

PATTERNS OF SUCCESS AMONG INTRODUCED BIRDS IN THE HAWAIIAN ISLANDS

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Abstract. At least 140 species of 14 different orders of birds have been introduced to the six main Hawaiian Islands. The introduced species came from six continents and the introductions were carried out by a variety of agents including state and local governments, private citizens, and the acclimatization society known as the Hui Manu. The introductions mostly occurred during the early to mid-twentieth century. Most (79%) of the intentional introductions were of species from three orders: Galliformes, Columbiformes, and Passeriformes.

Introduction success rates were significantly greater for passeriforms than for either columbiforms or galliforms, although the reasons for this are unknown. In predicting the fate of future introductions, only the columbiforms showed an “all-or-none” pattern of introduction history. Successful species had larger native geographic ranges than did unsuccessful species, which supports the hypothesis that range size is correlated with the ability to adapt to a new environment. Finally, in a partial test of the introduction effort hypothesis we found that galliforms successfully introduced to the island of Hawai‘i were introduced in significantly larger numbers than unsuccessful species.

Key Words: doves; game birds; introduced species; introduction effort; introduction success; native range size; perching birds; pigeons.

Numerous species of birds from six continents have been introduced to the Hawaiian Islands (Caum 1933, Berger 1981, Long 1981, Pratt et al. 1987). These species were introduced by a variety of groups for a variety of reasons. As noted by Berger (1981), the first avian introduction came with early Polynesians who brought the Red Junglefowl (*Gallus gallus*) for food. Since that time, a number of private citizens have brought species to Hawai‘i (e.g., Caum 1933). Some of these introductions were made inadvertently as individual birds escaped captivity (e.g., Melodious Laughing-thrush or Hwamei, *Garrulax canorus*, on O‘ahu), whereas others were intentionally released for aesthetic reasons or even as an attempt at biological control (Caum 1933). There also have been intensive efforts both by private citizens (e.g., Lewin 1971) as well as state and county agencies (Schwartz and Schwartz 1949; Walker 1966, 1967) to establish populations of various game birds for recreational hunting. In the early to mid-twentieth century, the acclimatization society known as the Hui Manu actively introduced several species to various islands (Caum 1933, Berger 1981).

Regardless of their source, a central question in any study of introduced birds is “Why do some species succeed and others fail?” In several papers we and our colleagues have argued that competition has played an influential role in determining the outcomes of passerine species’ introductions in Hawai‘i (Moulton and Pimm 1983, 1986a, 1987; Moulton 1985, 1993; Mountainspring and Scott 1985; Moulton et al. 1990; Moulton and Lockwood 1992). These arguments are based on three main findings. First, introductions tend to be less successful when more species of introduced birds are already present

(Moulton 1993; Moulton and Pimm 1983, 1986a). Second, there is a pattern of limiting similarity among congeneric pairs of introduced birds: differences in bill length are significantly greater in pairs that coexist than in pairs of species that were not able to coexist (Moulton 1985). And third, successful introduced passerines show a pattern of morphological overdispersion (Moulton and Pimm 1987, Moulton and Lockwood 1992); i.e., successful species are morphologically more different from each other than expected by chance.

Although these three patterns are consistent with predictions from competition theory, other explanations for patterns in introduction outcomes have been advanced. These include introduction history of a species (Simberloff and Boecklen 1991) and introduction effort (e.g., Pimm 1991, Veltman et al. 1996).

The idea that introduction history can predict future introduction outcomes is appealing in its simplicity. The concept comes from Simberloff and Boecklen (1991) who argued that whenever and wherever a given species is introduced, it tends to either always succeed or always fail. This leads to an “all-or-none” pattern in the distribution of birds introduced onto a series of islands: some species being successful on “all” the islands in the series and others being successful on “none” of the islands. If introduced birds actually follow this pattern, then predicting the outcome of future introductions would be greatly simplified. Moulton (1993) and Moulton and Sanderson (1997), however, argued that the all-or-none pattern reported by Simberloff and Boecklen (1991) for passerine birds was primarily an artifact of sample size.

Another factor that might influence the outcome of introductions is the effort invested in the introduction process. Griffith et al. (1989) found that introduction effort along with habitat quality were associated with introduction outcome. Similarly, Pimm (1991) studied introductions of seven game bird species (all of which had been successfully introduced somewhere in the world) in the western United States and found that there was a very high ($360/424 = 85\%$) failure rate. Pimm's analysis indicated that the failure rate was particularly high when fewer than 75 individuals were released. More recently, studies of introduced birds in New Zealand (Veltman et al. 1996, Duncan 1997, Green 1997) have concluded that introduction effort is the most influential variable in determining which species succeed. In each of the three studies, the authors reported that successful species were introduced in larger numbers and more frequently than were unsuccessful species.

Several authors have reported a positive relationship between the size of the native geographic range of a species and its average abundance (e.g., Bock and Ricklefs 1983, Brown 1984). If widespread species tend to be ecologically more generalized than species with narrow distributions, we would predict that successful introduced species would tend to be those that have larger native ranges.

Many analyses of avian introduction success in Hawai'i have focused on passerine birds (e.g., Moulton and Pimm 1983, 1986a,b, 1987; Williams 1987, Moulton and Lockwood 1992), yet passerines represent fewer than half the total number of birds that have been introduced to the Hawaiian Islands (Berger 1981, Long 1981). Our objectives in this paper were to examine patterns of success for introduced species in Hawai'i across three taxonomic orders of birds: Galliformes, Columbiformes, and Passeriformes. Specifically, are the success rates of nonpasserine birds different from those of the passerines? Second, is an all-or-none pattern evident in the nonpasserine orders? Third, is native range size greater for successful introduced species than for unsuccessful introduced species in passerines and nonpasserines? And, fourth, does introduction effort play a role in determining the success of introduced birds in Hawai'i?

METHODS AND MATERIALS

We used Caum (1933), Schwartz and Schwartz (1949), Munro (1960), Walker (1966, 1967), Lewin (1971), Berger (1981), Long (1981), Lever (1987), and Pratt et al. (1987) to compile lists of nonindigenous birds introduced to the Hawaiian Islands. In compiling our lists we attempted to ascertain not only the current status of each species but also the date of first introduction. In our analyses we considered species to be

successful if they were present on an island in 1990. We considered species to be unsuccessful if there were no recorded observations after 1990. Scientific names of 140 species introduced in the Hawaiian Islands are provided in Appendix 1. Scientific names of introduced species not included in our statistical analyses are provided in Appendix 2.

In order to determine success rates for the species in the different orders, we considered a species to be successful if it succeeded on any island, and unsuccessful only if it failed on every island on which it was released. By this approach, even if a species fails on all but one island, we believe that environmental conditions in the archipelago overall were potentially suitable for establishment and that perhaps differences in the mechanics of the release or interactions with other species might have occurred on islands where the species failed. We compared introduction success rates across orders with a chi-square test of equal proportions.

We used range maps in Long (1981) to estimate native range size for all introduced species, except *Garrulax caerulatus* and *Callipepla douglasii*, which were not included by Long. We used a grid method similar to the methods of Moulton and Pimm (1986b). We placed a small acetate grid over the native range map in Long (1981) and counted the number of squares that were intersected. Each square represented approximately 259,000 km². In earlier analyses of native range size of introduced passerines in Hawai'i (Moulton and Pimm 1986b), *Uraeginthus angolensis* and *U. cyanocephala* were omitted because of concern about the potential confusion with young *U. bengalus* in the field. However, we included all three *Uraeginthus* species in this analysis because Berger (1981) reported each was seen and identified in the wild.

We used Mann-Whitney tests for all our range size comparisons because data were not normally distributed. We compared native geographic range sizes of successful versus failed introductions, both within and across orders.

RESULTS

At least 140 species of nonindigenous birds from 14 orders have been released in the Hawaiian Islands (Table 1). Our results differ from earlier totals of 162 species (Long 1981) and 170 species (Berger 1981) for two reasons. First, those authors followed a somewhat different taxonomy. For example, Berger (1981) listed the Green Pheasant (*Phasianus versicolor*) as being a distinct species, whereas we followed Sibley and Monroe (1990) and treated it as being conspecific with the Ring-necked Pheasant (*Phasianus colchicus*). Second, at least among the passerines, we have excluded several species included by Long and Berger on grounds that simply too few individuals (i.e., < 5) were released. Simberloff and Boecklen (1991) list 14 of these species in their Appendix B, although based on Berger (1981) we included the two *Uraeginthus* species (*U. angolensis* and *U. cyanocephala*).

Although a great diversity of species has been released into the Hawaiian Islands, for the most

TABLE 1. SPECIES OF BIRDS INTRODUCED TO THE HAWAIIAN ISLANDS (CAUM 1933, BERGER 1981, LONG 1981)

Order	Number of species
Tinamiformes	1
Pelecaniformes	1
Ciconiiformes	3
Falconiformes	1
Galliformes	40
Turniformes	1
Gruiformes	1
Charadriiformes	2
Anseriformes	4
Columbiformes	18
Psittaciformes	14
Strigiformes	1
Apodiformes	1
Passeriformes	52

part three orders accounted for the bulk of the introductions. These are the game birds (Galliformes), pigeons and doves (Columbiformes), and perching birds (Passeriformes). These species represent 110 introductions (Appendices 3–5). Berger (1981) lists 14 species of a fourth order, Psittaciformes. However, according to Berger (1981), 13 of these species were accidental introductions. Moreover, Pratt et al. (1987) considered only one species of this order (*Psittacula krameri*) to be successful in Hawai'i. Thus, we restricted our tests to the three orders for which there was evidence for intentional in-

troductions: Galliformes, Columbiformes, and Passeriformes.

HISTORICAL PERSPECTIVE

In order to develop a historical perspective on the phenomenon of introductions for the galliforms, columbiforms, and passeriforms, we categorized introductions by time period (Fig. 1). Historical peaks in the number of introductions were evident for each order.

For galliforms, the number of species' introductions increased steadily from 1901 until the early 1960s and then declined to zero. There has not been an introduction of a new species of galliform into the Hawaiian Islands since 1965 (*Francolinus adsperus*). For columbiforms, the peak occurred in the 1920s. Indeed, there have been only two introductions (*Zenaida asiatica* in 1961 and *Zenaida macroura* in 1962) of species from this order since 1960. The passeriforms also appear to show a decline in the number of introductions after the 1960s (Fig. 1). Closer inspection reveals an even sharper decline in the frequency of introductions, with only one new passerine species introduced since 1980 (*Estrilda astrild* in 1981). The remaining nine species were all present on other islands in the archipelago prior to 1975 and possibly arrived onto new islands via interisland colonization.

SUCCESS RATES

Success rates differed significantly among orders ($\chi^2 = 14.59$, $df = 2$, $P < 0.005$). Among

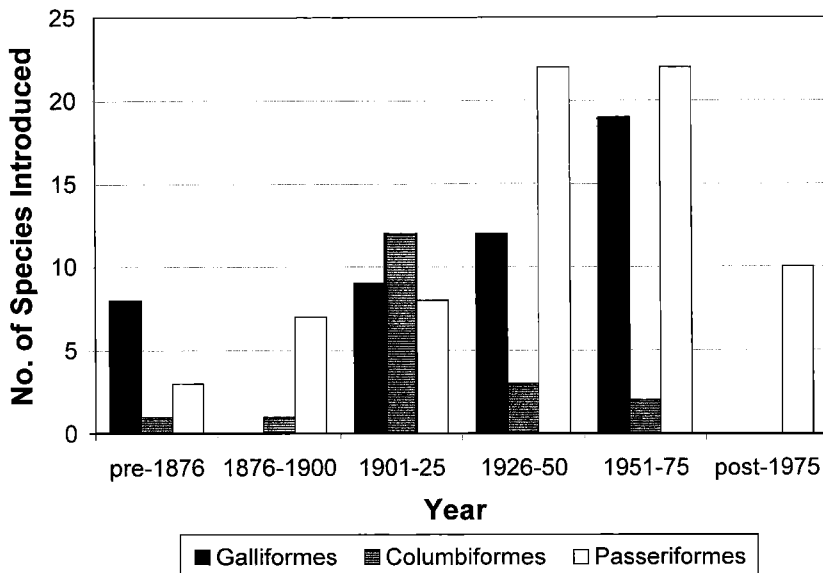


FIGURE 1. Chronology of species introductions to the Hawaiian Islands.

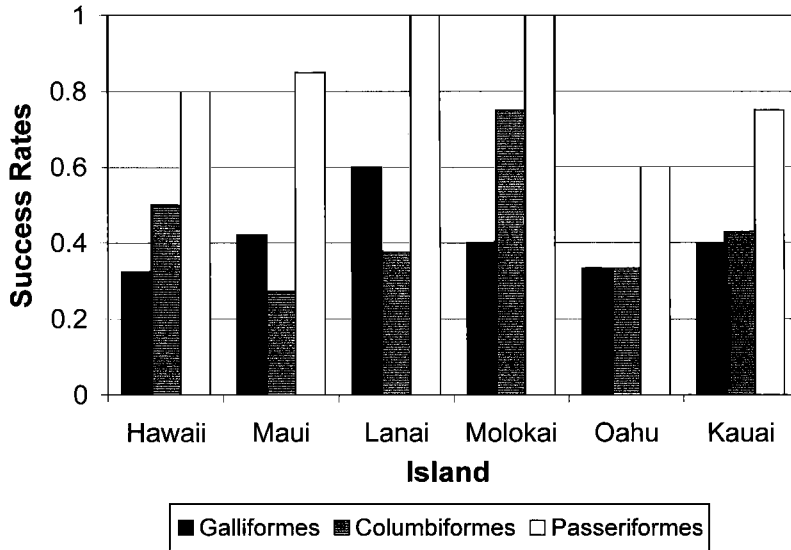


FIGURE 2. Success rates (number of successful introductions/total number of introductions) per order across the six main Hawaiian Islands.

passerines, 33 of 52 (64%) species have been successful on at least one island (Appendix 3). The success rates for galliform and columbiform species were not nearly so high. Only 12 of 40 (30%) introduced galliform species (Appendix 4) and 4 of 18 (22%) introduced columbiform species (Appendix 5) have been successful on at least one island.

Within islands the success rates also were variable (Fig. 2). For passerines, Moloka'i and Lāna'i shared the highest rates of success at 1.00 (13/13 for Moloka'i and 11/11 for Lāna'i). Lāna'i also had the highest success rate for galliforms (9/15, 0.60), whereas Moloka'i had the highest rate for columbiforms (3/4, 0.75; Fig. 2; Table 2). Although it is tempting to compare rates among islands across the different orders, results of any tests would be misleading because of the high potential for nonindependence. For example, with respect to passerines, only seven species were introduced to islands other than

O'ahu (five to Kaua'i and two to Hawai'i). For galliforms, only O'ahu and Hawai'i have any unique species.

ALL-OR-NONE PATTERNS

The hallmark of an all-or-none distributional pattern of introduced birds on islands would be presence of few, if any, mixed species. Mixed species are those that are successful on some islands and unsuccessful on others (Simberloff and Boecklen 1991). In principle, species released onto one island could show a mixed outcome if they spread to another island and then fail on one of the two islands. In practice this is very difficult to detect, because those species with the ability to spread to other islands could do so repeatedly giving the impression that they were established on the second island even if they were actually not able to survive there. This would be an example of what Brown and Kodric-Brown (1977) have termed a "rescue effect." With this in mind we believe that analyses for all-or-none patterns should be limited to those species that were physically introduced to more than one island.

In their analysis of introduced Hawaiian birds, Simberloff and Boecklen (1991) reported that among 19 introduced columbiform species, only one (*Pterocles exustus*) showed a mixed outcome, having succeeded on Hawai'i, and failed on Moloka'i and Kaua'i. However, Sibley and Monroe (1990) placed this species in the order Ciconiiformes. If this species is excluded, 18 columbiform species remain, 11 of which were

TABLE 2. SUCCESS RATES (NUMBER OF SUCCESSFUL INTRODUCTIONS/TOTAL NUMBER OF INTRODUCTIONS) PER ORDER ACROSS THE SIX MAIN HAWAIIAN ISLANDS

Island	Galliformes	Columbiformes	Passeriformes
Hawai'i	0.32	0.56	0.80
Maui	0.45	0.27	0.84
Lāna'i	0.53	0.43	1.00
Moloka'i	0.53	0.60	1.00
O'ahu	0.26	0.33	0.60
Kaua'i	0.40	0.375	0.75

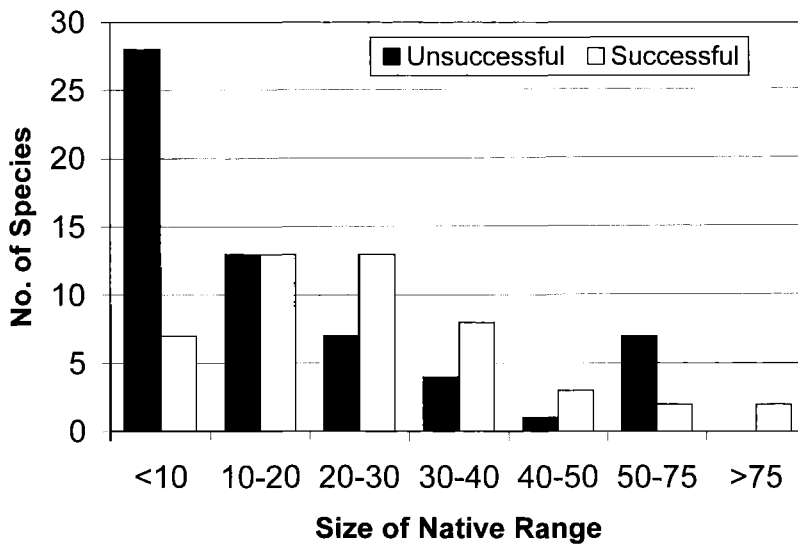


FIGURE 3. Size of native geographic range for unsuccessful versus successful introduced species. Range size measured in number of 259,000 km² map blocks (see Methods and Materials).

introduced onto more than one island. The observation of no mixed species out of eleven possible is evidence for an all-or-none pattern.

Among the Galliformes, 23 species were released onto two or more islands. At least seven of 23 (30%) have had mixed outcomes: *Callipepla californica*, *C. gambelii*, *Alectoris chukar*, *Coturnix japonica*, *Gallus gallus*, *Pavo cristatus*, *Meleagris gallopavo* (Appendix 4). Thus, there is not an all-or-none pattern among the introduced game birds.

Moulton and Sanderson (1997) and Moulton (1993) argued that mixed species tended to be those introduced onto more islands. With this in mind we compared the median numbers of islands of introduction for always unsuccessful, always successful, and mixed species. Medians differed significantly ($H = 8.95$, $P = 0.012$), with the highest median recorded for mixed species (6.0), and medians of 3.0 for always unsuccessful species and 6.0 for always successful species. As a further test we combined species that were always successful with those that were always unsuccessful and compared the com-

bined median with that of the mixed species. These medians also differed significantly ($H = 5.23$, $P = 0.022$).

RANGE SIZE

We estimated native range size for 108 introduced species. Range size was significantly larger in successful species than in unsuccessful species (approximate $\chi^2 = 10.95$, $df = 1$, $P < 0.001$; Fig. 3; Table 3). Within orders, range size differences were significant for passerines ($P = 0.015$) and marginally significant in game birds ($P = 0.099$). However median range size did not differ significantly between successful and unsuccessful columbiforms ($P = 0.123$). In all three orders, the successful species had larger median native range sizes than did unsuccessful species.

INTRODUCTION EFFORT

Data are available for only a partial test of the influence of introduction effort on introduction success. Lewin (1971) provided numbers of individuals released for 26 Galliformes on the island of Hawai'i (Table 4). Most of the data were derived from private releases by the owners of the Pu'u Wa'awa'a Ranch, but in some instances data from releases made by state agencies were included. We excluded *Coturnix japonica* because it already was successful, apparently having colonized the island from Maui and/or Lāna'i (Schwartz and Schwartz 1949), and there were no further releases by the state or the owners of the ranch. The median number of individuals introduced was 179 for successful galliform species ($N = 9$) and 14 for unsuccessful galliform species ($N = 17$). Medians

TABLE 3. RESULTS OF NATIVE RANGE SIZE COMPARISONS BETWEEN SUCCESSFUL (S) AND UNSUCCESSFUL (F) INTRODUCED SPECIES (MEAN NUMBER OF 259,000 KM² GRID SQUARES)

Order	S	F	P
Galliformes	22.2	16.6	0.099
Columbiformes	36.1	23.3	0.123
Passeriformes	33.0	17.5	0.015

TABLE 4. NUMBER OF INDIVIDUALS OF SPECIES OF GAME BIRDS, PIGEONS, AND DOVES RELEASED ON HAWAII (LEWIN 1971)

Species	Number released	Status
<i>Colinus virginianus</i> ^a	108	F
<i>Oreortyx pictus</i>	88	F
<i>Callipepla squamata</i>	14	F
<i>Callipepla californica</i>	412	S
<i>Callipepla gambelii</i>	546	F
<i>Callipepla douglasii</i>	113	F
<i>Ammoperdix griseogularis</i>	20	F
<i>Cyrtonyx montezumae</i>	8	F
<i>Alectoris chukar</i>	110	S
<i>Alectoris barbara</i>	104	F
<i>Francolinus francolinus</i>	226	S
<i>Francolinus pintadeanus</i>	10	F
<i>Francolinus pondicerianus</i>	214	S
<i>Francolinus adspersus</i>	4	F
<i>Francolinus icterorhynchus</i>	9	F
<i>Francolinus clappertoni</i>	10	F
<i>Francolinus erckelii</i>	179	S
<i>Francolinus leucoscepus</i>	27	F
<i>Coturnix chinensis</i>	8	F
<i>Bambusicola thoracica</i>	12	F
<i>Lophura leucomelanos</i>	67	S
<i>Gallus sonneratii</i>	14	F
<i>Phasianus colchicus</i>	244	S
<i>Syrnaticus reevesii</i>	180	F
<i>Pavo cristatus</i>	2	S
<i>Meleagris gallopavo</i>	115	S
<i>Zenaida macroura</i>	168	S
<i>Zenaida asiatica</i>	40	F
<i>Streptopelia risoria</i> (= <i>decaocto</i> ?)	11	F
<i>Streptopelia chinensis</i>	8	S
<i>Geopelia striata</i>	18	S

^a See Appendix 1 for common names.

were significantly different in a Kruskal-Wallis test ($H = 5.25, P = 0.02$).

Data for the columbiforms appear to be equally compelling, although we have not tested this group since there were just seven species introduced and two of these already were established on Hawai'i at the time of the introductions by the Pu'u Wa'awa'a Ranch (Lewin 1971).

DISCUSSION

The introduction process in the Hawaiian Islands has been highly nonrandom with respect to phylogeny. Thus 10 of the 14 orders are represented by five or fewer species. The three orders that are represented by more species are those that have been the focus of intentional introductions. Thus, most galliforms were likely introduced to enhance prospects for recreational hunting, and most columbiforms were introduced for recreational hunting or for aesthetic reasons. Passerines were introduced for a variety of reasons, including biological control and aesthetic reasons, as well as accidental releases of cage birds.

The phenomenon of avian introductions, at least

for the three orders we have focused on here, appears to be historical, with most introduction efforts having come to a close. There have been no columbiform or galliform introductions to the Hawaiian Islands in more than 30 years. Moreover, no new passerine species have been introduced to the islands since 1981. This is not to say that there will not be future introductions from these, or other, taxa. Indeed, there have been recent sightings of various parrot species since 1990. For example, Pyle (1994) reported that 10 to 15 Nanday Parakeets (*Nandayus nenday*) were seen on the island of Hawai'i.

In terms of success rates, we found that passerine species had a significantly higher overall success rate than either of the nonpasserine orders. The reasons for this are unclear, but the pattern is highly significant. It is possible to explain some of this result via the propagule size hypothesis. We found a significant relationship between propagule size (i.e., introduction effort) and the success rates of galliforms introduced to the island of Hawai'i. Caum (1933) also noted that several columbiform species apparently were introduced in very small numbers. However, it remains to be shown that passerines were systematically released in larger numbers.

The simplest potential predictor of the outcome of species' introductions is introduction history (Simberloff and Boecklen 1991). If introduction history alone were an adequate predictor of introduction outcomes we should have detected clear all-or-none patterns within the orders we analyzed. Moulton (1993) and Moulton and Sanderson (1997) argued that the all-or-none patterns reported for passerines introduced to the Hawaiian Islands and elsewhere may be due to sampling artifact. When we extended the analysis here to include the columbiforms and galliforms, only the columbiforms show any evidence for such a pattern. Thus, we found little evidence to support the notion that introduction history is an adequate predictor of future introduction outcomes.

Our analyses suggested that one consistent predictor of introduction success was size of native geographic range. In all three orders we observed that successfully introduced species had larger native ranges than unsuccessful species. These results are consistent with the hypothesis that species with larger ranges are ecologically more generalized (Brown 1984) and hence better able to adapt to a new environment.

In a partial test of the introduction effort hypothesis, we found that galliforms introduced successfully to Hawai'i were introduced in larger numbers than were unsuccessful species. However, it should be noted that some species were successful with initial releases of as few as two individuals; e.g., a single pair of Peafowl (*Pavo cristatus*) released on the Pu'u Wa'awa'a Ranch in 1909 led to the successful establishment of the

species on Hawai'i (Lewin 1971). Also, for 6 of the 15 unsuccessful species, >85 individuals were released (*Colinus virginianus*, *Callipepla douglasii*, *Callipepla gambelii*, *Syrnaticus reevesii*, *Oreotyx pictus*, *Alectoris barbara*; Table 4). We do not know if successful game birds on islands other than Hawai'i were introduced in higher numbers than were unsuccessful species. Because data are lacking for passeriform and columbiform species, a thorough test of the introduction effort hypothesis was not possible.

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APPENDIX 1. SCIENTIFIC AND COMMON NAMES OF 142 SPECIES INTRODUCED TO THE HAWAIIAN ISLANDS (NOMENCLATURE FOLLOWS SIBLEY AND MONROE 1990)

Scientific name	Common name
<i>Acridotheres tristis</i>	Common Myna
<i>Agapornis roseicapillus</i>	Rosy-faced Lovebird
<i>Alauda arvensis</i>	Skylark
<i>Alectoris barbara</i>	Barbary Partridge
<i>Alectoris chukar</i>	Chukar
<i>Amandava amandava</i>	Red Avadavat
<i>Amazona ochrocephala</i>	Yellow-crowned Parrot
<i>Amazona viridigenalis</i>	Red-crowned Parrot
<i>Ammoperdix griseogularis</i>	See-see Partridge
<i>Anas discors</i>	Blue-winged Teal
<i>Anas platyrhynchos</i>	Mallard
<i>Ara macao</i>	Scarlet Macaw
<i>Bambusicola thoracica</i>	Chinese Bamboo-Partridge
<i>Brotogeris jugularis</i>	Orange-chinned Parakeet
<i>Bubulcus ibis</i>	Cattle Egret
<i>Cacatua galerita</i>	Sulphur-crested Cockatoo
<i>Cacatua moluccensis</i>	Salmon-crested Cockatoo
<i>Callipepla californica</i>	California Quail
<i>Callipepla douglasii</i>	Elegant Quail
<i>Callipepla gambelii</i>	Gambel's Quail
<i>Callipepla squamata</i>	Scaled Quail
<i>Caloenas nicobarica</i>	Nicobar Pigeon
<i>Cardinalis cardinalis</i>	Northern Cardinal
<i>Carpodacus mexicanus</i>	House Finch
<i>Cettia diphone</i>	Japanese Bush-Warbler
<i>Chalcophaps indica</i>	Emerald Dove
<i>Chrysolophus amherstiae</i>	Lady Amherst Pheasant
<i>Chrysolophus pictus</i>	Golden Pheasant
<i>Colinus virginianus</i>	Northern Bobwhite
<i>Collocalia vanikorensis</i>	Uniform Swiftlet
<i>Columba livia</i>	Rock Pigeon
<i>Copsychus malabaricus</i>	White-rumped Shama
<i>Copsychus saularis</i>	Oriental Magpie-Robin
<i>Coturnix chinensis</i>	Blue-breasted Quail
<i>Coturnix japonica</i>	Japanese Quail
<i>Coturnix pectoralis</i>	Stubble Quail
<i>Crax rubra</i>	Great Curassow
<i>Cyanoptila cyanomelana</i>	Blue-and-White Flycatcher
<i>Cygnus olor</i>	Mute Swan
<i>Cyrtonyx montezumae</i>	Montezuma Quail
<i>Eclectus roratus</i>	Eclectus Parrot
<i>Eolophus roseicapilla</i>	Galah
<i>Erithacus akahige</i>	Japanese Robin
<i>Erithacus komadori</i>	Ryukyu Robin
<i>Estrilda astrild</i>	Common Waxbill
<i>Estrilda caeruleascens</i>	Lavendar Waxbill
<i>Estrilda melpada</i>	Orange-cheeked Waxbill

APPENDIX 1. CONTINUED.

Scientific name	Common name
<i>Estrilda troglodytes</i>	Black-rumped Waxbill
<i>Falco (rusticolus ?)</i>	Gyr Falcon?
<i>Fracolinus adspersus</i>	Red-billed Francolin
<i>Fracolinus clappertoni</i>	Clapperton's Francolin
<i>Fracolinus erckelii</i>	Erckel's Francolin
<i>Fracolinus francolinus</i>	Black Francolin
<i>Fracolinus icterorhynchus</i>	Heuglin's Francolin
<i>Fracolinus leucosepus</i>	Yellow-necked Spurfowl
<i>Fracolinus pintadeanus</i>	Chinese Francolin
<i>Fracolinus pondicerianus</i>	Grey Francolin
<i>Gallinolumba luzonica</i>	Luzon Bleeding-Heart
<i>Gallus gallus</i>	Red Junglefowl
<i>Gallus sonneratii</i>	Grey Junglefowl
<i>Garrulax albogularis</i>	White-throated Laughingthrush
<i>Garrulax caerulatus</i>	Grey-sided Laughingthrush
<i>Garrulax canorus</i>	Hwamei
<i>Garrulax chinensis</i>	Black-throated Laughingthrush
<i>Garrulax pectoralis</i>	Greater Necklaced Laughingthrush
<i>Geopelia cuneata</i>	Diamond Dove
<i>Geopelia humeralis</i>	Bar-shouldered Dove
<i>Geopelia striata</i>	Zebra Dove
<i>Geophaps lophotes</i>	Crested Pigeon
<i>Geophaps plumifera</i>	Spinifex Pigeon
<i>Geophaps smithii</i>	Partridge Pigeon
<i>Geotrygon montana</i>	Ruddy Quail-Dove
<i>Gracula religiosa</i>	Hill Myna
<i>Grallina cyanoleuca</i>	Maggie-Lark
<i>Lagonosticta senegala</i>	Red-billed Firefinch
<i>Larus novaehollandiae</i>	Silver Gull
<i>Larus occidentalis</i>	Western Gull
<i>Leiothrix lutea</i>	Red-billed Leiothrix
<i>Leptotila verreauxi</i>	White-tipped Dove
<i>Leucosarcia melanoleuca</i>	Wonga Pigeon
<i>Lonchura cantans</i>	African Silverbill
<i>Lonchura malacca</i>	Black-headed Munia
<i>Lonchura oryzivora</i>	Java Sparrow
<i>Lonchura punctulata</i>	Scaly-breasted Munia
<i>Lophura leucomelanos</i>	Kalij Pheasant
<i>Lophura nycthemera</i>	Silver Pheasant
<i>Melanocorypha mongolica</i>	Mongolian Lark
<i>Meleagris gallopavo</i>	Wild Turkey
<i>Melopsittacus undulatus</i>	Budgerigar
<i>Mimus polyglottos</i>	Northern Mockingbird
<i>Myiopsitta monachus</i>	Monk Parakeet
<i>Nandayus nenday</i>	Nanday Parakeet
<i>Neochen jubata</i>	Orinoco Goose
<i>Nothoprocta perdicaria</i>	Chilean Tinamou
<i>Numida meleagris</i>	Helmeted Guineafowl
<i>Oreortyx pictus</i>	Mountain Quail
<i>Ortalis cinereiceps</i>	Grey-headed Chachalaca
<i>Paroaria capitata</i>	Yellow-billed Cardinal
<i>Paroaria coronata</i>	Red-crested Cardinal
<i>Paroaria dominicana</i>	Red-cowled Cardinal
<i>Parus varius</i>	Varied Tit
<i>Passer domesticus</i>	House Sparrow
<i>Passerina ciris</i>	Painted Bunting
<i>Passerina cyanea</i>	Indigo Bunting
<i>Passerina leclancherii</i>	Orange-breasted Bunting
<i>Pavo cristatus</i>	Common Peafowl
<i>Penelope purpurascens</i>	Crested Guan
<i>Perdix perdix</i>	Grey Partridge
<i>Phalacrocorax carbo</i>	Great Cormorant
<i>Phaps chalcoptera</i>	Common Bronzewing
<i>Phasianus colchicus</i>	Ring-necked Pheasant
<i>Phoenicopterus ruber</i>	Greater Flamingo

APPENDIX 1. CONTINUED.

Scientific name	Common name
<i>Platycercus adscitus</i>	Pale-headed Rosella
<i>Porphyrio porphyrio</i>	Purple Swamphen
<i>Psittacula krameri</i>	Rose-ringed Parakeet
<i>Pterocles exustus</i>	Chestnut-bellied Sandgrouse
<i>Pycnonotus cafer</i>	Red-vented Bulbul
<i>Pycnonotus jocosus</i>	Red-whiskered Bulbul
<i>Rhipidura leucophrys</i>	Willie-Wagtail
<i>Rollulus rouloul</i>	Crested Partridge
<i>Serinus leucopygius</i>	White-rumped Seed eater
<i>Serinus mozambicus</i>	Yellow-fronted Canary
<i>Sicalis flaveola</i>	Saffron Finch
<i>Streptopelia chinensis</i>	Spotted Dove
<i>Streptopelia decaocto</i>	Eurasian Collared-Dove
<i>Sturnella loyca</i>	Long-tailed Meadowlark
<i>Sturnella neglecta</i>	Western Meadowlark
<i>Syrmaticus reevesii</i>	Reeve's Pheasant
<i>Syrmaticus soemmerringii</i>	Copper Pheasant
<i>Tiaris olivacea</i>	Yellow-faced Grassquit
<i>Turnix varia</i>	Painted Buttonquail
<i>Tympanuchis cupido</i>	Greater Prairie Chicken
<i>Tympanuchus phasianellus</i>	Sharp-tailed Grouse
<i>Tyto alba</i>	Barn Owl
<i>Uraeginthus angolensis</i>	Blue-breasted Cordonbleu
<i>Uraeginthus bengalus</i>	Red-cheeked Cordonbleu
<i>Uraeginthus cyanocephala</i>	Blue-capped Cordonbleu
<i>Urocissa erythrorhyncha</i>	Red-billed Blue Magpie
<i>Vidua macroura</i>	Pin-tailed Wydah
<i>Zenaida asiatica</i>	White-winged Dove
<i>Zenaida macroura</i>	Mourning Dove
<i>Zosterops japonicus</i>	Japanese White-Eye

APPENDIX 2. LIST OF 31 SPECIES FROM 11 ORDERS NOT INCLUDED IN STATISTICAL ANALYSES. WITHIN EACH CELL, THE FIRST LINE INDICATES DATE OF FIRST INTRODUCTION (OR FIRST REFERENCE TO INTRODUCTION) AND STATUS (S = SUCCESSFUL; F = FAILED); THE SECOND LINE INDICATES MODE OF INTRODUCTION (1 = PRIVATE; 2 = STATE OR COUNTY AGENCY; 3 = UNKNOWN, INCLUDES ESCAPE FROM CAPTIVITY; 4 = POLYNESIANS; 5 = HUI MANU); AND THE THIRD LINE INDICATES REFERENCE

Species	O'ahu	Kaua'i	Mau	Hawai'i	Moloka'i	Lāna'i
<i>Nothoprocta perdicaria</i>				1966 F 2 1		
<i>Phalacrocorax carbo</i>						1890s F 1 1
<i>Phoenicopter ruber</i>		1929 F 1 1				
<i>Bubulcus ibis</i>	1959 S 1 7	1959 S 1 7	1959 S 1 7	1959 S 1 7	1959 S 1 7	1959 S 1 7
<i>Pterocles exustus</i>		1961 F 2 5,11		1961 S 2 5,11	1961 F 2 5,11	
<i>Falco (rusticolus?)^a</i>				1929 F 1 1		

APPENDIX 2. CONTINUED.

Species	O'ahu	Kaua'i	Maui	Hawai'i	Moloka'i	Lāna'i
<i>Turnix varia</i>			1922 F 2 1		1922 F 2 1	
<i>Poopyrio porphyrio</i>	1933 F 3 1			1928 F 2 1		
<i>Larus novaehollandiae</i>	1924 F 3 1					
<i>Larus occidentalis</i>	1933 F 3 1		1933 F 3 1			
<i>Cygnus olor</i>				1920 F 1 1		
<i>Neochen jubata</i>	1922 F 2 1					
<i>Anas platyrhynchos</i> ^b				1955 S 1 6		
<i>Anas discors</i> ^c	1932 F 2 1					
<i>Tyto alba</i>	1959 S 2 7	1959 S 2 7	1959 S 2 7	1958 S 2 7	1959 S 2 7,11	
<i>Collocalia vanikorensis</i>	1962 S 2 7					
<i>Brotegeris jugularis</i>	1933 F 3 1					
<i>Cacatua galerita</i>	1933 F 3 1					
<i>Cacatua roseicapilla</i>	1933 F 3 1					
<i>Cacatua moluccensis</i>	1981 F 3 7					
<i>Ara macao</i>	1933 F 3 1					
<i>Melopsittachus undulatus</i>	1933 F 3 1					
<i>Psittacula krameri</i>	1933 S 3 1,7	1981 S 3 7,10		1981 S 3 7,10		
<i>Nandayus nenday</i>	1981 F 3 7			1981 U 3 13		
<i>Myiopsitta monachus</i>	1970 F 3 7					
<i>Amazona viridigenalis</i>	1971 U 3 7					

APPENDIX 2. CONTINUED.

Species	O'ahu	Kaua'i	Maui	Hawai'i	Moloka'i	Lāna'i
<i>Amazona ochrocephala</i>	1969 F 3 7					
<i>Eclactus roratus</i>	1981 F 3 7					
<i>Agapornis roseicapillis</i>	1973 F 3 7					
<i>Platycercus adscitus</i>			1877 F 1 1			
<i>Urocissa erythrorhyncha</i>	1966 F 1 7					

References: 1 = Caum 1933; 2 = Schwartz and Schwartz 1949; 3 = Munro 1960; 4 = Walker 1966; 5 = Walker 1967; 6 = Lewin 1971; 7 = Berger 1981; 8 = Moulton and Pimm 1983; 9 = Scott et al. 1986; 10 = Pratt et al. 1987; 11 = Simberloff and Boecklen 1991; 12 = Moulton 1993; 13 = Pyle 1994; 14 = Wunz 1992.

^a Caum (1933) listed *F. rusticolus* only as a tentative identification.

^b May have interbred with natural migrants, as well as feral individuals.

^c Species identity uncertain. Caum (1933) stated the species is *Querquedula discors* (Blue-winged Teal, *Anas discors*); however, he also reported that the individuals came from Australia where the Blue-winged Teal does not occur.

APPENDIX 3. INTRODUCED PASSERINES ON SIX MAIN HAWAIIAN ISLANDS (SEE APPENDIX 2 FOR EXPLANATION OF TERMS)

Species	O'ahu	Kaua'i	Maui	Hawai'i	Moloka'i	Lāna'i
<i>Acridotheres tristis</i>	1872 S 1 12	1883 S 3 8	1883 S 3 8	1883 S 3 8	1883 S 3 8	1883 S 3 8
<i>Alauda arvensis</i>	1867 S 3 12	1870 F 1 1,8	1886 S 3 8	1902 S 3 8	1917 S 3 8	1917 S 3 8
<i>Amandava amandava</i>	1900 S 3 12		1987 S 3 11	1987 S 3 11		
<i>Cardinalis cardinalis</i>	1929 S 3,5 1,8	1929 S 1 1,8	1949 S 3 8	1929 S 2 1	1951 S 3 8	1957 S 3 8
<i>Carpodacus mexicanus</i>	1870 S 3 12	1886 S 3 8	1886 S 3 8	1886 S 3 8	1886 S 3 8	1886 S 3 8
<i>Cettia diphone</i>	1929 S 1,2 1	1988 S 3 11	1980 S 3 11		1979 S 3 11	1980 S 3 11
<i>Copsychus malabaricus</i>	1939 S 5 11	1931 S 1 1				
<i>Copsychus saularis</i>	1932 F 5 1	1922 S 1 1,12				
<i>Cyanoptila cyanomelana</i>	1929 F 2,5 1,8			1937 F 5 8		
<i>Erithacus akahige</i>	1929 F 2 1					
<i>Erithacus komadori</i>	1931 F 3 8					
<i>Estrilda astrild</i>	1981 S 3 12					

APPENDIX 3. CONTINUED.

Species	O'ahu	Kaua'i	Mau	Hawai'i	Moloka'i	Lāna'i
<i>Estrilda caerulescens</i>	1965 S 3 12			1978 S 3 11		
<i>Estrilda melpoda</i>	1965 S 3 12		1989 S 3 MPM			
<i>Estrilda troglodytes</i>	1965 F 3 12			1975 S 3 11		
<i>Garrulax albogularis</i>		1919 F 1 1				
<i>Garrulax caerulatus</i>	1947 S 3 8					
<i>Garrulax canorus</i>	1900 S 3 1,8	1918 S 1 1,8	1902 S 1 1,8	1909 S 1 1,8	1909 S 1 1,8	
<i>Garrulax chinensis</i>		1931 F 1 1				
<i>Garrulax pectoralis</i>		1962 S 3 11				
<i>Gracula religiosa</i>	1960 S 3 11					
<i>Grallina cyanoleuca</i>	1922 F 2 1			1922 F 2 1		
<i>Lagonosticta senegala</i>	1965 F 3 11					
<i>Leiothrix lutea</i>	1928 S 2 1	1918 S 1 1	1928 S 2 1	1928 S 2 1	1928 S 2 1	
<i>Lonchura cantans</i>	1984 S 3 11	1984 S 3 11	1978 S 3 11	1972 S 3 11	1981 S 3 11	1979 S 3 11
<i>Lonchura malacca</i>	1936 S 3 8	1976 S 3 11				
<i>Lonchura oryzivora</i>	1964 S 3 12	1983 S 3 11	1986 S 3 11	1981 S 3 11		
<i>Lonchura punctulata</i>	1883 S 3 8,12	1883 S 3 8	1883 S 3 8	1883 S 3 8	1883 S 3 8	1883 S 3 8
<i>Melanocorypha mongolica</i>		1914 F 1 8				
<i>Mimus polyglottos</i>	1931 S 5 1,8	1946 S 3 8	1933 S 5 1,8	1959 S 3 8	1951 S 3 8	1970 S 3 11
<i>Paroaria capitata</i>				1973 S 3 11		
<i>Paroaria coronata</i>	1928 S 1,5 1,11	1928 S 3 8,11	1960 S 3 11	1976 S 3 11	1963 S 3 11	1976 S 3 11

APPENDIX 3. CONTINUED.

Species	O'ahu	Kaua'i	Maui	Hawai'i	Moloka'i	Lāna'i
<i>Paroaria dominicana</i>	1931 F 5 1					
<i>Parus varius</i>	1928 F 2 1,8	1890 F 1 1,8	1928 F 2 1,8	1928 F 2 1,8		
<i>Passer domesticus</i>	1871 S 3 1,8	1917 S 3 8	1917 S 3 8	1917 S 3 8	1917 S 3 8	1917 S 3 8
<i>Passerina ciris</i>				1937 F 5 8		
<i>Passerina cyanea</i>	1934 F 3 8			1937 F 5 8		
<i>Passerina leclancherii</i>	1941 F 5 8		1941 F 5 8,11			
<i>Pycnonotus cafer</i>	1966 S 3 11					
<i>Pycnonotus jocosus</i>	1965 S 3 11					
<i>Rhipidura leucophrys</i>	1926 F 2 1,8					
<i>Serinus leucopygius</i>	1965 F 3 11					
<i>Serinus mozambicus</i>	1964 S 3 11			1977 S 1 11		
<i>Sicalis flaveola</i>	1965 S 3 11			1966 S 3 11		
<i>Sturnella loyca</i>		1931 F 1 1				
<i>Sturnella neglecta</i>	1931 F 2 8	1931 S 1 1,11	1934 F 3 3			
<i>Tiaris olivacea</i>	1974 S 3 11					
<i>Uraeginthus angolensis</i>	1965 F 3 7					
<i>Uraeginthus bengalus</i>	1965 F 3 11			1973 S 3 11		
<i>Uraeginthus cyanocephala</i>	1969 F 3 12					
<i>Vidua macroura</i>	1962 F 3 12					
<i>Zosterops japonicus</i>	1929 S 2,5 1,11	1929 S 5 1,11	1938 S 3 8	1937 S 5 8	1938 S 3 8	1938 S 3 8

APPENDIX 4. INTRODUCED GAME BIRDS ON THE SIX MAIN HAWAIIAN ISLANDS (SEE APPENDIX 2 FOR EXPLANATION OF TERMS)

Species	O'ahu	Kaua'i	Mau	Hawai'i	Moloka'i	Lāna'i
<i>Crax rubra</i>				1928 F 2 1		
<i>Penelope purpurascens</i>				1928 F 2 1		
<i>Ortalis cinereiceps</i>				1928 F 2 1		
<i>Numida meleagris</i>	1928 F 1 1,10	1874 F 1 1,10	1928 F 1 1,10	1928 F 1 1,10	1908 F 1 1,10	1914 F 1 1,10
<i>Colinus virginianus</i>	1906 F 2 1,4	1906 F 2 1,4	1906 F 2 1,4	1906 F 1 4	1906 F 2 1,4	1906 F 2 1,4
<i>Oreortyx pictus</i>		1929 F 2 1		1929 F 2 1		
<i>Callipepla squamata</i>				1961 F 2 6		
<i>Callipepla californica</i>	1855 F 3 1,10	1855 S 3 1,10	1855 S 3 1,10	1855 S 3 1,10	1855 S 3 1,10	1855 S 3 1,10
<i>Callipepla gambelii</i>	1958 F 2 4,10	1958 F 2 4,10	1958 F 2 4,10	1958 S 1,2 6,10		1958 S 2 4,10
<i>Callipepla douglasii</i>				1959 F 1 6		
<i>Tympanuchus cupido</i>	1895 ^a F 1 1	1933 ^{a,b} F 1 1				
<i>Tympanuchus phasianellus</i>				1932 F 2 1		
<i>Cyrtonyx montezumae</i>				1961 F 1 6		
<i>Ammoperdix griseogularis</i>				1959 F 1 6		
<i>Alectoris chukar</i>	1923 F 2 1,10	1957 S 2 4,10	1957 S 2 4,10	1949 S 2 5,10	1923 S 3 4,10	1923 S 3 4,10
<i>Alectoris barbara</i>			1961 F 2 4,10	1959 F 1,2 4,6	1961 F 2 4,10	1959 F 2 4,10
<i>Francolinus francolinus</i>		1959 S 2 9	1959 S 2 9	1959 S 1,2 6	1959 S 2 9	
<i>Francolinus pintadeanus</i>				1962 F 1 6		
<i>Francolinus pondicerianus</i>	1958 S 2 4,5,10	1958 S 2 4,5,10	1958 S 2 4,5,10	1959 S 1 6	1958 S 2 4,5,10	1958 S 2 5
<i>Francolinus adsperus</i>				1965 F 1 6		
<i>Francolinus icterorhynchus</i>				1961 F 1 6		

APPENDIX 4. CONTINUED.

Species	O'ahu	Kaua'i	Maui	Hawai'i	Moloka'i	Lāna'i
<i>Francolinus clappertoni</i>				1961 F 1 6		
<i>Francolinus erckelii</i>	1957 S 2 5,10	1957 S 2 5,10	1957 S 2 5,10	1958 S 1,2 6	1957 S 2 5,10	1957 S 2 5,10
<i>Francolinus leucosepus</i>				1959 F 2 6		
<i>Perdix perdix</i>		1910 F 1 1	1926 F 1 1	1929 F 2 1		
<i>Coturnix chinensis</i>	1922 F 2 1	1910 F 1 1	1922 F 2 1	1922 F 2 1	1922 F 2 1	
<i>Coturnix pectoralis</i>			1922 F 2 3			1922 F 2 3
<i>Coturnix japonica</i>	1921 F 3 2,10	1921 S 3 2,10	1921 S 2 1,10	1921 S 3 2,10	1921 S 3 2,10	1921 S 2 1,10
<i>Rollulus rouloul</i>	1924 F 2 1					
<i>Bambusicola thoracica</i>			1959 F 2 4,5,10	1961 F 1 6		
<i>Lophura leucomelanos</i>				1962 S 1 6,10		
<i>Lophura nycthemera</i>	1932 F 2 1	1870 F 1 1				
<i>Gallus gallus</i>	PH ^c S 4 2,10	PH S 4 2,10	PH F 4 2,10	PH F 4 2,10	PH F 4 2,10	PH F 4 2,10
<i>Gallus sonnerati</i>				1962 F 1 6		
<i>Phasianus colchicus</i>	1865 S 1 1,10	1865 S 1 1,10	1865 S 1 1,10	1865 S 1 1,10	1865 S 1 1,10	1865 S 1 1,10
<i>Syrnaticus reevesii</i>	1960 F 2 4,10	1960 F 2 4,10	1960 F 2 4,10	1959 F 1 6	1960 F 2 4,10	1960 F 2 4,10
<i>Syrnaticus soemmerringii</i>	1907 F 2 1	1907 F 2 1	1907 F 2 1			
<i>Chrysolophus pictus</i>	1932 F 2 1	1870 F 1 1				
<i>Chrysolophus amherstiae</i>	1932 F 2 1					
<i>Pavo cristatus</i>	1860 S 1 1,10	1860 F 1 1,10	1860 S 1 1,10	1928 S 1 1,10	1860 F 1 1,10	1860 F 1 1,10
<i>Meleagris gallopavo</i>	1815 F 1 1,10	1815 F 1 1,10	1815 S 1 1,10	1815 S 1 1,10	1815 S 1 1,14	1815 S 1 1,10

^a May have been *Tympanuchus phasianellus* (Caum 1933).^b Based on "indefinite reports" (Caum 1933).^c Prehistoric introduction.

APPENDIX 5. INTRODUCED COLUMBIDS ON SIX MAIN HAWAIIAN ISLANDS (SEE APPENDIX 2 FOR EXPLANATION OF TERMS)

Species	O'ahu	Kaua'i	Moloka'i	Hawai'i	Moloka'i	Lāna'i
<i>Caloenas nicobarica</i>		1928 F 2 1	1922 F 2 1			
<i>Chalcophaps indica</i>	1924 F 2 1					
<i>Columba livia</i>	1796 S 3 1	1796 S 3 1	1796 S 3 1	1796 S 3 1	1796 S 3 1	1796 S 3 1
<i>Gallicolumba luzonica</i>		1929 F 1 1				
<i>Geopelia cuneata</i>	1928 F 2 1		1929 F 2 1			
<i>Geopelia humeralis</i>	1992 F 2 1	1922 F 1 1	1928 F 2 1			
<i>Geopelia striata</i>	1922 S 2 1	1922 S 2 1	1922 S 2 1	1922 S 2 1	1922 S 2 1	1922 S 2 1
<i>Geophaps lophotes</i>	1922 F 2 1			1922 F 2 1	1922 F 2 1	1922 F 2 1
<i>Geophaps plumifera</i>			1922 F 2 1			1922 F 2 1
<i>Geophaps smithii</i>			1992 F 2 1			1922 F 2 1
<i>Geotrygon montana</i>			1933 F 3 3			
<i>Leptotila verreauxi</i>			1933 F 3 3			
<i>Leucosarcia melanoleuca</i>			1922 F 2 1			1922 F 2 1
<i>Phaps chalcoptera</i>	1922 F 2 1					
<i>Streptopelia chinensis</i>	1879 S 3 1	1890 S 3 8	1890 S 3 8	1890 S 3 8	1890 S 3 8	1890 S 3 8
<i>Streptopelia decaocto</i>	1928 F 1 1	1920 F 1 1		1928 F 2 1		
<i>Zenaida asiatica</i>				1961 F 2 6		
<i>Zenaida macroura</i>				1962 S 1 9		