Evolutionary Ecology Research, 2001, **3**: 507–519

Patterns of success in game bird (Aves: Galliformes) introductions to the Hawaiian islands and New Zealand

Michael P. Moulton,[1]* James G. Sanderson[2] and Ronald F. Labisky[1]

[1]Department of Wildlife Ecology and Conservation, University of Florida, PO Box 110430, Gainesville, FL 32611-0430 and [2]Conservation International, 1919 M Street NW, Suite 500, Washington, DC 20036-3521, USA

ABSTRACT

Most species of birds introduced to oceanic islands belong to one of two orders, Passeriformes or Galliformes. Among passeriforms on several islands, interspecific competition has been identified as a factor limiting introduction success. One pattern associated with interspecific competition among introduced passeriform birds is morphological over-dispersion. We tested for morphological over-dispersion among surviving sets of introduced galliforms on the six main Hawaiian Islands and New Zealand. At least 45 galliform species have been introduced to these islands. Overall, we found that game birds were consistently over-dispersed morphologically. The effect was most pronounced on New Zealand and least evident on Moloka'i and Kaua'i. On four islands (Hawai'i, Maui, Lana'i, O'ahu), the surviving species showed intermediate levels of morphological over-dispersion. We also re-evaluated the role of introduction effort in limiting introduction success and found the evidence supporting this hypothesis to be weak. Our results suggest that community-level factors, including environmental factors and interspecific competition, play an important role in determining the outcome of galliform introductions.

Keywords: competition, game birds, introductions, morphological over-dispersion, oceanic islands.

INTRODUCTION

Many different species of birds have been introduced successfully to oceanic islands (Long, 1981). However, most introductions have involved species from just two orders, Passeriformes and Galliformes (Long, 1981). Although many studies of introduced birds on islands have focused on passeriform birds, the galliforms have largely been ignored. Case (1996) argued that this restriction is arbitrary and he noted that several galliform species have been highly successful where they have been introduced.

At least 40 species of galliform birds have been introduced onto one or more of the six main Hawaiian Islands (Moulton *et al.*, 2001) and Veltman *et al.* (1996) reported that 15 galliform species had been introduced to New Zealand. However, only 12 of the 40 (30%) galliform species introduced to the Hawaiian Islands succeeded on at least one island.

---

* Author to whom all correspondence should be addressed. e-mail: moultonm@wec.ufl.edu

Similarly, Veltman *et al.* (1996) found that only five of the 15 (33%) species of galliforms introduced to New Zealand were successful.

The low success rate for galliforms in the Hawaiian Islands stands in stark contrast to that of the passeriforms. Thirty-three of the 52 (64%) passeriform species released in the Hawaiian Islands have been successful on at least one island (Moulton *et al.*, 2001). One study from New Zealand reported that 15 of 41 (37%) introduced passeriforms have been successful there (Veltman *et al.*, 1996).

Whenever some species are successful and others are not, the question arises as to what factors are involved in deciding the fates of those introductions. In the Hawaiian Islands, studies of introduced passeriform birds (Moulton and Pimm, 1983, 1987; Moulton and Lockwood, 1992; Moulton, 1993) have indicated that competition has played a role in influencing introduction outcomes. In New Zealand, several authors (e.g. Veltman *et al.*, 1996; Duncan, 1997; Green, 1997) have argued that introduction effort (number of individuals per release), the number of separate releases, or both, have been the most important factors in deciding the fates of introductions.

With competition, species that are ecologically very similar would have reduced chances for co-existence and thus be expected to show a pattern of ecological over-dispersion. Basically, this means that the co-existing species would be more different from each other ecologically than expected by chance. Unfortunately, it is not possible to measure ecological similarity among all species introduced to an island, because on most islands a significant proportion of the introduced species were not able to persist and so are no longer present. However, several authors have shown that morphological similarity reflects ecological similarity (e.g. Newton, 1973; Wilson, 1975; Ricklefs and Travis, 1980; Schoener, 1984; Grant, 1986; Schluter, 1988). One can evaluate morphological similarity of all species introduced to an island, present or absent, by measuring ecologically meaningful morphological characteristics on museum specimens (e.g. Moulton and Pimm, 1986, 1987). Because of the relationship between ecological and morphological similarity, a pattern of morphological over-dispersion would provide evidence that competition had influenced patterns in introduction success.

With this in mind, we tested for morphological over-dispersion (e.g. Ricklefs and Travis, 1980; Moulton and Pimm, 1986, 1987; Moulton and Lockwood, 1992; Lockwood *et al.*, 1993, 1996; Lockwood and Moulton, 1994; Brooke *et al.*, 1995; Moulton *et al.*, 1997), as a measure of competition, in limiting success of galliform introductions in the Hawaiian Islands and New Zealand. We also re-evaluated the importance of introduction effort in influencing outcomes of galliform introductions (Veltman *et al.*, 1996; Duncan, 1997; Green, 1997).

METHODS AND MATERIALS

We used the presence/absence matrix for the six main Hawaiian Islands in Moulton *et al.* (2001) and determined the status of each species. We also calculated the success rates for galliforms on each island. We used a series of references to construct a list of galliform species introduced to New Zealand, including Heather and Robertson (1997), Veltman *et al.* (1996), Bull *et al.* (1985), Long (1981), Falla *et al.* (1978), Lamb (1964), Oliver (1955) and Thomson (1922).

We obtained morphological measurements from specimens of galliforms housed at the British Museum of Natural History and the Florida Museum of Natural History. One of

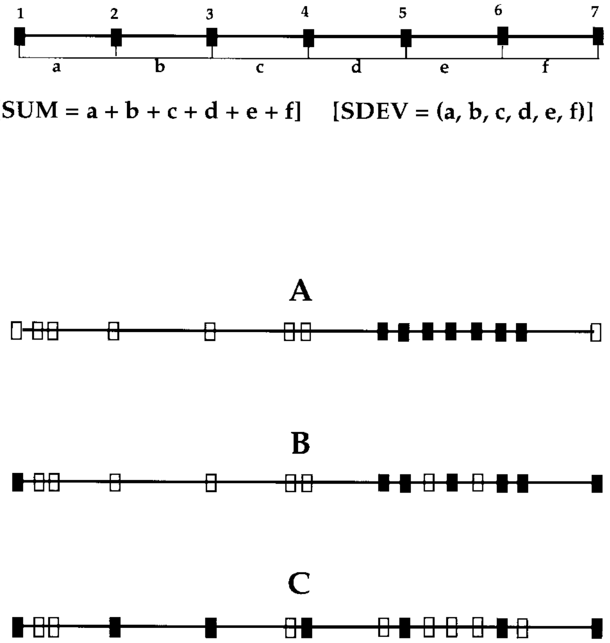


Fig. 1. (Top) Seven species indicated by solid black squares spaced out along a hypothetical morphological axis. The interspecies distances are indicated by the letters a, b, c, d, e and f. The SUM statistic is the sum of the $n - 1$ segments that join n species. The SDEV is the standard deviation of these line segments. (Bottom) In (A–C), the solid black squares represent successful species, whereas the open squares indicate unsuccessful species. In (A), the SUM is quite small and the SDEV is also very small. In (B), the SUM is very large, but so is the SDEV, as the individual line segments that join the species are quite different. In (C), the SUM is very large and the SDEV is very small.

the authors (M.P.M.) measured four characteristics on each specimen: the length of the culmen from the anterior margin of the nares to the tip of the beak; the length of the unflattened wing cord; the depth and width of the beak at the anterior margin of the nares. We measured as few as three and as many as 14 specimens of each species introduced to the Hawaiian Islands or New Zealand (see Appendix 1).

We conducted separate principal component analyses for the species introduced to each island to redefine variables as orthogonal, linear combinations of the original variables. Following Ricklefs and Travis (1980), we calculated the common logarithms of the raw measurements and we factored the covariance matrix of the log-transformed values to obtain our principal components. The principal components are eigenvectors of the covariance matrix, and the magnitude of the corresponding eigenvalue of each eigenvector represents the proportion of the total variance accounted for by that principal component.

For each island, we calculated the distances between surviving species. For a set of n species, there are $n - 1$ interspecific distances. We also calculated the mean and the standard deviation (SDEV) of these interspecific distances as well as a sum (SUM) of the segments that connect the species in the morphological space (see Fig. 1).

To test for morphological over-dispersion, we compared the SUM and SDEV of the observed sets of surviving species to distributions of randomly constructed assemblages of galliforms drawn from the pool of all galliform introductions to a particular island (see Fig. 1). To illustrate, 34 species of galliforms have been introduced to the island of Hawai'i. Of these 34 species, 11 have survived. Thus, we compared the SUM of the ten distances that connected the 11 surviving species to the SUMs of randomly selected sets of 11 species drawn from the pool of 34. There are $n!/(n-k)!\ k!$ ways of drawing a subset of k objects from a set of n objects. For Hawai'i, this comes to $34!/(34-11)!^{*}\ 11! = 286{,}097{,}760$.

We used a Monte-Carlo simulation technique to randomly select 5000 sets of galliform species on each island from the pool of all game bird species released on the island. We then compared the actual SUM and SDEV for each island to the random distributions of these statistics.

RESULTS

The numbers of galliform species introduced on each of the six main Hawaiian Islands were: Lana'i = 15, Moloka'i = 15, O'ahu = 19, Kaua'i = 20, Maui = 20 and Hawai'i = 34 (Table 1). The corresponding numbers of successful introductions were: Lana'i = 8 (53%), Moloka'i = 8 (53%), O'ahu = 5 (26%), Kaua'i = 8 (40%), Maui = 9 (45%) and Hawai'i = 11 (32%). The morphological relationships of successful and unsuccessful introduced game birds on each of the Hawaiian Islands are illustrated in Fig. 2.

In New Zealand, 20 galliform species were introduced, of which eight (40%) were successful (see Fig. 2). Our list for New Zealand differs in several instances from the list of Veltman *et al.* (1996); these differences are explained in Appendix 2.

The results of the seven principal component analyses were very similar. In all seven, the first principal component was positively correlated with all the log-transformed variables and accounted for at least 91% of the total variance. Thus, we conducted our analyses of over-dispersion using a single dimension. This simplification enabled us to use the simple sum (SUM) of the $n-1$ segments between the n species rather than the multi-dimensional minimal spanning tree used in other analyses (e.g. Lockwood and Moulton, 1994).

On all islands, the SDEV of the interspecific segments increased significantly with the SUM of the segments (see Fig. 3a–g). Therefore, our tests were based on the proportion of random SUMs that equalled or exceeded the observed SUM for an island and simultaneously had a SDEV that was equal to or smaller than the observed set of surviving species. With morphological over-dispersion, we would expect only a small fraction of the randomly generated SUMs to exceed the actual SUMs and also have SDEVs smaller than the observed set of species. Our simulation results are presented in Table 2.

On New Zealand and Lanai, the observed SUMs were equal to the maximum values calculated in any of the simulations. However, on both islands, several of the random combinations of species had equal or smaller SDEVs. On four of the remaining islands (Hawai'i, Maui, Lana'i, O'ahu), the proportions of random sets were larger (i.e. larger SUM) and more evenly spaced (i.e. smaller SDEV) than the actual surviving sets. Although not significant, these results were suggestive of over-dispersion.

Species with a large range of body sizes, as indexed by the first principal component scores, were introduced to each of the seven islands. The smallest species on any of the islands was *Coturnix chinensis*, which was released (unsuccessfully) on all of the Hawaiian Islands except Lana'i. The largest species, *Meleagris gallopavo*, was released (successfully) onto all islands in the study except O'ahu and Kaua'i.

Table 1. Distribution and introduction outcome for galliforms introduced to seven islands

Species	Ha	Ma	La	Mo	Oa	Ka	NZ
Ortalis cinereiceps	0.03279						
Penelope purpurascens	0.41385						
Crax rubra	0.64435						
Ammoperdix griseogularis	–0.17952						
Alectoris graeca							–0.01384
Alectoris chukar	**0.04408**	**0.08157**	**0.04731**	**0.03738**	0.03877	**0.04287**	**0.01209**
Alectoris barbara	0.00531	0.04280	0.00884	–0.00122			–0.02558
Alectoris rufa							–0.08426
Francolinus pondicerianus	**–0.01132**	**0.02583**	**–0.00777**	**–0.01912**	**–0.0168**	**–0.01267**	
Francolinus pintadeanus	–0.05726						
Francolinus francolinus	**0.02332**	**0.05969**		**0.01550**		**0.02110**	
Francolinus clappertoni	0.11391						
Francolinus icterorhynchus	0.08394						
Francolinus adsperus	0.08283						
Francolinus erckelii	**0.19475**	**0.23229**	**0.19819**	**0.18815**	**0.18959**	**0.19367**	
Francolinus leucosepus	0.23938						
Perdix perdix	–0.06762	–0.0304				–0.06885	–0.09646
Coturnix japonica	**–0.48616**	**–0.45213**	**–0.48220**	**–0.49666**	–0.49405	**–0.49046**	
Coturnix pectoralis		–0.39391	–0.42610				–0.45687
Coturnix ypsilophora							**–0.46723**
Coturnix chinensis	–0.73519	–0.70225		–0.74729	–0.74402	–0.74052	
Roulus rouloul					–0.14543		
Bambusicola thoracica	–0.19049	–0.15319					
Gallus gallus	0.06201	0.09675	0.06604	0.05254	**0.05480**	**0.05841**	0.03644
Gallus sonnerati	0.09404						
Lophura leucomelanos	**0.23116**						
Lophura nycthemera					0.28397	0.28784	0.26091
Syrmaticus soemmerringii		0.17096			0.12873	0.13249	
Syrmaticus reevesii	0.26943	0.30545	0.27295	0.26074	0.26304	0.26693	0.23949
Phasianus colchicus	**0.25628**	**0.29293**	**0.25994**	**0.24809**	**0.25047**	**0.25447**	**0.22553**
Chrysolophus pictus					0.09161	0.09561	
Chrysolophus amherstiae					0.13813		
Pavo cristatus	**0.55059**	**0.58484**	0.55503	0.54102	**0.54323**	0.54663	**0.52687**
Tetrao tetrix							0.18738
Tympanuchus phasianellus	0.05787						0.02962
Tympanuchus cupido							0.01508
Meleagris gallopavo	**0.60865**	**0.64612**	**0.61290**	**0.60334**	0.60389	0.60768	**0.58083**
Numida meleagris	0.42368	0.45901	0.42654	0.41411	0.41643	0.42027	**0.39263**
Oreortyx pictus	–0.20139					–0.20286	–0.23191
Callipepla squamata	–0.27445						
Callipepla douglasii	–0.24589						
Callipepla californica	**–0.33082**	**–0.29224**	**–0.32711**	**–0.33492**	–0.33501	**–0.33093**	**–0.36051**
Callipepla gambelii	**–0.32237**	–0.28453	**–0.31869**		–0.32719	–0.32319	
Colinus virginianus	–0.26794	–0.22812	–0.26474	–0.27096	–0.27134	–0.26701	**–0.30128**
Cyrtonyx montezumae	–0.18854						

Note: Values in the table are scores for the first principal component. Values in normal font represent unsuccessful species; values in bold represent successfully introduced species.
Abbreviations: Ha = Hawai'i; Ma = Maui; La = Lana'i; Mo = Moloka'i; Oa = O'ahu; Ka = Kaua'i; NZ = New Zealand.

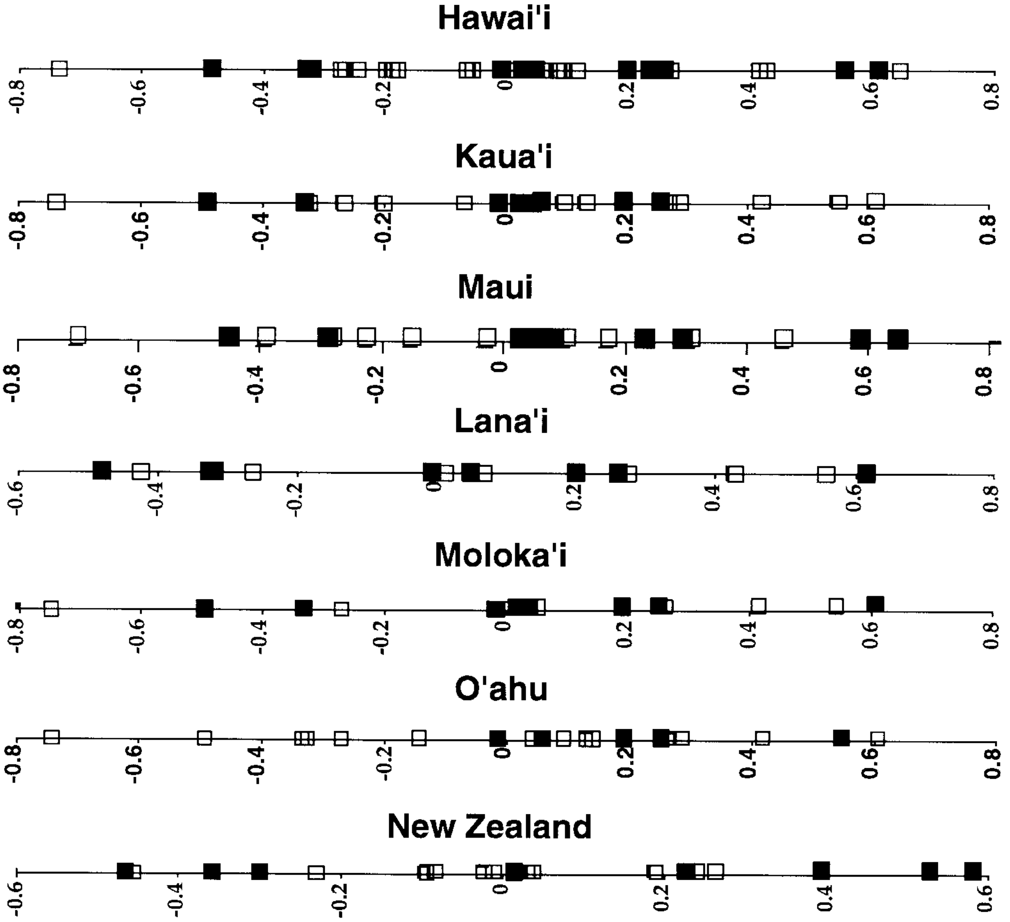


Fig. 2. The morphological relationships of the successful and unsuccessful birds introduced onto the seven islands. The open squares indicate species that have vanished, whereas the solid squares represent the surviving species.

On New Zealand, Hawai'i, Lana'i, Moloka'i and Maui, the surviving sets of species included small-, medium- and large-bodied species. On O'ahu, none of the six smallest species survived; on Kaua'i, the five largest species all failed. On both these islands, more than 4000 of the 5000 randomly generated SUMs were larger than the observed SUM. However, on O'ahu, far fewer of the randomly generated sets of species with SUMs greater than the actual SUM were also as evenly positioned in the morphological space as was the actual set of survivors.

On Kaua'i, the surviving species are not only less spread out than most of the random sets of species, but the surviving species also are highly clumped. On O'ahu, on the other hand, the surviving set of species is more evenly spaced-out even though none of the smallest species are included. Thus, O'ahu, but not Kaua'i, still shows a tendency towards morphological over-dispersion, on the basis of the more even spacing of the survivors.

Table 2. Results of one-dimensional analysis for seven islands

Island	SUM	SDEV	A	B	C
Lana'i	1.0951	0.1217	1331	3802	0.165
Maui	1.0983	0.1078	2237	3191	0.185
Kaua'i	0.7449	0.1009	4469	2390	0.377
Hawai'i	1.0948	0.1083	1996	3377	0.148
O'ahu	0.5600	0.0926	4229	1301	0.152
Moloka'i	1.1000	0.1238	3113	2783	0.245
New Zealand	1.0481	0.0850	713	1713	0.015

Abbreviations: SUM = sum of the interspecies distances; SDEV = standard deviation of segments; A = number of random SUMs ≥ actual; B = number of random SDEVs ≤ actual; C = proportion (#/5000) of random SUMs ≥ actual with SDEVs ≤ actual.

On all the islands, small proportions of random simulations had both SUMs greater than or equal to, *and* smaller than or equal to, the observed communities. One way to test the notion that these proportions were smaller than expected overall is with a maximum likelihood test. In this test, we calculate a G-value as:

$$G = -2\,\Sigma \ln p_i$$

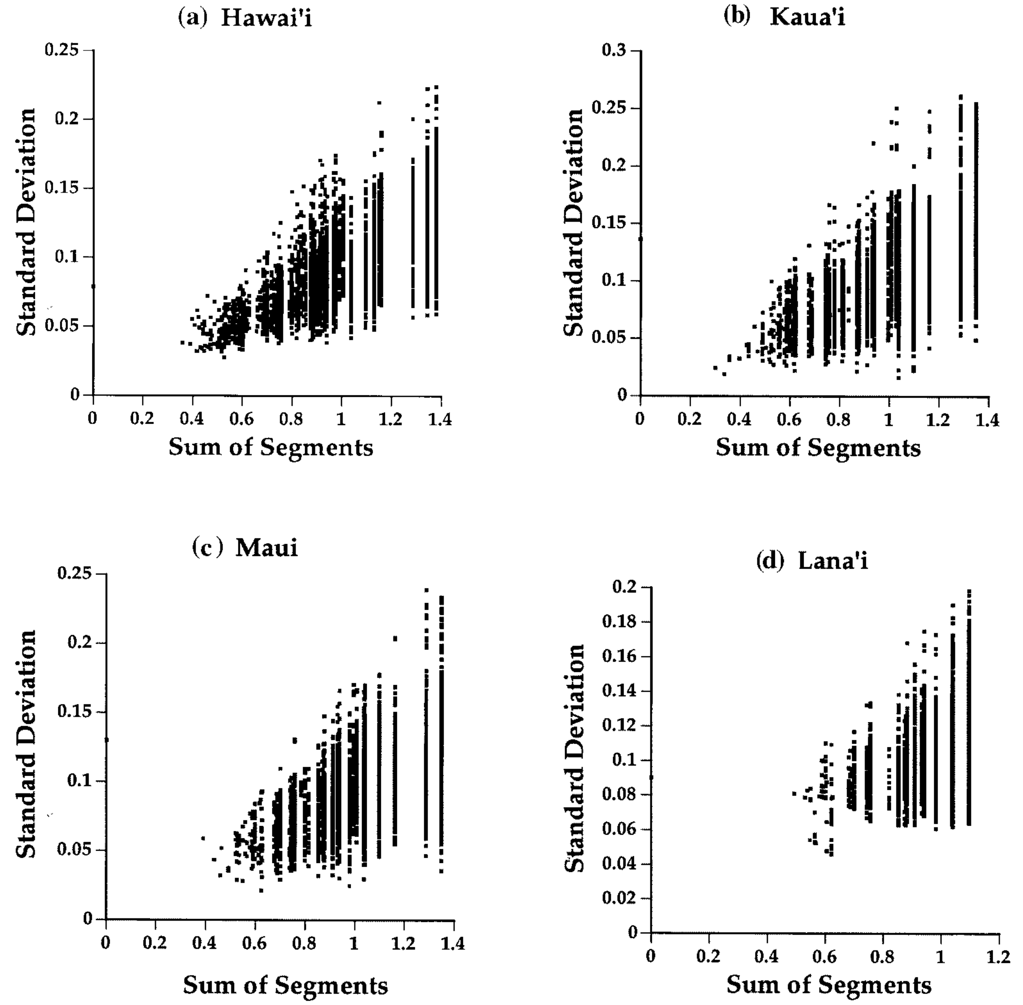
where p_i represents the ith of n proportions of interest. This statistic has a χ^2 distribution with $2n$ degrees of freedom. In this test, we calculated a χ^2 value of 27.73, which was highly significant ($0.025 < \chi^2 < 0.01$, d.f. = 14). This result further supports the idea that these sets of species are morphologically over-dispersed.

DISCUSSION

In our tests, New Zealand showed a pronounced pattern of morphological over-dispersion. Indeed, not a single one of the randomly generated sets of species for New Zealand had a larger SUM and only 76 of the random selections with equal sized SUMs had a SDEV that was smaller than that actually observed. On the remaining islands, the proportions of random sets were more spread out (i.e. had larger SUMs) and more evenly spaced (i.e. had smaller SDEVs than most of the randomly generated sets of species).

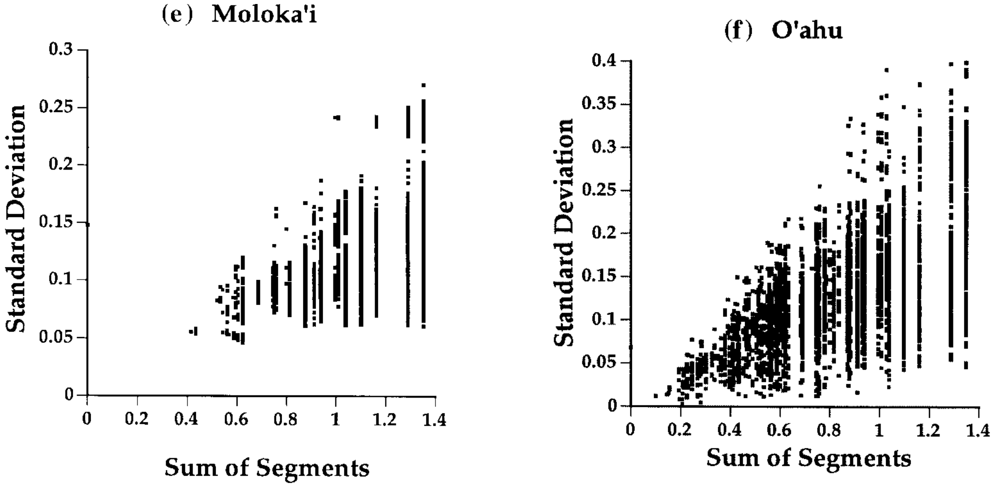
In interpreting these results, we emphasize that our test for over-dispersion may be conservative. To illustrate, consider the distribution of the principal component scores for the surviving species on the different islands. The principal component scores were highly correlated in each case with the body sizes of the species. On no island is there a pattern where all the surviving species had scores that were either small, medium or large.

The difference in galliform success between Moloka'i and Lana'i is notable. On both islands, eight of 15 species survived. Moreover, the islands differ by just two species. *Coturnix chinenesis* and *Francolinus francolinus* were released onto Moloka'i but not Lana'i, and *Coturnix pectoralis* and *Coturnix gambelii* were released onto Lana'i but not Moloka'i. Such differences seem subtle and indeed they are. However, many of the 5000 random sets for Moloka'i included the tiny species (*Coturnix chinensis*) as well as larger species such as *Pavo cristatus*, *Meleagris gallopavo*, or both. The SUMs generated for random sets that include *Coturnix chinensis* and one of the largest species inevitably exceed



that of the actual set of survivors. Thus, the inclusion of a single morphologically extreme species in a species pool of only 15 species can have a major impact on the results of our comparisons.

Veltman *et al.* (1996) argued that, in New Zealand, increased initial propagule sizes and increased numbers of releases were associated with increased success rates. However, we have re-examined the evidence supporting this generic argument and found it to be weak. The successful introduction of the Common Pheasant (*Phasianus colchicus torquatus*) on the North American mainland (Oregon) occurred in 1881 with a release of only 26 birds at a single site (Shaw, 1908). On the other hand, hundreds of thousands of Japanese quail (*Coturnix coturnix japonica*) were liberated at multiple sites in the Midwestern United States, principally in the late 1950s, without success (e.g. Labisky, 1959). Even Thomson's (1922) treatise on the naturalization of animals and plants in New Zealand reveals successes and failures among galliforms liberated in small numbers (< 5) and large numbers (> 100) at multiple sites. Obviously there is some minimum number of males and females associated



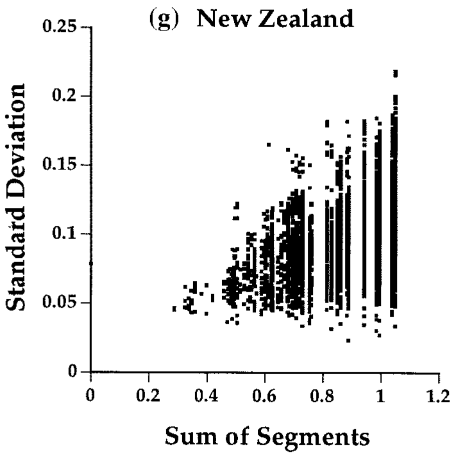


Fig. 3. Plots of SDEVs versus SUMs for 5000 randomizations for each of the seven islands.

with the successful introduction of any given species (Pimm, 1991). However, in all likelihood, this minimum number varies among species due to differences in mating systems and behaviours.

If accurate records of galliform introductions existed for the late 1800s and early 1900s, they would undoubtedly reveal that many failures were related to the source of stock. The euphoria associated with establishing populations of ‘new’ game birds in an area was overwhelming, resulting in the frenzied acquisition of eggs, chicks and adults from any available global source (Phillips, 1928). In too many instances, little effort was expended to select species with characteristics required for survival in the new environment: A pheasant was a pheasant and a quail was a quail! Thus, many introductions of species and subspecies were doomed from the onset because they were ecologically incompatible with the local environmental conditions and habitats. A further complication related to source is the probability that many introduced galliforms originated from domesticated stocks. Thus, most of the hundreds of thousands of *Coturnix c. japonica* that were released in North America came from a single source that originated in Japan, where the race had been domesticated for centuries (Stanford, 1957; Labisky, 1959). Labisky (1959) argued that the probable loss of wild vigour in the source of stock in this subspecies, as evidenced by aberrant behaviour and susceptibility to native predators, was a major factor contributing to its failure to become established on the North American mainland. However, we emphasize that this species has been successfully introduced to the Hawaiian Islands.

In the final analysis, the exact reasons for success or failure of many galliform introductions on islands remain obscure. We suggest that interspecfic competition between introduced galliforms is probably at least a contributing factor. Various species of galliform birds have been introduced in nearly every global environment. Typically, birds were released indiscriminately in the hope that the species or subspecies would become established and persist. This introduction paradigm resulted in many galliforms being liberated into environments that were outside their limits of environmental tolerance (i.e. right place, wrong bird or vice versa). Thus, the low success rate of galliform introductions may not reflect taxonomic inferiority when compared to passeriforms, but rather human disregard for rational approaches to introductions.

ACKNOWLEDGEMENTS

We thank Robert Prys-Jones of the British Museum of Natural History and David W. Steadman of the Florida Museum of Natural History for allowing us to examine and measure game bird specimens in their respective collections. This is contribution R-08006 to the Florida Agricultural Experiment Station.

REFERENCES

Brooke, R.K., Lockwood, J.L. and Moulton, M.P. 1995. Patterns of success in passeriform bird introductions on Saint Helena. *Oecologia*, **103**: 337–342.

Bull, P.C., Gaze, P.D. and Robertson, C.J.R. 1985. *The Atlas of Bird Distribution in New Zealand*. Wellington: The Ornithological Society of New Zealand.

Case, T.J. 1996. Global patterns in the establishment and distribution of exotic birds. *Biol. Conserv.*, **78**: 69–96.

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.

Falla, R.A., Sibson, R.B. and Turbot, C.G. 1978. *Collins Guide to the Birds of New Zealand*. Auckland: Harper Collins.

Grant, P.R. 1986. *Ecology and Evolution of Darwin's Finches*. Princeton, NJ: Princeton University Press.

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.

Heather, B. and Robertson, H. 1997. *The Field Guide to the Birds of New Zealand*. Oxford: Oxford University Press.

Howman, K. 1993. *Pheasants of the World*. Blaine, WA: Hancock House.

Johnsgard, P.A. 1988. *The Quails, Partridges and Francolins of the World*. Oxford: Oxford University Press.

Labisky, R.F. 1959. Report of attempts to establish Japanese quail in Illinois. *J. Wildl. Manage.*, **25**: 290–295.

Lamb, R.C. 1964. *Birds, Beasts & Fishes*. Christchurch: Caxton Press.

Lockwood, J.L. and Moulton, M.P. 1994. Ecomorphological pattern in Bermuda birds: The influence of competition and implications for nature preserves. *Evol. Ecol.*, **8**: 53–60.

Lockwood, J.L., Moulton, M.P. and Anderson, S.K. 1993. Morphological assortment and the assembly of communities of introduced passeriforms on oceanic islands: Tahiti versus O'ahu. *Am. Nat.*, **141**: 398–408.

Lockwood, J.L., Moulton, M.P. and Brooke, R.E. 1996. Morphological dispersion of the introduced land-birds of Saint Helena. *Ostrich*, **67**: 111–117.

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

Miles, D.B. and Ricklefs, R.E. 1984. The correlation between ecology and morphology in deciduous forest passerine birds. *Ecology*, **65**: 1629–1640.

Moulton, M.P. 1993. The all-or-none pattern in introduced Hawaiian passeriforms: The role of competition sustained. *Am. Nat.*, **141**: 105–119.

Moulton, M.P. and Lockwood, J.L. 1992. Morphological dispersion of introduced Hawaiian finches: Evidence for competition and a Narcissus effect. *Evol. Ecol.*, **6**: 45–55.

Moulton, M.P. and Pimm, S.L. 1983. The introduced Hawaiian avifauna: Biogeographic evidence for competition. *Am. Nat.*, **121**: 669–690.

Moulton, M.P. and Pimm, S.L. 1986. The extent of competition in shaping an introduced avifauna. In *Community Ecology* (J. Diamond and T.J. Case, eds), pp. 80–97. New York: Harper & Row.

Moulton, M.P. and Pimm, S.L. 1987. Morphological assortment in introduced Hawaiian passerines. *Evol. Ecol.*, **1**: 113–124.

Moulton, M.P., Sanderson, J.G. and Simberloff, D. 1997. Passeriform introductions to the Mascarene Islands: An assessment of the role of competition. *Ecologie* (*Paris*), **27**: 143–152.

Moulton, M.P., Miller, K.E. and Tillman, E.A. 2001. Patterns of success among introduced birds in the Hawaiian Islands. In *Evolution, Ecology, Conservation, and Management of Hawaiian Birds: A Vanishing Avifauna* (J.M. Scott, S. Conant and C. Van Riper III, eds), pp. 31–46. Studies in Avian Biology No. 22. Camarillo, CA: Cooper Ornithological Society.

Newton, I. 1973. *Finches*. New York: Taplinger.

Oliver, W.R.B. 1955. *New Zealand Birds*, 2nd edn. Wellington: A.H. & A.W. Reed.

Phillips, J.C. 1928. Wild birds introduced or transplanted in North America. *US Dept. Agric. Tech. Bull.*, **61**.

Pimm, S.L. 1991. *The Balance of Nature?* Chicago, IL: University of Chicago Press.

Ricklefs, R.E. and Travis, J. 1980. A morphological approach to the study of avian community organization. *Auk*, **97**: 321–338.

Schluter, D. 1988. The evolution of finch communities on islands and continents: Kenya *vs* Galapagos. *Ecol. Monogr.*, **57**: 229–249.

Schoener, T.W. 1984. Size differences among sympatric, bird-eating hawks: A worldwide survey. In *Ecological Communities*: *Conceptual Issues and the Evidence* (D.R. Strong, Jr., D. Simberloff, L.G. Abele and A.B. Thistle, eds), pp. 254–281. Princeton, NJ: Princeton University Press.

Shaw, W.T. 1908. *The China or Denney Pheasant in Oregon with Notes on the Native Grouse of the Pacific Northwest*. Philadelphia, PA: J.B. Lippincott.

Sibley, C.G. and Monroe, Jr., B.L. 1990. *Distribution and Taxonomy of Birds of the World.* New Haven, CT: Yale University Press.

Sorci, G., Moller, A.P. and Clobert, J. 1998. Plumage dichromatism of birds predicts introduction success in New Zealand. *J. Anim. Ecol.*, **67**: 263–269.

Stanford, J.A. 1957. A progress report of *Coturnix* quail investigations in Missouri. *Trans. North Am. Wild. Conf.*, **22**: 316–359.

Thomson, G.M. 1922. *The Naturalisation 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.

Watson, G.E. 1962. Three sibling species of Alectoris partridge. *Ibis*, **1962**: 353–367.

Wilson, D.S. 1975. The adequacy of body size as a niche difference. *Am. Nat.*, **109**: 769–784.

APPENDIX 1: MEANS OR MORPHOLOGICAL MEASUREMENTS OF GALLIFORMS INTRODUCED TO THE HAWAIIAN ISLANDS AND NEW ZEALAND

Species	*n*	Wing	Ncu	Nd	Nw
Ortalis cinereiceps	3	196.0	12.9	9.2	7.2
Penelope purpurascens	3	401.0	18.6	11.5	10.5
Crax rubra	2	413.5	24.3	22.8	13.0
Ammoperdix griseogularis	6	125.7	10.6	7.5	6.7
Alectoris graeca	4	161.2	12.7	9.2	8.8
Alectoris chukar	3	163.3	14.1	9.9	8.4
Alectoris barbara	5	159.0	13.2	9.0	8.3
Alectoris rufa	5	154.8	11.8	8.6	7.6
Francolinus pondicerianus	6	142.8	14.6	8.7	8.0
Francolinus pintadeanus	7	142.1	12.9	9.0	7.1
Francolinus francolinus	14	172.9	13.4	9.1	7.9
Francolinus clappertoni	12–13	177.1	16.3	9.9	9.0
Francolinus icterorhynchus	9–15	165.2	15.8	9.7	9.0
Francolinus adsperus	9–11	173.7	15.0	9.7	8.6
Francolinus erckelii	5–9	205.4	17.9	10.9	10.0
Francolinus leucosepus	2–5	204.6	18.6	11.1	10.2
Perdix perdix	4	151.7	11.9	7.8	7.8
Coturnix japonica	6	97.2	7.4	5.0	4.2
Coturnix pectoralis	5–6	98.0	7.5	5.6	4.9
Coturnix ypsilophora	4–9	91.7	7.6	6.0	4.8
Coturnix chinensis	4–10	70.3	5.9	3.9	3.1
Roulus rouloul	5	133.4	9.6	8.6	7.5
Bambusicola thoracica	5	128.4	9.9	7.5	6.7
Gallus gallus	6–12	209.9	14.0	8.4	7.9
Gallus sonnerati	4–12	219.0	14.9	9.2	8.2
Lophura leucomelanos	4–8	220.2	17.8	10.9	9.8
Lophura nycthemera	3–12	250.7	19.6	11.1	10.5
Syrmaticus soemmerringii	4–8	213.2	15.5	9.6	8.5
Syrmaticus reevesii	4–7	234.6	18.8	11.2	10.0
Phasianus colchicus	4	219.5	19.7	10.9	10.4
Chrysolophus pictus	4–9	183.7	14.9	10.2	9.6
Chrysolophus amherstiae	3–11	205.7	15.8	10.1	9.0
Pavo cristatus	4	449.5	23.5	12.3	13.0
Tetrao tetrix	5	243.2	14.6	11.9	10.4
Tympanuchus phasianellus	3	202.7	11.9	9.5	8.4
Tympanuchus cupido	4	206.7	11.7	8.8	8.3
Meleagris gallopavo	3–4	425.2	23.0	14.2	15.5
Numida meleagris	3	296.3	22.4	14.3	10.8
Oreortyx pictus	3	131.3	8.8	8.3	6.4
Callipepla squamata	4	114.2	8.7	7.1	6.2
Callipepla douglasii	5	110.0	8.5	8.1	6.9
Callipepla californica	4	107.7	7.6	6.6	6.2
Callipepla gambelii	4	111.2	7.8	6.6	6.0
Colinus virginianus	5	104.6	8.5	7.7	6.9
Cyrtonyx montezumae	5	122.6	8.5	8.8	7.5

Legend: number of specimens measured (*n*); means of unflattened wing cord (Wing); culmen from anterior of nares to tip (Ncu); depth (Nd) and width (Nw) at the anterior margin of the nares.

APPENDIX 2: NEW ZEALAND SPECIES LIST NOTES

Several papers dealing with introduced birds have appeared recently in the literature (Veltman *et al.*, 1996; Duncan, 1997; Green, 1997; Sorci *et al.*, 1998). Sorci *et al.* (1998) apparently used the same list as Veltman *et al.* (1996). Duncan (1997) focused on passerines only; Green's (1997) lists were just subsets of Veltman *et al.* (1996). These lists are all based on the work of Thomson (1922). We discuss differences between our lists and those of Thomson (1922) for each order below.

With respect to the galliforms, Thomson (1922) listed 34 species. One of these (*Turnix varia*) is now classified by Sibley and Monroe (1990) as belonging to a separate order (Turniciformes). Of the remaining 33 species, three ('Egyptian Quail', 'Black-breasted Quail' and 'Jungle Pheasant') are listed only by common name. It is impossible to discern which species 'Jungle Pheasant' pertains to in as much as the majority of the world's pheasants could qualify as 'Jungle Pheasants' (Howman, 1993), so we excluded this species. Thomson's (1922) listing of 'Egyptian Quail' may refer to *Coturnix coturnix* (Johnsgard, 1988; Long, 1981). Nevertheless, since its identity is unknown, we have also excluded this species. The 'Black-breasted Quail' of Thomson (1922) probably refers to *Coturnix coromandelica* (Sibley and Monroe, 1990). Thomson (1922) applied this binomen to 'Indian Quail'. Thus, there were apparently two listings for the same species. Moreover, it is possible that the two individuals of 'Black-breasted Quail' mentioned by Thomson (1922) were in fact two of the four individuals of *C. coromandelica* he also listed. Given the small number of individuals involved, we excluded both. Another apparent double listing involves '*Synoicus diemenensis*', which Thomson (1922) lists separately from '*Synoicus australis*', both of which are now treated by Sibley and Monroe (1990) as being conspecific under the name *Coturnix ypsilophora*. Thus, we excluded *S. diemenensis*.

We excluded several other species listed by Thomson (1922) chiefly because there was either no firm evidence of actual release or simply too few individuals (<5) were involved. Thus, we excluded *Alectura lathami*, *Crax rubra* and *Lagopus lagopus* on grounds that too few individuals were released. We also excluded *Chrysolophus pictus*, *Chrysolophus amherstiae*, *Phasianus ellioti*, *Tragopan temmincki* and *Coturnix chinensis* because these species may not have actually been released but rather just kept in aviaries (Thomson, 1922). Finally, we excluded *Lagopus mutus* because none of the inidividuals survived the voyage from England (Thomson, 1922). In sum, we excluded 14 of the 33 galliform species listed by Thomson (1922), leaving 19 of which seven were successful.

Another difference between our list and the game bird list of Thomson (1922) involves the partridges (*Alectoris*). Thomson (1922) lists three species in the genus 'Caccabis': *C. rufa*, *C. petrosa* and *C. saxatilis*. The genus is now called Alectoris and the species *A. rufa*, *A. barbara* and *A. graeca*. These three species were all introduced unsuccessfully. A fourth species, *A. chukar*, has been successfully introduced to the South Island (Heather and Robertson, 1997). However, this species was introduced after publication of Thomson's (1922) book, perhaps in 1926 (Oliver, 1955). Long (1981) and Veltman *et al.* (1996) treated the Chukar as a subspecies of the Rock Partridge (*A. graeca*). However, Watson (1962) argued in detail that the two were not conspecific. The significance here is that two species as opposed to one were actually introduced. Adding the Chukar (*A. chukar*) to the list of 19 leaves 20 species of game birds, eight of which were successful. Veltman *et al.* (1996) included 15 species. Those authors excluded *A. barbara*, *Gallus gallus*, *Numida meleagris*, *Meleagris gallopavo* and *Pavo cristatus*. They also considered *Alectoris graeca* and *Alectoris chukar* as a single species when they could have treated the two separately. Veltman *et al.* (1996) excluded *P. cristatus* because they could find no information on number released or number of releases. They list no reasons for the other exclusions. At the same time, Veltman *et al.* (1996) included *L. lagopus*, which we excluded (see above).