Successful population establishment from small introductions appears to be less common than believed

Alyssa Corbett King[1,2] and J. Michael Reed[1]

[1] Department of Biology, Tufts University, Medford, MA, USA
[2] Current affiliation: The School for Field Studies, Beverly, MA, USA

ABSTRACT

Although small populations are at high risk of extinction, there are regular reports in the scientific literature of purported small, isolated, persistent populations. One source of evidence of the viability of small populations comes from the alleged successful introduction of species to areas outside their original range from introductions of few individuals. We reviewed the examples from introduction compendia on deliberate translocations of birds, and the original sources, to identify and evaluate purported examples of successful establishments from small introductions. We found 23 purportedly successful introductions from few (<30) individuals. After assessing original sources, we found that two of the claims were substantiated; the rest were ambiguous or could be rejected as examples, primarily due to a lack of evidence in original sources of the number of birds released and because of supplemental individuals from other releases, releases in nearby regions, and the possibility of natural invasion. Our results suggest that reports of successful establishment of birds from introductions of few individuals have been overstated. These results strengthen the relationship previously reported between propagule pressure and likelihood of establishment, and support the lack of viability of small populations presumed by population theory. We suggest that analyses of introduction failure and success would benefit from excluding studies where introduction effort is unknown or unreliably documented.

Corresponding author
J. Michael Reed,
michael.reed@tufts.edu

INTRODUCTION

Despite wide acknowledgement that small populations are at greater risk of extinction than are larger populations (e.g., *MacArthur & Wilson, 1967*; *Gilpin & Soulé, 1986*; *Ludwig, 1996*), there are persistent caveats in the scientific literature that small, isolated populations can persist (e.g., *Simberloff, 1998*; *Walters & Crist, 2006*). The highest profile recent example is that of the purported rediscovery of the Ivory-billed Woodpecker (*Campephilus principalis*) (*Fitzpatrick et al., 2005*, but see *Sibley et al., 2006*; *Scott et al., 2008*; *Elphick, Roberts & Reed, 2010*). These examples appear to defy the small-population paradigm, described as the tendency for small populations to succumb to stochastic events and extinction vortices (*Gilpin & Soulé, 1986*; *Caughley, 1994*; *Fagan & Holmes, 2006*; *Brook, Sodhi & Bradshaw, 2008*). There are few examples of persistent, small, isolated populations of vertebrates,
and possibly none that have been investigated in detail. For example, although the Devil's Hole Pupfish (*Cyprionodon diabolis*) is endemic to a single pool in the Mojave Desert and the pond has been isolated for at least 60,000 years (*Riggs & Deacon, 2004*), it appears that the fish have not been there for more than a few thousand years, and possibly much less time (*Reed & Stockwell, 2014*; *Martin et al., 2016*; but see *Sağlam et al., 2016* for a contrary assessment). One source of evidence related to the potential viability of small populations comes from species introductions to new regions (*Duncan, Blackburn & Sol, 2003*; *Blackburn, Lockwood & Cassey, 2009*; *Blackburn et al., 2011*). Evaluating the success or failure of deliberate species introductions has provided important insight into population dynamics and invasion ecology.

Avian introductions have been of particular interest because of the extensive number of species introductions during the 19th and 20th centuries during and after colonial European expansion. The most distinctive pattern that has emerged from the analyses of bird introductions is that introduction effort, in terms of the number of individuals per release and number of releases (sometimes referred to as 'propagule pressure', e.g., *Simberloff, 2009*), is an important factor determining successful establishment (*Griffith et al., 1989*; *Wolf et al., 1996*; *Green, 1997*; *Sol & Lefebvre, 2000*; *Brook, 2004*; *Lockwood, Cassey & Blackburn, 2005*; *Blackburn, Lockwood & Cassey, 2009*; *Blackburn et al., 2011*; *Blackburn et al., 2013*; *Hufbauer et al., 2013*; but see *Moulton, Cropper & Avery, 2012*). Despite the common outcome that introductions of few individuals (low propagule pressure) tend to fail, there are regular reports of successful establishment from the introduction of very few individuals (*Newsome & Noble, 1986*; *Tomich, 1986*; *Pimm, 1989*; *Pimm et al., 1993*; *Green, 1997*; *Simberloff, 1998*; *Taylor, Jamieson & Armstrong, 2005*). The idea that successful introduction can occur from the introduction of few individuals has been called the Noah fallacy (*Simberloff, 2009*).

In impressive compendia, *Long (1981)*, *Lever (1987)* and *Lever (2005)* reviewed successful and failed attempts at bird species introductions, and they regularly report successful introductions from few individuals. In fact, *Long (1981)* is the primary source for most published studies that evaluate patterns of extinction risk. Our goal was to assess the quality of the evidence cited to support successful establishment from introductions of very few individuals. We did this specifically for birds because this taxon has the most extensive available data, and these data are regularly cited as providing examples of successful introductions. Previous studies have shown that invasion success by introduced birds is correlated with a variety of factors, including introduction effort (e.g., *Griffith et al., 1989*; *Wolf et al., 1996*; *Sol & Lefebvre, 2000*; *Lockwood, Cassey & Blackburn, 2005*). In addition, it is generally viewed that introductions of fewer than 5 individuals is not likely to lead to success (*Moulton & Pimm, 1983*; *Cassey, 2002*). However, assessments regularly identify apparent exceptions to the rule—purported introductions of few birds that somehow establish. One recent example is by *Moulton et al. (2010)*, who argue that there is no real evidence that House Sparrow (*Passer domesticus*) establishment in North America came from more than the original release of 16 individuals, rather than from multiple introductions of hundreds of birds, as is traditionally argued (*Long, 1981*). *Duncan* (*1997*, p. 905), for example, states that there are ''recorded instances of successful invasion

following the release of only two birds (*Drummond, 1906*).'' However, if one reads the original source for this example, *Drummond* (*1906*, p. 243) states: ''Many years ago a pair of these birds... nested in a kauri-tree about a hundred yards from a settler's house, and from that spot they completely spread throughout the whole country.'' So for this example there is no indication of the number of individuals originally introduced to the area, and the referenced pair could have been one of hundreds introduced to the region. Consequently, it would not be valid to assume that the existing population did indeed arise from a single introduction of two individuals.

Moulton et al. (2010) suggest that historical records need to be critically evaluated. Many of the examples reported of introduction success of birds from few individuals come from summary reports rather than from the original records. Here we evaluate alleged examples of introduction success of bird species from low introduction effort (low propagule pressure) from large summary reports (*Long, 1981*; *Lever, 1987*; *Ebenhard, 1988*) by examining original sources of these examples to determine the level of support that these were isolated introductions of the stated small size. This is not intended to be a review of all reported examples; it is an assessment of examples from the most commonly cited compendia. If we find any examples of understated introduction effort, or insufficiently documented support of introduction numbers, we will support our premise that successful introduction from few individuals is unlikely, or at least less likely than currently presumed.

METHODS

We gathered assertions of persistent populations arising from non-native introductions of few individuals reported in compendium volumes by *Long (1981)*, *Lever (1987)*, and *Ebenhard (1988)*; specific references were not available for some compendia (e.g., *Newsome & Noble, 1986*; they report introduction successes from few individuals but do not include references, citing a library repository that no longer has them). It was not our goal to do a thorough literature review or all alleged examples because it turned out to be unnecessary for our assessment, and the summary reports are the sources of most cross-species analyses. We considered an introduction to be ''few'' individuals if it was of 30 or fewer birds; this population size is easily small enough that extinction due to demographic and environmental stochasticity is expected to drive a species extinct, yet there are published assertions of successful establishment from these numbers. We ignore the lack of a standard definition of success, and assume that a population currently extant represents a successful introduction. We traced each cited example back to its original sources and scored the assertions for two measures: (1) confidence of the number released, and (2) confidence that there were no subsequent releases, no other nearby releases, and no likelihood of natural invasion. The confidence of number released was scored as: 0 = no evidence of actual number released; 1 = numbers reported, but no indication that it was of the complete introduction; 2 = second hand report of carefully documented release; 3 = quantitative documentation by person doing the release, and no other documentation of releases. The confidence that there was only one, isolated release was scored as: 0 = known other releases; 1 = suspected other releases; 3 = specifically addressed in literature

that no other releases occurred. (There was no similar intermediate value for a confidence score of 2; we skipped it so that 3 would represent a similar level of confidence.) We also included relevant information from other sources not cited by the analysis papers.

Because it is difficult to assess whether or not an introduced population remained isolated during colonization, we recorded documented instances of nearby introductions as possible sources of population augmentation. We defined "nearby" as any introduction that is within a plausible dispersal or individual exploration distance. For example, most of the New Zealand introductions have been considered as isolated in the specific province in which the release occurred. However, there is evidence of the song thrush (scientific names are found in Table 1) dispersing between provinces, suggesting that it is likely that other introduced populations were able to disperse in a like manner (*Lever, 1987*, p. 333). Similarly, *Long* (*1981*, p. 38) reported that black swans appeared hundreds of kilometers away from many of their release points in New Zealand (scientific names are found in Table 1), allowing for the complete colonization of the country and other offshore islands. Therefore, it is logical to include nearby releases as possibly augmenting the original founder population.

RESULTS

We evaluated 23 introductions that included 17 species, and recorded the confidence levels for each introduction (Table 1); details of what was reported in the original citations are found in Supplemental Information. Of the 23 introductions, we found only two that were strongly supported by original sources. One of the species reported as a successful introduction, the Cape Barren goose to New Zealand, has become extirpated so it cannot be considered a translocation success (*Lever, 1987*; *Falla, Sibson & Turbott, 1966*). Lack of support, or ambiguous support, for the reported number being released fell into four categories, including no first-hand documentation of release, no data available on introduction number, uncertainty about data available on introduction number, and additional releases at or near the original release site (Fig. 1).

Similarly, for 21 of the 23 introductions we had low confidence that the established population came from the introduction specified by the analytical review papers and compendium volumes. We found that the original literature for introductions report known additional introductions in the region, suspected additional introductions, had a lack of information addressing whether or not there were other releases in the general region as the original release in the same time period, acknowledged possibilities that a wild population of the species was already present in the same region, or that the current population might have come from a natural invasion (Fig. 2).

Finally, there can be complications from use of non-standard or inaccurate bird names that can cause both types of error. *Williams (1968)*, for example, reported that the European greenfinch was sometimes referred to as the green linnet, thus making it impossible to determine the exact number of birds released for some species.

Corbett King and Reed (2016), *PeerJ*, DOI 10.7717/peerj.2440

Peer J

Table 1 Evaluation of purported successful establishments of species from single introductions of few (<30) individuals; details from primary and secondary sources in Supplemental Information.

Species	Number reported released	Where introduced	Cited by	Confidence in		Rationale for confidence scores based on primary and secondary sources	Assertion accepted?
				Number released[a]	Lack of supplemental individuals[b]		
Mute swan *Cygnus olor*	12	Australia	*Duncan et al. (2001)*	0	0	Uncertainty about accuracy of introduction data; likely previously established wild population	No
	29	New Zealand	*Veltman, Nee & Crawley (1996)*	0	0	Additional birds released; possibility of earlier introductions	No
Black swan *C. atratus*	4	Auckland, NZ	*Lever (1987)*	2	0	No first-hand documentation of release; multiple releases to nearby regions	No
Cape Barren goose *Cereopsis novaehollandiae*	8[c]	New Zealand	*Veltman, Nee & Crawley (1996)*	1	0	Subsequent introductions; no first-hand documentation of release; possibility of natural invasion	No
Cattle egret *Bubulcus ibis*	18	Australia	*Duncan et al. (2001)*	2	0	Introduced birds apparently disappeared; no first-hand documentation of release; possible establishment via natural invasion	No
	12–21	Chagos Archipelago	*Lever (1987)*	1	–	Uncertainty about number released; possibility of other releases not addressed	No
Laughing dove (Senegal turtledove) *Streptopelia senegalensis*	4	Australia	*Duncan et al. (2001)*	0	–	No data available on number introduced; possibility of other releases not addressed	No
Laughing kookaburra *Dacelo novaeguineae*	21	New Zealand	*Veltman, Nee & Crawley (1996)*	0	–	No data available on number introduced; possibility of other releases not addressed	No
Australian magpie *Gymnorhina tibicen*	2	Australia	*Duncan (1997)*	0	–	No data available on number introduced; possibility of other releases not addressed	No
	10	Aukland, NZ	*Duncan (1997)*	2	0	No first-hand documentation of release; may have previously been present in the wild; multiple releases at nearby sites	No
Song thrush *Turdus philomelos*	8	Wellington, NZ	*Duncan (1997)*	2	0	No first-hand documentation of release; multiple releases at nearby sites	No
Red-whiskered bulbul *Pynconotus jocosus*	8	Australia	*Duncan et al. (2001)*	0	–	No data available on number introduced; possibility of other releases not addressed	No
	10–20	Miami, USA	*Lever (1987)*	0	–	No data available on number introduced; possibility of other releases not addressed	No

Corbett King and Reed (2016), *PeerJ*, DOI 10.7717/peerj.2440

Table 1 (*continued*)

Species	Number reported released	Where introduced	Cited by	Confidence in		Rationale for confidence scores based on primary and secondary sources	Assertion accepted?
				Number released[a]	Lack of supplemental individuals[b]		
Eurasian tree sparrow *Passer montanus*	20–24	St. Louis, USA	*Lever (2005)*	2	3	Supported	Yes
House sparrow *P. domesticus*	14[d]	Otago, NZ	*Duncan (1997)*	2	0	No first-hand documentation of release; 2 releases at introduction site; multiple releases at nearby sites	No
Scaly-breasted munia (spice finch) *Lonchura punctulata*	8	Australia	*Duncan et al. (2001)*	0	–	No data on number introduced; possibility of additional releases not addressed	No
Chaffinch *Fringilla coelebs*	16	Canterbury, NZ	*Duncan (1997)*	0	0	Additional birds were released at same site; multiple releases at nearby regions	No
Island canary *Serinus canaria*	12[e]	Midway Atoll, Hawaii	*Lever (1987)*	3	3	Supported	Yes
European greenfinch *Carduelis chloris*	8	Otago, NZ	*Duncan (1997)*	1	0	No first-hand documentation of release; use of the same common name for different species; multiple releases at nearby sites	No
Common redpoll *Carduelis flammea*	2	Wellington, NZ	*Duncan (1997)*	2	0	No first-hand documentation of release; multiple releases at nearby sites	No
Cirl bunting *Emberiza cirlus*	29[f]	New Zealand	*Veltman, Nee & Crawley (1996)*	1	0	For all 3 cases: no first-hand documentation of releases; multiple releases at nearby sites; other suspected introductions	No
	7	Otago, NZ	*Duncan (1997)*	2			
	4	Wellington, NZ	*Duncan (1997)*	2			

Notes.

[a]0, no evidence of actual number released; 1, numbers reported, but no indication that it was of the complete introduction; 2, second hand report of carefully documented release; 3, quantitative documentation by person doing the release.

[b]Via subsequent releases, other nearby releases, or natural invasion: 0, known other releases; 1, suspected other releases; 3, specifically addressed in literature that no other releases occurred; dash, not addressed by primary sources.

[c]Original records indicate 6 (*Williams, 1968*:67).

[d]*Duncan (1997)* cites *Long (1981)*, who says 23 were released, but Long cites *Thomson (1922)* who says 14 were released.

[e]Original records indicate 13 (*Bryan, 1912*).

[f]Original records indicate 11, as 18 released on an island failed (*Thomson, 1922*:175, *Long, 1981*:466).
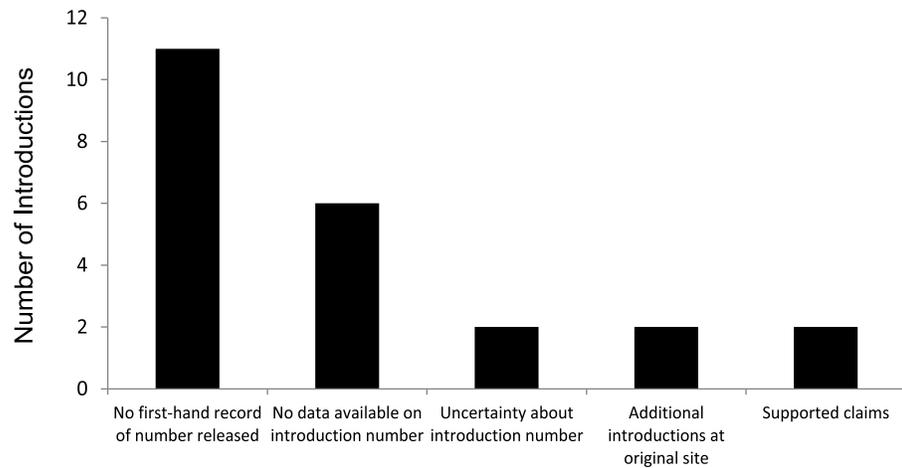
Figure 1 Assessments of 23 successful introductions of 17 species of birds alleged to have established from a single, isolated introduction of few (<30) individuals.
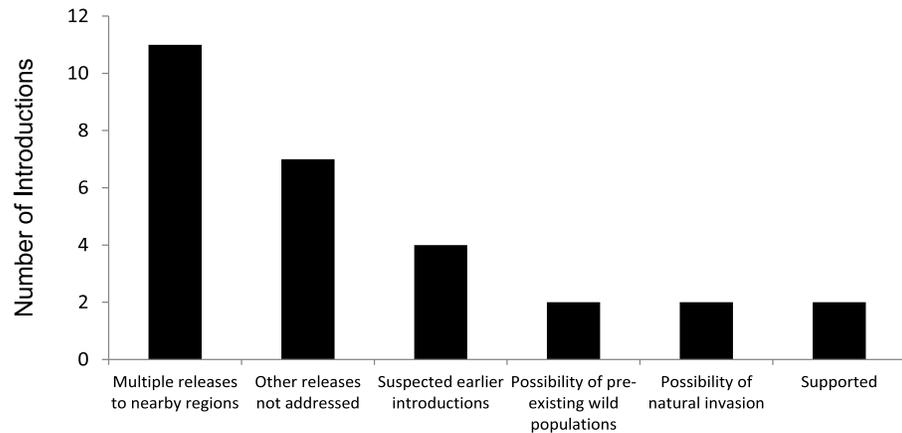
Figure 2 Assessment of support for releases being a single, isolated event for 23 successful introductions of 17 bird species alleged to have established from a single, isolated introduction of <30 individuals. (Note: 'Possibility of natural invasion' refers to species where there is the suggestion that the species' presence might have included unaided invasion.)

DISCUSSION

Although we found reports of 23 successful introductions from a total of 17 species of birds that were purported to have included fewer than 30 individuals in the introduction, only two appear to be strongly supported by data. The first is the island canary, which was introduced to the Hawaiian island of Midway in July of 1910. Only 11–14 canaries were released, but it was estimated that about 60 young were raised in the wild during the first breeding season, and the species is now common on the island (*Bryan, 1912*; *Munro, 1944*; *Berger, 1981*). The introduction, however, was facilitated by extensive human activities. Cats were removed from the island before birds were released, and released canaries were supplied for years with food from feeders (*Munro, 1944*; *Berger, 1981*). Also, a couple living
on the island kept caged canaries for years (*Munro, 1944*), so it is not impossible that there were additional releases or escapes. The other example of an apparently successful release from few individuals is the Eurasian tree sparrow in St. Louis (USA), which apparently originated from an introduced population of 20–24 birds released in 1870 (*Phillips, 1928*; *Wetmore, 1964*; *Barlow, 1973*). We were not able to find evidence of additional releases (*Cooke & Knappen, 1941*).

In contrast, 21 of the reported successful introductions from a small number of individuals were either not supported by original sources, or the information was ambiguous. The primary reason for rejecting the validity of a purported successful introduction from a small release group was a lack of evidence for the number of birds actually released. A particularly interesting example comes from the introduction of the red-whiskered bulbul to Florida (USA). The claim is that the initial introduction was of 10–20 birds, but this appears to be a guess based on possible population growth (*Carleton & Owre, 1975*, pp. 43–44): "To produce the present population, a founding population of fewer than five feeding pairs would have had an annual rate of increase of more than 50%—which seems excessive. An initial population of more than 10 pairs seems too large from accounts of residents…Thus, from tentative data, we hypothesize that between 5 and 10 breeding pairs founding the population…" This is an excellent example of how speculation can transform over retelling into apparent fact.

Another common error is that reports ignored multiple additional introductions of the same species to nearby regions before successful establishment was documented. An example of this is the Australian magpie introduction to Auckland, New Zealand. The implication in the analytical literature is that the 1867 introduction of 10 birds (and one more in 1870) was an isolated event that led to establishment of the Australian magpie in the province (*Duncan, 1997*). However, original sources show that there were at least 6 other releases to New Zealand within a decade of the original release (*Anderson, 1916*; *Thomson, 1922*; *Lamb, 1964*; *Wellwood, 1968*; *Williams, 1969*). The entire suite of releases might then form the basis for the current population, although without data that are apparently unavailable we cannot determine the functional size of the starting population.

Our results strengthen the importance of the observed relationship between propagule pressure to introduction success by showing that many apparent exceptions are, or might be, invalid. This supports the conclusions from earlier analyses, and is in contrast to results reported by *Nuñez, Moretti & Simberloff (2011)*, who reported plant invasion to be unrelated to the number of individuals introduced. Our analysis indicates that in fact 21 of those are not supported or have insufficient data to be evaluated, leaving only two apparently valid examples. These successes might be viewed as unusual chance events that are expected from a large number of attempts with a low likelihood of success, or as examples where there were additional releases not recorded any place we have found, or that records of actual additional releases were not kept. *Moulton et al. (2010)* provide another example of this regarding the history of introductions of house sparrows to North America, with assessments ranging from 8 pairs to over 50, with the actually number of birds released not determinable from the conflicting historic records.

We are not stating that successful introductions from few individuals are not possible, and they continue to be asserted (e.g., *Van Houtan et al., 2009*). Rather, that it is a statistical unlikelihood, so that claims of this type of success should be evaluated critically. One possibility that has not been raised in the small-population literature is that the dynamics of introduced populations are fundamentally different than those of naturally small or artificially reduced populations. This might make an interesting avenue for future investigation. In addition, it would be valuable to decide on unambiguous criteria for defining of success of introduction that distinguishes establishment from invasion and includes a time frame. For example, the crested myna *Acridotheres cristatellus* was introduced to Vancouver, British Columbia, Canada in the late 1890s. The species became established, invaded, increasing in numbers to a peak of around 20,000 birds in the late 1920s, and then decreased to extinction in 2003 (*Long, 1981*; *Simberloff & Gibbons, 2004*). The mynas certainly successfully established, as can occur from introductions of few individuals (e.g., *Szűcs et al., 2014*), but does this count as an invasion success because it became abundant and persisted over 100 years, or as a failure because failed to persist much longer? Consistent with our message in this manuscript of the importance of reading original sources, *Long (1981)* reports that this species was "certainly known" to be in British Columbia in 1894, citing *Wood (1924)* for the information. This assertion has been reprinted subsequently by later sources, e.g., *Lever (2005)*. However, reading the original source, Wood states that the species was "certainly unknown" in British Columbia in 1894 (emphasis ours).

Our results also suggest that analyses of invasion success should include a critical evaluation of the evidence for success and propagule size (also argued by *Moulton et al., 2010*; *Moulton, Cropper & Avery, 2011*; *Blackburn et al., 2013*). Studies that analyze introduction data are sometimes careful in their methods to state that the number of animals introduced that is analyzed is the *minimum* number released, but the results and interpretation often subsequently treat this value as the actual number released, which introduces a source of error into the statistical analyses and interpretations. What might be considered a gold standard is to only include species where the historical record is extensive—including number of animals released and a discussion that includes reference to a lack of other releases. Regardless, historic records will often be incomplete. In the absence of sufficiently robust records, one has few choices: (1) do not do the analysis, (2) do a qualitative analysis, (3) do the analysis, but carefully couch the conclusions in the context of perceived data quality, and perhaps (4) include sensitivity analyses of the effects of different data values on the results.

ACKNOWLEDGEMENTS

We thank M Romero for discussions on this topic, J Muller for translating an article from German, the Tufts Interlibrary loan office and R Broadfoot of the Ernst Mayr Library at Harvard University for assistance tracking sources, E Doerr for searching a library in Australia for unpublished information referenced by *Newsome & Noble (1986)*, and funding from the Tufts University Undergraduate Research Program.

Funding

ACK received funding from the Tufts University Undergraduate Research Program. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures

The following grant information was disclosed by the authors:
Tufts University Undergraduate Research Program.

Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Alyssa Corbett King performed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- J. Michael Reed conceived and designed the experiments, performed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.

Data Availability

  The raw data has been supplied as Supplemental Information.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.2440#supplemental-information.

REFERENCES

Anderson JC. 1916. *Jubilee history of South Canterbury.* Auckland: Whitcomb and Tombs.

Barlow JC. 1973. Status of the North American population of the European Tree Sparrow. In: Kendeigh SC, ed. *Symposium on the house sparrow and European tree sparrow in North America. Ornithological monograph,* vol. 14. Lawrence: American Ornithologist' Union, 10–23.

Berger AJ. 1981. *Hawaiian birdlife.* Honolulu: University Press.

Blackburn TM, Lockwood JL, Cassey P. 2009. *Avian invasions: the ecology and evolution of exotic birds.* Oxford: Oxford University Press.

Blackburn TM, Prowse TAA, Lockwood JL, Cassey P. 2011. Passerine introductions to New Zealand show a positive effect of propagule pressure on establishment success. *Biodiversity and Conservation* **20**:2189–2199 DOI 10.1007/s10531-011-0081-5.

Blackburn TM, Prowse TAA, Lockwood JL, Cassey P. 2013. Propagule pressure as a driver establishment success in deliberately introduced exotic species: fact or artefact? *Biolical Invasions* **15**:1459–1469 DOI 10.1007/s10530-013-0451-x.

Brook BW. 2004. Australasian bird invasions: accidents of history? *Ornithological Science* **3**:33–42 DOI 10.2326/osj.3.33.

Brook BW, Sodhi NS, Bradshaw CJA. 2008. Synergies among extinction drivers under global change. *Trends in Ecology and Evolution* **23**:453–460 DOI 10.1016/j.tree.2008.03.011.

Bryan WA. 1912. The introduction and acclimatization of the Yellow Canary on Midway Island. *Auk* **29**:339–340 DOI 10.2307/4071041.

Carleton AR, Owre OT. 1975. The red-whiskered bulbul in Florida: 1960–71. *Auk* **92**:40–57 DOI 10.2307/4084416.

Cassey P. 2002. Life history and ecology influences establishment success of introduced land birds. *Biological Journal of the Linnean Society* **76**:465–480 DOI 10.1046/j.1095-8312.2002.00086.x.

Caughley G. 1994. Directions in conservation biology. *Journal of Animal Ecology* **63**:215–244 DOI 10.2307/5542.

Cooke MT, Knappen P. 1941. Some birds naturalized in North America. *Transactions of the North American Wildlife Conference* **5**:176–183.

Drummond J. 1906. On introduced birds. *Transactions of the Proceedings of the New Zealand Institute* **39**:227–252.

Duncan RP. 1997. The role of competition and introduction effort in the success of Passeriform birds introduced to New Zealand. *American Naturalist* **149**:903–915 DOI 10.1086/286029.

Duncan RP, Blackburn TM, Sol D. 2003. The ecology of bird introductions. *Annual Review of Ecology, Evolution, and Systematics* **34**:71–98 DOI 10.1146/annurev.ecolsys.34.011802.132353.

Duncan RP, Bomford M, Forsyth DM, Conibear L. 2001. High predictability in introduction outcomes and the geographical range size of introduced Australian birds: a role for Climate. *Journal of Animal Ecology* **70**:621–632.

Ebenhard T. 1988. Introduced birds and mammals and their ecological effects. *Swedish Wildlife Research* **13**:1–107.

Elphick CS, Roberts DL, Reed JM. 2010. Estimated dates of recent extinctions for North American and Hawaiian birds. *Biological Conservation* **143**:617–624 DOI 10.1016/j.biocon.2009.11.026.

Fagan WF, Holmes EE. 2006. Quantifying the extinction vortex. *Ecology Letters* **9**:51–60 DOI 10.1111/j.1461-0248.2005.00845.x.

Falla RA, Sibson RB, Turbott EG. 1966. *A field guide to the birds of New Zealand.* London: Collings.

Fitzpatrick JW, Lammertink M, Luneau MD, Gallagher TW, Harrison BR, Sparling GM, Rosenberg KV, Rohrbaugh RW, Swarthout ECH, Wrege PH, Swarthout SB, Dantzker MS, Charif RA, Barksdale TR, Remsen Jr TV, Simon SD, Zollner D.

2005. Ivory-billed Woodpecker *Campephilus principalis* persists in continental North America. *Science* **308**:1460–1462 DOI 10.1126/science.1114103.

Gilpin ME, Soulé ME. 1986. Minimum viable populations; processes of species extinction. In: Soulé ME, ed. *Conservation biology: the science of scarcity and diversity*. Sunderland: Sinauer Press, 13–34.

Green RE. 1997. The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. *Journal of Animal Ecology* **66**:25–35 DOI 10.2307/5961.

Griffith B, Scott JM, Carpenter JW, Reed C. 1989. Translocation as a species conservation tool: status and strategy. *Science* **245**:477–480 DOI 10.1126/science.245.4917.477.

Hufbauer RA, Rutschmann A, Serrate B, De Conchard HV, Facon B. 2013. Role of propagule pressure in colonization success: disentangling the relative importance of demographic, genetic and habitat effects. *Journal of Evolutionary Biology* **26**:1691–1699 DOI 10.1111/jeb.12167.

Lamb RC. *Birds beasts and fishes*. Christchurch: Caxton.

Lever C. 1987. *Naturalized birds of the world*. New York: Longman Sci. Tech.

Lever C. 2005. *Naturalised birds of the world*. London: T and A.D. Poyser.

Lockwood JL, Cassey P, Blackburn T. 2005. The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution* **20**:223–228 DOI 10.1016/j.tree.2005.02.004.

Long JL. 1981. *Introduced birds of the world*. New York: Universe Press.

Ludwig D. 1996. The distribution of population survival times. *American Naturalist* **147**:506–526 DOI 10.1086/285863.

MacArthur RH, Wilson EO. 1967. *The theory of island biogeography*. Princeton: Princeton University Press.

Martin CH, Crawford JE, Turner BJ, Simons LH. 2016. Diabolical survival in death valley: recent pupfish Colonization gene flow and genetic assimilation in the smallest species range on earth. *Proceedings of the Royal Society of London B: Biological Sciences* **283**:2015–2334 DOI 10.1098/rspb.2015.2334.

Moulton MP, Cropper Jr WP, Avery ML. 2011. A reassessment of the role of propagule pressure in influencing fates of passerine introductions to New Zealand. *Biodiversity and Conservation* **20**:607–623 DOI 10.1007/s10531-010-9969-8.

Moulton MP, Cropper Jr WP, Avery ML. 2012. Historical records of passerine introductions to New Zealand fail to support the propagule pressure hypothesis. *Biodiversity and Conservation* **21**:297–307 DOI 10.1007/s10531-011-0165-2.

Moulton MP, Cropper Jr WP, Avery ML, Moulton LW. 2010. The earliest house sparrow introductions to North America. *Biological Invasions* **12**:2955–2958 DOI 10.1007/s10530-010-9692-0.

Moulton MP, Pimm SL. 1983. The introduced avifauna: biogeographic evidence for competition. *American Naturalist* **121**:669–690 DOI 10.1086/284094.

Munro GC. 1944. *Birds of Hawaii*. Honolulu: Tongg Publishing.

Newsome AE, Noble JJ. 1986. Ecological and physiological characters of invading species. In: Groves RH, Burdon JJ, eds. *Ecology of biological invasions.* Cambridge: Cambridge University Press, 1–20.

Nuñez MA, Moretti A, Simberloff D. 2011. Propagule pressure hypothesis not supported by an 80-year experiment on woody species invasion. *Oikos* **120**:1311–1316.

Phillips JC. 1928. *Wild birds introduced or transplanted in North America. US Department of Agriculture Technical Bulletin*, vol. 61. Washington, D.C: US Department of Agriculture.

Pimm SL. 1989. Theories of predicting success and impact of introduced species. In: Drake JA, Mooney HA, Di Castri F, Groves RH, Kruger FJ, Rejmanek M, Williamson M, eds. *Biological invasions: a global perspective, SCOPE 37.* Chichester: Wiley Press, 351–367.

Pimm SL, Diamond J, Reed TM, Russell GJ, Verner J. 1993. Times to extinction for small populations of large birds. *Proceedings of the National Academy of Sciences of the United States of America* **90**:10871–10875 DOI 10.1073/pnas.90.22.10871.

Reed JM, Stockwell CA. 2014. Evaluating an icon of population persistence: the Devil's Hole pupfish. *Proceedings of the Royal Society of London, B: Biological Sciences* **281**:20141648 DOI 10.1098/rspb.2014.1648.

Riggs AC, Deacon JE. 2004. Connectivity in desert aquatic ecosystems: the Devils Hole story. In: Sada DW, Sharpe SE, eds. *Conference proceedings. Spring-fed wetlands: important scientific and cultural resources of the intermountain region, 2002*, 1–38. *Available at* https://www.dri.edu/images/stories/conferences_and_workshops/spring-fed-wetlands/spring-fed-wetlands-riggs-deacon.pdf (accessed on 29 August 2010).

Sağlam İK, Baumsteiger J, Smith MJ, Linares-Casenave J, Nichols AL, O'Rourke SM, Miller MR. 2016. Phylogenetics support an ancient common origin of two scientific icons: Devils Hole and Devils Hole pupfish. *Molecular Ecology* **25**:3962–3973 DOI 10.1111/mec.13732.

Scott JM, Ramsey FL, Lammertink M, Rosenberg K, Rohrbauch R, Wiens JA, Reed JM. 2008. When is an "extinct" species really extinct? Gauging the search efforts for Hawaiian forest birds and the Ivory-billed Woodpecker. *Avian Conservation and Ecology* **3(2)**:3.

Sibley DA, Bevier LU, Patten MA, Elphick CS. 2006. Comment on "Ivory-billed woodpecker *Campephilus principalis* persists in continental North America". *Science* **311**:1555a DOI 10.1126/science.1122778.

Simberloff D. 1998. Small and declining populations. In: Sutherland WJ, ed. *Conservation science and action.* Oxford: Blackwell Press, 116–134.

Simberloff D. 2009. The role of propagule pressure in biological invasions. *Annual Review of Ecology and Systematics* **40**:81–102 DOI 10.1146/annurev.ecolsys.110308.120304.

Simberloff D, Gibbons L. 2004. Now you see them, now you don't!—population crashes of established introduced species. *Biological Invasion* **6**:161–172 DOI 10.1023/B:BINV.0000022133.49752.46.

Sol D, Lefebvre L. 2000. Behavioural flexibility predicts invasion success in birds introduced to New Zealand. *Oikos* **90**:599–605 DOI 10.1034/j.1600-0706.2000.900317.x.

Szűcs M, Melbourne BA, Tuff T, Hufbauer RA. 2014. The roles of demography and genetics in the early stages of colonization. *Proceedings of the Royal Society of London B: Biological Sciences* **281**:20141073 DOI 10.1098/rspb.2014.1073.

Taylor SS, Jamieson IG, Armstrong DP. 2005. Successful island reintroductions of New Zealand robins and saddlebacks with small numbers of founders. *Animal Conservation* **8**:415–420 DOI 10.1017/S1367943005002337.

Thomson GM. 1922. *The naturalization of animals and plants in New Zealand.* London: Cambridge University Press.

Tomich PQ. 1986. *Mammals in Hawaiʻi.* Second edition. Honolulu: Bishop Museum Press.

Van Houtan KS, Halley JM, Van Aarde RJ, Pimm SL. 2009. Achieving success with small, translocated mammal populations. *Conservation Letters* **2**:254–262 DOI 10.1111/j.1755-263X.2009.00081.x.

Veltman CJ, Nee S, Crawley MJ. 1996. Correlates of introduction success in exotic New Zealand birds. *American Naturalist* **147**:542–557.

Walters JR, Crist EL. 2006. Rediscovering the king of woodpeckers: exploring the implications. *Avian Conservation and Ecology* **1**:1–6.

Wellwood JM. 1968. *Hawke's Bay acclimitisation society centenary 1868–1968.* Hastings: Hawke's Bay Acclimatization Society.

Wetmore A. 1964. *Song and garden birds of North America.* Washington, D.C.: National Geographic Society.

Williams GR. 1968. The cape barren goose (*Cereopsis novaehollandiae* Latham) in New Zealand. *Notornis* **15**:66–69.

Williams GR. 1969. Introduced birds. In: Knox GA, ed. *The natural history of Canterbury.* Wellington: Reed, 435–451.

Wolf CM, Griffith B, Reed C, Temple SA. 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. *Conservation Biology* **10**:1142–1154 DOI 10.1046/j.1523-1739.1996.10041142.x.

Wood CA. 1924. The starling family at home and abroad. *Condor* **26**:123–136 DOI 10.2307/1363216.