

Inconsistencies Among Secondary Sources of Chukar Partridge (*Alectoris chukar*) Introductions to the United States.

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An important source of information concerning the fates of intentionally introduced exotic bird species has been collections of historical data that sometimes include species released, numbers released, locations of release, and establishment success. These data have been used to assess potential predictors of establishment success such as propagule pressure, site-level factors, and species characteristics. In order to better understand the limitations of such historical compilations, we compared data for the Chukar (*Alectoris chukar*) introductions to the USA from two often used compilations and from other sources associated with Chukar introduction programs. We found the major compilations of Long (1981) and Lever (1987) are inconsistent and likely to be incomplete, and inaccurate, in terms of the taxa introduced, the numbers introduced, and the fates of these introductions. Propagule pressure analyses have often assumed that every bird in every release must be summed to represent the propagule pressure necessary for establishment. We found, however, that large numbers of birds were released into states and counties with already established populations. Additionally, in numerous states very large numbers of Chukars were unsuccessfully released. We conclude that site-level factors were more important influences of establishment success than propagule pressure was.

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by

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Abstract

An important source of information concerning the fates of intentionally introduced exotic bird species has been collections of historical data that sometimes include species released, numbers released, locations of release, and establishment success. These data have been used to assess potential predictors of establishment success such as propagule pressure, site-level factors, and species characteristics. In order to better understand the limitations of such historical compilations, we compared data for the Chukar (*Alectoris chukar*) introductions to the USA from two often used compilations and from other sources associated with Chukar introduction programs. We found the major compilations of Long (1981) and Lever (1987) are inconsistent and likely to be incomplete, and inaccurate, in terms of the taxa introduced, the numbers introduced, and the fates of these introductions. Propagule pressure analyses have often assumed that every bird in every release must be summed to represent the propagule pressure necessary for establishment. We found, however, that large numbers of birds were released into states and counties with already established populations. Additionally, in numerous states very large numbers of Chukars were unsuccessfully released. We conclude that site-level factors were more important influences of establishment success than propagule pressure was.

Introduction

In attempting to identify the processes that deter or promote establishment of introduced bird populations, several empirical studies have concluded that propagule pressure, meaning the total number of individuals of a species released in some place, is the principal determining factor (e.g. Newsome and Noble 1986; Veltman et al. 1996; Duncan 1997; Green 1997; Cassey et al. 2004; Lockwood et al. 2005; Sol et al. 2012). Although this conclusion has been repeatedly criticized (Moulton et al. 2010, 2011, 2012a,b, 2013; Moulton and Cropper 2014a,b, 2015), and recent studies have emphasized the importance of species-level characteristics over propagule pressure (e.g. Sol et al. 2012; Cassey et al. 2014), some have persisted in touting its primary importance (e.g. Blackburn et al. 2015a, b). At the same time, site-level factors have largely been ignored by proponents of propagule pressure, despite numerous studies that have shown their importance in bird introductions (e.g. Gullion 1962; Diamond and Veitch 1981; Griffith et al. 1989; Moulton and Pimm 1983, 1987; Lockwood et al. 1993; Lockwood and Moulton 1994; Smallwood 1994; Case 1996; Gamarra et al. 2005; Moulton and Cropper 2014b; Allen et al. 2015).

A principal basis for the propagule pressure hypothesis, as applied to birds, has been compilations of historical records such as those by Thomson (1922), Phillips (1928) Long (1981) Lever (1987, 2005). In relying on such secondary sources, studies that claim to support propagule pressure make two assumptions: first that the chronicle of introductions presented in these sources is complete and accurate; and second that the principal, if not sole, motivation behind the

introductions was the establishment of self-sustaining populations. A corollary to this second assumption is that introductions would end once it was perceived that the species was established. We show that for Chukar (*Alectoris chukar*) introductions to the USA these assumptions are unmet, and we provide evidence that introduction outcomes in Chukars are likely to be mostly influenced by site-level factors.

Methods and Materials

To illustrate the hazards in depending on secondary sources, we analyzed historical records of introductions of the Chukar to the United States as reported in two major secondary sources: Long (1981) and Lever (1987). We then compare the compilations in these two references to the records reported by Christensen (1970) and then we show how they compare to the records used in a recent study (Sol et al. 2012).

The Chukar has a vast range throughout Asia (Watson 1962a), and was once considered a subspecies of the Rock Partridge (*Alectoris graeca*), which occurs in Europe. Watson (1962a,b) showed that subtle but consistent morphological differences exist between adjacent populations of *A. graeca* and *A. chukar* in extreme Eastern Europe. We follow the 4th edition of the Howard and Moore Checklist of Birds of the World (Dickinson and Remsen 2013), which also treats the two as distinct species.

Our initial motivation for conducting this study came from the observation that the compilations of Long (1981) and Lever (1987) often were quite different from that of Christensen (1970), although both cited Christensen (1970) in their

treatments of the Chukar. Long (1981) referred to the species as *A. graeca* but makes it clear that the subspecies involved in the USA were almost exclusively true Chukars (Asian origin) and not Rock Partridges (European origin). Lever (1987) noted that 'Greek Chukars' released in California were likely Rock Partridges. Christensen (1970) discussed the difference in nomenclature referring to North American introductions as *A. chukar*, following the work of Watson (1962a,b). Lever (1987) also noted that the species was *A. chukar*, and suggested that the so-called 'Greek Chukars' presented to the state of California were actually Rock Partridges.

We compiled lists of introduction records per state as reported by Long (1981) and Lever (1987). We then compared these lists to Christensen (1970, 1996). We compared the number of individuals released in the states for which all three references reported a total number of individuals released. We transformed the total numbers by calculating their common logarithms and then compared these values using a mixed linear model with state (location) of the introduction as a random factor and the three references as a fixed effect. We used the Proc Glimmix in (SAS 2009) for our analyses.

We then compare these lists to the records used in a recent study of introductions (Sol et al. 2012) to show their degree of reliance on the work of Long (1981) and Lever (1987).

Results

Bump (1951) claimed that Chukars had likely been released in every one of the 48 states in the US (Alaska and Hawaii did not become states until 1959) but none of the historical references (Long 1981; Lever 1987; Christensen 1970) listed

releases for all 48 states. Thus, Long (1981) reported introductions of Chukars to just 22 of the 48 conterminous states, but only listed propagule information for 16 states. Lever (1987) listed releases of Chukars to 30 states, but only reported propagule information for 18 states. In contrast Christensen (1970, 1996) reported Chukar releases to 40 of the conterminous 48 states (he also noted introductions to Hawaii and Alaska) and listed the total number of individuals released in 35 states (Figure 1). For five other states (Florida, Louisiana, Michigan, Mississippi, and Rhode Island) Christensen (1970) reported that a "few" individuals had been released (Table 1).

Although Long (1981) and Lever (1987) both cited Christensen (1970), neither followed his compilation very closely. Moreover, even in those states for which propagule information existed in all three references, only in Missouri did Long (1981) report the same number released as listed by Christensen (1970), and Lever (1987) did not report the same number as Christensen (1970) for any state.

For just 15 states Christensen (1970), Long (1981), and Lever (1987) all reported numbers of individuals released (Table 1). Long (1981) and Lever (1987), also reported numbers for New York, although Christensen (1970) did not. Lever (1987) reported numbers for Nebraska and Utah, as did Christensen (1970), but not Long (1981).

In our mixed linear model the logarithms of the numbers of individuals released across the three references and 15 states, with state of introduction as a random effect and reference as a fixed effect, differed significantly in a Type III test

(df. 2, 20; $F = 4.94$; $p = 0.014$). Clearly, most the variation in numbers released was due to the higher numbers Christensen (1970) reported.

Thus, it would seem that at least two references (Long 1981; Lever 1987) have included only about half the states, and significantly fewer individuals than Christensen (1970). We emphasize that none of these references were compiled for the purpose of testing the propagule pressure hypothesis. Nevertheless, we must conclude that results of any studies involving the Chukar that relied heavily on either Long (1981) or Lever (1987) would be based on incomplete and inaccurate information and so be suspect.

Studies that presumably include Chukar releases to the USA (e.g. Cassey et al. 2004) do not always make their data available. One exception to this is the recent study (Sol et al. 2012), which involved a global analysis aimed at disentangling the effects of species-level characters on introduction success in birds. Sol et al. (2012) claim to have updated the database used by Cassey et al. (2004).

We were able to match 38 of 40 records of Chukars reported by Sol et al. (2012), using their propagule sizes and ID numbers, to reports by Long (1981) or Lever (1987) for 16 (or 17) states in the USA (Table 2). Sol et al. (2012) did not specify individual states in their records, but we surmise that they included multiple releases to Arizona (2), California (8), and Utah (14), and single releases (sums) for 13 (or 14 -- see New York discussion below) others. Sol et al. (2012) listed an unsuccessful record with a propagule size of 175 (Sol et al. ID # - 61), but neither Long (1981) nor Lever (1987) listed a propagule of this size. It is possible that this represents a conflation of the record Long (1981) and Lever (1987) listed for

Delaware County, New York where 25-150 individuals were released yearly between 1936 and 1939. As shown in Table 2, this record in Sol et al. (2012) falls between exactly matching values and ID numbers we matched to Lever (1987) for Missouri (1900 - Sol et al. ID # 60) and Pennsylvania (2021 - Sol et al. ID # 62). If this record is actually for New York it would represent the fourteenth state as noted above.

Sol et al. (2012) also listed two unsuccessful releases of 17 individuals each. One of these possibly refers to 17 individuals released in Alaska (Lever 1987) but the other is uncertain. Lever (1987) listed releases to 17 *counties* in Nebraska of 27842, and it is possible that Sol et al. (2012) in the course of updating the data inadvertently included this as a separate release.

We summed multiple releases for Arizona, California and Utah listed by Sol et al. (2012) to make their records comparable to the work of Christensen (1970) Long (1981) and Lever (1987). In a separate mixed model again with state of introduction a random effect and log number of individuals released, we observed a highly significant difference in log number after controlling the random effect of state in the Type III test of fixed effects ($F_{3,45} = 5.88$; $p < 0.002$).

We further compared subsets of the sources using two orthogonal contrasts. First, we compared the numbers that Christensen (1970) reported per state to those reported by the combination of Long (1981), Lever (1987), and Sol et al. (2012). In this contrast we observed a significant difference ($t = 16.60$; $p < 0.0002$; $df = 45$). Next we compared the combination of Long (1981) and Lever (1987) versus Sol et al. (2012), and here the contrast was not significant ($t = 1.01$; $p > 0.32$; $df = 45$).

Discussion

The first assumption of the propagule pressure hypothesis mentioned above was that the historical record was complete and accurate. Whereas the record itself may well be complete and accurate secondary sources such as Long (1981) and Lever (1987) are incomplete and seemingly inaccurate. Sol et al. (2012) and presumably Cassey et al. (2004) apparently relied heavily on the reports in Lever (1987) and Long (1981) but as we have shown here neither author completely or accurately reflected the introduction data presented by Christensen (1970). Thus, for Chukar introductions to the USA we have shown that the record as presented by two sources is incomplete and inaccurate.

The second assumption was that all the individuals that were introduced were necessary for establishment. Chukars currently have self-sustaining populations in ten western states (see Table 1). In four of these states (California, Idaho, Nevada, and Washington) Chukars were considered established in 1954 (Christensen 1954); in the other six states (Arizona, Colorado, Montana, Oregon, Utah, and Wyoming) the status was considered uncertain, doubtful (Arizona) or hopeful (Utah, Oregon). More individuals were released in all ten states between 1954 and 1970 (Christensen 1970). If propagule pressure was important we might expect the six states where the status was uncertain to release larger numbers after 1954 than the four states where the Chukar was considered established. As indicated in Table 1, Christensen (1954) considered Chukars to be established in four states (California, Idaho, Nevada, and Washington). However, by 1970 additional individuals were released in all four states (California - 10,446; Idaho -

17,129; Nevada - 7256; Washington - 43879). Thus, even in those states where the population of Chukars was considered established, releases continued. Additionally, it is quite possible that thousands of individuals were also released into populations that were not thought to be established. In fact for many species the exact population status it is not easily determined, as noted by Phillips (1928) and Leopold (1931).

A final point that must be made is that in numerous states very large numbers of Chukars were unsuccessfully released. In Minnesota more than 80,000 individuals were released only to fail. Indeed the only states with successful Chukar populations are states that straddle or are west of the continental divide. These states share certain environmental characteristics: all are more arid and mountainous than states where Chukars failed (Johnsgard 1988, Christensen 1996). The overwhelming result is that site-level factors are more important than simply the number of individuals released.

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Table 1. Chukar releases according to Christensen (Ch 1954, Ch 1970); Lever (1987) and Long (1981). A question mark indicates that the state was mentioned by the source but no propagule information was available. Chukars are considered established in the ten states in italics: Chukars were considered established in 1954 in the 4 italicized states marked with an asterisk.

State	Ch 1954	Ch 1970	Lever 1987	Long 1981	Sol et al. 2012	FGIP
Alabama ¹	720	720	?	?	.	.
<i>Arizona</i>	9866	11737	1133	1133	1133	534
<i>California*</i>	44554	55000	75173	39186	14287	11837
<i>Colorado</i>	10433	24080	8000	9000	9000	.
Connecticut	100s	1500
Florida	few	few	?	.	.	.
Georgia	.	.	?	.	.	.
<i>Idaho*</i>	8581	25710	28000	28000	25000	.
Illinois	9000	9000	?	.	.	.
Indiana	.	7500
Iowa	1847	1847
Kansas	7879	7879	?	?	.	.
Kentucky	1500	5480	?	.	.	.
Louisiana	few	few
Maryland	.	.	?	.	.	.

Massachusetts	few	500	?	.	.	.
Michigan	few	few	?	?	.	.
Minnesota	85000	85000	84414	84414	84414	.
Mississippi	few	few
Missouri	1838	1838	1900	1838	1900	.
<i>Montana</i>	3629	7854	5365	5365	5365	.
Nebraska	14750	28142	27842	?	27842	26748
<i>Nevada*</i>	6399	13655	5339	6739	5000	.
New Hampshire	130	130
New Mexico	4943	31000	16621	7700	.	16471
New York			<600	<600	175 ^B	
North Carolina	449	449
North Dakota	2300	5600	?	.	.	.
Ohio	20	20
Oklahoma	1000s	1000s
<i>Oregon</i>	19898	113675	76000	76000	76000	.
Pennsylvania	2377	2377	2021	2021	2021	.
Rhode Island	.	few
South Carolina	few	200+
South Dakota	1459	1831	1368	1368	1368	75
Tennessee	5824	5824	?	?	.	.
Texas	.	703	?	.	.	.

<i>Utah</i>	8666	185911	458	?	515	73360
Virginia	100	100	.	.	.	
<i>Washington*</i>	7041	50920	64996	5841	5841	59155
West Virginia	4420	4429
Wisconsin	43013	43013	17550	17550	17550	.
<i>Wyoming</i>	14000	60000	17455	53455	17455	.
States	37	40	30	22	17 ²	7
Records	37	40	69	50	65	154
Individuals	320636	793424	451794	446788	294866	188180

¹ These could have been Rock Partridges. Imhof (1976) listed "Chukars" in one part of his book and "Rock Partridges" in another, and as *Alectoris graeca* in both places. Moreover he listed the origin of the birds as "southeastern Europe", and did not include the species in a previous publication on birds new to Alabama (Imhof 1958).

² Includes by assumption (see text) one unidentified report as being from the state of New York, possibly one for Nebraska (Table 2) and excludes a release attributable to Alaska.

341 Table 2. Presumed sources for Sol et al. (2012) records. ID refers to the ID number
 342 in Sol et al. (2012); Fate = 1 successful, 0 = unsuccessful; Prop = propagule size as
 343 listed by Sol et al. (2012). Lever and Long refer to the presence of the record in
 344 those two references (Long 1981; Lever 1987): .5 = fewer listed by the reference; 1 =
 345 identical number listed; 2 = additional releases to the state were listed by the
 346 reference. The Fates are those Sol et al. (2012) reported (S= Successful; F = Failed).
 347

ID	Fate	Prop	State	Lever	Long	Fate
81	1	333	AZ	1	1	S
3204	1	800	AZ	1	1	S
53	1	4600	CA	1	1	S
3197	1	423	CA	.	1	S
3198	1	444	CA	.	1	S
3199	1	440	CA	.	1	S
3200	1	440	CA	.	1	S
3201	1	440	CA	.	1	S
3202	1	7000	CA	1	1	S
3203	1	500	CA	.	1	S
3205	1	9000	CO	1	.5	S
82	1	25000	ID	1	1	S
59	0	84414	MN	1	1	F
60	0	1900	MO	1	.5	F

771	1	5365	MT	1	1	S
1897	0	27842	NE	1	?	F
84	1	5000	NV	2	2	S
61	0	175	NY?	2	2	F
475	1	76000	OR	1	1	S
62	0	2021	PA	1	1	F
1898	1	1368	SD	1	1	S
88	0	50	UT	1	.	F
85	0	13	UT	1	.	F
86	0	23	UT	1	.	F
87	0	50	UT	1	.	F
90	0	41*	UT?	2	.	F
91	0	28	UT	1	.	F
92	0	15	UT	1	.	F
93	0	15	UT	1	.	F
94	0	38	UT	1	.	F
95	0	100	UT	1	.	F
96	0	8	UT	1	.	F
98	0	8	UT	1	.	F
97	0	50	UT	1	.	F
99	0	76	UT	1	.	F
1587	1	5841	WA	2	.	S

467	0	17550	WI	1	1	F
100	1	17455	WY	1	.	S

348

349 * ID 90 of Sol et al. (2012) might be a typographical error, as Lever (1987) listed a

350 release of 46 to Utah.

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352 Table 3. Chukar release summary by various sources: Ch70 = Christensen (1970);
 353 Le87 = Lever (1987); Lo81 = (Long 1981); Sol = Sol et al. (2012).

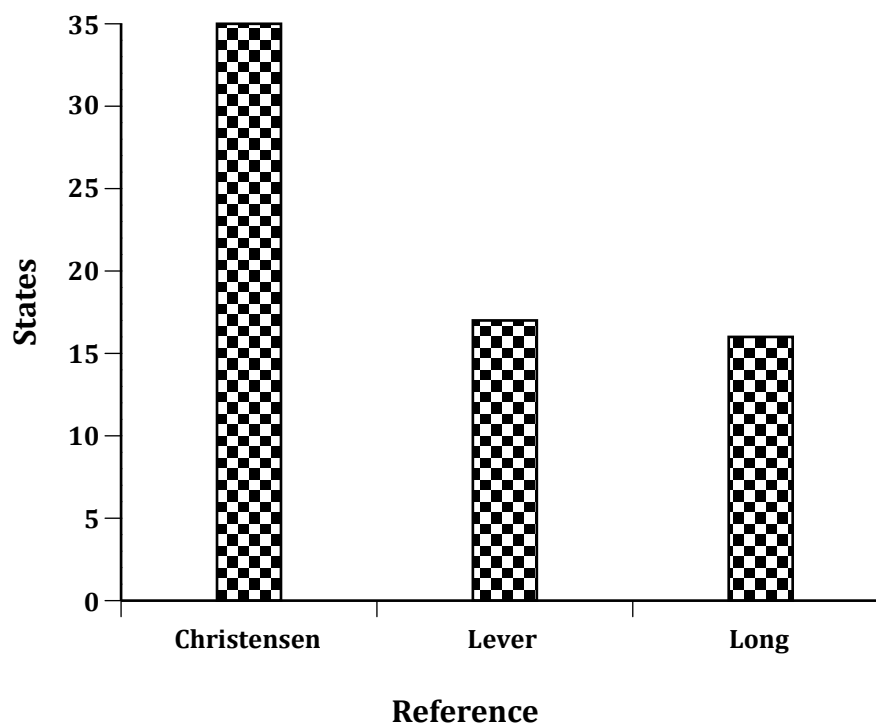
354

State	Ch70	Le87	Lo81	Sol
Nevada	13655	5339	6739	5000
California	55000	75173	39186	14287
Colorado	24080	8000	9000	9000
Wyoming	60000	17455	53455	17455
Idaho	25710	28000	28000	25000
Washington	50920	64996	5841	5841
Arizona	11737	1133	1133	1133
South Dakota	1831	1368	1368	1368
Missouri	1838	1900	1838	1900
Pennsylvania	2377	2021	2021	2021
Montana	7854	5365	5365	5365
Wisconsin	43013	17550	17550	17550
Oregon	113675	76000	76000	76000
Minnesota	85000	84414	84414	84414
New Mexico	31000	16621	7700	.
Utah	185911	458	.	515
Nebraska	28142	27842	.	27842
New York	.	<600	<600	175?

355

356 Figure 1. Number of states reporting total numbers of Chukars released: Christensen
357 (1970); Lever (1987); Long (1981).

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