Delayed plumage maturation increases overwinter survival in North Island robins

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Many bird species show delayed plumage maturation (DPM), retaining sub-adult plumage until after their first breeding season. Most explanations assume that DPM increases fitness over the breeding season. However, unless birds undergo a full moult before breeding, DPM could also be an adaptation to increase survival over the previous winter. The winter adaptation hypothesis has never been tested owing to the difficulty of measuring overwinter survival. We experimentally tested this hypothesis in North Island robins (*Petroica longipes*) using a closed island population where we could accurately estimate survival. The experiment involved dyeing 41 juveniles to mimic adult males, and comparing their survival with 41 control juveniles treated with the same peroxide base minus the pigment. The population was monitored with a series of resighting surveys, and mark-recapture analysis used to estimate overwinter survival. Survival probability was estimated to be 10% for dyed birds versus 61% for control birds in 2001, and 29% for dyed birds versus 40% for control birds in the winter of 2002, supporting the winter adaptation hypothesis for DPM. Access to suitable habitat is the key factor limiting juvenile survival in this population, and the locations where dyed juveniles were sighted suggest that they were often excluded from suitable areas.

Keywords: delayed plumage maturation; North Island robin; colour experiment; moult; survival

1. INTRODUCTION

Delayed plumage maturation (DPM) means that young birds do not acquire definitive (adult) plumage in their first year, so they spend their first breeding season looking different from older birds of their own sex. DPM is a widespread phenomenon among passerine birds. Cucco & Malacarne (2000) concluded that 96 out of 137 passerine species they assessed (70%) showed some form of DPM, and Hill (1996) noted that the distribution of DPM among species shows that it has evolved many times. The degree of DPM varies among species, yearlings looking completely different in some species and only subtly different in others. DPM is usually fairly consistent within species, but there are species where it occurs in some regions but not others (e.g. the scarlet robin (*Petroica multicolor*); Higgins & Peter 2002) and in some individuals but not others (e.g. the siskin (*Carduelis spinus*); Senar *et al.* 1998). DPM usually occurs in males, and a common pattern is for males of sexually dimorphic species to have female-like plumage in their first year (Hill 1996). However, DPM also occurs in females of some species (Lozano & Handford 1995; Thompson & Leu 1995; Senar *et al.* 1998). Birds with DPM are usually sexually mature and capable of breeding in their first year (Cucco & Malacarne 2000), raising the question of why they have evolved to retain a distinct plumage.

Several adaptive explanations for DPM have been proposed, mainly focusing on males (Cucco & Malacarne 2000). Most of these are 'summer adaptation hypotheses' (Rohwer & Butcher 1988) that are based on the two premises (i) that first-year males are competitively inferior to older males and (ii) that DPM increases the success of first-

year birds over the breeding season. These include the idea that DPM is an honest signal of subordinate status that reduces aggression from older males (Lyon & Montgomerie 1986). Alternatively, DPM may dishonestly mimic females or juveniles, allowing young males to sneak a foothold on a territory (Rohwer *et al.* 1980) or sneak extra-pair copulations (Trivers 1972). Finally, if there is little chance of breeding, DPM may simply avoid the cost of adult plumage, e.g. by making them more cryptic to predators (Selander 1965).

At present, there is little support for any of these hypotheses (Landmann & Kollinsky 1995). In some species with variable plumage development, juveniles with DPM have been shown to receive less aggression than adult-looking juveniles (Muechter *et al.* 1997; Senar *et al.* 1998; Conover *et al.* 2000). This is consistent with the status-signalling hypothesis, but the comparison is probably confounded by other differences between the two groups of juveniles. There have been experimental studies using models (e.g. Rohwer 1978; Flood 1984; Hill 1989) or cage birds (e.g. Slagsvold & Sætre 1991; Sætre & Slagsvold 1996), but these give no information on whether DPM affects reproductive success or survival or in the field. The only field experiment we know of is by Stutchbury (1991), who dyed first-year male purple martins (*Progne subis*) to mimic the appearance of older males. Stutchbury (1991) found that dyeing males increased their ability to acquire territories, and that all males acquiring territories quickly acquired mates. She also found that adult male territory owners were equally aggressive to non-dyed first-year males and to other adult males. These results are contrary to the predictions of summer adaptation hypotheses.

Although most of the literature on DPM has focused on summer adaptation hypotheses, Rohwer & Butcher (1988) noted DPM could increase overwinter survival, for

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example by reducing aggression on feeding grounds or reducing predation. They noted that all North American passerines with DPM lack a pre-alternate moult in the spring, meaning that the plumage they have over the winter is retained until after the breeding season. The 'winter adaptation hypothesis' can therefore potentially explain DPM through the first breeding season even if sub-adult plumage is maladaptive while breeding. This could potentially explain results such as the finding of Stutchbury (1991) that DPM apparently disadvantaged sub-adult purple martins. It is also possible that DPM may occur for non-adaptive reasons (Stutchbury 1991; Landmann & Kollinsky 1995), so the winter adaptation hypothesis should not be invoked uncritically in the absence of evidence for summer adaptation hypotheses.

It is therefore critical to test the adaptive significance of DPM in both winter and summer periods. However, testing the winter adaptation hypothesis is usually problematic. Among the North American and European species that have been studied, juveniles are migratory or otherwise disperse widely, making it difficult to follow the fates of marked birds. Even if behavioural interactions could be studied, it is unlikely that accurate estimates could be obtained for overwinter survival, which is the crucial parameter for the winter adaptation hypothesis. We test the effect of DPM on overwinter survival in a species and system that were ideal for addressing this question.

The North Island robin (*Petroica longipes*, henceforth 'robin') is a 26–32 g forest passerine endemic to the North Island of New Zealand and nearby offshore islands. Males in definitive plumage have dark charcoal grey feathers over most of their bodies whereas females have lighter brownish-grey feathers. Both sexes are white to pale grey on the lower breast. Juveniles look very similar to females by the time they reach independence, about one month after fledging, and both sexes retain this female-like plumage until after their first breeding season (Armstrong *et al.* 2000; Powlesland 2002). Robins are territorial and monogamous, usually remaining in their pairs until one member dies (Armstrong *et al.* 2000). We studied the Tiritiri Matangi Island (36°36' S, 174°53' E) robin population, which we have closely monitored since its reintroduction from the Mamauku Plateau in 1992. Because of the ongoing studies, over 95% of the birds are individually colour banded. The population is geographically closed, as robins are not expected to fly the 3.5 km necessary to reach the adjacent mainland and none has ever been seen there since the reintroduction. Owing to the small size of the island (220 ha) and confining nature of the species, we detect greater than 90% of the robins present in any survey (Armstrong & Ewen 2002). Consequently, we can estimate survival accurately. Armstrong *et al.* (2000) suggested that DPM might enhance overwinter survival of juveniles by reducing aggression from established territory holders. In this paper, we test this hypothesis experimentally by dyeing juveniles to mimic adult males.

2. MATERIAL AND METHODS

(a) *Study site and population*

Tiritiri Matangi is a 220 ha island in the Hauraki Gulf, 3.5 km east of Whangaparaoa Peninsula and 28 km north of Auckland off the North Island of New Zealand. The island was originally covered

by coastal broadleaf forest, but was largely cleared for Maori and European farming. When grazing stopped in 1971, the island was covered by pasture grass except for some small forest patches ranging from 0.1 to 4 ha. A revegetation programme between 1983 and 2002 has covered large parts of the remainder of the island with regenerating forest. Translocations of North Island robins in 1992 (Armstrong 1995) and 1993 resulted in a population that grew from seven pairs in the 1992/93 breeding season to 27 pairs in 2000/01 and 22 pairs in 2001/02, the two years of the current experiment. These pairs were mainly confined to the established forest patches totalling *ca.* 13 ha (see figure 1 in Armstrong & Ewen 2002), but a few pairs began to hold territories in the replanted vegetation during the current study.

(b) *North Island robin biology*

Previous research on the population has shown that juveniles failing to establish territories in good habitat do not survive to the breeding season, meaning there are no birds in the population living as 'floaters' without territories (Armstrong *et al.* 2000). It has also shown that first-year males surviving to the breeding season do not have a significantly lower chance of attracting mates than older unpaired males (Armstrong *et al.* 2000), and that pairs with first-year males do not have significantly lower reproductive success than pairs with older males (Dimond 2001). These results suggest that first-year males are not competitively inferior to older males, invalidating summer adaptation hypotheses. We also found no extra-pair paternity in 16 robin families sampled over 3 years (Ardern *et al.* 1997), suggesting that any ability to sneak access to other males' territories would not greatly enhance reproductive success. We have, however, found strong evidence that competition for space limits overwinter survival of juveniles. The proportion of juveniles surviving to adulthood each year is closely correlated with the current number of pairs (Dimond 2001; Armstrong & Ewen 2002), and the number of new immigrants to each patch is correlated with the current density of territory holders in that patch (Armstrong & Ewen 2002). Consequently, there will be strong selection for any trait allowing juveniles to better compete for territories.

(c) *Experimental treatment*

We monitored all pairs in the 2000/01 and 2001/02 breeding seasons from the time the first nests were initiated (September) until the last young were independent (March). Chicks were individually colour banded in the nest, and a growing feather was pulled from each bird at this time to determine its sex. The feather was sent to the Equine Blood Typing Unit at Massey University where a standard PCR-RFLP test was carried out using extracted DNA from the feathers. The sexing results were received within a week and before the juveniles were selected and captured. Birds were captured while still being fed by their parents, but when the feeding started to decrease (*ca.* 30 days after leaving the nest). Their first prebasic (post breeding season) moult was almost complete. Treating the birds at this time gave the opportunity to study the effect of the treatment on parental behaviour and on future interactions with other birds in the population during the juveniles' dispersal phase. Most juveniles were captured with a hand net after being trained to feed on mealworms (*Tenebrio molitor*) on the ground, and the most cautious birds were captured with a spring-loaded clapnet. Each juvenile captured was designated as either 'dyed', meaning it was dyed to mimic a male in definitive (adult) plumage, or 'control', meaning it did not receive the pigment. We assigned each bird to the treatment that currently had the lower sample size, but also took care to ensure that the

relative numbers for each treatment were similar for the two sexes. Robins typically have two young per brood, and the second sibling captured was always given the opposite treatment of the first. The numbers in each treatment were therefore balanced with respect to time, sex, and siblings.

The dye was created by mixing 2 g of Nyanzol D flakes (J. Belmar Inc., Andover, MA, USA) into 50 ml of a 17.5% hydrogen peroxide (H_2O_2) and water solution. New dye was mixed daily because the colouring properties of the solution decreased rapidly. Different concentrations of colour flakes produce feather colouring ranging from brownish grey to black, so we chose the concentration to mimic the colour of definitive male plumage. Control birds received the hydrogen peroxide and water solution alone, which does not affect plumage colour. The solution does not destroy the water repellent capacity of the feathers regardless of whether the pigment is added (Götmark 1987). Though bird's eyes have receptors for UV light, melanin-based plumage has not been found to show peaks in the UV portion of the spectra (McGraw *et al.* 2002). Also, Nyanzol-D-coloured feathers have not shown any difference in UV reflectance after treatment (Götmark 1997). These findings support our assumption that the method of feather dyeing employed in this study accurately mimics the dark plumage of the adult male.

Birds of both treatments were painted with a cotton-tipped applicator on their heads, upper wings, back and upper breast, following the pattern of the adult male. Care was taken to ensure that birds of both treatments were handled the same way, received equal coverage of solution, and that the procedure took the same time. We treated birds only on warm dry days to minimize the chilling effect of feather wetting, and kept water at hand in case any solution came in contact with the bird's eye. Because of careful application of the liquid, eye irrigation was never required. Birds were held in the hand during the procedure, and then held for 20 min in a dark box to allow the solution to dry. They were checked before release to ensure that they were in a good condition and that their eyes were not irritated, and were checked after release to ensure they were feeding normally and/or being fed by their parents. During the entire study only three juveniles did not fly away immediately when released from the box. These birds were held in the researcher's open hand for several minutes until they flew off. The appearance of birds was assessed in the following days, and any birds that did not adequately mimic the appearance of an adult male were removed from subsequent analysis. Four birds were also recaptured within a few weeks of treatment to ensure that the treatment had caused no damage to feathers.

(d) Monitoring

We conducted a series of surveys to obtain data for comparing survival rates for the two treatments. Surveys involved walking through each forest patch searching for juveniles, and also recording any juveniles seen while walking between fragments. We carried out surveys every two weeks from the time the first young reached independence (early to late November) until the end of the breeding season, then doing subsequent surveys in March, April, July and September. We recorded behavioural interactions for juveniles seen at any time. For juveniles still in their natal territories, we recorded whether or not they were still being fed by their parents. For juveniles that had dispersed from their natal territories, we recorded the location where it was found and any interactions with other robins. We assessed whether each location was suitable or unsuitable habitat, considering a location to be suitable if it was in a patch where robins bred (excluding some locations at patch edges where breeding has never taken place).

When a juvenile was found near another robin, we recorded the sex and age of that robin and any aggressive interactions, including displacements, chases and fights.

(e) Statistical analyses

We used mark-recapture analysis to test whether survival differed between the two treatment groups. Sightings of juveniles were treated as 'live recaptures', and analysed using program MARK (White & Burnham 1999; <http://www.cnr.colostate.edu/~gwhite/mark/mark.htm>). Each bird was recorded as first encountered on the survey closest to when it was treated, and was subsequently recorded as seen (1) or not seen (0) in each survey up to the following September (when the next breeding season began). Birds were effectively removed from the dataset at this point by fixing their subsequent survival probability as 0. We considered four factors that might affect survival probability (ϕ): treatment (dyed versus control), sex, year (2000/01 cohort versus 2001/02 cohort) and age (1–2-months-old, or older). The age distinction was based on the analysis of previous years' data showing that survival is lowest in the first two months after fledging, and is then relatively constant until the next breeding season (Dimond 2001). The treatment and sex of each bird was identified by dividing birds into four groups (dyed males, dyed females, control males, control females) in the encounter histories file. The effects of year and age were accounted for by manipulating the survival PIM (Parameter Index Matrix) for each group. For example, for dyed males, parameter 1 designated 1–2-month old birds in 2000/01, parameter 2 designated older juveniles in 2000/01, parameter 3 designated 1–2-month-old birds in 2001/02, and parameter 4 designated older juveniles in 2000/01. Consequently, there were four survival parameters for each of the four groups, and 16 survival parameters in total. To avoid any potential confounding effect of treatment on detection rate, we estimated resighting probability (p) separately for dyed and control birds. We assumed that resighting probability was otherwise constant, meaning that there were two resighting parameters.

The full model, with all 18 parameters, is called $\phi(\text{tment} \times \text{sex} \times \text{year} \times \text{age})$, $p(\text{tment})$, meaning that it includes all possible interactions among variables as well as the main effects. We used this as the global model, and tested whether it had an acceptable fit to the data using the bootstrap procedure in MARK (a poor fit indicates unexplained heterogeneity in the data, meaning that it is necessary to correct for the heterogeneity in model selection or find a better global model). We then created a set of simpler candidate models by removing terms, and compared these using Akaike's Information Criterion (AIC) to assess factors affecting survival. The most parsimonious model is that with the lowest AIC, indicating the best compromise between fit and simplicity. The set of candidate models should include all factors likely to affect survival, but should also be kept as small as possible to avoid overfitting (Burnham & Anderson 1998 recommend 4–20 models). We did not include 3- or 4-way interactions among variables, did not include interactions between treatment and age, sex and age, or sex and year, and did not allow interactive effects without main effects. We also did not consider models with no age effect, as we had *a priori* information that age was important. This left 19 candidate models, six with no treatment effect, six with a main treatment effect only, and seven with treatment interacting with sex or year (table 1).

We used a Wilcoxon two-group test to compare the length of time that dyed and control juveniles remained in their natal territories, and used a χ^2 contingency test to compare the proportions that were fed by their parents after treatment. We initially used χ^2

Table 1. Comparison of models to assess whether survival differed between dyed juveniles (plumage darkened to mimic adult males) and control juveniles (peroxide base applied with no colour pigment).

(Variables listed show the factors assumed to affect survival under each model: tment: dyed versus control; sex: male versus female; year: 2000/01 versus 2001/02; age: 1–2 months versus 2–10 months. (×) Indicates interactions among variables included, whereas (+) indicates additive effects only. K is the number of parameters in the model; AIC_c : corrected Akaike's information criterion; Δ_i : difference in AIC_c value from that of the best model; w_i : Akaike weights, showing the relative support for each model ($w_i = e^{-\Delta_i/2} / \sum e^{-\Delta_i/2}$). Models are listed in order of AIC_c , with the most parsimonious model at the top. Resighting probability was modelled as $\{p_{\text{tment}}\}$ in all cases, meaning that it was estimated separately for dyed and control birds but assumed to be unaffected by other factors.)

model	K	AIC_c	Δ_i	w_i
tment × year + year × age	8	537.00	0.00	0.17
tment × year + year × age + sex	9	537.36	0.35	0.14
tment + year × age	7	537.95	0.95	0.10
tment + sex + year × age	8	538.15	1.15	0.09
tment × year + age	7	538.74	1.74	0.07
tment + age	5	539.16	2.16	0.06
tment + sex + age	6	539.30	2.30	0.05
tment × year + sex + age	8	539.34	2.34	0.05
tment × sex + age × year	9	539.66	2.66	0.04
tment + year + age	6	540.12	3.12	0.04
year × age	6	540.35	3.35	0.03
tment + sex + year + age	7	540.53	3.53	0.03
sex + year × age	7	540.66	3.66	0.03
tment × sex + age	7	540.72	3.72	0.03
tment × sex + age + year	8	541.90	4.90	0.01
age	4	541.91	4.91	0.01
sex + age	5	542.19	5.19	0.01
year + age	5	543.35	6.35	0.01
sex + year + age	6	543.80	6.80	0.01

tests to compare the proportions of observations in which dyed and control juveniles were attacked by other robins, and the proportions of observations in which they were in good- or poor-quality habitat. However, these comparisons include pseudoreplicates, i.e. multiple observations per individual. If the raw χ^2 test suggested a significant difference ($p < 0.05$), we used permutation to assess whether the difference was still significant when pseudoreplication was accounted for. Each permutation involved randomly assigning each bird's set of observations to a treatment, keeping the number of birds in each treatment unchanged. The χ^2 statistic was calculated for each permutation, and the distribution of values was used to determine the probability of obtaining a χ^2 statistic as high as the observed by chance. The program was written as a Microsoft Excel spreadsheet, using the RAND() function, and a macro used to produce 10 000 permutations.

(f) *Ethical note*

Research preceding this study showed that robins had reached a carrying capacity of approximately 30 pairs, and that only 30% of juveniles were expected to survive to adulthood owing to the limited habitat available (Armstrong & Ewen 2002). While we had good reason to expect that darkening juveniles might reduce their ability to obtain territories in relation to control juveniles, there was no reason to expect that this would affect the overall proportion of juveniles surviving. The experiment was therefore unlikely to have a negative effect on the population, and this is supported by comparison with previous years' data (see § 3). In addition, our ability to closely monitor individuals of this species meant that any health problems associated with using the dye (such as dermatitis or apathy) would be noted immediately.

3. RESULTS

A total of 82 juveniles were treated, 28 in 2000/2001 and 54 in 2001/2002. There were 41 birds in each treatment (dyed or control), and the treatments were evenly distributed among 42 males and 40 females. Some birds appeared listless after release, but all recovered quickly and were confirmed to be feeding normally and/or being fed by their parents. Four of the dyed birds looked quite different from an adult male owing to poor feather colouring, and these were excluded from all analyses. Dyed birds showed no noticeable fading in colour. They remained unchanged for an average of 3.3 months then underwent a partial moult of head, back and breast feathers, resulting in a mottled appearance.

(a) *Survival*

Comparison of survival models indicates that dyeing juveniles significantly lowered survival, and that the effect may or may not have differed between years (table 2). The best survival model (table 1) was $\phi(\text{tment} \times \text{year} + \text{year} \times \text{age})$, where the effects of treatment and age on survival both differed between years. Under this model, the probability of a bird's surviving 10 months (the median time to the next breeding season) was 0.10 for dyed birds versus 0.61 for control birds in 2000/01, and 0.29 for dyed birds versus 0.40 for control birds in 2001/02. Three other models have at least half the AIC weight of the best model (table 1), showing it is unclear whether the effect of the treatment differed between years, and unclear whether sex may have also affected survival probability. However, there is little support for models with no treatment effect. The best of these, $\phi(\text{year} \times \text{age})$, has less than 20% of the

Table 2. Estimated survival probabilities for dyed and control birds.

(Monthly survival probabilities for 1–2-month-old birds ($\hat{s}_{1-2}$) and older birds ($\hat{s}_{2+}$) were estimated in MARK with model $\phi(\text{tment} \times \text{year} + \text{year} \times \text{age})$, $p(\text{tment})$ (table 1). Values in parenthesis show 95% confidence intervals. Survival over 10 months ($\hat{s}_{1-11}$) is estimated as $\hat{s}_{1-2} \times (\hat{s}_{2+})^9$, with the 95% confidence intervals obtained using the delta method.)

year	treatment	$\hat{s}_{1-2}$	$\hat{s}_{2+}$	$\hat{s}_{1-11}$
2000/01	dyed	0.47 (0.23–0.72)	0.84 (0.65–0.94)	0.10 (0.02–0.44)
	control	0.83 (0.56–0.95)	0.97 (0.88–0.99)	0.61 (0.27–0.87)
2001/02	dyed	0.87 (0.68–0.95)	0.89 (0.80–0.94)	0.29 (0.13–0.54)
	control	0.90 (0.74–0.97)	0.91 (0.84–0.96)	0.40 (0.20–0.64)

weight of $\phi(\text{tment} \times \text{year} + \text{year} \times \text{age})$, and a likelihood-ratio test between these models gives a p -value of 0.023. There is also little support for models including an interaction between treatment and sex, suggesting that the effects of the treatment were similar for males and females.

The goodness-of-fit test on the global model suggested there is some unexplained heterogeneity, but the above conclusions are robust to this. The bootstrap test (with 1000 runs) gave a p value of 0.042, indicating that there is a 4.2% probability of the deviance's being as high as that in the observed data if there was no unexplained heterogeneity. Examination of the deviance's residuals suggests that there was individual heterogeneity in resighting probability, which matches our impressions from the field. However, any overdispersion in the data is very mild, the observed deviance being only 12% higher than the mean deviance produced by bootstrapping. We therefore set the overdispersion parameter $\hat{c}$ to 1.12, and compared the resulting AIC adjusted for sample size and overdispersion (QAIC_c) values to assess the robustness of our results to overdispersion (Lebreton *et al.* 1992). This adjustment made little difference, the model $\phi(\text{tment} \times \text{year} + \text{year} \times \text{age})$ still having the highest weight and models without a treatment effect still having little support.

We cannot say conclusively whether the overall survival was affected by the treatments or remained unchanged. However, analysis of previous years' data gave 10-month survival probabilities of 0.30 (0.19–0.44) for 1999 and 0.40 (0.28–0.52) for 2000, which are similar to the overall values for this study: 0.30 (0.19–0.43) for 2001 and 0.41 (0.29–0.53). This suggests that overall survival was unaffected.

(b) Parental behaviour

Observations immediately after treatment suggest that dyeing triggered some parents to stop feeding juveniles. Out of the 71 juveniles included in our analyses, 48 had been fed recently at the time of treatment, including 20 dyed birds and 28 control birds. Out of these, 17 of the control birds (61%) were seen being fed by a parent after treatment, whereas only six (30%) of the dyed birds were seen being fed ($\chi^2 = 4.41$, d.f. = 1, $p = 0.035$). There were 25 observations of aggressive behaviours from the parents towards the fledglings and they were evenly distributed between the two treatment groups. There was also no difference between treatments in how long juveniles remained in their parents' territories (Wilcoxon two-group test, $n = 48$, $z = -0.78$, $p = 0.43$).

(c) Post-dispersal locations and interactions

Observations of juveniles after leaving their natal territories suggest that dyeing birds reduced their ability to occupy habitats suitable for long-term survival. We recorded 88 observations of dyed birds, involving 16 individuals, and 141 observations of control birds, involving 21 individuals. Out of these, 50% ($n = 44$) of the observations of dyed birds were in unsuitable habitat, whereas only 21% ($n = 29$) of the observations of control birds were in unsuitable habitat ($\chi^2 = 21.61$, d.f. = 1, $p \ll 0.001$). A permutation test on these data gave a p value of 0.048, showing that the difference was still significant when pseudoreplication was accounted for.

Dyed and control birds were both highly likely to be attacked when they were observed with other robins. Out of the 229 observations above, the juvenile was in proximity to another robin in 53 cases. Aggression from the other bird was recorded in 21 out of 21 cases (100%) for dyed birds, and 27 out of 32 cases (84%) for control birds ($\chi^2 = 3.62$, d.f. = 1, $p = 0.057$). The difference between dyed and control birds was also insignificant when aggression from adult males, adult females and other juveniles were analysed separately.

4. DISCUSSION

The dyeing procedure was successful at achieving the desired manipulation with no obvious side effects. The dyed birds were similar in appearance to males in definitive plumage, and their appearance remained unchanged over 2.2–4.6 months until a partial moult began. The lack of fading contrasts with previous studies (Götmark 1993), probably because North Island robins spend most of their time under dense forest cover and are rarely exposed to direct sunlight.

The reduced survival of dyed juveniles, in comparison to control birds, strongly suggests that delayed plumage maturation improves overwinter survival in North Island robins. The estimated survival probabilities suggest that dyeing juveniles reduced their overwinter survival from *ca.* 61% to 10% in 2001 and from 40% to 29% in 2002. The confidence intervals on these estimates are fairly large (table 2), so the effect may not be as extreme as suggested by these estimates. Nevertheless, the effect is clearly significant and suggests there could be strong selection pressure against any lineage that evolved immediate plumage dimorphism.

The mechanism underlying the effect of DPM on survival is currently unclear. Armstrong *et al.* (2000) proposed that DPM enhanced overwinter survival in North Island robins by reducing the amount of aggression from estab-

lished territory holders, enhancing their ability to compete for a territory. This idea is related to the status signalling and female mimicry hypotheses (Cucco & Malacarne 2000) in that these ideas also assume that DPM acts to reduce aggression. The difference is that these hypotheses assume that DPM reduces aggression in the summer rather than the winter. We found that dispersing juveniles were highly likely to receive aggression if another robin was present (100% of observations for dyed birds, 84% for control birds), meaning there was no power to compare treatments based on whether or not aggression was received. Among observational studies in other species conducted in the breeding season, Muechter *et al.* (1997), Senar *et al.* (1998) and Conover *et al.* (2000) found that adult males showed more aggression toward adult-looking juveniles than female-looking juveniles, and Stutchbury (1991) found no difference in the amount of aggression received by female-looking males and adult males.

Although there was no power to compare aggressiveness toward dyed and control robins, the fact that dyed juveniles were more likely to be found in unsuitable habitats supports the idea that their lower survival was due to exclusion by other robins. There is no reason why dyeing juveniles would affect their habitat preference, and the most likely reason for any juvenile's being found in an unsuitable habitat is that it had failed to establish a toehold in a suitable location. Stamps (1994) noted that aggressive interactions may be a poor indicator of ability to establish a territory, and that individuals receiving repeated aggression are sometimes the most likely individuals to establish. Understanding why dyed individuals were less likely to survive may require a more sophisticated understanding of the behavioural interactions leading to successful territory establishment. The problem is that the critical observations are likely to be missed in any study where juveniles cannot be followed continuously (Stamps 1994).

Although the literature on DPM focuses on coping with aggression from territorial males, aggressive interactions with resident males and females may both be important. In our observations of the whole set of treated individuals, we found almost as many instances of aggression from resident females (15) as from resident males (19). In addition, we recorded 31 observations of aggression from other juveniles. In principle, interactions with other juveniles could be the most important because it is juveniles that are competing for vacant territories. However, this is not supported by year-to-year variation in juvenile survival, which is inversely correlated with the number of pairs but uncorrelated with the number of juveniles in the cohort (Dimond 2001). Interactions with parents could also be important, as these may affect the condition of juveniles when they are searching for territories. Our results suggest that dyeing juveniles caused some parents to stop feeding them, raising the novel hypothesis that DPM could have adaptive value through prolonging parental feeding.

Another possibility for explaining for the lower survival of dyed juveniles is the cryptic hypothesis, the idea that DPM reduces predation risk. Like the status signalling and female mimicry hypotheses, the cryptic hypothesis was originally conceived as a summer adaptation (Selander 1965) but can potentially be applied to overwinter survival. It is not obvious, however, that dyed robins were any less cryptic than control robins or that adult males are any less

cryptic than adult females or juveniles. A cryptic plumage pattern is one that resembles the visual background as perceived by the predator at the time and place at which the bird is most vulnerable to predation (Endler 1991). The only predator known to take robins on Tiritiri Matangi is the morepork (*Ninox novaeseelandiae*), a medium-sized owl that hunts mainly at night (Imboden 1975). If anything, a dark plumage would probably make robins more cryptic than less cryptic in semi-darkness or darkness.

A final issue that needs to be considered is moult constraint (Cucco & Malacarne 2000). If young males initially moult into female-like plumage because they are constrained from moulting into definitive plumage, the female-like plumage could actually be maladaptive in both the winter and subsequent summer (Stutchbury 1991). This version of the moult constraint hypothesis is a potential alternative to the winter adaptation hypothesis. However, for this to be plausible, definitive plumage must be more costly to produce than female-like plumage, for example by the need to produce condition-dependent colours (McGraw *et al.* 2002). There is no reason to suspect this is the case in North Island robins given our evidence that female-like plumage enhances overwinter survival. However, the conventional version of the moult constraint hypothesis (Rohwer & Butcher 1988) does not require definitive plumage to be more costly, and is complementary to winter adaptation. In this version birds delay moulting until after the breeding season owing to energetic constraints; hence the maintenance of sub-adult plumage throughout the breeding season can be explained by winter adaptation in conjunction with moult constraint. This is applicable to North Island robins given that they do not undergo a complete moult until after their first breeding season.

Although robins do not moult their wing and tail feathers until after the breeding season, they do undergo a partial moult of other feathers 3–6 months after fledging, and replace these with female-like plumage. This raises the question of why young males do not produce definitive male plumage during this moult. The female-like plumage may still be adaptive at this stage. Stutchbury (1991) also noted that it could be maladaptive for birds to have a mixed plumage, and suggested this is why sub-adult male purple martins produce female-like plumage in late winter even though her experiments suggested it would be advantageous for them to have a definitive male plumage at this stage.

Given that North Island robins do not undergo a moult in the spring, the fact that female-like plumage enhances overwinter survival is sufficient to explain why males retain this plumage through their first breeding season, supporting the winter adaptation hypothesis of Rohwer & Butcher (1988). This hypothesis allows for the possibility that DPM is maladaptive during the breeding season. This is plausible, but not supported by our data for Tiritiri Matangi. First-year males surviving to the breeding season do not appear to suffer any competitive disadvantage in terms of attracting mates and fathering offspring (Armstrong *et al.* 2000). The population maintains an even sex ratio due to similar survival rates in males and females (Armstrong & Ewen 2002), all birds surviving to breeding age acquire territories suitable for breeding, and the species is monogamous with no evidence of extra-pair fertilization (Arden

et al. 1997). There therefore appears to be little potential for sexual selection, hence little potential for DPM to offer either an advantage or disadvantage during the breeding season. This raises the question of why North Island robins are sexually dimorphic at all.

It is possible that the selection pressures on the Tiritiri Matangi Island robin population are atypical for the species, but we do not believe this to be the case. In mainland populations that are at extremely low densities due to introduced predators (Powlesland *et al.* 1999), the selection pressures are probably quite different from the Tiritiri Matangi Island robin population. However, sites with intensive predator control have densities similar to those on Tiritiri Matangi, suggesting that high densities and intense competition would have been the norm historically. These sites also have relatively even sex ratios, no floaters, and monogamous breeding (Powlesland *et al.* 2000), suggesting little potential for sexual selection.

North Island robins may be sexually dimorphic in plumage simply because this is the ancestral condition. The North Island robin is one of 26 *Petroica* species in Australia and New Zealand (Holdaway *et al.* 2001; Higgins & Peter 2002). Two of these are melanistic species found on outlying islands (the black robin, *P. traversi*, and Snares Island tomtit, *P. dannefaerdi*). However, the other species all show a plumage pattern similar to the North Island robin but with stronger dimorphism. The New Zealand *Petroica* are all thought to be derived from migrants from Australia, and the Australian species are all strongly dimorphic. The North Island robin may be in the process of losing its dimorphism, and the dimorphism may even be maladaptive.

DPM may also be an ancestral trait, but this is less clear. All of the Australian species of *Petroica* have DPM, with males retaining female-like plumage until after their first breeding season similarly to North Island robins (Higgins & Peter 2002). One of these, the scarlet robin, is geographically variable in that males on Norfolk Island show DPM whereas those on the Australian mainland moult directly into male plumage. New Zealand has three sexually dimorphic *Petroica* species other than the North Island robin, and none shows DPM—i.e. males have a clear ‘male plumage’ in their first breeding season. This includes the closely related South Island robin (*P. australis*), which was considered to be the same species as the North Island robin until recently (Holdaway *et al.* 2001).

It is possible that North Island robins inherited DPM directly from an Australian ancestor, but it is also quite possible that they evolved it independently in New Zealand. If the latter is true, DPM may have evolved owing to selection for higher overwinter survival in juveniles, and DPM could be a stepping-stone to complete loss of dimorphism. If the former is true, the trait may have evolved under different selection pressures. Major *et al.* (1999) found that first-year male red-capped robins (*P. goodenovii*) tend to occupy poorer-quality habitats than older males during the breeding season, and a similar pattern has been observed for scarlet robins on Norfolk Island (D. Robinson, personal communication). These observations suggest competitive inferiority of first-year males, raising the possibility that DPM could be a summer adaptation in some *Petroica*.

Our research on North Island robins has given strong evidence that DPM enhances overwinter survival, and has

also shown that summer adaptation hypotheses are implausible for this species. This gives the most comprehensive evidence to date of the current selective forces maintaining DPM in a bird species. However, current selective forces can be quite different from those accounting for the evolutionary origin of a trait (Gould & Vrba 1982). Understanding the evolutionary origin of DPM in North Island robins presents an additional challenge.

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