Why some species of birds do not avoid inbreeding: insights from New Zealand robins and saddlebacks

Ian G. Jamieson, a Sabrina S. Taylor, a,b Lisa N. Tracy, a Hanna Kokko, c,d and Doug P. Armstrong e

aDepartment of Zoology, University of Otago, P.O. Box 56, Dunedin, 9054, New Zealand, bDepartment of Forest Sciences, Centre for Applied Conservation Research, 3041 - 2424 Main Mall, Vancouver, British Columbia, Canada V6T 1Z4, cDepartment of Biological and Environmental Science, P.O. Box 56, University of Helsinki, FIN-00014 Helsinki, Finland, dSchool of Botany and Zoology, Banks Wing Building, Australian National University, Canberra ACT 0200, Australia, and eWildlife Ecology Group, Institute of Natural Resources, P.O. Box 11 222, Massey University, Palmerston North, New Zealand

When dispersal options are limited and encounters with relatives are likely, individuals need to recognize and avoid mating with kin to avoid the fitness costs of close inbreeding. New Zealand robins and saddlebacks are genetically monogamous and possess life-history traits that predict they should show zero tolerance of close inbreeding. However, of 11 population-years of pedigree data, there was evidence of inbreeding avoidance in only 1 year. We also found no indication that incestuous pairings were avoided or that individuals were choosing genetically dissimilar mates based on microsatellite DNA analysis. Furthermore, a review of the literature revealed that inbreeding avoidance via kin recognition is common in cooperatively breeding birds, but pair-breeding birds such as robins and saddlebacks mate randomly with respect to relatedness. A model that incorporates encounter rates with close kin for various degrees of mate-searching effort shows that inbreeding avoidance is beneficial at intermediate to high levels of encounter rates with close kin (as found in cooperative breeders), but that random mating is more beneficial at low or extremely high encounter rates. We conclude that random mating normally results in such low rates of close inbreeding that it exerts negligible selection pressure to evolve kin recognition. Consequently, many threatened species are unlikely to have a natural “built-in” mechanism for avoiding close inbreeding, and the assumption of random mating built into many population viability models may be appropriate. Key words: genetic similarity, inbreeding avoidance, kin recognition, pedigrees, random mating. [Behav Ecol 20:575–584 (2009)]

Because mating with a close relative (i.e., inbreeding) generally results in reduced survival and/or reproductive success (inbreeding depression), natural selection should favor behavior that reduces the occurrence of inbreeding (Blouin and Blouin 1988; Pusey and Wolf 1996). The most commonly cited form of inbreeding avoidance in animals is dispersal (Greenwood 1980; Pusey 1987; Gandon 1999; Szulkin and Shelton 2007). However, if dispersal is not an option and encounters between kin are likely to occur, individuals need to recognize their close relatives and avoid pairing with them or engage in extrapair fertilizations (EPFs) (Pusey and Wolf 1996; Blomqvist et al. 2002). Individuals could learn to recognize and discriminate between kin and nonkin through experience or familiarity, a proposition that may work especially well in parent–offspring or litter–nestmate relationships (Komdeur et al. 2004; Wheelwright et al. 2006). Finally, independent of familiarity and experiences, individuals could use phenotypic cues that are correlated with genetic similarity in order to choose mates that are genetically dissimilar to themselves (Tregenza and Wedell 2000; Mays and Hill 2004).

Birds are ideal subjects for studying the occurrence of inbreeding avoidance in wild populations because adults and their offspring can be individually marked with colored leg bands, making subsequent identification of close relatives possible. Studies of small island populations are particularly relevant because encounters with close relatives are unavoidable, so the opportunity to detect inbreeding avoidance is enhanced (e.g., Gibbs and Grant 1989; Keller and Arcese 1998; Wheelwright et al. 2006). Despite an increase in such studies, few have clearly documented the occurrence of inbreeding avoidance in wild populations of birds (see Discussion).

Studies showing clear evidence of inbreeding avoidance via mate choice have been limited mostly to cooperative breeding species (e.g., Koenig et al. 1999; Daniels and Walters 2000; Hatchwell et al. 2000). By contrast, singular breeding species (i.e., species that breed as pairs on a defended territory) tend to exhibit random mating with respect to relatedness (i.e., the frequency of close inbreeding is consistent with the frequency expected from a random mating model) (e.g., Van Tienderen and van Noordwijk 1988; Gibbs and Grant 1989; Pärt 1996; Keller and Arcese 1998; Hansson et al. 2007; but see Kruuk et al. 2002; Wheelwright et al. 2006). Studies that base relatedness on genotype data give conflicting evidence on the prevalence of inbreeding avoidance via mate choice. Some species breeding in pairs prefer genetically dissimilar mates (e.g., Blomqvist et al. 2002; Freeman-Gallant et al. 2003), whereas others mate randomly with respect to genotype (e.g., Klevén and Lifjeld 2002; Schnell et al. 2005; Foerster et al. 2006; Van de Casteele and Matthysen 2006).

Variation in inbreeding avoidance among species could be due to a number of factors including variation in survival, natal dispersal, mate fidelity, mating system, constraints on breeding, and costs of inbreeding (Wäser et al. 1986; Kokko and Ots 2006). For example, Keller and Arcese (1998) argued that

Address correspondence to I.G. Jamieson. E-mail: ian.jamieson@stonebow.otago.ac.nz.
Received 30 June 2008; revised 26 January 2009; accepted 16 February 2009.

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short-lived birds would tolerate inbreeding if it were less costly than forfeiting mating opportunities, but that active rejection of relatives would be more likely in long-lived passerines. Lehmann and Perrin (2003) suggested that males might be more accepting of inbreeding as long as it did not reduce other opportunities for mating, but strictly monogamous species (i.e., species that do not engage in EFS) should not tolerate inbreeding. Furthermore, species with strong seasonal constraints on reproduction should be more tolerant of inbreeding or they may lose the opportunity to breed (Lehmann and Perrin 2003).

New Zealand saddlebacks (Philesturnus carunculatus) and robins (Petroica australis) are ideal species for examining inbreeding avoidance because their life-history characteristics and mating habits suggest that encounters with close relatives should be common and that there should be strong selection pressure for inbreeding avoidance. Like most New Zealand forest birds, saddlebacks and robins are nonmigratory, remain on their breeding territories over winter and show limited juvenile dispersal. They occur naturally on islands throughout New Zealand, although both species have been reintroduced to numerous offshore islands where introduced predators have been eradicated (Higgins and Peter 2002; Hooson and Jamieson 2003a; Higgins et al. 2006).

In the absence of introduced predators, saddlebacks (75 g) and robins (35 g) are relatively long lived for relatively small passerines. Saddlebacks have an estimated annual adult mortality rate ranging between 6.5% and 11% (Armstrong et al. 2005; Jamieson I, unpublished data), and some individuals have been known to live for up to 21 years (Higgins et al. 2006). Robins have an annual adult mortality rate between 10% and 20% (Dimond and Armstrong 2007; Jamieson I, unpublished data) and can live up to 16 years (New Zealand Department of Conservation, unpublished data). Both species exhibit biparental care of nestlings, remain resident on their breeding territories year round, and tend to pair for life (Higgins and Peter 2002; Higgins et al. 2006; Jamieson I, unpublished data). Furthermore, previous and concurrent molecular studies indicate that robins and saddlebacks are genetically monogamous (Ardern et al. 1997; Taylor et al. 2008; see Methods). They also have an extended breeding season that can last up to 6 months, during which they raise up to 3 clutches; hence, the breeding season does not appear to be seasonally constrained. These life-history traits imply that inbreeding depression should lead to prolonged and substantial reduction in fitness for the breeding pair. Previous studies of robins have indeed shown that substantial inbreeding depression can occur (Briskie and Mackintosh 2004; Jamieson et al. 2007), and the more general suggestion that many threatened bird species in New Zealand may have purged their deleterious alleles and exhibit little or no inbreeding depression has been strongly rebuked (Jamieson et al. 2006). Based on this information, current theory predicts that both species should show clear evidence of inbreeding avoidance by either avoiding breeding with close relatives (as determined from our pedigree data) or by choosing genetically dissimilar mates (as determined from microsatellite DNA data).

The aim of this paper is to document the level of inbreeding in 1 island population of saddlebacks and 2 island populations of robins based on 5–6 years of banding and nest monitoring data in each case. We use a randomization approach to test whether the frequency of close inbreeding is less than would be expected from a random mating model. We also examined whether incest avoidance was more likely between father–daughter pairs than mother–son or brother–sister pairs as predicted by the “asymmetrical incest avoidance model” (Wheelwright et al. 2006). We further tested the hypothesis of inbreeding avoidance by determining whether saddlebacks and robins were more likely to choose genetically dissimilar mates relative to the average genotype available at the time of pairing. In light of our results, which found no evidence that saddlebacks or robins regularly avoid mating with close relatives or prefer genetically dissimilar mates, we review the published evidence of random mating versus inbreeding avoidance in birds and develop a simple qualitative model to explain the conditions that are likely to promote the evolution of inbreeding avoidance.

METHODS

Study sites and sampling

Holdaway et al. (2001) consider the subspecies of saddlebacks and robins on North and South Islands of New Zealand as separate species, but we treat these as subspecies here following Higgins and Peter (2002) and Higgins et al. (2006). Both robins and saddlebacks were relatively common throughout the mainland of North and South Islands of New Zealand and on numerous islands around the coast before the introduction of exotic predators (Higgins and Peter 2002; Higgins et al. 2006). Our study sites were located on 2 islands (Ulva and Tiritiri Matangi) where robins and saddlebacks were recently reintroduced following the eradication of introduced predators. Saddlebacks are not capable of sustained flight (Newman 1980), and this usually confines them to individual offshore islands (saddlebacks are extinct on the mainland, i.e., North, South, and Stewart Islands). Robins have been known to fly from islands to return to their original breeding territories when displaced by human-assisted translocation (Oppel and Beaven 2002), but they tend to be reluctant fliers and resident birds are generally confined to individual offshore islands. Furthermore, there is no immigration into our study islands because there are no resident populations of either species on the adjacent mainland. Translocations themselves can induce short-term stresses on the birds, but postrelease survival in both species tends to be high, and all indications are that birds exhibit typical breeding behavior once they settle (Armstrong 1995; Armstrong and Craig 1995). Despite these island populations being reintroduced, the study species are free ranging and are not managed in any way that would affect their normal behavior or create differences with source populations.

Ulva Island

Ulva Island (259 ha, 168°08′E, 46°56′S) is a Department of Conservation open sanctuary located 800 m to the nearest shoreline within Stewart Island’s Paterson Inlet at the south end of the South Island, New Zealand. The island is primarily covered by lowland podocarp forest in its interior, surrounded by coastal scrub. Thirty banded saddlebacks were translocated in April 2000 from Big Island, off the southwest coast of Stewart Island, to Ulva Island, of which 23 survived to the first breeding season. There was no extensive nest monitoring in the first breeding season, but of the 16 birds for which we had DNA samples, 12 were identified as breeding pairs and 4 were single females based on both observations and subsequent parentage analysis (see below).

Robins were sourced from Freshwater Flats (Stewart Island) and were translocated on 3 separate occasions to Ulva Island, where they were closely monitored (Oppel and Beaven 2002). Sixteen banded birds were initially released in September 2000, but 5 adult birds returned to territories at Freshwater Flats and 6 died before breeding. This was followed by a second release of 4 banded juveniles in January 2001 (1 bird died) and a third release of 5 banded juveniles in November 2001 (1 bird died). In total, 12 of the released robins (5 females and 7 males) survived to the breeding season after they were released.
Following the translocations to Ulva Island, numbers of saddlebacks and robins have increased rapidly and have been monitored intensively. Over the course of the study (2000–2005), all robins were individually color banded (n = 197), and virtually all of these (98%) had a blood sample taken for microsatellite DNA analysis (protocols described in Boessenkool et al. 2007; Taylor et al. 2007, 2008). All robins hatched on Ulva were banded as nestlings or as fledglings inside their parents’ territory, giving us essentially complete data regarding pedigree relationships and genotypes of newly paired birds and available single birds. For saddlebacks, the origin of 17 juveniles that fledged and survived from the 2000–2001 cohort were unknown but were subsequently assigned to 6 breeding pairs with >90% confidence using an assignment program (Dodds et al. 2005; Taylor S, Jamieson I, unpublished data). Similarly, the origin of 27 of 38 juvenile saddlebacks from the 2001–2002 cohort were unknown, but 18 were subsequently assigned among 14 breeding pairs; the remaining 10 juveniles that could not be confidently assigned were left out of the analysis. Since the 2002 breeding season, virtually all saddleback (96%, n = 266) have been banded and bled in the nest or in their natal territory. Our annual monitoring program started in the spring (September) and continued through to early autumn (March).

Both saddlebacks and robins can be sexed as adults based on courtship feeding and incubation behavior (Armstrong et al. 2000; Armstrong 2001; Hooson and Jamieson 2003b). For 13 saddlebacks for which we had no behavioral data (9 were new 2000; Armstrong 2001; Hooson and Jamieson 2003b). For 13 saddlebacks for which we had no behavioral data (9 were new 2000–2001 cohort were unknown but were subsequently assigned to 6 breeding pairs with >90% confidence using an assignment program (Dodds et al. 2005; Taylor S, Jamieson I, unpublished data). Similarly, the origin of 27 of 38 juvenile saddlebacks from the 2001–2002 cohort were unknown, but 18 were subsequently assigned among 14 breeding pairs; the remaining 10 juveniles that could not be confidently assigned were left out of the analysis. Since the 2002 breeding season, virtually all saddleback (96%, n = 266) have been banded and bled in the nest or in their natal territory. Our annual monitoring program started in the spring (September) and continued through to early autumn (March).

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**Tiritiri Matangi Island**

Tiritiri Matangi Island (220 ha, 36°36′ S, 174°53′) is located in the Hauraki Gulf, 28 km north of Auckland, and is an open sanctuary under the control of the Department of Conservation. Tiri has undergone an extensive vegetation regeneration program, eradication of Pacific rats *Rattus exulans*, and reintroduction of several native birds (Armstrong 1999–2007). Forty-four banded robins were translocated from a mainland site near the city of Rotorua on the North Island, to Tiri in April 1992, and a further 14 banded robins were translocated in June 1993 (Armstrong 1995). The sex ratio in the first release was male biased; only 7 of the 33 birds that survived to the start of the first breeding season (1992–1993) were females. All 7 females acquired mates, but only 2 successfully fledged young (2 each) in the first breeding season. A follow-up translocation in 1993 increased the number of released adults alive at the beginning of the second breeding season (1993–1994) to 12 females and 21 males (Armstrong and Ewen 2001). The robin population has been monitored for 15 years, and nestlings were banded in all years except 1997–1998. This 1 year without banding created a major gap in our pedigree data, and thus, our analysis covers the first 6 years only, for which we knew the parents for all but 1 bird (99%, n = 145). The breeding population on Tiri reached a carrying capacity of about 65 robins by 1996/1997 (Armstrong and Ewen 2002). There have been no known cases of banded robins from the island being sighted on the mainland, approximately 3.5 km away.

**Estimates of inbreeding using pedigrees**

We constructed pedigrees of robin and saddleback populations assuming that the adults attending a nest were the genetic parents. Molecular studies of saddlebacks and robins on Ulva Island have indicated that EPFs are absent or extremely rare in both species. We found 0 incidences of EPFs in saddlebacks over 39 pair-years and 202 offspring sampled over a 4-year period, and 0 incidences in robins over 26 pair-years and 88 offspring over the same time period (Taylor et al. 2008). A previously published study found no evidence of EPFs in 16 robin pairs in 29 offspring on Tiri (Ardern et al. 1997). Similar findings have been found in 3 other robin populations in New Zealand (Ardern et al. 1997; Taylor et al. 2008). Although we cannot rule out that females engaged in extrapair copulation that did not lead to fertilizations, there is no evidence that saddlebacks or robins exhibit mate-guarding behavior.

From the pedigrees, we calculated inbreeding coefficients ($f$) for individual birds and kinship coefficients for breeding pairs ($f_{ij} =$ of their offspring) using PEDSYS (http://www.sfbr.org) with the Stevens-Boyce algorithm option (Boyce 1983). All inbreeding and kinship coefficients are relative to the founding birds, which are assumed to be unrelated and $f = 0$ (see Keller and Arcese 1998).

**Estimates of pairwise relatedness using microsatellite DNA**

Estimates of relatedness using microsatellite DNA were carried out on robins and saddlebacks on Ulva Island only, where blood samples had been collected as part of the paternity study (see above) plus other related work. Although levels of genetic variation were relatively low for both species (expected heterozygosity for saddlebacks and robins was 0.489 and 0.483, respectively (Boessenkool et al. 2007; Taylor and Jamieson 2007b), we nevertheless investigated whether there was any evidence that saddlebacks and robins were choosing genetically dissimilar mates relative to the average genotype available at the time of pairing.

DNA was extracted from blood using a Chelex resin protocol, and variation at microsatellite loci was investigated with denaturing and non-denaturing gels using standard protocols (see Taylor et al. 2007). MicroChecker (Van Oosterhout et al. 2004) was used to determine the likelihood of large allele dropout, null alleles, and scoring error due to stuttering. Genepop v3.4 (Raymond and Rousset 1995) was then used to check for deviations from Hardy–Weinberg equilibrium and linkage disequilibrium. Saddlebacks and robins were genotyped at 7 (Hru6, Pgm1, Pca08, Pca15, K13/14, Ase18, and CK5A4B) and 10 (2F9, Pca12, Pca13, Pgm3, Escu6, Pocc6, Ase18, GgaMut128, Indigo 28, and Ase64) polymorphic loci respectively. Genotypic data were missing for 2–7 saddlebacks, depending on the year, and could not be included in the pairwise-related analysis. Pairwise relatedness coefficients ($r$) were determined by the program Mark v2.1, using Wang’s (2002) estimator for relatedness, which performs well with small sample sizes and low levels of polymorphism.

**Expected inbreeding and pairwise relatedness under random mating**

We compared the mean inbreeding coefficient for all observed breeding pairs in any 1 year with the mean inbreeding coefficient expected under a random mating model. The latter was derived by pairing every locally available female with every locally available male (including her actual mate) in each year and calculating the mean from the resulting set of inbreeding coefficients. Available birds included those that paired for the first time, single birds, and those whose previous mates were not alive at the start of the breeding season, within the local population (Ulva or Tiri). We do not know the exact time when pairing occurs; thus, we simply quantified the availability of birds at the beginning of the breeding season of each year. Breeding pairs form over winter and are defending territories...
by the time we arrive at the study sites in early spring, although there were always a few unpaired birds each breeding season. A similar approach was used to estimate mean relatedness coefficients ($r$) for random matings. For both mean inbreeding and relatedness calculations, each year was analyzed separately because the resulting values were dependent on the birds that were available for mating, and the composition and size of this group changed from year to year. However, because sample sizes were small in some years, we also pooled data across years to increase statistical power.

Note that our approach assumes that birds that were paired with their previous mate were unavailable for remating because saddlebacks and robins have very high mate fidelity, ranging from 98% for saddlebacks on Ulva ($n = 88$ pairs), 94% for robins on Ulva, to 85% for robins on Tiri ($n = 48$ pairs). Some saddlebacks paired and settled on territories in their first year but did not normally breed until their second year. We included in our analysis first-year saddlebacks that had paired because 95% ($n = 20$) of these remained together and bred the following year. Robins pair and breed in their first year.

We believe our analysis is unaffected by temporal (e.g., spring migration/arrival; Pärt 1996), spatial (e.g., pairing with nearest neighbors; Keller and Arcese 1998), or social structuring (e.g., dispersing within family groups; Van de Casteele and Matthysen 2006) of available mates on our island study sites. All recruits originate from within the island populations (i.e., there are no adjacent populations on the mainland), and juveniles leave their parents’ territory soon after fledging to move widely in search for potential mates across the whole island. For example, individually banded juvenile robins have been observed at both ends of an island on a single day.

Statistical analysis

Because both the observed and expected levels of inbreeding are skewed toward 0, we used a randomization approach to test whether mean inbreeding coefficients, frequency of inbreeding with close/familiar kin, and mean relatedness of observed pairs were significantly different from those of randomly generated available pairs (see Keller and Arcese 1998; Wheelwright et al. 2006; Hansson et al. 2007). We constrained the number of randomly sampled pairs to equal the number of observed pairs for each year of the analysis. We then compared the mean inbreeding coefficients or % of close relatives of observed and random samples and repeated this sampling procedure 10,000 times. Because our main hypothesis was that robins and saddlebacks should avoid inbreeding or should pair with genetically dissimilar mates, we recorded the proportion of observed samples that was less than the randomized samples and subtracted from 1. This yielded the probability that the value for observed pairs was less than what was expected from a random mating distribution (i.e., 1-tailed test), with $P \leq 0.05$ indicating that pairs were significantly less inbred, or more genetically dissimilar, than what would be expected by chance.

The randomization macro developed in Microsoft Excel was unable to analyze observed yearly means based on sample sizes of 4 or fewer pairs, and thus, we excluded years with fewer than 5 pairs. The minimum proportion of related pairs ($f > 0$) that could form in any 1 year ranged from 12.5% to 16% across the 3 populations; thus, there was always the opportunity of inbreeding, and hence, inbreeding avoidance could occur. The probability of mating with close relatives ($f = 0.25$) in any 1 year was substantially lower (3.4–9.4%) but was never 0.

RESULTS

Is pairing with close relatives avoided?

Because mostly founding birds bred in the first 2 seasons after release, we began our analysis in the third year after release for the Ulva (2002) and Tiri populations (1995). Once first-generation birds started breeding, the mean level of inbreeding for new pairs gradually increased over 4 years for robins on Ulva but declined over 3 years for robins on Tiri (Table 1). The difference between the 2 populations was a result of a difference in the relative frequency of close

Table 1

<table>
<thead>
<tr>
<th>Species</th>
<th>Site</th>
<th>Year</th>
<th>No. of observed pairs</th>
<th>Mean observed pairs $f$</th>
<th>No. of random pairs</th>
<th>Mean random pairs $f$</th>
<th>$P$</th>
<th>No. (%) observed pairs $f = 0.25$</th>
<th>No. (%) random pairs $f = 0.25$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Robin</td>
<td>Tiriti</td>
<td>1995</td>
<td>13</td>
<td>0.063 ± 0.030</td>
<td>288</td>
<td>0.021 ± 0.0035</td>
<td>0.99*</td>
<td>3 (23.1)</td>
<td>16 (5.5)</td>
<td>0.99*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1996</td>
<td>10</td>
<td>0.045 ± 0.026</td>
<td>207</td>
<td>0.024 ± 0.0042</td>
<td>0.87</td>
<td>1 (10.0)</td>
<td>10 (4.8)</td>
<td>0.92</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1997</td>
<td>13</td>
<td>0.022 ± 0.019</td>
<td>286</td>
<td>0.027 ± 0.0040</td>
<td>0.42</td>
<td>1 (7.1)</td>
<td>19 (6.6)</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1995–1997</td>
<td>36</td>
<td>0.043 ± 0.015</td>
<td>781</td>
<td>0.024 ± 0.0022</td>
<td>0.96*</td>
<td>5 (13.9)</td>
<td>45 (5.8)</td>
<td>0.99*</td>
</tr>
<tr>
<td>Robin</td>
<td>Ulva</td>
<td>2002</td>
<td>8</td>
<td>0 ± 0</td>
<td>64</td>
<td>0.031 ± 0.0096</td>
<td>0.25</td>
<td>0 (0)</td>
<td>3 (10.5)</td>
<td>0.43</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2003</td>
<td>10</td>
<td>0.020 ± 0.0082</td>
<td>90</td>
<td>0.053 ± 0.0075</td>
<td>0.05*</td>
<td>0 (0)</td>
<td>7 (7.8)</td>
<td>0.43</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2004</td>
<td>17</td>
<td>0.057 ± 0.015</td>
<td>255</td>
<td>0.050 ± 0.0038</td>
<td>0.46</td>
<td>1 (5.9)</td>
<td>11 (4.5)</td>
<td>0.84</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2005</td>
<td>33</td>
<td>0.074 ± 0.010</td>
<td>960</td>
<td>0.070 ± 0.0018</td>
<td>0.68</td>
<td>2 (6.1)</td>
<td>37 (3.9)</td>
<td>0.84</td>
</tr>
<tr>
<td>Saddleback</td>
<td>Ulva</td>
<td>2002</td>
<td>7</td>
<td>0.036 ± 0.036</td>
<td>144</td>
<td>0.020 ± 0.0051</td>
<td>0.84</td>
<td>1 (14.3)</td>
<td>8 (5.5)</td>
<td>0.95</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2003</td>
<td>7</td>
<td>0 ± 0</td>
<td>180</td>
<td>0.031 ± 0.0056</td>
<td>0.28</td>
<td>0 (0)</td>
<td>16 (8.9)</td>
<td>0.52</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2004</td>
<td>10</td>
<td>0.028 ± 0.014</td>
<td>300</td>
<td>0.030 ± 0.0036</td>
<td>0.55</td>
<td>0 (0)</td>
<td>15 (5.0)</td>
<td>0.59</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2005</td>
<td>13</td>
<td>0.050 ± 0.020</td>
<td>1470</td>
<td>0.029 ± 0.0014</td>
<td>0.92</td>
<td>1 (7.7)</td>
<td>50 (3.4)</td>
<td>0.94</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2002–2005</td>
<td>37</td>
<td>0.032 ± 0.010</td>
<td>2994</td>
<td>0.029 ± 0.0013</td>
<td>0.67</td>
<td>2 (3.4)</td>
<td>89 (4.5)</td>
<td>0.79</td>
</tr>
</tbody>
</table>

$P$ refers to probabilities generated by randomization tests (10,000 runs each) for observed pair values being less than randomly generated pair values, thus indicating inbreeding avoidance, with significance levels set at $P < 0.05$. The analysis was a 1-tailed test (i.e., the observed value was “less than” expected from random), so years that yielded high $P$ values ($>0.95$) were reanalyzed to determine whether there was evidence for a preference for inbreeding (i.e., the observed value was “greater than” expected from random). Significant $P$ values for either inbreeding avoidance or preference are indicated with asterisks.
inbreeding \((f = 0.25)\) while the total number of breeding pairs was initially small. On Ulva, the level of inbreeding slowly increased, but there were initially no incidents of close inbreeding. By contrast, the frequency of close inbreeding on Tiri was initially high (3 of 13 new pairs in 1995), but declined thereafter, resulting in an overall decline in mean inbreeding levels for new pairs (Table 1). For saddlebacks on Ulva, the level of inbreeding remained relatively constant (Table 1).

We calculated 2 indices of inbreeding avoidance: comparison of mean inbreeding coefficients and percentage of inbreeding coefficients where \(f = 0.25\), for observed and randomly generated new pairs. The latter index aims to account for the possibility that birds might avoid pairing with close relatives only. When data were pooled across years, there was evidence that the mean level of inbreeding for Ulva robins was significantly lower than expected based on random mating, but this pattern appears to be primarily the result of data from 1 year (2003) when the observed mean was lower than the randomly generated mean in 9457 out of 10 000 randomizations \((N = 10\) pairs, \(P = 0.05\)) (Table 1). There were no such patterns in the following 2 years when the pool of available mates was larger \((2004: \ n = 17, 5409/10\ 000\ randomizations, \ P = 0.46; 2005: \ n = 33, 3227/10\ 000\ randomizations, \ P = 0.68)\). Furthermore, there was no indication that birds were avoiding pairing with close relatives at \(f = 0.25\) (Table 1).

The pooled data for Tiri robins also showed a significant departure from random, but in this case, the mean level of inbreeding was higher than expected, as a result of birds pairing with close relatives \((f = 0.25)\) at a greater frequency than was expected from random mating (Table 1). Again, this difference in the mean level of inbreeding was evident in the first year of the analysis \((1995: \ n = 13, 9803/10\ 000\ randomizations, \ P = 0.02)\), with a weaker trend in the second year \((1996: \ n = 10, 8689/10\ 000\ randomizations, \ P = 0.13)\), but not in the last year \((1997: \ n = 13, 3658/10\ 000\ randomizations, \ P = 0.63)\) (Table 1). There was no evidence in the yearly or pooled data of saddleback pairings departing significantly from random (Table 1). In summary, of a total of 11 population-years for which we ran randomization tests, 1 showed evidence of inbreeding avoidance, 1 showed evidence of inbreeding preference, and 9 were consistent with random mating.

It is worth noting that even when the frequency of observed pairings between close relatives \((f = 0.25)\) was very low (i.e., close to 0), the expected percentage of pairings between close relatives was also low because of the relatively small pool of close relatives that were available as mates. This meant that the likelihood of being able to reject the random mating hypothesis using the randomization tests with significance levels set at \(P \leq 0.05\) was low, especially in the case of saddlebacks. For example, based on randomization tests for the pooled data, the probability of observing 0 closely related pairings would have been 0.04 for Ulva robins assuming random mating (3 were actually observed), but for Ulva saddlebacks, the probability of observing 0 closely related pairings would have been 0.22 (2 were observed; Table 1). Nevertheless, the pooled percentage of pairings between close relatives was either very similar or slightly higher than that expected from random mating (Table 1), suggesting there was little evidence of consistent avoidance of close kin.

According to the asymmetrical incest avoidance model of female mate choice, pairings between mothers and sons or between sisters and brothers (from the same nest) are expected to be uncommon, but pairings between daughters and fathers are expected to be even less common. This is because asymmetries in complete knowledge of close kin occur as a consequence of juveniles maturing and molting into adult plumages and dispersing from their natal area. For example, daughters are more likely to recognize their fathers than mothers or sisters are likely to recognize their mature sons or brothers, which are likely to have dispersed as juveniles. It is also expected that incestuous pairings should involve more young males and older females due to the lower costs of age-specific inbreeding (for details see Wheelwright et al. 2006).

Of the 10 cases of incestuous pairings \((f = 0.25)\), 1 was between a mother and her son, 1 between a daughter and her father, 3 between siblings (brothers and sisters) that shared the same nest, and 5 were between siblings hatched in different years and therefore would not be socially familiar with each other. The proportion of unfamiliar sibling pairings of the total number possible from the randomly generated pairings \((5.7\%)\) was lower than the proportion of familiar sibling pairings \((11.5\%)\), which is in the opposite direction to that expected if females were avoiding close kin based on associative learning cues. The proportions of incestuous pairings among the 3 classes of familiar kin: sister–brother that shared a nest \((60\%)\), mother–son \((20\%)\), and daughter–father \((20\%)\) are similar to those expected by chance: of the 44 cases of randomly generated incestuous pairings that were possible in the same year as the observed cases, 59% were sister–brother (from the same nest), 16% were mother–son, and 25% were daughter–father. The age at which these incestuous pairings first occurred were evenly spread between the sexes: 4 1-year-old and a 6-year-old males and 4 1-year-old and a 4-year-old females. Finally, all of the above pairings lasted until 1 member of the pair died, that is, there was no evidence that incestuous pairings were of a short-term nature.

Is pairing with genetically similar mates avoided?

There is no evidence that saddlebacks or robins on Ulva Island choose genetically dissimilar mates (Table 2) (There was no DNA data from Tiri.) Saddlebacks in the 2000/2001 breeding season (founding individuals) showed the greatest departure from random mating (toward genetically dissimilar mates), but the pattern was not statistically significant \((P = 0.078)\). In all subsequent years, and with larger sample sizes, a random mating pattern with respect to genetic relatedness was much more evident for both species (Table 2).

**DISCUSSION**

Inbreeding in this study was defined as either pairing with relatives (including close kin) based on pedigrees or pairing with genetically similar mates based on microsatellite data. Our prediction was the inbreeding avoidance should be evident in our 2 study species, but the results of our analyses were mixed. In only 1 of the 11 population-years did we find evidence consistent with inbreeding avoidance. This occurred in a year when the pool of available mates was small and, if anything, we would have expected that inbreeding would be more common in such years because there would have been fewer choices of mates (but see below). We also found evidence of a preference for close relatives in 1 of the years. A preference for pairing with relatives in the Tiri robin population was unexpected, especially given that close inbreeding has a substantial cost on juvenile survival (Jamieson et al. 2007). However, the most common pairing pattern over all breeding seasons was random mating, leading us to believe that the relatively few cases of inbreeding avoidance and preference may have been spurious. Finally, although sample sizes were small, there was no evidence of asymmetrical incest avoidance (Wheelwright et al. 2006). When all the results are taken together, it appears that robins and saddlebacks normally chose their mates randomly with respect to relatedness or genetic similarity. Although this conclusion is contrary to the general expectation that animals...
should exhibit inbreeding avoidance mechanisms when dispersal options are limited (Waser et al. 1986; Pusey and Wolf 1996), it is consistent with many recent studies that indicate random mating may be common (Hansson et al. 2007).

Our study does differ from others in that we focused on species that had been recently reintroduced into areas of their former natural range. Although reintroduced populations start off with small numbers of birds, there is no evidence that this in itself caused a change in the mating behavior or the mating system of the study species. Indeed, our study system has several advantages that increase our confidence that random mating is the norm. Inaccurate pedigrees due to high levels of extrapair matings are a potential problem affecting many studies of inbreeding avoidance. Past and concurrent molecular studies have shown that saddlebacks and robins have extremely low rates of extrapair matings; indeed, no EPFs were detected in either species at our 2 study sites (Ardern et al. 1997; Taylor et al. 2004). We therefore conclude that not only were our pedigrees accurate and sufficiently deep (i.e., extended back to when the islands were first ‘colonized’), but also that the potential problem with our study as with most others of this kind is that the exact timing and order of pairing in each population is unknown. It is possible that early in the season individuals avoid pairing with close relatives through associative learning by offspring and by siblings.

Other problems identified in previous studies with constructing a proper null model of random mating for testing inbreeding avoidance (Pärt 1996; Keller and Arcese 1998) are unlikely to apply to our study species. For example, temporal variation in availability of mates due to variation in arrival after migration (Pärt 1996; Kruuk et al. 2002) is not an issue for these nonmigratory species, which also experienced no immigration from the mainland. In other species, the effective number of available mates is thought to be restricted to nearest neighbors where there is high annual turnover of pairs and high rates of pairing (Keller and Arcese 1998), but again this does not apply to our study species. One potential problem with our study as with most others of this kind is that the exact timing and order of pairing in each population is unknown. It is possible that early in the season individuals avoid pairing with close relatives, but as the season progresses and the number of available mates decline, the few remaining birds are forced to pair with close relatives (Kruuk et al. 2002). Again, because robins and saddlebacks are nonmigratory and do not exhibit long-distance dispersal, we believe juveniles that fledged 7–11 months previously would have plenty of time to locate a nonrelative and establish a pair bond if inbreeding avoidance was occurring. Casual observations suggest that pairing occurs in autumn or over winter, and by the time we arrive at the study sites in early spring, pairs are already established and defending territories. Also, if inbred matings occurred as a “best of a bad situation” such that they are perceived to be suboptimal by both individuals, one would also expect divorce when better opportunities arise, yet the pattern of lifelong monogamy persisted for inbred or even incestuous pairings.

Models that have examined the trade-offs between mate choice, mating system, and inbreeding avoidance predict the threshold for inbreeding tolerance should be 0 under strict monogamy (Lehmann and Perrin 2003), or more precisely, the threshold for inbreeding tolerance should be very low if an individual loses outbred mating opportunities by mating with a relative (Waser et al. 1986; Kokko and Ots 2006). Based on this plus other life-history traits (i.e., strong philopatry, lifelong partner bonds with biparental care, no extrapair matings and a relatively long lifespan) and that moderate inbreeding depression has been detected in at least 1 of our study populations (Jamieson et al. 2007), we predicted that saddlebacks and robins should be intolerant of close inbreeding. Our results, as with several other avian studies of inbreeding (see below), are contrary to the above predictions and instead supported a random mating model.

The likelihood of species evolving inbreeding avoidance through kin recognition and discrimination appears to be generally stronger in mammals than birds possibly because of the former group’s greater sense of smell (Pusey and Wolf 1996). Nevertheless, birds are capable of discriminating kin through other mechanisms such as plumage and song (Bateson 1982; Petrie et al. 1999; Russell and Hatchwell 2001; see also Reid 2007 for an unusual causal route from song to relatedness). Yet despite there being strong evidence for the costs of inbreeding in wild populations (Keller and Waller 2002), this study and others (e.g., Keller and Arcese 1998; Hansson et al. 2007) have found no evidence that females avoided pairing with close kin that they should recognize through associative learning.

So why have not kin recognition mechanisms evolved given the apparent high fitness costs of close inbreeding? Some have noted that the costs of avoiding inbreeding may be greater than the costs of tolerating it (Pärt 1996; Keller and Arcese 1998). The costs of inbreeding avoidance include delayed or missed opportunities for breeding or attaining a territory. However, because robins and saddlebacks tend to pair for life, the costs of tolerating inbreeding are likely to be significant compared with the costs of avoiding inbreeding. Hansson et al. (2007) came to a similar conclusion about great reed warblers (Acrocephalus arundinaceus); if dispersal opportunities

### Table 2

Comparisons of mean genetic relatedness between observed new pairs and randomly generated pairs for robins and saddlebacks on Ulva Island

<table>
<thead>
<tr>
<th>Species</th>
<th>Year</th>
<th>Observed pair relatedness (mean ± SE)</th>
<th>Random pair relatedness (mean ± SE)</th>
<th>n</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Robins</td>
<td>2002</td>
<td>0.07 ± 0.047</td>
<td>0.05 ± 0.020</td>
<td>7</td>
<td>0.80</td>
</tr>
<tr>
<td></td>
<td>2003</td>
<td>−0.12 ± 0.073</td>
<td>−0.05 ± 0.025</td>
<td>10</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>2004</td>
<td>−0.07 ± 0.068</td>
<td>−0.05 ± 0.015</td>
<td>17</td>
<td>0.23</td>
</tr>
<tr>
<td>Saddlebacks</td>
<td>2000</td>
<td>−0.11 ± 0.12</td>
<td>0.04 ± 0.048</td>
<td>5</td>
<td>0.078</td>
</tr>
<tr>
<td></td>
<td>2001</td>
<td>0.03 ± 0.085</td>
<td>0.05 ± 0.022</td>
<td>12</td>
<td>0.36</td>
</tr>
<tr>
<td></td>
<td>2002</td>
<td>0.04 ± 0.056</td>
<td>0.01 ± 0.012</td>
<td>22</td>
<td>0.72</td>
</tr>
<tr>
<td></td>
<td>2003</td>
<td>0.02 ± 0.053</td>
<td>0.02 ± 0.014</td>
<td>29</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td>2004</td>
<td>0.02 ± 0.048</td>
<td>0.03 ± 0.011</td>
<td>35</td>
<td>0.43</td>
</tr>
</tbody>
</table>

Genetic relatedness is based on Wang’s (2002) estimator. A negative pairwise relatedness value means that the 2 individuals are less related to each other than are 2 individuals chosen at random from the population. P values were generated by randomization tests as described in Table 1.
are limited and close kin are likely to regularly reside together, then kin discrimination should evolve to avoid close inbreeding, yet they too did not detect inbreeding avoidance.

More recently, Kokko and Ots (2006) have argued that inbreeding should be favored when the benefits outweigh the costs (i.e., kin selection), assuming that additional (inbred) matings do not harm overall mating success. In cases where the costs and benefits end up balancing, however, selection pressure to “prefer” or “avoid” mating becomes weak, including selection for kin recognition mechanisms. The costs of inbreeding would appear to be substantial in strictly monogamous breeders such as saddlesaddles and robins, but Kokko and Ots (2006) also note that kin recognition would fail to evolve if animals do not typically encounter kin in a mating context.

We believe this latter point may be the key to resolving this issue. Instead of focusing only on the cost/benefits of inbreeding, we also need to consider the predicted encounter rate with close kin. First, we note that encounter rates with close kin will be substantially higher in cooperative breeding species than in noncooperative, singular-pair species. A literature search for studies of inbreeding avoidance specifically using pedigree data from wild bird populations indicates that all but 1 species of singular-pair breeding showed evidence of random mating, whereas cooperatively breeding species showed evidence of inbreeding avoidance via kin discrimination (Table 3A). This list does not include studies of inbreeding and dispersal for which the results are also consistent with random mating (e.g., Szulkin and Sheldon 2007). Evidence for inbreeding avoidance based on mating preference for genetically dissimilar partners is also limited in singular breeders, although the overall pattern is more variable (Table 3B; see also Kempenaers 2007).

Second, Hansson et al. (2007) and Keller and Arcese (1998) have noted that inbreeding avoidance studies tend to be conducted on island or isolated mainland populations and that these may not be representative of larger populations on the

<table>
<thead>
<tr>
<th>Species</th>
<th>Social system</th>
<th>Inbreeding avoidance</th>
<th>Evidence</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A) Mate choice via kin discrimination (based on pedigree data)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Long-tailed tit</td>
<td>Cooperative</td>
<td>Yes</td>
<td>Forgo breeding with kin</td>
<td>Hatchwell et al. (2000)</td>
</tr>
<tr>
<td>Acorn woodpecker</td>
<td>Cooperative</td>
<td>Yes</td>
<td>Forgo breeding with kin</td>
<td>Koenig et al. (1999); Haydock et al. (2001)</td>
</tr>
<tr>
<td>Red-cockaded woodpecker</td>
<td>Cooperative</td>
<td>Yes</td>
<td>Forgo breeding with kin</td>
<td>Daniels and Walters (2000)</td>
</tr>
<tr>
<td>Superb fairy-wren</td>
<td>Cooperative</td>
<td>Yes</td>
<td>Forgo breeding with kin</td>
<td>Cockburn et al. (2003)</td>
</tr>
<tr>
<td>Savannah sparrow</td>
<td>Single pairs</td>
<td>Yes</td>
<td>Nonrandom mate choice</td>
<td>Wheelwright et al. (2006)</td>
</tr>
<tr>
<td>Great tit</td>
<td>Single pairs</td>
<td>No</td>
<td>Random mate choice</td>
<td>Van Tienderen and van Noordwijk (1988)</td>
</tr>
<tr>
<td>Medium ground finch</td>
<td>Single pairs</td>
<td>No</td>
<td>Random mate choice</td>
<td>Gibbs and Grant (1989)</td>
</tr>
<tr>
<td>Collared flycatcher</td>
<td>Single pairs</td>
<td>No</td>
<td>Random mate choice</td>
<td>Párt (1996)</td>
</tr>
<tr>
<td>Great reed warbler</td>
<td>Single pairs</td>
<td>No</td>
<td>Random mate choice</td>
<td>Hansson et al. (2007)</td>
</tr>
<tr>
<td>NZ robin</td>
<td>Single pairs</td>
<td>No</td>
<td>Random mate choice</td>
<td>This study</td>
</tr>
<tr>
<td>NZ saddleback</td>
<td>Single pairs</td>
<td>No</td>
<td>Random mate choice</td>
<td>This study</td>
</tr>
</tbody>
</table>

| (B) Mate choice via genetic dissimilarity (based on molecular data) |
| Splendid fairy-wren | Cooperative | Yes | Nonrandom EPM | Tarvin et al. (2005) |
| Mexican jay | Cooperative | Yes | Nonrandom EPM | Eimes et al. (2004) |
| Grey-crowned babblers | Cooperative | Yes | Forgo breeding with kin, EPM | Blackmore and Heinsohn (2008) |
| Seychelles warbler | Cooperative | No | Random mate choice, EPM (and MHC)* | Richardson et al. (2004, 2005) |
| Savannah sparrow | Single pairs | Yes | Nonrandom mate choice (MHC), EPM | Freeman-Gallant et al. (2003, 2006) |
| House finch | Single pairs | Yes | Nonrandom EPM | Oh and Badyaev (2006) |
| Shorebirds (3 spp.) | Single pairs | Yes | Nonrandom EPM | Blomqvist et al. (2002) |
| Frigatebird | Single pairs | No | Nonrandom mate choice b | Cohen and Dearborn (2004) |
| Barn swallows | Single pairs | No | Nonrandom EPM b | Kleven et al. (2005) |
| Great reed warbler | Single pairs | No | Random mate choice, EPM (and MHC) | Hanson et al. (2004, 2007); Westerdahl (2004) |
| Blue tit | Single pairs | No | Random mate choice, EPM | Foerster et al. (2006) |
| Coal tit | Single pairs | No | Random EPM | Schmoll et al. (2005) |
| Reed bunting | Single pairs | No | Random EPM | Kleven and Lifjeld (2005) |
| Superb starling | Single pairs | No | Random mate choice | Rubenstein (2007) |
| House sparrow | Single pairs | No | Random mate choice, EPM | Edly-Wright et al. (2007) |
| NZ robin | Single pairs | No | Random mate choice | This study |
| NZ saddleback | Single pairs | No | Random mate choice | This study |

Genetic dissimilarity was based on measures of relatedness (r) between social mates and/or extrapair mates (EPM) using micro or minisatellite DNA unless otherwise noted (e.g., major histocompatibility complex (MHC) genes). Evidence in the form of random mate choice is in reference to relatedness (e.g., females were no less related to EPM than to their social mate) but does not preclude mate choice based on criteria other than relatedness.

a Although primary female Seychelles warblers do not appear to facultatively avoid inbreeding with closely related mates, subordinate females did produce less inbred offspring as a result of indiscriminate extrapair matings (Richardson et al. 2004). There is also no evidence that Seychelles warblers show MHC-based social mate choice or extrapair mate choice in terms of disassortative genetic pairing, although MHC diversity of the extrapair male was higher than that of the social mate (Richardson et al. 2005).

b Frigatebirds and barn swallows showed preferences for mating with close kin.
mainland, where rates of dispersal and gene flow are much greater. In large mainland populations, normal encounter rates with close relatives are low, and hence, the chances of pairing with close kin even lower, resulting in weak selection pressure for kin discrimination. Gene flow from larger mainland populations to smaller islands might prevent local adaptation, if kin recognition is selectively favored only in small populations (Keller and Arcese 1998; Keller et al. 2001; Hansson et al. 2007).

To evaluate this argument, one should note that the overall frequency of close inbreeding in our island sites is still relatively low. We agree that the frequency of close inbreeding is likely to be higher on islands than on the mainland, but the encounter rates between close kin in island populations might still be too low to select for kin recognition, especially if kin recognition and discrimination mechanisms for adult breeders are generally associated with significant costs. Examples of such costs when encounter rates with kin are low are the additional mate-searching time/effort required to compare kin with non-kin; this is especially relevant when breeding habitat is near its carrying capacity and additional search effort can potentially lead to loss of a territory and ultimately death. Other types of mate-searching costs are imperfect recognition such that kin might be misidentified as nonkin and certain nonkin individuals might be passed over as suitable mating partners. In light of the above argument, it is interesting to note that the 1 case of inbreeding avoidance we detected (in Ulva robins) occurred when the pool of available mates including close kin was relatively small.

Whatever precise forms these costs take, one may contrast them with the varying benefits of avoidance behavior as the encounter rate with close kin changes. A simple conceptual model (Figure 1) shows that for each mate-sampling behavior, the relative benefits are the smallest when encounter rate with kin is either very low, or very high. This is because near the low end of encounter rate with close kin, the probability of an inbred mating is low regardless of whether mate searching is intensive or not. Likewise, if the encounter rate with close kin is extremely high, the probability of an inbred mating is not substantially reduced no matter how intensive mate searching is. However, for many mate-searching intensities, the benefits (the vertical difference between the diagonal and the curves in Figure 1a) stay substantial larger to the high than the low end of the kin encounter rate. We can conclude that conditions favoring inbreeding avoidance behaviors arise in situations that presumably apply to cooperative breeders, which have ample opportunity to recognize and avoid pairing with close kin by the time they are ready to breed.

This conceptual model shares some features with models proposed to explain variation in the expression of egg recognition and rejection in hosts of brood parasites (Davies et al. 1996). If correct, our model explains why inbreeding avoidance via kin discrimination is commonly observed in cooperative breeders, but not in noncooperative breeders where offspring disperse from their parents’ territory at independence. Whether the initial small founding population of robins on Ulva Island (n = 5 females) resulting from the reintroduction (which was less than half of that of robins on Tiri [n = 12]; see Methods) created a situation where the costs of kin discrimination were relatively low and hence resulted in inbreeding avoidance behavior, remains conjecture at this stage. In addition, our model does not rule out the importance of individual recognition in some noncooperative species of birds (e.g., petrels, Bonadonna et al. 2007) or the role of natal dispersal in facilitating inbreeding avoidance, which coupled with significant inbreeding depression, suggests that inbreeding avoidance could have played a major role in the shaping of the evolution of dispersal (Schieg et al. 2006; Szulkin and Sheldon 2007).

**Figure 1**

A model of the probability of avoiding inbreeding as a function of encounter rate with close kin and mate-searching effort. (A) The probability of a mate being close kin as a function of encounter rate with close kin for various mate-searching effort (i.e., sampling 2, 3, or 10 potential mates). Under a random mating strategy, the probability that a mate is a close kin equals the encounter rate with close kin. Increasing effort (number of mates sampled = n) with the rule “mate with a nonkin if the sample includes one,” leads to a probability α of mating with close kin, where α is the proportion of mates in the population that are related to the searcher. It follows that the benefit of mate search equals the vertical distance between random mating and α, i.e., a = a-α. (B) The costs/benefits of mate searching. The benefit of having spent mate search effort, exemplified here for n = 3, is directly proportional to α-αa, multiplied by the detrimental fitness effects of inbreeding (which we here arbitrarily scale as 1 fitness unit). A fixed cost of sampling together with a bumped benefit, predicts that individuals are likely to sample more potential mates at intermediate and fairly high encounter rates, while random mating should prevail at low and extremely high encounter rates.

**GENERAL CONCLUSIONS**

The main difference between avian species that show inbreeding avoidance via kin discrimination and those that exhibit random mating seems to be the type of social system they exhibit. Inbreeding avoidance is commonly observed in cooperative breeders, which should have a greater encounter rate with kin and a greater opportunity to learn to recognize close kin than noncooperative species, and thus avoid kin when it comes to mating. There is little evidence for inbreeding avoidance through kin discrimination in noncooperative, singular breeding species, with the exception of the Savannah sparrow (*Passerculus sandwichensis*) (Wheelwright and Mauck 1998;
Wheelwright et al. 2006), despite the availability of potential kin recognition mechanisms such as plumage and song (e.g., Bateson 1982). We hypothesized that the regular occurrence of natal dispersal along with random mating (with respect to relatedness) normally results in such low rates of close inbreeding that it exerts negligible selection pressure to evolve kin recognition, especially when kin recognition plays no part in other aspects of social behavior.

Finally, our results and conclusions have implications for conservation and management of endangered species. Most inbreeding in threatened wild populations is assumed to arise as an inevitable consequence of small population size (Frankham et al. 2002). Population viability models usually ignore inbreeding avoidance, instead employing the assumption of random mating. If species show variation in inbreeding avoidance, then the accuracy of these assumptions will depend on the mating system of the endangered species in question. Our results suggest that at least for socially monogamous birds, many threatened species are unlikely to have a natural “built-in” mechanism for avoiding inbreeding by kin discrimination, and the assumption of random mating may be appropriate and accurately reflect the true rate of inbreeding in small populations. Kin avoidance by cooperative breeders, on the other hand, may lead to slower inbreeding accumulation than models predict, but this can also combine with a possible demographic cost of lost breeding opportunities (Moller and Legende 2001). The balance of these factors is thus far unclear.

**FUNDING**

University of Otago; Department of Conservation (contract no. 3576); Landcare Research (contract no. C09X0503); Ulva Island Trust to L.J.; Massey University; Marsden Fund; Supporters of Tiritiri Matangi Inc. to D.A., and Academy of Finland to H.K.

The authors thank all those involved in the collection of robin and saddleback data on Ulva Island and Tiritiri Matangi Island, and the local area offices of Department of Conservation for logistic support over the period of the study. Meredith Trotter assisted with the development of area offices of Department of Conservation for logistic support over the period of the study. Meredith Trotter assisted with the development of the randomization macro. L.G.J. would like to thank Dave Shuter and colleagues at Acadia University for discussions during his visit there and Mark Hauber from Auckland University for his insightful comments during lunch at the 2007 Evolution meeting.

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