The bird trade in Taiwan: an analysis of an Eastern pathway to biological invasion

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This thesis is the result of my own work. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

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Abstract

The subject of this thesis is the bird trade as a pathway for invasions by alien species to the East Asian island nation of Taiwan. Most previous studies have considered bird invasions in a Western context, but cultural differences imply that drivers of human-mediated invasions in Eastern societies are likely to be different. Therefore, I analyse patterns in the composition of traded alien bird species in Taiwan, and identify characteristics associated with success or failure at different stages of the invasion pathway.

Data on the identities, numbers and prices of birds in the Taiwanese cage bird trade were obtained from non-structured interviews with bird shop owners and employees, as described in Chapter 2. In chapter 3, I showed that species with larger native range size, smaller body size, with songs attractive to people, and native to closer regions, are more likely to be traded in Taiwan. In chapter 4, I explore the determinants of the price of bird species for sale in Taiwan, as a proxy for assessing which species in trade are more likely to be introduced into the wild. Chapter 5 analyses characteristics associated with species success in introduction and establishment. Alien species commonly for sale, sold for a longer period in the trade and with attractive songs were more likely to be introduced. Successfully established alien species are also likely to be large-bodied. Chapter 6 explores the important role of environmental suitability in alien environments in establishment success. In addition, I show that species with larger native range sizes tend to have larger alien range sizes in Taiwan.

Overall, the results here show that bird species composition for sale in Taiwan is determined by the interaction of species availability and societal demands. The thesis concludes with some suggestions for the current market and future studies.

Table of Contents

List of Figures

green lines indicate individual observations, the solid black lines represent the means of the observations, the dotted line represent overall average and the purple areas show the distribution. Estimates and p-values represent: median value of phylogenetic regression coefficients (1st and 99th percentiles), calculated over 100 phylogenetic generalized linear models, each using a different likely phylogeny for the 167 species.

Figure 5.3 The relationship between whether alien species recorded for sale in pet shops in Chi's survey (n = 79) were introduced into the wild in Taiwan (1) or not (0), and (a) log number of birds for sale, (b) song attractiveness and (c) log body mass. The green lines indicate individual observations, the black lines the means of the observations, the dotted line represent overall average and the purple areas show the distribution. Estimates and p-values represent median value of phylogenetic regression coefficient, (1st and 99th percentiles) calculated over 100 phylogenetic generalized linear models, each using a different likely phylogeny for the 79 species).

Figure 6.1 The means of environmental suitability in Taiwan for failed introductions (n = 28) and established species (n = 29, established and potentially established species included). The blue lines indicate individual observations, the solid black lines represent the means of the observations in failed introductions and established species, the dotted line represents overall average and the purple areas show the distribution.

List of Tables

Table 3.1 Families with significantly (a) higher or (b) lower than expected numbers (Exp. number) of species in Taiwanese pet shops in 2012 ($\alpha = 0.05$), for all species or with analysis limited to alien species (i.e. species not native to Taiwan). Median expectation (Exp. median) is taken over the 10,000 iterations of the randomisation test, while the 97.5th and 2.5th percentiles are the upper and lower limits within which 95% of the iterated values lie. Bonferroni corrected expectation (Exp. Bonf) shows the upper or lower limits of significance under the Bonferroni correction, only for those families that exceed those limits. Asterisks (*) denote tests for which a bird family has a significantly higher (or lower) observed number of species for sale in bird shops than expected.

Table 3.2 The species recorded in trade during 2012 in Taiwan sorted by their realms of origin, and the number of species expected from the randomization test (2.5^{th} and 97.5^{th} percentiles), and with the sequential Bonferroni correction applied. Analyses are for all species or limited to alien species (i.e. species not native to Taiwan). Asterisks (*) denote tests for which a realm has a significantly ($\alpha = 0.05$) higher (or lower) observed number of species for sale in bird shops than expected.

Table 4.1 The ten traded bird species with the largest numbers and ten with highest price recorded for sale in Taiwanese pet shops in my survey. Table with numbers of birds recorded for sale, their price (US$) and whether species are alien or native to Taiwan (Status).

Table 4.2 The relationship between the log-transformed prices of traded bird species in Taiwanese pet shops and the predictor variables.

Table 4.3 The relationship between the price of traded bird species in Taiwanese pet market and the percentage of a given colour found on the species, and colour diversity.

Table 4.4 Model coefficients in PGLS models for determinants of the price of birds in Taiwanese pet shops.

Table 5.1 The numbers of introduced and established bird species recorded in each survey. The numbers of bird species recorded as introduced, and the numbers of those introduced species considered to be established, or not, in Taiwan under the criteria (Total), together with the number of these species also recorded for sale in Taiwanese pet shops in Su's, Shieh's and Chi 's survey. Percentages are provided for the species in each survey that were successfully introduced, and for the species subsequently considered to be established.

Table 5.2 The results of phylogenetic generalized linear models testing whether alien species recorded for sale in pet shops in my survey were introduced (n = 167). M1 – M3 are the most likely three models (those with ΔAICc < 4). The numbers for each variable represent the median, 1st and 99th percentiles of the model coefficients.

Table 5.3 The results of phylogenetic generalized linear model testing whether alien species, recorded for sale in pet shops in Chi's survey, were introduced (n = 79).

Table 5.4 The results of univariate phylogenetic generalized linear model testing whether alien species recorded in the wild were also breeding in the wild, based on species recorded for sale in a) my survey, n = 40; and b) species recorded in Chi's survey, n = 46.

Table 5.5 The results of phylogenetic generalized linear models testing whether introduced species were also recorded breeding there, based on alien species recorded in my survey (n = 40). M1 - M7 are the most likely models (ΔAICc < 4). The numbers for each variable represent the median (1st and 99th percentiles) of the model coefficients.

Table 5.6 The results of phylogenetic generalized linear model testing whether alien species recorded in the wild were also recorded breeding there, based on data from alien species recorded as for sale in pet shops in Chi's survey (n = 46). M1 - M4 are the most likely four models (those with ΔAICc < 4). The numbers for each variable represent the median (and 1st and 99th percentiles) of the model coefficient.

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Chapter 1 Introduction

1.1 Introduction to Invasion Biology

1.1.1 Introduction

The movement of individuals or species to a new environment can be a natural process. Individuals may disperse under their own steam, or be carried passively such as on wind or water currents. Natural dispersal is responsible for much of the natural diversity of remote landmasses and islands. However, natural methods of dispersal are being augmented and superseded. Increasingly, species are being spread accidentally or deliberately by human actions and there is hardly a landmass that is not being affected. Examples of accidental dispersal include species spread in ballast water, while deliberate dispersal can include species moved in the pet trade, for hunting and game, or as environmental ornaments.

Human-mediated dispersal is different from natural dispersal in many respects (Brown and Sax 2005; Cassey et al. 2005a). The first main difference is in geographical extent. For example, even the most isolated major landmass of Antarctica and the islands nearby are affected by a variety of human-mediated species which include plants, vertebrates, invertebrates, marine, freshwater and terrestrial microbial groups (Frenot et al. 2005). Second, natural and human-mediated invasions differ in terms of dispersal distance. Long-distance dispersal is more common in human-mediated than in natural dispersal. For example, 12 species of British passerine birds have established in New Zealand in the last 150 years. Apart from humans, 25 other non-volant terrestrial mammal species have established there in the last 800 years. However, prior to human arrival, no non-volant terrestrial mammals had colonised in the 80 million years since New Zealand became an isolated landmass (Cassey et al. 2005a). Third, human-mediated dispersal is different in invasion timescale: it is happening at a much quicker rate. For example, on Gough Island, 71 of the 99 pterygote insect species that now live there have established in the past 325 years. Thus the rate of species colonisation is approximately 218 per thousand years since Gough Island was discovered by humans. In contrast, only 21 colonisation events occurred in 2-3 million years after Gough Island emerged from the sea. Even supposing that 95% of indigenous species on Gough Island have gone extinct, the successful colonisation would thus be one event per thousand years (Gaston et al. 2003). Today, the colonisation of oceanic islands is primarily influenced by human activities (Frenot et al. 2005), rather than natural processes (Blackburn et al. 2008). Fourth, human-mediated introductions are different in agency of dispersal. In a natural colonisation, species rely on their own powers of dispersal and thus the population size and frequency of colonisations are likely to be small. Small populations may experience problems, such as inbreeding. In contrast, human-mediated dispersal often provides higher propagule pressure, which includes larger number of individuals. It is therefore the human mediated dispersal that is a more efficient process of introducing species into suitable habitats, avoiding the small population problems (Cassey et al. 2005a).

A further difference between human-mediated and natural invasions is the type of pathways by which species are moved. The pathways that species ‘take’ to reach the new environments have been modified by large-scale modern transportation and human intervention or demands. Today, the way and the reasons that species are transported into a new environment are more likely to be the results of human than natural processes. Human-mediated pathways are more diverse, dynamic and more rapid and different in many aspects to natural invasion (Lockwood et al. 2007). In this thesis, I will consider aspects of human-mediated invasion only, leaving aside the natural invasion processes. From here on in, I will use the term “invasion” to refer to the process driven by humans, unless otherwise stated.

1.1.2 The Definitions of Invasion and the Invasion Pathway

Before it is possible to engage in a detailed discussion on the invasion process, the framework and terms used to study the process need to be clarified. The growth of invasion biology has led to several different models of the invasion process (Williamson 1996; Richardson et al. 2000; Blackburn et al. 2011). In all of these models, invasions are divided into a sequence of stages within which are sequential barriers for species to overcome (Williamson 1996; Richardson et al. 2000; Kolar and Lodge 2001; Blackburn et al. 2011).

The most commonly used models in invasion biology over the last decade have been the Richardson et al. (2000) and Williamson (1996) models. These are broadly similar in many respects, but have two main differences. First, they focus on different subjects. Richardson et al. focus on barriers that alien species need to overcome and this model is commonly adapted for plant invasion, for example. It has been adopted in Global Strategy on Invasive Alien Species of the Global Invasive Species Programme (McNeely 2001;

Blackburn et al. 2011). On the other hand, Williamson focuses on stages through which species have to pass. Second, the stage after introduction and before spread is designed differently in both models. The Williamson model defines the stage after introduction as establishment, whereas the Richardson et al. model defines it with two barriers, environmental and reproductive barriers. This makes it difficult to align two models when species establishment success is not considered to result from either environmental or reproductive factors, but is linked to some other feature, such as the frequency of releases (Blackburn et al. 2011).

Recently, Blackburn et al. (2011) proposed a framework that integrates the key features of the Richardson et al. and Williamson invasion models, and this unified framework will be adopted in this thesis (**Figure 1.1**). Blackburn et al. consider the invasion pathway as a process that begins when a species is moved into a new location outside the limits of its native range as a result of human activities. Species that are transported by humans from their native continent or oceanic islands into the new environments, beyond their limited geographic regions, are termed alien species (Lockwood et al. 2007). Blackburn et al. (2011) divide the biological invasion processes into four main stages, as in the Williamson model, with each stage incorporating barriers to the progress of species to the next stage, analogous to the Richardson et al. model. The stages (with barriers) defined in this scheme are transport (geography), introduction (captivity or cultivation), establishment (survival and reproduction) and spread (dispersal and environmental). Species that pass these invasion steps are termed transported, introduced, established and invasive species, respectively. Alien species can be defined as invasive species only when they fully complete all the stages of the invasion process (Lockwood et al. 2007; Blackburn et al. 2011). Conversely, failure of an invasion can take place at any point of the process. Species that fail in any of the stages or their sub-stages, fail in invasion. However, a failure of species in any stage or a sub-stage of the invasion pathway does not preclude a future possibility of a success of the same species. The failure of species may predict the failure of the same species to establish at the same location at a later time, but success is not precluded from the next outcome.

The Blackburn et al. framework integrates the Richardson et al. and Williamson invasion models, but differs from them in four important ways. First, an additional barrier, captivity or cultivation, has been identified in introduction stage. Captivity or cultivation is a human-set barrier that prevents successfully transported species being introduced into a new environment directly. Second, Blackburn et al. replaced the environmental (local) barrier in the Richardson et al. model with a survival barrier. Together with a reproduction barrier, both are categorised under the establishment stage, which is a population process. In this stage, individuals from an alien population can fail in two ways: either fail in survival, or survive but fail in reproduction. An alien population can move onto next stage only when the population is self-sustaining.

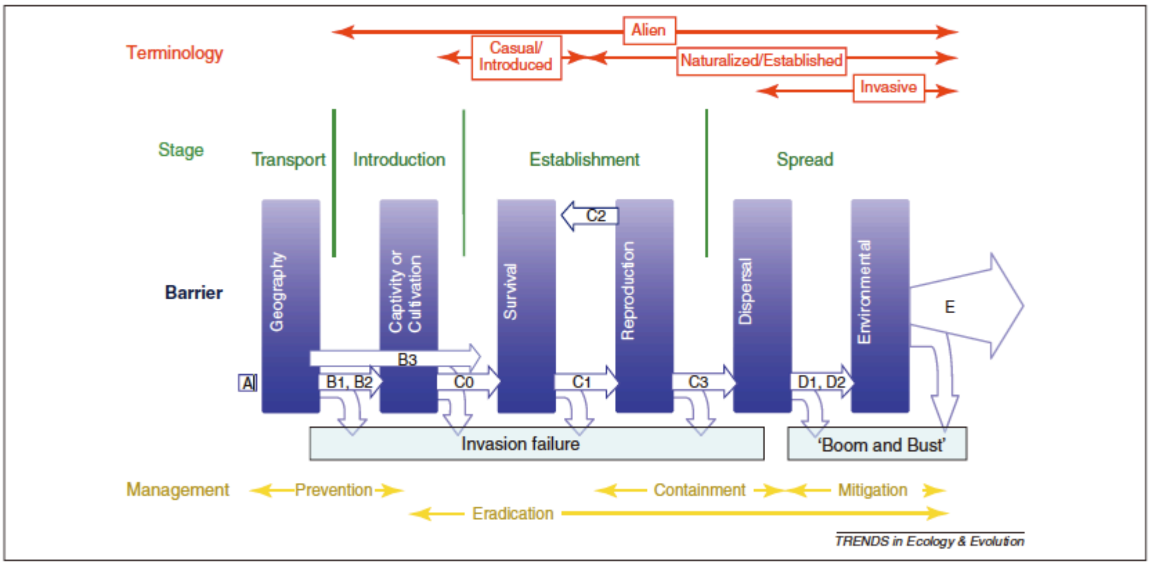

Figure 1.1 The framework for biological invasion proposed by Blackburn et al. (2010).

Third, Blackburn et al. added a dispersal barrier before naturalised species enter the spread stage and an environmental barrier when a spread population faces a greater range of environmental conditions. Once an alien population overcomes the dispersal barriers, this population would then spread into new locations significantly distant from their original introduced sites. The environmental barrier encompasses a range of geographic factors, which determine the extent of suitable conditions for populations. When species cross the geographic environmental barrier, they are referred to as fully invasive species. The environmental barrier in the Blackburn et al. model does not divide into disturbed or natural habitats, which is different from the Richardson et al. approach. Such distinction is neglected, because habitat disturbance is difficult to define and different species act differently in a variety of conditions. Fourth, the impacts of the economic or pest status are not included in the Blackburn et al. model, as the impacts of alien species are not always associated to their establishment (Blackburn et al. 2011).

The main limitation of the stage-based approach is that the sub-processes are not separate; the invasion process should be regarded as an on-going series, i.e. a continuous process. However, there are at least four advantages to viewing invasion as a stage-based process:

First, the stage-based approach allows researchers to focus on the constituent invasion steps. The common use of ambiguous invasion biology terminology renders comparison of studies difficult, and therefore it is important to work within a framework with well-defined invasion stages.

Second, a stage-based process can help to determine the characteristics that allow species to overcome each different stage successfully. If one relates the explicit series of stages to filters, it helps to explain the role of these stages. Each stage acts as a filter, therefore, the particular characteristics that affect species in success or failure in a given stage or barriers can be clarified.

Third, the mechanism of characteristic filters implies that species entering into the next invasion stage are a non-random subset of all species. The importance of species characteristics will also be different at each stage, therefore, some biological and social factors may possibly determine the likelihood that a species can succeed at each stage (Kolar and Lodge 2001). If viewing the invasion as one process, it is possible to include the bias applied by each stage and to draw different and potentially misleading conclusions. For example, if only large body size species are transported, it is expected that successful introduced species have large body size. If the comparison is made between species that succeed in establishment and species that fail in introduction, body size may emerge, incorrectly, as a successful characteristic. A stage-based approach allows characteristics of species to be discussed separately stage by stage, helps to define the source pool of species for each subsequent stage, avoids the confounding of characteristics determining success across stages, while determining what features of species are correlated to the success at each stage.

Fourth, a stage-based pathway can clearly show how different features act differently at any point of the process, thereby determining the factors which affect the multiple stages (Blackburn et al. 2009b). In order to comprehensively understand the invasion processes, separate studies of all stages are required (Blackburn et al., 2011). However, it is important to bear in mind that invasion is a continuous process. The processes that influence early stages will affect the composition of the later stages. Different patterns of species transportation and introduction will define the later invasion stages and affect the likelihood of success in the later stages. In fact, it has been shown that the frequency and the number of species released into an alien region in the early stages will affect the possibility of successful establishment in the subsequent stage (Lockwood et al. 2005; Wilson et al. 2009). For this reason, the different ways that species become entrained on a particular biological invasion pathway is important. For all of these reasons, I adopt a stage-based approach to analysing the invasion pathway in this thesis.

1.1.3 Transport and Introduction

To become an alien invader, species first need to be transported and introduced into a new (alien) environment. Animals are translocated for a variety of reasons such as game hunting, commercial concerns, food supply, aesthetics, nostalgia, conservation purposes, religious belief and ornamental interests.

Between 1820 and 1930, the population explosion in Europe led many people to leave their homeland to colonise "Neo-Europes" (Crosby 2004), the regions where Europeans emigrated successfully. Many species introductions occurred at this time as a result of this diaspora. Jeschke and Strayer (2005) showed that the number of introductions is positively correlated with the rate of human immigration in Europe and North America. Approximately, one species of North American vertebrate was introduced to Europe with every 200,000 immigrants to Europe. Introductions in this period were undertaken for a variety of reasons. For example, many species were transported to new environments for food or as game for hunting, which was very popular during the Victorian era (1837-1901). Thus, foxes were transported and introduced into Australia for the purpose of recreational foxhunting, while rabbits were intentionally transported and introduced as food animals. Brook trout and black bass were transported and introduced for fishing, due to the preference of settlers in the United States (Lockwood et al. 2007). These introductions were thought of as improvements to wildlife diversity (Lockwood et al., 2007). Transportation and introduction were not necessary always of species thought to be useful, however. For instance, many songbirds were transported and released into the new environment by settlers for nostalgic reasons (McDowall 1994).

Human actions determine which species to transport and introduce. Human-mediated introductions can be selected by choice, although direct choice is not always involved, for example, as in ballast water organisms. Either way, however, species imported by humans are not a random subset of all species (Blackburn et al., 2009). When active choice is involved, there must be some special features that make themselves attractive to a particular demand. As species characteristics do not evolve randomly but are rather shaped by the habitats where species evolved, and given the origins where species transported from are not random (Blackburn and Duncan 2001a), the characteristics of transported species are also very likely to be non-random.

Non-randomness has been studied particularly well for bird introductions. The distribution of bird introductions is non-random in respect of native geographic range size, taxon, introduced locations, origin and species features. For example, species with higher availability are more likely to be introduced. For British birds, resident birds with both large geographic range size and a large population size are more likely to be involved in introduction (Blackburn and Duncan 2001b). In respect of taxon and introduced location, bird introductions are concentrated in five bird families (Phasianidae, Passeridae, Psittacidae, Anatidae and Columbidae) and introduction events are concentrated in islands and temperate zones (Blackburn and Duncan 2001b). These five families are favoured as game birds, ornamental and pet species. Species that have been introduced outside of their origin have larger native geographic range and larger body mass than those that have never been transported (Gaston and Blackburn 1995; Jeschke and Strayer 2006; Blackburn and Cassey 2007). The mean body mass of introduced species is 116.6g which is significantly larger than the geometric mean mass of terrestrial bird species of 50.5g (Gaston and Blackburn 1995; Blackburn et al. 2008). Even within the same family, alien species have been shown to have larger body masses than those that have not been transported and introduced (Blackburn and Duncan 2001a).

Given that transport vectors are driven to a large degree by the demands of society, differences and changes in societies around the world are likely strongly to influence the types of species transported and introduced, and their characteristics (Blackburn et al. 2010). Different societal demands require the transport and introduction of different taxa from different regions with different traits, such as geographic range size, taxonomic composition and individual body mass (Blackburn et al. 2010). This may be particularly relevant to our understanding of the invasion process, given that most studies of the invasion process to date have concerned data from European-driven introductions in the Victorian era. In particular, language barriers mean that information from Eastern societies has been much less accessible to the majority of scientists studying invasion biology, who are mainly based in the West. Introductions during the Great European Diaspora are likely to be very different in time, space and motivation from introductions in the Eastern context. Therefore, the data that are used in large-scale comparative analyses may be biased. It follows that the conclusions drawn from the invasions driven by Western processes may not be applicable to the Eastern societies, since invasions in Eastern Asia may be driven by different processes and concern different species.

The social demand for birds is certainly different between Eastern and Western countries. Unlike the common movement for food, game hunting and ornamental purposes in Europe, birds can be traded in East and East-South Asia also for hobby, entertainment (singing competition), magic (occult) practices, traditional medicine and religion (Nash 1993; Shepherd et al. 2004). It is very popular to keep pet birds as a hobby in China and Indonesia. In China, it is common to walk birds in a cloth-covered bamboo cage. In

Indonesia, species such as Crows (*Corvus sp.*) are used in magic practices; Black-naped Oriole (*Oriolus chinensis*) is used as traditional medicine for pregnant women, who believe that it would make their babies prettier; Java Sparrow (*Padda oryzivora)* and Wagtails (*Motacilla* spp.) are used for animal releases (Shepherd et al., 2004; Environment and Animal Society of Taiwan (EAST) 2004). Singing competitions are common in China and Thailand. In Thailand, the Zebra Dove (*Geopelia striata*) is used in singing competitions and its high demand is due to the fact that its song is considered to be superior. In Songkla province, 80% of villages are involved in dove breeding. In seven provinces of Thailand, the income from dove trading is approximately US$3,900,000 (Nash 1993). The high demand results in large volumes of birds being imported to fulfil the social demands (Shepherd et al. 2004; Jepson and Ladle 2005). Overall, the neglect of transport and the associated potential for introductions driven by the demands of other societies from other regions and periods in time may cause significant biases in the view we have of what makes an introduced species.

1.1.4 Establishment and Spread

Once a species is introduced, it then faces several challenges before it can be considered to be a successful invasive species. Introduced species first face the challenges of survival and reproduction in the establishment stage. Once the population is successfully established, the next challenges relate to the ability of the population to spread and to cross the environmental barrier in the spread stage (Blackburn et al. 2009b).

Introduced species can fail to establish either because they fail to survive in the new environment, or because they can survive but fail to reproduce. Those that survive and reproduce successfully will either move on to the spread stage if the population is self-sustaining, but can remain in the establishment phase, or even fail to establish if survival and reproduction are not sufficiently high for the population to be self-sustaining (Davis 2009; Blackburn et al. 2011). Thus, certain individuals may manage to survive and reproduce in a new environment, but the population could still fail to establish unless it is supported by a regular supply of propagules from external sources. If the population does become self-sustaining, then it can enter the final invasion stage: spread. At this stage, the established species faces barriers to dispersal, and environmental barriers to establishment in new areas following spread. When an individual survives and spreads to a new habitat, the greater the distance an individual spreads, the greater the likelihood that the species arrives to a different habitat to where it had been originally introduced and established. The new environmental conditions could be more suitable to species or more hostile. However, in spreading further, a species will very likely eventually face an unsuitable environment that provides a limit for species dispersal.

Factors that influence the success of species in the establishment stage can be classified into three categories: species-level, location-level and event-level features (Blackburn et al. 2009b). Species-level factors include body mass, geographic range, origin of species, reproductive rate, whether migratory or not and species adaptability to introduced site. Location-level factors are for example, native biotic composition and climate in which species are introduced. Event-level traits are those factors that associate with the given introduction event, such as the number of individuals released, the frequency of releases, sex ratio, the time or weather when species are released and the condition of released species (Blackburn et al. 2009b). Event-level factors highlight that success at the establishment stage can vary even for the release of a given species to a given location, and hence is a stage where the focus is on the success of populations rather than species.

The factor that is argued most strongly to determine success in population establishment is in fact an event-level variable, introduction effort or propagule pressure (Lockwood et al. 2005). Propagule pressure is a measure of the frequency and number of individuals released into a site where the species is alien (Lockwood et al. 2005; Wilson et al. 2009). Propagule pressure is made up of two components: propagule size indicates the absolute number of individuals in a release event and propagule number specifies the number of separate release events (Lockwood et al. 2005). The higher the propagule pressure, the more likely it is that a species will succeed in establishment (Kolar and Lodge 2001). For example, releases of bird populations of more than 100 individuals resulted in 83% success in establishment in New Zealand, whereas only 21% success was reported for releases of fewer than 100 individuals (Green 1997). Cassey et al. (2004) analysed more than 600 bird introduction events at the global scale to show a strong correlation between propagule pressure and introduction success. Larger numbers of released alien individuals improve the ability of a population to avoid problems due to small population, such as demographic or environmental stochasticity or lack of genetic variation (Lockwood et al. 2005).

Success in establishment is also affected by species-level and location-level factors. For example, body size has been suggested to be a factor (Cassey 2008), while other factors, such as life-history strategies, larger propagule size, brain size, habitat generalism, island introduction or non-migratory status may also influence the probabilities of success in species establishment (Cassey 2008; Sol et al. 2012). In fact, bird species with smaller body size across taxa, but larger than other related species, are more likely to succeed in introduction (Cassey 2008). The success in small body size across taxa may result from species features or greater human effort. These species features include faster reproductive rate and shorter generation times of smaller bird species, as such species can grow their initially small population size faster. However, introduction effort was found to be greater in species with smaller body size in New Zealand (Cassey 2001; Cassey 2008). Introduction success may also depend on the native geographic range size of alien species, and on their adaptability or tolerance to a new environment (Blackburn and Duncan 2001b). Species with wider geographic range should have better tolerance to new environments, because a wider geographic range size implies that a species is not likely to be limited to a specific habitat, whereas is more likely to have ability to cope with multi-habitats (Blackburn and Duncan 2001a).

In terms of location-level factors, the origin of the species may at least partially determine the success of establishment (Green 1997; Blackburn and Duncan 2001a; Kolar and Lodge 2001). For instance for birds, the smaller the difference in latitude between native and alien ranges, the more likely the success of the introduction, as minor differences in latitude from the original location may still share similar climates and/or environments with the site of origin. This may reduce the need for major changes in foraging, or the likelihood of coming across new predators. In this latter respect, biotic resistance is also correlated to the success in establishment (Duncan et al. 1999; Kolar and Lodge 2001; Blackburn and Duncan 2001b; Blackburn and Duncan 2001a). For example, native predators provide resistance to some marine invertebrates at the establishment stage: introduced European Green Crab (*Carcinus maenas*) appear to be affected in their abundance and geographic range size by the predation from native Blue Crab (*Callinectes sapidus*) in eastern North America (DeRivera et al. 2005). Furthermore, alien birds are more likely to fail in establishment on islands where larger numbers of predator species have been introduced (Cassey et al. 2005b). Biotic resistance appears to affect introduction success on continental mainlands, or in the tropical zones (Blackburn and Duncan 2001a). It seem clear that species-rich continents and tropical regions should provide higher biotic resistance, but the lower number of alien species there seem mainly result from a lower likelihood of introduction to those areas. In fact, Blackburn and Duncan (2001b) showed for birds that the probability of establishment is highest for the species-rich Afrotropic and Central/South America.

1.2 Potential Drivers of Eastern Invasions

Prayer Animal Release

In East Asia and South-East Asia, one of the demands for animals is religion, which leads to a particular biological invasion pathway called “prayer animal release”. Prayer animal release is the practice of releasing animals as a form of prayer, and it has been commonly practised in these regions (Severinghaus and Chi 1999; Environment and Animal Society of Taiwan 2004).

The present day custom of prayer animal release has a long history in Eastern religious philosophy, primarily associated with Buddhism. Buddhism was introduced into China during the Han dynasty 206 BCE – 220 CE, however the custom of animal releases appeared even before Buddhism was introduced (Han 2005). The concept of animal release was originally simply to set free animals, often found randomly, which were suffering, harmed or destined to be slaughtered. This custom in China was broadly influenced by the philosophies of Taoism and Confucianism. Taoism is a philosophy and a religion founded during the Warring States period in China (4th to 3rd centuries BC) that has profound influences on Chinese culture, especially on attitudes to the nature. In Taoism, all beings are equal to humans under the Tao - the principle and essence of all existence. Confucianism originates in the teachings of Confucius, 551–479 BC, (Legge 1861), one of the leading philosophers of China, who greatly influenced Chinese culture and attitudes to nature. In his opinion, nature should be cherished and animals should have the opportunity to survive. Mencius (Legge 1895), a philosopher of Confucianism, wrote that: “Having seen them alive, he cannot bear to see them die; having heard their dying cries, he cannot bear to eat their flesh…” (Legge 1895). In addition, in Chinese folk religions, all beings have spirits and all have a possibility of becoming gods, such as fox spirit, turtle spirit, tree god, or river god. For this reason, animal killing is a sin and is thus forbidden.

The custom of animal release has also been adopted by Mahāyāna Buddhism, one of the two main branches of Buddhism today. Mahāyāna Buddhism originated in India and spread to various states in Asia. The Buddhist religious text *Brahmajāla Sutra* adapted the Chinese culture of filial piety into the practice of animal release (Cho 2004). Different Buddhist traditions follow different precepts. *Brahmajāla Sutra* identifies 10 major and 48 minor precepts. To refrain from killing living beings is one of the major precepts, while minor precepts cover the concepts of failing to rescue, eating meat and causing harm to living creatures. Therefore, one should rescue and set free animals if they are seen to be suffering. Compassion to living beings can be found in many other religious teachings. For instance, Zhiyi, (538-597 AC) the major founder of the Tiantai School of Buddhism (Ziporyn 2003) suggested that the emperor should limit hunting and fishing. It is said that he then went to explain the *Golden Light Sutra* to fishermen, with the result that the fishermen changed their occupation. The essential idea that nature should be cherished is therefore linked to the idea of animal release in Buddhism.

Given that one of the main precepts of Buddhism is to respect life and stop killing, the custom and value of animal release fused gradually with the belief of causality (karma) in the doctrine of Buddhism (Yan 2005). Karma originated from Indian religious thought, and is the cosmic principle according to which each person is rewarded or punished in one incarnation according to that person's deeds in the previous incarnation. Karma expresses the idea that an individual’s deeds and thoughts have consequences, and these consequences are apparent to the individual in their current life, in the afterlife, or in future lives where there is a belief in reincarnation. Positive deeds or thoughts are believed to result in positive consequences, and negative deeds in negative consequences. Hence, every action or thought of an individual creates either good or bad karma, which is reflected in an appropriate result in the current or eternal life.

One way to generate positive karma is to release life back to nature, as a form of prayer to the gods in the hope of achieving enlightenment. This is one of the main reasons why participants partake in animal release practises. In the *Great Treatise on the Perfection of Wisdom* (the genuine author of this ancient Indian sutra remains unknown, though it is commonly believed to be the work of Nāgārjuna (150–250 CE) and translated into Chinese by Kumārajīva (344–413 CE), it is said that the greatest meritorious action is the liberation of life. The notion of releasing animals is therefore mediated by virtue, and stems from respect and compassion for life and nature. In theory, such a deed should be committed out of selflessness (Shi 1991) and the life should be released out of sympathy. An example would be to buy and release fish destined to be killed in markets. The structure of animal release was later improved in the *Text of the Animal Releases* by Zhili (960-1028 AC), of the Tiantai School; and in the *Release of Animal Ritual* by Yunqi Zhuhong (Ming Dynasty 1368–1644 AC). These texts provided the basic ideas for animal release ceremonies, which were refined later.

The first animal release organizations can be traced back to Ming Dynasty. Yungi Zhuhong established two animal releases societies in China: *West Lake Society* and *Great Compassionate Society.* However, the features of such societies during the Ming Dynasty resembled regular meetings, akin nowadays to workshops or discussion groups. A better-structured animal release society called *Great Lotus Society* was established after the *Great Compassionate Society* closed. This society was well organised, held regular meetings and drafted its own conventions. For example, everyone had to prepare prayer animals at specific times and locations, otherwise they would be fined. The fines collected were in turn to be used to purchase prayer animals for the next meeting. The structure of the animal release ceremonies carried out by the *Great Lotus Society* followed the text of the *Ritual of Animal Release.*

The *Text of the Animal Releases* and *Release of Animal Ritual* have now become the main reference texts for present day animal releases. Animal releases are currently common in Malaysia, Thailand, Cambodia, Vietnam, Hong Kong (China), Korea, China and Taiwan (Severinghaus and Chi 1999; Environment and Animal Society of Taiwan 2004; Chan 2006; Liu et al. 2012). The details of the ceremonies vary from event to event. For example, some animal releases can be large-scale in abundance of prayer animals yet without accompanying ritual ceremonies or with very simplified ones; some releases may only involve a part of a large ritual for prayer animals; other releases can involve a few species but involve a complete ritual ceremony (Environment and Animal Society of Taiwan 2004). In China, releases may be to special purpose-built release ponds: man-made or natural. The first records of release pond records date back to the Han dynasty (206 BCE – 220 CE), and they were actively built by kings of the Han and Tang (618 CE-907 CE) dynasties (Han 2005). Animal releases and release ponds were supported by the government in China during Tang, Sung and Ming Dynasties. Zhiyi built an animal release pond next to a temple, and since this time, many temples have built animal release ponds on their properties. While there are still ponds and parks designated for animal releases, however, it is more common now to release animals to the wild, such as mountains, rivers, and coasts. In China, Hong Kong, Singapore and Taiwan, release events are mostly practiced in the wild, and thus animals are released into most available habitats (Environment and Animal Society of Taiwan 2004; Chan 2006; Lee 2011). The potential for invasion if the animals released are not native species is clear.

Bird Keeping

Bird-keeping is a popular hobby and an expression of social status in many Eastern Asian countries, such as Indonesia, Malaysia, Thailand, Vietnam, China, Hong Kong (China) and Taiwan (Nash 1993). To own rare or difficult to obtain species is can be particularly important in this regard. The culture of bird-keeping in Taiwan (the location for my study; see section 1.3) is strongly influenced by other nearby countries, in particular by China. Therefore, bird-keeping in Taiwan and China have similar features. In China, bird species have been commonly described in literature, and feature in symbolism. In the Qing dynasty (1644-1912), birds could symbolize social status, and were used as an identification of bureaucratic rank. In the current Chinese bird market, the most popular songbirds include Mongolian Lark *Melanocorypha mongolica*, Chinese Hwamei *Garrulax canorus*, White-eye species *Zosterops japonicus* (include several *Zosterops* spp.) and *Luscinia* spp. (Siberian Rubythroat *Luscinia calliope* and Bluethroat *Luscinia svecica*) (Xu and Dong 2007). In Taiwan, similar species are also in demand (see e.g. chapter 4).

Bird Singing Competitions

In addition to rare and ornamental species, songbirds are also popular for bird-keeping, and further, singing competitions are also very common in these countries. In these competitions, birdcages are hung outside onto frames or poles, and birds are judged based on the variety and volume of their songs. They are often also judged on other features that are not song related, for example their physical conditions and whether they are stable in the cages. Although the basic contexts of bird-keeping and singing competition are similar between Eastern countries, different countries or areas typically have their distinctive features. For example, different countries prefer different species for the contests, such as Zebra Dove *Geopelia striata* in Thailand (Nash 1993) and the Japanese White-eye *Zosterops japonicus* in Taiwan. The Taiwan Hwamei *Garrulax taewanus* used to be the most popular species in the competitions in Taiwan. However, since it is now listed as a protected species in Taiwan, the most popular species found in the competitions now are White-eye species *Zosterops japonicus* (and other *Zosterops* spp.). Nevertheless, different competitions can involve different species, such as Atlantic Canary *Serinus canaria* and White-rumped Shama *Copsychus malabaricus*. The prices of the winning birds in singing competitions usually are more expensive.

1.3 Taiwan as a Case Study of Eastern Pathways to Invasion

This study will explore Eastern pathways to invasion, using Taiwan as a case study (see Figure 1.2). Taiwan is an independent state in East Asia has n area of 36,193 km^2. It is located on an isolated island spanning 22°N - 25°18'N in latitude, and 120°27'E-122°E in longitude. The island has mountainous geography, ranging in altitude from sea level to a maximum elevation of 3952m, and 59% forest cover (Forestry Bureau 2010). It includes subtropical (in northern and central regions) and tropical (in the southern region) climates, with a highland climate in the mountains. In 2014, the average annual temperature was 23.6°C, and annual average precipitation was 2,207 mm (Central Water Bureau 2015). The Taiwanese bird list totals 626 species, of which many are vagrants, but also includes 25 species and 58 subspecies endemic to the country (Ding et al. 2014). I divided the study area into a total of 409,133 grid cells (300m x 300m, the finest scale of available maps used in Chapter 6).

Taiwan presents four main advantages to this study: the diverse culture related to birds that drives the trade in these species, the frequency of animal releases, Taiwan's island geography, and a good background of previous scientific research on alien species.

First, the main religions in Taiwan are Buddhism (Mahāyāna Buddhism), Taoism and I-Kuan Tao, all of which engage in prayer animal releases (Chen 1995; Severinghaus and Chi 1999; Lin 2002; Chen 2010). There were 11,875 registered temples in Taiwan in 2010 (report of Ministry of the Interior, Taiwan 2010) and almost a quarter of these are believed to be involved in the prayer animal release practice (Environment and Animal Society of Taiwan 2004). Furthermore, bird-keeping culture is popular in Taiwan. Specialised poles are commonly found in parks for owners to hang their birdcages while taking their caged birds out for fresh air (known as bird-walking). Then the owners can find places around the cages to have tea with other owners as a social activity. Bird singing competitions are also fashionable in Taiwan. Often these may involve more than 1,000 competitors.

Second, animal releases are frequently practised in Taiwan. Forty percent of Taiwanese people believe positive karma can be obtained by releasing animals (Keown 1996). The concept of animal release is so strongly engrained in the culture that non-religious releases are also practiced commonly. Animal releases are commonly practiced by individuals, but are mostly organised and have gradually evolved into commercial and large-scale events, rather than a religious ceremonies (Environment and Animal Society of Taiwan (EAST) and Kaohsiung Teacher's Association 2004; Chen 2005; Han 2005). The frequency with which temples release animals can be very high. Some temples release animals daily, some once a week, some once a month, while others only release animals in significant numbers on Buddhist holidays (Environment and Animal Society of Taiwan 2004). It is believed that the more animals released, the better the deed, which in turn leads to large quantities of prayer animals being required for ceremonial animal releases. Organised animal releases occur more than 2.1 times a day, an average (Environment and Animal Society of Taiwan 2004). 9.30% of the Taiwanese population have experienced large-scale ceremonial animal releases (Chen 2005); 29.5% of Taipei citizens from a range of religions participate and spend an estimated US$ 6 million annually to set free around 200 million wild animals (Environment and Animal Society of Taiwan 2004; Chen 2005). One religious organization, the Chinese Association of Life Preservation released an estimated 14,474,275 animals to the wild in a span of three months (Environment and Animal Society of Taiwan 2004; Yan 2005).

Animal releases are criticized as sources of alien species (Severinghaus and Chi 1999; Severinghaus 2003). Religious adherents counter that prayer animals are mainly wild-caught, and therefore the majority of prayer animals are native species. For example, 57 prayer species recorded in Phnom Penh are all native to Cambodia (Gilbert et al. 2012). However, the case may not apply to Taiwan. Although prayer birds tend to be caught from the wild, alien species have certainly not been excluded. A comparison between available data confirms that trend: Among the 41 prayer species defined in the report of Environment and Animal Society in 2004, in Hong Kong, 23 of 41 prayer bird species were found to be alien to Hong Kong (Chan 2006); similarly in Taiwan, there were 20 prayer species alien to Taiwan; and 6% of prayer birds in stock (n = 68,538) for sale were alien species (Severinghaus and Chi 1999), thus prayer birds are not all native to Taiwan as adherents claimed. Moreover, an online survey conducted by Taiwan Environmental Info Association in 2004 showed that 7% of alien pet bird owners have intentionally released their pets as prayer animals. It appears that native-only species ritual releases do not occur in Taiwan. Such releases may be a source of many of the alien bird populations in Taiwan.

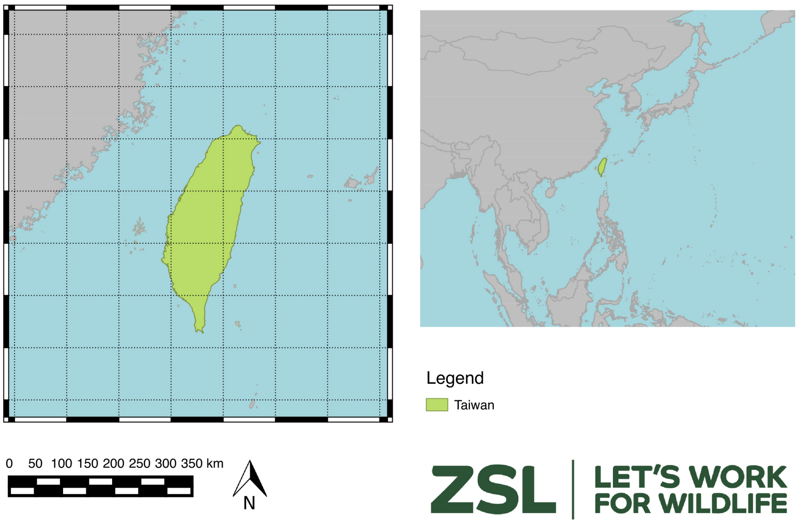

Figure 1.2 The location of Taiwan. Only the Island of Taiwan (the study site) is coloured green, other Taiwanese islands are coloured grey (as other countries). Maps were developed with QGIS 2.8.2-Wien.

Third, Taiwan is an isolated island, separated from the nearest continental mainland by >100km of open ocean. Hence, the geographical context of the research is well defined. Moreover, Taiwan's isolation means that opportunities for alien species to colonize are limited to those that are directly imported, and that the invasion stages will be relatively simple to define. (Note that this study considers introductions and invasions to the Island of Taiwan (see **Figure 1.2**): forming 99% of the land area of the country of Taiwan, and so excludes other Taiwanese islands, such as Penghu, Kinmen, Matsu and other minor islands.)

Finally, Taiwan has a strong history of scientific research on the bird trade, providing the background context for the research in this study, in particular the comprehensive pet trade surveys across Taiwan by Chi (1995) and Shieh et al. (2006). The legislation of the Wildlife Conservation Act in Taiwan was enacted on 23/6/1989. Sale of rare and endemic species is under a relatively better control than common species under the terms of this act. However, common species are still purchased in the bird market (Severinghaus and Chi 1999). The available surveys of pet shops in this thesis (Chi 1995 and Shieh et al. 2006 and my survey) were conducted after the legislation was enacted.

Chapter 2 Methods

As my thesis depended a lot on the data for bird species for sale in the bird market in Taiwan, non-structured interviews were conducted to obtain three core pieces of information from each shop for analyses: the identity of the species available, the number of birds of each species presented for sale in the shop, and their price. The survey was conducted from August to November of 2012.

2.1 Data Collection

2.1.1 Pet Shops Surveys

Data on pet shops and their locations were obtained through county and city government records in Taiwan and web databases. Information on registered pet shops was obtained from databases in the Commerce Industrial Services Portal and Yellow Pages, whereas information on non-registered pet shop and mobile hawkers was obtained from pet shop related blogs. The total number of recorded registered, mobile hawker and non-registered pet shops in Taiwan identified in this way was 154. This total excludes game pigeon shops, pet product-only shops, and aquarium pet shops. The resulting list differs substantially from that given in the previous empirical survey of bird species for sale in pet shops in Taiwan in 1995 (Chi 1995) as most of the shops surveyed then had subsequently closed down.

The survey was conducted in pet shops in Taiwan from August to November 2012. A total of 90 of the 154 pet shops were selected, including shops in 7 cities. A significant number of the pet shops were located in the vicinity of the main train station of a city. Therefore, the pet shops to survey were selected primarily by whether they were reachable within one hour from the main train station of a city, either by driving or public transportation. Eighteen of these shops had closed down or were run by owners who declined to respond to the survey. Therefore, the successfully surveyed sample comprised of 72 pet shops, or just under half of all shops identified in Taiwan. Of these 72 shops, 32 were in Taipei (mostly in Wan-Hua (Bird) Street), 7 in Hsinchu City, 11 in Taichung City, 1 in Taitung City, 14 in Kaohsiung City, 5 in Pingtung County, and 2 shops in Hualien City. All pet shops were visited once, apart from the selected pet shops in Taipei Wan-Hua Bird Street located in the central part of Taipei City. Wan-Hua Bird Street is the biggest bird market in Taiwan, with more than 15 bird shops which include three different main pet shops types in Taiwan: prayer bird shops, songbird shops and parrots shops. The type of the shop can be identified from the name of the shop and on the basis of the stock held: prayer bird shops display large volumes (100s) of a few key species with low price per bird, such as Red Collared-Dove *Streptopelia tranquebarica*, Light-vented Bulbul *Pycnonotus sinensis*, Japanese White-eye *Zosterops japonicus,* Scaly-breasted Munia *Lonchura punctulata,* White Wagtail *Motacilla alba*, Indian Silverbill *Lonchura malabarica* and Myna species. Some of them can cost less than US$1. Songbird shops seem to specialise in songbirds, especially in White-eye species. These singing birds are sold for a much higher price than an average bird price in pet market. Parrot shops were likely to specialise in parrot species with a wide range and higher cost.

Due to time constraints, the size and the significance of this bird market, I surveyed a number of selected pet shops in Wan-Hua Bird Street twice: in August and in November 2012.

Ethics approval for the study was given by the ZSL Ethics Committee. The non-structured interviews of the shop owners did not involve questions about their personal information or identity. This is because the sources of birds in trade in Taiwan are frequently illegal, and therefore owners will not provide signed documents and/or written consent. I aimed to record information on the numbers of species, their identity and their price in the shops, and I obtained shop owners' verbal agreements to obtain such information. The consent procedure was documented in writing by myself and had been approved by the Ethics Committee.

2.1.2 Semi-Structured Questionnaires for Pet Shops in Pilot Study

My initial aim was to obtain a clear picture of the bird trade market and its species combination in Taiwan. To this end, I drafted an open-ended structured questionnaire composed of 13 questions to obtain information about the sources of birds and details of the stock. To test the feasibility of this open-ended survey, I used the first 2 weeks of the available 13 weeks survey period to carry out a pilot survey in 13 randomly selected pet shops in Taipei. However, the targeted interviewers of all selected sites declined to cooperate, possibly because of the illegal nature of parts of the trade and the level of detail sought regarding the origin of the stock (it is likely that some of those were obtained from illegal sources). Therefore, I changed my approach from a structured survey to a non-structured interview to obtain the information from each shop: the identity of the species available, the number of birds of each species presented in the shop, and their price for sale.

2.1.3 Strategy and Data Limitations

To obtain these key pieces of information, in each shop visited I first asked the owner about the identities of the species offered for sale and their price, and then counted the number of birds of each species for sale by direct observation. I wrote down the name of the species presented in the shop including those that were consigned to the shop for sale and also those that were claimed to be the owner's pet birds (and hence not for sale). Species were declared as not-for-sale possibly due to regulatory concerns; nonetheless, owners will also give a price for the not-for-sale birds, if asked. Price can vary within species in the same shop; which is due to special qualities of the priced individual, such as skills, sex, age and colour morphs. For example, those birds that can speak words, recognize people or that are trained to hop from finger to finger would cost more. For many singing birds, the male is typically preferred in the bird market for their songs attractiveness; age also can affect the price charged because it is usually linked to other abilities, such as song or plumage quality, which improve with age. When the price was varied within a given species in the shop, and the owner didn't disclose the price for each individual, I recorded the price range.

I conducted counts of individuals of all species, except for Red Collared-Dove *Streptopelia tranquebarica*, Light-vented Bulbul *Pycnonotus sinensis*, Japanese White-eye *Zosterops japonicus,* Scaly-breasted Munia *Lonchura punctulata,* White Wagtail *Motacilla alba* and Indian Silverbill *Lonchura malabarica*. For these species, large numbers of birds were stored in standard wooden boxes with small windows, through which enough could be seen to identify species, but not to count them (**Figure 2.1**). These boxed birds were commonly sold by the box, with the number of birds in the box more or less fixed. Thus, when birds were available for sale in the standard wooden boxes, I enquired about the number of birds per box to the owner and then counted the number of boxes, which contained birds to arrive at a total count for that species in that shop. In some cases, birds were stored in regular cages that would have made a count possible, except that the cages were piled up densely (**Figure 2.2**). In such cases, I counted the number of birds in a cage and multiplied by the number of cages presented. Some pet shops can stock up to 4,000 individuals of the six listed species, and a box or cage count is the only way to obtain a reasonable estimate of the total.

My enquiries revealed that some of the pet shops (particularly prayer bird shops) get their bird supplies in the morning about once a week, or even daily for some species.

However, due to time constraints, the survey did not standardise the visiting time, which could therefore result in some inaccuracy in the bird count.

Figure 2.1 Prayer birds boxes. From left to right: a) the standard wooden bird boxes with small windows; b) Bird boxes placed on the alley after stock turnover.

Figure 2.2 Birdcages can be piled up densely, with large numbers of birds per cage. Right picture: Japanese White-eye *Zosterops japonicus* in a cage in a prayer birds shop.

2.1.4 Species Identification

I identified all taxa to species-level with the exception of two Myna species (Javan Myna *Acridotheres javanicus* and Great Myna *A. grandis*), three White-eye species (Oriental White-eye *Zosterops palpebrosus,* Lowland White-eye *Z. meyeni* and Japanese White-eye *Z. japonicus*) and all colour-morph lovebirds. The Mynas are commonly sold in mixed species cage of more than 50 individuals per cage, with up to 500 birds in stock at any one time. These cages are densely packed with birds, and often piled up (**Figure 2.2**), making species-level identification difficult. The three White-eye species were only identifiable to species-level by the owner, but this identification is unreliable due to the illegal sources of some White-eye species. The Lovebird species have a number of colour morphs bred in captivity in Taiwan, which makes the identification of the original species concerned complicated and more or less impossible from visual observations. I therefore recorded individuals of these species as Myna spp., White-eye spp. and Lovebird spp., respectively.

When pet shop owners did not or were not prepared to divulge the identification of birds in their stock, or in cases where I did not directly interview the owners, I identified species using field guides, in many cases taking photographs to aid the identification process. The guides used were: Birds of East Asia (Brazil 2009), Wild Birds of Taiwan (Liao 2012), Birds of China (MacKinnon 2000), Birds of Australia (Simpson et al. 2010) and Birds of East Africa (Stevenson and Fanshawe 2002). Some difficult to identify species were identified from photographs by T.M. Blackburn, using the books listed in Appendix A.

I used data from Jetz et al., (2012) to give the global taxonomic list for 9,993 extant bird species. The scientific name of these species followed Birdlife Version 3 and IOC Version 2.7 taxonomies, family names were following the Birdlife guide and the order names followed Sibley & Monroe (1990) (Jetz et al. 2012). The native or alien status of the bird species in Taiwan was defined based on the CWBF Checklist of the Birds of Taiwan (Chinese Wild Bird Federation 2012, Ding et al. 2012); the list was adjusted to exclude those transient migrant, pelagic seabird and vagrant by T.M. Blackburn.

2.1.5 Literature Data

Data from my survey were compared against existing data from two previous surveys:

(1) Chi (1995): the survey was conducted in 164 pet shops across cities in Taiwan in 1995. The focal birds include both native and alien species; it also recorded the total numbers of birds displayed in the shops.

(2) Shieh et al. (2006): an alien pet survey conducted in 2004, which included information the identity of 239 alien species for sale from 146 surveyed shops in Taiwan.

Chapter 3 Transport: Patterns of Non-randomness in the Composition and Characteristics of the Taiwanese Bird Trade

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3.1 Abstract

The invasion pathway is composed of a sequential series of stages that need to be quantified separately in order properly to understand the invasion process. This study examines the composition and characteristics of bird species being sold in the pet bird market in Taiwan. The bird trade in Taiwan is of high volume and financially lucrative. The identity of species in this trade is vital for informing later stages (introduction, establishment, spread) of the invasion pathway. I conducted interviews and surveys of 72 outlets selling pet birds from 7 cities across Taiwan, from which 247 bird species were identified (within 34 families) for sale. Of these, 170 bird species (from 27 families) are alien to Taiwan. Using randomization tests, the results show that nine families are significantly over-represented in the pet trade (Psittacidae, Muscicapidae, Timaliidae, Sturnidae, Turdidae, Estrildidae, Chloropseidae, Zosteropidae and Fringillidae), and three after sequential Bonferroni correction (Psittacidae, Muscicapidae and Sturnidae). Species that have been identified in Taiwanese pet shops tend to have a larger native geographic range, originate further from the equator, are smaller-bodied, and have more aesthetically-pleasing songs than expected by chance. The native ranges of pet shop species are more likely to be situated in the Indo-Malay and Palearctic biogeographic realms, while fewer species than expected derive from the Neotropic, Afrotropic and Nearctic realms. The results show that bird species for sale in Taiwan are determined by the interaction of species availability and societal demands.

3.2 Introduction

Alien species (also termed non-native, non-indigenous or alien) are species that have been moved beyond their native geographic range by human activity (Richardson et al. 2010;

Blackburn et al. 2011; Heger et al. 2013). Invasion by alien species represents one of the primary threats to the maintenance of global biodiversity, human health, and economic enterprises (Kolar and Lodge 2001; Fisher and Owens 2004). The best way to minimise their impact is to prevent new invasions taking place and to understand the factors that facilitate certain species to be introduced, established and spread into foreign environments.

The invasion process can be divided into a series of stages that are separated by barriers for an individual (or a population) to overcome (Williamson 1996; Blackburn et al. 2011). The stages (with barriers) defined in this scheme are: transport (geography), introduction (captivity or cultivation), establishment (survival and reproduction) and spread (dispersal and environmental). Only if an alien species passes through every stage can it be classed as an invasive. The early stages of invasion are particularly important in understanding the invasion process as a whole (Blackburn and Duncan 2001b; Cassey et al. 2004b; Jeschke and Strayer 2006; Blackburn and Cassey 2007), because they act as filters for species entering the later stages: species only get the chance to establish and spread if they are first transported and introduced. This means that the early part of the invasion process may substantially affect the outcome of the later part. For this reason, there is a growing interest in understanding which species are entrained onto the biological invasion pathway (Blackburn and Duncan 2001b; Duncan et al. 2003; Kark and Sol 2005; Blackburn and Cassey 2007). Here, I consider this issue in the context of the potential pool of bird invasions in Taiwan.

Bird species may be moved beyond the limits of their natural distributions for a variety of reasons, such as game hunting, commerce, food supply, aesthetic purposes, nostalgia, conservation, religious beliefs and ornamentation (Lockwood et al. 2007; Blackburn et al. 2009b). Most of the previous studies of the early stage of the invasion pathway for birds have been carried out in a Western context (Kolar and Lodge 2001; Cassey et al. 2004a; Jeschke and Strayer 2005; Jeschke and Strayer 2006), largely concerning species moved in association with the Great European diaspora (Crosby 2004). These studies were based on historical events because these data have been the most readily available. (Long and Agriculture Protection Board of Western Australia 1981; Lever 1994), and perhaps because fewer birds are imported nowadays to and from Western countries due to import and export bans (Cooney and Jepson 2005; Brooks-Moizer et al. 2008). However, the contemporary movement of birds may be driven by very different influences compared with that of previous centuries (Blackburn et al. 2009b). For example, there is a large trade in birds in Eastern societies, such as Vietnam, Indonesia, Malaysia, China, Hong Kong (China) and Taiwan (Lau et al. 1996; Jepson and Ladle 2005; Shepherd

2006; Shepherd et al. 2012). In comparison to the Acclimatization and Wildlife society introductions performed by some Western countries, the reasons for trading birds in Eastern cultures are very different. Rather, they are due to the region's unique culture with respect to the use of species for bird competitions, bird-keeping, and prayer animal release (animals released for religious reasons). The scoring factors in bird competitions frequently include song quality and bird condition (e.g. plumage, shape and stability); therefore such competitions are platforms to improve owners' training skills, to enhance birds' prices and to entertain bird-lovers. Bird-keeping is rooted deeply in East Asian culture (Jepson and Ladle 2005). It is often associated with a hobby of 'bird-walking', where owners air their caged birds outdoors, and hang these cages in especially designated areas, for social purposes. These factors have attracted relatively little attention, which may be due to the fact that information on alien species in East Asia is under-represented in the English-language (or other European language) literature. Thus, our understanding of which species are initially entrained on the invasion pathway may be biased.

The aim of this study is to assess the composition of species in the current cage bird market in Taiwan. The study focuses on Taiwan because it represents an excellent case study of the Eastern bird trade culture, where bird competitions, bird-keeping behaviours and prayer animal releases are commonly practiced. It is also one of the main importers of species re-exported by other Asian countries, such as from Malaysia and Singapore (Nash 1993; Severinghaus and Chi 1999; Shepherd et al. 2012). Moreover, because of its island geography (separated from the mainland of the nearest country by >100km of open ocean), the geographic condition of introduction can be precisely defined.

The bird trade is of high volume and financially profitable in Taiwan. Birds are bought for their superior songs, ornamented plumage, for bird contests and for prayer animal releases. Organised animal releases occur more than twice a day on average (Environment and Animal Society of Taiwan 2004), and almost 30% of Taipei citizens, from a variety of religions, participate and spend an estimated US$6 million annually to set free around 200 million animals for prayer animal release (Environment and Animal Society of Taiwan 2004; Severinghaus and Chi 1999). Furthermore, 7% of pet birds were intentionally released to the wild by their owners (TEIA 2004). Previous studies have shown that more than 90% of species recorded in the Taiwanese bird market are alien (Taipei Wild Bird Society 1996; Severinghaus 1999), and that more than 60% of alien species found in the wild were sold in the pet shops (Lee and Shieh 2005). The bird trade is likely a prominent source of species for invasion (Meyerson and Mooney 2007; Carrete and Tella 2008), especially given that higher propagule pressure and frequency of introduction events increase the potential of species to become invasive (Forsyth et al. 2004; Lockwood et al. 2005; Jeschke and Strayer 2006; Lockwood et al. 2007).

In this study, I conducted interviews in pet shops in cities across Taiwan to: 1) describe the composition of bird species available for sale in the current cage bird market in Taiwan; 2) assess whether bird species that are for sale in this market in Taiwan are a random selection of bird species with respect to taxonomy; and 3) test for non-random patterns in the cage bird fauna in Taiwan in terms of species characteristics. Specifically, I test for non-randomness in the native breeding range, latitudinal mid-point, biogeographic region of origin, body mass, and a measure of the (human-derived) attractiveness of song. This work focus on these characteristics, which, I predict, should determine why particular species are available in the trade market.

Species that are more widespread, and therefore more common (Gaston and Blackburn 2000; Blackburn et al. 2006), in their native range may be more likely to be traded, as they are more readily available for capture (Cassey et al. 2004a). I therefore predicted that birds in trade would tend to have larger native range sizes than expected by chance. There is a high demand for some particular species in the songbird market in China (e.g. Hwamei *Leucodioptron canorus* and White-eyes *Zosterops* spp.). Similar demand is likely to be observed in the bird market in Taiwan due to cultural similarities between the countries (Xu and Dong 2007). In addition, trade dealers may prefer species from closer regions, particularly if these species survive better during transportation to the shops in either the legal or illegal trade. For these reasons, I hypothesise that bird species available in the trade market will originate from closer regions, such as from East and South-East Asia. I test for origins of species using the latitudinal mid-point of their geographic range and their biogeographic region of origin.

Bird song is one of the main characteristics that drives the bird trade, as many species are traded for singing competitions in East Asia (Nash 1993). I predicted that species with songs that are relatively more attractive to people are more likely to be traded. I tested this hypothesis using a metric of attractiveness based on the frequency of song tracks lodged for a given species on the “Xeno-Canto” website (Blackburn et al. 2014b). For bird-keeping or bird-walking purposes, small-bodied birds are likely to be favoured, as they are more convenient to keep, feed and transport. Owners may also prefer convenient and transportable cages, in which they house a suitably sized bird for aesthetic purposes. Therefore, I hypothesised that small-bodied birds were more likely to be traded, and I tested whether cage birds in Taiwan are smaller-bodied than expected by chance.

3.3 Method

3.3.1 Data

I obtained data on the occurrence of bird species in pet shops from non-structured interviews with shop owners or staff between August and November 2012. Non-structured interviews were used because they present a better view of the species available for sale than official importation records, as the sources of animals in pet shops are frequently illegal (Shepherd et al. 2012). The capture of wild birds is restricted by the national Wildlife Conservation Act (but birds can be sold legally if they are not scheduled as protected species). Thus, when owners are aware that their animals come from illegal sources, they typically prefer to disclose the price only to a likely buyer. The aim of the non-structured interview was to obtain the identity of the species available from each shop (see more details in Chapter 2).

For each of the species recorded in the pet shops in Taiwan, I collated information on the following variables:

(1) Geographical range size (km^2): a measure of native geographical range extent (Gaston 1991; Gaston 1994a) was obtained from the data set used in (Orme et al. 2006). Total native breeding area of all species was measured as polygons and converted into equal area grids with a cell size of 96.3 x 96.3 km, which provided a scale identical to 1^o grids at the equator. The breeding area of each species was estimated by summing the areas of the cells in which they occurred (Orme et al. 2006; Blackburn and Cassey 2007). This information was available for 9,613 species, including all of the species in my survey.

(2) Latitudinal mid-point (degrees): The median latitude of the central cell grid in which that species occurs, from the geographical range size data. The absolute values of the median latitude points were used for analysis. This information was available for 9,613 species, including all of the species in my survey.

(3) Region of origin: the biogeographical region from which the native populations of alien species originate. Eight realms were defined using the World Wildlife Fund eco-regions map (Olson et al. 2001). Species were assigned to the region in which the largest part of their geographic range fell. This information was available for 9,677 species, including all of the species in my survey.

(4) Body mass (g): a measure of the body size of bird species from (Dunning 1992). Information on body mass is available for 7,433 bird species from (Dunning 1992) and for 202 of the total 247 (147 of the 170 alien) species recorded in my 2012 survey.

(5) Attractiveness of song: I used the number of song tracks lodged for the given species on the Xeno-Canto website (www.xeno-canto.org) to derive a metric of the attractiveness of bird song to humans (Blackburn et al. 2014b). Xeno-Canto provides more than 115,000 independent recordings of bird songs, which covers about 80-85 % of extant species, with up to 335 recordings per species. Song tracks were available for 245 of 247 recorded species with the range from 1-162 records. A general linear mixed model was used in R to model log number of songs lodged on Xeno-Canto as a function of log geographic range size (estimate ± s.e. = 1.16 ± 0.17). Geographic realm was included as a random effect, and the taxonomic factors order, family and genus as nested random effects to control for evolutionary relatedness among species in the model. The residuals from this model were calculated and used as the metric of song attractiveness controlling for the availability and taxonomy of species. Larger residuals have been shown to be associated with characteristics that may make songs more attractive to people (Blackburn et al. 2014b).

3.3.2 Analysis

A randomisation approach was conducted to test for the differences between the observed numbers of bird species within given families found in Taiwanese pet shops and the number expected if this species composition was a random selection of the world's bird species. The simulation involved picking 247 species from all of the 9,993 bird species, at random and without replacement, and then summing the number of these randomly selected species in each family. The simulation procedure was repeated 10,000 times in total to produce a frequency distribution of the number of birds in each family.

The observed species number within a given family is judged to be significantly greater than expected by chance ($\alpha = 0.05$) if a given number, S, of the randomly derived values for that family is greater than the observed value; and to be significantly lower ($\alpha = 0.05$) if the same given number (S) of randomly obtained values for that family is lower than the observed value, where S is calculated as $S=(\alpha/2) \times 10000$ (Rice 1989; Blackburn and Cassey 2007). These simulations were repeated just for alien species (n = 170), to test whether or not the results were influenced by the presence of native species. Because large numbers of families were compared, a sequential Bonferroni correction was applied to the significance level α, denoted β. First, the significance values (P-values) of each family were ranked from the smallest to the largest. The base value of α (0.05) was then divided by 2 for the two-tailed test, and divided by the sample size (n = 194 families) to give the adjusted significance value for comparison with the family with the smallest P-value, denoted β_1. The corrected value of α to compare with the second smallest P-value would be $\beta_2 = (\alpha/2) / (n-1)$, $\beta_3 = (\alpha/2) / (n-2)$, and so on (Rice 1989). Then, the observed P-value for each family is judged to be significantly greater or lower if the number (S_i) for that family is greater or lower than the relevant value of β. S_i can be expressed as $S_i=\beta_i \times 10000$.

The randomisation approach was used to address whether the bird species observed in the surveyed pet shops differed from a random sample of species in terms of native geographical range size (km^2; log transformed), latitudinal mid-point $\log_{10}$(absolute value + 1), eight biogeographic regions of origin, body size (g; log transformed) and song attractiveness (model residuals). For each simulation, 247 bird species were selected randomly and without replacement from the world's bird species, the geometric mean value was calculated, and the process repeated 10,000 times. These simulations were again repeated just for alien species (n = 170)

The simulation approach was repeated in each case constraining the family membership as well as the biogeographic origin of the species to that in the actual survey data. More closely related species are more likely to share the characteristics due to their evolutionary relatedness (Forsyth et al. 2004; Blackburn and Cassey 2007) and regions of origin. Thus the variation in trait values with respect to a random sample of birds may arise as a result of the non-randomness in the family and regional composition, rather than the traits favoured per se. All analyses were performed in R v2.15.2 (R Core Team 2014).

3.4 Results

My 2012 survey of Taiwanese pet shops recorded a total of 247 bird species from 34 different families. Of these, 170 species (from 27 families) were not native to Taiwan (**Figure 3.1**), while the remaining 77 species have either breeding or wintering ranges that include Taiwan. Nine families revealed a significantly (α = 0.05) greater number of species recorded in pet shops than expected if these species were a random sample of all birds (**Figure 3.2**), while seven families revealed significantly lower number than expected. Applying the sequential Bonferroni correction, three families had significantly higher numbers of pet species than expected by chance (Psittacidae, Muscicapidae and Sturnidae) and two significantly lower numbers (Tyrannidae and Trochilidae). The randomisation tests for alien species alone found that Psittacidae, Sturnidae and Chloropseidae were over-represented after Bonferroni correction, but no families were significantly under-represented (**Table 3.1**).

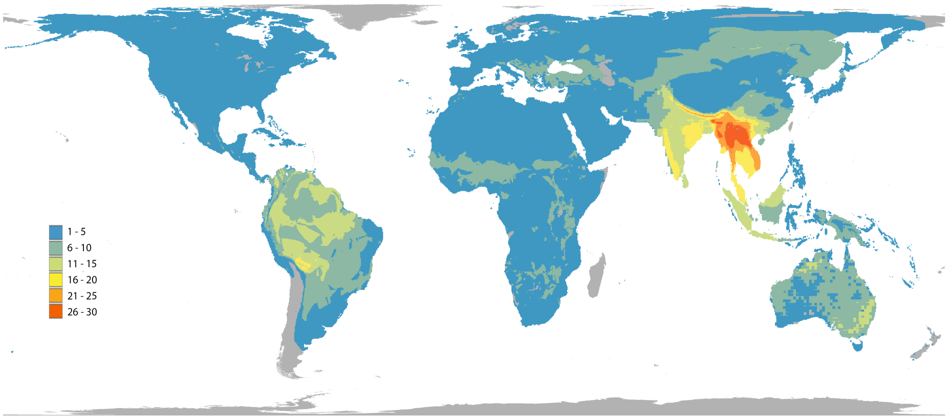

Figure 3.1 Areas with species richness for the alien species recorded in Taiwanese pet shops during the survey (n=170). The range of species richness is from 30 (the highest richness, red colour) to 1 (blue colour).

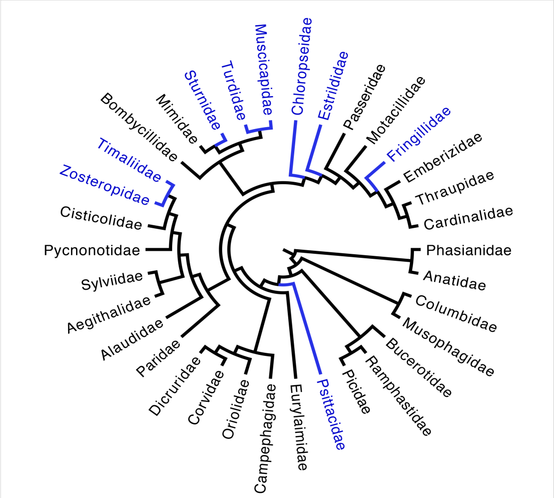

Figure 3.2 Species identified for trade in Taiwan (2012) were derived from 34 avian families. Nine of these families (marked in blue) have significantly (α = 0.05) higher than expected numbers of species in Taiwanese pet shops. The family level phylogenetic tree was constructed based upon the primary backbone tree of Hackett et al. (2008) in FigTree v1.4.0.

Table 3.1 Families with significantly (a) higher or (b) lower than expected numbers (Exp. number) of species in Taiwanese pet shops in 2012 (α = 0.05), for all species or with analysis limited to alien species (i.e. species not native to Taiwan). Median expectation (Exp. median) is taken over the 10,000 iterations of the randomisation test, while the 97.5th and 2.5th percentiles are the upper and lower limits within which 95% of the iterated values lie. Bonferroni corrected expectation (Exp. Bonf) shows the upper or lower limits of significance under the Bonferroni correction, only for those families that exceed those limits. Asterisks (*) denote tests for which a bird family has a significantly higher (or lower) observed number of species for sale in bird shops than expected. Observed numbers of species in the shops is denoted as Obs.

(a)

	All species				Alien Species only			
Family	Obs.	Exp. number	Exp. Bonf	Exp. median	Obs.	Exp. number	Exp. Bonf	Exp. median
Psittacidae	70	3-15*	1-20*	9	70	2-11*	0-15*	6
Muscicapidae	25	2-13*	0-18*	7	13	1-10*	0-14	5
Timaliidae	18	3-14*	0-18	8	4	2-10	0-15	5
Sturnidae	14	0-6*	0-10*	3	10	0-5*	0-8*	2
Turdidae	13	1-9*	0-15	4	10	0-7*	0-10	3
Estrildidae	11	0-7*	0-11	3	8	0-6*	0-10	2
Fringillidae	9	1-8*	0-11	4	7	0-6*	0-11	3
Zosteropidae	7	0-6*	0-9	2	5	0-5	0-7	2
Chloropseidae	4	0-2*	0-4	0	4	0-1*	0-3*	0

(b)

Family	Obs.	Exp. number	Exp. Bonf	Exp. median	Obs.	Exp. number	Exp. Bonf	Exp. median
Tyrannidae	0	5-17*	1-24*	10	0	3-13*	0-18	7
Trochilidae	0	3-14*	1-20*	8	0	2-11*	0-14	6
Thamnophilidae	0	1-10*	0-15	5	0	0-8	0-12	3
Strigidae	0	1-9*	0-14	5	0	0-7	0-11	3
Meliphagidae	0	1-9*	0-15	4	0	0-7	0-11	3
Furnariidae	0	2-11*	0-16	6	0	1-9*	0-12	4
Accipitridae	0	2-11*	0-16	6	0	1-8*	0-12	4

The geographic range size of the 247 pet shop species varies widely, from a minimum of 1,600 km^2 for Red-and-Blue Lory *Eos histrio* (Psittacidae) to 41 million km^2 for the Eurasian Tree Sparrow *Passer montanus* (Passeridae), with a geometric mean of 2.05 million km^2. The frequency distribution of these ranges is highly right-skewed, as most species have relatively small geographic ranges. The simulation test revealed an expected geometric mean range size of 0.59 million km^2 (99% confidence intervals (CI): 0.38-0.86 million km^2), meaning that the ranges of the species recorded in the survey are significantly greater than expected by chance. This is also true when the randomisation tests were constrained by taxonomy and region; expected geometric means of 0.42 million km^2 (99% CI: 0.28-0.59 million km^2) and 0.63 million km^2 (99% CI: 0.44-0.89 million km^2), respectively. The results also held when considering only alien species for sale in Taiwan (observed mean = 1.69 million km^2, expected mean = 0.59 million km^2, 99% CI: 0.37-0.88 million km^2), and for alien species when taxonomy (expected mean = 0.39 million km^2, 99% CI: 0.26-0.57 million km^2) and region (expected mean = 0.59 million km^2, 99% CI: 0.36-0.87 million km^2) were constrained.

The latitudinal mid-points of the 247 species ranged from 38.75°S for Red-Crowned Parakeet *Cyanoramphus novaezelandiae* (Psittacidae) to 64.28°N for the Little Bunting *Emberiza pusilla* (Emberizidae). The majority (76%) of the species identified in the 2012 survey originated from equatorial latitudes between 30°N and 30°S. The number of species generally declined as the absolute latitude increased; however, the mode of the frequency was between 20-30° of the absolute median latitude. This may be due to the influence of species native to Taiwan - if these are excluded, the mode lies between 5-10°. The geometric mean of the absolute latitudinal mid-point in the survey was 17.26° versus 12.04° (99% CI = 10.31-13.88°) from the randomisation test. Therefore, the origins of species recorded in the survey were significantly further from the equator than expected if pet shop species were selected by chance. This is also true when the randomisation tests were constrained by both taxonomy (99% CI = 10.18-13.43°) and region (99% CI = 11.89-15.36°), inferring that the results are not influenced by family composition or species origin. The geometric mean of the absolute median point for the alien species is 13.30°, which is not significantly different to the expected value of 12.04° (99% CI = 10.06 - 14.63°). Similar results were also obtained when taxonomy (expected mean = 11.41°, 99% CI = 9.67 - 13.39°) and region (expected mean = 12.64°, 99% CI = 10.85 – 14.84°) were constrained.

The largest bodied species in the survey was the Red-and-Green Macaw *Ara chloropterus* (Psittacidae), with a body mass of 1,380g, while the smallest was the Black-Throated Bushtit *Aegithalos concinnus* (Aegithalidae), with a mass of 6.2g. The geometric mean body mass for pet shop species was 43.7g (n = 202), which is not significantly different to the expected value of 39.1g from the randomisation test (99% CI = 30.6 - 51.0g). However, the observed body size was significantly smaller than expected based on both randomisation tests that constrained by family membership (expected mean = 53.7g, 99% CI = 46.5 - 61.3g) and their origin (expected mean = 58.5g, 99% CI = 45.2 – 76.7g). The geometric mean of mass of the alien species in Taiwanese pet shops (57.54g) is significantly greater than expected (39.2g, 99% CI = 29.53 – 52.99g), but not if the species origin (expected mean = 58.28g, 99% CI = 40.7 – 75.87g) or family membership (63.62g, 99% CI = 54.51 – 74.08g) are constrained.

Of the species identified in Taiwanese pet shops, more species than expected by chance had native distributions situated in the Indo-Malay and Palearctic biogeographic realms, even after Bonferroni correction (**Table 3.2**). Significantly fewer than expected species derived from the Neotropic, Afrotropic and Nearctic after Bonferroni correction was applied (**Table 3.2**). For alien species, those native to Australasia were present in the pet shops in a higher frequency than expected by chance, even after Bonferroni correction (**Table 3.2**).

Table 3.2 The species recorded in trade during 2012 in Taiwan sorted by their realms of origin, and the number of species expected from the randomization test (2.5th and 97.5th percentiles), and with the sequential Bonferroni correction applied. Analyses are for all species or limited to alien species (i.e. species not native to Taiwan). Asterisks (*) denote tests for which a realm has a significantly (α = 0.05) higher (or lower) observed number of species for sale in bird shops than expected.

	All Species			Alien Species only		
Realms	Numbers of species in shops	Expected number of species	Expectation after Sequential Bonferroni correction	Numbers of species in shops	Expected number of species	Expectation after Sequential Bonferroni correction
Indo-Malay	73	23 – 44*	19 – 48*	34	14-32*	12-35
Palearctic	65	16 – 33*	13 - 37*	27	10-25*	7-28
Neotropic	43	73 – 102*	67 - 108*	43	48-72*	44-77
Australasia	40	28 - 49	25 - 53	40	17-36*	15-39*
Afrotropic	23	36 – 59*	33 - 62*	23	23-43	21-45
Nearctic	3	6-19*	4 -21*	3	3-14	2-16

The maximum number of songs logged for any species from the survey was 162 recordings for the Eurasian Jay *Garrulus glandarius* (Corvidae). 161 of the 247 species for which there are song recordings on Xeno-Canto revealed positive residuals of song recordings (65.7%). Moreover, the arithmetic mean of the residuals of the song recording for the species identified was 0.24 (n = 245), which is significantly greater than expected from the randomisation test (expected mean = 0.0008, 99% CI = –0.13 - 0.14). Similar results are obtained for the alien species in Taiwan (mean = 0.21, expected mean = -0.001, 99% CI = –0.16 - 0.15).

3.5 Discussion

During the 1990s, the global bird trade involved an estimated 2 - 5 million birds per year and around a quarter of all extant bird species have been subjected to world trade markets (Inskipp 1990; FAO 2011). These large numbers are driven by a relatively few different types of demands for birds. In Taiwan, demand is shaped largely by the favoured characteristics of bird species in terms of religion, culture, and custom; as well as constrained by legislation (Wildlife Conservation Act, Taiwan). These demands in turn determine the types and characteristics of species found in the bird trade there.

Several previous studies have provided information on the wild bird trade in Taiwan (Chi et al. 1991; Chi 1995; Taipei Wild Bird Society 1996; Chen 2005a; Shieh et al. 2006; Wang 2010). These studies have addressed the species composition, origins and feeding behaviour of birds in trade (Severinghaus 1999). However, no previous study has provided quantitative analyses of the composition and species' characteristics of birds in the initial stage of the invasion pathway in Taiwan. Such an analysis is important, because understanding the factors involved in the early stages of the invasion pathway is key to understanding the wider invasion process (Duncan et al. 2003; Blackburn and Cassey 2007). This study provides a particular insight into the early stages of bird introduction into Taiwan by revealing significant non-randomness in the composition and characteristics of species for sale in pet shops.

Non-randomness in composition has previously been shown in bird species introduced into Florida (Blackburn and Cassey 2007), Europe and North America (Jeschke and Strayer 2005), and in bird introductions worldwide (Lockwood 1999; Blackburn and Duncan 2001b). At the global scale, introduced bird species are derived more often, than expected by chance, from five bird families: Anatidae, Phasianidae, Columbidae, Psittacidae and Passeridae (Blackburn and Duncan 2001b). In Florida, introduced species are more often, than expected by chance, derived from Anatidae, Psittacidae, Ciconiidae and Passeridae (Blackburn and Cassey 2007). Of these families, only the Psittacidae was over-represented in the Taiwanese pet shops. This difference in species composition in introduction may result from the fact that different introduction stages are being considered (transport vs introduction, *sensu* Blackburn et al. 2011), or may imply that preferences for species in Taiwan are different from those previously demonstrated in a primarily Western context.

Of the nine families significantly over-represented before sequential Bonferroni correction (**Table 3.1**), species of Timaliidae, Turdidae, Zosteropidae and Fringillidae are popular songbirds in Taiwan. For example, Hwamei (*Garrulax canorus*) (Timaliidae) is the most popular song bird in Chinese communities (Li et al. 2006), which strongly influences the pet market in Taiwan. Together with species of Zosteropidae, they are popular species for Taiwanese song competitions. Species of Estrildidae and Zosteropidae are also commonly sold as prayer birds. A previous survey found Zosteropidae to be the commonest birds in pet shops (Wang 2010), which indicates that they are likely to be heavily stocked for prayer releases. Fringillidae are also somewhat over-represented in pet shops when analysis is limited to alien species (**Table 3.1**). Finally, this study also found significantly higher than expected numbers of species in the family Chloropseidae (leaf birds), and also when native species were excluded in the analysis. This may result from a combination of their bright colours and availability, as all of the Chloropseidae found in the survey originated from the Indo-Malay realm.

The Psittacidae (parrots) was by far the most over-represented taxon in Taiwanese pet shops, whether or not native species are included in the analysis; indeed, there is no species of parrot native to Taiwan. More than 200 parrot species are known to be in aviculture in Taiwan, although not all species will be traded in pet shops in the country (Tang 2011). Nevertheless, I recorded 70 species for sale, in contrast to the random expectation of 15 species (or 20 after Bonferroni correction). Parrots are popular cage bird species the world over thanks to their diverse colours, high intelligence and ability to imitate human language (Juniper and Parr 1998), and an estimated 20% of international traded species are Psittaciformes (FAO 2011). For example, the Congo Grey Parrot (*Psittacus erithacus*) is well known for its imitative ability, and it is the most popular imported species in Taiwan (Tang 2011). The industry value of Psittacidae in Taiwan was estimated to be US$25 million from 2008 to 2010 (Tang 2011), which encourages the captive breeding industry. A Golden Conure (*Aratinga guarouba*) would cost the equivalent of more than US$8000 in Taiwan for its rarity and ornamental value.

Of the other two highly over-represented families (after sequential Bonferroni correction), species of Muscicapidae are traditionally popular in trade because of their rich and diverse songs (there was a positive mean value of song residuals for all Muscicapidae species in the survey). This may also explain the over-representation of Estrildidae, Sturnidae, Turdidae and Muscicapidae in the list of alien species. Species of Sturnidae are often used for prayer animal release (Severinghaus and Chi 1999), which may explain the high prevalence of Sturnidae in the pet shops: most Sturnidae in the shops originated from East Asia, and are not ornamental. Nevertheless, some of the species of Sturnidae I recorded are African species with glorious plumage. Colouration is a potentially desirable feature in the pet market. Unfortunately, I do not have the information necessary to assess the influence of colouration on the availability of birds in the pet market, as this would require quantitative data on the colour of all (or most) of the world's birds. My survey did find that different colour morphs of a species can fetch very different prices (e.g. the Ring-neck Parakeet (*Psittacula krameri*) and Barred Parakeet (*Bolborhynchus lineola*), although I do not analyse this variation here.

The observed numbers of Tyrannidae (tyrant flycatchers) and Trochilidae (hummingbirds) species in Taiwanese pet shops are significantly lower than expected after sequential Bonferroni correction (**Table 3.1**). Both of these families are species rich but comprise species with smaller breeding range and body size, compared to the subset of Taiwanese pet species. Species in both families are also almost entirely found in the Neotropic, a region which is under-represented in pet shop species (**Table 3.2**), and the complexity of transporting species from there could be one of the restrictions on trade. Finally, Trochilidae is one of the taxa with hypothermic (torpor) behaviour (McKechnie and Lovegrove 2002), which may increase the difficulties in keeping hummingbirds in captivity, and may subsequently also limit their representation in trade.

The analyses demonstrated that species found in Taiwanese pet shops are on average smaller-bodied, have more attractive songs, are more widespread in their native breeding range, and originate further from the equator, than would be expected if they were a random sample of the world's bird species. They are also more likely to be sourced from the Indo-Malay and Palearctic biogeographic regions. These patterns seem likely to result from the interaction of species availability and societal demands (Blackburn et al. 2010).

A species' availability is associated with its native range size and origin. For example, the Indo-Malay and Palearctic regions are the main sources for Taiwanese bird shop species, and significantly more species than expected derive from these regions; for alien species, the main source was from the Neotropic, and significantly more alien species derived from the Australasia than expected (**Table 3.2**). This is likely to be because Taiwan is ringed by these regions, and therefore species from them are more readily traded to Taiwan. Conversely, the Neotropic has more bird species than any other region, and by far the largest expectation of species numbers in the randomisation test. However, the number of bird shop species deriving from the Neotropic is significantly fewer than expected after I applied the Bonferroni correction. There are also fewer species than expected deriving from the Afrotropic and Nearctic regions, probably because they are distant from Taiwan. Taiwan lies between latitudes 20 and 25°N, and the results have shown that the species preferred in Taiwanese pet shops originate further from the equator, and closer to Taiwan than expected from the simulations (17.26° versus 12.04°), which is also true when taxonomy and region are constrained (17.26° versus 11.77° and 13.5°). The mode of the absolute mid-point of species origins fell in the range of 20N°-30N°, coinciding with the latitudes where Taiwan is located. The influence of Taiwanese native species on these results is also indicated by the fact that the latitudes of origin of alien species in pet shops did not differ from random expectation. Finally, species observed for sale in Taiwanese shops have larger geographic ranges than expected by chance, and this is also true when native species are excluded. Widespread species are normally also more abundant (Blackburn et al. 2006), and thus more likely to be encountered and captured than rarer species. In addition, the number of birds that can be purchased at a time is a significant factor in determining which species are normally sold for the prayer bird market. Widespread, abundant species that are available in large numbers may be the only species that can support such market demand, and may additionally help explain why species that are more widespread can be found in the pet shops.

Globally, introduced terrestrial birds are on average larger than extant terrestrial bird species (Gaston and Blackburn 1995; Cassey 2008). My analyses showed that species found for sale in Taiwanese bird shops are no different in body mass from a randomly selected subset of the world's species. However, this result is because pet shop birds are a non-random selection of species, while body mass is highly taxonomically conserved (Bennett 2002). If I control for taxonomic composition by constraining the random sample to the same family composition as pet shop birds, I find that species found for sale are actually smaller-bodied than expected by chance. This is also true when I controlled for the region of origin.

The body sizes of species for sale in Taiwan may be consequences of the societal demands of prayer animal release and bird-keeping behaviour in Taiwan. Prayer species tend to be small-bodied (Severinghaus and Chi 1999), because the practices of prayer animal releases involve the frequent liberation of large numbers of birds, and smaller-bodied species are likely to be easier to stock and transport in the numbers required for this trade –

and indeed prayer bird shops have created standard boxes to cage and transport these birds. Moreover, smaller-bodied species are favoured by bird-keepers, because the relatively smaller-sized birds are best matched with aesthetic demands, for example, to match with the typically small and delicate merchandise, such as carved bird-cages and designed china feeding pots. Also, simply, smaller-sized birds are more convenient for bird-walking. As a result, even though ornamental birds like parrots are also common cage birds and tend to be larger (Blackburn et al. 2009b), mainstream pet birds in Taiwan tend to be small-sized species. Alien species for sale in Taiwan are larger-bodied than expected by chance, but this is likely to be the result of their taxonomic composition, especially the high prevalence (40%) of parrots: alien species did not differ from the mean expectation in terms of body size when their taxonomy or origin were controlled for.

Bird-keeping behaviour is popular in East Asia and South East Asia (Nash 1993; Jepson and Ladle 2005). Species commonly kept for their songs include not only passerines (known colloquially as songbirds) but also non-passerines, such as doves, jungle fowl and barbets. Nevertheless, Passeriformes (songbirds) comprise 70% of the international bird trade market (Inskipp 1990), and are also identified as dominant (156 species, or 63%) species in the Taiwanese bird trade. Interestingly, the results show that 2/3 of the species in the survey (and more than 60% of the alien species) have positive song residuals (not only in passerines), where larger residuals imply that the species has a relatively more aesthetically pleasing song to human ears (Blackburn et al. 2014b). This not only suggests that the attractiveness of a bird’s song is one of the main desired characteristics in the early stage of invasion in Taiwan, but also suggests that the perception of the songbirds in Western societies may diverge from the one found in Eastern countries, where the contexts of song birds involve species other than Passeriformes. The results also provide the first demonstration that the metric of bird song (residual number of recordings on the Xeno-Canto website; Blackburn et al. 2014b)is related to the presence of bird species in trade, and so may be a reasonable way to quantify the attractiveness of bird song to human ears.

This study has shown that the characteristics of birds for sale in the shops may be influenced by Taiwanese cultural demands, like for example their preference for parrots, small-bodied species, and species with attractive songs. In addition, the species that are traded are also likely to be affected by the requirement for cheap, abundant animals for prayer release. Prayer releases typically concern the liberation of large numbers of animals, and shops sell birds for release in standardised boxes of 20. I also explore interspecific variation in the price and numbers of birds for sale in a subsequent chapter. However, religious practises do not exclude the use of alien species, and a previous pet shop survey in 2004 (Environment and Animal Society of Taiwan 2004) found almost equal use of alien (16) and native (19) species for prayer animal releases. This practice could promote the release of alien species, and thereby establishment success, especially if large numbers of individuals are concerned (e.g. high propagule pressure: (Cassey et al. 2004b; Lockwood et al. 2005). It has been shown that prayer animal release is one of the factors that drove the range expansion of the Light-vented Bulbul *P. sinensis* (a common prayer species) in Taiwan, with subsequent hybridization with the endemic Taiwan Bulbul *Pycnonotus sinensis* (Severinghaus 2007).

The source of alien birds released into a new environment has been suggested to be a key factor influencing success (Carrete and Tella 2008; Cabezas et al. 2012): wild-caught birds seem to be more likely to establish, and therefore to cross on to further invasion steps, than are captive-bred individuals. The broad range of regions of origin for species sold in Taiwanese pet shops (**Table 3.2**) suggests that wild caught individuals are from many other parts of the world, with potentially significant consequences for invasion should they make it into the wild. However, it is in fact difficult to determine whether individuals sold in Taiwanese pet shops are wild-caught or captive-bred. For example, Myna species can be captive-bred (or captured while they were just hatched in the wild) for pet birds or wild-caught for prayer birds. Furthermore, the capture of wild birds is illegal in Taiwan and imported birds have found to be wild-caught while stated/reported to be “captive-bred” (Shepherd et al. 2012). It is thus difficult to make any statements about the likely influence of origin on establishment success for any pet shop birds making it out into the wild in Taiwan, although this does clearly happen, not least because of the cultural practice of prayer release.

Chapter 4 Determinants of Bird Price in the Taiwanese Pet Market

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4.1 Abstract

International wildlife trade is the largest emerging source of vertebrate invasive alien species. In order to prevent invasions, it is essential to understand the mechanics of trade and, in particular, which traded species are most likely to be released or escape into the wild. A species' economic value is a key factor, because cheaper species were expected to be less assiduously secured against escaping, and more likely to be deliberately released. Here, I investigate determinants of the price of species in the Taiwanese bird trade. Taiwan is an international hub for bird trade, and several native species are threatened by alien bird species. I investigated the relationship between the traded species sale price in Taiwan and the species availability for trade (the number of birds for sale, geographic range size and their origin, conservation and CITES status) and traits (body size, coloration, song attractiveness). I used phylogenetic generalized least squares models, with multi-model inference, to assess the variables that are best related to the price of birds in the Taiwanese pet trade. I found that species available for sale in larger numbers, native to Taiwan, not globally endangered, and small-bodied are all relatively cheaper, as too are species lacking yellow coloration and with attractive songs. The models of price revealed high levels of phylogenetic correlation, and hence that closely related species tended to be sold for similar prices. I suggest that, on the basis of price, native species are more likely to be deliberately or accidentally released than alien species. Nevertheless, the first visit of the survey of bird shops recorded 160 species alien to Taiwan (7,631 individuals), several of which are for sale cheaply and in large numbers. Alien bird species in trade therefore present an ongoing, non-trivial invasion risk on the island.

4.2 Introduction

Geographical barriers that have naturally set limits species distributions are increasingly being breached as species are moved around by international trade (Lockwood et al. 2005; Davis 2009; Blackburn et al. 2009b; Wilson et al. 2009). This is a cause for considerable concern because alien species can have substantial negative impacts on the recipient regions (Kolar and Lodge 2001; Blackburn 2004; Frenot et al. 2005), including causing the extinction of native species (Blackburn 2004; Clavero and Garcia-Berthou 2005) and the homogenization of ecological assemblages (with a concomitant decrease in species diversity) (Lockwood and McKinney 2001).

One of the major pathways of human-mediated movement is the trade in wild animals and plants, including the trade in cage birds (Bush et al. 2014). Captivity places constraints on the invasion process (Wilson et al. 2009; Blackburn et al. 2011), because traded species are not directly introduced after transport and not all species in trade are introduced. Nevertheless, the wildlife vertebrate trade is an increasing source of invasive species (Meyerson and Mooney 2007; Hulme 2009; García-Díaz et al. 2014). Alien species in trade have been shown to be correlated, in terms of identity (Lee and Shieh 2005) and abundance (Carrete and Tella 2008), with those species that subsequently establish alien populations. Indeed, the most important correlate of variation in the number of invasive alien species across countries is currently the volume of merchandise imports (Westphal et al. 2008), suggesting that international trade is now the primary driver of species invasions (see also Colunga-Garcia et al. (Colunga-Garcia et al. 2013)). To characterise invasions effectively, it is therefore important to understand the mechanics of the wildlife trade, and in particular, which traded species are most likely to be released or escape into the wild.

The amount of care devoted to keeping a bird is likely to be associated with its value (International Traffic Network 1992). Therefore, I have assumed that sale price is one of the factors that will influence the likelihood that traded species are introduced into the wild. More valuable species are expected to receive better care and hence to be more assiduously secured against escaping, and less likely to be deliberately released by their owners. Here, this study use the example of the cage bird trade in Taiwan to explore reasons for variation in the price of species for sale.

Taiwan presents an excellent example for studying features of the bird trade in Asian countries (Severinghaus and Chi 1999). First, cultural practices relating to the bird trade, such as prayer release, singing competitions and 'bird-walking' (the avian equivalent of dog-walking, where birds are taken out in cages for fresh air), are very popular in Taiwan. Prayer animal release is a common religious activity in Asia (Severinghaus and Chi 1999): it is estimated that more than 200 million animals are set free through this practice in Taiwan every year (Environment and Animal Society of Taiwan and Kaohsiung Teacher's Association 2004; Agoramoorthy and Hsu 2007). Such a high frequency of releases may be an important factor contributing to invasions by alien bird species (Kolar and Lodge 2001; Blackburn and Duncan 2001b; Cassey et al. 2004a; Lockwood et al. 2005; Simberloff 2009). Second, Taiwan is a major wildlife trade hub from where species are re-exported to other Asian countries, such as Malaysia and Singapore (Nash 1993; Severinghaus and Chi 1999; Shepherd et al. 2012). Third, Taiwan is separated from the nearest continent by a >100 km ocean strait, meaning that it is relatively straightforward to define native versus alien species. Finally, alien bird species have proved to be a conservation threat in Taiwan through actual and potential hybridization with native bird species (Severinghaus 2007; Yao 2007; Li et al. 2010).

I predicted that the price of traded birds in the Taiwanese pet market would largely be determined by a species' availability, because supply costs would be lower for common species, and because people will pay higher prices for rarer species (the anthropogenic Allee effect (Courchamp et al. 2006)). I therefore hypothesised a negative relationship between price and the number of individuals of a species offered for sale. Species that are more widespread are normally more abundant (Gaston and Blackburn 2000; Blackburn et al. 2006), and more available for trade (Cassey et al. 2004a). I hypothesised that species that have more extensive native distributions would be less expensive. Similarly, I hypothesised that native species and species coming from closer regions, species not considered as threatened on the IUCN Red List, or species not listed on CITES Appendices, would also be cheaper. However, species availability is not the only factor suggested to affect market value. An extensive body of literature has shown that particular species traits can affect human attitudes towards species, including willingness to pay. Animal body size is a trait that influences human preference (Knegtering et al. 2010), and larger-sized species are more valued (Kellert 1985). Body size is negatively related to bird species richness (Blackburn and Gaston 1994; Blackburn and Gaston 1995) and abundance (Gaston 1994b; Gaston and Blackburn 2000), both of which may affect the availability of large-bodied birds for sale. Large-bodied birds also tend to be longer-lived and reproduce more slowly, and so will take longer to rear and be less productive if captive bred. For all these reasons, I therefore predicted that species with small body sizes should be less expensive. I also expected that more colourful species would be more attractive as cage birds (Frynta et al. 2010; Lišková and Frynta 2013; Tella and Hiraldo 2014), and hence predicted that drabber species would sell for lower prices. Finally, species are traded for singing competitions in Asia, and so I hypothesised that species with less attractive songs would fetch a lower price.

4.3 Method

4.3.1 Data

To obtain data on the occurrence and price of bird species in Taiwanese pet shops, I conducted non-structured interviews between August and November 2012. All shops were visited at least once with the aim of obtaining data on three variables: (i) the identity of species displayed for sale, (ii) their price (in Taiwanese Dollars, or TWD) and (iii) the numbers of birds of each species displayed. I identified birds to species level using monographs and bird guides, often from photographs taken by myself. In this way, a total of 247 bird species were identified (see Chapter 2 for more details). I used only species recorded in the first visit to each shop for analysis (n = 221) to standardise estimates of numbers for sale per shop (see Appendix B). Furthermore, the only two Nearctic species recorded for sale (Northern Mockingbird *Mimus polyglottos* and Red-bellied Woodpecker *Melanerpes carolinus*) were removed to ease regional comparisons. One further species (Taiwan Hwamei *Garrulax taewanus*) was excluded because an estimate of price was not available. For PGLS analysis (see below) I excluded Red-collared Lorikeet *Trichoglossus rubritorquis* when phylogenetic trees were selected based on (Jetz et al. 2012), because the authors treat it as a subspecies of Rainbow Lorikeet *Trichoglossus haematodus* (resulting in n = 217).

Based the analysis on the global taxonomic list of 9,993 extant bird species from Jetz et al. (Jetz et al. 2012). I identified species as native or alien in Taiwan based on the CWBF Checklist of the Birds of Taiwan (Ding et al. 2012), adjusted by excluding transient migrants, pelagic seabirds and vagrants.

I collated information for each of the species on the following variables:

(1) Geographical range size (km^2): a measure of native geographical range extent (Gaston 1991; Gaston 1994a), acquired from the data applied in (Orme et al. 2006). Maps of total native breeding area for all species were converted to equal area grid polygons with a cell size of 96.3 km x 96.3 km. This specified a scale identical to 1° grids at the equator. The breeding range of each species was estimated by summing the areas of the cells in which they occurred (Orme et al. 2006; Blackburn and Cassey 2007).

(2) Region of origin: the biogeographic region from which the native populations of alien species originate, defined using the World Wildlife Fund eco-regions map (Olson et al. 2001; Blackburn and Cassey 2007). Species were assigned to the region in which the largest part of their geographic range fell.

(3) Body mass (g): a measure bird species body size from Dunning (Dunning 1992), augmented by data used in Olson et al. (Olson et al. 2009).

(4) Conservation status of species: The conservation status of the identified species was obtained from the IUCN Red List of Threatened Species (IUCN 2013). Species recorded in the survey were classified into the following categories, treated as a multi-level categorical variable: least concern (LC), near threatened (NT), vulnerable (VU) and endangered (EN). All categories were tested in the univariate analysis. Species were separated by whether they were in the threatened categories (NT, VU and EN) or not (LC) in the multivariate analysis. None of the species in the survey of pet shops was data deficient (DD), critically endangered (CR) or extinct in the wild (EW).

(5) International trade status: The status of the identified species was obtained from Convention of International Trade in Endangered Species of Wild Fauna and Flora (CITES Appendices I, II and III). Species were separated by whether they were included in Appendices I, II and III (scored 1) or not (scored 0).

(6) Colour: Adult males of the nominal subspecies in breeding plumage (or females for species with reverse sexual dimorphism) were assessed for colouration on the basis of the plates in the Handbook of the Birds of the World. The colour of fourteen body parts of the bird (bill, face, cheek, head, throat, breast, belly, flank, back, wings, tail, rump, vent and legs) was assessed by eye, and the presence of eleven colours (blue, green, red, orange, brown, pink (including purple and violet), yellow, black, grey, white and ivory (pale flesh colour)) was scored. Two metrics were calculated from these data: 1) the percentage of the body surface covered by each colour, calculated over the fourteen body parts of the bird scored; and 2) colour diversity, calculated as the number of different colours on a given species (excluding colours covering <3% of the body). The data on plumage colour was developed by Miquel Vall-llosera.

(7) Song attractiveness: The number of song tracks lodged for a given species on the Xeno-Canto website [www.xeno-canto.org] was used to derive a metric of the attractiveness of bird song to humans (following Blackburn et al. 2014b). Xeno-Canto contains more than 115,000 independent recordings of bird songs, which cover about 80-85 % of the extant species, with up to 335 recordings per species. Only two of the species in

the data set do not have any song recordings on Xeno-Canto, while the range for the remainder is 1 - 162 records. The glm function in R v.3.0.3 (R Core Team 2014) was used to model the log+1 number of songs lodged on Xeno-Canto as a function of log geographic range size. It has been shown that larger residuals are correlated with the characteristics of songs associated with attractiveness to people (Blackburn et al. 2014b).

Of the nine predictor variables in the univariate analysis (see below), bird numbers, species status, region of origin, IUCN list and CITES listing, body mass and each colour, breeding range size and the attractiveness of bird song are available for 217 species. I log-transformed the data on body mass, number of birds of each species for sale, percentage of covered colour and their price, and applied arcsine square root transformations to the percentage of body surface covered in each colour.

4.3.2 Analysis

All analyses were conducted in R version 3.0.3 (R Core Team 2014). I constructed phylogenetic generalized least squares (PGLS) models for the prices of species recorded in Taiwanese pet shops (response variable) compared with all nine univariate predictor variables, using the *pgls* function in the package *caper* (region of origin, species status, IUCN status, and CITES list were treated as categorical variables). The *pgls* model specifies the structure of the variance–covariance matrix reflecting the phylogenetic associations among the species, and also includes an estimated parameter (λ) that governs the strength of phylogenetic signal in the dependent variable. Thus, *pgls* does not require the *a priori* assignment of phylogenetic signal but instead allows the data to dictate its magnitude in the statistical model (Revell 2010). Clearly, price is not an evolved trait, but it is correlated with species traits that are (see Results), and the phylogenetic approach provides a way to analyse the influence of these traits under a specified evolutionary hypothesis (i.e. a phylogeny) in a way that accounts for the non-independence of species in terms of price (c.f. (Fritz and Purvis 2010)). The significance of colour in univariate analysis was assessed after a Bonferroni correction, given that I test for the effects of 11 different colours. Collinearity amongst the different colour variables was low. Ivory colouration was found to have the strongest correlation with other colour variables; it exhibits the strongest positive correlation to brown (Pearson’s $r = 0.37$, $n = 217$, $P < 0.001$) and negative to black (Pearson’s $r = -0.33$, $n = 217$, $P < 0.001$). To find the most likely model for bird price, I fitted a global PGLS model including all predictors. I then used the *dredge* and *model.avg* functions (package *MuMIn*) to fit all possible models from these predictor variables, to identify the most likely models, and to calculate Akaike weights and variable importance (the sum of the Akaike weights across all models including that variable) based on the Akaike Information Criterion corrected for small sample sizes (AICc).

Based the phylogenetic analyses on the phylogenetic tree for birds proposed by (Jetz et al. 2012). The structure of this phylogenetic tree is not known for certain, and so I incorporated uncertainty over the true phylogenetic relationship by repeating the analyses over a number of different phylogenetic trees for the species, sampled at random from www.birdtree.org (Jetz et al. 2012). Initially, I used a sample of 100 random trees to calculate the univariate relationships. I then used ten trees (the smaller sample due to constraints on computer time necessary for the multi-model approach over hundreds of possible models) to identify the most likely set of models (those with ΔAICc < 4 of the best model) from the global PGLS model, and a further random selection of 100 phylogenetic trees to assess the fit and importance of models in this set. Thus, the simulation produced median estimates (over these trees) of the parameters of the best-fit models incorporating phylogenetic uncertainty. This approach allowed us to provide estimates of the variance in regression coefficients, which I calculated as the 5th and 95th percentiles in the coefficients across the 100 runs.

4.4 Results

The total number of birds for sale in the pet shops in the survey across all 217 species was 26,165, of which 7,612 individuals were of species alien to Taiwan (n = 159). The maximum recorded number of birds per species was 7,420 for Red Turtle Dove *Streptopelia tranquebarica*, while the highest single bird count in a single shop was 4,000 individuals, for this same species. The ten most abundant species in Taiwanese pet shops are listed in (**Table 4.1**). These ten species comprised 80% of all individuals for sale, while the five native species in (**Table 4.1**) account for 70% of all birds for sale. More than half of the alien bird individuals for sale came from just five species (**Table 4.1**). 67 of the alien species (2,778 individuals) for sale in the pet shops were parrots.

The prices of the 217 identified species sold varied widely, from US$0.86 (at an exchange rate of US$1:TWD30) per individual for Eurasian Tree Sparrow *Passer montanus* to US$8,000 for a single Golden Parakeet *Guaruba guarouba*. The total market value of displayed birds in the surveyed pet shops during the survey time was more than US$0.8 million, of which more than US$0.5 million (> 65%) was contributed by alien species.

Univariate PGLS models revealed that the prices of birds for sale in pet shops were related to the number of birds of each species for sale (**Figure 4.1**), body mass, whether or not the species is alien to Taiwan (**Figure 4.1**), whether or not the species is listed in CITES Appendices, breeding geographic range size, song attractiveness (**Table 4.2**) and colour (the percentage of a species' body that was yellow or grey; **Table 4.3**). There was also an effect of a species' categorisation on the IUCN Red List (adjusted r^2 ± s.e. = 0.084 ± 0.0008, $F_{3,177}$ ± s.e. = 5.41 ± 0.059, p ± s.e. = 0.002±0.0001, λ ± s.e. = 0.952±0.0007), and a marginal effect of biogeographic realm of origin (adjusted r^2 ± s.e. = 0.091 ± 0.0007, $F_{4,88}$ ± s.e. = 2.21 ± 0.01, p ± s.e. = 0.076 ± 0.002, λ ± s.e. = 0.95 ± 0.0004): in general, less threatened species and species from realms closer to Taiwan (Palaearctic, which include Taiwanese native species) were cheaper.

Model selection on the global model for the price of birds in Taiwanese pet shops identified 13 models for which the median ΔAICc across the ten trees was <4 relative to the most likely model (**Table 4.4**). As an indicator of fit, the variables in the most likely model explained 61% of the variance in bird price. The simulation over 100 randomly chosen but likely phylogenetic trees for each of these best 13 PGLS models recovered four variables - body mass, number of birds for sale, whether or not species are alien to Taiwan and song attractiveness - as present in all of the possible model combinations. The presence of yellow coloration also had relatively high variable importance (median importance [5th, 95th percentiles] = 0.96 [0.93, 0.98]). The variable importance of the CITES trade status is less than the previous five predictors but higher than the other variables (median importance [5th, 95th percentiles] = 0.71 [0.65, 0.79]). Thus, cheaper birds in Taiwanese pet shops tend to be physically small-bodied, not yellow in colour and not attractive singers, as well as highly available in the local markets, Taiwanese natives, and not included in any CITES Appendices.

Model coefficients (median estimates, [5th, 95th percentiles]) in PGLS models (ΔAIC from the best model is less than 4) for determinants of the price of birds in Taiwanese pet shops, were calculated over 100 randomly selected likely phylogenetic trees (**Table 4.4**). Model ranks (top 3 rankings shown) are based on ΔAIC. Parameter Lambda (λ) indicates the strength of phylogenetic signal in the price of birds for sale in Taiwan for each likely model. IUCN status divided species by whether they are classed in the category of least concern.

Table 4.1 The ten traded bird species with the largest numbers and ten with highest price recorded for sale in Taiwanese pet shops in my survey. Table with numbers of birds recorded for sale, their price (US$) and whether species are alien or native to Taiwan (Status).

Family	Species	Number of birds	Price (US$)	Status
Columbidae	*Streptopelia tranquebarica*	7420	1.63	Native
Zosteropidae	*Zosterops japonicus*	6381	35.50	Native
Estrildidae	*Lonchura punctulata*	2649	1.50	Native
Psittacidae	*Melopsittacus undulatus*	956	7.70	Alien
Estrildidae	*Padda oryzivora*	928	10.47	Alien
Sturnidae	*Acridotheres grandis*	722	10.00	Alien
Sturnidae	*Acridotheres fuscus*	492	6.83	Alien
Pycnonotidae	*Pycnonotus sinensis*	465	10.03	Native
Estrildidae	*Lonchura striata*	437	2.40	Native
Estrildidae	*Erythrura gouldiae*	405	13.03	Alien
Psittacidae	*Guaruba guarouba*	5	8000.00	Alien
Psittacidae	*Cacatua leadbeateri*	2	7500.00	Alien
Psittacidae	*Amazona oratrix*	1	6666.67	Alien
Psittacidae	*Ara macao*	1	4000.00	Alien
Psittacidae	*Cacatua moluccensis*	2	3333.33	Alien
Psittacidae	*Ara chloropterus*	2	2083.33	Alien
Psittacidae	*Cacatua ophthalmica*	1	2000.00	Alien
Psittacidae	*Primolius auricollis*	5	1916.67	Alien
Psittacidae	*Ara ararauna*	18	1818.17	Alien
Psittacidae	*Pionites leucogaster*	4	1777.77	Alien

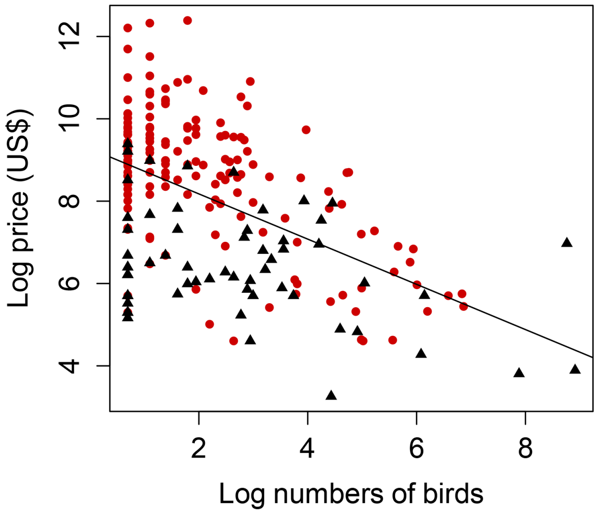

Figure 4.1 The relationship between log price and log abundance of alien and native species recorded in Taiwan. Red circles indicate the alien species and black triangles indicate the native species for sale in Taiwanese pet shops. The line indicates the best fit relationship between log price (in Taiwanese Dollars, or TWD) and log numbers irrespective of native or alien status ($r^2 = 0.27$, n = 217). Both transformations are natural logarithms.

Table 4.2 The relationship between the log-transformed prices of traded bird species in Taiwanese pet shops and the predictor variables. The averaged coefficients (median estimates [5th, 95th percentiles]) from univariate analysis on the relationship between the log-transformed price of bird species in Taiwanese pet shops (n = 217) and the predictor variables in the first column, were calculated over 100 randomly selected likely phylogenetic trees (see Methods for more details). Parameter Lambda (λ) indicates the strength of phylogenetic signal in the dependent variable (price of birds for sale in Taiwan).

Variables	Estimate	t value	Lambda (λ)	p value
Log number for sale	−0.14 [−0.15, −0.14]	−6.91 [−7.01, −6.77]	0.94 [0.94, 0.95]	< 0.001
Log mass	0.93 [0.89, 0.98]	6.27 [5.83, 6.89]	0.93 [0.92, 0.94]	< 0.001
Log geographic range	−0.18 [−0.2, −0.16]	−2.67 [−2.95, −2.44]	0.96 [0.95, 0.97]	0.008 [0.004, 0.01]
Song attractiveness	−0.09 [−0.1, −0.08]	−2.09 [−2.32, −1.91]	0.97 [0.96, 0.97]	0.03 [0.02, 0.05]
Status (native/alien)	−0.54 [−0.55, −0.52]	−2.5 [−2.7, −2.28]	0.95 [0.95, 0.96]	0.01 [0.007, 0.02]
CITES (listed/not)	0.69 [0.66, 0.72]	3.92 [3.71, 4.09]	0.94 [0.93, 0.95]	<0.001
Realm (Australasia, n=38)	0.06 [0.04, 0.1]	0.27 [0.16, 0.41]	0.95 [0.95, 0.96]	0.78 [0.67, 0.86]
Realm (Indo-Malay, n=64)	−0.35 [−0.39, −0.31]	−1.42 [−1.57, −1.23]	0.95 [0.95, 0.96]	0.15 [0.11, 0.21]
Realm (Neotropic, n=41)	0.4 [0.37, 0.43]	1.2 [1.09, 1.29]	0.95 [0.95, 0.96]	0.23 [0.2, 0.27]
Realm (Palearctic, n=52)	−0.45 [−0.47, −0.42]	−2.16 [−2.34, −1.95]	0.95 [0.95, 0.96]	0.03 [0.02, 0.05]

Table 4.3 The relationship between the price of traded bird species in Taiwanese pet market and the percentage of a given colour found on the species, and colour diversity. *significant applying a Bonferroni correction for multiple tests; N = 217 in each case

Colour (percentage of colour)	Estimate	t value	p value	Lambda (λ)
Black	3.95 [3.51, 4.34]	2.03 [1.79, 2.27]	0.04 [0.02, 0.07]	0.94 [0.93, 0.95]
Blue	1.45 [1.14, 1.74]	0.93 [0.76, 1.11]	0.34 [0.26, 0.44]	0.94 [0.93, 0.95]
Green	−2.12 [−2.64, −1.53]	−1.61 [−2.06, −1.14]	0.1 [0.04, 0.25]	0.94 [0.94, 0.95]
Red	4.49 [4.15, 4.82]	2.41 [2.24, 2.61]	0.01 [0.009, 0.02]	0.94 [0.93, 0.95]
Orange	−2.3 [−2.54, −1.86]	−1.31 [−1.44, −1.04]	0.19 [0.15, 0.29]	0.94 [0.94, 0.95]
Yellow	4 [3.72, 4.28]	2.89 [2.69, 3.06]	0.004* [0.002, 0.007]	0.95 [0.94, 0.95]
Brown	−2.69 [−3.05, −2.24]	−1.75 [−2.04, −1.46]	0.08 [0.04, 0.14]	0.94 [0.93, 0.95]
Pink	5.25 [4.55, 6.25]	2 [1.66, 2.57]	0.04 [0.01, 0.09]	0.95 [0.94, 0.95]
White	−0.55 [−1.17, 0.16]	−0.22 [−0.47, 0.06]	0.82 [0.63, 0.98]	0.94 [0.93, 0.95]
Grey	−6.2 [−6.64, −5.79]	−3.32 [−3.55, −3.12]	0.001*[0.0004, 0.002]	0.94 [0.93, 0.95]
Ivory	0.14 [−0.44, 0.82]	0.05 [−0.17, 0.33]	0.91 [0.72, 0.98]	0.94 [0.93, 0.95]
Colour Diversity	0.007 [0.002, 0.01]	0.26 [0.07, 0.59]	0.78 [0.55, 0.94]	0.94 [0.04, 0.95]

The averaged coefficients (median estimates, [5th, 95th percentiles]) from univariate analysis on the relationship between the log-transformed price of bird species for sale in Taiwanese pet shops and the arcsine square root transformed percentage of a given colour found on the species, and colour diversity (in the first column), were calculated over 100 likely phylogenetic trees. Parameter Lambda (λ) indicates the strength of phylogenetic signal in the price of birds for sale in Taiwan.

Table 4.4 Model coefficients in PGLS models for determinants of the price of birds in Taiwanese pet shops.

Intercept	Whether listed in CITES appendices	Grey colour	Log breeding range	Log numbers	Log mass	IUCN status	Song attractiveness
2.09 [1.99, 2.2]	0.28 [0.26, 0.31]	−2.61 [−2.9, −2.29]		−0.1 [−1.1, −1.1]	0.61 [0.57, 0.66]		−0.07 [−0.08, −0.06]
1.99 [1.89, 2.1]	0.28 [0.25, 0.31]			−0.1 [−0.1, −0.1]	0.64 [0.59, 0.69]		−0.07 [−0.07, −0.06]
2.1 [2, 2.21]	0.2 [0.251, 0.3]	−2.57 [−2.82, −2.24]		−0.1 [−1.1, −1.1]	0.61 [0.56, 0.66]	0.06 [0.04, 0.08]	−0.07 [−0.08, −0.06]
2.23 [2.1, 2.36]	0.28 [2.56, 0.31]	−2.61 [−2.89, −2.28]	−0.02 [−0.2, −0.008]	−0.1 [−1.1, −1.1]	0.61 [0.56, 0.66]		−0.07 [−0.08, −0.06]
2.02 [1.93, 2.14]		−2.51 [−2.83, −2.19]		−0.11 [−0.11, −0.1]	0.67 [0.62, 0.71]		−0.07 [−0.07, −0.06]
1.99 [1.9, 2.11]	0.27 [0.23, 0.3]			−0.1 [−0.11, −0.1]	0.64 [0.59, 0.69]	0.07 [0.04, 0.08]	−0.06 [−0.07, −0.05]
1.92 [1.82, 2.04]				−0.11 [−0.11, −0.11]	0.69 [0.65, 0.74]		−0.06 [−0.07, −0.05]
2.13 [2.01, 2.25]	0.27 [0.24, 0.3]		−0.02 [−0.03, −0.009]	−0.1 [−0.11, −0.1]	0.64 [0.59, 0.69]		−0.07 [−0.07, −0.06]
2.04 [1.94, 2.15]		−2.46 [−2.77, −2.12]		−0.11 [−0.11, −0.1]	0.66 [0.61, 0.7]	0.07 [0.05, 0.09]	−0.06 [−0.07, −0.05]
1.94 [1.83, 2.06]				−0.11 [−0.11, −0.11]	0.68 [0.63, 0.73]	0.08 [0.05, 0.09]	−0.06 [−0.07, −0.05]
2.16 [2.05, 2.27]	0.29 [0.26, 0.31]	−3.46 [−3.73, −3.14]		−0.1 [−0.1, −0.1]	0.61 [0.56, 0.65]		−0.07 [−0.08, −0.07]
2.15 [2.02, 2.29]	0.28 [0.24, 0.3]	−2.58 [−2.85, −2.24]	−0.009 [−0.01, 0.003]	−0.1 [−0.1, −0.1]	0.61 [0.56, 0.66]	0.05 [0.03, 0.07]	−0.07 [−0.08, −0.06]
2.19 [2.06, 2.32]		−2.51 [−2.82, −2.18]	−0.02 [−0.03, −0.01]	−0.11 [−0.11, −0.1]	0.66 [0.61, 0.7]		−0.07 [−0.07, −0.06]
Importance	0.71 [0.65, 0.79]	0.6 [0.5, 0.7]	0.23 [0.16, 0.29]	1	1	0.29 [0.22, 0.35]	1

Status (native/exotic)	Yellow colour	Model ranks			ΔAIC	Lambda (λ)	Akaike weight
		Rank 1	Rank 2	Rank 3			
−0.24 [−0.27, −0.22]	2.74[2.56, 2.95]	97	3	0	0 [0, 001]	0.92 [0.9, 0.93]	0.18 [0.15, 0.21]
−0.25 [−0.27, −0.22]	3.17 [0.002, 3.36]	3	84	9	0.71 [0.02, 1.44]	0.92 [0.9, 0.93]	0.12 [0.08, 0.17]
−0.24 [−0.27, −0.21]	2.66 [2.48, 2.85]	0	11	71	1.37 [0.98, 1.88]	0.92 [0.91, 0.94]	0.09 [0.07, 0.11]
−0.24 [−0.27, −0.22]	2.7 [2.52, 2.91]	0	0	2	1.82 [1.43, 2.11]	0.92 [0.9, 0.94]	0.07 [0.06, 0.09]
−0.24 [−0.27, −0.21]	2.74 [2.54, 2.95]	0	2	9	1.86 [1.33, 2.48]	0.92 [0.91, 0.94]	0.07 [0.04, 0.09]
−0.25 [−0.27, −0.23]	3.08 [2.91, 3.24]	0	0	8	2.03 [1.31, 2.66]	0.92 [0.91, 0.93]	0.06 [0.04, 0.08]
−0.25 [−0.27, −0.22]	3.16 [2.98, 3.36]	0	0	1	2.41 [1.49, 3.23]	0.92 [0.91, 0.94]	0.05 [0.03, 0.07]
−0.25 [−0.27, −0.22]	3.13 [2.96, 3.32]	0	0	0	2.54 [1.83, 3.10]	0.92 [0.91, 0.93]	0.05 [0.03, 0.06]
−0.24 [−0.27, −0.21]	2.65 [2.45, 2.85]	0	0	0	2.96 [2.13, 3.92]	0.93 [0.91, 0.94]	0.04 [0.02, 0.05]
−0.24 [−0.27, −0.21]	3.04 [2.87, 3.24]	0	0	0	3.47 [2.43, 4.31]	0.93 [0.91, 0.94]	0.03 [0.02, 0.04]
−0.28 [−0.31, −0.26]		0	0	0	3.48 [2.69, 4.28]	0.91 [0.89, 0.93]	0.03 [0.02, 0.04]
−0.24 [−0.27, −0.21]	2.65 [2.47, 2.85]	0	0	0	3.51 [3.03, 4.08]	0.92 [0.91, 0.93]	0.03 [0.02, 0.04]
−0.25 [−0.27, −0.21]	2.7 [2.49, 2.91]	0	0	0	3.53 [2.84, 4.42]	0.92 [0.91, 0.94]	0.03 [0.02, 0.04]
1	0.96 [0.93, 0.98]						

The 13 most likely models also included effects of IUCN listing, breeding area and grey colour, although these variables had lower importance than the others in the model (**Table 4.4**). Prices tended to be lower for species less threatened on IUCN status, with larger geographic range sizes and more grey colouration. The analyses of univariate models (**Table 4.2** and **Table 4.3**), the global PGLS model (median λ [5th, 95th percentiles] = 0.92 [0.90, 0.94] and the 13 most likely PGLS models (**Table 4.4**) all identified a high degree of phylogenetic correlation (Pagel's λ) in the models: price tended to be similar for closely related species (**Figure 4.2**).

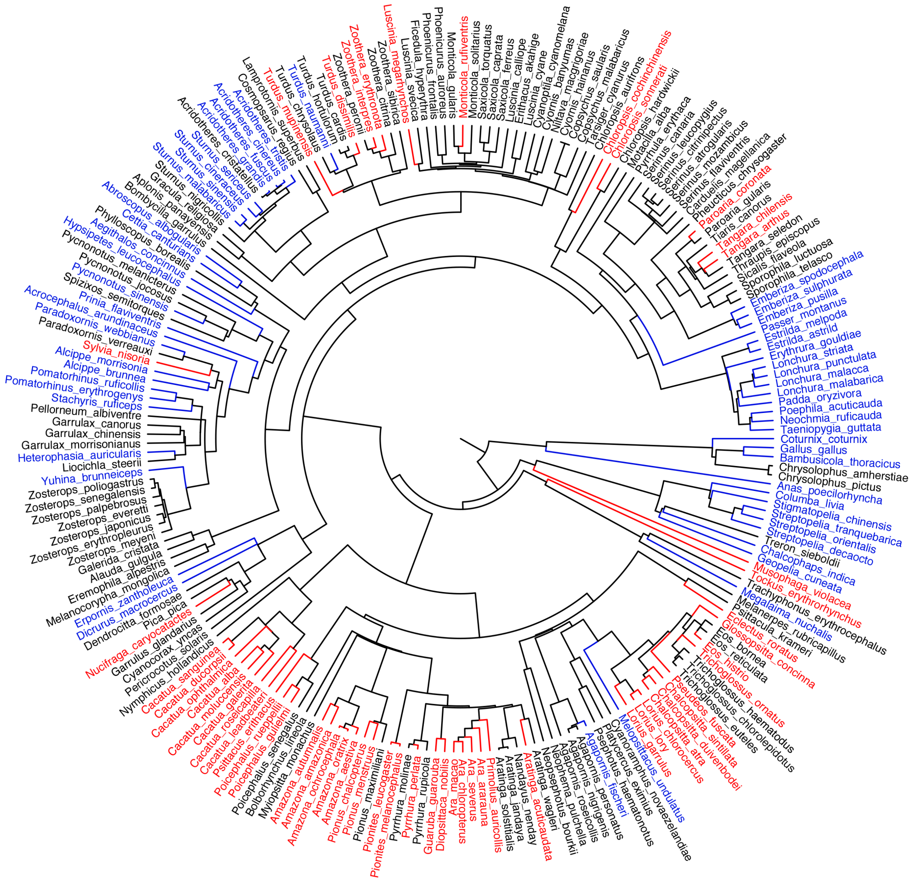

Figure 4.2 A phylogeny of the bird species included in the analysis.

Species were classed in three ranges by the price for every identified species (n = 217). Expensive bird species (species in the top quartile for price; n = 56) are marked in red; cheap bird species (species in the bottom quartile for price; n = 55) are marked in blue. The phylogeny was generated from birdtree.org (Jetz et al. 2012), visualised in FigTree v1.4.0.

4.5 Discussion

The most important correlate of variation in the number of invasive alien species across countries is currently the volume of imported goods (Westphal et al. 2008), suggesting that international trade is now the primary driver of vertebrate species introductions. The bird trade in East and South-East Asia is economically lucrative and active. The invasion pathway for birds has been well-studied in Western countries, but in Eastern countries birds are traded for different reasons, and trade concerns different species with different characteristics traded in different quantities (Severinghaus and Chi 1999; Jepson and Ladle 2005; Edmunds et al. 2011). It is particularly important to understand the trade in response to Eastern market demands, in comparison to Western trade, which has been curtailed since the unpopularity of past Acclimatisation Society activity and, currently, by wildlife trade bans. This is the primary motivation behind the analyses of the variation in price of bird species for sale in Taiwanese pet shops. The price of birds is a good indicator of the constraints and demands of the pet market, which allows us to identify the characteristics of traded species, and hence a key element in the process of human-mediated bird invasions in East and South-East Asia.

The analyses revealed that the price of species in pet shops is strongly associated with their availability. Thus, species that are for sale in large numbers, are native to Taiwan, and with healthy wild populations available for international trade (as assessed by CITES) all fetch a relatively low price in Taiwan. The first two of these variables were present in all of the identified most likely models, while the third was present in most of these models (**Table 4.4**). All also have model-averaged regression coefficients that differ significantly from zero with a high degree of confidence (**Table 4.2** and **Table 4.4**). For example, the Eurasian Tree Sparrow *P. montanus*, that is a common resident native species in Taiwan (Zhang et al. 2008), is not included in CITES Appendices, and is commonly sold species in Taiwanese pet shops, it costs around US$0.86 per individual. In contrast, the Golden Parakeet *G. guarouba* is native to South America (i.e. alien), is included on CITES Appendix I (at the time of my survey), and costs around US$8,000 per individual.

Alien species are probably more expensive because of reduced availability, as there are fewer alien birds for sale in Taiwanese pet shops than natives. Alien species must be imported from overseas (Low 2014), and higher prices presumably reflect importation costs (**Figure 4.1**). Moreover, higher prices could also reflect the scarcity of captive-bred individuals, particularly for species included on CITES Appendix I. The price inflation for species as alien versus as native is also illustrated by the comparative prices of species in bird markets in different countries. For example, the Red-crested Cardinal *Paroaria coronata* and Saffron Finch *Sicalis flaveola* are both native to South America. Their prices in local markets in Brazil were US$83.33 and US$16.11, respectively (where the lowest recorded price of any species is US$3.33) (Regueira and Bernard 2012), in comparison to US$750 and US$122.23 for the same species in Taiwanese pet markets (where the lowest recorded price of any species is US$0.86).

Whether or not a species was listed in the CITES appendices (and therefore restricted in international trade) has significant effects on the price of species in the Taiwanese pet market (**Table 4.2** and **Table 4.4**), albeit that the variable importance for CITES listing is less than that of the five primary predictors of price (**Table 4.4**). The sources of species in pet shops (captive-bred or wild-caught) are often unclear (Shepherd et al. 2012), but the bulk of pet trade is made up of wild-caught species (Nash 1993; Carrete and Tella 2008; Edmunds et al. 2011). Not only is the international trade of CITES-listed species restricted, but they are also likely to fall under local regulations such as the Wildlife Conservation Act in Taiwan (Severinghaus and Chi 1999; Agoramoorthy 2009), and so I would expect an effect of CITES listing on price. Courchamp et al. (2006) also showed that CITES listed amphibian and reptile species fetched a higher price in French trade than equivalent non-CITES species.

Larger-bodied species sell for a higher price in the Taiwanese pet market (**Table 4.2** and **Table 4.4**). Large-bodied species tend to have lower reproductive rates, require more food and space, and live at lower densities in the wild than smaller-bodied species (Bennett 2002). All of these factors will increase the costs of dealing in these species for pet shop owners, bird breeding farms, and bird catchers and export/importers. Large-bodied species also tend to be long-lived. For example, some of the larger parrot species have lifespans similar to humans (Wilson 1998; Robinson 2001; Young et al. 2012). Buying such a bird may be a once in a lifetime purchase, raising the price that is likely to be charged. A well-trained parrot may command a very high price, especially if it can imitate human language (Tella and Hiraldo 2014). This probably explains why species in birds such as macaws (*Ara*), amazons (*Amazona*) and cockatoos (*Cacatua*) fetch a high price in Taiwan (**Figure 4.2**).

I predicted a positive effect of the attractiveness of a bird's song on its price, because many species are traded for their ability as songsters and previous analysis showed that species for sale in Taiwanese pet shops had more aesthetically-pleasing songs than expected by chance (Chapter 3). In fact, I found the reverse relationship. It is possible that a higher demand for species with attractive songs has led to an abundance of such species in the market, and hence an associated lower price. However, the relationship is more likely to be a consequence of some birds, such as parrots, not being traded for their song, but for other reasons, such as the ability to mimic human voice (Tella and Hiraldo 2014). If I limit analysis to song birds (species in the order Passeriformes), then the negative relationship between song attractiveness and price disappears (univariate PGLS: estimate median [5th, 95th percentiles] = –0.03 [–0.04, –0.01], t = –0.48 [–0.66, 0.22], p = 0.063 [0.51, 0.82], λ = 0.90 [0.88, 0.93).

This study also found some evidence that the price of bird species in Taiwan is influenced by plumage colour, and specifically that species with a higher proportion of yellow colouration fetch a higher price, while species with a higher proportion of grey colouration fetch a lower price (**Table 4.3** and **Table 4.4**). Cultural factors may be key in driving such colour preferences (Soma and Saito 1997). For example, the colour grey has associations with low value in Asian countries (e.g., China and Japan), but associations with high quality and expense in the U.S. (Jacobs et al. 1991). In traditional Chinese culture, nature is composed of five elements - wood, fire, earth, metal and water - and each element has a colour and a compass point associated with it (Chen 2007). Yellow exemplifies the earth and represents the centre of the compass, and is therefore of high importance. Yellow was the colour for Imperial China: yellow was an exclusive colour of the imperial family during some Dynasties (e.g., the Qing dynasty)(Garrett 2008) and is a colour venerated in Buddhism. Taiwan has a Chinese-influenced culture, and it seems that yellow plumage convinces people to pay a higher price for bird species in the Taiwanese pet trade.

The price of birds was apparently less affected by variables relating to the realm of origin or native breeding range size. The effects of realm of origin and native breeding range size, which I predicted would affect price through availability, are presumably captured more directly by other availability measures, such as number for sale and whether or not a species is native.

Phylogenetic analysis identified a strong phylogenetic correlation in bird price. Related species thus tend to vary in price in a similar manner, which suggests that the factors that determine price are similar for related species. In fact, at least three of the four main predictors of price would be expected to show strong phylogenetic autocorrelation: body mass (Freckleton et al. 2002), threat status (Bennett and Owens 1997), and alien status, the last given that several of the families with birds for sale in Taiwan have no native species (e.g. parrots, turacos, tanagers). The phylogenetic correlation for analysis of the fourth main predictor - numbers of birds for sale - is also strong (**Table 4.2**). However, why this should be so is less clear, especially given that the abundances of bird species in the wild tend to show relatively low phylogenetic correlation (e.g. (Boehning-Gaese and

Oberrath 1999; Webb et al. 2007)). It may be that some bird taxa are easier to catch, survive better in transportation, and/or are easier to breed in captivity.

4.5.1 Implications

Alien invasive species have a wide range of environmental impacts (Blackburn et al. 2014a), and are one of the largest threats to the persistence of native species (Clavero and Garcia-Berthou 2005). In Taiwan, for example, the endemic Styan's bulbul *Pycnonotus taivanus* is categorised as vulnerable on the IUCN Red List due to hybridization with the introduced alien Chinese bulbul *P. sinensis*. The aim of this study was to provide insight into the contribution of the cage bird trade to bird invasions. Assuming that cheaper birds are more likely to be liberated (or conversely that more expensive birds are less likely to be so), and species more commonly sold also more likely to escape or be released, then one might conclude from the results that pet shop birds represent a low risk for alien bird invasions in Taiwan. The cheapest species in pet shops are native, as are the species most likely to be bought for prayer release. Prayer birds typically need to be readily and cheaply available (Environment and Animal Society of Taiwan 2009). Prayer animals are released regardless of whether or not they are alien to Taiwan, but alien bird species are often priced higher in the shops. Thus, cheaper native species are presumably much easier to source for shops, especially for sale for prayer release. The three most abundant species recorded in pet shops in the survey are all frequently released in religious ceremonies in Taiwan, and are native. All of this suggests that most of the individuals and species likely to be liberated in Taiwan do not present a risk of alien invasion because they are not alien. Pet shop birds nevertheless still present a non-trivial invasion risk. Most of the species sold are alien (68%), and some of them are available for sale in reasonable numbers and at relatively low price (**Figure 4.1** and **Figure 4.2**). There is therefore the potential and opportunity for some alien species to be introduced to the wild, and in the sort of numbers required to promote population establishment (which is a positive function of the number of birds introduced (Cassey et al. 2004a; Lockwood et al. 2005; Blackburn et al. 2009b; Blackburn et al. 2011). This likelihood may be further increased by the dynamics of the bird trade. Robinson (2001) showed that a high price for rare species can drive oversupply when traders and breeders rush to fulfil demand, with the result that market prices can decline rapidly. When demand is saturated and the market is low on profit, owners of breeding farms or pet shops would be more likely to release their birds (although not while species still sell for higher prices than other similar species). Alternatively, to minimise losses arising from the maintenance of unsold and unsellable birds in shops, pet shops may sell birds at a lower price for religious events.

Previous studies have also shown that when the sale of wild birds is prohibited (i.e. due to avian influenza), vendors were more likely to move to the illegal trade, or to release birds directly into the wild (Brooks-Moizer et al. 2008). Many Asian countries have gone through outbreaks of avian flu since 2004 (Forster 2013), and the bird trade in Taiwan is at risk of being affected by the disease or trade bans of nearby countries. A trade ban could therefore cause species to be released by vendors, whether alien or native. I suspect that species released this way would be likely to be those with lower economic value and to be more abundant in shops. However, maintaining higher value alien species costs more, and so owners may release the birds when their economic situation worsens. Therefore, I would not exclude the possibilities of pricier alien species also being released into the wild in these particular circumstances. I explored the influence of price on the likelihood of introduction and establishment in the Chapter 5.

Solutions for preventing alien bird releases could, and do, target both the sources of the birds in trade, and the customers sustaining the trade. The numbers of traded individuals could be reduced through control of the sources of birds (wild capture and illegal imports); some such controls are already in place in Taiwan (Severinghaus and Chi 1999; Agoramoorthy 2009). Educating the general population about the risk of releasing alien pet birds may have limited impact in the Asian context, because many purchases are for religious and cultural reasons and not only for companionship or status. Campaigns are already undertaken to discourage prayer release in Taiwan (Environment and Animal Society of Taiwan 2004; Environment and Animal Society of Taiwan 2009), although this practice continues to be commonplace there. An alternative approach (inspired by Venerable Bengkong Shi (Nuwer 2014)) would be to co-opt the religious reasons for buying and releasing animals, and so gradually to replace the ceremonial release of randomly chosen (and potentially harmful) prayer animals with planned releases of native species for conservation purposes, such as re-introductions. This process could incorporate ritual ceremonies to pray for the welfare of the animals before they are released.

Chapter 5 Establishment: The Wildlife Pet Trade as a Driver of Introduction and Establishment in Alien Birds in Taiwan

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5.1 Abstract

The global trade in alien cage birds is flourishing and is considered to be one of the major routes by which species are entrained into the human-mediated invasion pathway. Here, I explore the likely influence of the wild bird trade on alien bird invasions in Taiwan. Specifically, I analyse the characteristics of alien bird species that have been successfully introduced and established at large in the wild. I use phylogenetic regression models to compare the traits of alien species recorded in the cage bird trade in Taiwan that have (or have not) subsequently been recorded at large in the wild, and the traits of species recorded in the wild that have (or have not) established (using data on breeding success as a proxy). Alien species were more likely to be recorded as successfully introduced if they were commonly for sale in the Taiwanese pet bird trade, and possessed songs considered to be more attractive to people. Species that have been sold in the pet market for a longer period were also more likely to have been recorded in the wild. Establishment success was more likely for large-bodied bird species, but not strongly related to other predicted determinants of success, including proxies for propagule pressure and climate matching. I conclude that the pet trade influences bird invasions in Taiwan by determining which species are exposed to novel environments there, but which of those introduced species goes on to establish may depend more on their intrinsic life histories.

5.2 Introduction

Geographical barriers to species distributions are being increasingly broken down by human activities, such that species are transported beyond their natural ranges to locations where they do not naturally occur (Blackburn et al., 2009a, 2011; Davis, 2009; Wilson et al., 2009;

Richardson et al. 2011). These species (here termed aliens) may subsequently establish populations in new recipient areas, and some may proceed to spread widely (i.e., invasive species) causing negative economic and environmental impacts (Kolar and Lodge 2001; Blackburn 2004; Frenot et al. 2005; García-Moreno et al. 2007). These impacts have prompted an extensive body of research to understand the processes that lead species to become alien invaders.

The invasion process can usefully be studied as a sequence of stages, termed the 'invasion pathway' (Blackburn et al. 2011). In order to become 'invasive', species need to be successfully transported outside their native range, to escape or to be released from captivity or cultivation to new environments, to establish a sustainable population, and then to spread widely across the new environment. Fundamental to explaining the invasion process is an understanding of the identities and characteristics of the different species pools that lead them to complete each of these stages successfully (Kolar and Lodge 2001).

One route in which species become entrained in the invasion process is through the global wildlife trade and pet market (Westphal et al. 2008; Carrete et al. 2012). (BirdLife International 2008) estimated that, in the 1990s, 2-5 million birds were involved in the global bird trade annually, while Nash (1993) estimated that 1-3 million individual songbirds were traded in Eastern countries in the same period. The number of birds acquired for bird-keeping has been estimated to be more than 2 million annually in Indonesia alone. Studies have shown that the composition of species transported in the pet market is influenced by a combination of societal demands and species availability (Blackburn et al. 2009b; Chapter 3). For example, birds in the pet trade in Taiwan are more likely to be widespread species, of small body mass, with attractive songs, than expected by chance (Chapter 4).

Species in the pet trade can become alien invaders if they are released or escape from captivity, and subsequently succeed in establishing a viable population. A key question is whether we can identify characteristics that distinguish those alien species in the pet trade, which make these transitions, from those that do not. Here, I use the cage bird market in Taiwan as a case study to test for some of these characteristics.

Taiwan has an extremely active trade in alien cage birds. More than 180,000 individuals of over 200 parrot species were imported there between 2001 to 2011, from 20 countries (Wong et al. 2012). In a survey in 1995, Severinghaus and Chi (1999) found that 6% of the more than 68,000 prayer birds recorded for sale in Taiwan were alien species, but this had risen to more than 68% of the 7,634 birds recorded for sale in 2012 in (Chapter 3). Taiwan also has a large number of alien bird species known from the wild: 90 species have been recorded at large there, of which at least 25 have been recorded breeding (see Methods). More than 60% of alien bird species found in the wild are species known to have been traded in the Taiwanese pet market (Lee and Shieh 2005). I therefore predicted that the probability that an alien species is found in the wild in Taiwan is largely determined by the composition of the pet trade, and so depends on the same combination of societal demands and species availability that results in the mix of species in that trade (Chapter 3). I also predicted that availability determines the likelihood that an introduced species establishes a viable population, along with additional influences of the characteristics that relate to the likelihood that a species can cope with the Taiwanese environment.

Whether or not traded species get introduced into the wild depends on the likelihood that they will escape or be released. This is likely to be dependent on their abundance in shops - as commonly sold species by chance alone would be more likely to find their way into the wild - and on how much attention is provided to their care. Valuable species may be less likely to escape or be deliberately released, because more care is taken in their maintenance. Conversely, the common Taiwanese practice of prayer bird release (Shiu & Stokes 2008; Environment and Animal Society of Taiwan 2009), wherein large numbers of individuals bought from pet shops are deliberately freed, mainly concerns cheaper species (and species sold in large numbers), both native and alien (Chapter 4). I predicted that price will therefore be negatively correlated, and abundance in shops positively correlated, with the likelihood that an alien bird species in trade is also found in the wild. In Taiwan, the pet bird trade is also partly driven by bird singing competitions, and species with attractive songs may be more valued and better secured from escaping. I therefore also predicted that the attractiveness of bird songs to humans would be negatively correlated with the likelihood that a traded species is found in the wild.

Whether traded species are recorded as being introduced into the wild is likely to depend on how easily observable they are. The likelihood of being observed will again depend on the likelihood of escaping, but also on the species' conspicuousness. I expect larger-bodied, longer-lived birds to be more likely to be recorded, but given that these two traits are positively correlated (Peters 1983), I test only for the predicted positive effect of body size on the likelihood that a traded species is found in the wild.

Following introduction into the wild, subsequent establishment success has been shown to depend primarily on the number of individuals released, or 'propagule pressure' (Lockwood et al. 2005; Blackburn et al. 2009a; Blackburn et al. 2015). I do not have direct estimates of propagule pressure for alien birds in Taiwan, but would expect it to increase with the number of birds available for sale (and decrease with price), as more abundantly sold (and cheaper) species may escape or be deliberately released in larger numbers. Geographic range size and environmental matching have also been shown to be related to establishment success in birds (Blackburn and Duncan 2001a; Duncan et al. 2006), as has body size in some studies (Cassey 2002) Therefore, I predicted that species with larger native ranges, and that originate from biogeographic realms or latitudes closer to those of Taiwan, will be more likely to establish populations. I tested for an effect of body mass on establishment success, although previous studies of this effect have been inconsistent, finding positive (Green 1997; Cassey 2002), negative (Cassey 2008), or no significant effects (Duncan et al. 2006).

Liberated alien species may take decades or longer before their populations increase and they become classified as successfully established (Runde et al. 2007). Species for sale in Taiwanese pet shops earlier, or over a longer period, may therefore be more likely to have established populations, and indeed to be recorded in the wild. Hence, I also explored whether the time period when bird species were recorded for sale in shops relates to these metrics, using data from the most comprehensive independent pet shop surveys conducted across country in three well-separated years (1994, 2004 and 2012).

5.3 Method

5.3.1 Data

The analyses of the introduction and establishment of alien birds from the Taiwanese pet trade considered two dependent variables from the invasion pathway:

(1) Introduction success (or failure): whether or not an alien species recorded in a pet shop survey has been recorded at large in the wild. The records of alien bird species in the wild in Taiwan were obtained from (Severinghaus 1999) and the Chinese Wild Bird Federation (CWBF) database for the years 1980 to 2014. These sources provided a total of 90 alien bird species recorded in the wild (**Table 5.1**).

(2) Establishment success (or failure): whether or not a species recorded in the wild has also been recorded breeding there. While breeding records do not guarantee that an alien population is self-sustaining, species that are breeding have certainly progressed further along the invasion pathway than those have been observed in the wild but with no breeding records. Information on whether or not an alien species had been recorded breeding in the wild in Taiwan was obtained from the (Severinghaus 1999), CWBF database,

CWBF Checklist of Bird in Taiwan and its appendix in 2012-2014 (alien species with breeding records listed as introduced rather than established), Breeding Bird Survey Taiwan from 2009 to 2013 (Ko et al. 2013) and (Cheng 2010). To increase the likelihood that the population is actually established, I only considered a species as established if it was recorded breeding in more than one of these sources (n = 25, see **Table 5.1**). I obtained data on alien species for sale in Taiwanese pet shops from three surveys: Chi (1995), Shieh et al. (2006) and Chapter 4 (2015). Chi (1995) surveyed 164 shops in 1994, and included information on the identity and numbers of 84 alien species for sale. Shieh et al. (2006) surveyed 146 shops in 2004, including information only on the identity of 239 alien species for sale. Chapter 4 (2015) surveyed 72 shops from August to November 2012, and recorded information on the identity, price, and numbers of 170 alien bird species for sale. Hereafter I refer to these as: (i) 'Chi's survey'; (ii) 'Shieh's survey'; and (iii) 'my survey'.

I collected information on the following predictor variables for each of the species recorded across all three pet shop surveys:

(1) Geographical range size (km^2): a measurement of native geographic range extent (Gaston 1991; Gaston 1994a), acquired from the data collated by (Orme et al. 2006). Areas of total native breeding range for all species were converted to polygons on equal area grids with a cell size of 96.3 km x 96.3 km. This specified a scale identical to 1° grids at the equator. The native breeding area of each species was estimated by summing the areas of the cells in which they occurred (Orme et al. 2006; Blackburn and Cassey 2007). These values were natural log transformed for analysis.

(2) Biogeographic realms: Species were assigned to realms as defined using the World Wildlife Fund eco-regions map (Olson et al. 2001), on the basis of the region in which the largest part of their native range fell.

(3) Latitude of origin (degrees): this is defined as the latitudinal mid-point of the native geographic range, calculated as the median latitude of the central point of the grid cell where species occurs. The absolute values of the median latitude +1 were used for analysis. The values were natural log transformed for analysis. I incorporated a squared term to account for the fact that species from mid-latitudes (i.e. latitudes close to that of Taiwan) may be more likely to be able to breed in the wild in Taiwan.

(4) Body mass (g): a measurement of body size of bird species from (Dunning 1992), acquired from the data used in (Olson et al. 2009). The values were natural log transformed for analysis.

(5) Metric of song attractiveness: following the approach in (Blackburn et al. 2014b), the numbers of song tracks for a given species on the Xeno-Canto website (www.xeno-canto.org) were used to produce a metric of song attractiveness to humans. The metric is calculated as a species' residual deviation from a generalised linear model (GLM) of the natural log+1 numbers of songs lodged on Xeno-Canto versus natural log geographic range size, using Gaussian errors and an identity link. Larger residuals are taken to indicate that a species' songs are more attractive to humans (Blackburn et al. 2014b).

(6) Number of birds for sale: from the data collected in Chapter 2 and Chi (1995). The values were natural log transformed for analysis.

(7) Price of birds for sale (US$): From the data collected in Chapter 2. The values were natural log transformed for analysis.

As *Trichoglossus rubritorquis* is sometimes treated as a subspecies of *Trichoglossus haematodus* (e.g. Jetz et al. 2012), the numbers of alien birds for sale, song attractiveness, latitude of origin, native range size and their body masses were available for 169 of the 170 species recorded for sale in my survey. Data on the price of alien species displayed for sale was available for 167 species. Therefore the introduction analysis was conducted on 167 species.

5.3.2 Analysis

All analyses were conducted in R version 3.0.3, using the *caper* and *phylolm* packages.

I tested for phylogenetic correlation among species in terms of whether or not they were introduced, and whether or not they were established. These are both binary variables, and so I calculated the phylogenetic threshold model D statistic, (function *phylo.d* in the R package *caper*), a measure of phylogenetic signal strength in binary traits proposed by Fritz and Purvis (2010). D = 1 when the sum of sister-clade differences in a binary trait is phylogenetically randomly distributed throughout the tips of the phylogeny, whereas D = 0 if the trait evolved under a Brownian threshold model. Although introduction and establishment success are not evolved traits, they may be correlated with species traits that are (Cassey 2002), and the threshold model for calculating character dispersion on a phylogeny provides a way to scale phylogenetic signal strength under a specified evolutionary hypothesis (Fritz and Purvis 2010). The phylogenetic tree for birds is not known for certain (Jetz et al. 2012), and so I incorporated uncertainty about the true phylogenetic relationship by repeating the analyses on 100 different phylogenetic trees for the species, sampled at random from birdtree.org, and calculating the median, 1st and 99th percentiles value of D over all trees.

For the species recorded for sale in Taiwan by my survey, I tested for differences in the characteristics of species that have been recorded as introduced (n = 40) versus those that have not (n = 130). Likewise, for species recorded for sale in Taiwan by Chi's survey, I compared characteristics of the species recorded as introduced (n = 46) versus those not (n = 38). (Shieh et al. 2006) included information only on the identity of alien species for sale, and not on their numbers (a key predictor under my hypotheses), and so I did not test for differences in introduction success for the species in Shieh's survey.

I generated models of whether or not a traded species in my survey was introduced in terms of the variables I had predicted to affect it: price, numbers of bird for sale, song attractiveness, and body mass. I used the *phyloglm* function in the R package *phylolm* (Tung Ho and Ane 2014) to test each of the predictor variables separately, and to fit all possible multivariate models from these predictor variables, using a phylogenetic logistic regression approach (Phylogenetic Generalized Linear Model) (Ives and Garland 2010). I again repeated the analyses on 100 different phylogenetic trees to incorporate uncertainty about the true phylogenetic relationship. For each phylogenetic tree, the best model was identified based on Akaike's Information Criterion adjusted for small sample size (AICc), and the set of most likely models (those with ΔAICc < 4). I used these models to calculate the Akaike weight for each model and the variable importance for each predictor variable.

The same analytical methods were used to test for determinants of whether or not a traded species in Chi's survey was introduced into the wild. I used the numbers of birds for sale, song attractiveness and body mass as predictor variables.

The predictor variables for the determinants of establishment success were price, numbers of birds for sale, latitudinal mid-point of the range, body mass and native breeding range size. Latitudinal range mid-point is a significant predictor of biogeographic realm of origin in my data (adjusted $r^2 = 0.49$, $F_{4,161} = 40.3$, $p < 0.001$), and so I used only the former, continuous variable (including a quadratic term), in the analyses. I tested for difference in the characteristics of introduced species considered to be established (n = 18) versus those introduced but considered not to be established (n = 22). I again performed the analysis using data from Chi's survey, in which, 17 introduced species were considered to be established, and 29 not (**Table 5.1**).

I used the R package *VennDiagram* (Chen and Boutros 2011) to visualise the overlap between the numbers of introduced species across surveys, and the R package *beanplot* (Kampstra 2008) for box plots.

5.4 Results

The three pet shop surveys, together with the sources of data for introduced and established species, included a total of 341 alien bird species recorded in Taiwan, of which 312 species were recorded for sale in pet shops. Of the 90 alien species recorded as introduced in Taiwan, 29 (32.3%) were recorded in all three surveys (**Figure 5.1**), versus 15 of the 251 (6%) alien bird species not recorded as introduced; there is a strong relationship between whether or not species were traded and their wild record status ($\mathbf{c}^2 = 38.3$, df = 1, $p < 0.001$). A high percentage of both introduced and established species were those that had been recorded for sale: almost 70% of the introduced species (62/90) and more than 90% (23/25) of established species occurred in at least one of the three pet shop surveys (**Table 5.1**). The percentage of bird species in a survey that were introduced differs across surveys ($\mathbf{c}^2 = 33.9$, df = 2, $p < 0.001$), but the percentage of introduced alien bird species that have established does not ($\mathbf{c}^2 = 0.8$, df = 2, $p = 0.65$).

Table 5.1 The numbers of introduced and established bird species recorded in each survey. The numbers of bird species recorded as introduced, and the numbers of those introduced species considered to be established, or not, in Taiwan under the criteria (Total), together with the number of these species also recorded for sale in Taiwanese pet shops in Su's, Shieh's and Chi 's survey. Percentages are provided for the species in each survey that were successfully introduced, and for the species subsequently considered to be established.

Category of species	Total	Su	Shieh	Chi
Recorded for sale		170	239	84
Introduced	90	40 (23.5%)	55 (23.0%)	46 (54.8%)
Not introduced		130	184	38
Established	25	18 (45.0%)	20 (36.4%)	17 (37.0%)
Not established	65	22	35	29

Whether or not the alien species recorded in my survey were introduced into the wild showed an intermediate level of phylogenetic correlation (median D value = 0.46. 1st and

99th percentiles over 100 likely phylogenetic trees: 0.39, 0.52), and the same is true for the alien species recorded for sale in Chi's survey (D = 0.47, 1st and 99th percentiles: 0.42, 0.51). Likewise, establishment success showed an intermediate level of phylogenetic correlation across the species recorded in my survey (D = 0.38, 1st and 99th percentiles: 0.32, 0.44) and in Chi's survey (D = 0.55, 1st and 99th percentiles: 0.50, 0.59).

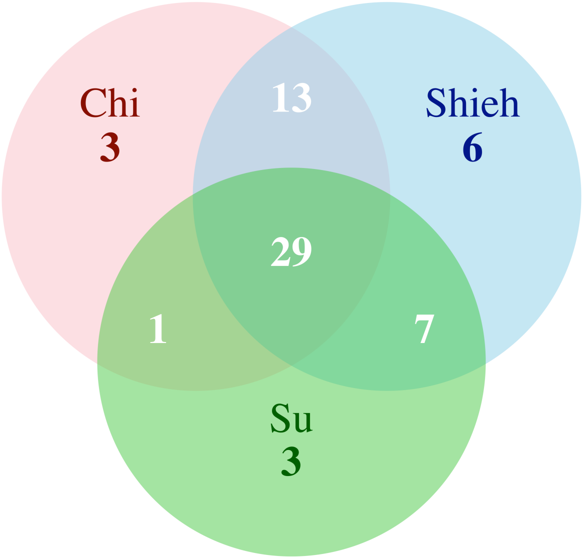


Figure 5.1 The numbers of the introduced species overlap across mine (Su, n = 40), Chi's (Chi n = 46) and Shieh's (Shieh n = 55) surveys.

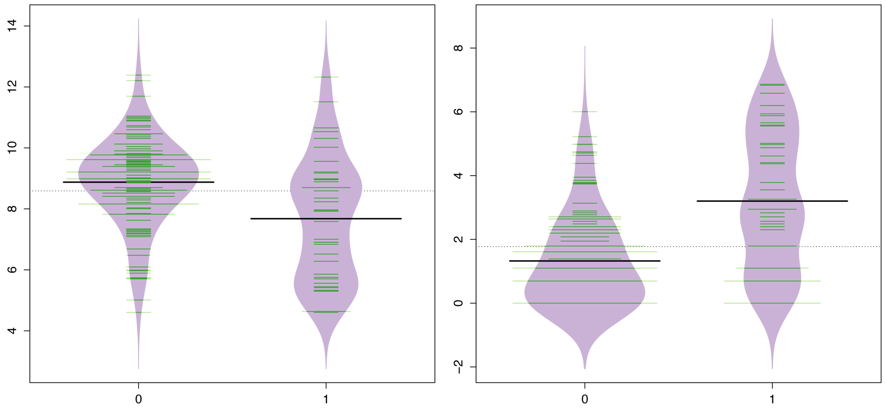
Univariate analysis revealed that introduction success for bird species recorded for sale in my survey was related to the numbers of birds for sale, their price and song attractiveness (**Figure 5.2**). The most likely model (of three models with ΔAICc < 4) was composed of just two factors: positive effects of both the numbers of birds for sale and song attractiveness (**Table 5.2**). These two variables were also present in all the most likely models (median variable importance = 0.99, 1st and 99th percentiles: 0.99, 0.99). Both of the other two predictor variables (price and body mass) were included in the other two most likely models as negative effects, albeit with lower variable importance (**Table 5.2**). The three most likely models accounted for >94% of the Akaike weight across all models.

Univariate analysis revealed that introduction success for bird species recorded for sale in Chi's survey was related to the numbers of birds for sale only (**Figure 5.3**). The best model (of four models with ΔAICc < 4; which accounted for 92% of the Akaike weight) also included the numbers of birds for sale, which had a median variable importance value of

0.93 (1st and 99th percentiles: 0.88, 0.96) (**Table 5.3**). Song attractiveness and body mass did not have strong effects on introduction success for the birds recorded in Chi's survey.

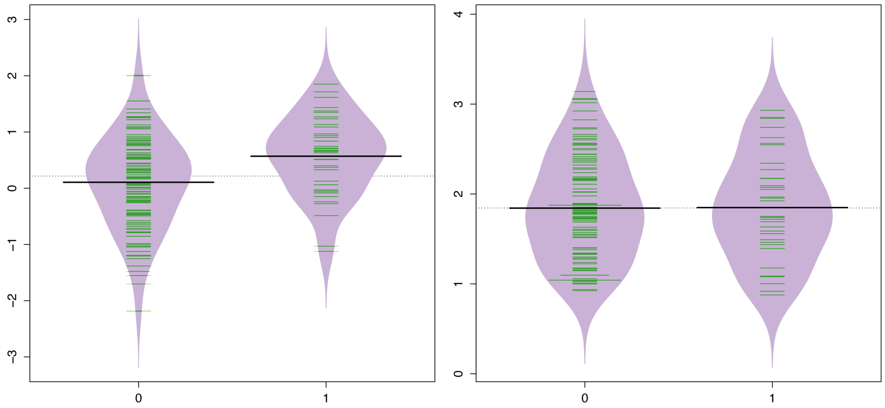
For establishment success, univariate analysis found that none of the tested variables had a strong effect on whether or not an introduced alien species recorded from my pet shop survey was established in Taiwan, although there was a moderate negative effect of price (**Table 5.4**a). Phylogenetic logistic regression analysis identified seven models with ΔAICc < 4, but only body mass was a consistent predictor of establishment success (**Table 5.5**); Body mass was present in all the most likely models, with a median importance value of 0.98 (1st and 99th percentiles: 0.96, 0.99).

None of the tested variables showed a strong effect on whether or not the introduced alien species recorded in Chi's survey were established in univariate analysis (**Table 5.4**b). Phylogenetic logistic regression analysis identified four models with ΔAICc < 4 (**Table 5.6**). Body mass was again the best predictor of establishment success. The most likely model, with an Akaike weight of 0.39, included just body mass, and body mass had a median importance value of 0.89 (1st and 99th percentiles: 0.75, 0.95) across all models. Latitudinal mid-point was not included in any of the most likely models.



(a) Estimate: −0.4 (−0.64, −0.26); P: 0.001 (< 0.001, 0.01)

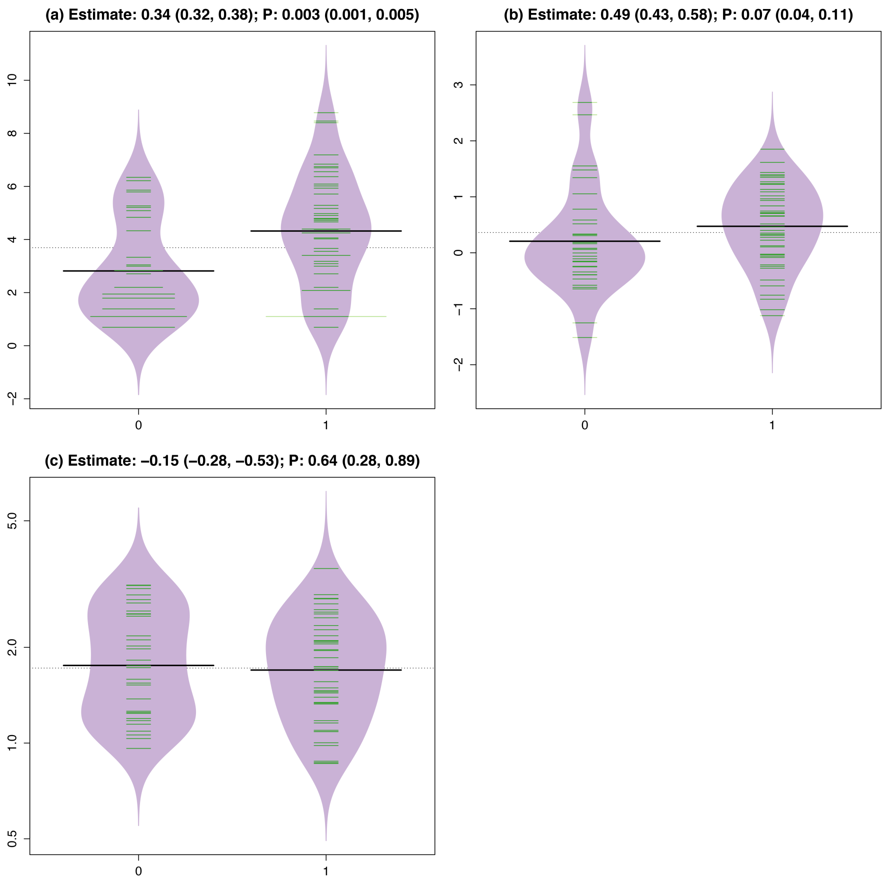
(b) Estimate: 0.5 (0.46, 0.54); p: < 0.001 (< 0.001, < 0.001)



(c) Estimate: 0.72 (0.68, 0.77) ; p: 0.001 (0.001, 0.002)

(d) Estimate: −0.23 (−0.4, 0.004); p: 0.59 (0.36, 0.91)

Figure 5.2 The relationship between whether alien species recorded for sale in pet shops in my survey (n = 167) were introduced into the wild in Taiwan (1) or not (0), and (a) log sale price, (b) log number of birds for sale, (c) song attractiveness and (d) log body mass. The green lines indicate individual observations, the solid black lines represent the means of the observations, the dotted line represent overall average and the purple areas show the distribution. Estimates and p-values represent: median value of phylogenetic regression coefficients (1st and 99th percentiles), calculated over 100 phylogenetic generalized linear models, each using a different likely phylogeny for the 167 species.



(a) Estimate: 0.34 (0.32, 0.38); P: 0.003 (0.001, 0.005)

(b) Estimate: 0.49 (0.43, 0.58); P: 0.07 (0.04, 0.11)

(c) Estimate: −0.15 (−0.28, −0.53); P: 0.64 (0.28, 0.89)

Figure 5.3 The relationship between whether alien species recorded for sale in pet shops in Chi's survey (n = 79) were introduced into the wild in Taiwan (1) or not (0), and (a) log number of birds for sale, (b) song attractiveness and (c) log body mass. The green lines indicate individual observations, the black lines the means of the observations, the dotted line represent overall average and the purple areas show the distribution. Estimates and p-values represent median value of phylogenetic regression coefficient, (1st and 99th percentiles) calculated over 100 phylogenetic generalized linear models, each using a different likely phylogeny for the 79 species).

Table 5.2 The results of phylogenetic generalized linear models testing whether alien species recorded for sale in pet shops in my survey were introduced (n = 167). M1 – M3 are the most likely three models (those with ΔAICc < 4). The numbers for each variable represent the median, 1st and 99th percentiles of the model coefficients.

Variable	M1	M2	M3	Importance
Log numbers of birds for sale	0.53 (0.48, 0.54)	0.51 (0.5, 0.53)	0.46 (0.35, 0.53)	0.99 (0.99, 0.99)
Song attractiveness	1.08 (0.98, 1.12)	1.07 (1.03, 1.1)	0.99 (0.83, 1.18)	0.99 (0.99, 0.99)
Log body mass		−0.16 (−0.23, −0.09)		0.29 (0.24, 0.33)
Log price			−0.12 (−0.17, 0.04)	0.15 (0.02, 0.24)
Intercept	−2.7 (−2.79, −2.43)	−2.34 (−2.46, −2.19)	−1.39 (−2.96, −0.97)	
ΔAIC	0 (0, 0)	1.73 (1.43, 1.96)	1.9 (3.32, 8.51)	
Akaike weight	0.59 (0.49 - 0.69)	0.24 (0.21, 0.28)	0.11 (0.009, 0.2)	

Table 5.3 The results of phylogenetic generalized linear model testing whether alien species, recorded for sale in pet shops in Chi's survey, were introduced (n = 79). M1 - M4 were the most likely four models (those with ΔAICc < 4). The numbers for each variable represent the median, 1st and 99th percentiles of the model coefficients.

Variable	M 1	M 2	M3	M4	Importance
Log numbers of birds for sale	0.34 (0.32, 0.38)	0.33 (0.31, 0.36)	0.35 (0.31, 0.37)	0.34 (0.32, 0.36)	0.93 (0.88, 0.96)
Song attractiveness		0.40 (0.35, 0.43)		0.41 (0.37, 0.45)	0.49 (0.44, 0.52)
Log body mass			0.03 (−0.06, 0.12)	−0.03 (−012, 0.03)	0.28 (0.26, 0.31)
Intercept	−0.91 (−1.09, −0.85)	−1.04 (−1.17, −0.95	−1.01 (−1.25, −0.71)	−1.01 (−1.2, −0.76)	
ΔAIC	0	0.34 (0.11, 0.64)	2.08 (1.96, 2.34)	2.35 (2.06, 2.65)	
Akaike weight	0.37 (0.34, 0.40)	0.31 (0.29, 0.33)	0.13 (0.11, 0.14)	0.11 (0.1 - 0.12)	

Table 5.4 The results of univariate phylogenetic generalized linear model testing whether alien species recorded in the wild were also breeding in the wild, based on species recorded for sale in a) my survey, n = 40; and b) species recorded in Chi's survey, n = 46.

a

Variable	Estimate	p
Log price	−0.4 (−0.42, −0.38)	0.05 (0.04, 0.05)
Log numbers of birds for sale	0.1 (0.07, 0.14)	0.47 (0.31, 0.6)
Latitudinal mid-point (quadratic)	−0.84 (−0.88, −0.72)	0.07 (0.06, 0.14)
Latitudinal mid-point (log+1)	3.78 (3.31, 4.04)	0.09 (0.06, 0.16)
Log body mass	1.13 (1.09, 1.17)	0.14 (0.13, 0.15)
Log geographic range	0.32 (0.23, 0.33)	0.06 (0.06, 0.22)

b

Variable	Estimate	p
Log numbers of birds for sale	0.01 (−0.08, 0.17)	0.93 (0.6, 0.99)
Latitudinal mid-point (quadratic)	−0.03 (−0.29, 0.09)	0.86 (0.24, 0.99)
Latitudinal mid-point (log+1)	0.25 (−0.15, 1.18)	0.18 (−0.11, 1.13)
Log body mass	1.05 (0.96, 1.6)	0.1 (0.04, 0.12)
Log geographic range	0.07 (0.59, 0.08)	0.62 (0.58, 0.7)

Table 5.5 The results of phylogenetic generalized linear models testing whether introduced species were also recorded breeding there, based on alien species recorded in my survey (n = 40). M1 - M7 are the most likely models (ΔAICc < 4). The numbers for each variable represent the median (1st and 99th percentiles) of the model coefficients.

Variable	M 1	M2	M3	M4
Log body mass	1.13 (1.09, 1.17)	2.03 (1.47, 2.54)	1.44 (1.36, 1.51)	1.15 (1.104 1.19)
Log price		−0.26 (−0.46, −0.15)		
Latitudinal mid-point (quadratic)		−0.51 (−1.01, −0.45)	−0.54 (−0.59, −0.49)	
Latitudinal mid-point (log+1)		2.13 (1.9, 4.23)	2.29 (2.15, 2.45)	
Log geographic range				
Log numbers of birds for sale				0.08 (0.07, 0.1)
Intercept	−2.94 (−3.03, −2.81)	−4.23 (−4.42, −3.16)	−5.56 (−5.71, −5.33)	−3.08 (−3.22, −2.83)
ΔAIC	0 (0, 1.97)	0.89 (0, 9.67)	1.46 (1.23, 3.84)	1.65 (1.56, 3.64)
Akaike weight	0.22 (0.13, 0.37)	0.15 (0.002, 0.27)	0.11 (0.05, 0.19)	0.1 (0.05, 0.16)

Variable	M5	M6	M7	Importance
Log body mass	1.84 (1.48, 2.04)	1.53 (1.42, 1.71)	1.75 (1.33, 2.42)	0.98 (0.96, 0.99)
Log price	−0.28 (−0.39, −0.17)		−0.25 (−0.53, −0.14)	0.45 (0.11, 0.69)
Latitudinal mid-point (quadratic)		−0.6 (−0.55, −0.46)	−0.83 (−0.9, −0.68)	0.38 (0.18, 0.53)
Latitudinal mid-point (log+1)		2.36 (2, 2.58)	3.64 (3.01, 3.73)	0.38 (0.18, 0.53)
Log geographic range	0.003 (−0.06, 0.06)		−0.008 (−0.02, 0.27)	0.27 (0.12, 0.4)
Log numbers of birds for sale	0.07 (0.05, 0.12)		0.22 (0.1, 0.34)	
Intercept		−2.33 (−2.09, −0.06	−5.89 (−6.09, −5.76)	−5.54 (−5.66, −5.31)
ΔAIC	2.03 (0, 5.05)	3.22 (2.91, 5.42)	3.53 (2.31, 14.21)	
Akaike weight	0.12 (0.02, 0.27)	0.04 (0.02, 0.07)	0.04 (0.0001, 0.08)	

Table 5.6 The results of phylogenetic generalized linear model testing whether alien species recorded in the wild were also recorded breeding there, based on data from alien species recorded as for sale in pet shops in Chi's survey (n = 46). M1 - M4 are the most likely four models (those with ΔAICc < 4). The numbers for each variable represent the median (and 1st and 99th percentiles) of the model coefficient.

Variable	M 1	M2	M3	M4	Importance
Log body mass	1.05 (0.96, 1.6)	1.05 (0.88, 1.6)	1.68 (1.01, 1.81)	1.35 (0.82, 1.8)	0.89 (0.75, 0.95)
Log numbers of birds for sale		0.07 (0.03, 0.12)	0.15 (009, 0.2)		0.37 (0.22, 0.52)
Log geographic range			0.02 (−0.03, 0.14)	0.09 (−0.09, 0.24)	0.28 (0.18, 0.47)
Intercept	−2.46 (−3.97, −2.17)	−2.67 (−4.5, −2.25)	−5.01 (−5.18, −4.09)	−4.59 (−4.72, −2.08)	
ΔAIC	0 (0, 0.33)	1.15 (0, 3.05)	3.01 (1.31, 6.43)	3.07 (0, 11.18)	
Akaike weight	0.39 (0.26, 0.56)	0.18 (0.1, 0.32)	0.09 (0.02, 0.17)	0.07 (0.002, 0.31)	

5.5 Discussion

The pet trade is one of the primary pathways by which bird species continue to be globally transported. Although it is not the primary aim of the pet trade to introduce birds to new wild environments, pet bird species can become alien invaders if they are released or escape from captivity, and subsequently go on to establish a viable population (Hulme et al. 2008). The situation in Taiwan, where the pet trade is extremely active, suggests that this can easily happen. More than 300 alien bird species have been recorded in the bird trade in Taiwan in just three surveys, and 90 alien bird species have been recorded in the wild. At least 25 alien bird species breed in Taiwan, and 23 of these species have been recorded for sale in Taiwanese pet shops. Thus, the wildlife pet trade appears to be a major driver of the introduction and establishment of alien birds in Taiwan.

Previous studies have shown that the level of international trade and the volume of merchandise imports are positively correlated with the numbers of invasive species across countries (Westphal et al. 2008). This implies that one of the key determinants of the likelihood that a species is introduced is its availability for release or escape (Lee and Shieh 2005; Severinghaus 2007; Blackburn et al. 2015) and therefore species abundance in captivity is predicted to provide important information for understanding the invasion process. My analysis revealed that, as expected, species abundance in captivity is a strong and consistent predictor of which pet shop species have been recorded at large in the wild. This result also holds for species abundance in captivity as recorded in Chi's survey, two decades earlier, and has also been shown by Lee & Shieh (2005) to apply to estrildid finches for sale in Taiwan.

Species that have been available in the pet market for a long period are also much more likely to find their way into the wild, again reflecting the influence of availability on introduction success. As species recorded in all three surveys were much more likely to have been recorded in the wild (32%) than those not (6%). However, what is more surprising is that 28 of the 90 species recorded in the wild were not recorded for sale in Taiwanese pet shops by any of the three surveys, even though these surveys recorded 312 species for sale in total. This suggests either that species are making their way into the wild from other sources, or perhaps more likely, that there are many more species traded in pet shops than have been identified by the three surveys.

The influence of the availability of species for sale on occurrence in the wild is exacerbated in eastern countries like Taiwan by prayer animal release. This is a common practice in Eastern religions such as Buddhism and Taoism, whereby animals are bought only to be released into the wild for good karma (Severinghaus and Chi 1999). Prayer animal release is extremely active in Taiwan, where it has been estimated that 200 million animals are released annually (Environment and Animal Society of Taiwan 2009). Indeed, in 2014, a religious TV channel in Taiwan (Life TV) launched the aim of having 1000 international animal release events, to be carried out in the shortest possible time. These events were practiced across China, Hong Kong, Thailand, Singapore and Malaysia, but mainly in Taiwan (Hai-Tao 2014). Prayer release often involves large numbers of alien species (Severinghaus and Chi 1999), providing a clear link from trade to wild.

Interestingly, while propagule pressure is the most consistent predictor of establishment success in birds (Blackburn et al. 2009a), and other organisms (Lockwood et al. 2005; Hayes and Barry 2008), I did not find strong evidence of an effect of numbers for sale on establishment success for birds in Taiwan (**Table 5.5** and **Table 5.6**). There is no direct information on the numbers of bird released in Taiwan, but the positive effect of numbers for sale on introduction probability (**Table 5.2** and **Table 5.3**) implies that species most commonly sold in Taiwan are more likely to escape or to be released; I would also expect numbers for sale to predict establishment success. The number of birds for sale is negatively correlated to price, while cheaper bird species are more likely to be purchased in abundance for release in religious events (Chapter 4), and I did find some suggestion of a negative effect of price on establishment success (**Table 5.4**). Nevertheless, this effect was weak and inconsistent (**Table 5.5** and **Table 5.6**). The lack of an effect of numbers on establishment success might reflect the poor condition of prayer release birds. These birds have high mortality before they are released. The released birds further suffer 1% mortality, and up to 35% of birds with bad condition that can only perform short flights, in the period immediately after release (Hsu 2008; Environment and Animal Society of Taiwan 2009).

Based on my survey, introduced species are likely to have more attractive songs (**Table 5.2**, **Figure 5.2** and **Figure 5.3**). My prediction was that species with higher song attractiveness would be more valuable to their owners, and hence would be better secured from escaping. However, the univariate relationship between introduction success and song attractiveness is not a simple consequence of co-linearity with price, as this relationship is also recovered in multivariate models. In fact, (Chapter 4) showed a negative correlation between song attractiveness and a species' price for sale in pet shops. One possibility is that the result is a consequence of the popular cultural activity of bird singing competitions in Taiwan. Bird owners often bring their “best singer” individuals to competitions, which are mostly held outdoors, thereby increasing the chance that such species might escape into the wild. I found that in some circumstances, songbirds can also be released deliberately by owners, for example, if purchased birds do not sing as well as expected. This would potentially increase the likelihood that such species would be released, and thus observed in the wild, producing the positive relationship between introduction probability and song attractiveness that I observed.

My analyses revealed no influence of body mass on introduction success in Taiwan. However, it is the most consistent predictor of which introduced species are subsequently recorded as breeding in the wild; this is true for analyses based on data both from my survey and Chi's survey. Some studies have suggested that species with faster population growth are more likely to succeed in establishing, because such populations can rapidly escape the dangers of small population size (Moulton and Pimm 1986; Cassey 2002). In contrast, other studies have suggested that these species are likely to fail in establishment because they face higher stochastic demographic variance than those with lower growth rate (Sæther et al. 2004; Blackburn et al. 2009a). Comparative studies of the relationship between establishment success and life history also suggest that species with slower population growth rates are more likely to succeed in establishing (Blackburn et al. 2009b). Species with slow population growth rate tend to have longer life-span, low rates of reproduction and larger body mass (Blackburn et al. 2009a). My finding of a positive relationship between body mass and establishment success supports the latter view: features associated with slow population growth rates are more likely to determine whether or not introduced species succeed in establishing in Taiwan, following introduction. Such species may be more likely to establish because they are less susceptible to the negative effects of demographic and environmental stochasticity on small founding populations (Sæther et al. 2004; Blackburn et al. 2009a).

My analyses are potentially affected by the difficulty of determining, for many alien species, whether individuals recorded in the wild derive from captivity or have occurred naturally as vagrants. There are 127 species identified as vagrants in the checklist of the birds of Taiwan (CWBF 2012), which is more than the numbers of alien species recorded in the wild since 1980 in my data (Ding et al. 2012). It is possible that some of the individuals of these species originated in captivity, or vice versa, that some of the species recorded as alien introductions are actually vagrants. I took the conservative line that all individuals of species that CWBF 2012 listed as vagrant in Taiwan were actually vagrants. Therefore, the numbers of alien species recorded in the wild is perhaps likely to be underestimated. Vagrants are more likely to come from regions in geographic proximity to Taiwan, but I do not think that this would alter my conclusions. For example, my survey showed that species from nearby geographic regions tend to be sold in larger numbers in pet shops, while species sold in larger numbers are more likely to be introduced (**Table 5.2**). Therefore, excluding vagrants that are actually aliens is likely to exclude species more abundant in shops, and hence bias my results away from the results I found.

In conclusion, my analyses combining records on alien bird species found in the wild in Taiwan with surveys of the pet bird trade spanning 20 years reveal that introduction success is dependent primarily on a species availability for release or escape. This is likely to be because species sold in large numbers are also liberated in large numbers, especially as a result of the practice of prayer animal release. However, this does not translate into an effect of numbers on establishment success, perhaps because many of those birds released are in poor condition. Rather, establishment success is greater for species that theory suggests will be less susceptible to the negative effects of demographic and environmental stochasticity on small founding populations. Thus, the pet trade influences bird invasions in Taiwan by determining which species are exposed to novel environments, but which of those introduced species goes on to establish may depend more on their intrinsic life histories (Sol et al. 2012; Cassey et al. 2014).

Chapter 6 Spread: Geographic Range Expansion of Alien Birds and Climate Match

6.1 Abstract

The international wildlife trade is a significant source of introduced alien species, some of which go on to become invasive and cause negative environmental and economic effects. However, not all introduced aliens establish viable populations, and it is important to identify the factors that determine establishment success. Here, I explore the role of environmental suitability (including anthropogenic influences, climate and habitat types) in establishment success for alien bird species introduced to Taiwan, using maximum entropy modelling. I employ a recursive feature elimination and AIC-based stepwise model selection approach to test whether the environmental suitability, native range size, body size, residence time and the numbers of birds for sale in the shops affect variation in the extent of alien bird range size in Taiwan. I show that species with larger native range sizes and larger body sizes also tend to have larger alien range sizes in Taiwan. There is no effect of environmental suitability on alien range size in Taiwan, but environmental suitability does influence bird species establishment success there.

6.2 Introduction

Human activities are moving species beyond their native geographic boundaries into areas where they do not naturally occur, where these species (here termed aliens) may become invasive, and cause negative environmental and economic impacts (Clavero and Garciaberthou 2005; Simberloff et al. 2013; Blackburn et al. 2014). These impacts provide a strong impetus to understand invasions over and above the intrinsic interest in studying the determinants of environmental change (Broennimann et al. 2007; Rödder and Lötters 2009; Lauzeral et al. 2011; Petitpierre et al. 2012; Strubbe et al. 2013). It is now recognised that the invasion process is most usefully analysed as a sequential series of stages (Blackburn et al. 2011): to become an alien invader, a species has to be transported (by humans) from its native range, be introduced into an area in which it does not naturally occur, establish a sustainable population, and finally spread out from the location of establishment. A species can only be termed an invasive alien if it succeeds in passing through all of these stages. It follows that to understand invasions, one must understand the entire pathway along which a species moves in the process of changing from native to alien (Blackburn et al. 2009a,b).

An interesting case study of the invasion process relates to alien birds in Taiwan (Chapter 3). Here, a variety of bird-related cultural activities, such as religious prayer animal release, bird singing contests and the keeping of cage-birds, shape societal demands for bird species. These demands interact with the availability of bird species in trade to shape the species composition of the pet bird market in Taiwan (Chapter 3), and to determine the characteristics of species that have the opportunity to establish alien populations there. Thus, the bird trade is an important source of introduced species, and at least 70% of introduced species, and 90% of established species, have been recorded in the bird markets in Taiwan (Chapter 5). Bird species are more likely to be released (e.g. as prayer animals) or escape if they are more frequently for sale in the Taiwanese pet bird trade and have been sold in the pet market for a longer period (Lee and Shieh 2005; Chapter 4; Chapter 5). Establishment success is more likely for large-bodied bird species, but not strongly related to other predicted determinants of success (Chapter 5). Here, I extend this work to the final stage of the invasion pathway, and explore determinants of variation in the extent of spread (geographic range size) for alien bird species in Taiwan.

Previous studies have suggested a number of variables that may be associated with alien bird geographic range sizes. One of the most consistent is the numbers of individuals introduced, or propagule pressure (Duncan et al. 1999; Cassey 2001; Blackburn et al. 2006; Signorile et al. 2014; Blackburn et al. 2015). It is not clear why species introduced in larger numbers may be able to spread further, but is possibly because they are less likely to suffer genetic effects arising from a population bottleneck, and are more likely to have individuals with appropriate adaptations to allow spread introduced to the new location (McCauley 1991; Blackburn et al. 2015). Propagule pressure is likely to be high in Taiwan because of prayer animal release and frequent escapes of birds from singing contests, and this should reduce genetic effects arising from population bottlenecks. In addition, a significant numbers of birds for sale in Taiwan are wild caught, and such individuals are more likely to survive after liberation than captive bred birds (Carrete and Tella 2008; Cabezas et al. 2012). The length of time since introduction (residence time) may also be related to alien range size, because species introduced longer ago will have had more time to spread (Duncan et al. 1999; Wilson et al. 2007; Albuquerque et al. 2011).

Species’ life history traits are known to be related to native geographic range sizes (Gaston 2003), and may also be related to alien range size if the same processes determine range size in the native and alien environments (Strubbe et al. 2013; Guisan et al. 2014). Species may experience high demographic variances during dispersal in new recipient environments, such that traits associated with the ability to overcome such stochasticity may help populations to survive (Blackburn et al. 2009b; Schröder et al. 2009). Larger-bodied species tend to have slower population growth rates, and so may be more likely to persist under such conditions (Sæther et al. 2004; Blackburn et al. 2009a); they may also be more readily recorded. Body size also tends to be positively related to native geographic range size (Gaston 2003). Conversely, small-bodied species tend to have faster population growth rates, and so may spread more rapidly for a given residence time (Duncan et al. 1999; Duncan et al. 2001; Mahoney et al. 2015).

Alien geographic range sizes should also be related to features of the recipient environment, and how those interact with the environmental tolerances of the species introduced: spread is not possible if the species cannot survive in the new location. The environmental requirements of many invasive species are conserved in the alien range (Petitpierre et al. 2012; Strubbe et al. 2013), and so the availability of suitable habitats, human interference (Blair 1996; Veech et al. 2011) and climate factors, such as temperature (Hitch and Leberg 2007; Illán et al. 2014) and precipitation (Tingley et al. 2012; Illán et al. 2014), are likely to be critical to the persistence of alien species (Gammon and Maurer 2002; Veech et al. 2011). Species traded in Taiwan are more likely to be derived from nearby biogeographic realms (especially the Indo-Malay and Palearctic) (see Chapter 3), such that the recipient environmental conditions are likely to be similar to those experienced in their native range. A larger native range may imply that species are more tolerant of a wider range of conditions, and hence more likely to encounter suitable environments when introduced (Duncan et al. 2001; Mahoney et al. 2015). Such species may be more likely to succeed in establishment (Croci et al. 2007; Bomford et al. 2009), and to spread across a larger range in the alien location.

Based on these previous studies, I test five predictions for variation in the extent of the alien range sizes of birds in Taiwan.

First, I predict that bird species more commonly for sale in Taiwan are likely to have larger alien range sizes in Taiwan than species rarely recorded for sale. Second, I predict that species with longer residence times are likely to have larger established range sizes in Taiwan. Third, I predict that large-bodied species will have larger alien range sizes than small-bodied species, as tends to be the case in the native range. Nevertheless, I may see a negative range size-body size relationship in Taiwan if small-bodied species attain their alien ranges more quickly. Fourth, I predict that alien range size in Taiwan is positively related to native range size, on the assumption that factors that determine native range sizes also influence alien range sizes. Finally, I predict that the extent to which a species can spread in Taiwan is positively related to the environmental match between Taiwan and the species' native range. I also test whether environmental suitability can distinguish between alien species that are introduced to Taiwan and that succeed or fail to establish.

6.3 Methods

6.3.1 Data

I obtained records on alien species found in the wild in Taiwan from Severinghaus (1999) and a dataset from the Chinese Wild Bird Federation (CWBF) for the years 1972 to 2014. These sources listed 62 alien bird species recorded in the wild and that were also found in at least one of three pet shop surveys (Chi 1995; Shieh et al. 2006; Chapter 4). Five of the 62 species had fewer than 10 occurrence records from their native ranges: two vulnerable species *Cacatua moluccensis* and *Padda oryzivora,* one critically endangered species *Cacatua sulphurea,* one near threatened species *Cacatua goffiniana,* and *Eos bornea* (IUCN 2015). This leads to small sample sizes in the environmental modelling algorithm (see Analysis) (Wisz et al. 2008), and so these five species were removed from the environmental suitability analysis. Hence, the total sample size is 57.

Twenty-eight of these 57 species are not classified as established or potentially established (see below), and therefore are considered in the analysis as failed introductions. A total of 29 species may be established in the wild, according to the Bird Checklist Taiwan (2011-2014). I assigned these to one of two groups: 1) Established: alien species that have had stable breeding records for more than ten consecutive years in the wild ($n = 15$); all 15 established species were recorded in the pet shop surveys. 2) Potentially established: alien species with wild breeding records but not for more than ten years ($n = 14$). All established ($n = 15$) and potentially established ($n = 14$) species were recorded in the pet shop surveys.

For established species, I calculated the current alien range size in Taiwan (2011-2013) based on information (x-y coordinates) in the Breeding Bird Survey (BBS) Taiwan (Ko et al. 2013). To estimate alien range size for each of these species, I created a GIS map polygon by buffering around the observed points to 4 km (the default maximum distance between survey points in a surveyed area), dissolving areas of overlap between observed points, and then summing the total area covered by the resulting distribution. The values were natural log transformed for analysis (Anderson-Darling normality test: untransformed alien range size ($A = 2.48$, $p < 0.001$); log-transformed alien range size ($A=0.65$, $p = 0.06$)).

There are no records available for *Cyanopica cyana* and *Streptopelia decaocto* from BBS Taiwan, such that the final sample size for established species in the range size analysis is 13.

I obtained the native geographical range (km^2) for all traded bird species considered to be failed introductions (n = 28), potentially established (n = 14) and established (n = 13) alien species in Taiwan, from data in (Orme et al. 2006), modified by removing alien ranges incorrectly included in some (Dyer et al. unpub. ms.). The data do not include the native range of *Amandava subflava,* which instead I obtained from the IUCN Red List (IUCN 2015). The total native range was measured as polygons and converted into equal area grids using a Behrmann projection with a cell size of 96.3 x 96.3 km (see Orme et al. 2006). Native range size was estimated by summing the areas of the grid cells in which species occurred. The values were natural log transformed for analysis (Anderson-Darling normality test: untransformed native range size ($A = 2.37$, $p < 0.001$); log-transformed native range size ($A=0.63$, $p = 0.07$)).

I recorded residence time for each established species as the number of years since it was first recorded in the wild in the CWBF database (1972-2014). The earliest recorded introduced species in CWBF database is *Columba livia* (1972; although it has certainly been present for much longer, since at least 1840, according to the National Museum of Nature Science, Taiwan); the most recently introduced species are *Cyanopica cyanus* and *Sturnus malabaricus* (both in 1998). I obtained information on body mass (g) for established species (n = 13) from (Olson et al. 2009). For established species, I also recorded the number of birds recorded for sale in the survey of Taiwanese pet shops (Chapter 4). The values of body mass and the numbers of birds for sale were natural log transformed for analysis.

The environmental suitability analyses are based on eight explanatory variables. I removed variables that were highly correlated and choose variables based on the biological meanings. Hence the selected environment mating variables include: global habitats cover (ESA Climate Change Initiative - Land Cover project 2014), annual maximum green vegetation fraction (MGVF) (Broxton et al. 2014), the accessibility (travel time to access closest city or areas of the population greater than 50,000) (from Nelson 2008), the climate variables include: annual mean temperature (°C), annual temperature range (°C), mean temperature of coldest quarter (°C), annual precipitation (mm) and precipitation of driest quarter (mm) (Hijmans et al. 2005; WorldClim 2015).

6.3.2 Analysis

All analyses were performed in R (version 3.0.3, R Core Team 2014), and species range maps were developed with ArcGIS 10.2.

I tested for phylogenetic correlation in alien range size in Taiwan by calculating variance components on the taxonomic levels of family and genus. The established species derived from only Psittaciformes and Columbiformes, and therefore I did not test for phylogenetic effects at the order level. Since the test detected no variance nested at these levels, I used generalized linear models (function *glm*) for subsequent tests related to alien range sizes in Taiwan.

I compared the alien range size of the established species in Taiwan with native range size, residence time, body mass, the numbers of birds for sale and the environmental suitability (see below) in Taiwan (n = 13) in univariate models. To find the most likely multivariate model for these variables, I used a recursive feature elimination approach, and AIC-based stepwise elimination of variables from a full model including all five predictors, carried out in R. The feature elimination approach removed variables with low t-statistic using cross-validation as the sampling method, implemented using the function *rfe*. The AIC-based stepwise elimination was carried out in the *caret* r package (Kuhn 2015), using function *train* with cross-validated and stepwise feature selection method (glmStepAIC). I calculated the relative importance values for tested variables (lmg importance, averaged r^2 contribution over orders, see (Lindeman et al. 1980)) with the *calc.relimp* function in the *relaimpo* package (Grömping 2006). I fitted a generalized linear model with selected variables derived from the above methods.

To test whether environmental suitability is a determinant of establishment success, I calibrated an environmental match model using MaxEnt (maximum entropy modelling, version 3.3.3k) (Phillips et al. 2006). I compared established (n = 15), potentially established (n = 14) and failed introductions (n = 28). First, I created an index of environmental suitability in Taiwan for each of the tested alien species. To do this, I obtained occurrence records within the species' native range from GBIF (GBIF.org 2015), using records of human observations, specimen records and machine observations (such as remote sensor camera records). To reduce sampling bias, duplicated observations of the same species were removed by setting MaxEnt to "remove duplicate presence records", thus the records also retained only one occurrence in a single grid cell (300m x 300m, see below and Appendix 1). I calibrated the MaxEnt model in the species native range using presence-only data with the environmental explanatory variables described above, and then projected the environmental requirements identified from the native range to Taiwan for each of the tested species (with grid cell size 300m x 300m). For each species, modelling was performed using 10-fold cross-validation resampling to evaluate the model performance. The performance of predictive models was judged using the rank-based AUC score (Fielding and Bell 1997). AUC is the area under the receiver operating characteristic curve, which indicates the probability that a randomly selected presence location is higher ranked than a randomly selected background location (Phillips et al. 2006; Phillips and Dudík 2008).

For each species, the model derived from the native range gave an estimated probability of presence ranging from 0 to 1 for each grid cell in Taiwan. These values can also be taken to represent environmental suitability (Phillips et al. 2006). The probability distribution model for each species is different, given that species have different environment requirements. I used the median value of the probability for each of the species as an index of environmental suitability to Taiwan.

To test whether environmental suitability is associated with the establishment success of bird species in the pet trade market, I compared established (n = 15), potentially established (n = 14) and failed introductions (n = 28), in terms of the environmental suitability index. I tested for phylogenetic correlation among species in whether introduced species succeed in establishment (become established or potentially established) in Taiwan, by calculating variance components on the taxonomic levels of order, family and genus. The family level comprised 85.84% of the variation, while 14.15% was found at the genus level. No variance was found nested at order level. I used generalized linear mixed-effects models (function *glmer* in the *lme4* package in R) with binomial errors and fitted family and genus as nested random effects to control for the phylogenetic association among species in the analysis. I also tested variance components on whether potentially established species succeed in becoming established in Taiwan. Variance was only found at the taxonomic level of family. Therefore, I fitted family as the random effect to control phylogenetic association for potentially established and established species. **Figure 6.1** was created with the R package *beanplot* (Kampstra 2008).

6.4 Results

The maximum entropy model calibrated from the native ranges for the tested species has a good model fit (median AUC score = 0.91, 1st and 99th percentiles = 0.67, 0.98). Note that an AUC score greater than 0.9 is considered to be a very good model, while an AUC between 0.7 and 0.9 is considered to be reasonable (Pearce and Ferrier 2000). The median value of the environmental suitability for all the tested species in Taiwan was 0.15 (1st and 99th percentiles = 2 x 10^-8, 0.91), for failed introductions was 0.08 (1st and 99th percentiles = 1.55 x 10^-8, 0.9) and for established and potentially established species was 0.24 (1st and 99th percentiles = 0.004, 0.79). A generalized linear mixed-effect model showed that environmental suitability is associated with the establishment success of alien species in Taiwan. Established and potentially established species have significantly higher environmental suitability indices than failed introductions (estimate ± standard error: 4.16 ± 1.87, z = 2.22, p = 0.02, see **Figure 6.1**). However, there was no significant difference between established and potentially established species (estimate ± standard error: 0.4 ± 2.27, z = 0.17, p = 0.85).

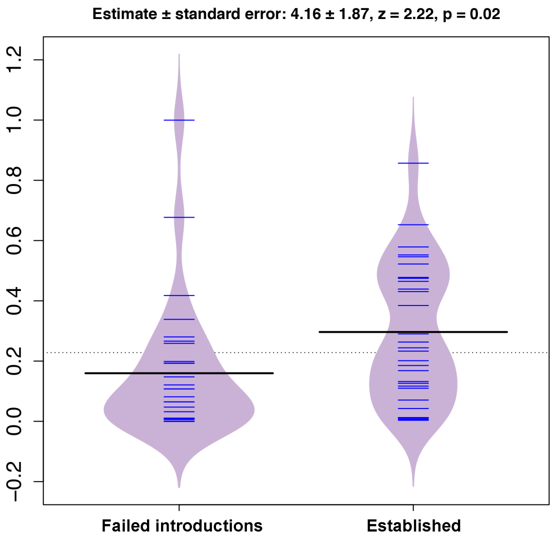


Figure 6.1 The means of environmental suitability in Taiwan for failed introductions (n = 28) and established species (n = 29, established and potentially established species included). The blue lines indicate individual observations, the solid black lines represent the means of the observations in failed introductions and established species, the dotted line represents overall average and the purple areas show the distribution.

Univariate analysis showed that alien bird range sizes in Taiwan were positively associated with native range size (estimate ± standard error: 1.08 ± 0.33, t = 3.26, p = 0.007), body mass (1.72 ± 0.66, t = 2.59, p = 0.02) and residence time (0.08 ± 0.03, t = 2.18, p = 0.05), but showed no relationship to the number of birds for sale (0.12 ± 0.15, t = 0.82, p = 0.42) or to the environmental suitability index (1.06 ± 1.43, t = 0.75, p = 0.47). Both cross-validated recursive feature elimination and AIC-based cross-validated selection approaches identified native range size and body mass as suitable variables for the model. A multivariate generalized linear model with the two selected variables showed that both native range size (estimate ± standard error: 0.89 ± 0.28, t = 3.18, p = 0.009, relative importance = 0.46) and body size (1.29 ± 0.5, t = 2.54, p = 0.029, relative importance = 0.36) have strong influences on alien range size in Taiwan (cross-validated adjusted $r^2 = 0.63$). Species' alien range sizes in Taiwan tend to be larger for larger-bodied species, and for species with larger native ranges.

6.5 Discussion

The pathway by which species become invasive aliens combines the influences of human mediated processes and the traits of the species involved. In the early stages of invasion, human preferences and actions are key determinants of which species get to be transported or introduced. For example, transported alien species are not a random subset of extant species (Blackburn and Cassey 2007; Chapter 3), locations where species are introduced are not distributed evenly (Blackburn and Duncan 2001b), and much of this variation is driven by the types of species chosen by people for translocation, and species' availability relative to these choices. However, in the later stages of invasion - establishment and spread - species traits matter more. Human activities largely dictate which species are exposed to novel environments, but intrinsic characteristics of these environments and species then influence whether or not these species subsequently succeed in colonising them.

For alien bird species introduced to Taiwan, I found that the extent of suitable environments on the island was significantly different between species that failed to establish and those that established (including those that were potentially established). The environmental suitability index used in the study incorporated anthropogenic influences (e.g. accessibility to human population centres), types of habitats (land cover) and climatic factors (precipitation and temperature variables). Therefore, it seems that species were more likely to establish if these features of the Taiwanese environment were more similar to those in their native ranges. Nevertheless, I still found established and potentially established species with low environmental suitability in Taiwan (e.g., the environmental suitability in Taiwan for *Cacatua alba* = 0.003), and conversely, species that failed to establish despite a very high environmental suitability (e.g. for *Serinus canaria* = 0.99). Hence, a low environmental suitability to an alien environment is not necessarily a bar to establishment success, and vice versa, a high environmental suitability is not a guarantee of success. It is likely that for some species, there are circumstances of the introduction that act above the environmental suitability. I have shown elsewhere that establishment success in Taiwan was higher for large-bodied bird species (Chapter 5), and it is interesting in this regard that the large-bodied

C. alba succeeded despite a low environmental suitability, and the small-bodied *S. canaria* failed despite a high environmental suitability.

Although the results suggest that environmental suitability is important for whether or not introduced species can succeed in establishing, the occurrence of higher environmental suitability in Taiwan does not appear to matter for the extent of species' alien range sizes in Taiwan: the environmental suitability index was not related to the size of alien range sizes in Taiwan in the analyses. It has been shown elsewhere that the number of introduction events influences alien bird range size worldwide (Dyer et al. unpub. ms.), and this effect may also be more important here. However, information on the number of releases is not available for birds in Taiwan. Bird invasions in Eastern countries are likely to be influenced by the indigenous cage bird culture, which includes elements such as religious prayer animal release, outdoor bird singing competitions, and bird-walking. These activities are likely to be important pathways for traded species to become introduced species. In particular, the practice of prayer animal release moves species beyond their natural barriers and into alien environments on a large scale. Previous studies have found that more than 200 million wild animals are released annually in Taiwan (Environment and Animal Society of Taiwan (EAST) 2009). A quarter of religious organizations (from several different religions) regularly practice prayer animal release (EAST and Kaohsiung Teacher's Association 2004), and there were 12,106 registered temples in Taiwan in 2014 (Ministry of the Interior 2014). In Taipei, around 30% of residents have participated in prayer animal releases (Severinghaus and Chi 1999). Both large-scale organised animal release and small-scale personal animal release are therefore common and widespread. For these reasons, the abundance of animals in trade, which I have shown elsewhere to be related to the probability of introduction, may be a useful surrogate for number of release events. Nevertheless, I found no effect of the number of birds for sale on alien range size in Taiwan (Chapter 5), unlike previous studies in alien birds and other species (Gammon and Maurer 2002; Liu et al. 2014). It is possible that the numbers of birds for sale predicts which bird species are introduced in Taiwan, but not how many individuals of those species make it into the wild, and that data on the latter would predict alien range size. Unfortunately, such data are also not available.

In fact, species traits appear to have the strongest influences on the alien range size of bird species in Taiwan. I found that alien species with larger body size and larger native geographic range size tended to have larger Taiwanese range sizes. Larger-bodied species tend to have slower population growth rates and to be longer-lived (Peters 1983; Gaston and Blackburn 2000), characteristics that have been argued to help colonising species to persist through environmental extremes (Sæther et al. 2004; Blackburn et al. 2009a). Taiwan is a sub-tropical island that mainly does not experience periods of extreme temperature or rainfall, but it is hit by regular typhoons (3-5 per year, according to Water Resources Agency, Taiwan). Tropical storms have been shown to cause high mortalities in wildlife (Ameca y Juárez et al. 2012) and have been argued to cause extinctions in small island populations of birds (Martínez-Morales et al. 2009; Şekercioğlu et al. 2012). These extreme events may differentially impact species of different body size, and so explain why larger-bodied species are more likely to establish (Chapter 5) and spread widely in Taiwan.

Positive relationships between native and alien range sizes for alien species, like that shown here for birds in Taiwan, have been argued to arise because species with larger native range sizes are likely to be able to exploit a broader range of habitats, or to have wider environmental tolerances (Blackburn and Duncan 2001a; Croci et al. 2007). However, I explicitly tested for environmental matches between native and alien distributions, and found no relationship between the environmental suitability in Taiwan and alien range size. Species with larger native range size do not have higher probability of occurrence across Taiwan.

The univariate analysis found the expected positive relationship between alien range size and residence time in Taiwan: established bird species present for longer on the island have had longer for their populations to grow and spread, and also more time to adapt to the novel environment (Vellend et al. 2007). They may also have benefitted from longer periods (and hence more) of introduction. However, residence time had no relationship with alien range size in the multivariate analyses, when the effects of native range size and body size were included. Dyer et al. (unpub. ms.) found that positive univariate effects of residence time on alien range size at the global scale disappeared in multivariate analysis, although there the relationship became significantly negative for reasons that are unclear. It seems that longer residence time is only a small advantage to established bird species, and matters less than other drivers in terms of the extent of their spread, at the time scales considered here.

Chapter 7 Conclusion

The trade in plants and wild animals, including cage birds, is one of the major pathways to invasions. Captivity places constraints on the invasion process because traded species are not directly introduced into the wild after transport and not all species in trade are subsequently introduced into the wild. Nevertheless, the pet trade is an increasing source of alien invasive species. Traded alien species have been shown to be correlated (Lee and Shieh 2005; Carrete and Tella 2008), in terms of identity and abundance, with those species subsequently established. Indeed, the most important correlate of variation in the numbers of invasive alien species across countries is currently the volume of imports. This suggests that international trade is now the primary driver of species invasions. To characterise invasions effectively, it is now more important than ever to understand the mechanics of trade, and in particular, which species in trade are most likely to be released or escape into the wild, and what species traits are associated with their success in establishment and spread.

Most studies on biological invasions by alien species have focused upon Western contexts, in particular considering the consequences of the planned movement of animal and plant species by acclimatisation societies and other organisations aiming to establish populations of beneficial species (Hursthouse 2011). Nevertheless, these organisations have largely passed away, and the bird trade is currently more active in Asian countries. There is growing awareness that invasions in these countries are driven by different social backgrounds and demands, and that the identities and characteristics of species concerned differ as a result. This study has shown that the attitude to the bird trade in at least one East Asian country, Taiwan, is heavily influenced by the culture of bird-keeping (and related activities) in East Asia, and that the characteristics favoured in the processes from transit through to subsequent invasion are distinctly different to the ones in the Western context.

7.1 Main Results

I have, for the first time, examined patterns of non-randomness in the composition and characteristics of traded alien bird species in Taiwan (Chapter 3). Transportation is the first stage of the invasion pathway, and only species that have been transported beyond the boundaries of their native range can get onto the following stages. My work revealed that the interaction of social demands and species availability strongly influences what specific characteristics of bird species are likely to be imported to Taiwan. The exposed scale of the bird trade is remarkable: a total of 247 bird species from 34 different families were identified during my survey from just 70 bird shops (Chapter 3). Of these, 170 species (from 27 families) were alien to Taiwan. A total of more than 25,000 individuals were recorded, of which more than 7,000 were alien birds. The highest single count in a single bird shop for a single species was around 4,000 individuals. The price range of species for sale was from US$ 0.86 up to US$8,000 per individual (Chapter 4).

The pet trade is the main animal source of introduced species in Taiwan, and most of the introduced bird species in Taiwan were traded species in this market. For a better view of the introduction stage of invasion, my survey was compared with the two most complete pet shop surveys, carried out in 1994 and 2004. My study (Chapter 5) showed that traded species are more likely to be found in the wild if they are commonly sold, good songsters and for sale for a longer period in the pet trade market. The likelihood of a species to be found in the wild is also related to bird-related social and religious activities in Taiwan, such as bird singing competitions, bird-keeping culture and prayer animal release.

To further understand which species have a higher risk of introduction, I used the price of bird species for sale as a proxy to determine the likelihood of species to be released or escaped into the wild. Sale price may be one of the factors that influence this probability, because the amount of care taken over the keeping of a bird is likely to be associated with its value. Furthermore, cheaper priced bird species are most preferred as prayer birds for larger scale prayer animal releases. My work (Chapter 4) found that cheaper priced species are most likely to be found in the wild. This study found that species for sale in larger numbers, not globally endangered, native to Taiwan, without attractive songs, with smaller body size and having no yellow coloration, are likely to be priced cheaper in the shops. One notable route of alien species to introduction is prayer animal release. Our understanding of larger scale prayer bird releases is that cheaper birds are preferred (Severinghaus and Chi 1999), which are likely to be native species. Prayer birds were purchased without reference to whether or not they are alien. Therefore, the risk of alien species, especially those with relatively cheaper price in Taiwanese pet shop, to be introduced through prayer animal release may be high. Species for sale as prayer birds are mostly wild caught in Taiwan, therefore some alien prayer birds may have been established in the wild but constantly involved in the cycle of being caught and released. In this case, prayer animal release is likely to play the role in increasing the chance for alien species to spread. In fact, during my survey, I uncovered some evidence that not only large-scale prayer animal releases practiced by organizations should be of concern. According to information from some of the surveyed pet shop owners, individual buyers looking for one or a few prayer birds are more likely to spend time over their selection, and are more willing to pay more for species different to the usual prayer bird species. For example, they may be more likely to choose species with colourful plumage, and hence to buy alien species. Therefore, from the perspective of invasion risk, individual buyers may be more likely to introduce aliens into the wild than large-scale organized prayer animal releases.

With regard to the establishment stage of invasion, my work (Chapter 6) has shown that environmental matching between native environments and recipient areas distinguishes species that fail or succeed in establishment. Successfully established alien species are likely to have similar environmental conditions in new environments to those experienced in their native ranges. Whether populations can grow and cope with the alien environment is also fundamental in establishment success. My work (Chapter 5 and 6) has shown that species traits selected in this stage in Taiwan are different to many other studied Western countries. In Taiwan, body size has a positive effect on species success in establishment. Species with larger body size may be more likely to have the ability to cope with demographic problems arising from slow population growth rates. As a result, they may be more likely to establish and their populations persist through the regular environmental extremes experienced in Taiwan.

Finally, for the spread stage of the invasion process for alien birds in Taiwan, my work (Chapter 6) showed that species with larger native range sizes tend to attain larger alien range sizes. Having a higher environmental suitability in the alien range for alien species does not affect their success in dispersal; rather, it seems that species that can tolerate broader types of habitats from a larger native range size can spread more widely in alien environments in Taiwan. Overall, the results from chapters 3 to 6 have given a novel view of the Eastern context of the biological invasion pathway for alien birds.

7.2 Constraints During the Survey

To study the invasion pathway in an Eastern context, Taiwan was chosen as the study site, and I conducted surveys of the identities, numbers and prices of bird species for sale in the Taiwanese bird market. The bird market may provide more accurate information for understanding the composition of imported species than official documents; this is because some of the animal sources and importations are illegal. My work on alien bird research in

Taiwan was motivated by the fact that pathways to Eastern invasion are relatively less well studied than Western ones. This seems to me likely to be due to the difficulties in accessing information about these markets, not only because of the language barrier to Western scientists who primarily carry out invasion research, but also because of the nature of some bird-related social activities. Those involved in the bird trade and religious animal releases in particular tend to be very reluctant to disclose information.

During my survey, some limitations on data collection were encountered. First, the main data limitation in my surveys was that the traders were suspicious of being questioned about their trade, and I was threatened several times during the survey. Therefore, in order to obtain information, it was important to build up a positive relationship and to reassure traders that information disclosed for research purposes was confidential and would not be used against them. For these reasons, the time needed to conduct the surveys was a lot longer than expected.

Second, the timing of my surveys was constrained. According to many of the surveyed traders, the high season for the wild-bird trade is during the winter. However, timing constraints meant that my survey was carried out just before this season, towards the end of November. Winter is claimed to be the high season for the wild bird trade because there are more native species available for sale due to altitudinal migration of bird species from higher to lower altitude in winter. These migrants are then more available for capture and trade. However, the timing constraint should affect the availability of alien species less, and therefore my analyses on alien species should still be reliable.

Third, many of the protected native bird species in Taiwan were probably under-recorded in my wild bird trade survey in 2012. These species are evidently only traded to people who know the market, as these protected bird species cannot be displayed legally. During my survey, I did not have access to all the hidden stocks of birds (although I was able to observe some stocks of some traders), and so the diversity and abundance of species in my survey are likely to be underestimated. In fact, to display an alien species has lower risk for owners; therefore, the numbers of native species are most likely to be underestimated in comparison to the alien species.

Fourth, there are limitations to the database I used on the species' wild records and breeding ranges in Taiwan. The main purpose of Breeding Bird Survey in Taiwan was to monitor native birds during breeding seasons. Although alien species were also recorded, these records do not always include evidence of breeding. Wild records from the Chinese Wild Bird Federation (CWBF) used in my analyses represent probably the most comprehensive dataset in Taiwan. These records still possibly underestimate the numbers of alien species found in the wild, because alien species are not as common as native species, and are more difficult to identify. For example, there are records only stated as “alien species” or only available in genus name in CWBF dataset. Nevertheless, the newly launched regional portal eBird Taiwan (on July 2015, in traditional Chinese language) will encourage and provide birders with a broad platform to upload their observations in the future. The combined observation records between CWBF, eBird and other platforms should increase the accuracy of records of birds from the wild for the future studies.

Finally, my study has a relatively small sample size for analyses in the later stages of invasion; this is because many species are filtered out during the process of invasion, and so the numbers of alien species established and spreading is always going to be less than the numbers transported in trade (or through other means). For this reason, the analytical methods used in this thesis tended to be conservative in order to avoid over-interpretation of the results. For example, we used Bonferroni correction for multiple comparisons in Chapter 3, the model selection simulations in Chapters 4 and 5 and the suitability index method in Chapter 6.

Despite these limitations, I consider the results to be robust. I have surveyed significant numbers of bird shops and earned support from many shop owners, trade unions and importers (in the restricted time), and so information obtained in the pet shops is reliable. To further improve the accuracy of the records, I also combined the records with other sources and the two surveys carried out in 1994 and 2004.

7.3 Current bird trade in Taiwan

The scale of bird trade in terms of the abundance and numbers of species recorded, and the strong links between the identities of species in the pet trade to those subsequently introduced and established, means that controls on the bird trade would provide one solution to deal efficiently in preventing species becoming invasive, and hence also minimising the effects of alien species in Taiwan. Education in terms of conservation awareness can gradually change the current social and religious demand for birds. However, in order to limit the probabilities of alien species to get onto the invasion pathway from the current bird trade market, a more important step is likely to be the enforcement of current regulations associated with alien species.

My survey confirmed that alien species in bird shops are also sourced from illegal importations. I was informed by the owners that holding larger numbers of an alien species makes a shop more likely to be investigated by authorities, or to be reported. However, this potential problem can simply be solved by reducing the numbers of illegally imported birds on display. With respect to animal welfare, illegal importations can cause the mortality of up to 80% of the individuals in shipments especially in the summer time, as estimated by the numbers of survivals within 48 hours since the shipped stock arrive (Mr Z., a bird importer, who would like to stay anonymous, personal communication, 2012). For these reasons, the enforcement of legislation relating to alien species sold in the market ought to be active and the monitoring of owners' registration ought to be increased.

7.4 Recommendations

My first recommendation for the current market in Taiwan is that there ought be a specific government intervention to enforce current legislation on bird importation, for example, the Wildlife Conservation Act: Article 27, the control of exotic wildlife in importation (Council of Agriculture 1989). As I observed during the survey, the sources of birds are not well checked. The current importation blacklist of alien species in Taiwan by Bureau of Foreign Trade in 2013 is an encouraging step to prevent species with high invasion risk being imported. Nevertheless, alien species still can be imported through illegal pathways or failures in customs, for example due to misidentification. Furthermore, only one bird species is listed, the Red-billed blue magpie *Urocissa erythrorhyncha*, while species not yet black listed do not imply no risk in invasion. The current situation in Taiwan is that once alien species have been imported, their subsequent pathway to biological invasion has no specific authorities assigned to control it. Therefore, I suggest developing an adequate tracking system in order to monitor alien species passage along the trade path. In addition to the blacklist, a specific legislation in how to deal with alien species is desired. The current parrot certification scheme promoted by Forestry Bureau Taiwan is a good start in bird source tracking. It encourages bird owners to register their parrots for identification of whether their parrots are captive bred individuals or not. However, again, this scheme is not enforced.

Second, I suggest tighter controls of animal sources, in particular from breeding farms and illegal importations. Breeding farms may be an important source of alien species in pet shops. My survey did not visit enough breeding farms to get sufficient information on species composition, but according to website trading information, the majority of captive bred species are alien to Taiwan. Furthermore, enormous numbers of breeding farms and home-based breeders are not registered or licensed, and this should be a serious concern in managing alien species in Taiwan.

7.5 Future work

In terms of biological invasions, my work on the traits of alien species in Taiwan should contribute additional information in aiding the alien blacklist in order to control alien importations. My work also provides valuable information in developing regulations in the alien bird trade. For future study, it is vital to monitor the sources of alien species, for example the bird-breeding farms. Although the survey was conducted only in Taiwan, its results have the potential to improve the regulation of the trade in birds more widely. I would also recommend undertaking a similar approach in the bird trade markets of neighbouring countries for a broad view of the invasion pathway in Asia and to carry out comparative studies in bird trade surveys between Eastern and Western societies. Finally, the Forestry Bureau Taiwan aims to establish an alert system for early detection and rapid eradication of alien species. By reviewing the current regulations and laws related to alien species between Taiwan, countries with similar scenarios of wildlife trade and those have well-established management framework of alien species can provide insight into the management of alien species before and after they are transported and introduced.

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Appendix A Books Used for Identifying Taiwanese Pet Shop Birds from Photographs

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Appendix B Species Recorded in the First Visit to Each Shop, n=221

Species	Numbers	Price (US$)	Status
Abroscopus albogularis	1	20	native
Acridotheres cinereus	43	10	alien
Acridotheres cristatellus	4	83	native
Acridotheres fuscus	492	7	alien
Acridotheres grandis	722	10	alien
Acridotheres tristis	82	9	alien
Acrocephalus arundinaceus	6	14	native
Aegithalos concinnus	1	17	native
Agapornis fischeri	266	18	alien
Agapornis nigrigenis	3	27	alien
Agapornis personatus	11	33	alien
Agapornis roseicollis	357	23	alien
Alauda gulgula	23	80	native
Alcippe brunnea	4	10	native
Alcippe morrisonia	1	7	native
Amazona aestiva	7	1458	alien
Amazona amazonica	5	583	alien
Amazona autumnalis	3	1056	alien
Amazona ochrocephala	2	1333	alien
Amazona oratrix	1	6667	alien
Anas poecilorhyncha	8	5	alien
Aplonis panayensis	1	200	alien
Ara ararauna	18	1818	alien
Ara chloropterus	2	2083	alien
Ara macao	1	4000	alien
Ara severus	3	1125	alien
Aratinga acuticaudata	5	611	alien
Aratinga jandaya	2	267	alien
Aratinga solstitialis	115	200	alien
Aratinga wagleri	1	267	alien
Bambusicola thoracicus	154	14	native
Bolborhynchus lineola	145	45	alien
Bombycilla garrulus	1	267	alien
Cacatua alba	2	1417	alien
Cacatua ducorpsii	6	713	alien
Cacatua galerita	15	1252	alien
Cacatua leadbeateri	2	7500	alien
Cacatua moluccensis	2	3333	alien
Cacatua ophthalmica	1	2000	alien
Cacatua roseicapilla	3	1528	alien
Cacatua sanguinea	2	1000	alien
Carduelis magellanica	2	40	alien
Cettia canturians	18	14	native
Chalcophaps indica	5	13	native
Chalcopsitta atra	3	1167	alien
Chalcopsitta duivenbodei	6	583	alien
Chalcopsitta sintillata	1	1167	alien
Chloropsis aurifrons	1	333	alien

Chloropsis cochinchinensis	2	422	alien
Chloropsis hardwickii	6	260	alien
Chloropsis sonnerati	1	400	alien
Chrysolophus amherstiae	3	200	alien
Chrysolophus pictus	9	103	alien
Columba livia	259	3	alien
Copsychus malabaricus	101	92	alien
Copsychus saularis	19	96	alien
Cosmopsarus regius	3	178	alien
Coturnix coturnix	13	3	alien
Cyanocorax yncas	1	250	alien
Cyanoptila cyanomelana	11	167	alien
Cyanoramphus novaezelandiae	1	50	alien
Cyornis banyumas	1	233	alien
Cyornis hainanus	3	142	alien
Dendrocitta formosae	34	38	native
Dicrurus macrocercus	1	10	native
Diopsittaca nobilis	11	493	alien
Eclectus roratus	17	1004	alien
Emberiza pusilla	1	7	native
Emberiza spodocephala	18	3	native
Emberiza sulphurata	1	10	alien
Eos bornea	12	258	alien
Eos histrio	1	533	alien
Eos reticulata	3	267	alien
Eremophila alpestris	1	267	alien
Erithacus akahige	2	267	native
Erpornis zantholeuca	8	15	native
Erythrura gouldiae	405	13	alien
Estrilda astrild	26	8	alien
Estrilda melpoda	6	12	alien
Ficedula hyperythra	1	67	native
Galerida cristata	1	183	alien
Gallus gallus	44	13	alien
Garrulax canorus	3	267	alien
Garrulax chinensis	2	322	alien
Garrulax morrisonianus	2	72	native
Garrulax taewanus	2	NA	native
Garrulus glandarius	5	233	native
Geopelia cuneata	42	15	alien
Glossopsitta concinna	5	433	alien
Gracula religiosa	1	333	alien
Guaruba guarouba	5	8000	alien
Heterophasia auricularis	13	16	native
Hypsipetes leucocephalus	5	20	native
Lamprotornis superbus	1	52	alien
Liocichla steerii	27	24	native
Lonchura malabarica	150	3	alien
Lonchura malacca	98	4	native
Lonchura punctulata	2649	2	native
Lonchura striata	437	2	native
Lorius chlorocercus	16	439	alien
Lorius garrulus	13	472	alien
Lorius lory	10	478	alien
Luscinia calliope	69	63	native
Luscinia cyane	1	150	alien
Luscinia megarhynchos	2	500	alien
Luscinia svecica	13	200	native

Megalaima nuchalis	24	19	native
Melanerpes carolinus	1	500	alien
Melanerpes rubricapillus	1	333	alien
Melanocorypha mongolica	17	333	alien
Melopsittacus undulatus	956	8	alien
Mimus polyglottos	2	167	alien
Monticola gularis	3	244	alien
Monticola rufiventris	1	833	alien
Monticola solitarius	66	35	native
Motacilla alba	34	31	native
Musophaga violacea	2	583	alien
Myiopsitta monachus	111	198	alien
Nandayus nenday	10	183	alien
Neochmia ruficauda	103	10	alien
Neophema pulchella	15	68	alien
Neopsephotus bourkii	23	47	alien
Niltava macgrigoriae	7	239	alien
Nucifraga caryocatactes	1	400	native
Nymphicus hollandicus	286	33	alien
Padda oryzivora	928	10	alien
Paradoxornis verreauxi	1	27	native
Paradoxornis webbianus	15	6	native
Paroaria coronata	1	750	alien
Paroaria gularis	2	350	alien
Passer montanus	83	1	native
Pellorneum albiventre	12	197	alien
Pericrocotus solaris	3	27	native
Pheucticus chrysogaster	2	142	alien
Phoenicurus auroreus	23	30	native
Phoenicurus frontalis	1	133	alien
Phylloscopus borealis	2	22	native
Pica pica	17	49	native
Pionites leucogaster	4	1778	alien
Pionites melanocephalus	10	667	alien
Pionus chalcopterus	1	833	alien
Pionus maximiliani	3	392	alien
Pionus menstruus	6	500	alien
Platycercus eximius	5	242	alien
Poephila acuticauda	146	12	alien
Poicephalus gulielmi	15	469	alien
Poicephalus rueppellii	1	500	alien
Poicephalus senegalus	15	190	alien
Pomatorhinus erythrogenys	2	22	alien
Pomatorhinus ruficollis	33	12	native
Primolius auricollis	5	1917	alien
Prinia flaviventris	1	10	native
Psephotus haematonotus	9	44	alien
Pseudeos fuscata	2	767	alien
Psittacula krameri	79	126	alien
Psittacus erithacus	52	562	alien
Pycnonotus jocosus	10	93	alien
Pycnonotus melanicterus	1	117	alien
Pycnonotus sinensis	465	10	native
Pyrrhula erythaca	1	50	native
Pyrrhura molinae	47	175	alien
Pyrrhura perlata	1	667	alien
Pyrrhura rupicola	2	200	alien
Saxicola caprata	19	242	alien

Saxicola ferreus	1	333	alien
Saxicola torquatus	1	333	native
Serinus atrogularis	9	150	alien
Serinus canaria	379	31	alien
Serinus citrinipectus	11	275	alien
Serinus flaviventris	14	177	alien
Serinus leucopygius	185	48	alien
Serinus mozambicus	35	66	alien
Sicalis flaveola	14	122	alien
Spizixos semitorques	16	41	native
Sporophila luctuosa	8	85	alien
Sporophila telasco	1	183	alien
Stachyris ruficeps	1	6	native
Stigmatopelia chinensis	135	4	native
Streptopelia decaocto	145	3	alien
Streptopelia orientalis	1	8	native
Streptopelia tranquebarica	7420	2	native
Sturnus cineraceus	41	10	native
Sturnus malabaricus	1	7	alien
Sturnus nigricollis	44	37	alien
Sturnus sericeus	11	18	native
Sturnus sinensis	19	10	native
Sylvia nisoria	3	422	alien
Taeniopygia guttata	131	7	alien
Tangara arthus	1	400	alien
Tangara chilensis	2	600	alien
Tangara seledon	1	300	alien
Tarsiger cyanurus	1	167	native
Thraupis episcopus	6	183	alien
Tiaris canorus	1	117	alien
Tockus erythrorhynchus	1	600	alien
Trachyphonus erythrocephalus	1	267	alien
Treron sieboldii	50	100	native
Trichoglossus chlorolepidotus	5	117	alien
Trichoglossus euteles	4	167	alien
Trichoglossus haematodus	26	179	alien
Trichoglossus ornatus	1	583	alien
Trichoglossus rubritorquis	NA	NA	alien
Turdus cardis	1	367	alien
Turdus chrysolaus	4	50	native
Turdus dissimilis	1	400	alien
Turdus hortulorum	2	42	alien
Turdus mupinensis	1	417	alien
Turdus naumanni	1	17	native
Yuhina brunneiceps	17	12	native
Zoothera citrina	14	271	alien
Zoothera erythronota	2	458	alien
Zoothera interpres	1	500	alien
Zoothera peronii	1	333	alien
Zoothera sibirica	1	150	alien
Zosterops erythropleurus	1	100	alien
Zosterops everetti	80	83	alien
Zosterops japonicus	6381	36	native
Zosterops meyeni	85	95	native
Zosterops palpebrosus	4	333	alien
Zosterops poliogastrus	1	83	alien
Zosterops senegalensis	2	117	alien

Appendix C Numbers of training samples in Maxent models for each of the tested species

Order	Family	Species	Numbers of training samples
PASSERIFORMES	Estrildidae	Padda oryzivora	2
PSITTACIFORMES	Psittacidae	Eos bornea	3
PSITTACIFORMES	Psittacidae	Cacatua moluccensis	4
PSITTACIFORMES	Psittacidae	Cacatua goffiniana	8
PSITTACIFORMES	Psittacidae	Cacatua sulphurea	9
PSITTACIFORMES	Psittacidae	Cacatua alba	15
PSITTACIFORMES	Psittacidae	Lorius garrulus	15
GALLIFORMES	Phasianidae	Chrysolophus amherstiae	16
PASSERIFORMES	Sturnidae	Sturnus nigricollis	17
PASSERIFORMES	Timaliidae	Garrulax chinensis	17
GALLIFORMES	Phasianidae	Pavo muticus	19
PASSERIFORMES	Estrildidae	Lonchura malabarica	27
PASSERIFORMES	Sturnidae	Sturnus malabaricus	32
PSITTACIFORMES	Psittacidae	Agapornis personatus	38
PASSERIFORMES	Estrildidae	Estrilda troglodytes	42
PASSERIFORMES	Estrildidae	Lonchura maja	52
PSITTACIFORMES	Psittacidae	Agapornis fischeri	61
PASSERIFORMES	Estrildidae	Amandava amandava	63
PASSERIFORMES	Muscicapidae	Cyornis hainanus	68
PSITTACIFORMES	Psittacidae	Agapornis roseicollis	77
PASSERIFORMES	Timaliidae	Garrulax canorus	89
PASSERIFORMES	Timaliidae	Garrulax monileger	91
PASSERIFORMES	Chloropseidae	Chloropsis hardwickii	97
PASSERIFORMES	Timaliidae	Leiothrix lutea	112
PASSERIFORMES	Paridae	Parus spilonotus	112
PASSERIFORMES	Estrildidae	Estrilda melpoda	126
PSITTACIFORMES	Psittacidae	Eclectus roratus	131
PSITTACIFORMES	Psittacidae	Cacatua leadbeateri	145
PASSERIFORMES	Timaliidae	Leiothrix argentauris	148
PASSERIFORMES	Ploceidae	Euplectes hordeaceus	150
PASSERIFORMES	Corvidae	Urocissa erythrorhyncha	180
PASSERIFORMES	Fringillidae	Serinus canaria	218
PASSERIFORMES	Timaliidae	Garrulax leucolophus	231
PASSERIFORMES	Sturnidae	Acridotheres fuscus	253
PASSERIFORMES	Sturnidae	Gracula religiosa	255
PASSERIFORMES	Emberizidae	Paroaria coronata	339
PASSERIFORMES	Sturnidae	Aplonis panayensis	353
COLUMBIFORMES	Columbidae	Geopelia striata	413
PASSERIFORMES	Muscicapidae	Copsychus malabaricus	429
PASSERIFORMES	Viduidae	Vidua paradisaea	449
PASSERIFORMES	Viduidae	Vidua regia	480

PASSERIFORMES	Muscicapidae	Saxicola caprata	676
PASSERIFORMES	Fringillidae	Serinus mozambicus	749
PASSERIFORMES	Sturnidae	Acridotheres grandis	846
PASSERIFORMES	Pycnonotidae	Pycnonotus jocosus	868
PASSERIFORMES	Corvidae	Cyanopica cyanus	1086
PASSERIFORMES	Muscicapidae	Copsychus saularis	1452
PASSERIFORMES	Ploceidae	Ploceus cucullatus	1543
PASSERIFORMES	Sturnidae	Acridotheres tristis	1736
PSITTACIFORMES	Psittacidae	Psittacula krameri	1755
PASSERIFORMES	Viduidae	Vidua macroura	1907
PASSERIFORMES	Estrildidae	Estrilda astrild	1932
PASSERIFORMES	Ploceidae	Euplectes orix	1968
PSITTACIFORMES	Psittacidae	Nymphicus hollandicus	3848
PSITTACIFORMES	Psittacidae	Melopsittacus undulatus	4042
PASSERIFORMES	Estrildidae	Amandava subflava	5460
PASSERIFORMES	Estrildidae	Taeniopygia guttata	6450
COLUMBIFORMES	Columbidae	Columba livia	7360
COLUMBIFORMES	Columbidae	Streptopelia decaocto	7805
PSITTACIFORMES	Psittacidae	Trichoglossus haematodus	7889
PSITTACIFORMES	Psittacidae	Platycercus elegans	11048
PSITTACIFORMES	Psittacidae	Cacatua galerita	11199