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Propagule size and patterns of success in early introductions of Chukar Partridges (*Alectoris chukar*) to Nevada

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ABSTRACT

Background: In an effort to combine the well-known evolutionary phenomenon of increased extinction probability in small populations with invasion biology models, some studies have concluded that propagule size is the primary determinant of establishment success in introduced birds.

Question: Is establishment success in Chukar Partridges (*Alectoris chukar*) introduced to the state of Nevada predicted by propagule size, by location of release, or by the source (game farm or wild-caught)?

Methods: We compared propagule sizes of successful and unsuccessful introductions of Chukar Partridges in Nevada, using logistic regression. We included tests for possible differences across introduction sites (i.e. counties) and between birds that originated from game farms or were wild-caught.

Findings: Propagule size was not a significant predictor of introduction success. Moreover, we found no significant differences across 17 sites, or between wild birds and those from game farms.

Conclusions: It appears most likely that site-level factors such as the availability of habitat are more important to the success of introductions than is propagule size.

Keywords: *Alectoris chukar*, exotic birds, propagule pressure, species introductions.

INTRODUCTION

Several studies have concluded that propagule pressure is the primary determinant of successful establishment in bird introductions (e.g. Newsome and Noble, 1986; Veltman *et al.*, 1996; Duncan, 1997; Green, 1997; Cassey *et al.*, 2004). Propagule pressure is defined as the total number of individuals, or the sum of propagule sizes, of a particular species released (Lockwood *et al.*, 2005; Blackburn *et al.*, 2009). Despite the seeming popularity of this conclusion, it has been challenged for several reasons, including a lack of scrutiny regarding the historical record, and more important, a failure to decide if species were successful because they were introduced in

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large numbers or if they were introduced in large numbers for other reasons (Moulton *et al.*, 2010, 2011, 2012a, 2012b, 2013, 2014, 2015; Moulton and Cropper, 2014, 2015).

Some supporters of the propagule pressure hypothesis in birds claim that such criticisms deny the well-known idea that small populations have higher chances for extinction (Blackburn *et al.*, 2015a, 2015b). However, it is the size of the effect, and not its existence, that is the important question. The relative importance of propagule size versus habitat quality, species characteristics, and event-level factors such as unusual weather patterns during and following the releases, cannot be determined by merely summing numbers released. Analyses touting propagule pressure have relied too heavily on secondary representations of the historical record (e.g. Thomson, 1922; Phillips, 1928; Long, 1981; Lever, 1987, 2005), which contain numerous errors and inconsistencies. Such analyses implicitly assume that the total number of individuals released was necessary for establishment. Other criticisms include the geographically limited nature of the historical records: most are for New Zealand and secondarily Australia.

A less equivocal test of propagule pressure requires the comparison of propagule sizes of a species in a place where there is a more accurate record of the releases and their fates. Ideally, such a situation would be free of any concerns that the species was already successful where it was being released, suggesting that subsequent releases were superfluous. Such conditions exist for the earliest releases of Chukar Partridges (*Alectoris chukar*) into Nevada (Christensen, 1954). We show that not only is there no evidence that propagule sizes influenced the fates of these introductions, but that in some cases releases occurred repeatedly in counties where the species was already established.

METHODS AND MATERIALS

Christensen (1954) listed 175 releases of Chukar Partridges in Nevada between 1935 and 1953. The fates were listed for 61 of the releases (www.evolutionary-ecology.com/data/3025Appendix.pdf). For two releases (one successful – Mineral County in 1945; and one unsuccessful – Nye County in 1947), the number of individuals released was not reported.

We tested the importance of propagule size using a logistic regression on the 59 releases with reported propagule size and specified outcomes, with fate (0 = unsuccessful; 1 = successful) as the dependent variable and common logarithm of number released, origin (game farm or wild-caught), and the county of release as predictor variables. We specified a binomial distribution for the dependent variable (i.e. fate) and used a logit link function. We used SAS Proc Glimmix for our logistic regressions (SAS, 2009).

RESULTS

Chukars were released in 17 counties (3025Appendix.pdf), including Ormsby County, which was merged with Carson City to form the Carson City Consolidated Municipality in 1969 (Anonymous, 2015). Christensen (1954) listed at least one successful release in ten counties (3025Appendix.pdf), but noted that immigrants from adjacent counties had spread into four other counties (Douglas, Humboldt, Ormsby, and Pershing); outcomes of all releases in these counties having been reported as uncertain (Table 1). Thus by 1954, Christensen considered Chukars to be successfully established in 14 of the 17 counties. A fifth county (Elko) also included releases that were all considered uncertain in outcome. In their

Table 1. Summary of releases in 17 Nevada counties

County	Suc	Uns	Unk1	Unk2	Total	Span	pp
Churchill	2	0	1	0	3	1	68
Clark	0	5	3	5	13	22	1189
Douglas	0	0	5	0	5	15	114
Elko	0	0	6	12	18	22	2006
Esmeralda	5	0	2	0	7	13	168
Eureka	1	3	3	0	7	9	195
Humboldt	0	0	4	1	5	22	211
Lander	1	0	2	0	3	7	75
Lincoln	0	15	7	9	31	26	2609
Lyon	3	2	3	1	9	22	911
Mineral	2*	0	3	0	5	3	114
Nye	6	8*	56	16	86	25	4223
Ormsby	0	0	2	0	2	15	43
Pershing	0	0	1	0	1	1	50
Storey	1	0	0	0	1	1	7
Washoe	4	0	10	3	17	23	992
White Pine	1	2	6	3	12	30	680
Totals	26	35	114	50	225		13655

Note: Suc = successful; Uns = unsuccessful; Unk1 = unknown outcome prior to 1954; Unk2 = releases after 1954 and before 1970 from Christensen (1970); Total = total releases; Span = span of years over which introductions occurred; pp = propagule pressure.
* Includes a single successful release in Mineral County and a single unsuccessful release in Nye County with no propagule size reported.

assessment of the distribution of the Chukar in Nevada, Gullion and Christensen (1957) showed that they occurred in all 17 counties. Thus in addition to Chukars spreading into unoccupied counties from adjacent populations, it is apparent that some of the uncertain releases in fact were ultimately successful.

Of the 59 releases with known propagule sizes, 34 were unsuccessful and 25 were successful; 114 releases had uncertain outcomes. The mean propagule size for unsuccessful releases was 61.1, whereas that for successful releases was 28. The distribution of successful and unsuccessful propagules in various propagule size classes is shown in Fig. 1. The figure suggests that small propagules (<15 individuals) were not doomed to extinction, but nor were large propagules mostly successful. Indeed, our analysis found that the fate of the introductions was not significantly related to the logarithm of the number of individuals released. That conclusion did not change if we included counties, or origins of the birds as class variables (see Tables 2 and 3).

Several authors argue that birds raised on game farms might have reduced colonization ability (e.g. Musil and Connelly, 2009; Rymešová *et al.*, 2013). Gruychev (2016) reported that Chukars raised on game farms were easily identified in the field owing to a lack of fear of humans, and poor feathering. However, in the present study a contingency test of introduction success rates of the 36 game-farm (0.40) and the 25 wild-caught birds (0.44) in Nevada showed they were nearly identical and not significantly different (Yates' $\chi^2 = 0.007$; $P > \chi^2 = 0.93$).

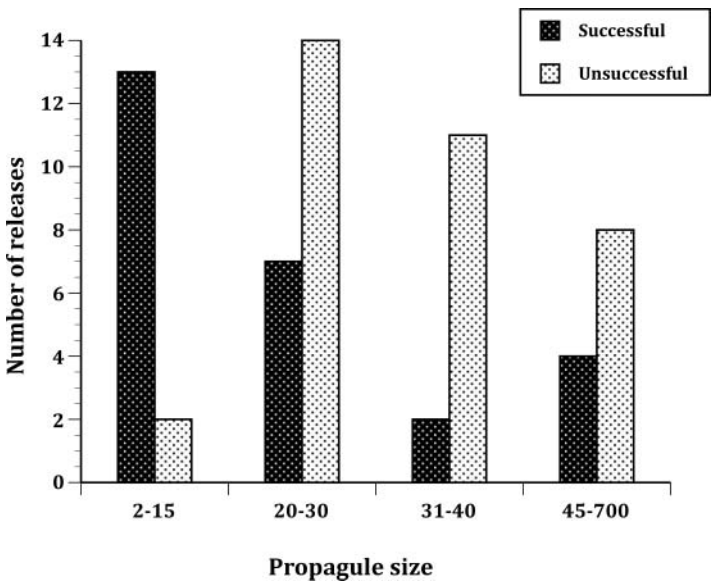

Fig. 1. Numbers of successful and unsuccessful releases of Chukars in Nevada by propagule size class.

Table 2. Parameter estimates for fixed effects in a generalized linear mixed model with a binomial response variable (logit link) for logarithm of propagule size, origin of the birds (wild-caught vs. game farm) in 12 counties of Nevada

Parameter	Estimate (SE)	*t*-value	$P > \lvert t \rvert$
Intercept	2.7407 (2.8736)	0.95	0.3453
Log_{10} propagule size	−1.4629 (1.3642)	−1.07	0.2893
Origin (1 = wild)	−1.1587 (1.1912)	−0.97	0.3359
Origin (2 = game farm)	0	—	—
County (Churchill)	12.2192 (623.97)	0.02	0.9845
Clark	−14.1590 (368.38)	−0.04	0.9695
Esmeralda	13.7784 (386.79)	0.04	0.9717
Eureka	−0.6356 (1.6995)	−0.37	0.7102
Lander	12.5459 (882.75)	0.01	0.9887
Lincoln	−13.8617 (223.30)	−0.06	0.9508
Lyon	0.3275 (1.9883)	0.16	0.8699
Mineral	14.2245 (882.74)	0.02	0.9872
Nye	−0.2637 (1.5283)	−0.17	0.8638
Storey	12.0617 (882.75)	0.01	0.9892
Washoe	12.9130 (423.78)	0.03	0.9758
White Pine	0	—	—

Table 3. Type III tests of fixed effects from the logistic regression model described in Table 2

Effect	d.f.	*F*-value	$P > F$
Log_{10} number	1,45	1.14	0.2893
Origin	1,45	0.95	0.3359
County	11,45	0.03	1.0000

Did those counties with at least one reported successful release discontinue releases following the first success? We answered this question by separating the 17 counties into two groups: first, the seven counties with only unsuccessful or uncertain results, and second, the ten counties with at least one successful release. In the first group, four of the counties (Clark, Elko, Humboldt, and Lincoln) made additional releases and three (Douglas, Ormsby, and Pershing) did not. In the successful group, four counties (Lyon, Nye, Washoe, and White Pine) made additional releases and six (Churchill, Esmeralda, Eureka, Lander, Mineral, and Storey) did not. A contingency analysis showed that the two groups did not differ (Yates' $\chi^2 = 0.041$; $P > \chi^2 = 0.84$). Thus there is no indication that people releasing Chukars in Nevada were following some sort of stopping rule, by which they would discontinue introductions after establishment.

DISCUSSION

Species introductions are essentially natural experiments that can generate insights for ecological and evolutionary biology (Sax *et al.*, 2007). Holt *et al.* (2005) argue that species introductions may be helpful for testing hypotheses about niche conservatism and evolution so long as information exists for both successful and unsuccessful introductions of a species in some location. These authors assume that propagule pressure played a key role in invasions of species 'outside the niche'.

In extolling the importance of propagule pressure, Blackburn *et al.* (2009) cite the well-known notion that smaller populations tend to suffer from loss of genetic diversity. It is not clear that loss of genetic material is inevitably a problem in introduced populations, or rather that any genetic loss that might occur will necessarily hamper the chances for successful establishment of small propagules.

Our results might seem to contradict the conclusion of Pimm (1991), who, in a separate analysis of game bird introductions to the USA, found a threshold in propagule size below which all introductions failed, and above which the chances for success were mixed. Perhaps such a threshold exists at extremely low propagule sizes? In our analysis, four propagules consisted of fewer than ten individuals: two of these were successful (seven individuals to Storey County in 1935; and eight to Churchill County also in 1935) whereas two were unsuccessful (four individuals to Clark County in 1939; and six individuals to Nye County in 1940). This could indicate that a threshold might exist at the very smallest propagule sizes. However, later releases of 32, 36, 40, and 63 individuals also failed in Clark County, whereas a release of ten individuals to Nye County succeeded. Thus the lack of success in Clark County cannot be attributed solely to small propagule size. A test is possible for Nye County where there were seven unsuccessful and six successful releases. The means

of these propagule sizes were 31.1 (unsuccessful) and 35.2 (successful). A Kruskal-Wallis test strongly suggests that these two groups were not significantly different (estimated $\chi^2 = 0.56$, $P > \chi^2 = 0.34$). So again no evidence exists that propagule size was the primary determinant of success.

In a logistic regression model, the common logarithms of the number of individuals per propagule, origin of the individuals released (game farm versus wild-caught), and county were not significantly related to introduction fate (Tables 2 and 3). Including county as a class variable would seem a reasonable approach to testing for site-level differences, but the results summarized in Table 2 indicate that county did not explain a significant amount of the variance. Of the 17 counties, the standard errors of the parameter estimates and the estimates themselves for the 13 counties that lacked both successful and failed introductions were extremely large (Table 2). This seems inconsistent, as in our analysis six counties (Churchill, Esmeralda, Lander, Mineral, Storey, and Washoe) had no known unsuccessful releases, two counties (Clark and Lincoln) had no known successful releases, and five counties (Douglas, Elko, Humboldt, Pershing, and Ormsby) had no known successes or failures (Table 1). Despite these seemingly stark differences, our logistic regression model did not detect a significant influence of county on introduction outcomes. This may imply that logistic regression is not the proper test for site-level factors.

Previous studies of propagule pressure have been criticized for relying too heavily on secondary representations of the historical record (e.g. Thomson, 1922; Phillips, 1928; Long, 1981; Lever, 1987, 2005), which are often incomplete and inaccurate (Moulton *et al.*, 2014, 2015; Pipek *et al.*, 2015a, 2015b). Moreover, it is impossible to discern whether multiple releases of individuals of a species are necessary for establishment, as assumed by Newsome and Noble (1986) for Australia and Veltman *et al.* (1996), Duncan (1997), and Green (1997) for New Zealand, or superfluous, as argued by Moulton *et al.* (2010, 2011, 2012a, 2012b, 2013, 2014; Moulton and Cropper, 2014). Blackburn *et al.* (2013) have termed the case where additional releases were made after initial successful establishment a Franklin Delano Roosevelt effect. But strictly speaking, a Franklin Delano Roosevelt effect could occur only if the people introducing the birds were aware of the success of previous introductions and decided to make additional releases, an assumption we have no evidence to test.

Gullion and Christensen (1957) show that Chukars occurred in all counties in Nevada. It is clear from these reports that introductions of Chukars continued for years following successful establishment, contradicting the assumption by proponents of propagule pressure that the correct measure of the number needed for success is the same as the total number released.

The record also shows very clearly that propagule size is not the most important consideration for establishment of Chukars in Nevada, a state that is larger in land area than entire nations involved in similar studies (e.g. New Zealand). Our results reinforce the conclusions of Gullion (1965), who noted in his criticism of the Foreign Game Investigation Program that sheer numbers are not as important as availability of adequate habitat.

REFERENCES

Anonymous. 2015. Carson City. < http:www.carson.org/index.aspx?page = 2? > [accessed 14 December 2015].

Blackburn, T.M., Lockwood, J.L. and Cassey, P. 2009. *Avian Invasions: The Ecology and Evolution of Exotic Birds*. Oxford: Oxford University Press.

Blackburn, T.M., Prowse, T.A.A., Lockwood, J.L. and Cassey, P. 2013. Propagule pressure as a driver of establishment success in deliberately introduced exotic species: fact or artefact? *Biol. Invasions*, **15**: 1459–1469.

Blackburn, T.M., Lockwood, J.L. and Cassey, P. 2015a. The influence of numbers on invasion success. *Mol. Ecol*., **24**: 1942–1953.

Blackburn, T.M., Dyer, E., Su, S. and Cassey, P. 2015b. Long after the event, or four things we (should) know about bird invasions. *J. Ornithol*., **156** (suppl. 1): s15–s25.

Cassey, P., Blackburn, T.M., Sol, D., Duncan, R.P. and Lockwood, J.L. 2004. Global patterns of introduction effort and the establishment success of birds. *Proc. R. Soc. Lond. B: Biol. Sci*., **271** (suppl.): s405–s408.

Christensen, G.C. 1954. The chukar partridge in Nevada. *Nevada Fish Game Comm. Biol. Bull.*, **1**: 77 pp.

Christensen, G.C. 1970. The Chukar Partridge: its introduction, life history, and management. *Nevada Dept. Fish Game Biol. Bull*., **4**: 82 pp.

Duncan, R.P. 1997. The role of competition and introduction effort in the success of passeriform birds introduced to New Zealand. *Am. Nat*., **149**: 903–915.

Green, R.E. 1997. The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. *J. Anim. Ecol*., **66**: 25–35.

Gruychev, G. 2016. Declining populations of Chukar Partridge (*Alectoris chukar*) in Bulgaria. *Turk. J. Zool*. [DOI: 10.3906/zoo-1508-5, published online 9 March 2016].

Gullion, G.W. 1965. A critique concerning foreign game bird introductions. *Wilson Bull*., **77**: 409–414.

Gullion, G.W. and Christensen, G.C. 1957. A review of the distribution of gallinaceous game birds in Nevada. *Condor*, **59**: 128–138.

Holt, R.D., Barfield, M. and Gomulkiewicz, R. 2005. Theories of niche conservatism and evolution: could exotic species be potential tests? In *Species Invasions: Insights into Ecology, Evolution, and Biogeography* (D.F. Sax, J.J. Stachowicz and S.D. Gaines, eds.), pp. 259–290. Sunderland, MA: Sinauer Associates.

Lever, C. 1987. *Naturalized Birds of the World*. Harlow: Longman Science and Technology.

Lever, C. 2005. *Naturalised Birds of the World*. London: T&AD Poyser.

Lockwood, J.L., Cassey, P. and Blackburn, T. 2005. The role of propagule pressure in explaining species invasions. *Trends Ecol. Evol*., **20**: 223–228.

Long, J.L. 1981. *Introduced Birds of the Eorld*. London: David & Charles.

Moulton, M.P. and Cropper, W.P., Jr. 2014. Establishment success in introduced passeriforms of New Zealand: evidence for a Franklin Delano Roosevelt effect. *Biol. Invasions*, **16**: 233–237.

Moulton, M.P. and Cropper, W.P., Jr. 2015. A comment on the role of propagule pressure in the establishment success of introduced birds. *Oecologia*, **177**: 317–319.

Moulton, M.P., Cropper, W.P., Jr., Avery, M.L. and Moulton, L.E. 2010. The earliest House Sparrow introductions of North America. *Biol. Invasions*, **12**: 2955–2958.

Moulton, M.P., Cropper, W.P., Jr. and Avery, M.L. 2011. A reassessment of the role of propagule pressure in influencing the fates of passerine introductions to New Zealand. *Biodivers. Conserv*., **20**: 607–623.

Moulton, M.P., Cropper, W.P., Jr., Moulton, L.E., Avery, M.L. and Peacock, D. 2012a. A reassessment of historical records of avian introductions to Australia: no case for propagule pressure. *Biodivers. Conserv*., **21**: 155–174.

Moulton, M.P., Cropper, W.P., Jr. and Avery, M.L. 2012b. Historical records of passerine introductions to New Zealand fail to support the propagule pressure hypothesis. *Biodivers. Conserv*., **21**: 297–307.

Moulton, M.P., Cropper, W.P., Jr. and Avery, M.L. 2013. Is propagule size the critical factor in predicting introduction outcomes in Passeriform birds? *Biol. Invasions*, **15**: 1449–1458.

Moulton, M.P., Santos, E.S.A., Cropper, W.P., Jr. and Nat Lim, J. 2014. New records for Passeriform introductions to the Otago acclimatisation region in New Zealand: evidence of a Franklin Delano Roosevelt effect. *Notornis*, **61**: 219–222.

Moulton, M.P., Cropper, W.P., Jr. and Broz, A.J. 2015. Inconsistencies among secondary sources of Chukar Partridge (*Alectoris chukar*) introductions to the United States. *PeerJ*, **3**: e1447.

Musil, D.D. and Connelly, J.W. 2009. Survival and reproduction of pen-reared vs. translocated wild pheasants *Phasianus colchicus*. *Wildl. Biol*., **15**: 80–88.

Newsome, A.E. and Noble, I.R. 1986. Ecological and physiological characters of invading species. In *Ecology of Biological Invasions* (R.H. Groves and J.J. Burdon, eds.), pp. 1–20. Cambridge: Cambridge University Press.

Phillips, J.C. 1928. *Wild Birds Introduced or Transplanted in North America*. US Dept. Agric. Tech. Bull. #61. Washington, DC: US Government Printing Office.

Pimm, S.L. 1991. *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities*. Chicago, IL: University of Chicago Press.

Pipek, P., Pyšek, P. and Blackburn, T.M. 2015a. How the Yellowhammer became a Kiwi: the history of an alien bird invasion revealed. *NeoBiota*, **24**: 1–31.

Pipek, P., Pyšek, P. and Blackburn, T.M. 2015b. A clarification of the origins of birds released by the Otago Acclimatisation Society from 1876 to 1882. *Notornis*, **62**: 105–112.

Rymešová, D., Tomášek, O. and Šálek, M. 2013. Differences in mortality rates, dispersal distances and breeding success of commercially reared and wild grey partridges in the Czech agricultural landscape. *Eur. J. Wildl. Res*., **59**: 147–158.

Sax, D., Stachowicz, J.J., Brown, J.H., Bruno, J.F., Dawson, M.N., Gaines, S.D. *et al.* 2007. Ecological and evolutionary insights from species invasions. *Trends Ecol. Evol*., *22*: 465–471.

SAS. 2009. *SAS/STAT (R) 9.2 User's Guide*, 2nd edn. Cary, NC: SAS Institute Inc.

Thomson, G.M. 1922. *The Naturalization of Plants and Animals in New Zealand*. Cambridge: Cambridge University Press.

Veltman, C.J., Nee, S. and Crawley, M.J. 1996. Correlates of introduction success in exotic New Zealand birds. *Am. Nat*., **147**: 542–557.