

The Influence of an Invasive Species, the Common Myna (*Acridotheres tristis*), on the Behavior of a Local Species, the House Sparrow (*Passer domesticus*)

DISSERTATION SUBMITTED FOR THE DEGREE

"DOCTOR OF PHILOSOPHY"

by

Itay Berger

School of Zoology, Tel-Aviv University

Submitted to the Senate of Tel-Aviv University

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This work was carried out under the supervision of

Prof. Tamar Dayan

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# **Abstract**

Studies of the influence of invasive species on local species have focused mainly on competition, predation, hybridization, and disease. Although many studies have also focused on the behavior of the invasive species, their influence on the behavior of the local species has been largely neglected to date, despite behaviors such as foraging or breeding having a great impact on survival and fitness. The invasion process encompasses several stages that act as a filter, selecting for specific traits in the introduced population, including behavioral traits. This filters out the unsuccessful would-be invasive species as well as the unsuccessful individuals within a successful species. Selection at the individual level is often realized in behavioral differences between the invasive and the local populations of the same species.

Behavior is a mediator of many interactions, affecting competition, predation, hybridization, and disease transfer, as well as constituting a mechanism of invasion. The presence of invasive species can alter the behavior of the indigenous species. Such behavioral changes can affect the fitness of the individual, especially if the affected behavior directly influences survival or breeding. Consequently, it may affect the population as a whole, with ecological implications.

Here, I examined the effect of the presence of the invasive common myna on the foraging and nesting behaviors of local house sparrows, by means of four main experiments, as follows:

Experiments 1 and 2 were conducted to examine the effect of the invasive mynas on the foraging behavior of the native sparrows, in the wild and in captivity, respectively. In order to measure the vigilance level of foraging sparrows, in experiment 1, flocks of sparrows were recorded on urban lawns. Six flocks were recorded foraging alongside a pair of mynas and eight flocks were recorded foraging alongside a pair of laughing doves, as control. Each video recording was analyzed frame-by-frame and the duration of the head-up posture was noted for individual sparrows. The findings were compared between the flocks that foraged in the presence of mynas and those that foraged in the presence of doves.

In order to determine whether sparrows will prefer to forage in the presence of mynas, Experiment 2 was conducted in captivity. Ten sparrows were introduced into an aviary, which had an additional aviary attached on either side. One of the side aviaries contained twenty sparrows and the other side aviary contained four mynas. The sparrows in the middle aviary were given two food trays, one close to the other sparrow aviary and the other close to the myna aviary. Sixteen grams of chicken feed mix were placed on each tray for 24 hours before measuring the giving-up density (GUD). I repeated this experiment for seven days. In the control experiments mynas were replaced in the first side aviary with doves while the second side aviary remained empty. GUD was measured for seven days for each control. Experiment 2 was conducted on six groups of experienced sparrows (sparrows captured in the wild and probably having previously encountered mynas or doves), and six groups of naïve sparrows (sparrows that had hatched in captivity and had no previous experience with mynas or doves).

Two additional experiments were conducted in order to examine the effect of the invasive mynas on the breeding behavior of the sparrows: Experiment 3 in the wild and Experiment 4 in captivity.

The effect of mynas on the nesting behavior of sparrows in the wild was examined by placing either a myna or a dove decoy near the sparrow nests for 30 minutes, while the nestlings were being fed. After 30 minutes the decoys were interchanged (dove for myna and myna for dove). The parents' behavior around the nest and rates and duration of visits were recorded.

Using a captive sparrow colony, I measured the breeding success in the presence and absence of mynas. Five pairs of sparrows (male and female) were introduced into each of six aviaries located next to each other in a row. Three of the aviaries contained a small cage with one myna and the other three contained a small cage with one dove. Although the sparrows could see the sparrows in the next aviary, the sparrows in aviaries with a myna could not see the doves in the other aviaries, and the sparrows in aviaries with a dove could not see the mynas in the other aviaries. The sparrows in all aviaries were provided with similar conditions in order to breed. After the first breeding cycle, all the mynas were replaced with doves and all the doves were replaced with mynas. Breeding success and fledgling physical condition were measured and compared between sparrows breeding next to mynas and those breeding next to doves.

Surprisingly, in the field, I found that sparrows that foraged alongside mynas were less vigilant than sparrows that foraged alongside doves. Alongside doves, sparrow vigilance was negatively influenced by group size, as expected from the literature. However, alongside mynas, vigilance was low, with no effect of group size.

In captivity, the experienced sparrows preferred to forage close to the myna cage than close to the other sparrow cage, while also preferring to forage close to the other sparrow cage than to the empty cage. In the presence of doves, the sparrows did not show any preference between doves and other sparrows. In regard to foraging location, the naïve sparrows preferred to forage close to both the myna and the dove cages than to the other sparrow cage, while also preferring to forage close to the other sparrow cage than next to the empty cage.

When the myna decoy was presented near the sparrow nest, nestling feeding rate decreased compared to when near the control, dove decoy. Furthermore, breeding success was significantly lower near the myna compared to near the dove. Fledgling physical condition (tarsus length) was also poorer when they were hatched and raised alongside mynas compared to fledglings that were hatched and raised alongside doves.

These findings suggest that sparrows perceive their environment as safer when foraging alongside mynas, but also treat mynas as a threat when encountering them in the vicinity of the nest. Consequently, invasive mynas may improve the foraging success of native sparrows but reduce their breeding success. This finding illustrates the complex potential influence of invasive species on local species. The findings from this study also highlight the importance of investigating the impact of biological invasions on the behavior of local species.

# **Introduction**

When I was a senior in high school, in 1998, I caught a glimpse, while on a bus, of a bird I could not identify. The bird, appearing for less than a second, was brown with white wing patches. It seems that this was my first sighting of a common myna, a newly-established invader. During that decade (the 1990s), the field of invasion ecology become established (Davis 2009) and in that year Wilcove et al. (1998) demonstrated how invasive species were becoming the second greatest threat to biodiversity, following habitat degradation or loss.

## Invasion Ecology

Invasive species are organisms introduced by humans into an area beyond their natural biogeographical range and which have established an expanding and independent population, while also impacting the local ecosystem. Although it was noticed as early as the 18th century by several scholars, the phenomenon of species' invasion was not studied in depth until the 20th century. The foundations of invasion ecology were established in 1958, with the publication of the book "*The Ecology of Invasions by Animals and Plants*" by Charles Sutherland Elton. This publication, describing invasions of islands, inland invasions, marine invasions and the influence on local populations, as well as engaging with conservation, is extensively cited in the professional literature.

During the 1990s, invasion ecology become established as a field separate from general ecology (Davis 2009) and publications started to grow exponentially (Richardson & Pyšek 2008). In 1997 the Global Invasive Species Programme (GISP) was founded as a partnership of IUCN, CABI, and SCOP with the aim of conserving biodiversity and sustaining human livelihoods, by minimizing the spread and impact of invasive species. The journal "*Diversity and Distributions*", which focused on biological invasions and biodiversity, was founded in 1998 and the journal "*Biological Invasions*" was founded in 1999.

During the first decade of the 21st century invasion ecology publication rate continued to grow (Shirley & Kark 2006; Richardson & Pyšek 2008; Davis 2009). At the same time, some studies started to challenge the basic perceptions and definitions of the field: that invasive is necessarily negative and native is necessarily positive; or that invasive species reduce local biodiversity (Davis & Thompson 2001; Slobodkin 2001; Rosenzweig 2001; Davis et al. 2011). Conservation practices against invasive species also emerged, such as the publication "Global Strategy on Invasive Alien Species" by GIPS in 2004, and the initiation of DAISIE (Delivering Alien Invasive Species Inventories for Europe) in 2005. In 2012, another institution was launched: the European Alien Species Information Network (EASIN). This advanced information database is open to the public, and can assist in estimating the pathways and gateways of alien invasions and in helping researchers and policy-makers (Katsanevakis et al. 2015).

## The Invasion Process

The invasion process can be divided into three stages: arrival or transport, establishment, and spread (Kolar & Lodge 2001; Davis 2009). Failure at any of the stages will prevent the invasion. The first stage occurs within the species' original distribution area. Individuals need to be transported via a pathway that will deposit them beyond a dispersal barrier, survive the transition, and become released into the wild. Following release, the introduced individuals will encounter the new ecosystem and need to survive the encounter and establish a sustainable population. An introduced species may be blocked at the establishment stage for a prolonged period, even decades, before spreading (Reise et al. 2006). After the population spreads beyond its introduction area and impacts the local ecosystem, it is then referred to as invasive. This stage is characterized by a sharp growth in population size (Reise et al. 2006). Reise et al. (2006) posited a fourth stage, adjustment, in which the invasive population growth halts and either becomes static or declines.

McNeely (2001) suggested three main pathways for the first stage of invasion:

1. Accidental introduction: for example, the brown tree snake in Guam (Pimm, 1987).
2. Limited purpose introduction: for example, the rose-ringed parakeet (*Pisttacula krameri*) which become introduced as an escaped pet in England.
3. Intentional introduction: for example, European starlings (*Sturnus vulgaris*) which were introduced into North America by the American Acclimatization Society.

Several variables can help to assess the probability of an invasion succeeding or failing at any of the invasion stages. As the number of introduction events (introduction effort) or the number of individuals in each introduction event (propagule pressure) increases, the probability of succeeding in the first two invasion stages and becoming established also increases (Kolar & Lodge 2001; Blackburn et al. 2009; Simberloff 2009; Blackburn et al. 2013). In contrast, there is not always a correlation between high propagule pressure and establishment success (Moulton et al. 2012). Other factors that may help to predict the probability of a species becoming invasive are those of the previous history of successful invasions of the species (Richardson et al. 1990; Scott & Panetta 1993; Richard & Hamilton 1997; Kolar & Lodge 2001; Bomford 2008; Hayes & Barry 2008), the family or the genus of the species (Pyšek 1998; Kolar & Lodge 2001), vegetative reproduction ability (Richrdson et al. 1990; Richard & Hamilton 1997; Kolar & Lodge 2001), high rate of population growth (number of broods per season, fast development, small body size) (Duncan et al. 1999; Kolar & Lodge 2001), large original distribution area (Goodwin et al. 1999; Kolar & Lodge 2001), large brain size (Sol et al. 2002; Sol et al. 2013), and climate and habitat match (Bomford 2008; Hayes & Barry 2008). It is, however, very difficult to identify these characteristics accurately and there is a great deal of contrasting information on the subject.

The probability of overcoming all the invasion obstacles and spreading in the novel environment may increase not only due to the traits of the invasive species, but also due to the properties of the invasion process. When the new environment lacks the introduced species' enemies, or contains a significantly lower number of enemies, there is greater probability that the introduced species will spread, become an invader, exert significant ecological impact, and become a pest (Keane & Crawley 2002). The invasion success due to an enemy-free or enemy-reduced environment is referred to as the 'enemy release hypothesis', and includes the freedom from predators (Keane & Crawley 2002), from pathogens (Mitchell & Power 2003), and from parasites (Torchin et al. 2001; Clay 2003; Torchin et al. 2003). In many cases, however, there is no simple correlation between enemy release and invasion success (Colautti et al. 2004).

Some invasions can be initially overlooked and are referred to as cryptic invasions. Cryptic invasions constitute the occurrence of species or genotypes that were not previously recognized as alien in origin or were not distinguished from other aliens (Novak 2011). Cryptic invasions can be divided into two categories: interspecific cryptic invasions that occur when the invasion goes unnoticed due to the invasive species being misidentified as a native species or as another invasive species; and intraspecific cryptic invasions that occur when one lineage of a species invades the area of another, distinct, local lineage of the same species (Morais & Reichard 2017).

Since the invaded ecosystems did not co-evolve with the new, exotic, species, an ecological impact of invasion is expected. Such impact may be immense and prominent or small and hard to measure. It can occur rapidly or it can take decades before the effect is felt.

## The Impact of Biological Invasions

Invasive species may have a negative impact on the economy through reducing agricultural productivity or increasing production costs, reducing/impacting property values, causing harm to people or to domestic animals, and raising the costs of control (Bomford 2008).

An exotic species may also have a positive impact on the economy if it functions as a biocontrol agent, is used for food production, or as a pet in the pet trade (Bomford 2008).

Biological invasions are the greatest threat to biodiversity after habitat loss (Wilcove et al. 1998; Pejchar & Mooney 2010). However, not all habitats have the same vulnerability. Arctic and alpine ecosystems are less vulnerable to biological invasions because of their harsh climate conditions, while tropical ecosystems are also less vulnerable because of the high local species diversity, which reduces the probability of successful establishment by invaders (Sala et al. 2000). Mediterranean and southern temperate forests, in contrast, are spread across the globe in isolated and remote patches and exhibit extensive convergent evolution, which makes them vulnerable to the breach of ecological barriers among the patches and to consequent biological invasions (Sala et al. 2000). Other isolated and low diversity habitats, such as islands, are also more vulnerable to invaders (Sala et al. 2000).

Invasive species often thrive in degraded or altered habitats and in proximity to human activity. While habitat alteration encourages biological invasions, it can also potentially have a negative effect on local populations and local biodiversity, with these three factors often co-occurring. Hence, a correlation between a rise in the invader population and a decline in the local population does not necessarily indicate a direct connection between them. Invasive species may be the drivers of the ecological change or merely passengers of ecological changes driven by habitat modification (Didham et al. 2005; MacDougall & Turkington 2005; Didham et al. 2007).

In order to distinguish between these pathways it is necessary to remove the invasion effect or the habitat alternation effect. Understanding the ecological interactions between the invasive and the native population may also indicate the pathway that drives the ecological change.

In order to recover a native population, it is necessary to distinguish between the different pathways. Eradication of an invasive population will not recover the local population if the invasive species is only a passenger of habitat degradation. Similarly, a restoration of the altered habitat may not be effective if the invasive species is the driver of ecological change.

As a driver of ecological change, the influence of invasive species on local populations can result from several interactions. Competition and predation are among the most studied interactions, as well as hybridization and disease vectors (Gurevitch & Padilla 2004; Baker et al. 2014). After successfully establishing and spreading, invasive species may outcompete local species over resources such as food, nesting sites or territory (Baker et al. 2014). Because it is essential for invasive species to find food in the newly invaded region, they will prey on local species. If the invasive population outcompetes, or the local species lack the ability to protect themselves, the latter might decline (Sih et al. 2010). If the invasive species can breed with the local species, the ensuing hybridization could harm the local population or even lead to assimilation (Vilà et al. 2000; Tracey et al. 2008). Hybridization between native and invasive lineages of the same species may be a common and important impact mechanism in intraspecific cryptic invasions, and can promote evolutionary change, as new genotypes and phenotypes may emerge (Morais & Reichard 2017). During the invasion process, the invasive species may carry invasive pathogens, to which the local species will be vulnerable since they did not co-evolve with them, unlike the invasive species that had introduced them. Invasive species can also function as a local disease vector and increase the vulnerability of the local populations. Gurevitch & Padilla (2004) re-analyzed Wilcove et al.’s (1998) data for 930 local species in the USA, regarding their interaction with the invasive species: 498 local species suffered from competition with the invasive species; 131 local species suffered from predation by the invasive species (including herbivores); 22 suffered from hybridization with the invasive species; and 33 suffered from local and invasive pathogens spread by the invasive species. Gurevitch & Padilla (2004) also analyzed data from the UNCN Red List on the interactions leading to local population decline. At the time, 911 species were listed as affected by invasive species (7,751 species updated), 137 of which were affected by competition and 161 by predation. Since it is difficult to demonstrate ecological interactions, in many studies the evidence remains solely anecdotal or theoretical, with no documented proof of population influence (Byers 2002; Baker et al. 2014). In many studies that did find a negative influence of invasion on local populations, the evidence was correlative (Byers 2002; Baker et al. 2014); while other studies found no evidence of actual threat to local populations, but only a potential threat (Baker et al. 2014).

Although competition, predation, hybridization, and disease are the main mechanisms by which local ecosystems are affected by invasive species, there are several less common interactions, such as parasitism (Woodworth 1997; Crystal-Ornelas et al. 2017).

In some cases, invasive species can become potential prey for the local species and thereby can have a positive effect (Glenn & Holway 2007; Stromberg et al. 2009; Ligon et al.2012).

## Avian Invasion

Red jungle fowl (*Gallus gallus*), transported from South-East Asia to northern China around 8,000 years ago offer the earliest evidence of avian species translocated by humans from their native distribution area (West & Zhou 1989). Since then, there have been many more avian translocations, especially, but not exclusively, for food (Grayson 2001; Hurles et al. 2003). The introduction rate of new avian species increased rapidly during the 18th century when Europeans started to spread out and colonialize many parts of the globe. About 40% of all known avian introductions occurred in only four regions: New Zealand, USA, Australia, and Hawaii, three of which are former British colonies (Blackburn et al. 2009). The reasons for those introductions were for food, hunting, biocontrol of local pests, aesthetic purposes, nostalgia and, sometimes, just as a hobby (Blackburn et al. 2009). The bird trade is a common pathway of modern avian invasions. The annual legal bird trade alone comprises one million individuals belonging to over 1,000 species (Gilardi 2006). Escaped pet birds are a main source of avian invasion today (Carrete & Tella 2008; Vall-Ilosera & Cassey 2017): for example, between 1999-2013 there were 1,900 reports of non-native escaped pet birds from 42 different species around cities in Australia, each of which can be referred to as an introduction attempt (Vall-Ilosera & Cassey 2017). Nevertheless, the more common, captive-bred, species do not tend to become invasive, despite their high introduction effort and high propagule pressure, while the less common, wild-caught, species have a higher potential to invade new environments (Carrete & Tella 2008). The reason for the low invasion potential of the captive-bred bird species may be the result of high artificial selection against those traits that enable survival in the wild (Carrete & Tella 2008).

It is difficult to characterize the specific life-history traits that might increase the probability of an exotic avian species becoming successfully introduced, since it is difficult to separate them from other life-history traits and other factors such as progagule pressure and phylogeny (Blackburn et al. 2009). Nevertheless, there is evidence that large body size and small clutches are positively correlated to introduction success (Blackburn et al. 2009). These traits are associated with slower population growth rate. Indeed, a meta-analysis by Blackburn et al. (2009) found that establishment success tends to be higher for species with slower population growth. Such traits may help the introduced population to contend with the conditions of the new environment. However, they also found that a short incubation period and higher number of broods per year too can increase introduction success. Therefore, it appears that the ideal strategy for the success of any introduced species is that of frequent reproduction with fast incubation, followed by long development to a large body size (Blackburn et al. 2009).

Another trait that influences introduction success is generalism (Blackburn et al. 2009; Sol et al. 2013). The wider the species’ niche, the more likely it is to achieve a successful introduction (Blackburn et al. 2009).

Relative brain size is also correlated positively with successful establishment in avian species and is associated with behavioral flexibility, which may assist the invader to contend with the novel environment (Sol et al. 2002; Sol et al. 2013).

From an analysis of 5,000 alien avian introductions (47% of which were successful), Sol et al. (2013) found that avian species with life-history strategies that prioritize future reproduction over current reproduction, are more successful in establishing than species that choose to invest in a current brood. Prioritizing future reproduction reduces the investment in the current brood and therefore increases the probability of the invasive population successfully passing the introduction and establishment stages (Sol et al. 2013).

Some bird families are more likely to be introduced than others. The most dominant of these are the Anatidae, Phasianidae, Psittacidae, Passeridae. and Columbidae (Blackburn et al. 2009). Shirley & Kark (2009) found that Columbidae, Psittacidae, Estrildidae and Ploceidae are more likely to have a negative impact on the economy (crops); Pycnonotidae and Threskiornithidae are more likely to have a negative impact on biodiversity; and Anatidae, Corvidae, Passeridae, Phasianidae, and Sturnidae are more likely to have a negative impact on both the economy and biodiversity. In Eurasia and Africa, introduced species originating from Indo-Malayan, Afrotropical, and Palaearctic zoogeographical regions were found to have a high impact on both the local ecosystem and the economy (Shirley & Kark 2009). Generalist avian invasive species were found to have a high economic impact; while invasive species that forage or roost in large flocks, as well as species with low body mass, were found to have a high impact on biodiversity (Shirley & Kark 2009).

Baker et al. (2014) reviewed 103 studies dealing with the interactions of 32 introduced avian species with local species. Eighty of these studies did not indicate a threat at the population level; 14 indicated a potential threat; and nine indicated a population level threat (Baker et al. 2014). Of those interactions, 68 were competition, 21 were hybridization, 17 were disease vector, 14 were predation, and one was brood parasitism (Baker et al. 2014). The invasive species subjected to the most studies, as reviewed by Baker et al. (2014), was the common myna (*Acridotheres tristis*), with 20 studies of its interaction with local species (followed by the myna’s relative, the common starling, with 13 studies reviewed).

## The Common Myna

The common myna was introduced into many parts of the world from South-East Asia (Feare & Craig 1998). This species is an aggressive intruder and there is considerable evidence regarding its aggression, competition, and predation on local species (Pell & Tidemann 1997; Blanvillain et al. 2003; Fitzsimons 2006; Holzapfel et al. 2006). Indeed, it was declared one of the 100 worst invasive species worldwide (Lowe et al. 2000), and it has been spreading in Israel since 1997 (Holzapfel et al. 2006).

Common mynas are part of the sub-group "Eurasian starlings", which belong to the Sturnudae family (Lovette et al. 2008). This sub-group shared common ancestors ca. 9.8 million years ago (mya), although most species started to diverge only from 7.2 mya, when this sub-group became divided into western and eastern Palearctic starlings (Zuccon et al. 2006; Zuccon et al. 2008). The Eurasian starling sub-group is composed of two main genera, *Sturnus* and *Acridotheres*, which separated ca. 3 mya (Lovette et al. 2008; Zuccon et al. 2008).

The common myna is an omnivore, feeding primarily on invertebrates but also on seeds (Feare & Craig 1998). Mynas prefer human-modified habitats such as irrigated lawns, agricultural fields, or urban areas in warm climates (Holzapfel et al. 2006; Peacock et al. 2007). Small open parks in urban environments are the mynas' preferred habitat, followed by urban habitats and rural habitats, and they are absent from the core bushland (Old et al. 2014). They usually forage in pairs or in flocks and demonstrate a high level of anti-predator vigilance that decreases as group size increases (Newey 2007).

Out of the 20 articles reviewed by Baker et al. (2014), only two demonstrated an ecological threat to local populations, both on islands. The first article associated poor breeding seasons of the endangered local flycatcher (*Pomarea nigra*) in Tahiti to the aggressive behavior of invasive mynas (Blanvillain et al. 2003). The second article dealt with myna interference with cavity nesting of the endangered Seychelles magpie-robin (*Copsychus sechellarum*) on Fregate Island in the Seychelles (Komdeur 1996).

Grarock et al. (2012) analyzed three decades of avian population data around Canberra, Australia, and found a correlation between the increased myna population and the decrease in the populations of 11 bird species (two of which are also invasive). However, this kind of correlation does not indicate an ecological impact of the invasive species. Grarock et al. (2013b) found that the common mynas in the Canberra area were mostly passengers of habitat degradation and urbanization.

One of the main mechanisms by which the common myna impacts native species has been claimed to be its highly aggressive interspecific behavior. There is evidence of myna aggression towards local birds (Holzapfel et al. 2006; Peacock et al. 2007; Trost & Olsen 2016) as well as towards mammals (Fitzsimons 2006; Trost & Olsen 2016). However, while much of the evidence is anecdotal, Lowe et al.’s (2011) comparison between the interspecific aggressive behaviors of the common myna and the interspecific aggressive behaviors of other avian species around Sydney, Australia, found that the mynas not only did not exhibit higher aggression levels than the local species, but actually exhibited lower levels than the local species (Lowe et al. 2011). Haythorpe et al. (2012) too did not find high interspecific aggression by mynas compared to local species during foraging, and also did not find an avoidance by local species of the presence of common mynas at feeding stations. Furthermore, Haythorpe et al. (2013) compared the invasive common myna around Newcastle, Australia, with the native noisy miner (*Manorina melanocephala*), whose population has increased due to human activity. They found that the noisy miner demonstrated a higher level of interspecific aggressive behavior compared to the common myna. Noisy miners were associated with a decrease in local avian biodiversity, were more abundant than common mynas, and were found in a larger variety of habitats, including the natural environment, while the common mynas were almost entirely restricted to urban and suburban habitats (Haythorpe et al. 2013).

Another potential impact mechanism of invasive mynas on native avian species is that of competition over nest cavities. Grarock et al. (2013a) found, using nest boxes around Canberra, that although common mynas preferred to breed in nest boxes at low tree density, the population of the native crimson rosellas (*Platycercus elegans*), abundant at high tree density, its favorite habitat, decreased in the presence of breeding mynas. Charter et al. (2016) demonstrated competition over nest cavities between the invasive common mynas and local passerines. Nonetheless, since mynas prefer human-modified habitats, and often breed in artificial structures, they may not necessarily compete with the local species in more natural habitats (Lowe et al. 2011). Orchan et al. (2013) studied the interactions among cavity-nesting species in Tel-Aviv. They found that the local Syrian woodpecker (*Dendrocopos syriacus*), which is a primary excavator, is negatively affected by an invasive, relatively small, competitor – the vinous-breasted starling (*Sturnus burmannicus*); which is in turn negatively affected by the common myna. Since common mynas are too large to occupy woodpecker nests, they can only use such nests after the woodpecker has finished breeding and the entrance hole has been widened by a secondary excavator, the rose-ringed parakeet. Consequently, the mynas do not directly compete with or affect woodpeckers. The eradication or reduction of myna populations may therefore negatively affect the local woodpecker population (Orchan et al. 2013).

Although most evidence of the ecological impact of mynas on the local ecology are anecdotal or correlative, the myna's high success as an invader and its potential threat have led to many attempts to eradicate or reduce the invasive populations. In 2006, the Canberra Indian Myna Action Group (CIMAG) was formed as a community group with the aim of reducing the impact of the invasive common myna on native birds (CIMAG, 2013). CIMAG uses public education and a culling program in order to achieve its goal. Culling is based on food bait that lures mynas into valve traps. However, an analysis of three decades of data indicates that although culling attempts have some impact over a fine scale of 1 km2, they have no effect on the invasive myna population over a broader scale of approximately 70 km2 (Grarock et al. 2014). Reducing myna populations can be difficult, since it is necessary to overcome their high reproduction rate of up to seven eggs per clutch, and up to three clutches per year. Furthermore, mynas can be very suspicious and have learned to avoid baits and traps after observing other individuals being captured (Griffin & Boyce 2009).

A different approach to the control of invasive myna populations is that of using starlicide bait (DRC1339, 3-chliri-p-toluidine hydrochloride). Starlicide was developed during the 1960s in order to reduce the common starling invasive population in North America, and its toxicity is higher for starlings (Sturnidae), icterids (Icteridae), crows (Corvidae), and gulls (Laridae) than for other avian taxa (Feare 2010). Furthermore, because starlicide breaks down under UV light, uneaten baits do not retain the poison residue and, following consumption, the poison completely metabolizes, thereby preventing any danger of secondary poisoning (Feare 2010). Starlicide was tested for its efficacy in controlling invasive myna populations on two islands in the Atlantic: St Helena and Ascension island (UK). A high mortality of the mynas was found as a result of the starlicide on both islands, with the Ascension myna population being reduced by 70% (Feare 2010). However, in the long term, the population recovered, probably due to bait avoidance and site aversion (Feare 2010). Complete eradication of the mynas was achieved on Fregate Island in the Seychelles, after eight months of continuous effort using a combination of methods, mostly traps, but also actively destroying nests and shooting the birds (Canning 2011). On Sigatoka Island in Fiji, an eradication attempt, using nest destruction, did not affect the myna populations, despite 40% of the nests being destroyed (Prasad & Christi 2014). Eradication of myna mainland invasive populations has never been accomplished.

In its native range, common myna foraging flocks are often associated with foraging black drongos (*Dicrurus macrocercus*), which are attracted to the flying insects that flee from the mynas (Veena & Lokesha 1993). This presents an example of a species that benefits from its interaction with the myna. Mynas, in their native range, have been found to be more tolerant and less aggressive, during foraging, towards house sparrows (*Passer domesticus*) than towards larger species, while house sparrows maintain a 'tolerance distance' from the mynas (Gupta et al. 2014). It thus seems that, in their native range, mynas and sparrows derive some mutual benefits from foraging together. In New Zealand, where both mynas and house sparrows are invasive, a caged common myna decoy was deployed next to bird feeding stations. Although 11 different bird species approached the feeding stations, house sparrows (together with the silvereye, *Zosterops lateralis*), were the most common and also the most likely to demonstrate high-risk behavior, such as standing on the decoy's cage and feeding at the station (Borowske et al. 2012).

## The House Sparrow

House sparrows, one of the few species that generally persist when urbanization increases, are traditionally associated with human habitation (Summers-Smith 1988; Shaw et al. 2008). The genus *Passer* emerged in Africa and its radiation started about 11 mya (Allende et al. 2001). The earliest known house sparrow fossil is from Bethlehem, Israel, and is dated to around 400,000 years ago (Tchernov 1962). When agricultural societies emerged in the Middle East around 10,000 years ago, house sparrows exploited the new niche, where they fed on crops and spillage, nested in man-made constructions, and developed commensalism with humans (Sætre et al. 2012). They spread from the Middle East, with human agriculture, into Europe, the Indian subcontinent, and North Africa, and various subspecies evolved (Ericson et al. 1997; Sætre et al. 2012).

Although house sparrows are well adapted to human populations, there is evidence that house sparrow populations are declining in some areas. The first such indication is from the village of Denver, Britain, in the early 20th century, and is linked to a reduced spillage of oats from the nosebags of horses as horses became replaced by motor vehicles (Bergtold 1921). At the end of the 20th century, a rapid population decline of the house sparrow was found in Western Europe (Crick et al. 2002; Robinson 2005; Balmori & Hallberg 2007; De Laet & Summers-Smith 2007) and in India (Dandapat et al. 2010). The decline was due to food reduction as a result of industrial agriculture intensification (De Laet & Summers-Smith 2007). In traditional agriculture rural areas, such population decline was not seen. However, the urban populations of house sparrows are still in decline, with the reasons for this being unclear (De Laet & Summers-Smith 2007), although competition with invasive species, chemically-treated seeds, reduction in nest site availability, and increased electromagnetic radiation have all been suggested (Balmori & Hallberg 2007; Dandapat et al. 2010).

House sparrow breeding in Israel takes place between March and August (pers. obs.), with each pair breeding on average 2-3 times per season, and producing an average clutch of 5 eggs (Singer & Yom-Tov 1988; Aslan et al. 2005). The nestling feeding rate in birds is determined by many different factors, such as brood size, food supply and weather, as well as the risk of predation (Nur, 1984; McGillivray 1984; Martin 1987; Fontain & Martin 2006). The house sparrow female feeding rate is higher than that of the male, and is positively correlated with it (Voltura et al. 2002; Ringsby et al. 2009). Parental feeding rate correlates with brood size and reproduction success, while parental age also positively correlates with reproduction success (Hatch & Westneat 2007; Ringsby et al. 2009). There are several observations of predation of sparrow nestlings by the common myna, where the distribution of the two species overlaps (Holzapfel et al. 2006). It is thus possible that sparrows adapt their behavior to myna presence while nesting.

## Objective

Using the common myna as a model for invasive species, and the house sparrow as a model for native species, and under the assumption that behavioral changes can have a significant impact on local ecology, in this study I sought to investigate whether the mere presence of an invasive species can influence the behavior of a native species. The null hypothesis was that sparrow behavior remains the same in both presence and the absence of mynas; and, therefore, that there is no indication of ecological impact. The research hypothesis was that the behavior of sparrows changes in the presence of mynas, with either negative or positive implications for the sparrows' fitness.

In order to determine whether the presence of an invasive species can influence the behavior of a native species, I conducted a literature review to uncover the knowledge gaps as well as to examine the captive experiments, field experiments, and field observations, in order to elucidate the influence of an invasive species on the foraging and breeding behaviors of a native species, which are crucial for the survival and fitness of the latter.

## Outline

In this work I present the interactions between common mynas and house sparrows as a case study.

In the Introduction I review the field of invasion ecology and its main research foci. One of the major difficulties frequently encountered by this field, as I demonstrate, is to validate the assumption that invasive species affect the local ecosystem and to determine the precise nature of any such effect. I contend that, by studying the effect of the presence of invasive species on the behavior of local species, it is possible to uncover the complex effect of biological invasions.

Chapter One: Review

In this chapter I review the current literature that deals with the behavioral effects of biological invasions, in order to define the knowledge gap. First I review the impact of invasion on the behavioral traits of the invader, and I then define the interaction between invaders and local species in terms of behavior by reviewing studies that, while focusing on the classic impact mechanisms, also describe behavioral changes. In the third part of the chapter I demonstrate how such behavioral changes can impact the ecology of local species independently of the classic impact mechanisms. Finally, I demonstrate how behavioral changes can have implications for the invaded ecosystem.

While most studies engaging with the ecological impacts of biological invasions focus on simple negative or positive impacts, here I argue that studying the behavioral impact can help to reveal the complexity of the effects of invasion.

Chapter Two: Foraging and Vigilance

In this chapter I demonstrate, through two experiments, the influence of the presence of mynas on the vigilance behavior of foraging sparrows.

In the Introduction I review the definition of vigilance and the variables that influence it, as well as the visual properties of house sparrows and common starlings (the common starling is the closest organism to the common myna whose visual properties have been studied). I also review the different types of vigilance and the methods used to measure it, as well as other topics of importance for the discussion, such as safety cues and mixed foraging flocks.

The Methods section presents two experiments. Experiment 1 was designed to determine the effect of the presence of mynas on sparrow vigilance behavior by measuring the sparrow's vigilance level in the presence and absence of mynas. Experiment 2 was designed to determine the affinity of foraging sparrows to the presence of mynas and whether this affinity is innate or learned.

The results show that sparrows are less vigilant in the presence of mynas, that they prefer to forage alongside mynas, and that this affinity is partially learned.

I discuss these results in light of the contribution of the current knowledge to our understanding of foraging and vigilance, while also referring to the results of unpublished studies in order to further interpret the results. I determine the potential positive impact of myna presence on foraging sparrows, and I discuss the potential biases.

Chapter Three: Breeding

In this chapter I demonstrate, through two experiments, the influence of the presence of mynas on the breeding behavior of foraging sparrows.

In the Introduction to this chapter I review the factors that influence nesting behavior in birds, in light of predation risk. I also focus on perceived predation risk, and its influence on parental care. The effect of parental care on offspring development is also reviewed. Finally, I review the current literature on the breeding biology of house sparrows.

The Methods section presents two further experiments. Experiment 3 was designed to determine the effect of myna presence on parental care of the sparrows by measuring the parents' feeding rate and duration. Experiment 4 was designed to determine the effect of the presence of mynas on the sparrows' breeding success, by measuring the laying, hatching, and fledging rates, as well as the fledglings’ physiological parameters.

My findings demonstrate that sparrows both reduce their parental care and display lower breeding success in the presence of mynas.

I discuss these results in the light of our current knowledge on the effect of perceived predation risk on parental care and I determine the mynas' presence as exerting a potential negative impact on nesting sparrows. I also discuss possible interpretations of the results regarding paternal and maternal investments and I compare the breeding success results found here to those of previous studies on sparrow breeding biology. Finally, I discuss the potential biases of the study.

Conclusions

This section offers a synthesis of the results presented in the previous chapters. I demonstrate the importance of studying the behavioral impacts of invasions in order to reveal their ecological impacts. I also discuss the importance of understanding the complexity of the invasion effect and the consequent potential for conservation applications.

# **Chapter One – Review: The Behavioral Effects of Biological Invasions**

Invasion biology, as a discipline, focuses mainly on the invasion process and its ecological and economic impacts. The references to behavior in this field have been limited, in most cases, to the behavior of the invasive species, usually as part of the questions "What traits characterize invasive species?" and, more recently, "How do the traits of invasive species change as part of the invasion process?". The behavior of the local species, however, has been largely neglected. Nevertheless, since behavior is often central in interactions, many studies that focus on the ecological impact of invasive species have noted, indirectly, behavioral changes by the local species in the face of invasion.

In this chapter I review the current literature in order to understand how invasive species may change the behavior of local species, and whether understanding behavioral change can help to understand the ecological impact of invasion. Finally, I define the current knowledge gap regarding this subject.

## *The Importance of Behavioral Traits in the Invasion Process*

The invasion process involves several stages, as noted previously, comprising transportation, release/escape, establishment, and spread. In order to become a successful invader, it is necessary to succeed at every stage – and only a few species have indeed managed to become invasive. The invasion process acts as a filter, at both the species and the individual level, selecting for the necessary traits for success (Mooney & Cleland 2001). Feeding innovation, for example, appeared more in invasive bird species than in non-invasive ones (Sol & Lefebve 2000; Sol et al. 2002). Large brains, in relation to body size, are associated with more flexible behavior, and were found to correlate to species' invasion success among amphibians (Amiel et al. 2011), birds (Sol et al. 2002), and mammals (Sol et al. 2008). Such flexibility offers another example of a behavioral trait filter during the invasion process, at the species level. Several other behavioral traits that are associated with successfully completing the invasion process are those of high activity level, preference or tolerance for human habitation, boldness, high dispersal, exploration behavior, foraging flexibility, habitat preference flexibility, sociality tendency, and thermoregulatory behavior flexibility. Behavioral traits such as anti-predator/anti-parasite behavior and interspecific aggression, however, have been found only in the establishment and spread stages (reviewed by Chapple et al. 2012).

Behavioral traits often differ not only among species, but also among individuals. They are referred to in this case as personality or temperament. The correlation among behavioral traits is referred to as a behavioral syndrome (which can occur either via a behavioral genotype and environmental link, or via a genetic correlation among the behavioral traits), and may lead to behavioral types (Sih et al. 2004; Réale et al. 2007). The result of selection pressure on the behavioral types of the non-native species during the invasion process can manifest in behaviors in the invasive population differing from those in the local population in its native range. There are many examples of the invasion process filter selecting for behavioral traits among individuals. Two synonyms of the DRD4 SNPs gene, which are associated with a neophobic/neophilic personality and activity level in the presence of a novel object, were found in an invasive population of the yellow-crowned bishop (*Euplectes afer*) in Iberia (Mueller et al. 2014). Mueller et al.(2014) suggested that these alleles were introduced via the local population and were selected under the invasion process filter. Crayfish (*Pacifastacus leniusculus*) in an invasive population were more aggressive towards conspecifics, bolder in the presence of predators, and demonstrated more active foraging, compared to crayfish in their native range, where prey were more abundant (Pintor et al. 2008). Argentinian ants (*Linepithema humile*) establish large unicolonial nests in their invasive range, while in their local range they usually establish on average smaller supercolonies (Suarez et al. 2008). Ants in unicolonial nests demonstrate lower conspecific aggression than ants in supercolonies; and, indeed, Argentinian ants in their invasive range are less aggressive toward conspecifics than Argentinian ants in their native range (Suarez et al. 2008). The tendency to establish large unicolonies with low conspecific aggression may have been selected under the conditions encountered by the invasive Argentinian ants.

Differences between invasive species and their local relative species are also expected to result from the invasion process selection. Two related wasps that coexist in Europe, the local *Vespa crabro* and the invasive *Vespa velutina,* show different behavioral traits associated with invasion (Monceau et al. 2015). Monceau et al. (2015) measured the activity, boldness, and exploration traits within and among individuals, and found that the invasive *V.velutina* were more active, bolder, and more explorative than the local *V.crabro*. While the local *V.crabro* presented a low behavioral variation for all three traits within each individual (each individual was more persistent in retaining its behavior), the invasive *V.velutina* presented a similar variation both within and among individuals (Monceau et al. 2015), probably due to the narrow bottleneck resulting from single female introduction (Monceau et al. 2014), which left the invasive population with low variation among individuals.

The conditions that the invader has to cope with may vary between the core of the invasion range and the front line of the invasion, leading to different behavioral traits among individuals in these two parts. Cane toads (*Bufo marinus*) have been invasive in Australia for the last 70 years. Behaviors associated with dispersal abilities were measured in both the established population and the current invasion frontline and were compared to the initial invasion front (Alford et al. 2009). The probability of continued dispersal was higher in the current invasion front compared to the initial invasion front, and higher in the initial invasion front compared to the established population (Alford et al. 2009). Three other behavioral traits associated with dispersal – path straightness, mean distance moved per move, and displacement rate – did not differ between the initial invasion front and the established population (Alford et al. 2009). These results demonstrate not only the difference between the established population and the initial invasion front, but also the rapid shift (within about 50 generations) in behavioral traits under invasion conditions.

The challenges facing an invasive species and the low proportion of successful invasions often drive the selection of behavioral traits at both the species and the individual level (Holway & Suarez 1999). The selected behavioral traits of the invader can become part of the new challenges that a local species faces in its invaded environment. For each interaction there are at least two sides: the invader and the native (although there can be more the one invader and more than one native which can also interact among themselves), whose interaction can be mediated through behavior.

## *Behavior as a Mediator of Invasion Impact*

The study of the behavioral impact of invasive species on local species has been largely neglected. The few studies carried out to date have mainly focused on competition, predation, hybridization, and disease transfer as the main impact mechanisms of the introduced species on the native species. Phillips & Suarez (2012) contended that almost all of these impact mechanisms are mediated by behavior, both of the invader and of the native species. Sih et al. (2010) explain how the predation impact, both on the native prey and on the invasive predator, as well as on the native predator, is mediated by an anti-predator behavior; and they present a comprehensive model that deals with several scenarios of invasive predator encounters with local ecosystems and how the anti-predator behavior will effect these encounters. However, those authors hardly deal with behavioral changes, although they do describe a situation in which, although the invasive predator is recognized as a threat by the native species, the anti-predator behavior of the latter is inefficient (this is the worst scenario for the native prey, since it will suffer both large consumptive and non-consumptive effects). In this case, a behavioral shift by the native species is expected over time. Sih et al. (2010) also emphasize that the mediator of predation impact is not limited to the native prey’s anti-predator behavior, but also to the anti-predator behavior of the invasive predator itself, since it too can fall prey to native top-predators (with the behavior of the latter also being important, since they are naïve to the new potential prey and therefore need to recognize it and perform the appropriate predation behaviors). Anti-predator behaviors may also mediate competition impact. When the local prey does not recognize the invasive predator as a threat or engages in inefficient anti-predator behaviors, the invasive predator will have an advantage over local predators that forage on the same prey (Sih et al. 2010).

One example of predation impact mediated by anti-predator behavior is that of parental defense by the local arrow cichlid (*Amphilophus zaliosus*) (endemic to Lake Apoyo in Nicaragua) against the invasive predator, the bigmouth sleeper (*Gobimorus dormitor*). *G.dormitor* prey on the broods of *A. zaliosus*, but while *A. zaliosus* recognizes *G. dormitor* as a threat and demonstrates anti-predator behavior, its response is inefficient, since it only initiates this behavior when the predator is already too close to the brood (Lehtonen et al. 2012). While *A. zaliosus’s* population in Lake Apoyo has declined, its relative, *A. sagittae*, which coevolved with *G. dormitor*, demonstrates an effective anti-predator behavior and maintains a stable population in the lake (Lehtonen et al. 2012).

One example of a competition impact mediated by behavior is demonstrated in bird breeding behaviors. The preference for cavity nesting has benefits such as shelter from the weather and protection from predators. However, it can also be a limiting resource. There are many examples of cavity competition mediated by breeding behavior. In Australia, the invasive common myna and common starling, which breed in cavities, compete with the local crimson rosella, with the local eastern rosella (*Platycercus eximius*), and with each other for nesting boxes and natural cavities (Pell & Tidemann 1997; Grarock et al. 2013a). Charter et al. (2016) deployed large-entrance-hole nest boxes in which both invasive and local species can breed, including the invasive common myna and rose-ringed parakeet, the local house sparrow, and the great tit (*Parus major*); and small-entrance-hole nest boxes in which only the local species can breed. Mynas occupied 62%-74% of the large entrance hole nest boxes, while the native species occupied only 8.7% of the large entrance hole nest boxes and 36.5% of the small-entrance-hole nest boxes (Charter et al. 2016). Furthermore, great tits that bred in the large-entrance-hole nest boxes fledged fewer offspring than those breeding in the small-entrance-hole nest boxes. All failed breeding attempts of the great tits in the large-entrance-hole nest boxes occurred due to their active eviction by mynas (Charter et al. 2016).

Disease transfer can also be mediated by behavior. For example, similar foraging behaviors of the feral buff-tailed bumblebee (*Bombus terrestris*) and local white-tailed bumblebee (*Bombus lucorum*) can result in interspecific transfer of a trypanosome parasite (*Crithidia bombi*) from *B. terrestris* to *lucorum* after feeding on the same flower (Durrer & Schmid-Hempel 1994).

In plants, hybridization between local and invasive plants is most likely to occur, and have a significant impact, when the pollinator of the local plant recognizes the invasive plant and the hybrid as a food source. Generalist foraging behavior by the pollinator can therefore mediate hybridization impact (Vilà et al. 2000). The invasive *Carpobrotus edulis*, which has magenta flowers, hybridizes with the local *Carpobrotus chilensis*, which has yellow flowers. Both species are pollinated by the same thysanoptera and coleopteran species, providing an example of a foraging behavior hybridization mediator (Vilà et al. 2000). *Bombus terrestris dalmatinus* and *Bombus terrestris sassaricus* are two bumblebee subspecies that were introduced into many parts of the world as commercial pollinators of greenhouse crops. Because these species pose a threat to local subspecies due to hybridization risk, farmers should prevent the escape of queens and males (Kenis et al. 2009). However, when entering an unrelated conspecific colony, bumblebee workers can choose selfish reproductive strategies, usually avoided under kin-selection conditions, and lay unfertilized eggs that produce male offspring (Lopez-Vaamonde et al. 2004). Thus, reproduction behavior may mediate a hybridization impact.

Since behavior can mediate the mechanism of the invasion impact, changes in behavior, as a result of invasion, can in themselves produce an ecological impact.

## *Behavioral Change as Impact*

Behavior can not only reflect a large variety of adaptive traits that can have a tremendous impact on the survival and fitness of an individual, but it can also be very plastic. A specific behavior may change under different circumstances, either through learning or through other, innate, mechanisms. Hence, an environmental change, such as the establishment of an exotic species, is expected to drive behavioral changes in the local species that interact with it (Wong & Candolin 2015). Behavior not only influences the survival and fitness of individuals, in addition to influencing ecological processes such as food consumption or nutrient distribution, but can itself be affected by environmental changes such as caused by invasive species, and the resulting behavioral change can have an ecological impact in itself (Wong & Candolin 2015). Notwithstanding, only a few studies have dealt directly with the impact of behavioral change under invasion conditions.

Local birds in and around London are well adapted to urban and human environments, and often forage in artificial feeders. The rose-ringed parakeet is an invasive competitor for food with local birds and also often forages in artificial feeders. Peck et al. (2014) deployed next to artificial feeders around London, at 41 sites (30 sites within parakeet range and 11 outside parakeet range), a parakeet decoy in a cage and parakeet calls / parakeet decoy only / parakeet calls only, and measured the visit rates of local birds to the feeders. As control, they presented next to the feeders an approximately same-sized, caged, decoy of the local great spotted woodpecker (*Dendrocopos major*) and woodpecker calls / woodpecker decoy only / woodpecker calls only / empty cage and no calls. Most local avian visitors to the feeders were blue tits (*Cyanistes caeruleus*) and great tits. Inside the parakeet range the number of visits and the time spent on the feeder was lower in all parakeet manipulations compared to the control, while time spent in vigilance was higher (Peck et al. 2014). Outside the parakeet range, the results showed a similar pattern, albeit with visit rate being lower in the presence of the parakeet decoy than in the same treatment within the parakeet range (Peck et al. 2014). Although these results do not directly demonstrate an ecological impact of the behavioral change, such impact can be reasonably assumed, since a change in foraging behavior can impact fitness, either through reduced nutrition (due to shorter time spent in feeding), increased foraging investment (due to changing feeding locations more frequently and thus flying more between food patches), lower feeding rate to offspring (due to longer time spent in foraging for self-feeding, resulting in reduced in nutrition, shorter time left to locate invertebrates to feed the nestlings), and an increase in predation risk (due to time allocation shift). Peck et al.'s (2014) results demonstrate only the behavioral effects of the invasive species, but not competition or predation, since the demonstrated behavioral changes result simply from the presence of the invader. These findings also show how behavioral plasticity can moderate the impact of behavioral changes through habituation.

Another example of a study dealing directly with the effect of an invader on the behavior of a native species, was conducted by Ligon et al. (2012) on the impact of the invasive red imported fire ant (*Solenopsis invica*) on the breeding behavior of the eastern bluebird (*Sialia sialis*). Red imported fire ants are known to negatively affect arthropod communities (Eubanks et al. 2002) and thereby also to affect insectivores. Ligon et al. (2012) compared the breeding behavior of an insectivore, the eastern bluebird, among 28 nest boxes located in areas with abundant fire ants, and 28 paired nest boxes located in similar habitats in areas where fire ants were treated with ant-specific hydramethylnon bait in order to reduce their populations. In the treated areas, where fire ant abundance was significantly reduced, nesting bluebirds fed their chicks more frequently, foraged for shorter distances, and fed more frequently within a radius of 50 m from the nest, compared to nesting bluebirds in the non-treated, fire ant abundant areas (Ligon et al. 2012). In this example too, the behavioral change of the local species that resulted from the presence of the invasive species might have reduced the local species' fitness; and could also, although there is no direct evidence for this, have impacted the bluebird population.

Hentley et al. (2016) engage directly with the behavioral effects of invasion. In the presence of an invasive competitor *Harmonia axyridis*, a local coccinellid, *Adalia bipunctata*, increased its feeding rate, while the local coccinellid, *Coccinella septempunctata*, reduced its feeding rate (Hentley et al. 2016). While this example also demonstrates a change in the local species' behavior in the presence of an invader, its implications for fitness and ecology are less easily assumed, especially since the *A. bipunctata* population is in decline while the *C. septempunctata* population is stable. Although this is an example of behavioral change that occurs in the presence of an invasive species, and may very well have an ecological impact since it affects foraging behaviors that directly influence the survival and fitness of an individual, it also emphasizes the difficulty in associating this behavioral change to an ecological impact.

Although very little research has been directed at studying the direct influence of invasive species on the behavior of native species, there are many studies dealing with the ecological impact of invasive species and the mechanisms behind such impact, which describe behavioral changes. Since many mechanisms, such as competition, predation, disease transfer, and hybridization are mediated by behavior, many of the studies examining these mechanisms describe, albeit indirectly, behavioral changes.

Some studies have described habitat shifts under competitive conditions, with invasive species forcing the native species into a new environment (Kats & Ferrer 2003; Baker et al. 2014). The natives may change their behaviors such as foraging or breeding, to accommodate to the new environment. Although Grarock et al. (2013a), for example, do not deal directly with behavior, or even niche shift, they do demonstrate how the invasive common myna, which prefers to nest under low tree density, has reduced the abundance of the native crimson rosella, which prefers high tree density, under both low and high tree densities but not under medium tree density. If crimson rosellas will shift their habitat to the medium tree density, they may be expected also to adapt their behaviors, such as foraging, to the new habitat. These behavioral changes might affect other components of the environment, such as the prey species of the rosella.

Another, more detailed, example of a habitat shift under invasion conditions is that of the native Duvaucel's gecko (*Hoplodactylus duvaucelii*) on Ohinau Island in New Zealand, which was invaded by Pacific rats (*Rattus exulans*). Following the invasion, the geckos were found mostly on coastal cliffs and boulders, where rats were scarce. Six months after the rats' eradication from the island, geckos began to be found in a variety of habitats, especially in coastal forests, and less frequently on coastal cliffs (Hoare et al. 2007).

Other studies describing environmental changes caused by invasive species mention behavioral changes that may have an ecological impact, but do not focus on them. Rodewald et al. (2011) studied evolutionary and ecological traps (in which once-adaptive behavior becomes maladaptive in the new selective environment, or in which individuals actively select habitats that ultimately reduce their fitness, Leston & Rodewald 2006; Rodewald et al. 2011). They referred to environmental change caused by the invasive Amur honeysuckle (*Lonicera maackii*). The honeysuckle fruit is rich in carotenoids that, when eaten by northern cardinals (*Cardinalis cardinalis*), helps the males to become more attractive to females. Rodewald et al. (2011) showed that when honeysuckle fruit are abundant, the sexual signal becomes less effective. Furthermore, while honeysuckle locations were favored for nesting, these locations were also associated with high predation (Rodewald et al. 2011). The cardinal's preference for the honeysuckle might therefore have affected their mating and nesting behaviors, and consequently impacted their fitness and ecology.

Honeysuckle invasion has a behavioral effect in other cases too. A removal experiment of invasive honeysuckle cover and fruit demonstrated that, under cover removal, raccoons (*Procyon lotor*) and opossums (*Didelphis virginiana*) reduced their activity, while under fruit removal, raccoons increased their activity (Dutra et al. 2011). Honeysuckle introduction can thus increase predator activity (Dutra et al. 2011) and bird nest predation (Rodewald et al. 2011). These findings may imply a mechanism of ecological impact by means of behavioral alteration triggered by invasive species.

Another way in which behavioral change can influence the local ecosystem is that of the effect of invasive plants on the behavior of local pollinators and, consequently, the effect on local plants that are pollinated by the same pollinators. Local pollinators may prefer the invasive plant due to stronger signals or higher rewards; and, therefore, the invasive plant will be a superior competitor to the local plant (Bjerknes et al. 2007). King & Sargent (2012), for example, showed that bumblebees, the main pollinators of both the invasive purple loosestrife (*Lythrum salicaria*) and the native swamp loosestrife (*Decodon varticillatus*), prefer to visit the native species only outside the invasion area (where the pollinators are probably naïve regarding the invader). Within the invasion area, the pollinators did not show a preference for one of the species and visited them both at the same rate, even though the invasive species offered much lower rewards (about a 7-fold lower nectar volume) than the native species (King & Sargent 2012). These results suggest a behavioral change in pollinator preference following the invasion, which may have increased competition between the two species. Alternatively, the attractiveness of the invasive species may lure more pollinators, which may increase visit rate also to the native plant, creating a facilitation effect (Bjerknes et al. 2007). It may therefore be difficult to assess the impact of invasive plant species, a priori, on local competitors. Pollinator behavior toward invasive plants, as noted earlier, can also increase hybridization and its spread (Vilà et al. 2000). Invasion can affect the behavior of local pollinators, and this behavioral alteration may in turn affect local plants, which constitute the basis of the ecosystem trophic structure. Such behavioral impact may therefore be highly significant for an invaded ecosystem. Notwithstanding, there has been very little research to date on the subject.

Behavioral changes can also affect physiological traits. Lower growth rates and metamorphosis at a smaller size in the presence of an invasive predator, for instance, were demonstrated among amphibians in several studies, and were linked to movement and reduced feeding in the presence of the invasive predator (reviewed by Kats & Ferrer 2003). Kiesecker & Blaustein (1998) showed a similar effect on the native red-legged frog (*Rana aurora*), caused by two invasive predators – the bullfrog (*Lithobates catesbeianus*) and the amallmouth bass (*Micropterus dolomieui*), using a field enclosure experiment. Lawler et al. (1999) demonstrated that the same effect, in several native species, was caused by the invasive mosquitofish (*Gambusia affinis*), and Nyström et al. (2001) demonstrated the same effect on the native common frog (*Rana temporaria*) by the invasive rainbow trout (*Oncorhynchus mykiss*), but not by the invasive signal crayfish. In all these studies, only the presence of the predator was tested, without actual predation being observed, and it was linked to a low prey survival rate, in addition to the physiological impact. The changes in physiological traits due to behavioral changes not only affect the fitness of the native species itself (which might in turn affect its population), but also other trophic levels (e.g. it might affect its prey choice or its predator preferences). It may also affect competitors and, consequently, the native ecosystem.

Although the occurrence of behavioral changes in response to biological invasion impact on the local ecosystem is a reasonable assumption, behavioral adaptation may reduce the impact. The invasive brook stickleback (*Culaea inconstans*) is a predator of local long-toed salamander (*Ambystoma macrodactylum*) larvae. The larvae's anti-predator behavior is to reduce their in activity, and it is chemically-mediated by kairomones. When exposed to kairomones from sticklebacks fed on salamander larvae diet, salamander larvae reduced their activity, but when exposed to kairomones from sticklebacks fed on earthworms (*Lumbricus terrestis*), salamander larvae did not reduce their activity (Reed 2016). Following exposure to kairomones from sticklebacks fed on salamander larvae, the salamander larvae were again exposed to kairomones, but from sticklebacks fed on earthworms, and their activity was measured. These salamander larvae reduced their activity even in the presence of kairomones from stickleback that had been fed on earthworms only. Apparently, the salamander larvae can learn and generalize predation threat cues, even if the predator is naïve and had not previously encountered salamander larvae (Reed 2016). This presents an example of a behavioral adaptation that can increase predator identification as a threat, converting the anti-predator response into a more appropriate one, and thereby reducing the impact of the invasive predator (Sih et al. 2010).

Although there is little direct evidence to date regarding the impact of behavioral changes in response to biological invasions, it is not unreasonable to assume that this impact is nonetheless quite common, since it affects many of the aspects that are important for fitness, such as predation, competition, foraging, and breeding. Therefore, behavioral changes may also have an effect at both the population level and on the entire ecosystem, with associated ecological and evolutionary implications.

## *The Implications of Behavioral Changes*

Uncovering the an ecological impact of an invasive species may be difficult, since it is necessary to determine the impact mechanism and link it to a correlative study, demonstrating a change in the native species population associated with a growth in the invasive species population. Even then, it may be difficult to prove the impact, since invasion is often associated with other anthropogenic changes such as habitat degradation or climate change. Consequently, the invader may be only a passenger of other ecological changes and not itself the driver of the ecological change (Diham et al. 2005; MacDougall & Turkington 2005). Furthermore, it can be difficult to determine which ecological changes have been caused by behavioral alterations. Such ecological changes can be nonetheless inferred from the findings of studies dealing with behavioral changes driven by biological invasions, and these changes might have major implications for biodiversity and ecosystem stability.

Behavioral changes that can alter key demographic parameters, such as reproduction rate, can be expected to influence both the population level and the ecosystem (Wong & Candolin 2015). For example, Yang et al. (2011) studied the interaction between two invasive plants, the spiny plumeless thistle (*Carduus acanthoides*) and the musk thistle (*Carduus nutans*), and found that the co-occurrence of both plant species led to changes in foraging behavior (patch visits rate, plant visits rate, and proportions of moves within the same plant) of various pollinators, which reduced the proportion of seed set available for both species. This example reveals the potential effect of local species' behavioral changes not only on their own fitness, but also on that of other species in the ecosystem (in this case invasive, but the behavioral change can affect other local species too).

Stout & Morales (2009) reviewed the impact of invasive species on bees and refer to 15 studies dealing with the impact of invasive plant species on local plant species by influencing pollination. Of those 15 studies, four found a negative impact on seed set and fruit set (Grabas & Lavery 1999; Chittka & Schurkens 2001; Brown et al. 2002; Jakobsson et al. 2007). Using fluorescent dyes Brown & Mitchell (2001) found interspecific pollination between the invasive purple loosestrife (*Lythrum salicaria*) and the native winged loosestrife (*Lythrum alatum*) caused by bumblebees and honey bees. In their experiment, a mixture of conspecific pollen and interspecific pollen resulted in almost 29% lower seed set compared to conspecific pollination (Brown & Mitchell 2001). This presents another example of a behavioral change caused by biological invasion that subsequently affects reproduction levels and therefore may also affect the population size of the native species and thereby affect the entire ecosystem.

Blanvillain et al. (2003) associated the decline in the local Tahiti flycatcher (*Pomarea nigra*) population to behavioral interactions (aggression) with the invasive common myna. The interaction of these two species did not involve predation or competition, but aggressive behavior by the myna during the flycatcher's breeding period. Although that study did not measure the breeding behavior variables of the flycatchers, it did associate the interaction with mynas to very poor breeding success in the breeding season of 1999-2000 when only 26% of the nests managed to fledge young. It is possible that some change in breeding behavior or parental care was the cause for the poor success. That study associated between population decline and invasive species behavior because the flycatcher population at the beginning of the study (1998) had comprised only 25 individuals and 12 breeding pairs. The flycatcher's behavioral change may therefore have had significant biodiversity implications, but not necessarily ecological implications.

Native species may use environmental cues in order to assess habitat quality. However, following environmental alteration by an invasive species, the appropriate response to these cues may change too, resulting in an ecological trap (Wong & Candolin 2015). One example of an ecological trap was presented earlier: northern cardinals were shown to prefer nesting in invasive amur honeysuckle vegetation, despite suffering from high predation there (Rodewald et al. 2011). Another example of an ecological trap caused by inappropriate behavioral change in response to an invasive species, is the amplexus preference shown by the local, vulnerable, California red-legged frog (*Rana draytonii*). D'Amore et al. (2009) found a high preference among red-legged frog males for interspecific amplexus with juvenile invasive bullfrogs. They documented 43 cases of interspecific amplexus over three years, compared to only five appropriate intraspecific amplexus acts. Ecological traps can have a significant negative impact on a population since they cause a reduction in fitness behavior.

Another implication of behavioral change is that of a shift in behavioral traits. Large variation in behavioral traits among a native population, or large behavioral plasticity, may shift a common behavior following environment change as a consequence of biological invasion. Invasive cane toads in Australia are venomous and are eaten by local death adders (*Acanthophis praelongus*), which also feed on a variety of local toxic and non-toxic amphibians. The adders handle the local prey relative to their toxicity level: non-toxic prey are eaten immediately; prey that secrete a sticky glue are envenomed and consumed about ten minutes after being bitten; and neurotoxic prey are envenomed and consumed at least 40 minutes after being bitten (Phillips & Suarez 2012). When encountering a toad for the first time, adder response varies: some eat it immediately as a non-toxic prey, some envenom it and then eat it as glue-secretion prey, some envenom it and then eat it as a neurotoxin prey, and some avoid the toads entirely. Because almost all adders that consume toads die, there may be a strong selection for prey avoidance preferences (Phillips & Suarez 2012). Toad toxicity following a native naïve predator's behavioral shift also occurs in other Australian frog predator species. Australian black snakes (*Pseudechis porphyriacus*) have adopted avoidance behavior towards cane toads, in addition to physiological resistance to the toad's toxin (Phillips & Shine 2006). This avoidance behavior may have been evolutionarily adapted (in this particular case, it developed over 23 generations), but it may also have been learned, although Phillips & Shine (2006) did not manage to teach black snakes to avoid cane toads under lab conditions.

Another behavioral shift that can occur following the introduction of an invasive species was demonstrated by Singer et al. (1993) in two populations of the local Edith's checkerspot butterfly (*Euphydryas editha*), which shifted its food preference after its local food source became scarce due to habitat degradation and the spread of the invasive herb, ribwort plantain (*Plantago lanceolate*). The butterflies rapidly shifted their foraging behavior, and the proportion of individuals that preferred the introduced plantain increased (Singer et al. 1993).

The adaptation of behavioral traits under selection pressure following biological invasions may moderate the ecological implications (e.g.: Hoare et al. 2007; Sih et al. 2010). If the native species' behavior is flexible enough or is varied enough, it can adopt a more appropriate behavior and remain ecologically unaffected by the environmental change caused by the invasion. On the other hand, the behavioral adaptation may itself have an ecological impact.

If the invasion affects the native species' fitness, if this effect is not random and the traits under selection have a heritable component, then the behavioral change can have evolutionary implications (Mooney & Cleland 2001; Strauss et al. 2006). Such implications can be moderated through a high gene flow with a population that was not affected by the invasion; or can increase through genetic isolation of the invaded population (Strauss et al. 2006). Behavioral trait shifts that occur due to learning and to behavioral plasticity may be reversible after the invasion conditions are removed, as in Hoare et al.'s (2007) example. Behavioral trait shifts that occur due to evolutionary selection might not be reversible, however, since this requires a longer time, high selection pressure, and enough variation among individuals.

Strauss et al. (2006) reviewed 42 studies dealing with the evolutionary influence of invasive species on native species. Ten of those studies incorporated a behavioral component, five of them dealt with anti-predator behavior, and three dealt with foraging behavior.

Although native species' behavior can be modified under invasion conditions, and can have ecological and/or evolutionary implications, there are very few studies that have directly engaged with this issue. Finding and proving an ecological impact of an introduced species on local ecosystems can be difficult. However, focusing on the behavioral impact of invasion (which can be easily manipulated and measured on a short time scale, compared to a solely ecological study; and since behavior is a very plastic trait and may be strongly impacted by ecological change), may reveal new mechanisms of the invasion impact and can lead to a better understanding of biological invasions with consequent implications for conservation.

Since behavior can mediate the mechanism of the invasion impact, while native species can alter their behavior in the presence of alien species, and this behavioral response can have evolutionary, ecological, and conservation implications, it is important to study behavioral changes in order to better understand biological invasions.

## *Discussion*

Since invasive and local species did not co-evolve, it is clear that the effect of invasion will usually be negative in regard to the local ecosystem. Most studies that engage with the impact of invasive species on the local ecosystem deal with conservation and, therefore, are focused on those ecological variables that may have a negative effect on the local populations (although a few studies have demonstrated a positive effect), such as on predation, competition, disease transfer, or hybridization. Measuring these ecological variables, in most cases, can be challenging and, therefore, make it difficult to reach a comprehensive understanding of the ecological impact. For example, in avian invasions, one of the most common forms of competition is over nesting cavities. While most of the secondary cavity breeders use abandoned or natural cavities, many of the studies dealing with cavity competition used artificial nest boxes, since it is easier to examine and manipulate them. When dealing with predation, many studies focus on predation success, but do not take into consideration the costs of anti-predator behavior, whether successful or unsuccessful. Many studies, especially in large ecosystems, thus fail to fully demonstrate the ecological impact of invasive species. Furthermore, most studies simplify the invasion impact to either positive or negative based on a single mechanism. However, the impact may be much more complex and involve a network of several mechanisms, even regarding the interaction of one invasive species with one local species.

Most studies that deal with the ecological impact of biological invasions, and in particular those that involve animals, can be viewed from a behavioral aspect, even when they do not test behavior directly. Looking at the behavior that lies at the basis of the studied interactions may indeed reveal more complex interactions. In each of the above noted examples, the particular behavior is initiated or altered by a signal: the presence of the invasive species. Unlike competition, predation, hybridization, and disease transfer, which require the active participation of the invasive species in the interaction, behavioral impact may occur simply through the presence of the invasive species. For example, while a small entrance hole to a nest box may prevent competition and predation by larger species, the very presence of an invader may in itself have a behavioral impact on the local species breeding in that nest box. Invasive species that are recognized by local species as potential predators may elicit costly anti-predator behavior, even if the invader does not pose a real predation risk. Such behavioral impact may take a toll on the local species – a toll that will not be revealed by measuring competition or predation.

Most of the invasion biology studies that have focused on behavior have examined a selection of behavioral traits during the invasion process, or the shift in behavioral traits along the invasion gradient of the invasive species. Comparing the behavioral traits of individuals from the invasive population to those of individuals from the original population is the most common method of elucidating the selection pressure of the invasion process on behavioral traits. However, in many studies that have found differences between the original and the invasive populations, these differences can also be explained by the founder effect and not necessarily by selection. It is therefore more appropriate to explain differences in behavioral traits between original and invasive populations as a result of selection when a resemblance in traits is found among the different invasive populations, but not in comparison to the original population.

Studies that found differences in the behavioral traits between individuals at the core of the invasive population and individuals at the forefront of the invasion have demonstrated an interesting selection and behavioral trait shift or behavioral plasticity along the invasion gradient. These findings can have important evolutionary and ecological applications. However, those studies focused only on the behavioral traits of the invasive species. It is expected that the behavioral traits of local species will undergo change too along the invasion gradient. Local individuals at the core of the invasion, which have interacted with the invasive species for several generations, may adopt different behaviors to those of individuals at the forefront of the invasion, which have only just encountered the invasive species, or individuals outside the invasion range that did not encounter the invasion species. This behavioral difference can be the result of a trait shift as well as the result of behavioral plasticity. Furthermore, behavioral differences between individuals at the forefront of the invasion and those outside the invasion range can indicate behavioral plasticity – but not a trait shift, since the interaction of the local species with the invader is new, encompassing only a few generations (or even first generation).

Studying behavioral changes of a local species along the invasion gradient presents an opportunity to study the evolutionary and ecological implications of biological invasions. Such an approach provides a better control through comparing individuals from the same population but at different invasion stages. It also it avoids a founder effect interpretation. Furthermore, in some cases it may provide the opportunity to examine the same population in the same location as it changes from being free from invasion to being at the forefront of the invasion, and then to being at the core of the invasion as this proceeds. The local species' behavioral changes, either through trait shift or through behavioral plasticity, may reveal more of the ecological impact than the invasive species' behavioral changes, since the former deals directly with changes in the local ecosystem.

Studying the behavioral changes of a local species under invasion may assist us to draw a clearer picture of the complex impact of biological invasions. This better understanding can have implications for conservation, either by helping to target the more serious invasion threats or by finding other solutions, rather than eradication of the invader, to assist the local populations.

# **Chapter Two: Foraging and Vigilance**

## Introduction

Foraging birds frequently interrupt their feeding to scan their surroundings.

Scanning typically occurs in order to detect predation threats, and may be a marker of vigilance. Vigilance can be defined as the state of monitoring the surroundings for potential threats (Beauchamp 2015). Measuring vigilance according to this state, however, is problematic (Beauchamp 2015). Another, simpler, way to define vigilance is as the probability that an animal will detect a given stimulus at a given time (Dimond & Lazarus 1974). Although it is possible to measure vigilance according to Dimond & Lazarus's (1974) definition, most field studies use behavioral markers, such as scanning, head position, or sniffing (Dimond & Lazarus 1974), even though an animal may be vigilant without demonstrating the marker behavior, or present the marker behavior without being vigilant. Reliable vigilance markers are those that demonstrate consistent association with threat detection (Beauchamp 2015). In birds, head posture and scanning appear to be related to predator detection ability (Fernández-Juricic et al. 2008; Tisdule & Fernández-Juricic 2009; Beauchamp 2015).

The more time that an individual invests in scanning, the greater its probability of detecting and escaping a predator. However, investing more time in scanning means investing less time in feeding, and a lower rate of energy intake. Individuals have certain minimum metabolic requirements. Scanning increases the probability of detecting a predator, but reduces the rate of energy intake. Consequently, in order to accumulate sufficient energy, the overall time spent in foraging, that is, in being exposed to predation rather than being in shelter, is necessarily longer and the probability of encountering a predation attempt is accordingly higher (Lima 1987). Since in order to survive a predation attempt it is necessary to detect the predator from a far enough distance to enable a successful escape to shelter, several factors must be taken into account by the prey: the predator's speed and its own speed, as well as the distance to the nearest shelter, in order to determine the scanning rate that will maximize the probability of detecting a predator from far enough away (Lima 1987). Another factor that should be taken into account regarding time allocation and food patch exploitation is that of food availability or marginal value: when food availability is high, marginal value decreases and the forager needs to spend less time foraging in the patch (Tsurim et al. 2010).

There is a trade-off between predation risk and food density, which can be measured as an energy cost using a titration experiment (Abramsky et al. 2002; Brown & Kotler 2004). The forager can determine the time and the foraging area in order to reduce predation risk or to increase food intake (Brown 1999; Abramsky et al. 2002; Brown & Kotler 2004), as well as to increase or decrease vigilance behavior at the expense of feeding rate (Lima 1987). However, it is not only food availability that can characterize the preferred environment and influence the readiness to forage in a riskier environment, but also other factors, such as temperature, which can affect the energy cost (Grubb & Greenwald 1982). Predation risk in the environment can be affected by the forager's behaviors, such as vigilance rate and allocation of time, but also by its rate of encounters with a predator, which increases with the number of predators, the activity of the predators, and the ability of a predator to detect its prey; while predation risk decreases with an increase in forager group size (Brown 1999). Predation risk can also be affected by the degree of lethality of the predator: i.e. the probability of the forager not surviving a predator attack when it is not vigilant (Brown 1999). While direct predation carries a high cost, vigilance and anti-predator behaviors may also carry an energetic cost and physiological consequences for the forager that might a dramatically affect the individual forager's survival and reproduction, as well as that of the population (Creel & Christianson 2008).

A common theoretical assumption in many empirical studies is that feeding and scanning are mutually exclusive all-or-none activities (Pulliam el al. 1982; Ward 1985). Thus, a forager can be in only one of two states at a time: either vigilance in a head-up posture, or feeding in a head-down posture (Pulliam et al. 1982; Ward 1985). There are, however, many studies that consider the birds' visual perception and demonstrate that non-vigilant feeding birds can also detect a predator threat (Lima & Bednekoff 1999; Fernández-Juricic et al. 2004; Fernández-Juricic et al. 2008; Tisdale & Fernández-Juricic 2009). Using a decoy hawk attack, Lima & Bednekoff (1999) demonstrated that dark-eyed juncos (*Junco hyemalis*) were able to detect an attack even from the head-down posture, although from a much shorter distance than from the head-up posture (over both gray and camouflaged backgrounds, detection distance during head-up posture was almost always at a maximum of 15 m, while during the head-down posture it was about 6-15 m over the gray background and about 0-4 m over the camouflaged background). It seems that the attention to predation risk and to feeding activity is a continuum between total anti-predator vigilance on the one hand, which maximizes the ability to detect and escape predator attacks but does not enable any attention to other activities; and total 'blind' feeding on the other hand, which maximizes the ability to consume food but leaves predator detection unattended (Dall et al. 2001). On this continuum, "any reduction in attention to other activities, such as feeding, as a result of increasing the allocation of attention to detecting and/or responding to potential predator activity" can be referred to as apprehension (Dall et al. 2001). Apprehension can be measured by measuring patch use under different predation risks (Dall et al. 2001).

The visual field of house sparrows reflects that of birds that use visual guidance to find food items that are then taken up in the bill (Fernández-Juricic et al. 2004; Fernández-Juricic et al. 2008). The visual field extends horizontally from 46º of binocular overlap in the direction of the bill and 47º of blind area behind the head with eyes converged, to 3º of binocular overlap in the direction of the bill and 18º of blind area behind the head with eyes diverged (Fernández-Juricic et al. 2008). The house sparrow's binocular field, which extends vertically more than 180º, even to 70º below the plane of projection of the bill, suggests it can potentially observe food items using binocular vision while its head is raised, with the bill parallel to the ground (Fernández-Juricic et al. 2008). Tisdule & Fernández-Juricic (2009) showed, experimentally, that in house sparrows the chances of detecting a predator decreased from about 97% in the head-up posture to about 2% in the head-down posture. Thus, although feeding and scanning are not mutually exclusive, the body posture in house sparrows indicates their current ability to detect a predator, and that the detection of a predator while head-down may not be as effective as in the head-up posture (Lima & Bednekoff 1999; Fernández-Juricic et al. 2008; Tisdule & Fernández-Juricic 2009).

One of the major factors that influences an individual's time spent in vigilance in many species, including house sparrows, is group size: as the size of the group increases, each individual invests less time in vigilance and more time in foraging (Barnard 1980; Elgar 1987; Beauchamp 2015). Two main hypotheses shed light on the inverse relationship between group size and individual vigilance (Roberts 1996). One maintains that animals benefit from flocking, since the vigilance of flock-mates leads to an increase in the probability of detecting a predator before it attacks (Pulliam 1973). This hypothesis, referred to as the 'many eyes effect', posits that individuals in larger groups can enjoy the same or even an improved predator detection rate, while scanning less frequently and having more time to feed (Pulliam 1973; reviewed by Roberts 1996). The 'many eyes effect' hypothesis implies that each individual can rely on the vigilance of its neighbors and, therefore, the best strategy is expected to be to reduce vigilance to zero and invest only in feeding (in which case, each scanning act is in fact an altruistic act). However, a vigilant individual apparently has a higher probability of escaping predation attempts than a non-vigilant individual, since the predator may be closer to the non-vigilant individual than to the vigilant individual (Van der Post et al. 2013). Relying on the vigilance of other group members may be difficult since, in some species, such as house sparrows, false alarms may be quite frequent (Boujja-Miljiour et al. 2017) and it is necessary for the individual to assess the level of reliability of the neighbor's vigilance. The other hypothesis, referred to as the 'dilution effect', posits that if vigilance depends on predation risk, and if that risk declines with increasing group size, the greater the number of individuals in a group, the lower the probability of a certain individual being taken in a predation attempt and, therefore, vigilance is expected to decline with increasing group size (Pulliam et al. 1982; Packer & Abrams 1990; Lima 1996; Dehn 1990; McNamara & Houston 1992; reviewed by Roberts 1996). In an analysis of data from 53 studies demonstrating individual vigilance reduction as group size increases, Beauchamp (2017) noted that the findings from about 30% of these studies were best explained by a model that represented the 'many eyes effect', in which the time spent in vigilance is predicted to decrease proportionally to group size. About 40% of the data-sets were best explained by a model that represented the 'dilution effect', in which the time spent in vigilance is predicted to decrease with natural increase in group size, and about 30% were best explained by a combination of the 'many eyes effect' and the 'dilution effect' (Beauchamp 2017). This finding is quite surprising, because it implies that, in some cases, individuals in the group do not rely on their conspecifics' vigilance but only on a lower chance of being caught when in a large group (this may occur if the individual itself detects the predator and thereby increase its probability of escape). In other cases, individuals ignore the lower chance of being caught and rely on other group members' vigilance (which may occur when it is difficult for an individual to estimate group size).

Although group size affects individual vigilance in house sparrow flocks, there are additional parameters that may also influence individual vigilance. Beveridge & Deag's (1987) study on vigilance in house sparrows demonstrated that the magnitude of the group-size effect on scan duration was larger in females than in males. Predation risk also influences the time invested in vigilance (reviewed by Beauchamp 2008): in house sparrows, a larger reduction in time spent in vigilance in a larger group occurred more under high risk than under low risk (Barnard 1980; Lima 1987). Barnard (1980) showed that sparrows that foraged in a habitat where predation risk was relatively high, scanned more frequently than sparrows that foraged in a habitat relatively protected from predators. The scanning frequency of the high-risk habitat foraging sparrows was negatively influenced by flock size but positively influenced by distance from cover (Barnard 1980).

An individual may be vigilant not only in order to detect predation risk (anti-predator vigilance), but also in order to detect conspecific risks (social vigilance), such as aggressive group members, mating rivals, group members that might steal food items, or group members that might kill offspring (reviewed by Beauchamp 2015). Whereas anti-predator vigilance decreases as group size increases (either through the 'dilution effect' or the 'many eyes effect'), social vigilance is expected to increase with group size, since in larger groups the risks from conspecific are more frequent (Beauchamp 2015). However, finding markers that separate social vigilance from anti-predator vigilance is difficult, and requires a distinction between the objectives of the scanning, either within-group scanning or outside scanning (Beauchamp 2015). Only a few studies have engaged to date with the difference between anti-predator vigilance and social vigilance, and have focused on mammals with forward-facing eyes, for which it is easier to find the target of the vigilance (Beauchamp 2015). Social vigilance studies in birds are even scarcer, since the birds' large lateral visual field makes it difficult to distinguish between social and anti-predator vigilance (Beauchamp 2015). Some studies, however, have been carried out in common starlings (Fernández-Juricic & Kacelnik 2004; Fernández-Juricic et al. 2004; Butler & Fernández-Juricic 2014). Fernández-Juricic et al.'s (2004) experiment on foraging and vigilance in common starlings at different group densities found that, at high density, the scanning birds tended to face away from the group, since their visual field allows them, using peripheral vision, to monitor both conspecific and predation risks. At medium density (one meter apart), the starlings were not able to monitor both risks, and tended to face the group. At greater distances (three meters apart) it was difficult for the starlings to see their conspecifics and they did not show any preference regarding scanning direction. Fernández-Juricic et al.'s (2004) study not only demonstrates both social vigilance and anti-predator vigilance in birds, but also the influence of group density, and not only group size, on the different types of vigilance. Furthermore, Butler & Fernández-Juricic (2014), using a 'starling robot', demonstrated that foraging starlings may reorient their attention in response to the visual orientation of their conspecifics.

Although a negative correlation between vigilance and group size was demonstrated in many studies, Beauchamp (2008) found, by analyzing data from 172 publications, that in nearly a third of them the correlation was not significant (and that about 4% were significant, but the correlation was positive). These results demonstrate the complexity inherent in the study of vigilance in the field, since it can also be explained by unreliable vigilance markers (efficient predator detection also while feeding) or by social vigilance that is not separated from anti-predator vigilance.

While it may be adaptive to possess an innate affinity to certain safety cues, such as group size, other cues would be better learned. Individuals can learn to rely on their own experience or they can rely on the experience of others by copying their behavior. The 'costly information hypothesis' suggests that since individual/private learning is more accurate, but also more costly, while social learning is less accurate but also less costly, individual learning will be adaptive where learning costs are low, and social learning will be adaptive when learning costs are high. Since learning the environmental cues for predation risk may be costly, social learning can be more adaptive (Webster & Laland 2008).

Because foraging can be costly, it is assumed that animals have evolved to optimize their foraging strategy to balance the costs and benefits of efficient foraging. When food availability decreases with time, the optimal point at which to leave the foraging patch is described by the "marginal value theorem" (Parker 1992). "Giving-up density" (GUD) is the food density at which the foraging animal will leave the patch and it is assumed to represent the optimal food density at which the animal should give-up and leave to seek another patch. GUD may be influenced, inter alia, by marginal value, competition, conspecific and predation risks, and energy demands. When predation risk decreases, due to low predator density, close shelter, large group or other variables, GUD decreases as well. However, while group size may reduce predation risk, it also might increase competition. Foraging individuals may leave a high-quality patch in favor of another, less good one, because of high competition, while taking the safety aspect with them through reducing the group size or group density in the first patch while increasing these factors in the second patch (China et al. 2008).

While foraging alongside conspecifics may reduce predation risk, it may also increase competition. However, foraging in a group composed of several species may have the advantage of lower predation risk alongside lower competition, if each species specializes in a different microhabitat (Alatalo 1981; Hutto 1988; Harrison & Whitehouse 2011). Different species that actively seek each other and maintain their association can be referred to as mixed species flocks, unlike species that merely aggregate around a source such as food or water (Harrison & Whitehouse 2011). Mixed species flocks are extremely varied (Harrison & Whitehouse 2011). They can occur in many habitats, can contain a few individuals or over a hundred (Moynihan 1962; Diamond 1987; Herzog et al. 2002), can be composed of two species to over eleven species (Croxall 1976; Herzog et al. 2002), and the relationship between the mixed flock species can be very short and transient or very long-term, stable, and obligatory (Munn & Terborgh 1979). The mixed species flock gathers around one or a few 'core species' that are essential to the flock formation (Hoffman 1981; Hutto 1994; Hino 1998), and is followed by 'satellite species' that may join or leave the flock under various circumstances (Munn & Terborgh 1979; Hutto 1994).

In addition to the benefits of higher safety as a consequence of the 'many eyes effect' and 'dilution effect', mixed-flock foragers may enjoy the vigilance of species with greater sensory acuity and greater likelihood of detecting predators or of detecting them from a greater distance (Harrison & Whitehouse 2011). As a result of the safer environment, mixed-flock foragers can acquire higher foraging efficiency (Sridhar et al. 2009; Harrison & Whitehouse 2011), they can allocate more time to feeding, their marginal value is expected to be higher, and their GUD to be lower. However, a high feeding rate in mixed species flocks is more significant for the satellite species than for the core species (Sridhar et al. 2009). This is probably because species that are more vulnerable to predation tend to join and follow species that may reduce predation risk and create safer environments (Sridhar et al. 2009), either through their superior visual and vigilance properties that reduce predator lethality, or through reducing the probability of a predator attack.

Common mynas often forage alongside other species (pers. obs.). In urban environments common mynas are highly vigilant, and their level of vigilance is lower when foraging in a group compared to foraging in pairs or alone (Newey 2007). Although this indicates lower levels of anti-predator vigilance in a group, it appears that foraging rate and food intake do not increase respectively (Newey 2007). In their native range, large flocks of foraging mynas (both jungle mynas *Acridotherus fucscus* and common mynas) are often associated with foraging black drongos (*Dicrurus macrocercus*) (Veena & Lokesha 1993). This relationship between the two foraging species, however, is not mutualism but amensalism, since the drongos benefit from the insects that flee from the foraging myna flocks, while the mynas are not affected by the drongos (Veena & Lokesha 1993). A field experiment conducted by Gupta et al. (2014) in the native range of both common mynas and house sparrows found that there was a strictly kept feeding distance between the two species. The mynas were tolerant of the sparrows' presence as long as this distance was respected. However, this distance, which was observed to be about 45 cm when food was plentiful, was reduced to zero (sparrows were observed to be feeding at the mynas' feet) when food was patchy and scarce (Gupta et al. 2014). Although the sample size of this study was very small (one myna pair), its results imply that the two species gain some benefit from foraging together. Furthermore, Borowske et al. (2012) showed, using caged decoys of two large aggressive birds (Australian magpie *Cracticus tibicen* and common myna) and two large non-aggressive birds (rock pigeon *Columba livia* and ringneck dove *Streptopelia risoria*), that house sparrows preferred to forage around mynas than to forage around the other three decoy species. House sparrows also preferred to forage around mynas compared to around ten other small species (Borowske et al. 2012). That study was conducted outside the native range of both common mynas and house sparrows, and the findings further reinforce the assumption that house sparrows benefit from foraging alongside mynas. Sparrows also prefer to forage alongside other large species that resemble mynas in appearance, size, and behavior. Clergeau (1990) used stuffed decoys of the European starling and demonstrated that house sparrows preferred to forage next to these compared to next to conspecifics.

In Israel, house sparrows are a native species and their population mainly comprises the subspecies *P.d. biblicus* which ranges from Israel to Iran and Turkey (Sætre et al. 2012). Since this study was conducted where house sparrows are indigenous while common mynas are invasive, it focuses not only on the relationship between these two specific species, but may also represent the relationship between invasive and local species. In this chapter I focus on the effect of the presence of mynas on the foraging and vigilance of house sparrows, both in the field and in captivity.

## Objectives

The objective of the first experiment was to understand whether the presence of common mynas affects the vigilance behavior of foraging house sparrows. The null hypothesis was that the sparrows' vigilance behavior would remain the same whether in presence or absence of mynas. The research hypothesis was that the vigilance behavior of the sparrows would change in the presence of mynas.

Since common mynas are an aggressive species with much evidence of interspecific aggression and the predation of small passerine chicks, including house sparrows, it can be assumed that sparrows will be vigilant around mynas. However, it can also be assumed that the presence of mynas will create a safer environment for sparrows from predation and, therefore, they will reduce their vigilance.

The primary objective of the second experiment was to understand the degree of affinity of foraging sparrows toward mynas. The null hypothesis was that the sparrows have no preference for the presence or absence of mynas. The research hypothesis was that the sparrows prefer to forage alongside mynas.

The results of the second experiment are expected to contribute to understanding not only whether the sparrows alter their vigilance behavior in order to consume more or less food, but also whether they alter their foraging preference accordingly, demonstrating higher levels of potential ecological implications.

A secondary objective of this experiment (should the null hypothesis of the primary objective be rejected) was to understand the motivation behind this affinity: Hypothesis 1) the affinity to forage alongside mynas is inherent; Hypothesis 2) the affinity to forage alongside mynas is learned.

Since the sparrows and mynas did not coevolve, similar to many invasive and local species, the results here are expected to contribute to understanding the motivation that may drive such behavioral alteration.

## Methods

The study comprised two experiments. Experiment 1: foraging in an open lawn environment; and Experiment 2: foraging in a controlled environment.

**Foraging in the wild**: Experiment 1 was conducted on urban irrigated lawns in the city of Tel Aviv in the central coastal plain of Israel. In the city, a 100-year-old urban metropolis, common mynas are abundant and have been spreading since 1997. House sparrows (*P.d. Biblicus*) are a native, widespread, and common species in the area.

Different-sized flocks of foraging sparrows were located and video-recorded on urban irrigated lawns in and around Tel Aviv; at a recording speed of 30 frames per second. Frame-by-frame analysis revealed, the duration of head-up posture for randomly selected sparrows in each film (the individuals in the frame were numbered and chosen randomly using Excel; about 50% male and 50% female). Head-up posture was determined as the sparrow's eyes being positioned well above the grass and its bill parallel to the ground (Fig. 1). In this position the bird was more likely to be displaying vigilance and not foraging. The head-up posture also appeared in food handling, but in those cases the bird was also vigilant; and the head-up posture here was therefore considered as vigilance.

 

Figure 1: an example for the head posture. Two frames of the same bird (in the red circle) that were taken from one of the records. On the left picture, the bird is feeding in the head-down posture and its ability to detect a predator is very low. On the right picture, the bird is vigilant in the head-up posture.

The records were divided into two groups: sparrow flocks that foraged alongside a pair of mynas (n=6); and a control, sparrow flocks that foraged alongside a pair of laughing doves *Streptopelia senegalensis* (n=8). Laughing doves were used as control since they are a common, non-aggressive myna-sized species. The records were saved under code names, preventing recognition of the two groups, and thus making it a blind test. Each frame lasted five minutes and featured up to six individuals. The analyses focused on a few individuals for each record and ended when the analyzed individual stopped foraging (usually fleeing to shelter). The number of foraging sparrows in each flock was counted in the field, in order to compare the duration of the "head-up" posture between the two groups as a function of flock size (Table 1). Although group size was larger in the myna group (Table 1), the difference was not significant.

Table 1: Details of the sampled data

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Sparrows that foraged alongside mynas | | | Sparrows that foraged alongside doves | | |
| group size | number of sparrows sampled | video duration | group size | number of sparrows sampled | video duration |
| 8 | 3 | 05:23 | 3 | 3 | 03:55 |
| 15 | 3 | 07:41 | 6 | 2 | 05:35 |
| 22 | 3 | 07:22 | 8 | 3 | 05:13 |
| 55 | 3 | 05:38 | 15 | 3 | 07:48 |
| 55 | 4 | 06:03 | 22 | 3 | 06:32 |
| 60 | 2 | 08:16 | 25 | 5 | 08:43 |
|  |  |  | 25 | 2 | 05:51 |
|  |  |  | 32 | 3 | 07:24 |

**Statistical analysis:**

The dependent variable in this experiment was the average time of head-up posture per minute for each flock. The independent variables were the presence of mynas or doves (experiment/control groups), group size, sex ratio (sex ratio among the sampled sparrows), and the rate and duration of head-up posture (head-up bout). The dependent variable was compared between the experiment and control groups in correlation to group size using ANCOVA test (Fig. 3). The correlation of the dependent variable to all the independent variables was analyzed using a linear model with Stepwise method. All statistical analyses were performed using IBM SPSS Statistics 25.

**Experiment in captivity:** Experiment 2 was conducted in captivity in an aviary in the I. Meier Segals Garden for Zoological Research, and lasted from October 2012 to early March 2014, outside the breeding season. The aviary was divided into five cages (Fig. 2). Cages 1 and 5 contained 20 (±5) sparrows each, comprising both adults that had hatched in captivity and adults caught in the wild (with equal ratio between the two cages). The sparrows in these cages were fed daily with one egg, one cucumber, and 100 g of chicken-feed mixture, placed in the middle of the cage. Cage 2 contained 10 sparrow adults (5 females and 5 males) that had been caught in the wild and probably had previous experience of foraging alongside mynas (experienced sparrows). Cage 4 contained 10 sparrow adults (5 females and 5 males) that had hatched in captivity and had not encountered mynas (naïve sparrows). All sparrows were ringed with aluminum rings (AB) and could be identified individually. Some of the sparrows were also ringed with colored plastic rings (up to four rings in total).

Food tray

Food tray

Food tray

Food tray

Cage 1

Cage 2

Cage 3

Cage 4

Cage 5

Figure 2: schematic illustration of the second experimental cage setting and food trays.

The sparrows in cages 2 and 4 were held there for 5-7 days for acclimation before the experiment. Following acclimation, two trays with 16 g of chicken-feed mixture mixed with sand were placed at either side of the cage (Fig. 2). In order to prevent mice eating from the trays, they were placed on shelves at a height of 1.5 m and mouse tracks (footprints, stools, and urine) were monitored. The chicken-feed mixture and sand were filtered to provide chicken-feed mixture grains >0.5 mm and sand grains <0.5 mm. GUD was measured for each tray every 24 hours by separating the chicken-feed mixture from the sand and weighing it. In addition to the food on the trays, the sparrows were fed daily with half an egg, half a cucumber, and 50 g of chicken-feed mixture, placed in the center of the cage. Fresh water was supplied daily. The occupants of cage 3 were changed every 7 days according to three stages: 4 mynas, or 4 laughing doves, or an empty cage; and the GUD measured in cages 2 and 4 was compared for each of these stages. After completion of all three stages in cage 3, the sparrows in cages 2 and 4 were replaced with the next group, which I had captured using a 9 m mist net. Six groups of naïve sparrows and six groups of experienced sparrows were replaced during this experiment. The order of the stages in cage 3 was different for each of the six sparrow groups in order to control for habituation that might occur during the experiment (Table 2).

Table 2: The order of the stages in the cage experiment. In each stage, the central, cage 3 (Fig. 2) had different occupants. For each of the six sparrow groups the order of the stages differed.

|  |  |  |
| --- | --- | --- |
| sparrow group | stage | occupants of cage 3 |
| 1 | first | 4 mynas |
| second | 4 doves |
| third | empty |
| 2 | first | empty |
| second | 4 doves |
| third | 4 mynas |
| 3 | first | 4 mynas |
| second | empty |
| third | 4 doves |
| 4 | first | 4 doves |
| second | 4 mynas |
| third | empty |
| 5 | first | 4 mynas |
| second | empty |
| third | 4 doves |
| 6 | first | 4 doves |
| second | 4 mynas |
| third | empty |

**Statistical analysis:**

In order to determine whether the sparrows showed a preference to forage on one of the trays, a paired t-test was conducted to compare between the amounts of food consumed on the two trays over the six trials. Three paired t-tests were conducted: the difference between the amounts of food consumed on the tray next to the cage with the sparrow (cage 1 or 5) and the tray next to the cage with the mynas/doves/empty (cage 3). For a likelihood of 0.05 for the three paired t-test, Bonferroni correction requires a significance of 0.016; therefore, p<0.016 indicates a significant difference.

## Results

**Experiment 1: foraging in the wild.** Fig. 3 demonstrates that sparrows were less vigilant while foraging alongside a pair of mynas compared with the control (doves) (ANCOVA: F1,41=12.945, P=0.01). The vigilance of the sparrows was negatively influenced by group size in the presence of laughing doves (exponential regression: F1=7.087, P=0.015, R2=0.26), but not in the presence of mynas (Fig. 3). In the presence of laughing doves, the foraging sparrows allocated, on average, over 40% (25.32±9.59 seconds per minute) of their time to vigilance with head up; while sparrows that foraged in the presence of mynas allocated, on average, only about 17% (10.22±2.91 seconds per minute) of their time to vigilance with head up (t12=-3.697, p=0.003) (Fig. 4). However, the average group size of the sparrows that foraged alongside doves (17±10.56) was smaller than that of those foraging alongside mynas (35.8±23.32), which may have biased these results (Table 1), although the difference was not significant (t12=2.042, p=0.64).

Neither the head-up bout nor the head-up rate was correlated with group size. There was no significant difference between the duration of head-up bout of the sparrows foraging alongside mynas (average: 1.27±2.34 seconds) and that of those foraging alongside doves (average: 1.29±0.81 seconds). However, among the sparrows foraging next to mynas, there was one individual that displayed unusually long head-up bouts of 11.86±14.68 seconds on average (representing three extremely long head-up bouts of 17.33, 30.2, and 32.57 seconds). This sparrow also displayed a relatively small, but not unusual, head-up rate of 9.14 per minute. Excluding this individual, the average head-up bout of the sparrows that foraged alongside mynas was 0.78±0.29 seconds.

A linear model reveals a significant correlation of vigilance only in the presence of mynas or of doves (t1,12=3.7, p=0.003, Fig. 4). The sex ratio (t1,12=1.2, p=0.27), group size (t1,12=-0.8, p=0.46), head-up bout (t1,12=0.6, p=0.55, Fig. 5), and head-up rate (t1,12=2.1, p=0.06, Fig. 6) were excluded from the model.

**Experiment 2: foraging in captivity.** In experiment 2, the sparrows were given two trays to forage on. The naïve sparrows tended to forage more on the trays than the experienced sparrows (Mann-Whitney U test: p=0.008). The naïve sparrows consumed 9±4.05 g per day, while the experienced sparrows consumed 6.58±2.9 g per day. During the myna presence stage, both experienced and naïve sparrows consumed more food from the tray that was close to cage 3 (average of 9.7±1.53 g and 12.5±1.65 g respectively) than from the tray further from cage 3 (average of 3.8±2.37 g and 4.26±0.9 g respectively; paired t test: t5=8.85, p<0.0001 and t5=15.99, p<0.0001 respectively) (Figs. 7 & 8). At the empty-cage stage, experienced sparrows did not consume significantly more food from the tray further from cage 3 than from that closest to cage 3 (average of 8.7±2.13 g and 4.7±2.45 g respectively; paired t test: t5=-2.48, p=0.032) (Fig. 7), similar to the naïve sparrows (10.8±2.9 g from the tray that farther from cage 3 and 6.9±2.06 g from the tray closest to cage 3; paired t test: t5=-1.69, p=0.153) (Fig. 8). At the laughing dove stage, the naïve sparrows consumed more food from the tray closest to cage 3 than from that farthest from cage 3 (average of 11.9±2.03 g and 6.6±2.43 g respectively; paired t test: t5=3.8, p=0.013) (Fig. 8), while the experienced sparrows consumed the same amount of food from both trays (average of 5.7±2.08 g from the further tray and 5.9±2.25 g from the closest tray; n=6; paired T test: t5=0.47, p=0.658) (Fig. 7). No significant difference was found between the naïve and experienced sparrows during the myna and empty-cage stages for both trays. At the laughing dove stage, the naïve sparrows preferred to forage near the doves, while the experienced sparrows did not show any preference (Fig. 7 & 8).

Figure 3: the correlation between the average vigilance (duration of "head up" posture per minute) to the flock size of sparrows that foraged alongside mynas and sparrows that foraged along-side laughing doves in the wild (±SD).

Figure 4: the average vigilance (head-up posture in second per minute) of sparrows that foraged alongside mynas and alongside doves (±SD).

Figure 6: head up posture per minute (±SD). There is no significant difference between the groups.

Figure 5: duration of head up bout, excluding one individual with unusual long head up bouts (±SD). Sparrows that foraged alongside mynas had significantly shorter head up bout then the control.

Figure 7: average GUD of the six groups of experienced sparrows at the three stages of cage 3 (±SE, N=6).

Figure 8: average GUD of the six groups of naïve sparrows at the three stages of cage 3 (±SE, N=6).

## Discussion

In this section I describe the marginal experiments featuring a small sample size or whose methods were insufficient for inclusion in the Methods and Results sections, but which nevertheless contribute to the discussion of the results of the other experiments.

I set out to investigate how the presence of invasive common mynas may affect the foraging behavior of native house sparrows. My findings suggest that although mynas are aggressive invaders, house sparrows may benefit from foraging alongside them.

In the first experiment, I analyzed the sparrows' "head-up" posture in mixed flocks, together with either mynas or doves, as a measurement of vigilance. Although feeding and scanning are not mutually exclusive, body posture in house sparrows has an impact on their ability to detect potential predators (Tisdale & Fernández-Juricic, 2009). Furthermore, while foraging, the sparrow converges its eyes, making its binocular vision filed and the anterior blind area wider, and the tip of the bill visible. However, in this position, detecting a predator is less likely (Fernández-Juricic, 2012; Tyrrell & Fernández-Juricic, 2017). During foraging, in the head down-posture, wide binocular overlap can assist the sparrow to locate multiple small food items over large angular distances; but in order to detect predation risk in this position it has to use the ventral part of the visual field (Fernández-Juricic et al. 2008). The ventral part of the passerine retina has a high concentration of double-cone photoreceptors (Hart, 2001), which are associated with motion detection and can detect a fleeing flock member; while possessing low acuity, preventing detection of imminent predator attack and estimating distance (Fernández-Juricic et al. 2008). Therefore, body posture in house sparrows can be used as a reliable measure or marker of vigilance.

Sparrows spent less time vigilant in the presence of mynas (Fig. 4). While vigilance correlated with group size when sparrows foraged alongside doves, it did not correlate with group size when they foraged alongside mynas (Fig. 3). The lower vigilance in the presence of mynas related to shorter scanning bouts (Fig. 5), and not to lower scanning rate (Fig. 6).

The results of the first experiment imply that the presence of mynas creates a safer environment for the foraging sparrows. Sparrows may be less concerned about potential predators while foraging with mynas and, therefore, can allocate more time to feeding and less time to scanning. The head-up posture, presented in Fig. 3, represents not only anti-predator vigilance, but also social vigilance (Beauchamp, 2015). Assuming that social vigilance is not affected by foraging alongside mynas or doves, but is positively correlated with group size (Fernández-Juricic et al. 2004; Beauchamp, 2015), the effect of the presence of mynas on anti-predator vigilance may be even greater (Fig. 9). If we do not separate between the two different targets of vigilance, anti-predator and social, it seems that when in the presence of doves, sparrow vigilance reduces with group size, whereas in the presence of mynas, sparrow vigilance remains the same even when group size increases (Fig. 3). However, if social vigilance increases with group size (alongside both doves and mynas), then sparrow anti-predator vigilance alongside mynas decreases, increasing the relative difference between the two groups (Fig. 9; social vigilance – the area below the dashed line; anti-predator vigilance – the area between the dashed line and the curve). Social vigilance may explain the lack of correlation between sparrow vigilance in the presence of mynas and group size. The presence of mynas may increase the safety level, allowing anti-predator vigilance to decrease to social vigilance level and mask the group size effect (Fig. 9). Social vigilance may create a minimum level of vigilance that may not be affected by predation risk. However, food handling too, which may occur in the head-up posture, requires a minimum vigilance level, although food handling in the head-up posture might require converged eyes and, therefore, reduce the ability to detect predation risk. Since there is no differentiation in the data analysis between scanning and food handling in the head-up posture, or between the different eye orientations, food handling can also explain the low vigilance limit and the lack of correlation between the vigilance of the sparrows in the presence of mynas and the group size. Even a completely non-vigilant individual will remain for a certain amount of time in the "head-up" posture for handling food, which is recorded as vigilance in this experiment.

Figure 9: the results of the first experiment, showing a speculation of social vigilance (dash line), under the assumption that social foraging is not influenced by the presence of neither mynas nor doves. The area under the dashed line represents social vigilance while the area between the dashed line and the vigilance results represents anti-predator vigilance. This speculation represent a possible explanation for the unaffected vigilance by the group size in the presence of mynas.

To better understand these results, it is essential to differentiate between the visual properties of sparrows and mynas. However, while there are several studies on the visual perception of the house sparrow, data are lacking regarding that of the common myna. There are however some studies dealing with the visual perception of the myna's relative, the European starling (European starlings separated from mynas about 9.85 mya, Zuccon et al. 2008). European starlings have a 28.5% higher visual acuity than house sparrows (Dolan & Fernández-Juricic 2010), a wider blind area at the rear of the head, longer scan bout durations, and are able to detect a predator risk from a longer distance than house sparrows (Tisdule & Fernández-Juricic 2009).

Reducing predation risk is a very common motivation for forming mixed foraging flocks (Harrison & Whitehouse 2011; Sridhar et al. 2009). Consequently, there are two main explanations for the sparrows' low vigilance in the presence of mynas, based on the lower predation risk of foraging in a mixed flock: one explanation is that mynas can detect and be alert to approaching predators more efficiently and from a greater distance than sparrows. In this case, the mynas reduce predation risk, increasing the ability of non-vigilant sparrows to escape predators; and the other explanation is that mynas’ aggression towards potential predators causes such predators to avoid patches where mynas forage. In this case, mynas reduce the rate of encounters with predators for the sparrows too. By detecting and alerting to predator attack from a greater distance, the presence of mynas may increase the distance between the sparrows and the predator at the point of detection and thereby also increase the distance necessary for the predator to overtake an escaping sparrow (Lima 1987). This will allow sparrows to increase their distance from cover while foraging (Lima 1987). In this case, if the presence of mynas creates a safer environment for sparrows, through detecting and alerting to predator attacks from greater distances, we should expect the sparrows to be less vigilant, but also to forage at greater distances from shelter. On the other hand, if mynas create a safer environment for foraging sparrows by deterring potential predators, due to their high level of aggression, we should expect that while the sparrows will be less vigilant, their distance from cover will remain the same as in the absence of mynas, since while predation attempts will be less frequent, they will occur from the same distance as in the absence of mynas.

In collaboration with an undergraduate student (Marina Kats), we completed a study in which we measured the flight distance of sparrows that foraged in the presence or absence of mynas. Marina observed sparrow flocks that foraged alongside a pair of mynas (N=7) and sparrow flocks that foraged in sparrow only flocks (N=8). She approached the flock and measured the distance in which the sparrows were fleeing to shelter. We found that in the presence of mynas, flight distance was shorter than in the in absence of mynas (Fig. 10). Shorter flight distance can indicate a shorter distance to shelter (Lima 1987). These results support the assumption that mynas reduce the sparrows' predation risk by deterring potential predators, rather than by detecting predator attacks from a greater distance. The study results imply that sparrows "trust" mynas to deter potential predators, and therefore reduce their vigilance. We also focused on the individual bird that first responded to the threat in the mixed flocks, and determined whether it was a myna or a sparrow. Among the seven tested mixed flocks, the average number of sparrows was 4.5±1.8 and the number of mynas was always two. The probability that a myna would first detect the risk was thus 0.3. However, mynas detected the threat in five out of the seven trials, while a sparrow detected the threat in only two trials (binomial test: p=0.029). This implies that mynas can detect predators better than sparrows, either through different vigilance tactics or through better visual properties. Sparrows, however, do not necessarily rely on mynas’ vigilance in mixed flocks, since they also respond to threats from a greater distance in the absence of mynas. While Marina's study results may shed some light on the results of the first experiment, it is essential to consider that although she sought to approach the sparrows at the same speed in each trial, her actual speed was not monitored. Furthermore, humans are not typical sparrow predators, and the results might have differed if the approaching predator had been a cat or a hawk (Tisdule & Fernández-Juricic 2009).

Foraging mynas search for food mostly in the head-up posture, and lower their head to the head-down posture only to catch food items or to probe. In this study, together with Marina, we measured the time spent in the head-down posture of mynas foraging only with conspecifics (N=14) or alongside sparrows (N=4). We found that myna head-down time was longer alongside sparrows than alongside conspecifics only (Fig. 11). This suggests that mynas may benefit from foraging alongside house sparrows through an increase in feeding rate. However, mixed flocks of sparrows and mynas were larger, with an average of 6.5±1.9 members, than myna only flocks, with an average of 1.45±0.69 members (t3.29=-5.15, p=0.011). Mynas may thus benefit too from foraging alongside sparrows, by reducing predation risk, simply due to the safety of foraging in larger groups, reflecting either the 'many eyes effect' or the 'dilution effect'.

Figure 11 (Marina Kats project): the rate of mynas head down posture when foraged in the presence of house sparrows and in the absence of house sparrows (t16=-4.53, p<0.0001, ±SD).

Figure 10 (Marina Kats project): the minimal distance that a potential threat could approach the flock before fleeing to cover in mixed flocks of mynas and sparrows and in flocks of only sparrows (t13=-5.054, p<0.0001, ±SD).

The results of the second experiment suggest that sparrows prefer to forage alongside mynas and thus support the conclusion of the first experiment. The difference found between naïve and experienced sparrows suggests that previous experience of mixed foraging with mynas and doves may influence the preference to forage alongside those species. It is possible that naïve sparrows prefer to forage in mixed species flocks with almost any larger species as an innate mechanism, in order to provide a safer environment. On the other hand, sparrows that have experienced mixed-flock foraging may be able to discriminate among the species they join, relying on their experience, in order to reduce interspecific competition or in order to select the species that creates the safer environment for them. A sparrow may learn that foraging alongside some species, such as laughing doves, may increase competition, through their experience of low food availability or increased interspecific aggression. Learning that foraging alongside some species may be safer then foraging alongside other species, might be more challenging. Such learning might result from linking a lower rate of predator attacks to the presence of one species compared to a higher rate of predator attacks in the presence of other species. However, in order to make such a connection, it is essential that predator attacks will be quite common and it can explain the creation of safer environments only through a reduction of predator attack rates (by deterring potential predators) and not through a reduced lethality of the predator (by better threat detection), since while the surviving sparrows will be aware of the predation attempt, they may not be aware of whether it was successful. Learning that mynas can detect predators from greater distances might be a challenge, since the sparrows will experience frequent myna alerts and link them to predation attempts. However, if mynas alert a potential predation attack from greater distances than sparrows, sparrows might perceive it as a false alarm. In South Asia, mixed flocks of sparrows and mynas, which are both native, are common, and mynas display a high tolerance toward sparrows compared to other birds (Gupta et al. 2014). In Europe, sparrows prefer to forage alongside European starlings, which are also native, and they form mixed flocks (Clergeau 1990). One possible explanation is that foraging in mixed flocks with Sturnidae species provides a safer environment for the sparrows and thus invasive mynas may fulfill that function where other suitable species are scarce. In Israel, European starlings are common during winter and may forage in large flocks, but usually in agricultural fields and rural environments and not on urban irrigated lawns (during all the observations in the first experiment, carried out when starlings are present in Israel, no starling was seen foraging on an urban lawn). Therefore, invasive mynas may fulfill the role of preferred core species for mixed species flocks and attract foraging house sparrows as a satellite species.

By tracking six sparrow flocks (for an average of 17±10.9 minutes) on urban irrigated lawns I measured the time allocated to foraging alongside mynas, doves, only other sparrows, or other species. I found that foraging sparrows spent most of their foraging time next to mynas or alongside conspecifics only, compared to the time they spent next to doves or other species (Fig. 12). This observation supports the results of the second experiment and suggests an affinity between sparrows and mynas, and that these two species form mixed species flocks. However, during these observations there was no control over the proportion of mynas, doves, and other species. Theoretically, however, this result could be explained by the high myna density compared to that of doves and other species. Indeed, when myna density is very high (over 100 individuals on a single lawn), sparrows are usually absent. The proportion of mynas and doves, in this observation, was approximately the same. It is also possible that sparrows and mynas aggregate at the same patch, feeding partially on the same food source, but that mynas have a wider food niche than sparrows and their diet is based more on invertebrates than the sparrows' diet.

Figure 12: the proportion of time that foraging sparrows spent next to mynas, doves, only conspecifics or other species. Foraging sparrows spent more time next to mynas and conspecifics compared to the time they spent next to doves and other species (ANOVA: F3=23.8, p<0.0001, ±SD, N=6; the table details the Post-Hoc tests).

|  |  |  |
| --- | --- | --- |
|  |  | sig. |
| Conspecific | Dove | 0.00 |
| Myna | 0.38 |
| Other | 0.00 |
| Dove | Conspecific | 0.00 |
| Myna | 0.00 |
| Other | 0.17 |
| Myna | Conspecific | 0.38 |
| Dove | 0.00 |
| Other | 0.01 |
| Other | Conspecific | 0.00 |
| Dove | 0.17 |
| Myna | 0.01 |

The mixed species foraging of native sparrows and invasive mynas presents an unusual example of a native species that may benefit from the presence of an invasive species. Facilitation (interaction between two species that results in an increase in the density or biomass of at least one of those species) has been little studied in regard to invasion biology (Rodriguez 2006). Rodriguez (2006) reviewed 61 papers published between 1993 and 2004 and dealing with any form of invasive species that facilitates native species. The most common mechanism described regarding the facilitation of the native species is that of habitat modification caused by the invasive species (21 papers) (Rodriguez 2006). Facilitation by predation release is described in only seven papers, all of which refer to invasive species that reduced the population of local predators and, therefore, facilitated local prey species (Rodriguez 2006). In this study I did not find direct evidence of facilitation, since it focused on the behavioral level and not on the population level. Nevertheless, the results indicate that sparrows may suffer less predation and increased food consumption when foraging alongside mynas; and, if such benefit is reflected in higher reproduction, more offspring or higher offspring survivorship, the positive behavioral effect may also impact at the population level.

In many cases it is extremely difficult to trace the ecological impact of an invasive species. The present study emphasizes the importance of understanding the behavioral impact of invasive species on local species. Studying this impact may provide us with a better understanding of biological invasions.

# **Chapter Three: Breeding**

## Introduction

While sparrows may benefit from foraging alongside mynas, the mynas might pose a predation threat to the sparrow nestlings (Holzapfel et al. 2006). In most bird species, predation is the main cause of breeding failure and may alter breeding strategies, such as number of broods per breeding season and the time that nestlings remain in the nest before fledging (Martin 1995). Under high predation risk, reducing parental investment is one of the breeding strategies that parents employ in order to allocate resources to future broods and to maximize total fitness. This strategy can result in lower clutch size (Travers et al. 2010; Zanette et al. 2011; Hua et al. 2014), lower egg mass (Fontaine & Martin 2006), or lower clutch mass (Martin et al. 2006; Martin & Briskie 2009). Reduced parental investment as a breeding strategy to cope with high predation risk can also be a behavioral alternative, manifested in lower parental care, such as lower offspring provision rate (Fontaine & Martin 2006; Zanette et al. 2011; Ghalambor et al. 2013; Mutzel et al. 2013; Hua et al. 2014) or lower incubation visitation rate (Sofaer et al. 2012). Reducing parental investment is a breeding strategy that can be applied when breeding in high-risk environments, in order to reduce the resources that parents invest when benefit is uncertain (low reproductive value). In contrast, by estimating predation risk prior to breeding, parents may employ another breeding strategy to cope with high predation risk, such as altering settlement decisions and selecting breeding sites with lower predation risk (reviewed by Ibáñez-Álamo et al. 2015). Pre-nesting assessment of predation risk can be based on a variety of signals, such as cues indicating predator activity, the presence of 'protector species' (species that may deter potential predators), previous offspring loss to predation, and the breeding success of conspecifics and heterospecifics (reviewed by Ibáñez-Álamo et al. 2015). Not only might predation risk lead to parents reducing their parental investment, but uncertainty too regarding genetic relationship to the offspring (due to extra-pair copulation and extra-pair paternity) can result in a reduction in parental care (Matysioková & Remeš 2013) or nest defense (Berger et al. 2014b).

Parents can reduce their care not only in order to reduce their investment in the young, but also to reduce the probability of nest detection by predators (Skutch1949). Skutch (1949) contended that when predation risk is high, parents will reduce visit rate to the nest in order to avoid nest detection by predators, and that there is a trade-off between parental care and nest safety. Therefore, although it might be expected that during the incubation stage, when visit rates to the nest are low, nest predation rate will be lower than during the nestling feeding stage, when visit rates to the nest are high, nest predation rate is nonetheless not higher during the feeding stage than during the incubation stage (Roper & Goldstein 1997; Farnsworth & Simons 1999; Martin et al. 2000; Lloyd 2004). On the other hand, it is possible that, during the incubation stage, many of the poorly hidden nests and nests that are easy to approach become a target for predation, with predators ignoring the better hidden and harder to approach nests until the nestling stage. This could explain the evidence of a lower predation rate during the nestling stage, in line with the Skutch hypothesis. Martin et al. (2000) separated between these two factors of parental visit rate and nest site choice by observing parental care during the incubation stage and during the nestling stage. They ranked nest sites of four ground-nesting species: orange-crowned warbler (*Vermivora celata*), Virginia's warbler (*Vermivora virginiae*), red-faced warbler (*Cardellina rubrifrons*), and dark-eyed junco, by placing a zebra finch (*Taeniopygia guttata*) egg in the nests in the following year and noting whether it was found by predators. Their results show a strong effect of nest site on the probability of predation – nests that were in poor locations failed, due to predation, in both years; with predation tending to occur during the incubation stage rather than the nestling stage (Martin et al. 2000). When controlling for nest site effect, nest predation during the nestling stage is higher than during incubation stage, supporting Skutch's hypothesis (Martin et al. 2000).

In order to determine a behavioral breeding strategy during nesting, it is necessary to estimate predation risk. Using a predator removal experiment, Fontaine & Martin (2006) found that parents (from 12 studied species) successfully estimated a lower predation rate and consequently increased investment in the hatched young by increasing their feeding rate. Playing voice recordings of nest predators can influence parental care and reduce offspring feeding rate (Zanette et al. 2011; Ghalambor et al. 2013, Hua et al. 2014). Furthermore, when predation risk was actually low, but perceived predation risk was manipulated to be high, parents responded to the manipulation and reduced offspring feeding rate. Hua et al. (2014) exposed cavity-nesting eastern bluebirds (*Sialia sialia*) to voice recordings of nestlings and an adult predator, the Cooper's hawk (*Accipiter cooperii*). Although all pairs were breeding in artificial nest boxes, with entrance holes that prevented predation by Cooper's hawks, the breeding pairs reduced offspring feeding rate under the voice recording manipulation compared to the control (Hua et al. 2014). Zanette et al. (2011) eliminated all nest predation risk for breeding song sparrows (*Melospiza melodia*) by protecting each nest with an electric fence and seine net. Predator signal manipulation comprised a vocal recording of a combination of predators such as raccoon, corvid, hawk, owl, and cowbird, while the control record was a combination of non-predators, such as seal, goose, flicker, loon, and hummingbird. Although there was no actual predation risk, the manipulated pairs employed different breeding strategies to those of the control pairs and had lower clutch size, lower clutch mass, shorter incubation bout, and lower offspring feeding rate. The manipulated pairs also had more eggs that failed to hatch, higher chick mortality, and 40% lower breeding success than the control pairs, despite not suffering any predation (Zanette et al. 2011). Exposure to visual stimuli, such as a stuffed predator decoy, can produce the same effect (Ghalambor & Martin 2000; Ghalambor & Martin 2001; Ghalambor & Martin 2002; Tilgar et al. 2010). Ghalambor & Martin (2002) did not control predation risk, but manipulated breeding pairs of five cavity breeders (*Sitta pygmaea*, *Sitta canadensis*, *Sitta carolinensis*, *Poecile gambeli,* and *Certhia americana*) by placing stuffed decoys of red squirrels (*Tamiasciurus hudsonicus*) as a predator model or dark-eyed juncos as control. Under manipulation, males fed the incubating females less frequently than in the control. Ghalambor & Martin (2001) also used stuffed decoys of predators (hawk as a model for predator of adults, jay as a model for predator of nestlings, and tanager as control) to manipulate predation risk in ten bird species. The parents strongly reduced offspring feeding rate under manipulation of either the nestling predator decoy or the adult predator decoy (Ghalambor & Martin 2001). Perceived predation risk may thus have more influence on breeding strategy than actual predation risk; and since breeding strategy may have a significant impact on breeding success (e.g. Zanette et al. 2011), perceived predation risk may have a significant impact on both fitness and ecology.

Predation may pose a threat not only to nestling and eggs, but also to adults. In response to adult predation risk, parents may reduce offspring feeding rate, in order to reduce the probability of predation at the expense of parental care. Whether the parents choose self-risk and provide food for the nestlings, or choose lower self-risk at the expense of parental care, depends on reproductive value: the mean amount of future reproductive success for individuals of that age and sex in the population (Williams 1966). Life-history should therefore predict parental preference for increasing risk to themselves or for reducing parental care at the expense of nestling survival. Species that produce more offspring and have a shorter life expectancy are predicted to prefer self-risk and higher parental care in the presence of a predator; while species that produce fewer offspring and have a longer life expectancy are predicted to prefer lower parental care and lower self-risk in the presence of a predator (Ghalambor & Martin 2000; Ghalambor & Martin 2001). Ghalambor & Martin (2000) compared male feeding rate to incubating females in the presence of an egg predator, the house wren (*Troglodytes aedon*), and in the presence of an adult predator, the sharp-shinned hawk (*Accipiter striatus*) in two species: the high offspring producer and short life expectancy white-breasted nuthatch (*Sitta carolinensis*), and the low offspring producer and high life expectancy red-breasted nuthatch (*Sitta canadensis*). Males of both species reduced their feeding rate to the females in presence of both predators; but, as expected, *S. carolinensis* reduced its feeding rate more in the presence of the egg predator, while *S. canadensis* reduced its feeding rate more in the presence of the adult predator (Ghalambor & Martin 2000). In contrast, Tilgar et al. (2010) found that breeding pied flycatchers (*Ficedla hypoleuca*) reduced their offspring feeding rate in the presence of the adult predator, the Eurasian sparrowhawk (*Accipiter nisus*), but not in presence of the nest predator, humans. Tilgar et al. (2010) explain their findings as resulting from the necessity to silence the begging call of the chicks that might attract the predator and reveal the nest. Tilgar et al. (2010) also found that under controlled conditions and nest predator manipulation, parents provided more food to the older chick than to the younger one, while under adult predator manipulation the parents reduced their feeding rate to the older chick and provided food at the same rate for both chicks. There are two possible explanations for this. First, the parents control the food distribution among the chicks. They can relate to the reduction in offspring feeding rate, caused by the presence of an adult predator, as a short-term decrease in food supply. Consequently they reduce food to the older chick, which can handle a short-term food deficiency, rather than to the younger chick, which may not survive short-term food deficiency. The parents can thereby keep all the nestlings alive without impairing breeding success (Tilgar et al. 2010). In the second scenario the chicks control food division by competition and begging. Tilgar et al. (2010) could not explain their results according to this latter option, since the chicks were too young to respond to the parents' alarm calls and were only able to raise their heads and open their beaks.

The consequence of reducing offspring feeding rate by the parents is not necessarily a negative regarding nestling development. After the predator threat is removed, parents can compensate for the temporary food deficiency by increasing offspring feeding rate (Bengtsson & Rydén 1983). Furthermore, the feeding rate dues not necessarily indicate the amount of food delivered in each visit, for low feeding rate parents may bring larger food items than when feeding at a high rate (Blondel et al. 1991; Grieco 2002). In great tits, high offspring feeding rate has been related to poor-quality habitat, while low offspring feeding rate has been related to high-quality habitat; and, therefore, high offspring feeding rate has also been related to poor nestling condition, lower weight, and shorter tarsus length (Mägi et al. 2009). However, under perceived nest predation risk and lower offspring feeding rate, eastern bluebird nestlings fledged at a younger age, had higher growth rate, lower seasonal fecundity and, during the second breeding cycle, had higher mortality (Hua et al. 2014). Under perceived adult predation risk, nestlings did not fledge at a younger age, but had higher mortality and lower seasonal fecundity.

Interspecific comparison also revealed a correlation between feeding rates, predation risk, and offspring growth rate. By analyzing data from 64 passerine species, Martin et al. (2011) found that while offspring feeding rate was negatively correlated with predation risk, growth rate was also negatively correlated with offspring feeding rate: growth rates were faster in species that had higher predation risk, but lower offspring feeding rates. Cheng & Martin (2012) analyzed data from 12 passerine species and found a positive correlation of nestling wing growth rate and mass growth rate to predation risk, but a negative correlation of the age of endothermy to predation risk. Cheng & Martin (2012) linked their results to a higher ability to escape from predators after fledging. High nestling predation risk may encourage earlier fledging and, therefore, higher growth rate. However, there could be differences between ecological (e.g. Hua et al. 2014; Yoon et al. 2016) and evolutionary (e.g. Martin et al. 2011; Cheng & Martin 2012) responses to predation risk, since these may influence different traits (Ibáñez-Álamo et al. 2015).

Predation risk may also influence offspring development through maternal effect. Maternal effect is the influence of the mother on the phenotype of the offspring: and, if that influence assists the offspring to cope with the environment, it may be adaptive (Storm & Lima 2010). By being exposed to predation stress, females may influence nestling development. Coslovsky & Richner (2011) exposed great tit females to sparrowhawk decoys and voice recording before the egg laying and incubation stages, or to song thrush (*Turdus philomelos*) decoys and voice recording as control. The offspring were then transferred to foster parents that were not exposed to any manipulation. The results revealed that nestlings of mothers that had been exposed to predator manipulation were smaller (tarsus length, wing length, and sternum length) and had higher wing growth rate than the control nestlings (Coslovsky & Richner 2011). In an experiment that may shed light on the mechanism of maternal effect, barn swallow (*Hirundo rustica*) females were exposed to predator (cat decoy) or control (rabbit decoy) after laying the first egg (Saino et al. 2005). Corticosterone concentration measured in the eggs showed significantly higher concentrations in those laid by predator treatment mothers than by the controls (Saino et al. 2005). The eggs laid by mothers that were not exposed to the treatment were additionally injected with corticosterone or oil, or no injection as control. Nestlings that hatched from corticosterone-injected eggs were smaller, with shorter tarsus and lower mass than the control nestlings (Saino et al. 2005).

Predation risk may affect nestlings through lower parental investment and lower parental care, especially when predation risk is continuous or frequent, or through maternal effect. Offspring under predation risk may have a higher growth rate, may fledge earlier, and may be smaller. Not all body features are similarly affected by predation risk, and some (like wings or endothermy) may develop faster than others (like tarsus or mass). Differential growth and faster growth rate (Arendt, 1997) may result from allocation of resources and it can indicate that they may be adaptive (Øyan & Anker-Nilssen 1996; Kunz & Ekman 2000; Coslovsky & Richner 2011; Cheng & Martin 2012).

House sparrows are secondary cavity breeders, building their nests in existing holes (Summers-Smith 1988). Among avian species, cavity nests are more protected from predators compared to open nests, since fewer predators can reach and enter them (Martin & Li 1992; Martin 1995; Fontain et al. 2007). Consequently, cavity breeders suffer less predation, have larger clutch sizes, higher annual fecundity, higher nesting success, shorter nestling period (Martin & Li 1992; Martin 1995), higher mate feeding rate during incubation (Martin & Ghalambor 1999; Fontain et al. 2007), and higher offspring feeding rate (Martin et al. 2000; Martin & Briskie 2009; Ghalambor et al. 2013). Cavity nests also have a more stable temperature during the day, while open nests suffer from more extreme peaks of high and low temperatures (Martin & Ghalambor 1999). Since cavity nest safety is based on low accessibility for predators, the entrance hole size (e.g. Yoon et al. 2016) and the depth of the nest (Ghalambor & Martin 2002) play a large part in predation risk. Therefore, primary cavity breeders, which build their own nests to the required size, suffer lower predation risk than secondary cavity breeders, which rely on existing cavities (Martin & Li 1992; Martin 1995). Furthermore, cavities may be a limited resource in some habitats and, therefore, secondary cavity breeders may be limited by the available cavities (Von Haartman 1957; Cornelius 2008). In contrast, Wiebe (2011), who analyzed 31 studies that tested cavity nests as a limiting factor using manipulation (nest box addition, nest box removal, or cavity blocking) in mature forests, found that most studies (81%) did not find a significant effect of the manipulation on breeding densities, and he concluded that cavities are not necessarily a limiting factor for cavity breeders in mature forests. Nevertheless, in many cases there is evidence of strong competition for breeding places among secondary cavity breeders, and that this is a major source for breeding failure (Orchan et al. 2013; Charter et al. 2016). Since different species of secondary cavity breeders are of different sizes, the size of the entrance hole is a major factor for nest cavity competition, with smaller species able to use cavities inaccessible to larger species (Orchan et al. 2013; Charter et al. 2016).

House sparrows often breed in cavities and both parents take part in incubation and offspring feeding (Summers-Smith 1988; Bartlett et al. 2005). House sparrows are socially monogamous, but extra-pair copulation and extra-pair paternity are common (Wetton et al. 1995; Václav et al. 2003) and there is evidences of intra-specific brood parasitism (Kendra et al. 1988).

Breeding success in house sparrows depends on many factors, such as temperature, rainfall (Peach et al. 2008), food abundance, especially invertebrate availability (Peach et al. 2008; Peach et al. 2014), nest environment (rural or urban) (Seress et al. 2012), and also nest predation (Murphy 1978; Cordero 1991) and cavity competition (Charter et al. 2016). Cordero (1991) estimated the proportion of breeding failure due to predation out of the total breeding failure as 4.1%-17.2% (the cause of 13.1% of the breeding failures was uncertain). However, since house sparrows are very widespread across the globe, predation risk and cavity availability, as well as potential predators and potential cavity competitors, may vary across different locations and habitats. In Spain, Cordero (1991) found that sparrow nests were predated mostly by least weasels (*Mustela nivalis*) and black rats (*Rattus rattus*), but also by competing birds such as the wryneck (*Jynx torquilla*) or other sparrow species. In Kansas and Alberta, USA, Murphy (1978) found that the sparrow nests' most common predator was the black rat snake (*Pantherophis obsoletus*), which preyed on sparrow eggs. In Britain, domestic cats (*Felis catus*) are a major predator of house sparrows, both adults and nestlings (Churcer and Lawton 1987; Woods et al. 2003). In Israel, the common myna can be a dominant cavity competitor for house sparrows, but it is restricted by the size of the entrance hole (Charter et al. 2016).

In this work I conducted two experiments in order to test the effect of the presence of the common myna on breeding in house sparrows.

## Objective

The objective of the first experiment (parental care) was to determine whether the presence of mynas around the nest would alter parental behavior. The null hypothesis was that the sparrows' parental behavior would remain the same in both the presence and the absence of the mynas. The research hypothesis was: the parental behavior of the sparrows would change in the presence of mynas, with either negative or positive implications for parental care.

Parental behavior, such as visit rate, is linked to parental care, which may be affected by perceived risk. Changes in parental behavior in the presence of mynas could therefore indicate changes in perceived risk.

The objective of the second experiment (breeding success) was to understand whether the presence of mynas around the nest would affect the breeding success parameters. The null hypothesis was that the sparrows’ breeding success would remain the same in both the presence and the absence of the mynas. The research hypothesis was that the breeding success of the sparrows would change in the presence of mynas.

The findings from the second experiment were expected to indicate whether the behavioral change demonstrated in the first experiment (if the null hypothesis was rejected) can affect breeding success and consequently also fitness, and potentially have implications for the ecosystem.

## Methods

**Parental care experiment**: In order to better understand the influence of invasive common mynas on the breeding behavior of local house sparrows, I conducted an experiment on wild breeding sparrows. Nine breeding pairs were located at the stage of feeding their chicks, whose age and brood size, however, were unknown. A stuffed myna decoy was placed next to five of the nests, 5 m from the nest entrance, and left there for 30 minutes. A laughing dove decoy was placed next to the other four nests, as a control, again 5 m from the nest entrance, for 30 minutes. After 30 minutes the decoys were interchanged – myna for dove and dove for myna, in the same locations and left for another 30 minutes. Three different myna decoys and three different dove decoys were used for this experiment.

During the experiment the nest entrance and surroundings were recorded using a video camera at a rate of 30 frames per second. The camera was located at a distance of 15 m from the nest and was left unattended. Analysis of the recordings revealed the parents' visit rate, visit duration, and their behavior around the nest. Because the decoys were not visible in the recordings I could not distinguish between myna manipulations and dove manipulations in the analyses, which can thus be considered as blind.

All the nests were located at the I. Meier Segals Zoological Research Garden at Tel-Aviv University and around other locations on the Tel-Aviv University campus. There was no evidence of real predators around the nest during the experiment.

**Statistical analysis**

Four variables were compared between the presence of a myna decoy and the presence of a dove decoy: rate of visits, rate of pre-entry behavior, time spent inside the nest, and time spent in pre-entry behavior. The four dependent variables were measured for all parental visits, regardless of sex, and were compared using a MANOVA model. Another MANOVA model was used to compare between the separate visits of the male and the female for all four dependent variables in the presence of a myna or a dove decoy. All data from the four variables were transformed with square root transformation to normalize distribution.

**Breeding success experiment**: In early March 2015, six aviaries (3m×3m×3m) at the I. Meier Segals Zoological Research Garden at Tel-Aviv University were populated with five pairs of house sparrows (Fig. 13). Each aviary contained five nesting boxes located 2 m above the ground on its eastern wall (Fig. 13). The three northern aviaries were separated from the three southern aviaries by an opaque divider (Fig. 13). Each of the northern and southern aviaries was separated from the adjacent aviary by 1 m of fence (on the east side of the cage, next to the nesting boxes) and 2 m of opaque divider (Fig. 13). Each aviary also contained a smaller cage with either one common myna or one laughing dove (Fig. 13). The laughing dove was used as a control since it is approximately the same size as a myna and is a non-aggressive species. (See Fig. 13 for scheme of aviaries and the specific location of the smaller cages). As a result of the fence divider, the sparrows in the three northern aviaries could see each other, and the sparrows in the three southern aviaries could see each other. Sparrows that shared their aviary with a myna, however, could not see any laughing doves, and sparrows that shared their aviary with a laughing dove could not see any mynas. Since the mynas and doves were caged inside the aviary, they could not compete with the sparrows for food or harm the sparrows or their chicks in any way. All sparrows were adults that had been captured in the wild and probably had previous experience with both mynas and laughing doves.

The sparrows were kept on a basic diet of one shredded egg, half a cucumber, and 200 g of grain (mixed grain chicken feed) per aviary per day. From 08/03/2015 100 g of maggots per aviary per day were added to the diet in order for the sparrows to start breeding. All food was placed in the center of the aviary. Each aviary was supplied with straw and cotton wool for nesting.

The sparrows were given two weeks to start breeding, after which all eggs that had been laid in new nests were removed in order to synchronize the breeding cycles.

M

M

M

D

D

D

18 m

Figure 13: the six aviaries in the first breeding cycle. The sealed dividers are represented by solid lines and the nets by dashed lines. Each aviary contained five nesting boxes on the east side (black squares) and a small cage with either one laughing dove (D) or one common myna (M). During the second breeding cycle each myna was replaced with a dove and each dove was replaced with a myna.

After the first breeding cycle had been completed and all surviving fledglings had been removed to a distant aviary, all the nest boxes were cleaned and the second breeding cycle was initiated with the same adults. In the second breeding cycle, the locations of the myna and the doves were reversed. The eggs that were laid in the new nests after two weeks were similarly removed in order to standardize the results of the second breeding cycle with the results of the first breeding cycle.

For both breeding cycles, I documented the number of eggs laid, the number of chicks hatched, and the number of fledglings. Between one to two days prior to fledging, the chicks were weighed and tarsus length and skull + bill length were measured. Although body mass is a good indicator of current body condition and nutritional status, it may fluctuate on a daily basis and cannot be used as a reliable measure of size (Piersma & Davidson 1991). Tarsus length, in contrast, is a stable measurement that does not change after fledging and is a good indicator of body size (Johnston & Selander, 1971; Piersma & Davidson 1991; Senar & Pascual 1997). Skull and bill lengths are also indicators for early development and, together with body mass and tarsus length, are associated with survival after fledging (Lindström 1999; Freed & Cann 2009).

**Statistical analysis**

Four dependent variables were compared between the myna and the dove treatments: the number of nests built per aviary, the number of eggs laid per aviary, the number of eggs hatched per aviary, and the number of chicks fledged per aviary. The differences between treatments for each variable were analyzed using paired T test. The number of chicks fledged per aviary was also compared between the two breeding cycles using paired T test. In order to determine whether the treatment, the breeding cycle, or a correlation between them affected the survival rate (number of chicks fledged/number of chicks hatched) a two-way ANOVA model was used.

The hatchling measurements comprised three dependent variables: skull length, body mass, and tarsus length. The difference between the treatments for each variable was analyzed using paired T test.

## Results

**Parental care experiment**: All nine nests in this experiment were observed to be regularly visited by both parents, prior to any experimental manipulation. The nine nests received together a total of 143 visits during which one or the other of the parents entered the nest, in both the control and the myna manipulation (total of 87 female visits and 56 male visits). Of those 143 visits, 90 were preceded by a "pre-entry behavior" characterized by the parent standing on or next to the entrance, holding a food item and scanning. In the other 53 visits, the parent entered the nest immediately, without any pre-entry behavior (total of 15 "immediate entries" by males and 38 by females). There was no significant difference between the number of "immediate entries" (divided by the total number of entries) between the control and manipulation groups (average in the control group: 0.3±0.07; average in the manipulation group: 0.22±0.09; Paired samples T test: T7=-0.83, p=0.44). On 16 occasions a parent displayed pre-entry behavior, but this was not followed by entering the nest (12 events by the female and 4 events by the male). There was no significant difference between the number of events in which the pre-entry behavior was not followed by entering the nest (divided by the total number of pre-entry behaviors) between the control and manipulation groups (average in the control group: 0.1±0.04; average in the manipulation group: 0.26±0.13; Mann-Whitney Test: U=25.5, p=0.32).

In the MANOVA model, the test of equality covariance did not reject the null hypothesis (F=1.7, p=0.074). The MANOVA model revealed a significant difference in variance between the presence of the myna decoy and that of the dove decoy (Wilks' Lambda test: F=3.1, p=0.04, observed power=0.588), indicating that the between-subjects effect was appropriate. The rate at which the parents entered the nest was higher in the presence of the dove decoy than in that of the myna decoy (Fig. 14). The rate of the parents' pre-entry behavior was also higher in the presence of the dove decoy than in that of the myna decoy (Fig. 15). The total time spent by the parents inside the nest was significantly shorter in the presence of the myna decoy than in that of the dove decoy (Fig. 16); while the total time spent by the parents in pre-entry behavior did not significantly differ between treatments (Fig. 17). The average time spent by the parents inside the nest on each visit in the presence of the myna decoy was 23.6±7.9 seconds, and did not significantly differ from that in the presence of the dove decoy, 39.6±16.3 seconds (square root transformation, Paired samples T test: T7=-1.26, p=0.25). The average time the parents spent in pre-entry behavior on each visit in the presence of the myna decoy was 10.3±2.5 seconds, and did not significantly differ from that in the presence of the dove decoy, 13.1±4.1 seconds (square root transformation, Paired samples T test: T8=-0.084, p=0.94).

Figure 14: the rate of parents visits inside the nest (number of visits in 30 minutes) under both treatments (±SE). F=-6.6, p=0.021, observed power=0.67, N=9.

Figure 15: the rate of parents pre-entering behavior (number of visits in 30 minutes) under both treatments (±SE). F=5.33, p=0.035, observed power=0.58, N=9.

Figure 16: the time parents spent inside the nest in 30 minutes under both treatments (±SE). F=6.92, p=0.018, observed power=0.695, N=9.

Figure 17: the time parents spent in pre-entering behavior in 30 minutes under both treatments (±SE). Paired samples T test: F=1.58, p=0.227, observed power=0.219, N=9.

While both males and females reduced their entry visit rate to the nest and the time they spent inside the nest in the presence of a myna decoy compared to in the presence of a dove decoy, there was no effect of sex on the rate of visits inside the nest (Fig. 18), or on the rate of pre-entry behavior (Fig. 19), on the time spent inside the nest (Fig. 20), or on the time spent in pre-entry behavior (Fig. 21) in the presence of the myna decoy compared to in the presence of the dove decoy.

Figure 18: the difference between the rates of visits inside the nest in the presence of dove decoy and myna decoy in 30 minutes, for the male and the female (±SE). F=0.07, p=0.8, observed power=0.057, N=9.

Figure 19: the difference between the rates of pre-entering behavior in the presence of dove decoy and myna decoy in 30 minutes, for the male and the female (±SE). F=0.49, p=0.49, observed power=0.1, N=9.

Figure 20: the difference between the times spent inside the nest in the presence of dove decoy and myna decoy in 30 minutes, for the male and the female (±SE). F=0.21, p=0.65, observed power=0.07, N=9.

Figure 21: the difference between the times spent pre-entering behavior in the presence of dove decoy and myna decoy in 30 minutes, for the male and the female (±SE). F=1.56, p=0.22, observed power=0.23, N=9.

**Breeding success experiment**:

*Breeding success*

Average brood size was 5.36±0.15 and did not differ between the groups (average brood size was 5.31±0.08 in the myna group and 5.42±0.31 in the dove group, Paired samples T test: T5=-0.34, p=0.75), nor between breeding cycles (average brood size in the first cycle was 5.63±0.24 and in the second cycle it was 5.1±0.13, Sign test: p=0.063). There was no difference in the number of nests built (Fig. 22), or in the number of eggs laid between the experimental and the control group (Fig. 23). The number of chicks hatched was also similar between the two groups (Fig. 24). However, the number of chicks that fledged was significantly higher in the control group (Fig. 25). The sparrows that bred in the presence of mynas fledged fewer offspring than those that bred in the presence of doves. The number of fledglings was similar in both breeding cycles (Fig. 26). The hatching rate (number of chicks hatched/number of eggs laid) was similar for both groups, as well as for the two breeding cycles (χ21=0.324, P=0.569). The survival rate (number of chicks fledged/number of chicks hatched) differed between the groups but not between the breeding cycles (Table 3).

Figure 22: number of nests built per aviary (paired t test: T5=-0.7, P=0.53, ±SE, N=6)

Fig 23: the numbers of eggs laid in the two groups (paired t test: T5=-1.006, P=0.361, ±SE, N=6).

Fig 24: the number of chicks hatched in the two groups (paired t test: T5=0, P=1.0, ±SE, N=6).

Fig 25: the number of chicks fledged in the two groups (paired t test: T5=-4.108, P=0.009, ±SE, N=6).

Figure 26: number of fledglings per aviary (paired t test: T5=-0.95, P=0.39, ±SE, N=6).

Table 3: Average survival rate (number of chicks hatched/number of chicks fledged) in the two groups and in the two breeding cycles (R2=0.43).

|  |  |  |  |
| --- | --- | --- | --- |
|  | df | F | p |
| Corrected model | 3 | 3.72 | 0.061 |
| Cycle | 1 | 1.25 | 0.3 |
| Group | 1 | 6.82 | 0.03 |
| Cycle\* Group | 1 | 3.09 | 0.12 |

*Offspring measurements*

No correlation was found between any of the offspring measurements and brood size. Consequently, comparisons between the experiment and control groups exclude brood size. There was no significant difference between the two breeding cycles in any of the measurements.

There was no significant difference between the two groups in offspring weight (Fig. 27) or in offspring skull length (Fig. 28). However, the offspring of the sparrows that bred in the presence of mynas had significantly shorter tarsus than those of sparrows that bred in the presence of doves (Fig. 29).

Fig 27: The weight of sparrow offspring alongside mynas and alongside doves (T4=-2.350, P=0.079, ±SE, N=5).

Fig 28: The skull length of sparrow offspring alongside mynas and alongside doves (T4=-0.253, P=0.813, ±SE, N=5).

Fig 29: the tarsus length of sparrow offspring alongside mynas and alongside doves (T4=-5.017, P=0.007, ±SE, N=5).

## Discussion

The parental care experiment suffers from low statistical power due to the small sample size, as well as variation among the sampled nests due to variation in offspring age and number (which were not controlled due to the access to natural nests being limited, while parental care is affected by both offspring age and number). However it appears that the sparrows did alter their behavior in the presence of the myna decoy.

This experiment involved similar human interference with the breeding pair when approaching the nest in order to place either the myna or the dove decoy. The nest locations were close to human activity, however, and people often walk around and remain near the nests (although not during the experiments).

Mynas are known as potential predators of sparrow hatchlings (Holzapfel et al. 2006), and it is therefore possible that parental concern not to expose the nest to predation can lead to their reducing feeding rate (Skutch 1949; Fontaine & Martin 2006). The myna decoy could have been perceived as an increased predation risk, leading to a reduction in parental care, either because the parents sought to avoid exposure of the nest, or in order to conserve resources for allocation to future broods. Predation risk is not the only threat that mynas may pose to breeding sparrows. Mynas can compete with sparrows for nest cavities and can threaten an existing brood in order to usurp the breeding cavity (Charter et al. 2016). The perceived threat, whether predation or competition, may result in a reduction in parental care.

Since cavity nests may become a trap for the parents as well as for their offspring when detected by predators, it is possible that the adult sparrows may perceive the myna as a threat to themselves when they are inside the nest, but not when involved in other behaviors, such as foraging. Therefore, reducing the time spent inside the nest in presence of the myna decoy may be the result of reducing self-risk by the parent. If the parents do reduce their time in the nest in order to reduce self-risk, this reduction should be influenced by the reproductive value of each parent. Since extra-pair copulation is common among house sparrows (Wetton et al. 1995; Václav et al. 2003), the male might be expected to reduce its time in the nest more than the female in the presence of the myna decoy; this difference, however, was not found (Fig. 20); whereas in the presence of the dove decoy, the male did spend less time inside the nest (134±61 sec/30 min) than the female (338±131 sec/30 min), and therefore had less overall time for reduction.

It is expected that under increased predation risk, the male will allocate its time differently to that of the female and invest more in other activities, such as extra-pair copulation, which may maximize its fitness. The male may be less willing than the female to invest time and other resources in a high-risk brood since it may have other offspring as a result of extra-pair copulation; and it may also, similarly, be less certain of its own paternity (Berger et al. 2014a). In the present study no effect of the sex of the parent was found in regard to behavioral changes in the presence of the myna decoy compared to in the presence of the dove decoy. However, the statistical power of those results is very low (Fig. 18-21) due to small sample size. Because male parental care is less than that of the female and, hence, its activity around the nest is very low, measurement of any change in its activity compared to the female requires a larger sample size. Furthermore, the ratio between male and female parental care can be affected by offspring age, which was not controlled in this experiment and can increase the data variation.

While in this experiment no data were collected regarding parental care when not under interference; and, therefore, we can only compare parental care in the presence of the dove or the myna decoy, we can conclude that parental care was lower in presence of the latter. The breeding success experiment sheds additional light on the results of the parental care experiment.

A reduction in parental care, reflected in both visit rates and time spent inside the nest in presence of mynas, may affect the breeding success of the sparrows by reducing the food available for the chicks and thereby reducing their fitness.

The results of the breeding success experiment can be compared to those of Singer & Yom-Tov (1988), who studied the breeding biology of house sparrows in Israel. The average brood size in the present study, 5.36±0.15, was similar to that found by Singer & Yom-Tov (1988): 4.9-5.62 eggs/nest. The hatching rate (eggs/hatchlings) too was similar between this study (65% with no significant difference between treatments) and Singer & Yom-Tov (1988) (70%). The survival rate (fledglings/nestlings) in Singer & Yom-Tov (1988) was 75%, similar to the survival rate of our sparrow and dove group (69%), and higher than the survival rate of the sparrow and myna group (38%). This comparison between Singer & Yom-Tov’s (1988) results in the wild and the results of the present breeding success experiment in captivity, supports the use of a dove decoy as a good control. It also indicates that although there was no increase in the breeding success in the presence of doves, breeding success in the presence of mynas was reduced.

Since in both sparrow groups the number of eggs laid was similar (Fig. 24), as was the number of chicks hatched (Fig. 25), we can assume that the difference in fledgling numbers (Fig. 26) reflects chick mortality. Our findings suggest that the mere presence of mynas next to breeding sparrows can significantly reduce their breeding success. A lower feeding rate may result in malnutrition, which may well explain the shorter tarsus of the surviving fledglings in the myna treatment group (Fig. 30), although there were no significant differences in other measurements between groups (Figs. 28-29). The shorter tarsus is an indicator of smaller body size and can also indicate lower fledgling survival rate (Lindström 1999; Freed & Cann 2009), in addition to the low nestling survival rate. The effect of myna presence on tarsus length, while body mass and skull length remained unaffected, may indicate resource allocation by the chicks towards particular physiological factors, such as thermoregulation, at the expense of others. It is also possible that in the presence of mynas, chicks were smaller due to malnutrition, reflected in the shorter tarsus, but that this malnutrition created strong selection pressure for the fatter chicks (the thinner chicks may not have been able to withstand the malnutrition and died). Thus, in the presence of mynas the hatchlings were smaller, but presented the same body mass as the hatchlings raised in the presence of doves. This suggests that the presence of mynas may not only affect the breeding success of sparrows, but can also create new selection pressure.

The breeding success experiment demonstrates a strong potential influence of the sheer presence of mynas on the local ecosystem, even though this experiment was conducted in captivity. In this experiment, although the sparrows were safe from predation and interspecific competition, the mynas were present constantly, whereas in the wild mynas are not constantly near the sparrow nests. Sparrows in the wild, in contrast to in this experiment, may have a wider choice regarding nest location, mates, and food resources. This difference between sparrows in the wild and in captivity may have biased the results and the effect of mynas on wild sparrows may be smaller.

Although the parental care experiment has low statistical power and the breeding experiment was conducted in captivity, it would nonetheless seem that mynas are perceived by breeding sparrows as a potential threat. This perception might affect parental care, and could constitute the mechanism behind a reduced breeding success. This effect of an invasive offers a unique example, in not being the result of direct predation, competition, hybridization, or disease transfer; but, rather, the result of behavioral changes due to the mere presence of the invader.

# **Conclusions**

Many organisms may modify their behavior in the face of environmental change. This behavioral modification, especially if it involves behaviors that are associated with breeding, foraging, or anti-predator behavior, may affect the fitness of individuals, trends at the population level, or even affect the ecosystem. Invasive species can trigger such environmental changes and there is evidence of the effect of biological invasions on the behavior of local species (Ligon et al. 2012; Peck et al. 2014; Wong & Candolin 2015; Hentley et al.). Nevertheless, most studies that deal with the impact of invasive species on the local ecology have focused on predation, competition, disease transfer, and hybridization as the such impacts (Gurevitch & Padilla 2004; Baker et al. 2014), while only a few studies have focused on the impact of behavioral change in itself.

In general "successful" invasion should have a negative impact on the local ecosystem as it triggers a significant and rapid change in the environment to which the local species are not adapted. On a global scale collapsing ecological barriers may unite previously separate ecosystems and reduce biodiversity. In order to cope with and mitigate such threats it is necessary to understand the ecological changes created by invasion and the mechanism of such invasion. Revealing the effect of biological invasions on local ecosystems can be difficult in many cases, and for many reasons: e.g. the difficulty in distinguishing between invasive species that are the drivers of ecological change and invasive species that are merely passengers of such change (Didham et al. 2005; MacDougall & Turkington 2005; Didham et al. 2007; Hermoso et al. 2011; Bauer 2012); the difficulty in determining the effects at the population level (since this requires a long-term survey, e.g. Grarock et al. 2012); and the difficulty inherent in uncovering cryptic invasions (Morais & Reichard 2017). Understanding the behavioral changes may contribute to revealing the impact caused by invasions. Many of the mechanisms behind the ecological consequences of biological invasions are mediated by behavior (Phillips & Suarez 2012). Studying the behavioral impact of an invasive species can thus reveal previously unknown ecological impacts. Furthermore, although a direct ecological impact is difficult to study by means of controlled experiments in captivity, the behavioral effects of biological invasions can be tested in captivity, where many variables, such as food availability, nesting materials, previous experience, group size, predation risk etc., can be controlled by experiments, in addition to observations in the wild. Through experiments in captivity it is possible to manipulate the effect of the presence of invasive species, and thereby uncover the underlying mechanisms, which might be cryptic in the wild. For example, in the present study, a GUD experiment in captivity revealed the affinity of foraging sparrows to mynas, whereas in the wild such an experiment could be strongly affected by the variety of food resources available to the sparrows, and by the difference in predation risk (food availability and predation risk may be very difficult to control in the wild).

In this work I have demonstrated how the study of behavioral changes in a local species, caused by the presence of an invasive species, can reveal a potential mechanism behind the invasion effect on native populations. While sparrows that forage alongside mynas may benefit, and increase their fitness, by increasing food intake or reducing perceived predation risk, those same sparrows, when breeding in the presence of mynas, might pay a cost and reduce their fitness due to increased perceived predation risk. Moreover, the sparrow hatchlings that survive and fledge in the presence of mynas, while they might be smaller compared to sparrow fledglings in an uninvaded habitat, may nonetheless benefit from a safer foraging environment alongside mynas. In order to understand the overall effect of myna presence on sparrow populations, further experimental and long-term correlative studies are needed. Measuring the energetic benefit gained by foraging sparrows in the presence of mynas, and calculating their fitness gain compared to their fitness loss caused by the mynas’ presence around the nest, can reveal the net impact of mynas on local sparrow populations. Studying additional behavioral effects, such as that of anti-predator behavioral changes in the presence of mynas on the predation rate of sparrows (e.g. by monitoring the mynas' behavior, do sparrows increase their probability of escaping a predation attempt?); or the effect of the presence of mynas on the length of the sparrows' breeding season (e.g. does increased food availability in the presence of mynas enable sparrows to produce more breeding cycles?). Such studies can contribute to calculating the net impact of invasions. This kind of research should be supported in the future by population trend correlative and experimental research that will distinguish between the driver and the passenger of the ecological change.

While most experimental studies that deal with the effect of biological invasions on local populations have found no influence or a negative influence, and a minority of studies have a found a positive influence, the present study found a complex influence that contains both negative and positive components: not at the ecosystem level, nor even at the population level; but at the individual level (which may provide insights into the population and ecosystem levels). An individual sparrow may experience a positive effect while foraging alongside mynas and a negative effect while breeding in the presence of mynas. Since ecosystems are complex systems with numerous and different interactions taking place among its components, complex effects can be expected following the introduction of a new species, and not only negative or only positive effects. The nature of the behavioral study can assist to uncover, experimentally, this complexity. However, while studying the behavioral effects of invasions may help to reveal the complex mechanisms behind these, it is also necessary to combine such research with a long-term correlative study that can indicate population trends.

Most biological invasion studies that deal with conservation have focused on the negative impact of the invasion, and consequently on the eradication or control of the invasive population. One example of a different conservation approach to biological invasions is that of the "city parrots" project that promoted the conservation of endangered parrot species, which suffer from habitat loss in the wild, but may thrive as invaders in an urban environment (Roelant Jonker pers. comm.).

Since ecological systems are complex, and invasion impact too might be complex, it is necessary to understand it in order to employ more appropriate conservation tactics. One of the major problems facing invasion biology conservation lies in grading the invasive population according to its impact on the environment and allocating resources accordingly. Since it is difficult to uncover the ecological impact of an invasive species, it may be problematic to classify the different invasions according to their ecological impact. Understanding the complexity of the invasion impact, by studying the local species' behavioral changes, can help to reveal those invasive species that exert the greatest impact, and to allocate conservation resources accordingly.

Furthermore, because an invasion impact may be complex, the net impact of some invasions may be positive for certain local populations. In cases in which those populations are declining or endangered as a result of other, human actions, the eradication of the invasive species can have a negative effect on the local species.

Davis et al. (2011) stated "Don’t judge species on their origins, but on their environmental impact". Assessing this impact is undoubtedly a difficult task. The present study, which has demonstrated the ability to shed light on the complex interactions that take place between local and invasive species by focusing on behavioral changes, together with future research that will similarly focus on this impact, can assist us to accomplish this task.

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# **תקציר**

המחקר אודות מינים פולשים מתמקד בעיקר בארבעה מנגנונים: תחרות, טריפה, הכלאה והעברת מחלות. עד כה, ההשפעה של מינים פולשים על ההתנהגות של מינים מקומיים כמעט ולא נחקרה באופן ישיר, למרות שלהתנהגויות כמו שיחור מזון ורבייה יש השפעה מכרעת על השרידות והכשירות של הפרט. עם זאת, מחקרים רבים התמקדו בהתנהגות של המין הפולש. תהליך הפלישה כולל מספר שלבים המשמשים כמסננת הבוררת תכונות מסוימות מאוכלוסיית המקור, בכלל זה תכונות התנהגותיות. ברירה זו חלה הן ברמת המין והן ברמת ברירה של פרטים מתוך האוכלוסייה. הברירה ברמת האוכלוסייה באה לידי ביטוי בהבדלים התנהגותיים בין הפרטים באוכלוסייה הפולשת לפרטים באוכלוסיית המקור.

התנהגות מתווכת באינטראקציות רבות, כולל תחרות, טריפה, הכלאה והעברת מחלות, לכן ניתן להתייחס להתנהגות כמנגנון השפעה של פלישה ביולוגית בפני עצמו. נוכחותם של מינים פולשים יכולה להשפיע על ההתנהגות של מינים מקומיים. שינוי התנהגותי יכול להשפיע על הכשירות של הפרט, בעיקר אם ההתנהגות קשורה באופן ישיר לשרידות או לרבייה, לכן שינוי זה יכול להשפיע ברמת האוכלוסייה ולהוביל לשינוי אקולוגי.

בעבודה זו בחנתי את השפעת נוכחות המאינה ההודית הפולשת על התנהגות שיחור מזון והתנהגות הקינון של דרור הבית המקומי בעזרת ארבעה ניסויים מרכזיים. שני ניסויים נערכו במטרה לבחון את ההשפעה של נוכחות המאינה על התנהגות שיחור מזון של דרורים. ניסוי אחד נערך בבר וניסוי נוסף נערך בשבי. במטרה לבחון את מידת הערנות של דרורים במהלך השיחור תועדו קבוצות של דרורים המשחרים על מדשאות בסביבה עירונית. שש קבוצות תועדו כשהן משחרות לצד זוג מאינות ושמונה קבוצות תועדו כשהן משחרות לצד זוג צוצלות כביקורת. כל תיעוד וידאו נותח במטרה למדוד את משך הרמת הראש של פרטים שונים בקבוצה. התוצאות הושוו בין הקבוצות ששיחרו בנוכחות מאינות לקבוצות ששיחרו בנוכחות צוצלות.

בכדי לבחון את ההעדפה של דרורים לשיחור בנוכחות מאינות, נערך ניסוי בשבי. עשרה דרורים שוחררו בכלוב שמשני צדדיו שני כלובים נוספים. כלוב בצד אחד הכיל כעשרים דרורים בעוד שהכלוב בצד השני הכיל ארבע מאינות. לעשרת הדרורים בכלוב האמצעי ניתנו שני מגשי מזון, אחד בסמוך לכלוב של הדרורים והשני בסמוך לכלוב של המאינות. 16 גרם של מזון הונחו בכל אחד מהמגשים למשך 24 שעות, שלאחריהן נמדדה כמות המזון שנותרה בכל אחד מהמגשים. הניסוי נערך במתכונת זו במשך שבעה ימים. כביקורת ניסוי זה נערך, במתכונת זהה, לאחר שהמאינות הוחלפו בצוצלות ובכלוב ריק. נערכו שש חזרות של ניסוי זה על קבוצות שונות של דרורים מנוסים (דרורים שנלכדו בבר וניתן להניח שהתנסו בשיחור לצד מאינות ולצד צוצלות) ועל שש קבוצות שונות של דרורים נאיביים (דרורים שבקעו וגדלו בשבי ולא התנסו מעולם בשיחור לצד מאינות או צוצלות).

שני ניסויים נוספים נערכו בכדי לבחון את ההשפעה של נוכחות המאינה על התנהגות הרבייה של הדרורים. ניסוי אחד נערך בבר וניסוי נוסף נערך בשבי.

ההשפעה של נוכחות המאינה על התנהגות הקינון של דרורים נבחנה ע"י הצבת פוחלץ של מאינה או צוצלת למשך 30 דקות בסמוך לקן של דרורים בשלב האכלת הגוזלים. לאחר 30 דקות הפוחלץ הוחלף. פוחלץ של מאינה הוחלף בצוצלת ופוחלץ של צוצלת הוחלף במאינה. התנהגות ההורים סביב הקן תועדה וקצב ההאכלות ומשך ההאכלות נמדדו.

באמצעות מושבת דרורים בשבי, בחנתי את הצלחת הרבייה של דרורים בנוכחות מאינה. חמישה זוגות דרורים שוחררו בשישה כלובים צמודים זה לזה ומסודרים בשורה. בשלושה מהכלובים הוצב כלוב קטן ובתוכו מאינה ובשלושת הכלובים האחרים הוצב כלוב קטן ובתוכו צוצלת. למרות שהדרורים היו מסוגלים לראות את הדרורים בכלובים הסמוכים, דרורים שקיננו בנוכחות מאינה לא היו יכולים לראות צוצלת ודרורים שקיננו בנוכחות צוצלת לא היו מסוגלים לראות מאינה. הדרורים בכל הכלובים קיבלו תנאים זהים המאפשרים קינון. לאחר שמחזור הקינון הראשון הסתיים, כל המאינות הוחלפו בצוצלות וכל הצוצלות הוחלפו במאינות ולדרורים ניתנה האפשרות לקיים מחזור קינון נוסף. הצלחת הרבייה ומצב הפירחונים הושוו בין קינון בנוכחות מאינות לקינון בנוכחות צוצלות.

באופן מפתיע, הדרורים בבר היו פחות ערניים במהלך השיחור לצד מאינות בהשוואה לשיחור לצד צוצלות. כפי שצפוי מהספרות, הערנות של הדרורים ששיחרו לצד צוצלות ירדה עם העלייה בגודל הקבוצה, אך הערנות לצד מאינות נשארה נמוכה ללא קשר לגודל הקבוצה.

בשבי, דרורים מנוסים העדיפו לשחר בסמוך למאינות מאשר בסמוך לדרורים אחרים, אך הם העדיפו לשחר בסמוך לדרורים האחרים מאשר לשחר בסמוך לכלוב ריק. בנוכחות צוצלת לדרורים אלו לא הייתה העדפה ברורה. דרורים נאיביים העדיפו לשחר בסמוך גם למאינה וגם לצוצלת מאשר בסמוך לדרורים האחרים, אך הם העדיפו לשחר בסמוך לדרורים האחרים מאשר בסמוך לכלוב הריק.

בנוכחות פוחלץ של מאינה, שני ההורים הורידו את קצב ההאכלות של הגוזלים בהשוואה לביקורת. בנוסף לכך, הצלחת הרבייה בשבי הייתה נמוכה יותר בנוכחות מאינות בהשוואה לצוצלות והמצב הגופני של הפירחונים היה ירוד יותר.

תוצאות אלו מצביעות על כך שבעוד שבמהלך השיחור נוכחות של מאינות גורמת לדרורים לחוש שהם בסביבה בטוחה יותר, הדרורים תופסים את נוכחות המאינה בסמוך לקינון כאיום. כתוצאה מכך, נוכחותן של מאינות יכולה לשפר את יכולת השיחור של דרורים, אך לפגוע בהצלחת הרבייה שלהם.

זוהי דוגמה להשפעה המורכבת שיכולה להיות למין פולש על מין מקומי. מחקר זה מדגיש את היתרונות בהתמקדות בהשפעה של מינים פולשים על התנהגות של מינים מקומיים.

עבודה זו נעשתה בהדרכת

פרופ' תמר דיין

השפעת המאינה המצויה (*Acridotheres tristis*) כמין פולש על ההתנהגות של דרורי בית (*Passer domesticus*) כמין מקומי

חיבור לשם קבלת התואר "דוקטור לפילוסופיה"

מאת:

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