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Sexual selection and the fate of introduced pigeons and doves (Aves: Columbidae)

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ABSTRACT

Background: Recent research has indicated that a response to sexual selection as manifested by plumage dichromatism predicts the introduction success of passeriform birds but not that of galliform birds.

Question: Does the response to sexual selection predict patterns of introduction success in species of the family Columbidae?

Data description: We compiled lists of introduced columbids using published references for ten island systems. We examined specimens of introduced columbid species housed at the Museum of Natural History in Tring, England. We measured wing lengths of individuals of each species and we categorized species as being either plumage dichromatic or monochromatic. We also compared success with native range size and wing length.

Conclusions: We found no difference in introduction success rates of monochromatic versus dichromatic columbids. Moreover, we found no significant differences in wing lengths between the two groups or in sizes of geographic ranges.

Keywords: Columbidae, introduced birds, sexual selection

INTRODUCTION

Sexual selection has favoured exaggerated development of male traits used in epigamic displays and agonistic contests (Andersson, 1994). Such exaggerated traits have long been argued to impair male survival (Darwin, 1871; Wallace, 1889; Fisher, 1958) and depress population fitness (Lande, 1987; Kirkpatrick and Barton, 1997). Allocation of energy to sexually selected structures and mate acquisition can result in poor male condition (Maney *et al.*, 2008) and reduce energy allocated to coping with harsh or changing environments (McLain, 1993; McLain and Vives, 1998; but see Whitlock, 2000; Rankin and Arnqvist, 2008). Thus, some theoretical models indicate that sexual selection can increase the risk of extinction (Tanaka, 1996; Gavrilets *et al.*, 2001; Arnqvist and Rowe, 2002; Kokko and Brooks, 2003).

In birds, male-brighter sexual dichromatism may reflect an evolutionary response to strong sexual selection pressures (Scott and Clutton-Brock, 1989; Møller and Birkhead, 1994; Dunn *et al.*,

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2001; Badyaev and Hill, 2003) that could reduce mean fitness. For instance, brightly coloured males suffer higher rates of mortality, which then increases female mortality during the breeding system (Promislow *et al.*, 1992, 1994; Møller and de Lope, 1994; Delhey and Kempenaers, 2006). Moreover, the cost of bright colours (e.g. McGraw *et al.*, 2002; Andersson *et al.*, 2007) reduces the energy available for paternal care, selecting for reduced clutch size (Badyaev, 1997; Bókony and Liker, 2005). Such costs may account for the greater propensity for local extinction of sexually dichromatic species (Doherty *et al.*, 2003; see also Morrow *et al.*, 2003).

Costs associated with response to sexual selection fostered the prediction that among bird species introduced into new habitats outside their native ranges, dichromatic species would be more vulnerable to extinction and, therefore, less likely to become established. Among 78 bird species introduced to New Zealand (Veltman *et al.*, 1996), dichromatic species have been more likely to fail (Sorci *et al.*, 1998). Similarly, dichromatism is associated with introduction failure among more than 130 species of passeriform birds introduced onto oceanic islands (McLain *et al.*, 1995, 1999). However, among galliforms introduced onto the same islands, the association did not hold (Donze *et al.*, 2004). Thus, other, intrinsic, characteristics of taxa may affect their risk of extinction (Wedekind, 2002; Blackburn and Cassey, 2004; Thomas *et al.*, 2006). It now becomes important to determine if other groups of introduced birds will provide general support for a negative effect of sexual selection on population survival.

Although species from as many as 20 taxonomic orders of birds have been introduced one place or another around the world (Long, 1981; Lever, 1987), the vast majority are from five orders: Passeriformes ($n = 196$), Galliformes ($n = 74$), Psittaciformes ($n = 51$), Anseriformes ($n = 29$), and Columbiformes ($n = 32$). Other taxonomic orders are represented by far fewer species. Thus, possibilities for testing hypotheses are limited.

Each of the four non-passeriform orders listed above poses unique problems in studying the dynamics of species introductions. The Galliformes includes a number of species that were released principally for sport hunting. The Chinese Bamboo Partridge (*Bambusicola thoracica*) may have failed to become established on the islands of Maui and Hawaii because of hunting (Moulton *et al.*, 2001). Moreover, individuals of several species of francolins (*Francolinus* spp.) introduced in the Hawaiian Islands may have suffered from reduced genetic variability (e.g. Lockwood *et al.*, 2007), having been raised on game farms in the USA. The combined effects of recreational hunting and inbreeding depression may have doomed some, but not all, introductions of francolins (Berger, 1981; Moulton *et al.*, 2001).

Introductions from the order Psittaciformes (see Long, 1981) include many species that were released in very small numbers, principally as cage escapes. Many others were released just beyond the boundaries of their native range, making it impossible to determine if individuals present after an introduction event were survivors or extra-limital sightings.

There are two central problems with ascribing failure to anseriform introductions. First, many of the introduced species were capable of flying home after introduction. Second, some species (e.g. Mallards, *Anas platyrhynchos*; Ruddy Ducks, *Oxyura jamaicensis*) appear to inter-breed readily with native species (e.g. *Anas superciliosa*, *Oxyura leucocephala*) (see Williams, 1969; Gillespie, 1985; Muñoz-Fuentes *et al.*, 2007).

The order Columbiformes offers the most potential, outside the passeriforms and galliforms, to determine if response to sexual selection, as manifested in plumage dichromatism, affects introduction success. This is because a number of columbids have been introduced onto most of the same islands as the passeriforms (McLain *et al.*, 1999) and galliforms (Donze *et al.*, 2004) that have contrasting associations between introduction success and dichromatism. The islands or island systems onto which columbids have been introduced represent eight of the 13 localities receiving more than 20 species (see Long, 1981). In the current study, we tested the notion that male-brighter dichromatism in columbids is associated with reduced introduction success.

METHODS AND MATERIALS

Study species

We compiled lists of columbids introduced onto ten island systems: Hawaii, Maui, Oahu, Kauai, Tahiti, Mauritius, La Reunion, Saint Helena, Bermuda, and New Zealand. Only Maui, with five introductions, was not included in the studies of McLain *et al.* (1999) and Donze *et al.* (2004). We include Maui here because five species were released only to this island (see Table 1).

To compile our list, we started with Long (1981) and then refined our list using island-specific references. We used: (1) Moulton *et al.* (2001) and references therein for the Hawaiian Islands, (2) Diamond (1987) and Barre *et al.* (1996) for Mauritius and La Reunion, (3) Rowlands *et al.* (1998) for Saint Helena, (3) Thomson (1922), Heather and Robertson (1997), and Falla *et al.* (1978) for New Zealand, (4) Thibault and Rives (1975) for Tahiti, and (5) Wingate (1973) for Bermuda.

Of the 33 species included by Long (1981) (see Table 1), 23 (72%) have been introduced to one or more of the 10 islands included in this study. As noted by Long (1981), some uncertainty surrounds several of the possible introductions. Therefore, we excluded Rock Doves (*Columba livia*), as they commonly occur in a semi-wild state on some of the Hawaiian Islands, and likely elsewhere too, and because it is not possible to assess accurately the species' plumage status. Hutton (1871) similarly listed this species as having been introduced to New Zealand but not having 'gone wild'. We assume that this could have been the case on other islands as well.

Thomson (1922) lists 16 species of the order Columbiformes as having been introduced to New Zealand. However, he was unable to identify five species, providing only common names ('New Caledonia Green Dove', 'Solomon Island Pigeon', 'Indian Pigeon', 'Java Dove', and 'Moreton Bay Dove'). For two other species, Thomson suggested a scientific name. Following Hutton (1871), Thomson (1922) reckoned that the 'Queensland Dove' could have been *Geopelia cuneata*, and the 'Indian Dove' might have been *Turtur ferrago*. It is unclear whether he was entirely convinced by this latter identification, as he put a question mark in parentheses after the name. According to Peters (1937), *Turtur ferrago* is a synonym for *Streptopelia orientalis*, but, according to Gibbs *et al.* (2001), several species of the genus *Streptopelia* occur in India and so might be considered 'Indian Doves', including *S. chinensis*, *S. tranquebarica*, *S. decaocto*, and *S. senegalensis*. With this in mind, we excluded *S. orientalis* from our analyses. Thomson (1922) also listed two species (*Phaps histrionica* and *Geophaps scripta*) for which Long (1981) did not provide species' accounts. According to Thomson (1922), just a single pair of individuals of the species *P. histrionica* was introduced to New Zealand (by the Auckland Society). Similarly, Thomson (1922) reported that *G. scripta* was represented by two pairs of individuals 'received' by the Canterbury Society. Long (1981) reckoned that *P. histrionica* might not have actually been released into the wild, and Thomson (1922) suggests the same possibility for *G. scripta*. Thus we excluded these two

Table 1. Plumage status and distributions of introduced columbiform species on ten islands

Species	CL	SS	H	O	K	M	T	Mr	Re	SH	Be	NZ
Zenaida macroura	A	2	1	1							1	
Zenaida asiatica	A	1	0									
Streptopelia picturata	A	1						1	1	0		
Streptopelia decaocto	A	1	0	0	0							
Streptopelia roseogrisea	A	1										1
Streptopelia bitorquata	A	1										0
Streptopelia chinensis	A	1	1	1	1	1		1				1
Geopelia striata	C	1	1	1	1	1	1	1	1	1		
Geopelia cuneata	C	2		0				0				0
Geopelia humeralis	C	1		0	0							
Columbina passerina	B	2									1	
Oena capensis	C	2										0
Chalcophaps indica	C	2		0								
Phaps chalcoptera	C	2		0								0
Ocyphaps lophotes	C^{b}	1	0	0								0
Geophaps smithii	C	1				0						
Geophaps plumifera	C	1				0						
Leptotila verreauxi	A	1				0						
Geotrygon montana	A	2				0						
Gallicolumba luzonica	C	2			0							
Leucosarcia melanoleuca	C	1				0						0
Starnoenas cyanocephala^{a}	A^{b}	2	*	*	*	*						
Caloenas nicobarica	C	1			0	0						
Total			6	9	6	8	1	4	2	2	2	8

Note: Nomenclature follows Dickinson (2003). CL indicates the major clade as identified by Pereira *et al.* (2007); SS indicates plumage state: 1 = monochromatic, 2 = dichromatic. Distributional data: '1' indicates successful introduction, '0' indicates a failed introduction. Islands listed are: H = Hawaii; O = Oahu; K = Kauai; M = Maui; T = Tahiti; Mr = Mauritius; Re = La Reunion; SH = Saint Helena; Be = Bermuda; NZ = New Zealand.

[a] It is unknown which of the Hawaiian islands *Starnoenas cyanocephala* was released on, but we assume it was released and failed to become established. [b] Likely clade membership of genera that were not listed by Pereira *et al.* (2007).

species from our analyses. Finally, we follow Long (1981), who presumed that the 'Java Dove' of Thomson (1922) was *Streptopelia bitorquata*.

Starnoenas cyanocephala was apparently introduced to at least one island in the Hawaiian archipelago (Caum, 1933). However, we are unable to discern how many other islands this species might have been released on, as the references are too vague (e.g. Caum, 1933). Thus, this species is not included in some analyses below.

In addition to *Columba livia*, *Streptopelia orientalis*, and *Geophaps scripta*, we excluded nine species listed by Long (1981) because they were not released on any of the islands that are the focus of this study. These species are *Ducula rosacea*, *Columba palumbus*, *Streptopelia turtur*, *Streptopelia tranquebarica*, *Streptopelia semitorquata*, *Streptopelia senegalensis*, *Scardefella inca*, *Phaps histrionica*, and *Leptotila jamaicensis*.

Plumage type, body size, and range size

To classify species as either monochromatic or dichromatic we (M.P.M. and L.E.M.) examined specimens at the Natural History Museum in Tring, England. We also measured the lengths of un-flattened wings of 2–4 specimens of each species. Range sizes were estimated from the range maps in the *Handbook of Birds of the World* (del Hoyo *et al.*, 1997), as provided by W. Jetz (personal communication).

As noted by Harvey and Pagel (1991), a potential problem of independence of observations may arise in analyses such as this due to phylogenetic constraint. Briefly, characteristics such as plumage status and probability of successful introduction might be constrained at the generic or at some other level, such as the major clade level. If this were the case, then treating species within multi-species genera or clades as independent observations might lead to biased results. Initially, we considered all the species to represent independent observations. Then we conducted the analysis at the generic level, by calculating the average probability of introduction success among all dichromatic and all monochromatic species within each genus. As noted by McLain *et al.* (1999), this procedure treats all the dichromatic (and all monochromatic) species within a genus as having arisen from a common dichromatic (or monochromatic) ancestor. Recently, Johnson and Clayton (2000) and Pereira *et al.* (2007) conducted phylogenetic analyses of the Columbiformes. The two studies reported similar but not identical results. We used Pereira *et al.* (2007) because these authors sampled 48 species from 33 of 41 Columbiform genera as opposed to Johnson and Clayton (2000), who sequenced 32 species. Both studies grouped genera based on mitochondrial and nuclear DNA sequences. As a further attempt to compensate for non-independence due to phylogenetic constraints, we compared average probabilities of introduction success between monochromatic and dichromatic species at the major clade level.

RESULTS

Distribution of introductions

Eleven of the 23 columbid species (48%) were released onto a single island, four were released onto two islands, five onto three islands, one (*Streptopelia chinensis*) onto six islands, and one (*Geopelia striata*) onto eight islands. The mean number of islands onto which a species was released was 2.18 (S.D. = 1.79; $n = 22$). Monochromatic (2.50 islands per species) and dichromatic species (1.625 islands per species) did not differ significantly in the number of islands onto which they were introduced (Kruskal-Wallis test, approximate $\chi^2_1 = 0.85$, $P = 0.36$), although only 14 of 49 introductions were of a dichromatic species (ascribing a single introduction to *Starnoenas cyanocephala*).

The number of species introduced onto an island ranged from one to nine (or ten) (mean = 4.80, S.D. = 2.97). Oahu had the greatest number of introductions, nine species – or ten if *S. cyanocephala* was released there. Eight species were released onto New Zealand and Maui. Only one species (*Geopelia striata*) was released on Tahiti (Table 1).

Success of introductions

Only six of 23 species of columbids were successfully introduced onto at least one of the islands (Table 1). This success rate is significantly lower than for passeriforms introduced onto the same islands [64 of 132 species successfully introduced onto at least one island (McLain *et al.*, 1999); $\chi^2_1 = 3.97$, $P = 0.05$].

The columbid species exhibited a pronounced all-or-none pattern (Simberloff and Boecklen, 1991), with 10 of 11 species (excluding *Starnoenas cyanocephala*) always failing or always succeeding when introduced to two or more islands. The exception to the pattern, *Streptopelia picturata*, succeeded on two islands but failed on Saint Helena, where, perhaps, as few as two individuals were released in the 1650s (Rowlands *et al.*, 1998). Among genera with at least two species being introduced, the all-or-none pattern breaks down, as three of the four genera (*Streptopelia*, *Geopelia*, and *Zenaida*) had mixed outcomes. The lone exception to this was the genus *Geophaps*, which had two species that failed twice. Two of the three major clades identified by Pereira *et al.* (2007) in our study were represented by more than one species (see Table 1). Both of these clades had successful and unsuccessful species. So the all-or-none pattern seen at the species level vanishes at higher taxonomic levels.

Nine of 23 study species (39%) were dichromatic (Table 1). Of the six species that succeeded on at least one island, two were dichromatic. These were *Zenaida macroura* and *Columbina passerina*. The success rate (successful introductions/total introductions) of the nine dichromatic species was not significantly different from that of the 14 monochromatic species (Kruskal-Wallis test, approximate $\chi^2_1 = 0.06$, $P = 0.81$). If *Caloenas nicobarica*, a species that exhibits bright monomorphism (Kimball and Ligon, 1999) – that is, bright plumage in both sexes – is included with the dichromatic species, there is still no significant association between plumage and introduction success (Kruskal-Wallis test, approximate $\chi^2_1 = 0.24$, $P = 0.63$).

Islands with more introduced columbid species had lower rates of introduction success (Spearman rho = –0.87, $P = 0.001$). The number of dichromatic species introduced to islands was not significantly correlated with island success rate (Spearman rho = –0.41, $P = 0.24$), but it was for monochromatic species (Spearman rho = –0.93, $P = 0.001$). Moreover, excluding the dichromatic *Starnoenas cyanocephala*, for reasons noted above, across the islands the introduction success rates differed significantly between dichromatic species with 13 introductions and monochromatic species with 35 introductions (Kruskal-Wallis test, approximate $\chi^2_1 = 5.1$, $P = 0.02$).

Phylogenetic constraint

We attempted to compensate for possible non-independence by conducting our analysis on average introduction success within genera and major clades for dichromatic and monochromatic species. There were four multi-species genera in our study: *Streptopelia* (five species, all monochromatic), *Geophaps* (two species, both monochromatic), *Zenaida* (two species, one monochromatic and one dichromatic), *and Geopelia* (three species, one dichromatic and two monochromatic). Using the average introduction success within genera reduced the original 23 observations to 16. Here the dichromatic group did not differ significantly from the monochromatic group (Kruskal-Wallis test, approximate $\chi^2_1 = 0.08$, $P = 0.78$).

As noted above, Pereira *et al.* (2007) identified three major clades in the order Columbiformes. The genera in our study fall into these three clades as follows: Clade A – *Streptopelia*, *Leptotila*, *Zenaida*, and *Geotrygon*; Clade B – *Columbina*; Clade C – *Oena*, *Chalcophaps*, *Caloenas*, *Phaps*, *Geophaps*, *Geopelia*, *Leucosarcia*, and *Gallicolumba*. Current taxonomic treatments such as Dickinson (2003) list the one species of *Geophaps* (Clade C) that Pereira *et al.* (2007) sampled as actually belonging to the genus *Ocyphaps*. Thus we included *Ocyphaps* in Clade C. Similarly, we included the genus *Starnoenas* in Clade A, even though Pereira *et al.* (2007) did not sequence this species. Our decision follows Goodwin (1983) and also Gibbs *et al.* (2001), both of whom asserted that *Starnoenas* was most closely related to *Geotrygon*, which is in Clade A. Mahler *et al.* (2003) made a similar judgement.

In Clade A, seven species were monochromatic and had an average probability of introduction success of 0.38, whereas five species were dichromatic with an average probability of introduction success of 0.33. In Clade C, the seven monochromatic species had an average probability of introduction success of 0.14, and the five dichromatic species had an average probability of introduction success of 0.00. Clade B had just a single dichromatic species (*Columbina passerina*). We compared the average probabilities of introduction success for monochromatic and dichromatic species in Clades A and C and found no significant difference (Kruskal-Wallis test, approximate $\chi^2_1 = 0.60$, $P = 0.44$).

Effects of body and range size

Overall, un-flattened wing length was not significantly associated with introduction success (Spearman rho = –0.06, $P = 0.78$; $n = 23$). Wing length did not differ significantly between monochromatic (mean = 155.0 mm; $n = 14$) and dichromatic (mean = 131.4 mm; $n = 9$) species (Kruskal-Wallis test, approximate $\chi^2_1 = 2.48$, $P = 0.12$) (Table 2).

The size of the native range of introduced columbid species varied by more than 166-fold, with *Streptopelia decaocto* having the largest and *Starnoenas cyanocephala* the smallest range size (Table 3). Overall, the size (Table 3) of the native range was not significantly correlated with introduction success rate (Spearman rho = 0.19, $P = 0.38$). Rank in range size was not significantly different between dichromatic and monochromatic species (Kruskal-Wallis test, approximate $\chi^2_1 = 0.89$, $P = 0.35$).

DISCUSSION

Among introduced columbids, dimorphic species have been no more likely to fail than monomorphic species. Moreover, this result holds regardless of the level at which we conducted our comparisons – among species, genera or major clades. This suggests that the strength of sexual selection, assumed to be stronger for male-brighter dichromatic species (reviewed in Badyaev and Hill, 2003), has no impact on the probability of local extinction when these birds are introduced into new habitats. Yet, a greater response to sexual selection has been argued to reduce introduction success in passeriforms (McLain *et al.*, 1995, 1999) and other birds (Sorci *et al.*, 1998), suggesting that male-brighter species are especially vulnerable to local extinction (Doherty *et al.*, 2003). Additionally, changes in habitat are associated with reduced dichromatism (Schluter and Price, 1993; Barraclough *et al.*, 1995; Price, 1998; Cuervo and Møller, 1999; Badyaev and Snell-Rood, 2003), suggesting that new natural selection pressures reduce allocation to sexually selected characters (McLain, 1993; McLain and Vives, 1998). However, plumage dichromatism is not associated with lower rates of successful introduction in all groups of birds (Donze *et al.*, 2004), suggesting that response to sexual selection need not impair mean fitness (e.g. Morrow and Pitcher, 2003; Thomas *et al.*, 2006; Candolin and Heuschele, 2008).

The lack of an association between plumage type and introduction success in the current study is a consequence of the low rate of successful introductions in columbids (26% of species with ≥1 success). The greater rate of failure in columbids versus passeriforms

Table 2. List of sample sizes and wing lengths of introduced columbids

		Wing lengths			
Species	*n*	mean	S.D.	max	min
Zenaida macroura	4	143.5	6.61	135	151
Zenaida asiatica	4	154.7	4.57	148	158
Streptopelia picturata	4	166.2	4.35	162	172
Streptopelia decaocto	4	161.7	1.26	160	163
Streptopelia roseogrisea	2	163.0	7.07	158	168
Streptopelia bitorquata	4	161.5	3.87	156	165
Streptopelia chinensis	4	151.0	5.29	146	158
Geopelia striata	4	94.2	4.57	89	99
Geopelia cuneata	4	89.0	3.65	85	93
Geopelia humeralis	4	138.2	3.30	136	143
Columbina passerina	4	85.7	2.5	83	89
Oena capensis	4	104.2	3.20	102	109
Chalcophaps indica	4	143.0	5.35	138	149
Phaps chalcoptera	4	192.7	5.56	187	198
Ocyphaps lophotes	4	161.0	5.03	154	166
Geophaps smithii	4	131.5	2.65	128	134
Geophaps plumifera	4	107.2	3.86	103	111
Leptotila verreauxi	4	134.5	3.70	132	140
Geotrygon montana	4	141.0	4.83	137	148
Gallicolumba luzonica	4	141.0	4.69	136	147
Leucosarcia melanoleuca	3	195.7	10.02	188	207
Starnoenas cyanocephala	2	142.5	2.12	141	144
Caloenas nicobarica	4	250.2	12.84	232	261

introduced to the same islands or island systems may reflect differences in life history and natural history or, perhaps, that most introductions of columbids occurred on islands where their success rate was low. In either case, the low rate of introduction success of monochromatic columbids (23.5%), coupled with the low rate of dichromatism among introduced columbids (26.1%), is sufficient to ensure that no rate of failure among dichromatic columbids could produce a significant difference. In contrast, among passeriforms introduced onto the same islands, the rate of dichromatism was nearly twice as high (50.0%), as was the proportion of monochromatic species successfully introduced to at least one island (57.6%) (see McLain *et al.*, 1999).

The contrasting associations between plumage type and introduction success among passeriforms (McLain *et al.*, 1999), galliforms (Donze *et al.*, 2004), and columbids suggests the prudence of analysing groups separately, if sample sizes permit, so that a pattern characteristic to one group is not inferred to apply across all groups. The contrasting results between columbids and passeriforms may reflect the distribution of plumage types as well as differences in natural history. In fact, differences in the frequency of dichromatism may reflect natural history differences.

Plumage colour is produced by carotenoid pigments, melanin pigments or feather microstructure (Hill and McGraw, 2004). Carotenoid-based yellow, red, and green colours, rarely

Table 3. Zoogeographic regions, native range sizes (km^2), and probability of introduction success

Species	Zoogeographic region	Native range size	Probability of introduction success
Zenaida macroura	2	10,662,967	1
Zenaida asiatica	1	2,143,801	0
Streptopelia picturata	4	576,851	0.67
Streptopelia decaocto	6	16,964,852	0
Streptopelia roseogrisea	4	5,049,352	1
Streptopelia bitorquata	5	482,006	0
Streptopelia chinensis	5	8,575,190	1
Geopelia striata	3	772,816	1
Geopelia cuneata	3	5,456,331	0
Geopelia humeralis	3	2,350,962	0
Columbina passerina	1	12,899,190	1
Oena capensis	4	10,202,951	0
Chalcophaps indica	5	7,598,154	0
Phaps chalcoptera	3	4,681,341	0
Ocyphaps lophotes	3	5,827,478	0
Geophaps smithii	3	149,051	0
Geophaps plumifera	3	1,803,608	0
Leptotila verreauxi	1	15,447,429	0
Geotrygon montana	1	15,058,570	0
Gallicolumba luzonica	5	102,957	0
Leucosarcia melanoleuca	3	577,411	0
Caloenas nicobarica	5	436,096	0
Starnoenas cyanocephala	1	101,696	0

Note: Zoogeographic regions are as follows: 1 = Neotropical; 2 = Nearctic; 3 = Australasia; 4 = Ethiopian; 5 = Oriental; 6 = Palearctic).

utilized by columbids (Mahler *et al.*, 2003), are most often associated with sexual dichromatism (Hill, 1996; Badyaev and Hill, 2000) and female choice in passeriforms (e.g. Dunn *et al.*, 2001; Hill, 2006; Pryke and Griffith, 2007). Birds obtain carotenoids from their diet (Siefferman and Hill 2005), rendering carotenoid pigmentation sensitive to food deprivation. Consequently, in dichromatic species, males in better condition express more intense coloration (e.g. Hill, 1990, 1996; Rosen and Tarvin, 2006; Andersson *et al.*, 2007; Siefferman *et al.*, 2007). Seveal authors have argued that the connection between male condition and coloration favours female choice for bright plumage (Hill, 1996; Pryke and Griffith, 2007) because choosy females obtain mates that survive better (Jennions *et al.*, 2001; Delhey and Kempenaers 2006), offer more paternal care (Siefferman and Hill, 2005; Balenger *et al.*, 2007), and may produce offspring of superior genetic constitution (Hamilton and Zuk, 1982; Møller and Alatalo, 1999; Foerster *et al.*, 2003). However, Møller and Jennions (2001) conducted a meta-analysis of several species from various taxa and concluded that the expression of male secondary sexual characters might not provide a reliable metric of male food provisioning to offspring. Moreover, bright colours that attract predators (Badyaev, 1997; Götmark *et al.*, 1997; Post and Götmark, 2006) and that are costly to acquire (McGraw *et al.*, 2002; Andersson *et al.*, 2007) may render small, introduced populations especially vulnerable.

In passerines, granivores display carotenoid-based dichromatism (Badyaev and Hill, 2000).

Among columbids, it is frugivores that utilize carotenoid pigmentation (Mahler *et al.*, 2003). Only two species of introduced columbid, *Gallicolumba luzonica* and *Caloenas nicobarica*, are largely frugivorous (Mahler *et al.*, 2003). Thus, in introduced columbids, the coloration of males may not provide females with information on male quality, reducing the strength of sexual selection for bright plumage. Perhaps as a consequence, plumage tends to be largely reddish, brown, grey or bluish in colour. Moreover, the costs associated with bright carotenoid-based plumage that are borne by passeriforms could be largely absent in columbids, which are typified by a dull dichromatism. Thus, it is not surprising that the introduction success of monochromatic and dichromatic columbids does not vary, as it does for passeriforms (McLain *et al.*, 1999).

Bright monochromatism (see Kimball and Ligon, 1999; Wiens, 2001) may occur because the sexes share most of their genes in common and results in female phenotypes that are not optimal with respect to survival (Lande, 1987). Such intra-locus sexual conflict (Chippendale *et al.*, 2001) is resolved when sexual dimorphism evolves, permitting each sex to evolve independently towards its own optimum phenotype (Bonduriansky and Rowe, 2005). Among introduced columbids, three species exhibit bright monomorphism, the two frugivores and *Starnoenas cyanocephala*, which includes some fruit in its diet (Baptista *et al.*, 1997). Thus, it is likely that carotenoids derived from fruit account for the bright colours (Mahler *et al.*, 2003). None of the bright monomorphic columbids was successfully introduced onto an island.

Among introduced passeriforms, neither the number of nest-attending parents nor clutch size had a significant effect (McLain *et al.*, 1999). However, the small clutch size of doves, typically two (Campbell, 1974; Baptista *et al.*, 1997; Gibbs *et al.*, 2001), is much less than that of most introduced passeriforms, where 90% of species produce larger clutches (McLain *et al.*, 1999), and may contribute to the relatively low rate of introduction success among columbids. Also, among introduced passeriforms, species eating seeds but not fruit, which is also characteristic of introduced columbids (Mahler *et al.*, 2003), had lower success rates (McLain *et al.*, 1999). Eating seeds on the ground but not fruit in trees may result in greater exposure to predators, which could render populations more susceptible to extinction. Greater exposure to predators may also explain the lower success rates of ground-nesting introduced passeriforms (McLain *et al.*, 1999). However, nest location is not likely to account for the relatively low rate of successful introductions among introduced columbids because, with two possible exceptions (*Geophaps smithii* and *Starnoenas cyanocephala*), columbids nest in shrubs or trees (Campbell, 1974; Baptista *et al.*, 1997; Gibbs *et al.*, 2001).

Ten of 11 columbid species introduced onto more than one island were either always successfully introduced or always unsuccessfully introduced. These 11 species were introduced a total of 35 times, with 14 of 17 successful introductions belonging to just two monomorphic species, *Streptopelia chinensis* (6 of 6 introductions successful) and *Geopelia striata* (8 of 8 introductions successful). The dichromatic species, *Zenaida macroura*, accounted for the other multiple successes. The all-or-none pattern (Simberloff and Boecklen, 1991) observed for columbids, which passeriforms exhibit to a reduced degree (McLain *et al.*, 1999), suggests, given the low rate of success for columbids overall, that intrinsic factors not under study, such as competitive ability (Moulton, 1993), can strongly influence success. Consequently, the effect of factors under study (i.e. plumage type) may be obscured. Interestingly, as noted previously, the all-or-none pattern does not extend to genera or to clades within the columbids. Thus, the species level appears to be an appropriate level of analysis.

A final concern deals with variation in introduction effort. Several authors have argued that introduction effort is an important factor in influencing introduction success (Veltman *et al.*, 1996; Duncan, 1997; Green, 1997; Cassey *et al.*, 2004; Lockwood *et al.*, 2005). Unfortunately, we are unable to test this idea, as the propagule sizes for the all species in this study are unknown. However, there is evidence for the Hawaiian Islands (e.g. Caum, 1933) and New Zealand (e.g. Thomson, 1922) that some species were introduced in small numbers. However, we have no reason to assume that successfully introduced species were introduced in greater numbers than unsuccessful species.

McLain *et al.* (1999) observed a significant difference in probability of introduction success between dichromatic and monochromatic passeriform species. Does the present result involving just columbiform species in any way invalidate the notion that different orders of birds should be treated separately in analyses of introduction outcomes? The question boils down to deciding if the significance levels of the two studies are significantly different from each other. Thus, Rosenthal (1991) compared the significance levels of two analyses (one that found a significant difference and one that did not) by calculating a standardized Z-score using the formula $[(Z_1 - Z_2)/\sqrt{2}]$, and examining the associated probability level for this new combined Z-score. With this in mind, we combined the standardized Z-scores for the present analysis with one for introduced passeriforms (using probabilities of introduction success calculated across just the islands in this study). The Z-scores were 2.226 for passeriforms and –0.2056 for columbiforms. The resulting Z-score was 1.72 with an associated probability of 0.09. Although not significant at the 0.05 level, the comparison, nonetheless, suggests that the effect of response to sexual selection is indeed not the same in these two groups.

In conclusion, our results indicate that dichromatism is not associated with reduced rates of successful introduction in doves and pigeons. These results together with those of previous studies (McLain *et al.*, 1999; Donze *et al.*, 2004) suggest that the impact of sexual selection on population fitness, as assessed by rates of successful introduction, varies among higher taxa. Therefore, combining different taxonomic orders (e.g. Sorci *et al.*, 1998) might obscure patterns that exist within some orders but not others. Variation among orders may reflect differences in natural history and life history. For example, doves and pigeons typically lay only two eggs (Campbell, 1974; Baptista *et al.*, 1997; Gibbs *et al.*, 2001), whereas 90% of the introduced passeriforms produce larger clutches. Also, columbids, unlike passerines, rarely employ carotenoid-based plumage, which may indicate that the strength of sexual selection in dichromatic species varies among groups. Within an order it appears that other powerful intrinsic factors, evidenced in the all-or-none pattern, may obscure decrements to population fitness arising from response to sexual selection.

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