

A test of the Darwin–Fisher theory for the evolution of male secondary sexual traits in monogamous birds

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Abstract

The Darwin–Fisher theory proposes that the presence of male secondary sexual traits in monogamous birds is selected for by early season breeding of females that are in good condition. These early breeding females have high fecundity because of their good condition, and they select mates based on secondary sex traits. We tested whether this hypothesis may be responsible for the presence of male sexual ornaments in the great frigatebird, a socially and genetically monogamous seabird. Consistent with the Darwin–Fisher theory, we found that reproductive success declined over the season. However, males with more exaggerated ornaments were not chosen as mates earlier in the season than males with less exaggerated ornaments, and selection gradients on these ornaments were not significantly different from zero.

Introduction

Male secondary sexual traits reach their extreme in polygynous and lekking species of birds, such as peafowl (Petrie *et al.*, 1991) or birds of paradise (Beehler & Pruett-Jones, 1983). One explanation for the evolution of these traits in polygynous and lekking species is that female mate choice causes males with more elaborate ornaments to obtain more mates (Darwin, 1871). Indeed, the predictions of this hypothesis have generally been well-supported (Andersson, 1994).

Male sexual ornaments, however, are often exhibited by monogamous species as well (e.g. New World warblers, Parulinae; Morse, 1989). Darwin (1871) recognized this dilemma and proposed that variance in male reproductive success resulted from variation in female fecundity. This idea was expanded upon by Fisher (1958) and later explored in single-locus models by O'Donald (1972, 1980a,b) and in broader quantitative-genetic models by Price *et al.* (1988) and Kirkpatrick *et al.* (1990). The scenario is that males arrive at the breeding grounds earlier in the season than do females. When the first females arrive, all males are available to be chosen as

mates. Early arriving females are in better condition, and hence more fecund, than late-arriving females. The good-condition females choose mates from the full pool of males and make their selection based upon male secondary sexual traits. Late-arriving females, who are in poor condition, are forced to choose mates from the reduced pool of unpaired males that exhibit dull, small, or otherwise less exaggerated secondary sexual traits. Thus, males with more exaggerated secondary sexual traits will pair earlier in the season and will achieve higher reproductive success, not because of early season breeding *per se*, but because good-condition females choose mates earlier in the season than poor-condition females.

The Darwin–Fisher mechanism has the potential to explain male secondary sexual traits in a wide array of monogamous birds. However, the recent advent of molecular ecology techniques has revealed that many species of socially monogamous birds are not genetically monogamous – the frequency of extra-pair paternity in such species is often as high as 40% (Fleischer, 1996; Gowaty, 1996). In these species, it is quite possible that male secondary sexual traits are selected for by variance in male reproductive success resulting from differential ability of males to obtain extra-pair paternity. Indeed, Møller & Birkhead (1994) have shown that, across taxa, male plumage brightness is correlated with frequency of

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extra-pair fertilizations. Thus, an accurate test of the Darwin–Fisher theory should be based upon a species that exhibits male secondary sexual traits in conjunction with not only social monogamy but also genetic monogamy.

Here, we test whether the Darwin–Fisher theory explains the presence of male secondary sexual traits in the great frigatebird (*Fregata minor*). Males of this species have two striking morphological ornaments that females lack: a ruff of long iridescent feathers on the back of the neck, and a red inflatable throat pouch (Fig. 1). Great frigatebirds exhibit short-term social monogamy, forming pair bonds that last for the duration of a breeding attempt; males and females share in all aspects of parental care. Furthermore, great frigatebirds are genetically monogamous: in a group of 92 families sampled over 2 years, Dearborn *et al.* (2001) found only one instance (1.1%) of extra-pair paternity. Understanding the selective mechanism responsible for male ornaments in frigatebirds is intriguing because the sexual dimorphism of frigatebirds is a uniquely derived trait in a large clade of otherwise monomorphic species (Dearborn *et al.*, 2001).

In this paper, we test two critical predictions of the Darwin–Fisher theory for the evolution of male sexual ornaments in great frigatebirds. First, we test whether reproductive success is higher for early season nests. Secondly, we test whether males with more exaggerated secondary sexual traits are chosen as mates earlier in the season than are males with less exaggerated sexual traits.



Fig. 1 Male great frigatebirds possess two striking morphological ornaments that females lack: a ruff of long iridescent feathers on the back of the neck, and a red inflatable throat pouch. These ornaments are prominently displayed to females during courtship but are infrequently (iridescent ruff) or never (throat pouch) used in male–male interactions.

Materials and methods

Study population

Great frigatebirds forage pelagically and gather on small remote islands to breed. We are studying a breeding colony of great frigatebirds on Tern Island (23°45′N, 166°17′W), in the north-western Hawaiian Islands. Males arrive at the island sooner than females and begin performing courtship displays as females arrive to evaluate mates. Males display to females by inflating the red throat pouch, erecting the iridescent ruff, tilting and wagging the head and throat pouch, extending and shaking the wings and vocalizing. Displays are conducted while males are perched in bushes.

Females choose mates by first making low inspection flights around the colony and then making closer inspections by landing next to individual males. When a female flies over a group of males, they erupt in display. A particular male continues to display intensely if a female lands next to him for closer assessment. At our study site, hundreds of males display on a 14-ha island, allowing females to quickly and effectively evaluate a wide array of males.

Male–male competition is minimal and occurs only in contests for access to abandoned (failed) nests; such nests, and hence such contests, are rare because failed nests are usually dismantled by males collecting sticks to build new nests. Male–male interactions do not involve throat pouch inflation; instead, males vocalize, snap/bite at each other, and sometimes erect their ruffs. Based on time budget observations of 17 males over a 2-day period, males spent 0.3% of time engaged in aggressive interactions with other males; in contrast, these males spent 29.3% of their time performing courtship displays (Dearborn and A. Anders, unpublished data).

After a female has chosen a mate, the pair builds a nest together, with the male bringing sticks to the nest site and the female constructing the nest. This nest construction process lasts several days. When the nest is complete, the female lays a one-egg clutch. Throughout the population, egg-laying occurs over a 3-month season, allowing ample opportunity for us to detect seasonal variation in both nesting success and pairing dates of males with different trait values.

Field methods

In 1998, we marked and measured males at the start of the breeding season. Males were captured by hand at night, when they were sleeping perched in shrubs. Birds were fitted with leg bands and with numbered wing tags. We measured the length of the iridescent ruff with a cloth tape, and we measured wing length to obtain a measure of structural size. All measurements were made by the same person (D.C.D.). The brightness of the

iridescent ruff was scored as one of three categories: dull, moderate or bright. The ruff was illuminated at night with a fluorescent lantern held at a standard distance and angle, and the score assigned to a bird was based on consensus of two observers (D.C.D. and A. Anders). Scores were assigned when birds were still unpaired; thus, observers were blind to the eventual reproductive status of the birds.

Colour of male throat pouch was scored during daytime when males had their pouches inflated for courtship display. The nature of the behaviour of these birds prevented the measurement of colour with a spectrophotometer, which would have had the advantages of incorporating the ultraviolet spectrum and of not relying on human visual perception (Cuthill *et al.*, 1999). Because this approach was not possible, colour was scored by comparison with Munsell colour chips from a distance of 5 m. For consistency, scores were made only under outdoor viewing conditions recommended by Munsell and by the American Society for Testing and Materials: during periods of light overcast and from a position such that line of sight was perpendicular to the surface of the throat pouch and illumination was at 45° to this axis. The throat pouch was viewed through a hole cut in a photographic grey card to eliminate any perceptual effects of variation in background coloration. All colour scores were made by the same individual (D.C.D.). Repeatability of measurements was assessed for three traits by measuring the correlation between two measurements of the same individual bird. Repeatability was high for all three traits: wing length (Pearson $r = 0.991$, $n = 260$, $P < 0.001$), pouch colour value ($r = 1.0$, $n = 8$, $P < 0.001$) and pouch colour chroma ($r = 1.0$, $n = 8$, $P < 0.001$).

To monitor pairing status of marked birds, we walked around the breeding colony twice per day. Because of the open nature of the habitat, the large size of the birds (2-m wingspan), and the small size of the island, breeding activities of individuals do not go unnoticed. Because pair bond formation is a gradual process that takes several days, we used date of egg-laying (which can be objectively determined) as an index of pairing date; egg-laying typically occurs 5–7 days after pair formation.

Nests were monitored twice a day (08:00 and 17:00) to determine nest fate. We used incubation success as a measure of reproductive success in this study. The incubation period is generally viewed as the most critical stage of breeding for seabirds (Prince *et al.*, 1994). Incubation in our population of great frigatebirds lasts 56 days, and over 50% of nests fail during this period (Dearborn, 2001). Body condition is a key determinant of incubation effort and incubation success in this population, and three of the four causes of nest failure are at least partially dependent upon the body condition of the incubating bird (Dearborn, 2001).

Data analysis

First, we used logistic regression to ascertain if incubation success (hatch vs. fail) was highest for eggs laid early in the breeding season.

Secondly, we used linear regression to test for relationships between egg-laying date and four continuous male sexual traits: absolute ruff length, ruff length scaled by overall body size (= ruff length/wing chord length) and two aspects of throat pouch colour (value and chroma). The Munsell colour system measures colour along three axes: hue (the 'colour' of the object), value (lightness/darkness) and chroma (saturation, or 'amount' of colour). Hue did not vary among these males and was thus excluded from analysis.

Thirdly, we compared the egg-laying dates of males in different categories of ruff iridescence. Because our sample of marked males with known egg-laying dates included only two males with dull ruffs, we used a *t*-test to determine whether males with moderate vs. bright ruffs differed in date of egg laying.

To allow for the possibility that male pairing date is determined by a multivariate combination of traits, we used principal components analysis to generate a reduced number of uncorrelated factors that were used as predictors in a regression model with egg-laying date as the dependent variable.

We calculated selection gradients for male ornaments by regressing relative reproductive success against each male trait, and also against the factors from the principal components analysis, and measuring the slope of the resulting least-squares lines. Reproductive success, a component of fitness, was based on whether the male's nest survived to hatch and was expressed relative to the average hatch success for this sample of nests. The distribution of each phenotypic trait was standardized to mean = 0 and variance = 1.

For the linear regressions, we conducted *post-hoc* power analyses according to Neter *et al.* (1989), using the following values from our initial analyses: the residual error term (MSE), the sum of the squared deviations in the predictor variable, and the degrees of freedom. With an alpha of 0.05, we used these parameters to estimate the probability of detecting a linear relationship of a particular slope. Because successful nests were initiated on an average of 13 days earlier than failed nests (see Results), we present power analysis based on two slopes of interest: one in which males with a trait value of mean + 1 SD are chosen by females 13 days earlier than males with a trait value of mean -1 SD, and another in which males with a trait value of mean + 0.5 SD are chosen 13 days earlier than males with a trait value of mean -0.5 SD.

Power analysis for the ruff iridescence *t*-test was conducted with G-Power (Buchner *et al.*, 1996), using our data to estimate the variance in nest initiation date. For this power analysis, we specified that bright-ruffed

males would pair 13 days earlier, on average, than moderate-ruffed males.

Results

We monitored 66 nests with known egg-laying dates. Nests that were initiated early in the breeding season were more likely to survive to hatching than nests that were initiated later in the season (Wald $\chi^2 = 9.78$, d.f. = 1, $P = 0.002$, $R = -0.293$; Fig. 2); the mean egg-laying date of successful nests was 13 days earlier than that of failed nests. However, males with early season nests did not have more exaggerated secondary sexual traits than did males with late-season nests (Fig. 3): egg-laying date did not vary with pouch colour value ($n = 17$, $t_{\text{slope}} = 0.76$, $P = 0.458$), pouch colour chroma ($n = 17$, $t_{\text{slope}} = 0.07$, $P = 0.946$), ruff length ($n = 33$, $t_{\text{slope}} = 1.69$, $P = 0.101$), ruff length scaled by body size ($n = 33$, $t_{\text{slope}} = 1.34$, $P = 0.189$) or ruff iridescence ($n = 28$, $t = 0.76$, $P = 0.451$). Although the relationship with one trait (ruff length) did approach significance, this relationship was not in the predicted direction.

Power was low to moderate for detecting a 13-day difference in egg-laying date between males with trait values of +1 SD and -1 SD for each sex trait, and power was moderate to high for detecting a 13-day difference in egg-laying date between males with trait values of +0.5 SD and -0.5 SD for each sex trait (Table 1). Power was 0.48 (effect size $d = 0.617$, $n_1 = 13$, $n_2 = 15$) for a t -test to detect a 13-day difference in mean egg-laying date between males with bright ruffs and males with moderate ruffs.

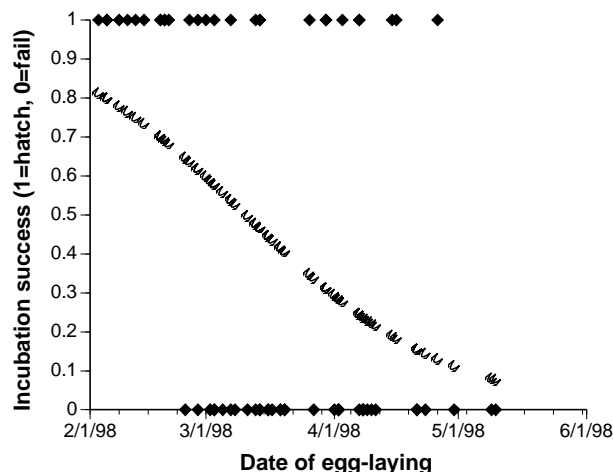


Fig. 2 Early season nests were more likely to survive to hatching than were late-season nests (probability of hatching = $[1 + e^{-(6.223.4 - 0.00000047 \times \text{laydate})}]^{-1}$; Wald $\chi^2 = 9.78$, d.f. = 1, $P = 0.002$, $R = -0.293$). Filled diamonds are observed values, and open circles are predicted values from the logistic regression.

In the principal components analysis, two factors had eigenvalues greater than one and were retained for use as predictors in the regression analysis (factor 1: eigenvalue = 2.298, accounting for 46.0% of variance in male trait values; factor 2: eigenvalue = 1.377, accounting for 27.6% of variance). In a multiple regression model, egg-laying date was not predicted by factor 1 ($t_{\text{slope}} = 0.803$, d.f. = 11, $P = 0.439$) or factor 2 ($t_{\text{slope}} = 0.794$, d.f. = 11, $P = 0.444$); for model with both factors, adjusted $R^2 = -0.059$.

Consistent with these results, the selection gradient did not differ from zero for any of the traits we examined – absolute ruff length (gradient = -0.791 , 95% CI = -2.833 to 1.252), ruff length adjusted for body size (0.547 , -1.286 to 2.380), ruff iridescence (0.268 , -0.294 to 0.832), pouch colour value (-0.049 , -0.859 to 0.761), pouch colour chroma (-0.188 , -0.831 to 0.455), principal components factor 1 (-0.221 , -0.697 to 0.254) and principal components factor 2 (0.274 , -0.201 to 0.749).

Discussion

Despite the considerable theoretical attention given to the Darwin–Fisher mechanism (Fisher, 1958; O’Donald, 1972, 1980a,b; Price *et al.*, 1988; Kirkpatrick *et al.*, 1990), surprisingly few empirical tests of this theory have been published: three positive findings (Arctic skuas, *Stercorarius parasiticus*, O’Donald, 1980c; barn swallows, *Hirundo rustica*, Møller, 1988, 1991; house finches, *Carpodacus mexicanus*, McGraw *et al.*, 2001) and no negative findings. It is unclear whether this is because of a bias against publishing negative findings (Csada *et al.*, 1996) or, alternately, whether the Darwin–Fisher theory has seldom been tested empirically.

In our study of great frigatebirds, we found support for one critical prediction of the Darwin–Fisher theory: early season nests were more successful than late-season nests. The probability of successful incubation in this population of frigatebirds is linked to adult body condition, particularly for females (Dearborn, 2001). Thus, the seasonal decline in hatching success is consistent with the Darwin–Fisher theory, in which early breeding females are proposed to have greater reproductive success because of their better nutritional condition.

The cause of the seasonal decline in frigatebird incubation success is not known – it could be because of condition-related female fecundity, as posited by the Darwin–Fisher theory, but it could also be the result of seasonal changes in age or experience of breeders, oceanographic conditions, or weather at the breeding colony. Seasonal declines in reproductive output are widespread among bird species and have been linked to a variety of causes. In many cases, such declines are because of changes in clutch size (reviewed in Rowe *et al.*, 1994; Siikamaki, 1998), and a few studies have shown that such trends are because of early season

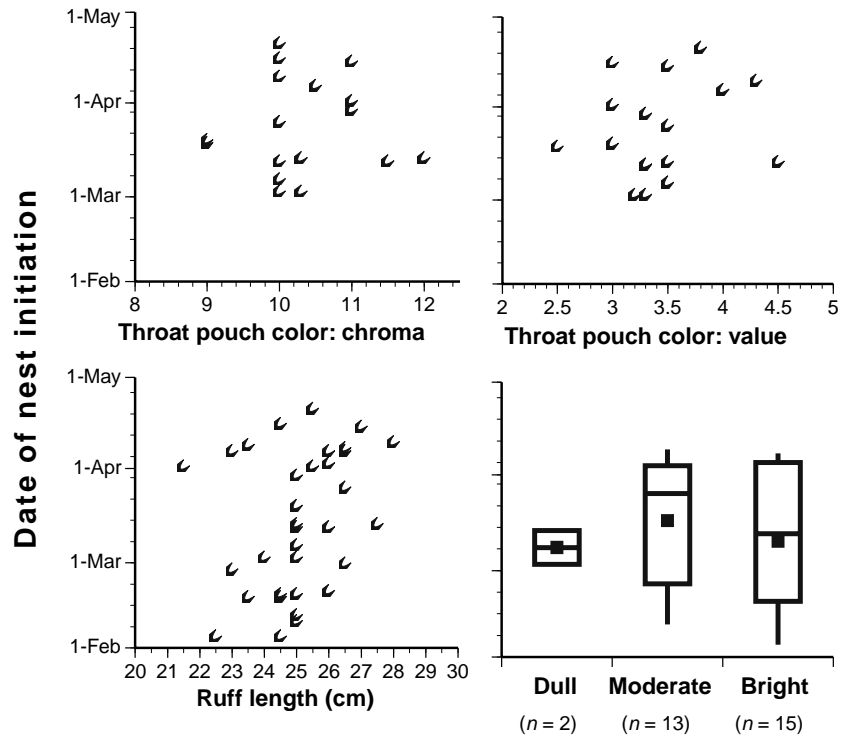


Fig. 3 Males with more exaggerated secondary sexual traits were not more likely to obtain mates and initiate nests earlier in the season than males with less exaggerated traits. See text for tests of significance and Table 1 for power analyses.

Table 1 Power analysis for regression of nest initiation date vs. male sexual trait exaggeration. Slope of regression is based on interest in detecting a 13-day difference in nest initiation date for males with trait values of either mean + 0.5 SD vs. mean – 0.5 SD, or mean + 1 SD vs. mean – 1 SD. The 13-day criterion corresponds to the difference between mean initiation date of successful nests and failed nests.

Male sexual trait	Power to detect	
	Mean \pm 0.5 SD vs. mean – 0.5 SD	Mean \pm 1 SD vs. mean – 1 SD
Ruff length (absolute)	0.83	0.30
Ruff length (adjusted)	0.67	0.23
Throat pouch colour value	0.78	0.28
Throat pouch colour chroma	0.78	0.27

breeding by females that are more fecund because of good body condition (Møller, 1991; McGraw *et al.*, 2001), as posited by the Darwin–Fisher explanation. Seasonal variation in the reproductive success of frigatebirds is not because of variation in clutch size, because frigatebirds lay a single egg per clutch. However, seasonal changes in avian reproductive success can be driven by seasonal changes in other factors, including egg size (Magrath, 1992), food availability or other aspects of environmental quality (Verhulst & Tinbergen, 1991; Lepage *et al.*, 1999), intrinsic quality of breeding adults or their territories (Högstedt, 1980; Verhulst *et al.*, 1995; Brinkhof, 1997), energetic constraints of adults

that are preparing to molt at the end of the season (Siikamaki, 1998), risk of nest predation because of changes in breeding synchrony (Hatchwell, 1991) or predator behaviour (Schaub *et al.*, 1992), and probability of post-fledging survival (Spear & Nur, 1994). We do not know whether the seasonal decline in frigatebird incubation success is driven by early breeding of fecund females, as outlined by the Darwin–Fisher theory, or by one of these other factors.

We did not find support for the second key prediction of the Darwin–Fisher theory, that males with more exaggerated secondary sex traits should be chosen as mates earlier in the season. There was no relationship between date of egg laying and any male-specific ornament: colour of throat pouch, length of iridescent nape, and brightness of iridescent nape; likewise, nest initiation date was not predicted by principal components that account for multivariate variation in male sex traits. Our power to detect such relationships was reasonable, and graphical inspection of the data (Fig. 3) suggests that the lack of relationship is an accurate finding rather than an artefact of low power. In accord with these results, none of the selection gradients for these male ornaments was significantly different from zero.

Because some birds can see into the ultraviolet (UV) spectrum and sometimes incorporate UV traits in mate choice decisions (Bennett *et al.*, 1996; Johnsen *et al.*, 1998), it is possible that unmeasured UV features of male frigatebird ornaments are predictive of male pairing date.

In studies that have demonstrated the occurrence and importance of UV in avian plumage, feathers were generally found to have a UV reflectance peak that was strong and distinct relative to other wavelengths (Andersson, 1996; Andersson & Amundsen, 1997; Hunt *et al.*, 1998). Results of a preliminary spectrophotometric analysis, at a variety of viewing angles, do not suggest substantial UV reflectance in the nape feathers of male frigatebirds (Dearborn and Ryan, unpublished data). Although we cannot entirely discount the possibility that male frigatebirds have hidden UV ornaments that are predictive of early season pairing success, the available evidence does not support the Darwin–Fisher prediction that early mated males have more exaggerated sex traits.

The lack of support for the Darwin–Fisher mechanism could be because we tested this idea in an atypical year. Some long-term studies of sexual selection do find that male mating success is correlated with different traits in different years (Fiske *et al.*, 1994). However, the 1998 season was similar to other years in which we have worked on Tern Island (1996, 1999, 2000) in terms of phenology of breeding, operational sex ratio (OSR), overall nesting success, the process of mate choice, the rarity of male–male competition and the weather during the breeding season.

Explanations other than the Darwin–Fisher theory for the presence of male ornaments may be more plausible in frigatebirds. Extra-pair fertilizations are rare, but there is a pronounced male bias in the OSR (Dearborn *et al.*, 2001). If this skew in OSR leads to variance in male reproductive success, such variance could favour the evolution of male ornaments (Kvarnemo & Ahnesjö, 1996). The mechanism of the skew in OSR is still under investigation, as are the effects of OSR on variance in male reproductive success.

An alternate interpretation is that females currently choose mates based primarily on display behaviour (perhaps in the manner envisioned by Darwin and Fisher) but that ornament-based choice in the past may have selected for exaggeration of male traits. In such a scenario, ornaments are now a necessary component of courtship (analogous to an ante in betting; Kodric-Brown & Brown, 1984) but are not in themselves the basis of female choice. We do not currently have enough data to evaluate this idea for frigatebirds, but it is a plausible hypothesis. A similar mechanism may underlie variation in male mating success in several lekking birds with male ornaments, such as sage grouse (*Centrocercus urophasianus*; Gibson & Bradbury, 1985) and black grouse (*Tetrao tetrix*; Höglund & Alatalo, 1995; Höglund *et al.*, 1997); in these species, behavioural traits are better predictors of male success than are morphological ornaments.

In a related scenario, ornaments could be a necessary component of displays, but females choose males on the

basis of display site. This seems unlikely to explain the evolution of ornaments in male frigatebirds, on two counts: (1) males would presumably compete for good or central display sites, yet male traits are not frequently used in male–male interactions, and (2) males in our population voluntarily shift display sites frequently, suggesting that there may not be intrinsically good or bad sites.

In general, the occurrence of any of these alternate mechanisms of sexual selection on male ornaments would not necessarily preclude the simultaneous operation of the Darwin–Fisher mechanism (Kirkpatrick *et al.*, 1990), but we did not find support for the Darwin–Fisher theory in this study. The current and historical importance of male ornaments in frigatebirds remains unclear.

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