completion nests are not parasitized), the presence of eggs automatically includes a nest among those susceptible to egg predation. If a nest was not depredated (censored cases), the observation period ended the day before hatching began. Any cause of nest failure, predation but also nest desertion or destruction due to inclement weather, was considered to have occurred on the day of the mid-point between the two last nest checks (Mayfield 1961, 1975). Due to logistical constraints in monitoring each nest every day, Mayfield (1975) formulated a method to compute the exposure of a nest to predation with the available nest checks. Establishing the failure date as the middle day between two checks has been considered an objective method used in several investigations of population demography (Boal et al. 2005) and dynamics (Woodworth 1999). To determine nest survival until nestlings were depredated, I used all the nests that contained nestlings at the time of inspection and they were recorded as censored if no nestlings were missing at the time of the last inspection.

To compare nest survival between study years, I compared the distributions of nest survival time using Gehan-Wilcoxon and Log-Rank tests (Fox 2001). These tests analyze the early and late portion of the failure-time curves, thus comparing nest survivorship at each step.

Effect of Nest Defence on Nest Success

In both warbler populations, parasitism and egg and nestling predation were recorded during both years of study. To test the effect of nest defence on nest success, I ran a model analogous to nonparametric multiple regression analysis used to test whether continuous variables predict survival time (Cox 1972, Cox and Oakes 1984). This model computes the maximum likelihood parameter estimates and evaluates the overall goodness-of-fit. I tested whether nest defence responses (continuous variables) were predictors of nest survival time (dependent variable). From the three samples described in the previous section only from part of them could I record defensive responses. This limitation was due to the small temporal windows of laying/incubation and nestling stages used to perform the model presentations described in Chapters 2-4 and to the nesting synchrony of individuals in populations. In other words, because a high number of individuals started nesting simultaneously, I could not perform model presentations in all of them before their eggs hatched or their nestlings fledged because of time constraints. The nests exposed to models were used as subsamples. To test whether the subsamples provided a reliable representation of underlying relative samples, I compared their survival functions by using Gehan-Wilcoxon and Log-Rank tests (Fox 2001).

Behavioural responses analyzed were those recorded at: (1) nests exposed to parasite models before and after trainings. These were simulated parasitism and egg removal events, as well as conspecifics defending their nest during a visit by a parasite (Chapters 3 and 4; Tab. 3.1 and 3.2); (2) a control group of nests exposed twice to parasite models but not to the training (Tab. 3.1 and 3.2); (3) nests that were exposed to pre-training only as they were depredated, parasitized, or destroyed by inclement weather before the end of the experiment, and, (4) nests already parasitized when found and successively exposed once to a parasite model. In this last case, I considered warbler responses as post-training nest defence.

I expected that the following behaviours were predictors of nest survival to parasitism because they were significantly different between the pre- and post-training presentations in Chapters 3 and 4 when the ability to refine antiparasite response was tested. For Yellow Warblers, the number of *seet* calls, attacks on the model, time spent in distraction displays, and time spent out of sight, whereas for Reed Warblers, perch changes, bill snaps, *huit* and *churr* calls, and time spent uttering *zirr* calls.

I expected that the following behaviours were predictors of nest survival to egg predation because they differed in response to parasites and predators (Hobson and Sealy 1989, Gill and Sealy 1996, Chapter 2). For Yellow Warblers, the number of *chip* and *seet* calls, perch changes and attacks on the model, and the time spent sitting on the nest, out of sight, and performing distraction displays and displacement activities, whereas for Reed Warblers, the number of perch changes, strikes, bill snaps, close flights, *churr* and *huit* calls, and songs, and the time spent uttering *zirr* calls, watching the model silently, and out of sight.

I expected that the following behaviours were predictors of nest survival to nestling predation because they differed in response to predator models between egg and nestling stages (Hobson and Sealy 1989, Gill and Sealy 1996, Chapter 2). For Yellow Warblers, the number of *chip* and *seet* calls, whereas for Reed Warblers, the number of perch changes and *churr* calls, and time spent out of sight and silently watching the model.

Given the numerous independent and continuous variables, when a behaviour is a significant predictor of nest survival, its effect is not immediately visible in the model analysis outputs. It is necessary to run a set of model simulations that changes the mean value, obtained by the model analysis, of the variable of interest (Cox 1972, Cox and Oakes 1984). Accordingly, to accomplish this, I modeled nest survival rates by entering the lowest and highest values of the nest survival predictors recorded during presentations. Survival rates from these simulations and from the subsamples were compared using Student's *t*-test (Zar 1999).

I used Spearman's Rank Correlation test (Zar 1999) to reveal possible correlations between predictors of nest survival, and Principal Component Analysis (PCA, Digby and Kempton 1987) to show the distribution of warbler responses along gradual intensities of the nest survival predictors.

RESULTS

Yellow Warblers

Rate of survival to parasitism of Yellow Warbler nests inspected during 2002 and 2003 was 88% (Tab. 5. 1). There was no significant difference in the number of nests that survived to parasitism between years (Log-Rank Test statistic = -0.45, P = 0.652, Tab. 5.2). A subsample of 164 nests was exposed to cowbird models before and after training (Chapters 3 and 4). The final survival rate of this subsample was higher than that obtained from the entire population (Log-Rank Test statistic = 3.01, P = 0.003, Tab.5.1). No single behaviour predicted survival to parasitism; however, I could not run a single survival analysis simultaneously testing all responses recorded during presentations as there were not enough uncensored cases tested before parasitism (i.e., five nests, Tab. 5.1) to compute the appropriate number of interactions. Instead, I ran three different analyses with the responses recorded during the pre-training (Cox Model, $\chi^2 = 3.07$, df = 4, P = 0.545), post-training ($\chi^2 = 0.002$, df = 4, P = 1.000), and the difference between the two ($\chi^2 = 0.002$, df = 4, P = 1.000), and in all three cases, no behaviour significantly predicted nest survival, indicating that no single defensive responses were associated reliably with parasitized or unparasitized nests.

Rate of survival to egg predation of all nests in 2002 and 2003 was 35%, however, predation was significantly lower in the first year than in the second year (Log-Rank Test = 2.73, P = 0.006, Tab. 5.2). To test the effect of defence on nest survival to egg predation, I performed a survival analysis on a subsample of 199 nests for which I recorded behavioural data (Tab. 5.1). The final survival rate of this subsample was significantly higher than that of the entire sample (Log-Rank Test = 2.53, P = 0.011, Tab.

Table 5.1. Sample sizes and survival rates determined on Yellow Warbler nests at Delta Marsh (Manitoba) in 2002 and 2003 (All nests) and on a fraction of them exposed to models (Subsample). Depending on their susceptibility to threatening events, nests could be used in Survival Analyses to determine survival distributions relative to parasitism, and egg and nestling predation events. Subsample nests were used to test behavioural responses as predictors of nest survival. Results of Wilcoxon Matched-Pairs show differences of nest survival functions between all nests and the subsamples exposed to models.

	Parasitism				Egg Predation				Nestling Predation			
	All nests	Subsample	Test statistic	P	All nests	Subsample	Test statistic	P	All nests	Subsample	Test statistic	P
Survival rate	88%	97%	-2.89	0.004	35%	45%	-2.91	0.004	50%	47%	0.01	0.997
N[1]	338	164			425	199			120	61		
Parasitized/ depredated	36	5			154	57			29	20		
Unparasitized/ not depredated	302	159			271	142			91	41		

[1] Number of nests.

Table 5.2. Sample sizes and survival rates determined on all Yellow Warbler nests at Delta Marsh (Manitoba) in 2002 and 2003. Depending on their susceptibility to threatening events, nests could be used in Survival Analyses to determine survival distributions relative to parasitism, and egg and nestling predation events. Results of Wilcoxon Matched-Pairs show differences of nest survival functions between the two years of study.

	Parasitism				Egg Predation				Nestling Predation			
	2002	2003	Test statistic	P	2002	2003	Test statistic	P	2002	2003	Test statistic	P
Survival rate	90%	87%	0.32	0.751	26%	42%	-2.53	0.011	70%	47%	-0.89	0.372
N[1]	132	206			171	254			23	97		
Parasitized/ depredated	13	23			71	83			5	24		
Unparasitized/ not depredated	119	183			100	171			18	73		

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[1] Number of nests.

5.1). All behavioural responses recorded during presentations had a combined effect on nest survival to egg predation (Cox Model, $\chi^2 = 54.43$, df = 24, P = 0.0004) with *chip* calls, perch changes, attacks on the model, and nest-protection behaviour emerging as significant predictors positively associated with nest survival rates (Tab. 5.3).

Rates of survival to egg predation obtained in simulations with the lowest and highest values recorded for each predictor were significantly lower and higher than the actual survival rate, respectively (Student's *t*-test, $P < 0.001$) except for the rate resulting from entering the lowest number of attacks on the model (P = 0.841, Tab. 5.4). Correlation analyses showed that, among the above survival predictors, *chip* calls and perch changes were positively correlated with each other whereas they both were negatively correlated with nest-protection behaviour. This indicates alternative forms of nest defence that I designated as the distractive strategy, composed of *chip* calls and perch changes, the protective strategy composed of nest-protection behaviour, and the aggressive strategy involving mostly strikes (Tab. 5.5). Consequently, I ran two sets of survival function simulations, one with the lowest and highest numbers of both *chip* calls and perch changes (Fig. 5.1) and the other with the shortest and longest bouts of nest-protection behaviours (Fig. 5.1). In both cases, the actual nest survival rate was significantly higher than that obtained with less intense nest defence responses (45% versus 0%, *t*-test, $P < 0.001$) but significantly lower than that which resulted among highly responsive individuals (45% versus 99% and 97%, respectively, $P < 0.001$, Fig. 5.1). A Principal Component Analysis using survival predictors as variables similarly revealed the alternative strategies of Yellow Warblers that responded either with high numbers of *chip* calls and perch changes or spent much more time protecting their nests.

Table 5.3. Results of Cox Model that tested the effect of the defensive responses of Yellow Warblers at Delta Marsh (Manitoba) on the survival of their nests to egg predation. Pre-training and post-training refer to responses recorded before and after, respectively, simulations of parasitism and egg removal, whereas training difference refers to response differences determined between pre-training and post-training trials.

	Wald Statistic	P
Chip call (pre-training)	7.50	0.006
Chip call (post-training)	4.31	0.038
Chip call (training difference)	5.98	0.014
Seet call (pre-training)	3.83	0.050
Seet call (post-training)	2.49	0.114
Seet call (training difference)	2.54	0.111
Perch change (pre-training)	24.58	< 0.001
Perch change (post-training)	21.38	< 0.001
Perch change (training difference)	20.38	< 0.001
Strike (pre-training)	1.33	0.248
Strike (post-training)	1.11	0.292
Strike (training difference)	4.09	0.043
Nest protection (pre-training)	16.59	< 0.001
Nest protection (post-training)	10.51	0.001
Nest protection (training difference)	12.93	< 0.001
Distraction display (pre-training)	3.04	0.081
Distraction display (post-training)	1.88	0.170
Distraction display (training difference)	2.47	0.116
Displacement activities (pre-training)	0.00	0.988
Displacement activities (post-training)	0.25	0.616
Displacement activities (training difference)	0.03	0.857
Out of sight (pre-training)	2.44	0.119
Out of sight (post-training)	0.02	0.896
Out of sight (training difference)	1.76	0.184

Table 5.4. Rate of nest survival to egg predation obtained with all Yellow Warbler nests at Delta Marsh (Manitoba) exposed to models (All tested nests) compared with those obtained by entering in the model the lowest and highest values of each behaviour that predicted nest survival. Different superscripts indicate significantly different survival rates (t-test, $P \leq 0.05$).

Nest survival predictors	Rates of nest survival to egg predation (%)		
	Lowest	Highest	All tested nests
Chip calls	20^b	99^c	
Perch changes	0^b	99^c	45^a
Strikes	44^a	83^b	
Nest-protection	3^b	97^c	

Table 5.5. Correlation matrix among Yellow Warbler behaviours that predict nest survival to egg predation at Delta Marsh (Manitoba). Spearman Rank correlation *r* and P values are indicated in the top and bottom rows, respectively.

Nest survival predictors	Chip calls	Perch changes	Strikes	Nest protection
Chip calls		0.20 0.004	-0.17 0.016	-0.35 0.000
Perch changes			-0.12 0.920	-0.48 0.000
Strikes				-0.11 0.882
Nest protection				

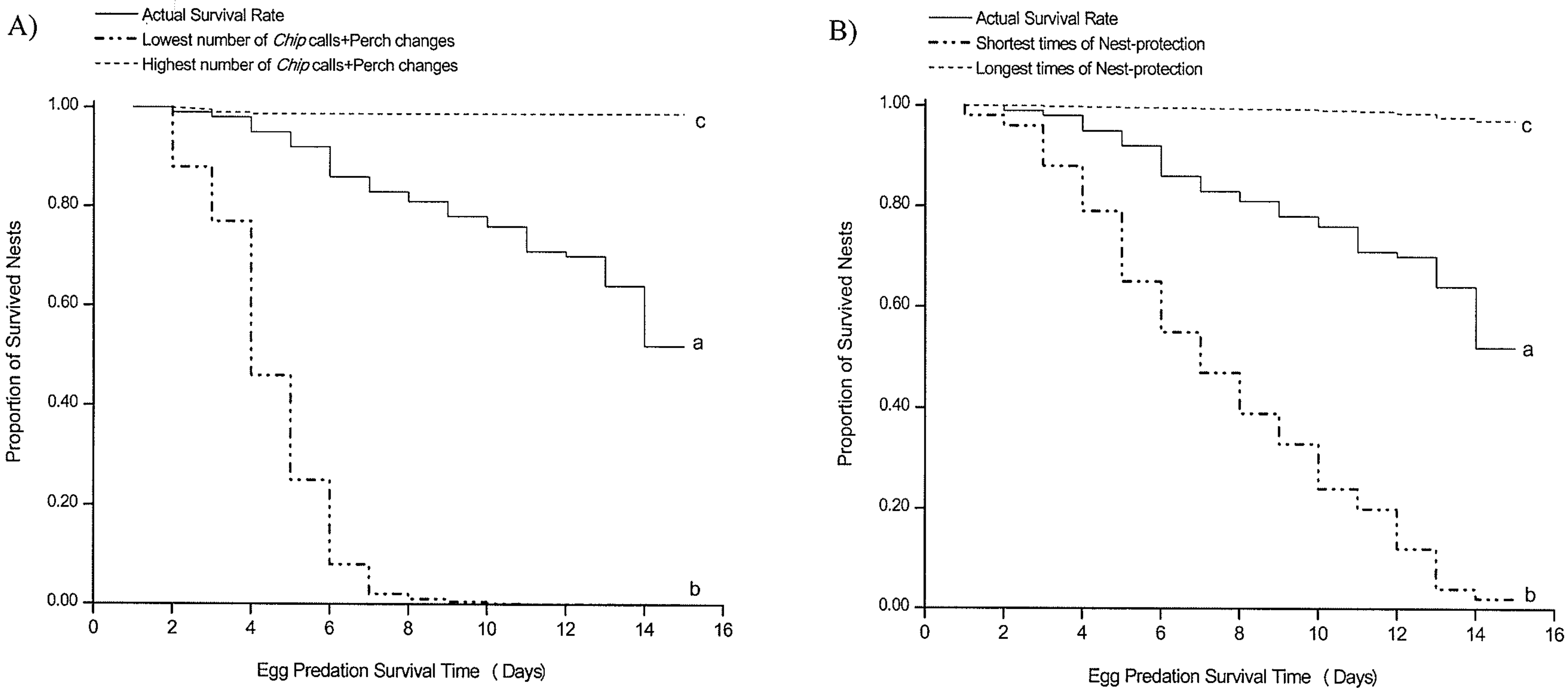

Figure 5.1. Curve of survivorship to egg predation that resulted from all Yellow Warblers at Delta Marsh (Manitoba) exposed to models (solid line) is compared to those obtained by entering in the model the lowest (dash-dot line) and highest (dashed line) values of (A) *chip* calls and perch changes and (B) nest-protection behaviour recorded during presentations. Different superscripts indicate significantly different survival rates (t-test, $P \leq 0.05$, see text for exact values).

Nest-protection behaviour was also associated with a high number of attacks on the model (Fig. 5.2).

The survival rate of Yellow Warbler nests to nestling predation was 50%, for all nests in 2002 and 2003 (Tab. 5.1), and there was no significant difference in the distribution of survival times between years (Log-Rank Test = -0.14, P = 0.887, Tab. 5.2). I tested the influence of nest defence on the survival of Yellow Warbler nests to nestling predation on a subsample of 61 nests that were also exposed to models and monitored during the nestling stage (Tab. 5.1). Survival of this subsample was 47%, not significantly different from that obtained from the entire sample (Log-Rank Test = - 0.11, P = 0.916, Tab. 5.1). No behaviour predicted nest survival to nestling predation events (Cox Model, $\chi^2 = 5.70$, df = 6, P = 0.457).

Reed Warblers

Survival to parasitism of Reed Warbler nests inspected during 2004 and 2005 was 76% (Tab. 5.6). There was no significant difference in the distributions of nest survival to parasitism between years (Log-Rank Test statistic = -0.16, P = 0.872, Tab. 5.7). A subsample of 117 nests was exposed to cuckoo models before and after training sessions (Chapters 3 and 4). The survival function of this subsample did not differ significantly from that for the entire population (Log-Rank Test statistic = 0.04, P = 0.966, Tab.5.6). Although all the variables did not have a combined effect on nest survival to parasitism (Cox Model, $\chi^2 = 18.43$, df = 15, P = 0.241, Tab. 5.8), *zirr* calls emerged a significant predictor (Tab. 5.8). The most vocal individuals during the first cuckoo encounter were parasitized significantly less frequently than the most silent (*t*-test, P < 0.001); however, the most flexible individuals, increasing their level of *zirr* calls after

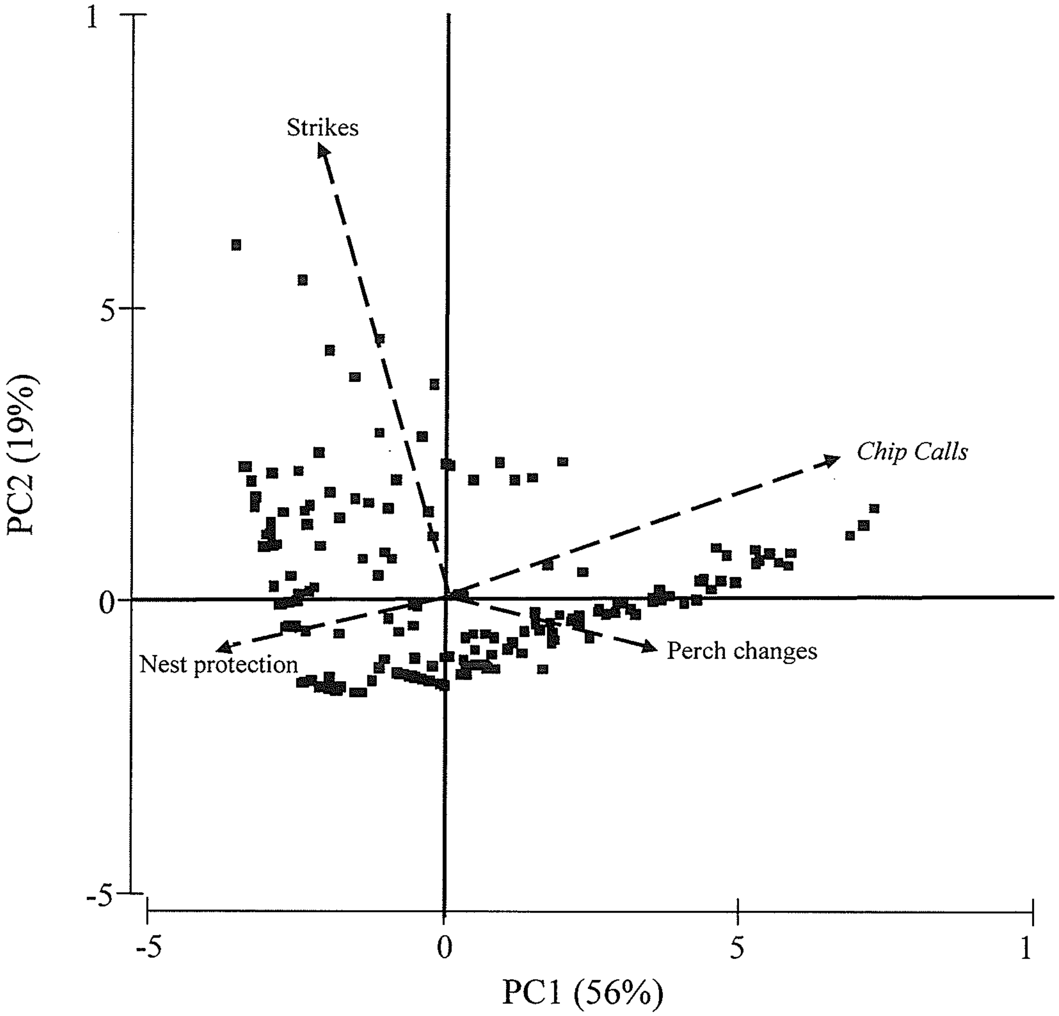

Figure 5.2. Distribution of Yellow Warbler responses that predicted nest survival to egg predation (dashed vectors) at Delta Marsh (Manitoba). Direction of vectors indicates a higher contribution to the first (PC1) or second components (PC2) and an increasing expression of the relative behaviour along the component axes.

Table 5.6. Sample sizes and survival rates determined for Reed Warbler nests at Tomina (Italy) in 2004 and 2005 (All nests) and on a fraction of them exposed to models (Subsample). Depending on their susceptibility to threatening events, nests could be used in Survival Analyses to determine survival distributions relative to parasitism, and egg and nestling predation events. Subsample nests were used to test behavioural responses as predictors of nest survival. Results of Wilcoxon Matched-Pairs show differences of nest survival functions between all nests and the subsamples exposed to models.

	Parasitism				Egg Predation				Nestling Predation			
	All nests	Subsample	Test statistic	P	All nests	Subsample	Test statistic	P	All nests	Subsample	Test statistic	P
Survival rate	76%	73%	-0.12	0.907	71%	73%	-1.01	0.311	78%	76%	0.25	0.804
N[1]	169	117			187	123			113	69		
Parasitized/ depredated	25	18			38	24			15	11		
Unparasitized/ not depredated	144	99			149	99			98	58		

[1] Number of nests.

Table 5.7. Sample sizes and survival rates determined for all Reed Warbler nests at Tomina (Italy) in 2004 and 2005. Depending on their susceptibility to threatening events, nests could be used in Survival Analyses to determine nest survival distributions relative to parasitism, and egg and nestling predation events. Results of Wilcoxon Matched-Pairs show differences of nest survival functions between the two years of study.

	Parasitism				Egg Predation				Nestling Predation			
	2004	2005	Test statistic	P	2004	2005	Test statistic	P	2004	2005	Test statistic	P
Survival rate	85%	68%	-0.05	0.956	75%	67%	-0.55	0.581	82%	72%	-0.67	0.500
N[1]	85	84			93	94			53	60		
Parasitized/ depredated	12	13			19	19			8	7		
Unparasitized/ not depredated	73	71			74	75			45	53		

[1] Number of nests.

Table 5.8. Results of Cox Model that tested the effect of the defensive responses of Reed Warblers on the survival of their nests to parasitism at Tomina (Italy). Pre-training and post-training refer to responses recorded before and after, respectively, simulations of parasitism and egg removal, whereas training difference refers to response differences determined between pre-training and post-training trials.

	Wald Statistic	P
Perch change (pre-training)	0.99	0.321
Perch change (post-training)	2.48	0.115
Perch change (training difference)	1.07	0.301
Bill snap (pre-training)	0.62	0.432
Bill snap (post-training)	0.15	0.697
Bill snap (training difference)	1.22	0.268
Churr call (pre-training)	0.03	0.853
Churr call (post-training)	0.01	0.934
Churr call (training difference)	0.22	0.643
Huit call (pre-training)	0.20	0.657
Huit call (post-training)	0.08	0.783
Huit call (training difference)	0.54	0.463
Zirr call (pre-training)	6.26	0.012
Zirr call (post-training)	7.76	0.005
Zirr call (training difference)	6.55	0.011

the first threat encounter, suffered significantly higher parasitism than individuals that remained relatively unresponsive during subsequent encounters with cuckoos (P = 0.0004, Tab. 5.9). The Cox model run with the highest increase of *zirr* calls recorded during model presentations resulted in a rate of survival to parasitism similar to that which resulted from the sample (P = 0.1473, Tab. 5.9).

Survival to egg predation of all nests in 2004 and 2005 was 71% and there was no difference recorded between years (Log-Rank Test statistic = - 0.55, P = 0.821, Tab. 5.6 and 5.7). I tested the defence responses elicited during model presentations as possible predictors of survival to egg predation using a subsample of 123 nests for which I recorded behavioural data (Tab. 5.6). The survival function of this subsample did not differ from that of the entire sample (Log-Rank Test statistic = 0.70, P = 0.483, Tab. 5.6). All behavioural categories recorded during presentations had a combined effect on nest survival rate (Cox Model, $\chi^2 = 37.68$, df = 22, P = 0.020) although the model did not allow me to test the response differences recorded between pre-training and post-training trials. The number of perch changes was a significant predictor positively associated with survival rates, whereas the presence of other birds during pre-training presentations appeared as a factor associated negatively with nest survival to egg predation (Tab. 5.10). The actual survival rate was significantly lower than the rate obtained with the most mobile individuals (Student's *t*-test, P = 0.004) and the least number of other birds seen during presentations (P = 0.000, Tab. 5.11a). Instead, it was significantly higher with the most static individuals and the highest number of other birds (P = 0.000, Tab. 5.11a).

Survival to nestling predation was 78%, for all nests in 2004 and 2005, and there was no significant difference between years (Log-Rank Test statistic = 0.77, P

Table 5.9. Nest survival to parasitism obtained with all Reed Warbler nests at Tomina (Italy) exposed to models (All tested nests) compared with those obtained by entering in the model the lowest and the highest values of *zirr* calls, and the highest and lowest changes in *zirr* calls recorded between pre- and post-training presentations at the same nest. Different superscripts indicate significantly different survival rates (t-test, $P \leq 0.05$).

	Rate of nest survival to parasitism (%)		
Nest survival predictor	Model Results		All tested nests
zirr calls	Lowest	12^b	73^a
	Highest	98^c	
	No change (at lowest values)	96^c	
	Highest increase	81^a	

Table 5.10. Results of Cox Model that tested the effect of the defensive responses of Reed Warblers on the survival of their nests to egg predation at Tomina (Italy). Pre-training and post-training refer to responses recorded before and after, respectively, simulations of parasitism and egg removal.

	Wald Statistic	P
Perch change (pre-training)	11.22	0.001
Perch change (post-training)	8.64	0.003
Strike (pre-training)	1.66	0.197
Strike (post-training)	2.36	0.125
Bill snap (pre-training)	0.08	0.774
Bill snap (post-training)	1.20	0.273
Close flight (pre-training)	2.50	0.114
Close flight (post-training)	3.37	0.066
Churr call (pre-training)	3.28	0.070
Churr call (post-training)	0.01	0.917
Huit call (pre-training)	1.42	0.234
Huit call (post-training)	0.94	0.332
Song (pre-training)	0.01	0.925
Song (post-training)	0.27	0.606
Other birds (pre-training)	5.89	0.015
Other birds (post-training)	0.85	0.356
Zirr call (pre-training)	0.57	0.448
Zirr call (post-training)	0.04	0.839
Silent watching (pre-training)	2.24	0.135
Silent watching (post-training)	0.01	0.915
Out of sight (pre-training)	0.18	0.676
Out of sight (post-training)	1.45	0.229

Table 5.11. Nest survival to (A) egg predation and (B) nestling predation obtained with all Reed Warbler nests at Tomina (Italy) exposed to models (All tested nests) compared with those obtained by entering in the model the lowest and the highest values of each behaviour that predicted nest survival. Different superscripts indicate significantly different survival rates (t-test, $P \leq 0.05$).

A	Nest survival to egg predation (%)		
Nest survival predictors	Lowest	Highest	All tested nests
Perch changes	55^b	99^c	73^a
Other Birds	93^b	20^c	

B	Nest survival to nestling predation (%)		
Nest survival predictors	Lowest	Highest	All tested nests
Perch changes	43^b	96^c	76^a

= 0.439, Tab. 5.6 and 5.7). I tested the influence of defence on the survival of nests to nestling predation on a subsample of 69 nests that were exposed to models and monitored throughout the nestling stage (Tab. 5.6). Survival of this subsample was 76%, not significantly different from that obtained from the entire sample (Log-Rank Test statistic = -0.43, P = 0.670, Tab. 5.6). Among the behaviours that changed significantly between the egg and the nestling stage, only the number of perch changes was associated positively with nest survival to nestling predation (Wald = 4.26, P = 0.039), whereas a combined effect of all variables was not detected (Cox Model, $\chi^2 = 5.50$, df = 4, P = 0.240). Survivorship functions calculated with the lowest and the highest values of perch changes observed during model presentations resulted in a survival of 43% and 96%, respectively. These were significantly lower and higher, respectively, than the nest predation survival rate obtained from the subsample (*t*-test, P < 0.001, Tab. 5.11b).

Zirr calls and perch changes, the behavioural predictors of nest survival to parasitism and predation, respectively, were significantly and positively correlated (Spearman Correlation Test, R = 0.52, P < 0.001). Individuals defending with the highest number of *zirr* calls and perch changes enjoyed a higher rate of nest survival to parasitism (Fig. 5.3a) and to egg (Fig. 5.4.a) and nestling (Fig. 5.4b, *t*-test, P < 0.001) predation. As seen in the singular effect of *zirr* calls, and the additive effect of *zirr* calls and perch changes, individuals that maintained a low level of responsiveness survived better to parasitism than the most flexible ones (P = 0.004, Fig. 5.3b). The actual rate of nest survival to parasitism was similar only to that achieved by the most flexible individuals (P = 0.066, Fig. 5.3b), whereas the actual rates of nest survival to both egg

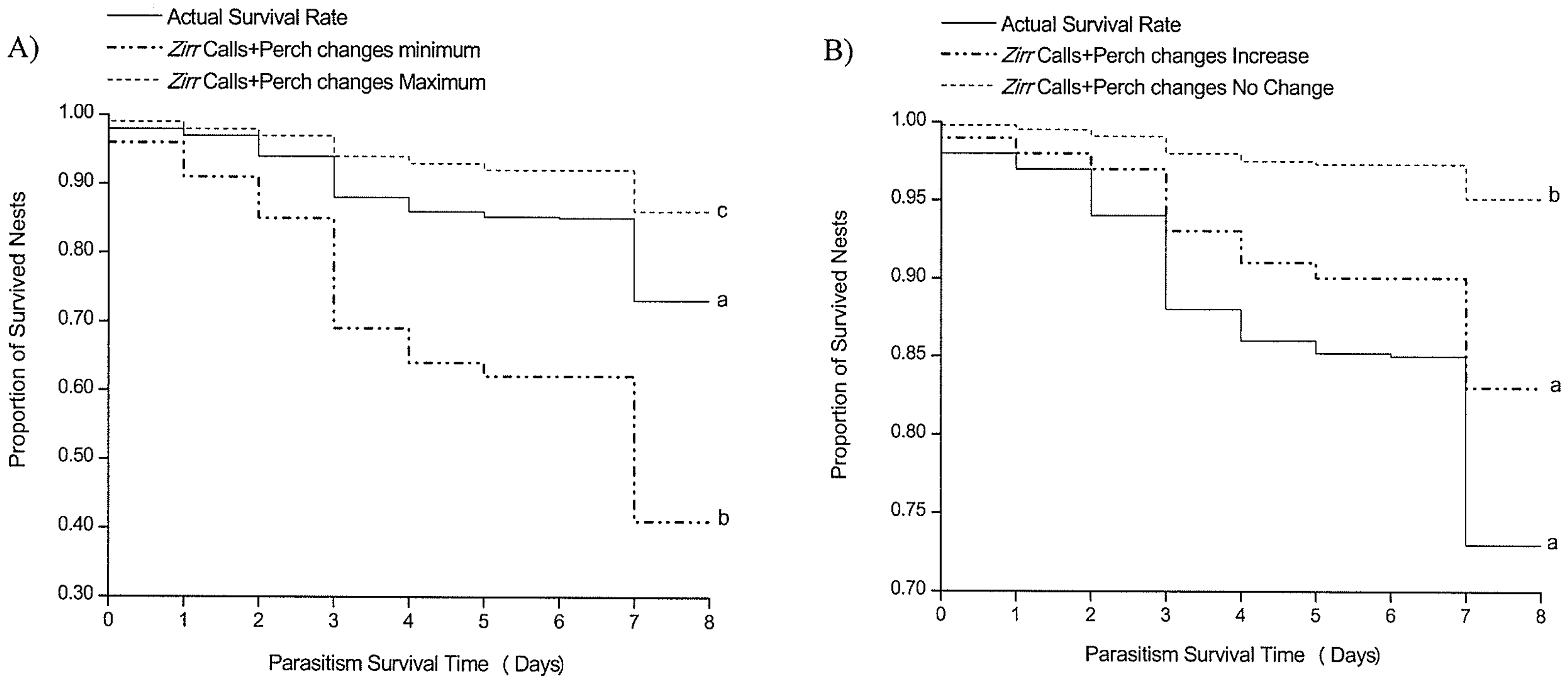

Figure 5.3. Curve of survivorship to parasitism that resulted from all Reed Warbler nests at Tomina (Italy) exposed to models (solid line) is compared to those obtained by entering in the model (A) the lowest (dash-dot line) and highest (dashed line) values of *zirr* calls and perch changes and (B) the highest (dash-dot line) and the lowest (dashed line) changes of *zirr* calls and perch changes recorded between pre- and post-training presentations at the same nest. Different superscripts indicate significantly different survival rates (t-test, $P \leq 0.05$, see text for exact values).

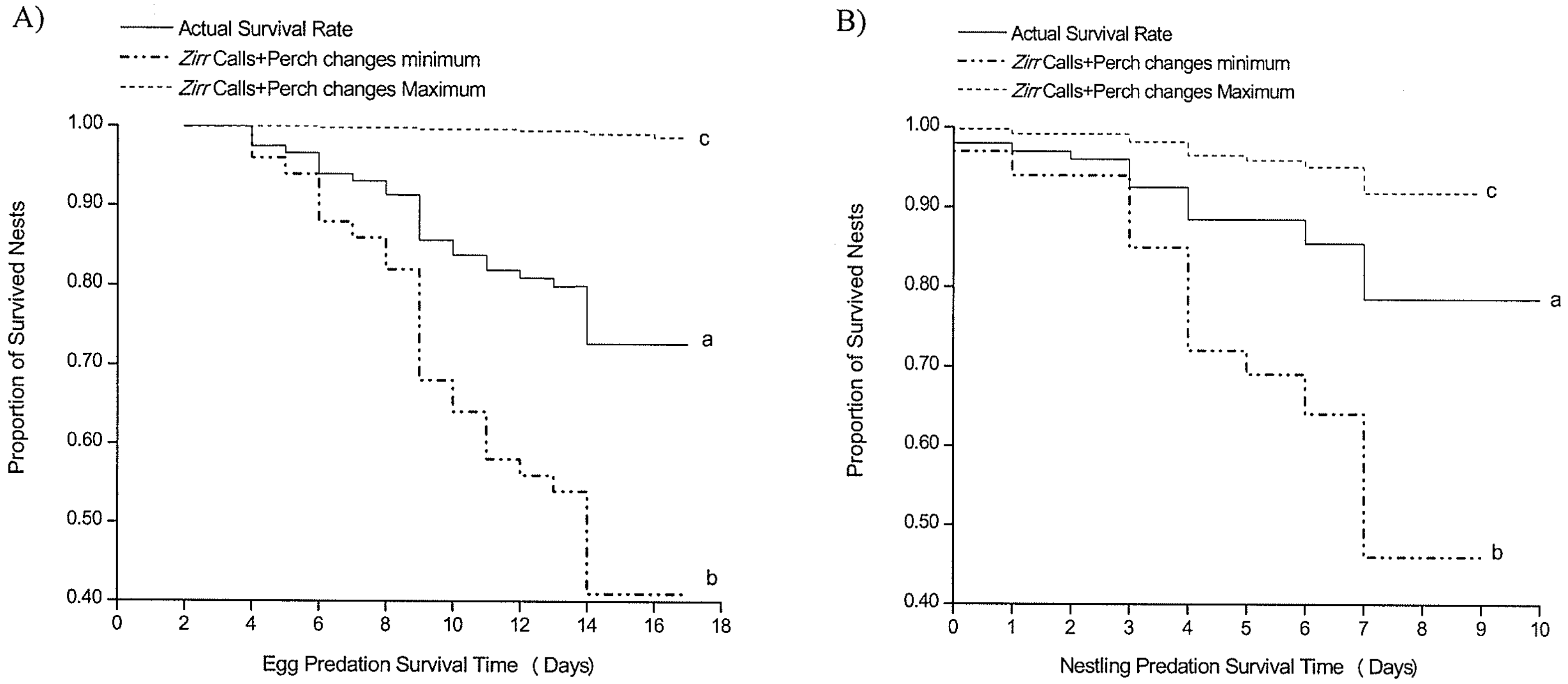

Figure 5.4. Curves of survivorship to (A) egg and (B) nestling predation that resulted from all Reed Warbler nests at Tomina (Italy) exposed to models (solid line) are compared to those obtained by entering in the model the lowest (dash-dot line) and the highest (dashed line) values of *zirr* calls and perch changes recorded during presentations. Different superscripts indicate significantly different survival rates (t-test, $P \leq 0.05$, see text for exact values).

and nestling predation were significantly higher than the least responsive (P < 0.001, Fig. 5.4) and significantly lower than the most responsive individuals (P < 0.01, Fig. 5.4).

DISCUSSION

Nest Defence as a Parasitism Deterrent

Yellow Warblers respond to cowbirds with specific defences (Hobson and Sealy 1989, Gill and Sealy 1996, 2004), which implicitly suggested fitness benefits (Sealy et al. 1998). My results confirm this (Chapter 3-4); however, in this study, higher or lower nest survival to parasitism was not associated with particular behaviour. Individuals that vocalized or moved more did not benefit through higher survival to parasitism than less responsive individuals. This result should be interpreted cautiously because, although the sample size was large, I recorded responses at only a few nests before they were parasitized.

Past investigators proposed that not only does nest defence against cowbirds not serve as a deterrent against parasitism, but that instead, cowbirds may exploit warbler defences to locate nests (i.e., nesting-cue hypothesis, Robertson and Norman 1976, 1977). One investigation on nest defence of Red-winged Blackbirds and Yellow Warblers (Gill et al. 1997b) showed no support for this hypothesis. In fact, the intensity of responses did not differ between models placed at different distances from nests and between parasitized and unparasitized hosts, both results which fail to conform to the predictions of the nest-cue hypothesis (Gill et al. 1997b). Although these results support my findings that nest defence did not affect the likelihood of Yellow Warblers being parasitized, recent observations at nests have revealed that hosts similar in size to Yellow Warblers occasionally thwart parasitism by their attacks, with cowbird eggs being laid on the ground (Ellison and Sealy 2007). This indicates a clear effect of nest defence on the incidence of parasitism that I did not detect in my study.

Reed Warblers that uttered more *zirr* calls during the first cuckoo encounter also tended to escape parasitism. This call was also uttered more frequently to cuckoos (Chapter 2). Use of defensive behaviours toward specific threats has been described in several organisms, from fleeing behaviour in fish (Chivers and Smith 1994, 1998) to alarm calls in birds (McLean and Rhodes 1991, Gill and Sealy 1996) and mammals (Seyfarth et al. 1980, Owings et al. 2001), and their specificity has been explained to serve precise functions (Bradbury and Veherencamp 1998). To explain how the *zirr* call can deter a parasitism event, and then provide fitness benefits, it is useful to examine its acoustic characteristics. The *zirr* call appeared to have a similar broadband sound typical of mobbing calls that recruit conspecifics, and this function was supported by the observed increase in birds attracted to the nest area during defensive responses elicited by cuckoo models (Chapter 2).

In many studies, mobbing did not thwart parasites. Videorecordings of natural parasitism events have shown that cuckoos chased Reed Warblers off the nest (Moksnes et al. 2000). However, because video cameras were set for close-ups of the nests, it was not possible to record host mobbing intensity and whether other birds than the nest owners were present (Moksnes et al. 2000, Tab. 1.1). If group mobbing is the ultimate deterrent of cuckoo parasitism, it should be elicited when the cuckoo is around the nest, not at the nest, given the few seconds a cuckoo takes to parasitize a nest (Sealy et al. 1995). In two studies, Reed Warblers instead responded more when a threat was at their nest rather than some distance from it. However, one of these studies did not distinguish between different models and different nesting stages when responses were recorded (Duckworth 1991, Tab. 1.1), whereas the other study recorded a higher aggression index in response to a cuckoo model placed closer rather than farther from the nest. The use of an aggressiveness index and the non-distinction between alarm calls do not permit an interpretation of whether a higher aggression index meant that individuals uttered more *zirr* calls (Røskaft et al. 2002b, Tab. 1.1). Single behaviours recorded when a cuckoo model is presented at different distances from the nest would test whether *zirr* calls and the consequent group mobbing are also elicited when cuckoos are approaching the nest and, therefore, giving the mobbers more opportunities to chase the cuckoos away.

Parasitism occurrence in relation to nest defence has been quantified in few studies. In addition to tests of the nest-cue hypothesis (see Smith et al. 1984, Gill et al. 1997b), recent results have revealed a higher intensity of defensive responses toward cuckoo intrusions by Great Reed Warblers compared with Reed Warblers (Dyrcz and Halupka 2006). The frequent attacks of Great Reed Warblers were suggested but not confirmed to be the cause of their lower parasitism rate. In this study, I detected another defence used by Reed Warblers that possibly deters parasitism. Reed Warblers attacked cuckoos more frequently than the other models (Chapter 2), probably because they are one third the size of Great Reed Warblers (Cramp 1992), but their attacks were not predictors of nest survival to parasitism. On the contrary, their *zirr* calls were associated with low parasitism incidence. Whether the *zirr* call recruits conspecifics for group mobbing warrants a study of its functional information.

Nest Defence as a Deterrent of Nest Predation

Survival of Yellow Warbler nests to egg predation was associated with high intensities of specific and alternative defensive strategies. Individuals that responded with many *chip* calls, perch changes, attacks on the model, and long bouts of nest-protection behaviour were among those that were most likely to escape egg predation. These responses were segregated into three sets of alternative defensive strategies that I designated, for brevity, aggressive, distractive and protective. The number of perch changes also emerged as a predictor of nest survival to both egg and nestling predation, in Reed Warblers. Changing perches, the common survival predictor in the two species, has been suggested to distract an intruder's attention from the nest by attracting it toward the performer (Greig-Smith 1980). Gill and Sealy (1996) reported that distraction displays were elicited more by a predator than cowbird models and, in Chapter 2, this behaviour increased toward nest predators at the nestling stage, which indicates an increased defensive effort toward nest predators at the more valuable nestling stage (Patterson et al. 1980, Montgomerie and Weatherhead 1988).

Nest defence is often considered to be suboptimal behaviour not only because predation is seldom deterred (Ghalambor and Martin 2000) but because future reproduction is diminished by the energy expended protecting the nest (Smith et al. 2007). Comparisons between predator-free populations and populations with predators have attempted to quantify the alleged lower nest success. Despite highly aggressive responses, Arctic Terns (*Sterna paradisaea*) sympatric with the predatory American Mink (*Mustela vison*) achieved lower nest success than those in allopatry; however, there was no indication that nest success varied with the intensity of aggression within the sympatric population (Nordström et al. 2004). Still, solitary-nesting terns suffered higher nest predation than colonial nesters, despite a similar frequency of attack on a predator model (Lemmetyinen 1971). An increased level of mobbing, as measured by an aggression index, had no effect on the reproductive outcome of American Robins (*Turdus migratorius*, McLean et al. 1986) but it was found to be positively associated with nest success in Stonechats (Greig-Smith 1980) and in Eastern Kingbirds (*Tyrannus tyrannus*, Blancher and Robertson 1980). There are indications that similar life history traits would select for similar nest defence expressions, which suggests ultimately a similar fitness return (Ghalambor and Martin 2000). Yellow Warblers and Reed Warblers possess similar life history traits as they have a similar body mass, lifespan, age of sexual maturity, clutch size, mating system, and parental care (Cramp 1992, Lowther et al. 1999), all traits that might have played a role in the convergence of their nest survival predictors toward predator distractions such as perch changes coupled with frequent vocalizations.

Yellow Warblers adopted more strategies associated with a decreased nest predation rate. Aggressive and protective responses were in fact absent in the repertoires of Reed Warblers at Tomina. Mutually exclusive antipredator behaviours are apparently influenced by urgency of the threat (i.e., imminent danger of attacks), by the predator type, and by the frequency of encounter between predator and prey (Ricklefs 1969, Le Roux et al. 2001, Warkentin et al. 2001, Caro 2005, Jackson et al. 2006). When confronted with Spotted Leopards (*Panthera pardus*), Bonnet Macaques (*Macaca radiata*) uttered a specific type of alarm call that alerted all troop members, which immediately escaped to trees, whereas the slow-moving Indian Python (*Python molurus*) did not elicit this refuge-seeking behaviour (Coss et al. 2007). Each strategy, therefore, potentially increased fitness if used with the appropriate predator. The different nesting habitat and the different predator types to which Yellow Warblers are exposed should be investigated in order to determine whether they serve as factors selecting these other strategies, although they accounted for less than 0.001% of the variability in explaining the aggressive nest defence in several species of waders (Larsen et al. 1996).

Flexibility of Nest Defence in Stable/Unstable Threatening Conditions

Survival Analyses have partially confirmed the annual variation in parasitism and nest predation frequencies provided earlier (Chapter 1, Tab 1.4). Between two years, Yellow Warblers were parasitized at similar frequencies but predation pressure was different, whereas Reed Warblers were exposed to consistent levels of parasitism and nest predation (Tab. 5.2 and 5.7). Past studies provide evidence of longer term parasitism pressure in the population of Yellow Warblers at Delta Marsh, although great changes were also recorded (Tab. 1.3). Nest predation frequency recorded in this study was higher than that recorded in the past (Tab. 1.1); however, there are no past records of its fluctuation between years. There is no information of parasitism and predation frequencies on the Reed Warbler population at Tomina. Due to the reduced number of cuckoos, a drastic change in parasitism was recorded in an English population after 10 years (Brooke et al. 1998), but populations of Reed Warblers in Czech Republic and Tuscany (Italy) did not experience such changes (Øien et al. 1996, Quaglierini 2006), whereas there are no records of fluctuations of nest predation frequencies in any Reed Warbler population.

Results of the variation in parasitism and predation frequencies between years are consistent with the environmental conditions suggested to select preferentially for individual or social learning (Johnston 1982, Kendal et al. 2005). Despite their high nesting density (Woolfenden et al. 2003), Yellow Warblers apparently ignored defensive responses they saw performed by conspecifics, whereas the intensity of their defence increased after a threat had been presented at their nest. The opposite results were obtained for Reed Warblers; they intensified their defence after observing conspecifics defending their nest, but did not do so after exposure to the same threatening situation at their nest (Chapters 3 and 4).

In this study, it was not possible to test the adaptiveness of behavioural flexibility adopted by Yellow Warblers because I could not record enough defensive responses at nests before they had been parasitized and there is no available means to predict which nest will be parasitized. A population with a higher frequency of parasitism may provide experimenters more opportunities to collect an adequate sample size of responses in "to-be-parasitized" nests and compare the behaviour of owners of those nests with that of individuals that remain unparasitized.

In Reed Warblers, nest survival to parasitism was predicted by changes in the number of *zirr* calls following threatening experiences. There was an apparent maladaptive value of learning as low responsive individuals that maintained the same low response intensity during further threat encounters benefited by having the highest nest survival rates, whereas individuals increasing their response were more likely to be parasitized. (Tab. 5.9). However, less flexible and less responsive individuals would respond with the same non-aggressive defence during successive nesting attempts, and therefore, would be particularly vulnerable to parasitism in the first place, as shown by the increased survival rates obtained with the most responsive individuals during their first parasite encounter (Tab 5.9). Thus, more flexible individuals might benefit from their refined defence as their stronger reactions might enable them to escape parasitism more easily during their first encounter with a threat.

The flexibility shown by Reed Warblers in defensive responses was acquired mostly by observing conspecifics (Chapter 4). Given its occurrence in many animal species (Cheney and Seyfarth 1985, Dukas and Real 1991, Carlier and Lefebvre 1997, Galef and Laland 2005), social learning has been proposed to be adaptive (Galef 1995, Danchin et al. 2004, Kendal et al. 2005, but see Laland 1996, Laland et al. 2005). Fitness consequences of socially acquired behaviours have been largely documented in song acquisition (Payne 1982), including in Yellow Warblers (Cosens and Sealy 1986). In Brown Rats (*Rattus rattus*), the opening of pine cones to consume their contents has been shown as a socially transmitted ability to enable individuals to exploit another ecological niche (Terkel 1996). Further, antelopes (*Kobus kob thomasi* and *K. leche fafuensis*) and Collared Flycatchers (*Ficedula albicollis*) use public information to choose good-quality patches to breed, which suggests that favourable conditions increase their reproductive success (Deutsch and Nefdt 1992, Doligez et al. 2002, Pärt and Doligez 2003). Evidence of fitness advantages accrued by learning antipredator responses are scarce (Griffin 2004) and there are no studies that have tested the effects of behavioural flexibility in antiparasite acquisition. In my study, I found a relationship between socially acquired defences and breeding success. Other hypotheses relative to socially acquired traits have suggested that copying conspecific behaviours might transmit maladaptive traits (Boyd and Richerson 1985). To test whether the acquired defence is retained during successive nesting attempts is an attractive avenue that would either support the indications of this study, thus that flexibility in antiparasite responses conveys fitness benefits, or that an apparent maladaptive trait is maintained in this population.

Defending from Parasites and Nest Predators at a Population Level

In Yellow Warbler and Reed Warbler populations, enhanced intensities of some defence were associated with increased nest survival. In both cases, an increased intensity of these nest survival predictors was the most common strategy spread in the populations. In fact, survival rates quantified among all individuals responding at different intensity levels were higher than those obtained with individuals showing the lowest levels of response (Fig. 5.1, 5.3, 5.4). Defensive responses are considered energetically expensive and potentially dangerous (Sealy et al. 1998, Lima and Dill 1990, Lind and Cresswell 2005), therefore, a population mostly composed of highly responsive individuals that achieved higher reproductive outcomes indicates a directionality in selection toward optimal nest defensive responses.

The only exception to this scenario was the intensity of one of the predictors of survival to predation in Yellow Warbler nests, attacks on the model. As for the distractive and protective strategies, an enhanced aggressiveness was also associated with high rates of survival to egg predation. However, high intensity expression of this strategy was uncommon in the population, as indicated by a survival rate similar to that of the least responsive individuals (Tab.5.4). From invertebrates (Hedrick and Kortet 2006) to mammals (Berger et al. 2001), as well as fish (Chivers et al. 2001) and birds (Beauchamp 2004), natural selection apparently favours stronger antipredator responses as predation risk increases (i.e., high predator encounter rates), whereas less appropriate defence is used if the encounters with a predator type are rare. Contrary to the example summarized in the previous section, macaque populations less experienced with pythons responded by climbing trees, a response optimal against leopards but not against slow-moving snakes (Coss et al. 2007). In this investigation, I identified the defensive strategies adopted by individuals whose nests were depredated or those whose nests were not, and I quantified nest survival rates for individuals adopting those strategies. However, I did not determine the most common predator. Yellow Warblers discriminate between an avian predator and a brood parasite (Hobson and Sealy 1989, Gill 1995, Gill and Sealy 2003), therefore, it is plausible that different predators elicit specific antipredator responses, as has been documented for species able to discriminate between at least terrestrial and aerial predators (Cheney and Seyfarth 1985, Seyfarth and Cheney 1990, Evans et al. 1993). On these bases, the occurrence of low levels of the aggressive strategy may be explained if these responses were triggered preferentially by rare predators.

Except for the aggressive strategy in Yellow Warblers, nest survival rates of the populations were higher than those recorded among the least responsive individuals. At the same time, mean nest survival relative to all individuals was lower than the rates obtained among the most responsive individuals (Fig. 5.1, 5.3, 5.4). In other words, the first comparison indicates a tendency toward increased responsiveness, whereas the second indicates some constraints that prevented all individuals in the population from acquiring the highest intensity in nest defence.

Suboptimal defensive behaviours have been proposed to result from pressures imposed by multiple predators whose impact may constrain the evolution of intense and specific antipredator defences (Sih et al. 1998). Predator-specific defences might enhance prey mortality as a response that proves optimal in avoiding one predator type (e.g., climbing trees to avoid a terrestrial predator), may also render the prey more vulnerable to another predator (e.g., attack by an aerial predator; Soluk and Collins 1988, Soluk 1993). In some cases, compensatory prey defences include the evolution toward more generalized or attenuated responses (Krupa and Sih 1998). In Reed Warblers, other birds at the nest were associated with decreased survival to nest predation (Tab. 5.11), which is consistent with the hypothesis that other birds attracted by the defending pair were exploited by predators to better locate their targets. Exploitation of animal signals is known across the animal kingdom. Fringe-lipped Bats (*Trachops cirrhosus*) eavesdrop on mating calls to better locate their prey, Tungara Frogs (*Physalaemus pustulosus*, Ryan et al. 1982). Frogs, in turn, compensate by attenuating their mating calls when females are absent or competition with males is low (Ryan et al. 1982). The highest numbers of *zirr* calls and hence attraction of other birds were elicited during cuckoo presentations (Chapter 2). *Zirr* calls were also associated with a reduced frequency of parasitism, whereas the presence of other birds was associated with increased nest predation. Therefore, the alarm call intensity expressed at less than the most optimal level predicted in terms of deterring parasitism is consistent with a compensatory response of Reed Warblers to attenuate the enhanced predation risk imposed by other birds' presence (i.e., to prevent an effective antiparasite response from turning into a detrimental strategy that increases predation; Charnov and Krebs 1975, Sih et al. 1998).

For Yellow Warblers, I was not able to detect a similar constraint, thus there were no factors particularly associated with increased frequency of parasitism or predation. The nest-cue hypothesis suggested that nest defence activities and vocalizations are exploited by cowbirds to better locate nests to parasitize (Robertson and Norman 1976, 1977). However, evidence did not support this hypothesis in Yellow Warblers as they responded with the same intensity when cowbird models were placed at different distances from their nest (Gill and Sealy 1997b). Despite frequent vocalizations during model presentations, males of the breeding pair joined the defending females inconsistently (Hobson and Sealy 1989, Gill and Sealy 1996) and the presence of other birds at the nest has not been quantified. In light of my findings on Reed Warblers, an investigation of the recruitment properties of Yellow Warbler vocalizations and their effect on nest success is warranted.

In conclusion, defences of Yellow Warblers had a neutral effect on parasitism frequency but alternative strategies were evident as deterrents of nest predation. Reed Warbler defences, on the other hand, produced a positive effect on nest survival in response to both parasitism and predation. Different environmental pressures in the two populations were consistent with the conditions suggested to favour the different learning mechanisms adopted by the two species in acquiring defensive behaviours. In Reed Warblers, there were indications that acquired defensive responses might convey fitness benefits if they are retained during successive nesting attempts, a hypothesis that should be addressed in Reed Warblers. Finally, in both species, there was a significant tendency toward enhanced defensive responses at the population level. However, in Reed

Warblers, there were indications that this tendency was also constrained by other elements involved in their defensive responses. Further studies are required to investigate Yellow Warbler populations with higher frequencies of parasitism to enable a more robust analysis of the effects of defence and its modulation on nest success. Long-term studies should focus on variation in parasitism and predation to further address the role such variation plays in selecting for the different learning mechanisms adopted by the two species. Finally, examining more variables involved in nest defence of Yellow Warblers might shed light on the constraints preventing them from adopting optimal responses.

CHAPTER 6

CONCLUSIONS

In this study, I examined the role of experience in the nest defence of Yellow Warblers and Reed Warblers. Defensive responses and their intensity were also tested for their adaptiveness. While past investigations consistently revealed Yellow Warblers discriminate among threats, some studies showed that Reed Warblers reacted differently to parasites and adult predators, whereas in others they failed to distinguish between even cuckoos and pigeons.

Because of these contrasting results, I first tested the enemy discrimination ability of Reed Warblers by exposing them to models of cuckoos (brood parasites), magpies (nest predators), and pigeons (control species), during the egg and nestling stages. Reed Warblers responded differently to the three models at different nesting stages, indicating their ability to discriminate among threats and to adjust their responses according to the risk each poses. When the risk of parasitism was high, Reed Warblers mobbed cuckoos more frequently, performed numerous bill snaps, uttered more *zirr* calls, and significantly more birds, other than the breeding pair, were attracted to the nest site during cuckoo presentations, whereas when presented with nest predator models, they watched silently and from a distance. When the reproductive value of their nest contents increased, and the risk of parasitism was over, they responded as mildly to cuckoos as they did to the non-threatening pigeons, whereas they approached the predator models more closely and moved more frequently among perches. Intensity of defensive responses was not affected by the number of experimenter visits at the nests, the day and time of presentations, or the size and age of clutches and broods. In one exception, the number of the Reed Warbler *churr* calls was influenced by clutch or brood age but not by the model type presented. Further studies of the two alarm calls of Reed Warblers, *zirr* and *churr* calls, are warranted to test whether they function to recruit neighbours for group mobbing and to silence the offspring, respectively, as my findings suggest.

I tested whether defence was modified by a threatening event at the nest or by observing conspecifics defending their nests from brood parasites by exposing Yellow and Reed warblers to multiple presentations that simulated events of parasitism and egg removal. Yellow Warblers significantly increased the number of alarm calls, attacks, and distraction displays after being confronted with a threat at their nest, whereas they did not change their defence after the social experience. The opposite results were obtained in Reed Warblers. After observing conspecifics defending their nest during a parasite's visit, they changed perches and bill-snapped toward cuckoos more frequently, whereas they did not modify their defence after parasitism and egg removal events had been simulated at their nests. These results indicated that individual learning affects nest defence in Yellow Warblers, whereas social learning does in Reed Warblers. In my study, to provide experimental simulations of a parasite intrusion, I exposed each nest to two trainings. It is possible that two trainings were not sufficient to trigger individual learning in Reed Warblers and social learning in Yellow Warblers. Future studies should address this question, keeping in mind that more exposures to a still model may result in habituated or sensitized responses. The occurrence of different learning mechanisms in other behaviours has been proposed as the selective result of differential variability in environmental conditions, as stable environmental pressures should favour social learning, whereas unpredictable fluctuations would select for individual learning.

Although such conditions were detected in parasitism and predation frequencies in the two populations during the course of this study, a long-term study that records both annual changes in parasitism frequencies and warbler learning abilities may support this explanation for the selection of differential learning mechanisms acting on the refinement also of defensive behaviours.

In the last chapter of this dissertation, I tested whether intensity of nest defence and its adjustment following a threatening event were associated with increased survival of Yellow and Reed warbler nests by performing survival analyses coupled with the defensive responses recorded during the model presentations. Results showed that intensities of the defensive responses of Yellow Warblers did not predict whether a nest would be parasitized, whereas numerous *zirr* calls were mostly associated with unparasitized Reed Warbler nests. Aggressive, distractive, and protective responses of Yellow Warblers and frequent perch changes by Reed Warblers were instead predictors of low nest predation rates. In Reed Warblers, a low survival to nest predation was also predicted by numerous other birds being attracted at the nest while the warblers were defending it.

The adjustment of nest defence that followed a threatening event was apparently maladaptive in Reed Warblers because individuals that responded with less intensity also during the successive parasite encounters were the least parasitized. Results, however, also indicated that the individuals that responded more intensely in the first place were those that most escaped parasitism. This suggests that high defensive intensity acquired during past encounters and retained during successive nest attempts would be advantageous to more plastic individuals. Further studies should focus on the ability of

Reed Warblers to retain defensive changes detected in the short-term for support of this hypothesis. In Yellow Warblers, I could not test the effect of defence flexibility on nest survival because too few nests were tested with model presentations before they were parasitized. Higher frequencies of parasitism would allow studies to achieve statistically analyzable data.

Results of survival analyses showed that specific defensive behaviours predicted the occurrence of parasitism and nest predation, suggesting that these behaviours prevented or contained parasitism or nest predation. The adaptiveness of these defensive responses was supported by the large extent to which intense responses of the nest survival predictors were spread throughout the population. The same analyses, however, revealed that the two populations did not adopt the optimal intensity of the nest survival predictors. For Reed Warblers, constraints were suggested as a trade-off between antiparasite and antipredator responses. In fact, many *zirr* calls simultaneously predicted survival to parasitism and were correlated with a high number of other birds at the nest. These in turn predicted a low survival to nest predation, suggesting that *zirr* calls expressed at high, but not at the highest, intensity may result in a trade-off between effective group mobbing against parasites and preventing predators from better locating nests. As suggested above, a study examining the referentiality of this call may shed light not only on its function but also on its use in conjunction with other defensive responses of Reed Warblers. I did not find possible constraints preventing Yellow Warblers from adopting the optimal intensity of the predictors of nest survival. Alarm calls of Yellow Warblers possess referential information of the environmental context for the breeding pair and young. In the light of findings on Reed Warblers, a future investigation of

Yellow Warbler defence should be conducted to test whether these vocalizations also function to recruit nesting neighbours for group mobbing and whether their presence is a predictor of warbler nest survival.

Implications of my findings address different facets, from dynamics of brood parasitism to ecological aspects of learning. In the arms race between parasites and their hosts, rejection of parasitism has been considered the only antiparasitic response possible to reduce the impact of parasitism on host nest success (Rothstein 1975a, Davies 2000). Although suggested by different studies (Sealy et al. 1998, Lindholm and Thomas 2000), a specific test of the effectiveness of nest defence to deter or diminish the impact of parasitism has not been conducted. In this study, specific responses predicted whether a nest would be parasitized or depredated and, therefore, let nest defence to enter among the components taken into account when evaluating the coevolutionary race between brood parasites and hosts. If parasites are deterred by host aggressiveness, the stealthy habit of brood parasites fits well as a coevolutionary response to host attacks. Moreover, the process of host specialization by parasites, and their consequent egg mimicry, might be favoured or prevented according to the effectiveness of nest defence among the potential hosts in the avian community.

The comparative approach allowed me to reduce the speculation in the interpretation of results that emerged from this study. The adoption of one learning mechanism and the investigation of the adaptive value of nest defence for only one species would have not revealed how the different environmental pressure and parasite system would have come together to produce the detected effects. Instead, the comparative approach allowed divergence or convergence of defensive traits and their adaptiveness to be revealed with respect to particular sets of environmental factors (Shettleworth 1993), such as the frequencies of parasitism and nest predation.

Probably because antipredator responses have often been considered optimal if expressed at their best since the first predator encounter, the ecological approach to learning of the last decades has neglected to investigate to what extent defensive strategies are also shaped by the interaction between environmental variables and individual experiences (Griffin 2004, Galef and Laland 2005). In my study, species under two parasite systems adopted different mechanisms of learning. Accordingly, implications of these findings would be to re-consider the complex pressures imposed by environmental variables as agents able to select, via learning, not only optimal foraging techniques, habitat preferences, and mate choices, but also effective defence.

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