Patterns of Success in Game Bird Introductions in the United States

by

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"There is no safety in numbers, or in anything else." James Thurber, The Fairly Intelligent Fly, The New Yorker, February 4, 1939.
Abstract

Better predictions of the success of species’ introductions require careful evaluation of the relative importance of at least three kinds of factors: species characteristics, characteristics of the site of introduction, and event-level factors such as propagule pressure. Historical records of bird introductions provide a unique method for addressing the relative importance of these factors. We compiled a list of introductions of 17 Phasianid species released in the USA during the Foreign Game Investigation Program (FGIP). These records indicate that releases for some Phasianid species in the USA continued long after establishment. For many of the 13 species that always failed, even numerous releases and large numbers of individuals per release were not enough for successful establishment, yet several of these species were successfully introduced elsewhere. Only four species were successful in at least one state. Yet, all four were unsuccessful either in other states, or in other regions of states where they were not already successfully established, or both. These results support the notion that the number of individuals released and the number of releases are less important than characteristics of the location where the introductions occurred.
Introduction

Several studies have argued that the total number of individuals of a species released at some locality is the key predictor of establishment success in exotic birds (Newsome and Noble 1986; Veltman et al. 1996; Duncan 1997; Green 1997; Cassey et al. 2004; Lockwood et al. 2005; Blackburn et al. 2009a, 2011, 2013). This notion was based on the observation, in the historical record, that successfully established populations of introduced birds tend to be those released in significantly larger numbers. This observation was later formalized as the propagule pressure hypothesis (i.e. Lockwood et al. 2005). Propagule pressure is defined as the total number of introduced individuals of a species.

The propagule pressure hypothesis as stated assumes has two parts. First, is the assumption that just as small populations have increased chances of extinction, so must small propagules of introduced species suffer increased chances of failing to become established. The second aspect of the propagule pressure hypothesis predicts that increasing the numbers of individuals that are released, increases the probability of successful establishment, up to a point. Thus, even the staunchest proponents of propagule pressure (i.e. Blackburn et al. 2009a) acknowledge that for unsuccessfully introduced species with propagule pressures greater than 100, releasing more individuals would not alter that outcome.

The propagule pressure hypothesis has numerous criticisms but the chief concern is the accuracy and reliability of the historical record as well as its interpretation (Moulton et al. 2010, 2011, 2012a,b, 2013, 2014, 2015; Moulton and Cropper 2014a,b, 2015). For example, in examining the historical record, were
species successful because they were introduced in large numbers or released in large numbers because they were initially successful?
The large number of Phasianid introductions carried out under the Foreign Game Investigation Program (FGIP) initiated under the old Bureau of Sport Fisheries and Wildlife in the U.S. Department of the Interior provides an experiment of sorts into the relative importance of components of the propagule pressure hypothesis as well as factors related to the site of introduction. Specifically, we ask: do releases of larger numbers of individuals leads to increased chances for successful establishment?

**Methods**

We compiled a list of release records for introduced Phasianid species involved in the FGIP using five summary reports (Bump and Bohl 1964; Chambers 1965, 1966; Bohl and Bump 1970; Banks 1981). These FGIP reports typically listed details such as county of introduction, source of the birds (wild, game farm, or both), and in several cases the actual subspecies involved in the introductions (see Table s1 for a summary and Appendix s1 for a detailed listing by reference).

Despite the detail of the FGIP reports (Bump and Bohl 1964; Chambers 1965, 1966; Bohl and Bump 1970; and Banks 1981) there were still several instances where we could not discern what were the sizes and fates of individual releases. Thus, 47 cases involving releases of eight species listed a span of years ranging from two to five years over which only a sum of individuals was released. Banks (1981) noted that not all of the conterminous 48 states participated in the FGIP but many, if not all, were involved in releases of Phasianid species.
Although Bohl and Bump (1970) reported that the FGIP had signed cooperative agreements with 44 states, summaries of release records (Bump and Bohl 1964; Chambers 1965, 1966; Bohl and Bump 1970; Banks 1981) included just 30 of the conterminous 48 states. Some states also introduced species from families other than Phasianidae (e.g. Tinamidae, Columbidae; Pteroclididae) as part of the FGIP but we did not include them. Both Long (1981) and Lever (1987) listed releases of Phasianid species to the USA other than those made by the FGIP so our compilation represents only a sample of all Phasianid releases to the USA.

Results

Our final dataset included 1691 introduction records for 17 Phasianid species included in the FGIP in 30 states. Of these, 47 involved a span of years, ranging from two (13 cases, 5 species) to five years (2 cases involving 2 species). In these cases, we assumed, minimally, only that separate releases must have occurred in the first and last years. The number of species released in each of the 30 states ranged from 1 to 8 (see Table s1 for a summary and Appendix s2 for a detailed list), with a mode of 3 (Figure 1). As shown in Table s3, the overall success rate was low with just 234 successful introduction records (234/1691= 13.8%) all of which came from just four species: Chukar Partridge (*Alectoris chukar*); Common Pheasant (*Phasianus colchicus*); Himalayan Snowcock (*Tetraogallus himalayensis*); and Grey Partridge (*Perdix perdix*). All 17 species were unsuccessful in one state or another and all releases of 13 species ended in failure regardless of where they were released or the number of individuals released. Figure 2 maps the states into which species were released. The common pheasant and chukar partridge represented the bulk of the
introduction records with just under half the total release records (837/1691 = 49.5 \% ) and most of the individuals (479249 / 683494 = 70.1 \% ).

Most of the releases (1457) involved individuals from game farms but 57 involved wild-caught birds, 26 involved presumed translocations (generally these releases listed the origin of the birds as another state) and 146 records did not specify any origin and this pattern held for both successful and unsuccessful releases (Figures 3a,b).

Several patterns emerged from our analyses the FGIP data. First, and most obvious was the importance of location-level factors. Ten of the 13 species in the program that did not register a single success anywhere in the continental US were successfully introduced elsewhere in the world. Moreover, all four of the species that succeeded in one state or another exhibited geographical patterns related to where they were released. Thus, common pheasants invariably failed in southeastern states: Alabama, Arkansas, Florida, Georgia, Kentucky, Louisiana, Maryland, South Carolina, Tennessee, and Virginia (MPSG 2013), despite the fact that in some cases there were numerous releases of large numbers of individuals (Table s4). In Texas and Oklahoma, releases of common pheasants in the southeastern regions of both states invariably failed, whereas those in more western and northern regions were classified as successful. This was mostly the case for Missouri too, except introductions of common pheasants in the "Bootheel" region of extreme southeastern Missouri may have been successful (MPSG 2013). In Arizona and New Mexico, common pheasant success was limited to farmed areas in river valleys (Brown 1989; Campbell 1976). Banks (1981) reported that FGIP
releases of common pheasants into two counties (Garfield and Mesa) in western Colorado failed. However, common pheasants may still occur in both counties (Andrews and Righter 1992) possibly as a result of the FGIP releases, although pheasants occurred there prior to the FGIP (Aldrich and Duvall 1955; Bailey and Niedrach 1965). As shown in Figure 4, among the five states with mixed outcomes for common pheasant introductions, both Texas and Oklahoma had far more unsuccessful than successful introductions.

Chukar partridges, the second most frequently introduced species in the FGIP program (Table s5), had mixed outcomes in Arizona (Brown 1989), California (Harper et al. 1958) and Washington (Barnett 1952), and invariably unsuccessful in Nebraska, South Dakota and New Mexico. As noted elsewhere (Gullion 1965; Christensen 1970; Moulton et al. 2015b), in numerous states, releases of chukar partridges were unable to successfully establish wild populations despite introductions of large numbers of individuals (e.g. 17 releases totaling 26,748 individuals were unsuccessful in Nebraska).

Grey partridges also showed a geographical pattern. Releases of this species succeeded only in the northern states of Iowa and Washington. Grey partridges were unsuccessful in Colorado, Nebraska, western portions of Oregon (Willamette Valley) and Washington (See Table s6). Banks (1981) lists the release of 67 individuals into two counties (Dawes and Frontier) in western Nebraska as a probable failure and indicated that the releases to Colorado and western Oregon were unsuccessful. Mollhoff (2001) reported that grey partridges do not occur in that region of Nebraska, indicating that those releases failed. Three of the four
releases to southwestern Iowa were to Shelby County whereas the fourth was to Cass County. The status of these releases is uncertain. Dinsmore (2001) reported that this species was declining in Iowa and had disappeared from the southern part of the state. Jackson et al. (1996) showed no records of grey partridges in Cass County and only one for Shelby County. However, as Carroll (1993) included the entire state of Iowa as being within the North American range of the species we treated these releases as being successful.

Lastly, all releases of Himalayan snowcocks occurred in Nevada, with some succeeding in the Ruby Mountains but failing in other parts of the state (Bland and Temple 1993; Christensen 1998). There is, however, some uncertainty as to the outcomes of the releases. The first 19 wild-caught birds were said to have vanished shortly after release (Bland and Temple 1993), if this was the case the fact that later and larger releases succeeded would appear to support a role for propagule pressure. However, Christensen (1998) reported that state agency personnel observed six adult-sized snowcocks in 1966 in the area three years after the original release—it is not possible to determine whether these individuals were simply survivors from the original release in 1963 or the progeny of a small but established population. Christensen (1970) was of the opinion that a lack of suitable habitat existed in places other than the Ruby Mountains. Bland and Temple (1990) found that predation risk, a location-level factor, significantly influenced habitat use in Himalayan snowcocks in Nevada.

Blackburn et al. (2009a) suggested that unsuccessful introductions with propagules of more than 100 individuals indicate that factors other than numbers
were responsible for the lack of success. Among the 13 FGIP species that were always unsuccessful, 12 had propagules of 1000 or more: Only one species (*Pternistis erckelii*) had a propagule of fewer than 100 (Table 1).

**Discussion**

Clearly, the patterns of success in introductions of Phasianids to the US were impacted largely by location-level factors (Duncan et al. 2003) rather than characteristics of the individual releases (i.e. propagule pressure). Literally thousands of individuals of all but two species (*Pternistis erckelii* and *Tetraogallus himalayensis*) were released unsuccessfully in one state or another.

Additional evidence, albeit indirect, for an important role for location-level factors comes from the observation that ten of the 13 FGIP species that always failed in the continental USA may have been introduced successfully elsewhere. These include: *Francolinus francolinus, Francolinus pondicerianus, Pternistis erckelii, Lophura leucomelanos, Gallus gallus* (Pyle and Pyle 2009), and *Phasianus versicolor* (Schwarz and Schwarz 1951) in Hawaii; *Bambusicola thoracicus* in Japan (Eguchi and Amano 2004); *Alectoris rufa* in the U.K. (Potts 2012); and possibly *Alectoris barbara* in Madeira — Schmitz (1905) listed this species as occurring in Madeira, but Clarke (2006) did not — and possibly *Syrmaticus reevesii* in Germany and France (Lever 1987, 2005). Moreover, the four presumably successfully introduced species apparently were already successfully established in the states where the FGIP releases (see references in Tables s4-s6) appeared to succeed.

Analyses of the propagule pressure hypothesis based on summing all introduction numbers (e.g. Newsome and Noble 1986; Veltman et al. 1996; Duncan...
1997; Green 1997), implicitly assume that introductions were aimed chiefly at, and were necessary for, establishing wild populations (e.g. Blackburn et al. 2009a, 2011b, 2013, 2015a, b). Simple establishment of wild populations was clearly not the only goal of the FGIP releases, or of Acclimatization Societies in New Zealand.

McDowall (1994) listed multiple reasons for avian introductions to New Zealand besides simple establishment, including maintenance of populations, bolstering populations and extending the ranges of species. Moreover, as noted by Phillips (1928) and Leopold (1931) in some cases introduced populations might appear to succeed initially only to decline and vanish later. An awareness of this phenomenon could have encouraged additional releases as a hedge against local extinctions.

Barnett (1952), for instance, discussed the need for shoring up already established populations of Chukar Partridges in Washington State, as did Gullion and Christensen (1957) for the same species in Nevada. Banks (1981) noted that FGIP releases of Chukar Partridge s in Washington State also were aimed at trying to provide more hunting opportunities in the western counties where populations were not established. Similar arguments can be made for repeated releases of Common Pheasants `in states such as Virginia, Kentucky, and Tennessee, where wild self-sustaining populations never existed, despite the release of thousands of individuals.

In the USA, there was also a financial aspect regarding Phasianid releases. Campbell (1976), for example, figured that the cost of harvesting a single Common Pheasant in New Mexico was $12, which was twice the price of a resident small game-hunting license. This led him to conclude that further releases of this species
would not be financially sustainable. Stiver (1984) noted that the Himalayan Snowcock introduction effort in Nevada cost approximately $750,000, or roughly $370 per bird for 2025 birds that were ultimately released (1533 were listed by the FGIP reports).

Our results support the findings of numerous professional wildlife scientists and ecologists who emphasize location-level factors over simple considerations of numbers of individuals released. Characteristics of the environments where the introductions occur have been shown to play a significant role in introduction outcome (e.g. Blair 1942; Elton 1958; Gullion 1962; Gullion and Christensen 1957; Robertson 1958; Nagel 1945; Diamond and Veitch 1981; Nelson 1964; Moulton and Pimm 1983, 1987; Lockwood et al. 1993; Smallwood 1994; Bland and Temple 1990, 1993; Case 1996). Studies touting propagule pressure, generally relegate characteristics of the target environment and of the species themselves to secondary status, if indeed they consider them at all (e.g. Sorci et al. 1998; Sol et al. 2005, 2008, 2012; Blackburn et al. 2009b; 2013, 2015a,b). This is despite substantial evidence that location-level factors (e.g. Moulton and Cropper 2014b; Case 1996; Diamond and Veitch 1981) need to be considered before invoking propagule pressure to explain establishment patterns.

Propagule pressure does not explain patterns of establishment success in introduced Phasianid species to the USA. Similar results have been shown for various assemblages of Passeriform birds (i.e. Moulton et al. 2010, 2011, 2012a,b, 2013, 2014a,b, 2015). As shown here, with respect to Phasianid species, propagule pressure not only fails to explain past patterns of introduction success, the available
data are clearly incapable of predicting the minimum necessary propagule pressure necessary for successful establishment. Even if these data were available, it would likely lead to minimum necessary numbers that were functions of species and introduction sites, and not a simple summed number.
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Table 1. A list of the number of successful (Rl S) and unsuccessful (Rl U) releases and number of successful (Ind S) and unsuccessful (Ind U) individuals introduced for 17 species released as part of the FGIP. We calculated p(s) as the number of successful releases divided by the total number of releases.

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<th>States</th>
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<th>Rl U</th>
<th>Ind S</th>
<th>Ind U</th>
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Figure 1. Distribution of numbers of Phasianid species released in each of 30 states.
Figure 2. Numbers of states in which each of 17 species was released. Species codes for the 13 unsuccessful species light stippling: Agra= *Alectoris graeca*; Abar= *Alectoris barbara*; Aruf= *Alectoris rufa*; Agri= *Ammoperdix griseogularis*; Perc= *Pternistis erckelii*; Ffra= *Francolinus francolinus*; Fpon= *Francolinus pondicerianus*; Btho= *Bambusicola thoracicus*; Ggal= *Gallus gallus*; Pcol= *Phasianus colchicus*; Sell= *Syrmaticus ellioti*; Sree= *Syrmaticus reevesii*; Pver= *Phasianus versicolor*; Lleu= *Lophura leucomelanos*. Species codes for the four successful species dark stippling: Thim= *Tetraogallus himalayensis*; Achu= *Alectoris chukar*; Pcol= *Phasianus colchicus*; Pper= *Perdix perdix*. 
Figure 3a. Distribution of origins of 234 successful releases of game birds.

![Pie chart showing distribution of origins of 234 successful releases of game birds.]

Figure 3b. Distribution of origins of 1455 unsuccessful releases of game birds.

![Pie chart showing distribution of origins of 1455 unsuccessful releases of game birds.]

Figure 4. Number of successful (S) and unsuccessful (U) releases of Common Pheasants for states with mixed introduction outcomes: (AZ= Arizona; MO=Missouri; NM= New Mexico; TX=Texas; OK=Oklahoma.)