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Patterns of success in passeriform bird introductions on Saint Helena

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Abstract Ecologists have long attempted to predict the success of species that are introduced into foreign environments. Some have emphasized qualities intrinsic to the species themselves, whereas others have argued that extrinsic forces such as competition may be more important. We test some of the predictions made by both the extrinsic and intrinsic hypotheses using passeriform birds introduced onto the island of Saint Helena. We found direct evidence that extrinsic forces are more important predictors of successful invasion. Species introduced when fewer other species were present were more likely to be successful. In a direct test of the alternative hypothesis that intrinsic forces play a more prominent role in success or failure, we found a tendency for species which successfully established on Saint Helena to be also successful when introduced elsewhere. However, the vast majority of species unsuccessful at establishing on Saint Helena had probabilities of success outside Saint Helena of 50% or greater, making this result somewhat equivocal. Finally, we found no evidence to support the hypothesis that species that are successful early are those that are intrinsically superior invaders. These results are consistent with similar analyses of the introduced avian communities on Oahu, Tahiti, and Bermuda.

Key words Saint Helena · Introductions · Competition · Birds · Community

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Introduction

Many ecological studies have attempted to deduce explanatory principles for predicting which species of plants and animals are likely to succeed and which to fail when released into foreign environments (Elton 1958; volumes edited by Mooney and Drake 1986; Drake et al. 1989). Some authors have emphasized the importance of properties intrinsic to the particular species being released (Simberloff and Boecklen 1991; Simberloff 1992), whereas other have argued that extrinsic forces such as competition may be more important (Moulton and Pimm 1983, 1986a,b, 1987; Moulton 1985, 1993; Lockwood and Moulton 1994; Lockwood et al. 1993). In this paper we test some of these predictions in the light of a hitherto unexplored case history: the introduced passeriform birds on the island of Saint Helena in the South Atlantic.

The Saint Helena case history offers three attractive features for testing these predictions. First, the island is quite small, making species composition more easily ascertained. Second, a relatively large number of passeriform species have been released there (at least 31). Third, the first introductions took place in 1776, so the time span over which introductions have occurred exceeds 200 years.

If extrinsic forces such as competition influence introduction success, then species introduced when fewer other species are present should have greater chances for success (Elton 1958; Moulton and Pimm 1983; Moulton 1993). Alternatively, if intrinsic properties govern species' chances to succeed, then species successfully introduced into one environment should be intrinsically more likely to succeed anywhere else they are introduced. This would be true regardless of when they are introduced or which other species are present (Simberloff and Boecklen 1991; Simberloff 1992).

We begin by testing the "competition" hypothesis that avian introductions are more likely to succeed when fewer other introduced species are present (Elton 1958; Pimm 1989; Simberloff and Boecklen 1991; Moulton

1993). We then test the "intrinsic colonization hypothesis" of Simberloff and Boecklen (1991) and Simberloff (1992) that species which successfully invade one locale are likely to be successful at other locales simply because they are intrinsically "good" invaders. Finally, we test a similar hypothesis that earlier introductions are intrinsically more likely to succeed.

Materials and methods

The island of Saint Helena at 15° 58′S, 05° 43°W is volcanic and rises nearly 6000 m from the mid-Atlantic ridge. The island has an area of 122 km^2 and a maximum height of 830 m above sea level. Introductions of terrestrial birds began shortly after the first Europeans arrived around 1550 (Teale 1981). The earliest introductions involved non-passeriforms, whereas the first introductions of passeriform species occurred in 1776 (Haydock 1954). The early European settlers exterminated nearly all the indigenous terrestrial birds and converted most of the original native forest to plantations of exotic trees, agricultural land and rough grazing land (Haydock 1954; Teale 1981).

To be consistent with other recent work we consider only the introduced passeriforms (Moulton and Pimm 1986, 1987; Lockwood et al. 1993; Moulton 1993; Lockwood and Moulton 1994). Faaborg (1977) argued that non-passerines exhibit physiological differences from passerines, and Ricklefs and Travis (1980) also argued that these two groups should be treated separately. Moreover, no native passeriforms survive on Saint Helena (Baker 1868).

We compiled the list of introduced passeriform birds (Appendix 1) from a series of published references: Phillips (1805); Brooke (1808); Barnes (1817); Layard (1867, 1871); Baker (1868); Melliss (1870, 1871); Janisch (1908); Huckle (1924); Moreau (1931); Winterbottom (1936); Benson (1950); Haydock (1954); van Bruggen (1958); Watson (1966); Basilewsky (1970); Loveridge (1977); Teale (1981); and Hartog (1984). As in some other studies of introduced birds (i.e. Moulton and Pimm 1983; Simberloff and Boecklen 1991; Moulton 1993), we adopted the convention of excluding those species where five or fewer individuals were known to have been released: none of these introductions were likely to have led to self-perpetuating populations.

In our first test, we calculated the number of species present at the time of introduction, using the technique of Moulton (1993). Briefly, we ranked each species by introduction date and then summed the number of other introduced species present at the time of the introduction. The actual number of other species present at the time of introduction (NSP) was obtained by subtracting the number of extinctions of introduced species from the total number of other introduced species. We then used a Kruskal-Wallis test to compare the number of other species present at the time of introduction for failed versus successfully established species. If extrinsic forces such as competition were not an influencing factor, then we would expect no significant difference in the mean number of other species present between groups. However, if these extrinsic forces were important, at the time of introduction the average number of other species present would be higher for the group of species which failed to establish than for the group that successfully established.

As a direct test of the alternative view of Simberloff and Boecklen (1991), which emphasizes intrinsic properties, we calculated an index of success for each species. The success index is based chiefly on data in Long (1981), updated using Lever (1987). We excluded any introductions for which the outcome was uncertain. Our calculation is based on the index used by Simberloff (1992) and Moulton (1993). An index of success for each species was calculated by dividing the number of times that a species was successfully introduced, excluding Saint Helena, by the total number of places that species was introduced. Often a species was intentionally introduced on several occasions in one geographic location. However, because information concerning multiple introduction events is unlikely for other species, we count each species as having only one attempt at invasion in one geographic location. We were able to calculate a probability index of success, or P(success), for 21 of the 31 species released on Saint Helena: the remaining species were only released on Saint Helena. We then compared the mean success index value for the group of species that successfully colonized Saint Helena versus those that failed. If intrinsic properties influence successful establishment, then those species successfully introduced outside Saint Helena should have a greater probability of success on Saint Helena. Similarly, if species tend to fail wherever introduced, they will tend to fail when introduced to Saint Helena. The introduction dates and success index values that we used in our calculation are listed in the Appendix.

In the analyses of the introductions to the Hawaiian islands, there is a tendency for the number of introduced species on the island to increase over time (Moulton and Pimm 1983, 1986a,b, 1987). Thus, it is argued that early introductions typically succeed because they encounter fewer competitors. The alternative is that these early introductions were intrinsically more successful – perhaps because only the most hardy species could survive the rigors of mid-nineteenth century sea transport or something of the like. The dynamics of species introductions to Saint Helena are different and do not show the same rough increase in species numbers over the years. The last addition, for example, was in 1850 while the Hawaiian islands may be continuing to accrue species. These differences in the timing of introductions allow us to examine the effects of timing on success with what is essentially a different experimental design.

We can thus test another prediction of the "intrinsic colonization hypothesis" that early introductions are more likely to be successful due to intrinsic properties rather than later introduction. We compared the success values for early versus late introductions using the median and mean date of all introductions as our criterion for classification. In addition, we used a Spearman rank correlation of success index value against date of introduction. If intrinsic properties determine successful invasion, we would expect that in each of these tests, species introduced earlier are also the species with high success index values.

Results

At least 31 species of passeriform birds have been released on Saint Helena. The first introduction took place in 1776, and the last in 1929 (see Appendix). The introductions were not evenly spaced over time, rather they were highly episodic. Thus, 8 of the introductions occurred in the year 1820, 2 in 1850 and 1870, and 14 in 1929. No species introduced after 1850 successfully colonized Saint Helena, but 4 of the 11 introductions prior to 1850 were successful. These include the Yellow Canary (*Serinus flaviventris*), Java Sparrow (*Padda oryzivora*), Common Myna (*Acridotheres tristis*) and Common Waxbill (*Estrilda astrild*). The fifth successful introduction, the Madagascar Weaver (*Foudia madagascariensis*), was introduced in 1850. Thus, the overall success rate for passeriform introductions on Saint Helena is very low at 5/31 or 16%.

As noted in the Appendix, none of the 14 species released in 1929 was successful. The failure of such a large proportion of the introduced species when the greatest number of other introduced species were present superficially appears overwhelmingly to support the "competition" hypothesis. However, we have no information on propagule sizes or sex ratios for these introductions. Moreover, all were introduced by a single individual whose methods of release may have, for some unknown reason, doomed all these species to failure. Thus, it could be argued that for our analyses to be conservative these species should be excluded. For this reason, we have conducted each test with and without these 14 species.

When we look at the number of other species present at the time of introduction and its influence on successful establishment, we see that successful species on average faced fewer potential competitors. (Kruskal-Wallis, approximate $\chi^2 = 10.99$; $P > \chi^2 = 0.009$). The mean number of species encountered by successful species on Saint Helena was 5.4 and for unsuccessful species 14.15. This result is consistent with the competition hypothesis: successful species, on average, faced fewer potential competitors when they were initially released. When all 1929 releases were excluded, we still observe a significant difference (Kruskal-Wallis, approximate $\chi^2 = 6.94$, $P > \chi^2 = 0.008$), with the mean number of species encountered for successful introductions being 5.4 and 9.67 for failed introductions.

Supporters of the idea that intrinsic properties are most important (e.g. Simberloff and Boecklen 1991) have predicted that the outcomes of several introductions of a given species into separate locales would be correlated. To test this, we compared success index values between the group of successful versus the group of failed introduced species on Saint Helena. Ideally, this test would include success index values for all species; however, this was not possible. Only 21 (all 5 of the successful species and 16 of the unsuccessful species) of the 31 passeriforms introduced to Saint Helena have also been introduced in some other locale. Ten of these species were introduced by H. Bruins-Lich in 1929 (Haydock 1954). Thus, most of the 1929 introductions (10 of the 14 species) were, by default, not included in this and the following tests. However, following arguments made above, we conducted this test and each of the below tests with and without those four 1929 species.

We found that the success index values for the group of species that successfully established on Saint Helena did differ significantly from the group that failed, regardless of whether we included the 1929 introductions (approximate $\chi^2 = 8.74$, $P > \chi^2 = 0.0031$) or excluded them (approximate $\chi^2 = 7.34$, $P > \chi^2 = 0.0067$). Thus, the species successfully establishing on Saint Helena tend to have a high success index value. This result superficially supports the "intrinsic colonization hypothesis" of Simberloff and Boecklen (1991). However, if we look closely at the results, of the 16 species that failed, 11 had better than a 50% chance of succeeding elsewhere. For example, the generally extremely successful European Starling (*Sturnus vulgaris*) and House Sparrow (*Passer domesticus*) failed when introduced to Saint Helena. Thus, although there is a statistical tendency for intrinsic properties influencing successful establishment on Saint Helena, this result is somewhat negated on closer examination.

Finally, we can test a hypothesis advanced by Simberloff and Boecklen (1991) that species introduced earlier are simply more likely to succeed (perhaps for reasons not involving competition), while more recent introductions are more likely to fail. As indicated in the Appendix, the first passeriform introductions occurred in 1776, whereas the last took place in 1929. In classifying introductions as being either late or early, we used the median and mean dates of all 31 introductions (see Moulton 1993). The median date for all passeriform introductions on Saint Helena was 1870, and the difference in probability of success values between early versus late introductions was not significant (Kruskal-Wallis, approximate $\chi^2 = 1.48$, $P > \chi^2 = 0.22$). In this test, 15 species were classified as "early" and 6 as "late". We also did this test using the mean date of all introductions (1874). In this test we did observe a significant difference in probability of success values between early and late introductions (Kruskal-Wallis, approximate $\chi^2 = 4.90$, $P > \chi^2 = 0.03$). In this test, the four species that were classified as "late" were the four introduced in 1929, which, as we have argued, are best excluded.

When we exclude the 1929 introductions, the difference in probability of success values between early and late introductions is not significant, whether we use the mean date of 1829 (Kruskal-Wallis, approximate $\chi^2 = 0.00$, $P > \chi^2 = 0.99$) or the median date of 1820 (Kruskal-Wallis, approximate $\chi^2 = 2.04$, $P > \chi^2 = 0.15$). When using the median date of 1820, we classified all species introduced in 1820 "late". However, if we had classified them as "early", the analysis is the same as using the mean date of 1829.

If earlier introductions were more likely to succeed, we would further expect a significant correlation between date of introduction and probability of success. We used a Spearman rank correlation and observed no significance (Spearman's ρ of = -0.39, $P >$ absolute $\rho = 0.08$). A correlation excluding those species released in 1929 was also not significant (Spearman's $\rho = 0.098$, $P >$ absolute $\rho = 0.71$).

Discussion

Overall, we contend that our results are consistent with the hypothesis that competition played a prominent role in influencing the fates of species introduced onto Saint Helena. Our results do not support the hypothesis that species successfully introduced onto Saint Helena were intrinsically destined to be so. We have two major results. First, species that were unsuccessful on Saint Helena were released when there were about two to three times as many species present than when the successful species were released. The criticism of our interpreting this result as indicating competition is that the successful species could be intrinsically successful and the unsuccessful species could be intrinsically unsuccessful. The relationship to the number of species present could just be spurious.

We can evaluate this criticism, because there are 21 species for which we were able to calculate a probability of success outside of Saint Helena. There is indeed a significant tendency toward successful introduced species on Saint Helena being those that had high probabilities for success outside of Saint Helena. However, 11 of the 16 species which failed to become established had overall probabilities of success at or above 50%. This can hardly be interpreted as supporting the hypothesis that these species were destined to fail no matter where introduced. Indeed, the chance that all 11 would fail is the same as tossing a coin 11 times and getting 11 heads, i.e. less than one in 2000. Thus, our second major result is that some species seem to have intrinsic qualities that make them superior invaders. Intrinsic factors are not however, prevalent enough to mask the effects of competition.

We found no support for the hypothesis that species successful early were intrinsically more likely to be so. Unlike Hawaii, species introduced earlier to Saint Helena (pre-1829, or pre-1870 depending on the analysis) were not more likely to succeed outside of Saint Helena than those released later. In addition, there was no trend for the probability of success elsewhere to decline with the date of introduction on Saint Helena.

Although the effects of interspecific competition are notoriously difficult to prove in extant communities (Connell 1980), we can deduce these effects using the introduced communities on oceanic islands (for the benefits of such analyses see Moulton and Pimm 1983). Our results lend further evidence to support the hypothesis that extrinsic properties, specifically interspecific competition, strongly influence the success or failure of introduced species (Moulton and Pimm 1983, 1986a,b, 1987; Moulton 1985, 1993; Lockwood and Moulton 1994; Lockwood et al. 1993).

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Appendix

Species introduced to Saint Helena, followed by the date of introduction, present status on Saint Helena and calculated probability of success, P(success). All other places introduced and those introduction fates are listed as well. All information is taken from Long (1981) or Lever (1987).

Serinus flaviventris **(Yellow Canary)**: 1776, Successful, P(success) = 1.00
Successful (1) – Ascension
Unsuccessful (0)

Padda oryzivora **(Java Sparrow)**: 1790,Successful, P(success) = 0.81
Successful (25) – China, Hong Kong Island, South Vietnam, Singapore Island, Pinang Island, Myanmar, Sumatra, Lesser Sunda Islands, Pemba Island, Thailand, Sri Lanka, Borneo, Sulawesi, Moluccas, Philippines, Christmas Island, Cocos-Keeling Islands, Zanzibar, Hawaiian Islands, Fiji, USA, Puerto Rico, Tanzania, Japan, Taiwan
Unsuccessful (6) – Seychelles, Mauritius, Réunion, Archipel des Comores, New Zealand, Australia

Erithacus rubecula **(European Robin)**: 1820, Failed, P(success) = 0.00
Successful (0)
Unsuccessful (4) – Australia, New Zealand, Canada, USA

Fringilla coelebs **(Chaffinch)**: 1820, Failed, P(success) = 0.50
Successful (2) – New Zealand, South Africa
Unsuccessful (2) – Australia, USA

Euplectes orix **(Red Bishop)**: 1820, Failed, P(success) = 0.60
Successful (3) – Australia, Puerto Rico, Hawaiian Islands
Unsuccessful (2) – Tahiti, Bermuda

Estrilda astrild **(Common Waxbill)**: 1820, Successful, P(success) = 0.79
Successful (15) – Mauritius, Ascension, Rodrigues, Amirante Islands, Seychelles, Réunion, Cape Verde Islands, Tahiti, New Caledonia, Brazil, Puerto Rico, São Tomé, Portugal, Bermuda, Hawaiian Islands
Unsuccessful (4) – Fiji, Madagascar, Archipel des Comores, Principé

Turdus merula **(Blackbird)**: 1820, Failed, P(success) = 0.50
Successful (3) – Australia, New Zealand, Tasmania
Unsuccessful (3) – South Africa, USA, Fiji

Turdus philomelos **(Song Thrush)**: 1820, Failed, P(success) = 0.50
Successful (2) – Australia, New Zealand
Unsuccessful (2) – South Africa, USA

Acridotheres tristis **(Indian Myna)**: 1820, Successful, P(success) = 0.92
Successful (22) – Australia, New Zealand, South Africa, Seychelles, Réunion, Rodrigues, Mauritius, Madagascar, Archipel de Comores, Chagos Archipelago, Ascension Island, Solomon Islands, Cook Islands, Fiji, New Caledonia, Society Islands, Hawaiian Islands, New Hebrides, Agalega Islands, Laccadive Island, Maldive Island, South Africa
Unsuccessful (2) – USA, England

Alauda arvensis **(Skylark)**: 1820, Failed, P(success) = 0.88
Successful (7) – New Zealand, Australia, Hawaiian Islands,Vancouver Island (Canada), Tasmania, Kangaroo Island, Lord Howe Island
Unsuccessful (1) – USA

Gracula religiosa **(Hill Myna)**: 1829, Failed, P(success) = 0.75

Successful (3) – Hawaiian Islands, USA, Puerto Rico
Unsuccessful (1) – Christmas Island

***Serinus canicollis* (Cape Canary)**: 1850, Failed, P(success) = 0.33
Successful (1) – Réunion
Unsuccessful (2) – Mauritius, Tahiti

***Foudia madagascariensis* (Madagascar Weaver)**: 1850, Successful, P(success) = 1.00
Successful (7) – Amirante Islands, Seychelles, Chagos Archipelago, Mauritius, Reunion, Rodrigues, Agalega Islands
Unsuccessful (0)

***Sturnus vulgaris* (European Starling)**: 1852, Failed, P(success) = 0.50
Successful (6) – North America, Jamaica, South Africa, Australia, New Zealand, Puerto Rico
Unsuccessful (3) – Cuba, Venezula, Russia

***Mimus gilvus* (Tropical Mockingbird)**: 1853, Failed, P(success) = 0.75
Successful (3) – Colombia, Panama, Trinidad and Tobago
Unsuccessful (1) – Barbados

***Passer domesticus* (House Sparrow)**: 1870, Failed, P(success) = 0.85
Successful (29) – North America, South America, Easter Island, Falkland Islands, Cuba, St. Thomas, Bermuda, Hawaiian Islands, Australia, Norfolk Island, New Zealand, New Hebrides, New Caledonia, Senegal, Kenya, South Africa, Zanzibar, Archipel des Comores, Seychelles, Mauritius, Réunion, Rodrigues, Chagos Archipelago, Azores Islands, Cape Verde Islands, Amirante Islands, Puerto Rico, Java, Andaman Islands
Unsuccessful (5) – Greenland, Philippines, South Georgia, New Guinea, Jamaica

***Carduelis chloris* (Greenfinch)**: 1870, Failed, P(success) = 0.80
Successful (4) – Australia, New Zealand, Azores Islands, Uruguay and Argentina
Unsuccessful (1) – USA

***Uraeginthus angolensis* (Blue Waxbill)**: 1929, Failed, P(success) = 0.50
Successful (1) – Hawaiian Islands
Unsuccessful (1) – Tahiti

***Amandava subflava* (Orange Waxbill)**: 1929, Failed, P(success) = 0.00
Successful (0)
Unsuccessful (1) – Tahiti

***Serinus mozambicus* (Yellow Canary)**: 1929, Failed, P(success) = 0.75
Successful (6) – Mauritius, Réunion, Rodriques, Hawaiian Islands, USA, Puerto Rico
Unsuccessful (2) – Amirante Islands, Tahiti

***Euplectes albonotatus* (Whitewinged Whydah)**: 1929, Failed, P(success) = 1.00
Successful (1) – Australia
Unsuccessful (0)

Introduced only to Saint Helena:

***Estrilda erythronotos* (Blackcheeked Waxbill)**: 1929 Failed

***Estrilda melanotis* (Yellow-bellied Waxbill)**: 1929 Failed

***Euplectes progne* (Longtailed Whydah)**: 1929 Failed

***Pytilia melba* (Green-winged Pytilia)**: 1929 Failed

***Ploceus velatus* (Redeyed Masked Weaver)**: 1929 Failed

***Serinus atrogularis* (Blackthroated Canary)**: 1929 Failed

***Sporopipes squamifrons* (Scalyfronted Finch)**: 1929 Failed

***Uraenginthus granatinus* (Grenadier Waxbill)**: 1929 Failed

***Vidua paradisaea* (Longtailed Paradise Widow)**: 1929 Failed

***Vidua regia* (Short-tailed Widow)**: 1929 Failed

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