Evolutionary Ecology Research, 1999, **1**: 549–565

Sexual selection and extinction: The fate of plumage-dimorphic and plumage-monomorphic birds introduced onto islands

Denson Kelly McLain,[1]* Michael P. Moulton[2] and James G. Sanderson[2]

[1]*Department of Biology, Georgia Southern University, PO Box 8042, Statesboro, GA 30460 and* [2]*Department of Wildlife and Conservation, University of Florida, PO Box 110430, Gainesville, FL 32611-0430, USA*

ABSTRACT

Correlates of the fate of 132 species of birds introduced onto one or more oceanic islands (Hawaii, Kauai, Oahu, Tahiti, La Reunion, Saint Helena, Bermuda, New Zealand and Mauritius) were examined. Introduction success rate was less for species with sexually dichromatic plumage than for species with sexually monochromatic plumage. The diet of introduced sexually monochromatic and dichromatic species did not differ, but a broader diet was associated with higher introduction success rates. In a two-way analysis, plumage and diet had significant effects on the introduction success rate. Species nesting primarily in bushes had higher success rates than those nesting on the ground or in trees. Plumage type was not associated with nest location. Both plumage type and nest location had significant effects on introduction success rate in a two-way analysis. Species of introduced sexually dichromatic birds had a lower rate of bi-parental care than did species of introduced sexually monochromatic birds. However, neither the number of nest-tending parents nor clutch size significantly affected the rate of successful introduction. Sexual selection drives the evolution of sexual dichromatism. Thus, our results suggest that sexual selection indirectly promotes extinction of small, colonizing populations encountering new environmental demands by constraining ecological plasticity and evolutionary response to natural selection pressures.

Keywords: community structure, extinction, introduced birds, islands, sexual selection.

INTRODUCTION

Elucidation of the processes that determine community membership continues to be an important focus in ecology (Law and Morton, 1993; Luh and Pimm, 1993; M'Closkey *et al.*, 1997). The aim of this study was to determine the association between prior response to sexual selection pressures and membership in island bird communities. Theoretical models suggest that response to sexual selection may result in reduced population fitness (Lande, 1980; Kirkpatrick, 1982, 1996; Tanaka, 1996). If response to sexual selection constrains phenotypic plasticity or response to natural selection pressures, species that are more

* Author to whom all correspondence should be addressed. e-mail: dk_mclain@gsvms2.cc.gasou.edu

strongly sexually selected may be more likely to suffer extinction within local communities. To test this, we contrasted the fate of plumage-monomorphic and plumage-dimorphic bird species introduced into communities on oceanic islands. We also tested whether sexually monochromatic or dichromatic plumage is associated with factors that might determine the rate of successful introduction, such as clutch size, number of attending parents, diet and nest location.

In most animal species, male reproductive success is limited by the number of females mated (Trivers, 1985). When variance in mating success is attributable to variation in male traits, sexual selection arises (Hubbell and Johnson, 1987), favouring the evolution of male traits in the directions that confer a mating advantage (Darwin, 1871). In birds, a common response to strong sexual selection pressures is the elaboration of male plumage characters, including sexual dimorphism in feather colour (Darwin, 1871; Hamilton and Zuk, 1982; Bjorklund, 1984; Thompson, 1991; Prum, 1997), either because females prefer males with the most extreme or bright plumage (e.g. Andersson, 1989; Møller, 1988, 1990) or because colourful plumage provides an important signal in competition between males for access to females (e.g. Mateos and Carranza, 1997a).

Because the pressure of sexual selection is applied to a population with every mating (West-Eberhard, 1983), sexual selection is a powerful micro-evolutionary force (Endler, 1986). Consequently, the elaboration of male traits under the force of sexual selection may proceed to the point that viability is significantly reduced (Fisher, 1958). In fact, the mortality rates of male birds are higher in plumage-dimorphic species (Promislow *et al.*, 1992; Promislow, 1992), suggesting that strong sexual selection pressures have reduced or retarded response to natural selection pressures. Male traits reflect a compromise between elaboration under sexual selection for greater mating success and optimization under natural selection that reflects the ecological niche (e.g. Rohwer *et al.*, 1996; Wikelski and Trillmich, 1997). Over part of the course of evolution of sexually selected male traits, female traits may change in non-adaptive ways due to the genetic correlation that initially exists between homologous traits of males and females (Lande, 1980). The evolution of sexual dimorphism represents an approach to the state in which the female phenotype resides at its optimum under natural selection.

Environmental heterogeneity causes the intensity of natural selection to vary in time or space. The equilibrium that may be established between the conflicting pressures of natural and sexual selection in one environment may translate into reduced potential for population survival in another environment. As the environment changes, the composition of a community is also expected to change with regard to the proportion of strongly sexually selected species within it. Yet, few studies have attempted to relate community structure and population survival to the prior response of resident species to sexual selection pressures (McLain, 1993; McLain *et al.*, 1995).

Introducing species onto islands mimics a colonization event that subjects the founders to a new environment. This may render an introduced population more susceptible to extinction if the previously evolved balance between countervailing natural and sexual selection pressures requires adjustment (see Wilkinson, 1987). Strong sexual selection may be correlated with other factors that impact colonization and extinction dynamics. For example, in polygynous species or in socially monogamous species with frequent extra-pair copulations and fertilizations (e.g. Krokene *et al.*, 1996; Sundberg and Dixon, 1996; Yezerinak *et al.*, 1996; Gray, 1997; Freeman-Gallant, 1997), effective population sizes may be much smaller than the number of adults (Collias and Collias, 1996) and could lead to

critical loss of genetic variation (but see Waite and Parker, 1997). Furthermore, females of socially polygynous or effectively polygynous species may receive less help rearing offspring (Hannon and Martin, 1992; Eens and Pinxten, 1996), which could result in higher rates of nest predation and less viable fledglings (Markman *et al.*, 1996). Therefore, we predict that bird species exhibiting plumage dimorphism are more susceptible to local extinction than plumage-monomorphic species when introduced into island habitats.

This prediction contrasts with expectations based on some good genes models. Here, female preference for bright, colourful male plumage favours underlying alleles conferring better disease resistance, viability and physiological responsiveness. Indirect choice for good genes is predicted to maintain high mean population fitness and enhance population survival. For example, Hamilton and Zuk (1982) hypothesized that brightly coloured plumage evolves in males in response to pressure to demonstrate health to females. As infection by parasites reduces some plumage colours (Thompson *et al.*, 1997), brightly plumaged males would be favoured if offspring of choosy females received alleles from males that conferred resistance to parasitism (Hamilton and Zuk, 1982). More brightly coloured males may forage over greater distances (Hill, 1991), live longer (Sundberg and Dixon, 1996), possess superior physiology (Thompson *et al.*, 1997) and defend breeding territories more effectively (Mateos and Carranza, 1997a,b). Heritable variation in viability and condition would favour female choice due to its impact on offspring fitness. The heritability of some plumage traits has been demonstrated (e.g. Saino *et al.*, 1997) and there may be sufficient heritable variation in fitness that female preference for bright or colourful plumage generally yields a genetic reward reflected in offspring health, condition or viability (Rice, 1988). The genetic reward might, in turn, favour population persistence.

METHODS

Scoring plumage

Two plumage types were recognized in this study, sexually dichromatic and sexually monochromatic. Breeding plumage differences among males and females were scored by examining specimens of each introduced species in the bird collection at the US Museum of Natural History, Washington, DC. Nine different plumage regions were examined and sexual differences were scored on a line drawing of a House Sparrow (from Pettingill, 1970) that had the nine regions delimited. A species was scored as dichromatic if for any of the nine regions there was: (a) a difference in the degree of colour, (b) a difference in colour, (c) a difference in pattern, or (d) a difference in colour and pattern. Otherwise, a species was scored as monochromatic. We chose not to score plumage differences based on published photographic or artistic records as others have done (e.g. Pruett-Jones *et al.*, 1991), because subtle differences in plumage might not be represented in references. Assessing the presence of sexual dichromatism (colour difference between sexes) at the museum allowed us to control the conditions under which the assessments were made.

Statistics

We used a Kruskal-Wallis test to ascertain if sexually dichromatic species were more likely than sexually monochromatic species to suffer extinction after introduction onto an island. Here, ranks of the rate of successful introduction were grouped according to plumage type.

The rate of successful introduction is the proportion of islands where a species still persists out of all the islands onto which the species was introduced. These probabilities were generated from data in Long (1981), as well as from updated personal observations. In instances where the fate of an introduction is uncertain, the introduction was omitted from our analyses. We report one-tailed probabilities because the null hypothesis we tested is that dichromatic species were not more likely than monochromatic species to fail as introductions. This is the appropriate null hypothesis to test our contention that prior response to sexual selection did, in fact, increase the extinction vulnerability of introduced populations.

Other characteristics of introduced species were also examined for their effect on the rate of successful introduction: (a) the number of parents engaged in rearing, (b) clutch size, (c) nest location and (d) diet. These data came from: Mackworth-Praed and Grant (1955), May (1955), Watson and Campbell (1965), Godfrey (1966), Ali and Rippley (1974), Campbell (1974), Penny (1974), Medway and Wells (1976), Blakers *et al.* (1985), Stiles and Skutch (1989) and Harrison and Greensmith (1993).

Species in which both parents attend nestlings and species with larger clutches may experience faster population growth, reducing the risk of extinction due to demographic stochasticity (Lande, 1993). Predation rates may be higher for species nesting in shrubs, with the result that natural selection favours duller colours in females due to their general presence at the nest (Martin and Badyaev, 1996). If plumage dimorphism reflects a constraint on female colour, not sexual selection on males, and if predation puts populations at risk, an unexpected association may have resulted between extinction rates and plumage type. Diet may influence the potential for males to produce colourful plumage (Hill, 1991; but see Thompson *et al.*, 1997). Sexual dichromatism could then be associated with specific dietary needs. As species introduced onto islands may lack access to important components of their typical diet, it is possible that sexually dichromatic species could have suffered higher extinction rates even if sexual selection did not compromise their survival.

Paternal care (present or not), nest location (ground, bush, bush and tree, or tree; categories followed Martin and Badyaev, 1996) and plant component of the diet (seeds, fruit, or fruit and seeds) were used as grouping variables in Kruskal-Wallis tests of the introduction success rate (Table 1). As virtually all the introduced species eat some insects and often other invertebrates, only the plant component of the diet was incorporated into the analyses. The effect of clutch size was investigated using analysis of variance (ANOVA) because clutch size was approximately normally distributed and contained too many categories for a powerful non-parametric test.

When a non-plumage parameter was found to have a significant effect on the introduction success rate, two-way Scheirer-Ray-Hare extensions of the Kruskal-Wallis test (Sokal and Rohlf, 1995) were used to reassess the impact of plumage type. All statistical tests were performed with Systat (Wilkinson, 1988).

Phylogenetic constraint

Phylogenetic constraint is a potential problem in comparative data sets that examine the association between two or more traits because the terminal branches of a cladogram, representing taxa of potential interest, are not independent when the associations between traits trace to a smaller number of ancestors (Harvey and Pagel, 1991). Thus, if the species of a genus are constrained with regard to plumage characteristics (see Pruett-Jones *et al.*,

1991), and if the probability of a successful introduction is also characteristic of the species of a genus (Simberloff and Boecklen, 1991), then any apparent association between the fate of introduction and plumage type could be an artifact of phylogenetic constraint. Ideally, phylogenetic information is available with which to determine the number of independent evolutionary transitions.

Although we did not have phylogenies for the genera in our data set, we attempted to control for potential phylogenetic constraint. Here, the one species of every single-species genus was included in an analysis together with the average success of all monochromatic species in each multi-species genus and the average success of all dichromatic species within each multi-species genus. This was tantamount to assuming that, within a genus, all the dichromatic species arose from one ancestor and all the monochromatic species arose from another ancestor.

RESULTS

Phylogenetic constraint

To control for potential phylogenetic constraint, our very conservative analysis reduced the sample size from 132 species to 74 groups. Nevertheless, sexual dichromatism was marginally significantly associated with a lower introduction success rate relative to sexual monochromatism (Kruskal-Wallis test: $H = 2.27$, d.f. = 1, $P = 0.066$).

However, we do not consider phylogenetic constraint a problem for this data set because success of introduction is not a trait that characterizes species or a set of species within a genus (Moulton and Sanderson, 1997), as plumage characteristics might. Typically, a species that has been introduced to more than a couple of islands has mixed fates, surviving on some and suffering extinction on others (Moulton and Sanderson, 1997).

Moreover, the number of multi-species genera fixed for fate (= 13) was not significantly greater than the number expected by chance (= 10.6; $\chi^2_1 = 0.81$, $P > 0.25$), which is inconsistent with phylogenetic constraint for fate of introductions. Here, the expected number was obtained from the binomial distribution and is given by $x(p^n + q^n)$ summed over $n = 2$ to $n = 8$ (the greatest number of species within a single genus), where p and q are the proportions of species with some successful introductions (56/132) or no successful introductions (76/132), and x is the number of multi-species genera with n species.

Plumage and fate of introductions

The preceding arguments suggest that is statistically justifiable to treat congeners as independent. The mean (±S.E.) probability of a successful introduction was 0.445 ± 0.055 for the 65 sexually monochromatic species but only 0.258 ± 0.050 for the 67 sexually dichromatic species (Table 1). For both monochromatic and dichromatic species, the range was 0–1.0. For the entire data set of 132 species, sexually monochromatic species were significantly less likely than sexually dichromatic species to fail after introduction (Kruskal-Wallis test: $H = 6.31$, d.f. = 1, $P = 0.006$).

Table 1. Plumage type (M = sexually monochromatic, D = sexually dichromatic), success rate (= [number of successful introductions]/[number of introductions]), mean clutch size,[a] number of attending parents,[a] plant component of diet[a] (S = seeds; F = fruits, buds, flowers or nectar; 0 = neither) and nest location (G = ground, B = bush, T = tree) of 132 species of birds introduced onto islands

Family[b]	Species	Plumage type	Success rate	Mean clutch size (no. parents)	Diet	Nest
Alaudidae	*Alauda arvensis*	M	0.77	4.0 (2)	S	G
	Lullula arborea	M	0.00	3.5 (2)	SF	G
	Melanocorypha mongolica	M	0.00	4.0 (2)	SF	G
Cisticolidae	*Cettia diphone*	M	1.00	4.5 (2)	0	B
	Leiothrix lutea	M	0.50	4.0 (2)	S	B
	Sylvia atricapilla	D	0.00	5.0 (2)	F	B
Corvidae	*Corvus albus*	M	0.00	5.5 (2)	SF	BT
	Corvus brachyrhynchos	M	1.00	6.0 (2)	SF	BT
	Corvus frugilegus	M	1.00	5.0 (2)	SF	T
	Corvus splendens	M	0.82	4.5 (2)	SF	T
Cracticidae	*Gymnorhina tibicen*	D	0.80	3.5 (1)	S	T
Emberizidae	*Cardinalis cardenalis*	D	1.00	3.5 (2)	SF	B
	Cyanerpes cyaneus	D	0.50	2.0 (1)	F	B
	Emberiza cirlus	D	1.00	2.5	S	B
	Emberiza citrinella	D	0.33	4.0 (2)	SF	G
	Emberiza hortulana	D	0.00	5.0 (1)	S	G
	Paroaria capitata	M	1.00	2.0	SF	B
	Paroaria coronata	M	1.00	3.5	SF	B
	Paroaria dominicana	M	0.00	3.5	SF	B
	Passerina ciris	D	0.00	3.5 (2)	S	BT
	Passerina cyanea	D	0.00	3.5 (2)	SF	BT
	Passerina leclancherii	D	0.00	3.5 (2)	S	BT
	Ramphocelus bresilius	D	0.00	2.0	SF	B
	Ramphocelus carbo	D	0.00	2.0	SF	BT
	Ramphocelus dimidiatus	D	1.00	2.0	SF	BT
	Sicalis flaveola	D	1.00	2.5 (2)	SF	B
	Tachyphomus rufus	D	0.00		F	
	Tangara arthus	M	0.00	2.0 (2)	F	T
	Tangara larvata	M	0.00	2.0 (2)	F	T
	Thraupis episcopus	M	0.00	2.5 (2)	F	B
	Tiaris olivacea	D	1.00	2.5 (2)	SF	T
Estrildidae	*Chloebia gouldiae*	D	0.00	6.0 (2)	S	G
	Amandava amandava	D	0.67	8.0 (2)	S	B
	Amandava subflava	D	0.00	4.5 (2)	S	G
	Amadina fasciata	D	0.00	5.5 (2)	S	T
	Erythrura cyaneovirens	M	0.00		S	G
	Erythrura prasina	M	0.00		S	G
	Erythrura psittacea	M	0.00		S	G
	Erythrura trichroa	D	0.00		S	G
	Estrilda astrild	M	0.82	6.0 (2)	S	B
	Estrilda caerulescens	M	1.00	5.0	S	B
	Estrilda erythronotus	D	0.00	4.0	S	B
	Estrilda melanotis	D	0.00	2.5 (1)	S	B

Table 1. *continued*

Family[b]	Species	Plumage type	Success rate	Mean clutch size (no. parents)	Diet	Nest
	Estrilda melpoda	M	0.67		S	B
	Estrilda troglodytes	M	0.50	4.5	S	B
	Lagonostica senegala	D	0.00	4.0 (2)	S	B
	Lonchura castaneothorax	M	0.67	5.5 (2)	S	B
	Lonchura cucullata	M	0.50	6.0 (2)	S	B
	Lonchura fringilloides	M	0.00	5.0 (2)	S	B
	Lonchura malabarica	M	1.00	6.0 (2)	SF	B
	Lonchura malacca	M	0.71	5.5 (2)	S	B
	Lonchura oryzivora	M	0.77	7.5 (2)	SF	T
	Lonchura punctulata	M	0.78	6.0 (2)	SF	B
	Lonchura striata	M	0.00	5.0 (2)	S	BT
	Neochmia modesta	D	0.00	5.5 (2)	S	BT
	Neochmia ruficauda	D	0.00	6.0	S	BT
	Neochmia temporalis	M	1.00	5.0 (2)	S	BT
	Pytilia melba	D	0.00	4.5 (2)	S	BT
	Stagonopleura bella	M	0.00		S	
	Stagonopleura guttata	M	0.00		S	
	Taeniopygia bichenovii	M	0.00		S	B
	Taeniopygia guttata	D	0.25	5.5 (2)	S	BT
	Uraeginthus angolensis	D	0.00	5.0 (2)	S	BT
	Uraeginthus bengalus	D	0.25	4.5 (2)	S	BT
	Uraeginthus cyanocephala	D	0.00	5.0 (2)	S	BT
	Uraeginthus granatina	D	0.00	4.0 (2)	S	BT
	Vidua macroura	D	0.33		S	G
	Vidua paradisea	D	0.00		S	B
	Vidua regia	D	0.00		S	B
Fringillidae	*Carduelis cannabina*	D	0.00	5.5 (2)	S	B
	Carduelis carduelis	M	0.75	5.5 (2)	S	T
	Carduelis chloris	D	0.67	5.0 (2)	SF	BT
	Carduelis flammea	D	1.00	5.5 (2)	S	BT
	Carduelis flavirostris	D	0.00	5.5 (2)	S	T
	Carduelis spinus	D	0.00	4.5 (2)	S	T
	Carduelis tristis	D	0.00	5.0 (2)	S	T
	Carpodacus mexicanus	D	1.00	4.5 (1)	SF	B
	Fringilla coelebs	D	0.40	4.5 (2)	SF	BT
	Fringilla montifringilla	D	0.00	6.0 (2)	SF	T
	Serinus atrogularis	M	0.00	3.5 (2)	S	BT
	Serinus canaria	D	0.33	3.5 (2)	S	BT
	Serinus canicollis	D	0.50	3.5	S	BT
	Serinus flaviventris	D	1.00	3.0 (1)	S	BT
	Serinus leucopygius	M	0.00	3.5	S	BT
	Serinus mozambicus	M	0.63	5.0 (1)	SF	BT
Grallinidae	*Grallina cyanoleuca*	D	0.00	3.5 (2)	SF	T
Icteridae	*Sturnella loyca*	D	0.00		SF	G
	Sturnella neglecta	M	0.33	5.0 (1)	S	G
Maluridae	*Malurus cyaneus*	D	0.00	3.5 (2)	S	B

Table 1. *continued*

Family[b]	Species	Plumage type	Success rate	Mean clutch size (no. parents)	Diet	Nest
Meliphagidae	*Manorina melanocephala*	M	0.50	3.5 (2)	F	T
Monarchidae	*Rhipidura leucophrys*	M	0.00	3.0 (2)	0	T
Muscicapidae	*Copsychus malabaricus*	D	1.00	4.0 (2)	F	T
	Copsychus saularis	D	0.50	3.5 (2)	SF	BT
	Cyanoptila cyanomelana	D	0.00	4.0 (2)	F	T
	Erithacus akahige	D	0.00	4.0 (2)	F	G
	Erithacus komadori	D	0.00	4.0 (2)	F	G
	Erithacus rubecula	M	0.00	6.0 (2)	SF	G
	Sialia mexicana	M	0.00	5.0	F	T
Paridae	*Parus caeruleus*	M	0.00	11.5 (2)	SF	T
	Parus varlus	M	0.00	8.0	F	T
Passeridae	*Passer domesticus*	D	0.81	4.5 (2)	SF	T
	Passer montanus	M	0.80	5.0 (2)	S	T
	Poephila acuticauda	M	0.00	6.0 (2)	SF	T
Ploceidae	*Euplectes albonatus*	D	0.00	2.5 (1)	S	B
	Euplectes orix	D	0.20	3.0 (1)	S	B
	Euplectes progne	D	0.00	2.0 (1)	S	B
	Foudia madagascarensis	D	1.00	2.0 (2)	S	T
	Foudia rubra	D	0.00	2.0 (2)	F	T
	Ploceus capensis	D	0.00	2.5 (1)	S	T
	Ploceus cucullatus	D	0.80	2.0 (1)	SF	T
	Ploceus velatus	D	0.00	2.5 (1)	SF	T
	Sporopipes squamifrons	M	0.00	4.0	S	T
Prunellidae	*Prunella modularis*	M	0.50	4.5 (2)	F	B
Pycnonotidae	*Pycnonotus cafer*	M	0.83	3.0 (2)	F	B
	Pycnonotus jocosus	M	1.00	2.0 (2)	F	T
Sturnidae	*Acridotheres tristis*	M	0.88	4.5 (2)	SF	T
	Fregilupus varius	M	0.00		SF	
	Gracula religiosa	M	0.40	2.5 (2)	F	T
	Sturnus roseus	D	0.00	4.0 (2)	SF	G
	Sturnus vulgaris	M	0.70	5.5 (2)	SF	G
Timaliidae	*Garrulax albogularis*	M	0.00	3.5 (2)	SF	B
	Garrulax caerulatus	M	1.00	3.0 (2)	SF	BT
	Garrulax canorus	M	0.83	4.5 (2)	SF	B
	Garrulax chinensis	M	0.00	4.5 (2)	SF	B
	Garrulax pectoralis	M	1.00	4.0 (2)	SF	B
Turdidae	*Mimus gilvus*	M	0.00	3.5 (2)	SF	B
	Mimus polyglottos	M	0.40	4.5 (2)	SF	B
	Turdus merula	D	0.43	4.0 (2)	F	BT
	Turdus philomelas	M	0.40	4.0 (2)	F	BT
Tyrannidae	*Pitangus sulphuratus*	M	1.00	4.5 (2)	F	T
Zosteropidae	*Zosterops japonicus*	M	1.00	3.0 (2)	SF	B
	Zosterops lateralis	M	0.50	3.5 (2)	F	B

[a] Data from: Mackworth-Praed and Grant (1955), May (1955), Watson and Campbell (1965), Godfrey (1966), Ali and Rippley (1974), Campbell (1974), Penny (1974), Medway and Wells (1976), Blakers *et al.* (1985), Stiles and Skutch (1989) and Harrison and Greensmith (1993). [b] Follows Clements (1991).

Parents, clutch size, diet and nest location

There were significantly more species without paternal care among the introduced sexually dichromatic birds (12/53) than among introduced sexually monochromatic birds (2/49) ($\chi^2_1 = 7.41$, $P = 0.006$; Table 2). However, paternal care was not associated with the rate of successful introduction (paternal care: 0.38 ± 0.11; no paternal care: 0.39 ± 0.04; Kruskal-Wallis test: $H = 0.007$, d.f. = 1, $P = 0.935$). Introduced species with paternal care did average significantly larger clutches (4.45 ± 0.15, $n = 88$) than introduced species without paternal care (3.21 ± 0.33, $n = 14$) ($F_{1,100} = 9.42$, $P = 0.003$). Also, clutch size varied significantly among species of introduced sexually dichromatic (3.93 ± 0.17, $n = 61$) and monochromatic (4.52 ± 0.22, $n = 57$) birds (ANOVA: $F_{1,116} = 4.69$, $P = 0.032$). Clutch size was not correlated with the rate of successful introduction ($r = -0.04$, $t_{116} = -0.43$, $P = 0.67$).

Diet had a significant effect on the rate of successful introduction (Kruskal-Wallis test: $H = 8.36$, d.f. = 3, $P = 0.039$, including two species eating neither seeds nor fruit; $H = 8.23$, d.f. = 2, $P = 0.016$, omitting two species eating neither seeds nor fruit). Species that eat both seeds and fruit had the highest rate of successful introduction, whereas species that eat seeds but not fruit had the lowest rate (Table 2). Overall diet did not vary significantly by plumage type ($\chi^2_2 = 4.81$, $P = 0.090$; analysis necessarily omits two species not eating seeds or fruit). Introduced sexually monochromatic species were marginally significantly more likely to include fruit in their diet than sexually dichromatic species ($\chi^2_1 = 3.69$, $P = 0.055$). In a two-way analysis of variance for ranked data (Scheirer-Ray-Hare test), both diet ($\chi^2_2 = 6.51$, $P = 0.036$) and plumage ($\chi^2_1 = 3.53$, $P = 0.028$) had a significant effect on the rate of successful introduction. This test could not be conducted unless the two species that eat neither seeds nor fruit were omitted from the analysis.

Nest location did not vary by plumage type for introduced species when all four categories (ground, bush, bush + tree, tree) were included in the analysis ($\chi^2_3 = 7.16$, $P = 0.067$). However, introduced sexually monochromatic species were more likely to use bushes and less likely to use trees than sexually dichromatic species ($\chi^2_2 = 9.85$, $P = 0.007$; analysis combined bush + tree and tree categories; Table 2). Nest location was associated with the rate of successful introduction ($H = 9.88$, d.f. = 3, $P = 0.020$), with bush nesting being associated with the highest and ground nesting with the lowest success rates (Table 2). In a two-way analysis of variance for ranked data (Scheirer-Ray-Hare test), both nest location ($\chi^2_3 = 8.20$, $P = 0.039$) and plumage ($\chi^2_1 = 4.52$, $P = 0.016$) had a significant effect on the rate of successful introduction.

Table 2. Number of introduced sexually monochromatic and dichromatic species eating seeds (S), fruits (F) or seeds and fruits (S&F), nesting on the ground (G), in bushes (B), bushes and trees (B&T) or trees (T), and introduction success rate as a function of diet and nest location

	Diet			Nest location			
Plumage	S	F	S&F	G	B	B&T	T
Monochromatic	24	11	28	9	27	9	17
Dichromatic	38	10	19	11	17	21	17
Success rate	0.264	0.307	0.496	0.123	0.468	0.345	0.392
Standard error	0.047	0.081	0.065	0.055	0.064	0.073	0.076

DISCUSSION

Plumage, natural history and life history

The results demonstrate that sexually dichromatic species are more likely than sexually monochromatic species to fail when introduced onto islands. We predicted this pattern based on arguments that sexual selection constrains response to natural selection pressures and, thereby, increases the risk of population extinction. However, it is possible that sexual dichromatism is correlated with biological features not directly related to sexual selection but that significantly limit the potential for successful introduction.

Diet, for example, may be correlated with sexual dichromatism but not constrained by response to sexual selection pressures. Gray (1996) has shown that sexual dichromatism is associated with use of dietary carotenoids and loss of use of melanin and structural colour. Female preference for carotenoid-based colouration in males is selected for to the extent that the ability to produce bright, colourful displays honestly signals male quality (e.g. Hill, 1994). Sexual dichromatism is then expected to be more common among species of insectivorous or granivorous birds, since the diet contains less total carotenoid, rendering the ability to acquire carotenoids a reflection of foraging ability or physiological condition (Gray, 1996). In the present study and consistent with the expectations of Gray (1996), introduced sexually dichromatic species were marginally significantly more likely than sexually monochromatic species to eat seeds but not carotenoid-laden fruits. However, although diet was associated with the rate of successful introduction, plumage type of introduced species continued to be significantly associated with the introduction success rate even when the effect of diet was statistically controlled.

Like diet, nest location may be associated with plumage type but may not be constrained by sexual selection. Martin and Badyaev (1996) found that species nesting in shrubs are more likely to be sexually dichromatic and suffer more nest predation. They argued that bright colouration attracts nest predators, imparting selection against bright colouration. Predator-imposed natural selection is expected (a) to constrain female colouration more than male colouration due to the greater time that females spend on the nest, and (b) to constrain male colour less in species nesting in the canopy where predation rates are lowest (Martin and Badyaev, 1996). Nest predation does not appear to account for the lower success rates of some introduced species because introduced species that nest in trees had lower introduction success rates than species nesting in bushes. Thus, higher introduction success rates were associated with nesting in what are expected to be more vulnerable locations. Both sexual dichromatism and tree nesting were associated with lower introduction success rates, but the significant association between sexual dichromatism and tree nesting suggests the possibility that the effect of plumage type on success rates could be spurious. This is not the case, however, as plumage type retained its significant effect in the two-way model that also tested the effect of nest location on success rates.

The potential for a small, introduced population to increase rapidly in size should be correlated with the rate of successful introduction. Life-history parameters such as clutch size, extent of bi-parental care and number of broods per year may all affect the rate of population increase. The values of these parameters may be correlated and may be constrained by sexual selection acting on males. In general, sexual dichromatism is associated with reduced male care of offspring (Andersson, 1994). Reduced male care may: (a) limit

clutch size, as seen in the larger clutches of introduced species with versus without paternal care; (b) limit body size (e.g. Lozano and Lemon, 1996; Markman *et al.*, 1996) and, therefore, competitive ability and stamina; and (c) increase nest predation rates (e.g. Hannon and Martin, 1992; Markman *et al.*, 1996). In reducing population growth rates, reduced male care increases susceptibility to extinction via demographic stochasticity, the population sum of realized probabilities of death and reproduction (see Lande, 1993). The effect of demographic stochasticity on population survival is most pronounced in small populations (Lande, 1993), such as was initially present when a bird species was first introduced onto an island. Among introduced bird species, however, the number of attending parents was not associated with the introduction success rate. The dichotomy, one versus two parents, may not provide sufficient resolution to test if the indirect effect of sexual selection on population extinction rates stems from limits on the extent of male care.

Mating systems and the intensity of sexual selection

The strength of sexual selection is greater in polygynous than monogamous mating systems (Kirkpatrick *et al.*, 1990; but see Andersson, 1986). Consequently, sexual dichromatism is more common among polygynous species in some groups of birds (Bjorklund, 1990, 1991). However, for many groups of birds, sexual dichromatism and conspicuous colouration are equally likely in polygynous and socially monogamous species (i.e. species with a stable pair bond) (Møller, 1986; Johnson, 1991). Often, this may indicate substantial potential for polygyny in socially monogamous species (e.g. Korpimäki *et al.*, 1996; Krokene *et al.*, 1996; Sundberg and Dixon, 1996; Wagner *et al.*, 1996; Freeman-Gallant, 1997; Gray, 1997; Saino *et al.*, 1997; Sandell and Smith, 1997). Thus, dichromatic species may be characterized by smaller clutches, fewer broods and greater nest predation rates, even if socially monogamous, if pursuit of extra-pair matings by males compromises rates of nest attendance and vigilance. Among introduced species, clutch size was significantly smaller for dichromatic species. However, the indirect effect of sexual selection on population extinction rates of introduced birds does not appear to stem from constraints on the rate of population growth, as clutch size was not associated with the rate of successful introduction. Perhaps dichromatic species are less likely to produce multiple broods per year, especially if females receive little assistance from males.

The effective population sizes of sexually dichromatic species may be smaller than those of monochromatic species if sexual dichromatism is associated with polygyny or frequent extra-pair fertilizations (Collias and Collias, 1996). Smaller effective population sizes could result in more rapid loss of genetic variation and reduce the efficiency of natural selection within local populations (Kimura and Ohta, 1971; Wright, 1978). In birds, signal diversity is known to decrease in island populations relative to mainland counterparts (Baker, 1996), suggesting that genetic drift and founder events could have a significant impact on small, introduced populations. The larger effective population sizes on mainlands may preserve sufficient genetic variation to favour female choice for good genes. This might, in turn, promote population survival by compensating for indirect negative consequences of sexual selection, such as reduced male care. On islands, however, loss of genetic variation may render choice for good genes ineffective, in which case sexual selection may promote extinction.

For birds introduced onto islands, species that have responded to strong sexual selection pressures, as indicated by sexual dichromatism, are more susceptible to local extinction.

Specific ecological or life-history attributes responsible for the association between plumage type and rate of successful introduction have not been identified but may arise for several reasons:

1. *Principle of allocation* (Levins, 1968) – energy allocated to sexually selected traits is not available for other adaptations.
2. *Genetic correlations* (Lande, 1980) – pleiotropy can cause the evolution of traits under sexual selection to pull other traits away from their phenotypic optima under natural selection.
3. *Countervailing selection* (Arnold and Wade, 1984) – natural and sexual selection may favour opposite directions of trait evolution, resulting in a phenotypic compromise. Stronger sexual selection pressures result in greater constraint on adaptive response.

The principle of allocation may be especially relevant because the survival of birds on islands is dependent on reducing energy expenditures (McNab, 1994). Dietary and physiological support of sexual dichromatism may impart high energetic costs, especially when carotenoids are used to produce yellow, orange and red colours (Hill, 1994; Gray, 1996). Energy allocated to expression of sexual displays is not available for dealing with competitors, predators, parasites or inclement conditions. Consistent with this argument is the observation that, among island waterfowl, there is a reduction in elaborate feather patterns such as barring and reduction or loss of sexual dichromatism (Weller, 1980).

Good genes and mean population fitness

Our hypothesis, that more strongly sexually selected species are more likely to go extinct, suggests that sexual dichromatism is reflective of a load on population fitness. This reasoning runs counter to the good genes hypothesis that the evolution of bright colouration in males permits females to choose males on the basis of their resistance to co-evolving parasites (Hamilton and Zuk, 1982), which could have the effect of increasing population fitness (Kodric-Brown and Brown, 1984). Comparative evidence for the role of parasites in the evolution of sexual dichromatism has been questioned (Read and Harvey, 1989; but see Møller, 1990; Thompson *et al.*, 1997). Nonetheless, females choose those males that are less parasitized (e.g. Hillgarth, 1990; Zuk *et al.*, 1990; Zuk, 1992; Buchholz, 1995) and brightness of carotenoid-based plumage colours does reflect male parasite load prior to moulting and physiological condition at the stressful time of moulting (Thompson *et al.*, 1997). Moreover, female choice for bright plumage can translate into higher offspring fitness (Norris, 1993; Petrie, 1994; see Rice, 1988).

By choosing males with greater stamina (e.g. Hannon and Dobush, 1997) females may garner critical assistance during nesting (Markman *et al.*, 1996) and reduce the risk of acquiring a sexually transmitted disease (Hunter *et al.*, 1993; Thrall *et al.*, 1997). Such direct benefits of mate choice reduce the potential for evolving choice for good genes and reduce the potential for the run-away evolution of elaborate plumage displays (see Kirkpatrick, 1996). Female choice in some brightly coloured species may not even be based on plumage colouration (e.g. Hillgarth, 1990; Buchholz, 1995; Ligon and Zwartjes, 1995). Bright plumage may, however, signal dominance and willingness to fight with other males (Evans and Hatchwell, 1992; Mateos and Carranza, 1997a,b) if its expression is an honest advertisement of male condition (Kodric-Brown and Brown, 1984).

The honest advertisement hypothesis (Kodric-Brown and Brown, 1984), like the hypothesis of Hamilton and Zuk (1982), posits heritable variation in fitness, condition-dependent expression of a costly sexually selected trait, and greater survival and mating success for males with the most extreme expression of the trait. Success at mating, whether via intra- or inter-sexual selection, selects for those alleles that underlie good condition, eliminating the trade-off between natural and sexual selection (Kodric-Brown and Brown, 1984; but see Kirkpatrick, 1996). Nonetheless, honest advertisement leaves open the question of whether populations of two species will be equally likely to survive if one species has a mating system that selects for honest but costly advertisements, whereas the other species has a mating system that permits the energy allocated to advertisement in the former species to be allocated to feeding young or vigilantly guarding the nest.

As suggested by the hypothesis of Hamilton and Zuk (1982), the weaker the direct selection on female preferences, the more likely a good genes process is to actually reduce mean population fitness, because as the male trait becomes a better indicator of fitness, the female preference is pulled from its optimum under natural selection (Pomiankowski *et al*., 1991; Kirkpatrick, 1996). Therefore, if males provide less care in sexually dichromatic versus monochromaic species, direct selection on female preferences is likely to be weaker in dichromatic species and, consequently, there will be more potential for good genes processes to reduce mean population fitness. Our results provide empirical support for models predicting that sexual selection can lead to trait and preference distributions that compromise population fitness and, ultimately, survival.

Species diversity and environmental change

The greater rate of extinction of sexually dichromatic species may be a population-level consequence of poorer survival, under stressful or harsh conditions, of phenotypes favoured by sexual selection (Rohwer *et al.*, 1996; Wikelski and Trillmich, 1997; see also Wilkinson, 1987). Sexual dichromatism as part of the response to sustained sexual selection would then be associated with higher individual mortality rates under stressful or harsh conditions (Promislow, 1992; Promislow *et al.*, 1992). Higher individual mortality rates may imperil the small populations that characterize introductions or colonizations.

Sexual selection is a powerful, diversifying micro-evolutionary process (West-Eberhard, 1983); as such it may promote rapid speciation between disjunct populations and those in secondary contact (Lande, 1982). In birds, the diversifying effect of sexual selection is especially strong in polygynous versus monogamous species (Prum, 1997) and species richness is greater in polygynous taxa (Mitra *et al*., 1996). Our results indicate that response to sexual selection can also promote extinction, especially when populations are exposed to different or changing environmental conditions (see Tanaka, 1996). Thus, species selection (Stanley, 1979) may move a biota towards greater numbers of strongly sexually selected species during periods of environmental stability and benignity but towards lesser numbers of such species during periods of change or harshness (McLain, 1993).

ACKNOWLEDGEMENTS

We thank J.H. Brown and A. Kodric-Brown for their many helpful suggestions regarding revision of the original manuscript.

REFERENCES

Ali, S. and Rippley, S.D. 1974. *Handbook of the Birds of India and Pakistan*, Vols 1–10. Oxford: Oxford University Press.

Andersson, M. 1986. Evolution of condition-dependent sex ornaments and mating preferences: Sexual selection based on viability differences. *Evolution*, **40**: 804–816.

Andersson, M. 1994. *Sexual Selection*. Princeton, NJ: Princeton University Press.

Andersson, S. 1989. Sexual selection and cues for female choice in leks of Jackson's widowbird, *Euplectes jacksoni*. *Behav. Ecol. Sociobiol.*, **25**: 403–410.

Arnold, S.J. and Wade, M.J. 1984. On the measurement of natural and sexual selection: Theory. *Evolution*, **38**: 709–719.

Baker, M.C. 1996. Depauperate meme pool of vocal signals in an island population of singing honeyeaters. *Anim. Behav.*, **51**: 853–858.

Bjorklund, M. 1984. The adaptive significance of sexual indistinguishability in birds: A critique of a recent hypothesis. *Oikos*, **43**: 414–416.

Bjorklund, M. 1990. A phylogenetic interpretation of sexual dimorphism in body size and ornament in relation to mating system in birds. *J. Evol. Biol.*, **3**: 171–183.

Bjorklund, M. 1991. Evolution, phylogeny, sexual dimorphism, and mating system in the grackles (*Quiscalus* spp.: Icterinae). *Evolution*, **45**: 608–621.

Blakers, M.S.J., Davies, J.F. and Reilly, P.N. 1985. *The Atlas of Australian Birds.* Carlton, Victoria: Melbourne University Press.

Buchholz, R. 1995. Female choice, parasite load and male ornamentation in wild turkeys. *Anim. Behav.*, **50**: 929–943.

Campbell, B. 1974. *The Dictionary of Birds*. New York: Exeter.

Clements, J.F. 1991. *Birds of the World: A Check List*. Vista, CA: Ibis.

Collias, N.E. and Collias, E.C. 1996. Social organization of a red junglefowl, *Gallus gallus*, population related to evolutionary theory. *Anim. Behav.*, **51**: 1337–1354.

Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. London: John Murray.

Eens, M. and Pinxten, R. 1996. Female European starlings increase their copulation solicitation rate when faced with the risk of polygyny. *Anim. Behav.*, **51**: 1141–1147.

Endler, J. 1986. *Natural Selection in the Wild*. Princeton, NJ: Princeton University Press.

Evans, M.R. and Hatchwell, B.J. 1992. An experimental study of male adornment in the scarlet-tufted malachite sunbird: I. The role of pectoral tufts in territorial defense. *Behav. Ecol. Sociobiol.*, **29**: 413–419.

Fisher, R.A. 1958. *The Genetical Theory of Natural Selection*. New York: Dover.

Freeman-Gallant, C.R. 1997. Extra-pair paternity in monogamous and polygynous Savannah sparrows, *Passerculus sandwichensis*. *Anim. Behav.*, **53**: 397–404.

Godfrey, W.E. 1966. *The Birds of Canada*. Ottawa: National Museum of Canada.

Gray, D.A. 1996. Carotenoids and sexual dichromatism in North American passerine birds. *Am. Nat.*, **148**: 453–480.

Gray, E.M. 1997. Do female red-winged blackbirds benefit genetically from seeking extra-pair copulations. *Anim. Behav.*, **53**: 605–623.

Hamilton, W.D. and Zuk, M. 1982. Heritable true fitness and bright birds: A role for parasites? *Science*, **218**: 384–387.

Hannon, S.J. and Dobush, G. 1997. Pairing status of male willow ptarmigan: Is polygyny costly to males? *Anim. Behav.*, **53**: 369–380.

Hannon, S.J. and Martin, K. 1992. Monogamy in willow ptarmigan: Is male vigilance important for reproductive success and survival of females? *Anim. Behav.*, **43**: 747–757.

Harrison, C.J. and Greensmith, A. 1993. *Birds of the World.* New York: Eyewitness Handbooks, DK Publishing.

Harvey, P.H. and Pagel, M.D. 1991. *The Comparative Method in Evolutionary Biology*. New York: Oxford University Press.

Hill, G.E. 1991. Plumage coloration is a sexually selected indicator of male quality. *Nature*, **350**: 337–339.

Hill, G.E. 1994. Trait elaboration via adaptive mate choice: Sexual conflict in the evolution of signals of mate quality. *Ethol. Ecol. Evol.*, **3**: 351–370.

Hillgarth, N. 1990. Parasites and female choice in the ring-necked pheasant, *Phasianus colchicus. Am. Zool.*, **30**: 227–233.

Hubbell, S.P. and Johnson, L.K. 1987. Environmental variance in lifetime mating success, mate choice, and sexual selection. *Am. Nat.*, **130**: 91–112.

Hunter, F.M., Petrie, M., Otronen, M., Birkhead, T. and Møller, A.P. 1993. Why do females copulate repeatedly with one male? *TREE*, **8**: 21–26.

Johnson, S.G. 1991. Effects of predation, parasites, and phylogeny on the evolution of bright coloration in North American male passerines. *Evol. Ecol.*, **5**: 52–62.

Kimura, M. and Ohta, T. 1971. *Theoretical Aspects of Population Genetics*. Princeton, NJ: Princeton University Press.

Kirkpatrick, M. 1982. Sexual selection and the evolution of female choice. *Evolution*, **36**: 1–12.

Kirkpatrick, M. 1996. Good genes and direct selection in the evolution of mating preferences. *Evolution*, **50**: 2125–2140.

Kirkpatrick, M., Price, T. and Arnold, S.J. 1990. The Darwin–Fisher theory of sexual selection in monogamous birds. *Evolution*, **44**: 180–193.

Kodric-Brown, A. and Brown, J.H. 1984. Truth in advertising: The kinds of traits favored by sexual selection. *Am. Nat.*, **124**: 309–323.

Korpimäki, E., Lahti, K., May, C.A., Parkin, D.T., Powell, G.B., Tolonen, P. and Wetton, J.H. 1996. Copulatory behaviour and paternity determined by DNA fingerprinting in kestrels: Effects of cyclic food abundance. *Anim. Behav.*, **51**: 945–955.

Krokene, C., Anthonisen, K., Lifjeld, J.T. and Amundsen, T. 1996. Paternity and paternity assurance behaviour in the bluethroat, *Luscinia s. svecica*. *Anim. Behav.*, **52**: 405–417.

Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution*, **34**: 292–307.

Lande, R. 1982. Rapid origin of sexual isolation and character divergence in a cline. *Evolution*, **36**: 213–223.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am. Nat.*, **142**: 911–927.

Law, R. and Morton, R.D. 1993. Alternative permanent states of ecological communities. *Ecology*, **74**: 1347–1361.

Levins, R. 1968. *Evolution in Changing Environments*. Princeton, NJ: Princeton University Press.

Ligon, J.D. and Zwartjes, P.W. 1995. Ornate plumage of male red jungle fowl does not influence mate choice by females. *Anim. Behav.*, **49**: 117–125.

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

Lozano, G.A. and Lemon, R.E. 1996. Male plumage, paternal care and reproductive success in yellow warblers, *Dendroica petechia. Anim. Behav.*, **51**: 265–272.

Luh, H.-K. and Pimm, S.L. 1993. The assembly of ecological communities: A minimalist approach. *J. Anim. Ecol.*, **62**: 749–769.

Mackworth-Praed, C.W. and Grant, C.H.B. 1955. *Birds of Eastern and North Eastern Africa.* Melbourne, Victoria: Longmans, Green and Co.

Markman, S., Yoram, Y.-T. and Wright, J. 1996. The effect of male removal on female parental care in the orange-tufted sunbird. *Anim. Behav.*, **52**: 437–444.

Martin, T.E. and Badyaev, A.V. 1996. Sexual dichromatism in birds: Importance of nest predation and nest location for females versus males. *Evolution*, **50**: 2454–2460.

Mateos, C. and Carranza, J. 1997a. The role of bright plumage in male–male interactions in the ring-necked pheasant. *Anim. Behav.*, **54**: 1205–1214.

Mateos, C. and Carranza, J. 1997b. Signals in intra-sexual competition between ring-necked pheasant males. *Anim. Behav.*, **53**: 471–485.

May, J.R. 1955. *A Natural History of American Birds of Eastern and Central North America*. New York: Bramhall House.

M'Closkey, R.T., Hecnar, S.J., Chalcraft, D.R., Cotter, J.E., Johnston, J. and Poulin, R. 1997. Colonization and saturation of habitats by lizards. *Oikos*, **78**: 283–290.

McLain, D.K. 1993. Cope's rules, sexual selection, and the loss of ecological plasticity. *Oikos*, **68**: 490–500.

McLain, D.K., Moulton, M.J. and Redfern, T.P. 1995. Sexual selection and the risk of extinction of introduced birds on oceanic islands. *Oikos*, **74**: 27–34.

McNab, B.K. 1994. Resource use and the survival of land and freshwater vertebrates on oceanic islands. *Am. Nat.*, **144**: 643–660.

Medway, L. and Wells, D.R. 1976. *The Birds of the Malay Peninsula.* Kuala Lumpur: Penerbit University.

Mitra, S., Landel, H. and Pruett-Jones, S. 1996. Species richness covaries with mating system in birds. *Auk*, **113**: 544–551.

Møller, A.P. 1986. Mating systems among European passerines: A review. *Ibis*, **128**: 234–250.

Møller, A.P. 1988. Female choice selects for male sexual tail ornaments in the monogamous swallow. *Nature*, **332**: 640–642.

Møller, A.P. 1990. Parasites and sexual selection: Current status of the Hamilton and Zuk hypothesis. *J. Evol. Biol.*, **3**: 319–328.

Moulton, M.P. and Sanderson, J.G. 1997. Predicting the fates of passeriform introductions on oceanic islands. *Conserv. Biol.*, **11**: 552–558.

Norris, K. 1993. Heritable variation in a plumage indicator of viability in male great tits *Parus major. Nature*, **362**: 537–539.

Penny, M. 1974. *The Birds of the Seychelles*. New York: Taplinger.

Petrie, M. 1994. Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature*, **371**: 598–599.

Pettingill, O.S. Jr. 1970. *Ornithology in the Laboratory and Field*. Minneapolis, MN: Burgess.

Pomiankowski, A., Iwasa, Y. and Nee, S. 1991. The evolution of costly mate preferences: I. Fisher and biased mutation. *Evolution*, **45**: 1422–1430.

Promislow, D.E.L. 1992. Costs of sexual selection in natural populations of mammals. *Proc. Roy. Soc. Lond. B*, **247**: 203–210.

Promislow, D.E.L., Montgomerie, R. and Martin, T.E. 1992. Mortality costs of sexual dimorphism in birds. *Proc. Roy. Soc. Lond. B*, **250**: 143–150.

Pruett-Jones, S.G., Pruett-Jones, M.A. and Jones, H.I. 1991. Parasites and sexual selection in a New Guinea avifauna. *Curr. Ornithol.*, **5**: 213–245.

Prum, R.O. 1997. Phylogenetic tests of alternative intersexual selection mechanisms: Trait macro-evolution in a polygynous clade (Aves: Pipridae). *Am. Nat.*, **149**: 668–692.

Read, A.F. and Harvey, P.H. 1989. Reassessment of evidence for Hamilton and Zuk theory on the evolution of secondary sex characters. *Nature*, **339**: 618–620.

Rice, W.R. 1988. Heritable variation in fitness as a prerequisite for adaptive female choice: The effect of mutation–selection balance. *Evolution*, **42**: 817–820.

Rohwer, S., Langston, N. and Gori, D. 1996. Body size and harem size in male red-winged blackbirds: Manipulating selection with sex-specific feeders. *Evolution*, **50**: 2049–2065.

Saino, N., Primmer, C.R., Ellegren, H. and Møller, A.P. 1997. An experimental study of paternity and tail ornamentation in the barn swallow (*Hirundo rustica*). *Evolution*, **51**: 562–570.

Sandell, M.I. and Smith, H.G. 1997. Female aggression in the European starling during the breeding season. *Anim. Behav.*, **53**: 13–23.

Simberloff, D. and Boecklen, W. 1991. Patterns of extinction in the introduced Hawaiian avifauna: A reexamination of the role of competition. *Am. Nat.*, **138**: 300–327.

Sokal, R.R. and Rohlf, F.J. 1995. *Biometry.* New York: W.H. Freeman.

Stanley, S.M. 1979. *Macroevolution: Pattern and Process.* San Francisco, CA: W.H. Freeman.

Stiles, F.G. and Skutch, A.F. 1989. *A Guide to the Birds of Costa Rica*. Ithaca, NY: Cornell University Press.

Sundberg, J. and Dixon, A. 1996. Old, colourful male yellow-hammers, *Emberiza citrinella*, benefit from extra-pair copulations. *Anim. Behav.*, **52**: 113–122.

Tanaka, Y. 1996. Sexual selection enhances population extinction in a changing environment. *J. Theor. Biol.*, **180**: 197–206.

Thompson, C.W. 1991. The sequence of moults and plumages in painted buntings and implications for theories of delayed plumage maturation. *Condor*, **93**: 209–233.

Thompson, C.W., Hillgarth, N., Matthias, L. and McClure, H.E. 1997. High parasite load in house finches (*Carpodacus mexicanus*) is correlated with reduced expression of a sexually selected trait. *Am. Nat*., **149**: 270–294.

Thrall, P.H., Antonovics, J. and Bever, J.D. 1997. Sexual transmission of disease and host mating systems: Within-season reproductive success. *Am. Nat*., **149**: 485–506.

Trivers, R. 1985. *Social Evolution*. Menlo Park, CA: Benjamin Cummings.

Wagner, R.H., Schuz, M.D. and Morton, E.S. 1996. Confidence of paternity, actual paternity and parental effort by purple martins. *Anim. Behav*., **52**: 123–132.

Waite, T. and Parker, P.G. 1997. Extrapair paternity and the effective size of socially monogamous populations. *Evolution*, **51**: 620–621.

Watson, D. and Campbell, B. 1965. *The Oxford Book of Birds*. Oxford: Oxford University Press.

Weller, M.W. 1980. *The Island Waterfowl*. Ames, IA: Iowa State University Press.

West-Eberhard, M.J. 1983. Sexual selection, social competition, and speciation. *Q. Rev. Biol.*, **58**: 155–183.

Wikelski, M. and Trillmich, F. 1997. Body size and sexual size dimorphism in marine iguanas fluctuate as a result of opposing natural and sexual selection: An island comparison. *Evolution*, **51**: 922–936.

Wilkinson, G.S. 1987. Equilibrium analysis of sexual selection in *Drosophila melanogaster*. *Evolution*, **41**: 11–21.

Wilkinson, L. 1988. *Systat: The System for Statistics*. Evanston, IL: Systat Inc.

Wright, S. 1978. *Evolution and the Genetics of Populations. Vol. 4: Variation Within and Among Natural Populations*. Chicago, IL: University of Chicago Press.

Yezerinak, S.M., Weatherhead, P.J. and Boag, P.T. 1996. Cuckoldry and lack of parentage-dependent paternal care in yellow warblers: A cost–benefit approach. *Anim. Behav.*, **52**: 821–832.

Zuk, M. 1992. The role of parasites in sexual selection: Current evidence and future directions. *Adv. Study Behav*., **21**: 39–68.

Zuk, M., Thornhill, R., Ligon, J.D. and Johnson, K. 1990. Parasites and mate choice in red jungle fowl. *Am. Zool*., **30**: 235–244.