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RESEARCH ARTICLE

Island size predicts the frequency of melanic birds in the color-polymorphic flycatcher *Monarcha castaneiventris* of the Solomon Islands

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ABSTRACT

Observations that similar traits repeatedly evolve across independent taxa on islands—such as loss of flight in birds or reduction of body size in large mammals—suggest that deterministic processes, rather than drift, drive the convergent evolution of these traits. One such repeated pattern on islands that has received little attention is the evolution of entirely black coloration, or “melanism.” In several taxa, including birds, reptiles, and insects, melanism has evolved on islands despite the proximity of mainland populations with different colors. We explored the evolution of melanism on islands by testing how island size predicts the frequency of melanic birds in *Monarcha castaneiventris obscurior*, a subspecies of flycatcher from the Solomon Islands that is polymorphic for plumage color (i.e. melanic vs. chestnut-bellied). While accounting for potential spatial autocorrelation because some islands are <1 km apart, we found that island size predicted the frequency of melanic birds, with smaller islands having higher frequencies of melanism than larger islands. As with other traits that have repeatedly evolved on islands, this pattern suggests that melanism on small islands is likely mediated by deterministic processes like natural selection.

Keywords: color polymorphism, island ecology, melanism, *Monarcha*, spatial autocorrelation

El tamaño de la isla predice la frecuencia de pájaros melánicos en el *Monarcha castaneiventris* con polimorfismo de color en las Islas Salomón

RESUMEN

En islas, ciertos caracteres han evolucionado de manera similar en varios taxones diferentes, como la pérdida de vuelo en pájaros o la reducción de tamaño en mamíferos, lo cual sugiere que la evolución convergente es producto de procesos determinantes en lugar de la deriva genética. Por ejemplo, la evolución de coloración negra conocida como melanismo, presenta un patrón repetitivo encontrado en islas y no ha sido estudiado en detalle. El melanismo ha evolucionado en islas a pesar de su cercanía con poblaciones en tierra firme en varios taxones, incluyendo pájaros, reptiles e insectos. En este estudio, exploramos la evolución del melanismo en islas al investigar si el tamaño de la isla predice la frecuencia de pájaros melánicos en *Monarcha castaneiventris obscurior*, una subespecie de monarca ventricastaño de las Islas Salomón que presenta un polimorfismo en el color del plumaje con variaciones melánicas y castaños. Dado que algunas islas se encuentran a menos de 1 km de distancia una de otra, analizamos el posible efecto de la correlación espacial, y nuestros resultados sugieren que el tamaño de la isla predice la frecuencia de pájaros melánicos en este archipiélago con islas que varían de tamaño. Las islas pequeñas tienen una frecuencia de melanismo mayor que las islas grandes. Al igual que otros caracteres que han evolucionado en islas, este patrón sugiere que el melanismo en islas pequeñas es mediado por procesos determinantes como lo es la selección natural.

Palabras clave: polimorfismo de color, isla ecología, melanismo, *Monarcha*, autocorrelación espacial

INTRODUCTION

Island systems have featured prominently in our understanding of key evolutionary and ecological processes (Darwin 1859, Wallace 1864, Mayr 1942, Diamond 1977, MacArthur and Wilson 1963, Kaneshiro 1980, Grant 1986, Losos et al. 1998). For instance, variation among islands inspired Darwin's (1859) and Wallace's (1864) hypothesis that gradual changes among populations driven by natural selection can accumulate to yield large differences that

result in new species. Similarly, the universal species–area relationship was largely inspired by patterns observed in tropical archipelagoes from a diverse set of taxa (MacArthur and Wilson 1963). More recently, island systems have provided clear evidence for the operation of natural selection in the wild, including the now classic examples of adaptation to feeding in Darwin's finches (Grant and Grant 2007) and convergent evolution of limb morphology in Caribbean lizards in the genus *Anolis* (Losos 2011). As such, island systems remain fertile grounds for testing key

ecological and evolutionary processes (Losos and Ricklefs 2009).

Island populations are often distinct in behavior and morphology from their continental counterparts, and this has been attributed to the unique biotic and abiotic conditions of islands or to the operation of genetic drift in small populations (Losos and Ricklefs 2009). For instance, loss of flight in birds and insects (McNab 1994), and reduction or increase in body size of large and small mammals, respectively (Lomolino 2005), have evolved repeatedly in oceanic islands, which suggests that deterministic processes like natural selection are driving such convergent changes.

One less explored pattern of convergence is the evolution of entirely black coloration, or “melanism,” on islands. Examples of melanism on islands and in other small, peripheral populations include species of birds, reptiles, spiders, and insects (see Table 1). In these examples, island populations evolved entirely black coloration despite being in proximity to larger populations of a different color, where gene flow could prevent the fixation of melanism on small islands. In a few cases, the possible mechanism seems evident, such as selection for more effective thermoregulation (Theron et al. 2001, Tanaka 2007). However, in the majority of cases, the underlying drivers of the recurring evolution of melanism are poorly understood. Given the repeated evolution of this trait in islands across independent taxa (Table 1), melanism may evolve by deterministic processes and not by drift alone.

Because color, typically, is either fixed or nearly fixed between island and mainland populations, the general pattern discerned thus far is that some small island populations evolve darker coloration than their mainland counterparts (see Table 1), making it difficult to test how island size, in itself, predicts the frequency of melanism. Taxa with multiple, coexisting color forms (i.e. color polymorphic) would provide a unique test of how the frequency of melanic individuals is predicted by island size. Here, we test the hypothesis that island size predicts the frequency of melanism by taking advantage of a color-polymorphic avian species found in the Solomon Islands. If small islands favor melanism, we predicted a negative relationship between island size and the frequency of melanic birds, even after controlling for spatial autocorrelation because neighboring islands can be <1 km apart.

METHODS

Study System

In his seminal book on speciation, Ernst Mayr (1942) presented the *Monarcha castaneiventris* flycatcher complex of the Solomon Islands as a case of incipient speciation (see also Mayr and Diamond 2001). There are at least 6 named subspecies in this complex that differ in

body size and plumage color, despite small geographic separation (Mayr 1942, Diamond 2002; Figure 1A). *Monarcha castaneiventris* are insectivorous leaf-gleaners found primarily in the middle and lower strata of forests (Filardi and Smith 2008). They are socially monogamous, and pairs defend breeding or nesting territories from other breeding pairs (Uy et al. 2009a, 2009b). The subspecies in the Russell Islands, *M. c. obscurior*, is unique in being the only population that is polymorphic in plumage color (Mayr 1942; see Figure 1). Individuals of this subspecies typically have chestnut bellies and blue-black upperparts; however, melanic birds coexist with chestnut-bellied birds on a few islands (Mayr 1942; Figure 1). In this subspecies, the sexes do not differ significantly in body size and plumage color (Uy et al. personal observation).

Field Survey

The Whitney South Seas Expedition (WSSE), the most expansive collecting expedition in the South Pacific, sampled scores of islands from New Guinea through Pitcairn Island for more than a decade (1921–1932; Chapman 1935). From July 30 to August 7, 1927, the WSSE visited the Russell Islands of the Solomon Islands and collected from the large islands Pavuvu and Banika, and from the smaller islands Moie and Kiomie (detailed in the field journal of one of the collectors on the expedition, F. C. Drowne, courtesy of the American Museum of Natural History; see Figure 1B). On the largest island, Pavuvu, the WSSE collected 13 *M. c. obscurior* specimens, all with chestnut bellies; on Banika, it collected 1 melanic, 1 mostly melanic, and 11 chestnut-bellied; on Moie, 1 mostly melanic and 3 chestnut-bellied; and on Kiomie, 4 chestnut-bellied specimens. According to Drowne's journal, the WSSE opportunistically collected samples for a few hours on each island, taking birds as they moved from the shore to the interior of the island on trails established by indigenous communities or by workers for large coconut plantations.

We visited the Russell Islands from June 24 through July 1, 2011, sampling the same islands and localities visited by the WSSE (as recorded by Drowne). Similar to the WSSE, we sampled each island by following established trails on the big islands of Banika and Pavuvu, and on the smaller island of Moie, for 4 hr each (0600–1000 hours). We were able to survey the entire islet of Kiomie within 4 hr because of its small size (0.10 km²). We returned to the Russell Islands during October 1–7, 2011, to survey 9 additional islands, for a total of 13 islands surveyed in 2011 (Appendix Table 2). As with the surveys in June, we spent ≥4 hr on each island (0600–1000 hours), either following trails established by indigenous communities ($n = 3$ large islands) or sampling the entire island ($n = 6$ islands; see Appendix Table 2). The 9 additional islands visited in October were likewise opportunistically sampled to match the methods of the WSSE and our sampling of 4 islands earlier in June.

TABLE 1. Examples of melanism evolving on small islands in birds, reptiles, and invertebrates.

Taxa	Alternative color morphs	Frequency of melanism on islands	Evolutionary mechanism	References
Birds				
<i>Coereba flaveola</i>	Yellow and black	Nearly fixed in habitat	Possibly thermoregulation	Theron et al. 2001
<i>Malurus leucopterus</i>	Blue and black	Fixed	Unknown	Doucet et al. 2004
<i>Monarcha castaneiventris obscurior</i>	Chestnut and black	Polymorphic	Unknown	Mayr 1942
<i>M. c. ugiensis</i>	Chestnut and black	Fixed or nearly fixed	Unknown, but evidence for selection	Mayr 1942, Uy et al. 2009b, personal observation
<i>Myzomela</i> spp.	Red and black	Fixed	Unknown	Mayr and Diamond 2001
<i>Rhipidura fuliginosa</i>	Rufous	Nearly fixed	Unknown	Atkinson and Briskie 2007
<i>Turdus poliocephalus</i>	Several other morphs	Fixed	Unknown	Jones and Kennedy 2008
Reptiles				
<i>Elaphe quadrigata</i>	Striped	Nearly fixed	Thermoregulation	Tanaka 2007
<i>Nerodia sipedon</i>	Striped	Polymorphic	Drift, gene flow, and selection for thermoregulation	King 1993
<i>Podarcis lilfordi</i>	Several other morphs, including blue and red	Nearly fixed	Unknown	Buades et al. 2013
<i>Thamnophis sirtalis</i>	Striped	Polymorphic	Drift, gene flow and selection for thermoregulation	Bittner and King 2003
Invertebrates				
<i>Nephila maculata</i>	Yellow and green	Polymorphic	Prey capture and crypsis	Tso et al. 2002
<i>Oeddaeus senegalensis</i>	Green and brown	Nearly fixed	Unknown	Ritchie 1978
<i>Philaenus spumarius</i> (several peripheral and insular populations in Europe)	Six other morphs	Polymorphic	Balancing selection based on thermoregulation and habitat	Berry and Willmer 1986, Brakefield 1990, Halkka et al. 2001

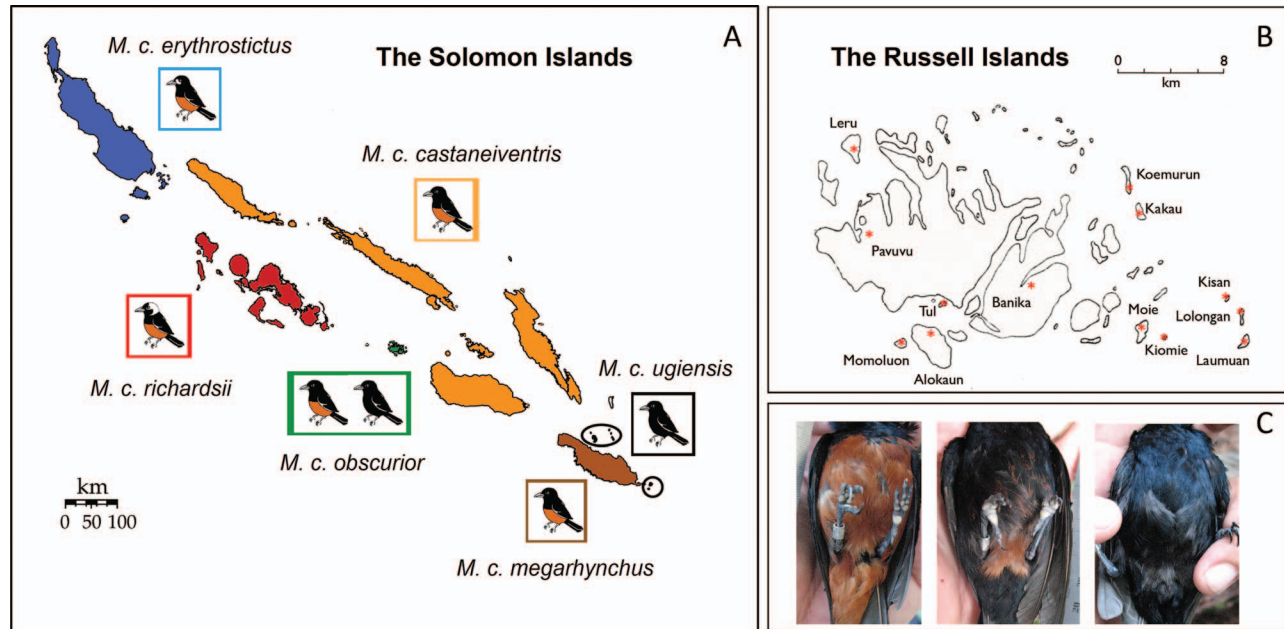


FIGURE 1. Variation in plumage color and distribution of flycatchers in the *Monarcha castaneiventris* species complex. **(A)** Geographic variation among subspecies throughout the Solomon Islands. Six subspecies are shown, but in the present study we focused on *M. c. obscurior* of the Russell Islands, which is the only polymorphic subspecies (green box and islands). **(B)** Map of the Russell Islands. Asterisks indicate the 13 islands sampled in 2011 (Appendix Table 2). **(C)** The color morphs of *M. c. obscurior* (from left to right): chestnut-bellied, mostly melanic, and melanic.

To survey each island, a team of observers, which included J.A.C.U. and 3 local field guides, started at the shore and proceeded into the interior of each island, stopping every 10 min to survey birds immediately around the group. Confirmed *M. castaneiventris* individuals were identified and classified as “chestnut-bellied,” “mostly melanic,” or “melanic” by sighting with binoculars, after complete agreement of the team. Adult *M. c. obscurior* have blue-black upperparts and light, blue-gray bills. While netting birds for a separate long-term study, we captured several immature individuals with dark bills, light chestnut bellies, and gray instead of black upperparts. We did not capture immature individuals lacking the light chestnut belly (i.e. entirely gray). As such, it remains unclear whether all individuals, regardless of their adult plumage color, started as chestnut-bellied and gray before molting into either a chestnut-bellied or a melanic adult. Further, we do not know when individuals acquired their adult plumage, although preliminary mark–recapture data suggest that this would require at least 2–3 yr. Given that we know little about the transition from immature to adult plumage, immature individuals sighted during the surveys were not included in the test of the predictors of the frequency of melanic birds.

The habitats we surveyed were all similar among islands, consisting primarily of secondary forests and mangroves. Because these forests are relatively open, identification and classification of birds were unambiguous. Further, the assistance of local field guides with intimate knowledge of

the islands’ flora and fauna and excellent tracking skills ensured that we found all the *M. c. obscurior* individuals in the vicinity of the group. These included birds that were foraging or not calling. Sampling was conducted only once per island, to avoid counting the same individuals multiple times during subsequent visits.

Establishing a standard transect for the 6 large islands would provide a more unbiased and systematic survey of the relative abundances of chestnut-bellied and melanic *M. c. obscurior* (as in Smucker et al. 2005). However, given the small size of most of the islands (Appendix Table 2), standardized transects were not feasible. Further, *M. castaneiventris* is a very abundant and conspicuous species, and so the opportunistic sampling provided an unbiased estimate of the *M. c. obscurior* color morphs. Note also that some islands had as few as 6 individuals sighted (Appendix Table 2). These numbers may represent a small sample size for statistical tests and be prone to error; however, most of the islets were small, and so the few individuals that we observed likely represented most, if not all, of the birds on that island. That is, we sampled the entire island, and so the sighting of few birds provided a biologically relevant and likely accurate estimate of population composition.

Without knowledge of the genetic basis of melanism, we combined the counts of melanic and mostly melanic birds as a measure of the number of melanic birds, because mostly melanic birds look more like melanic than like

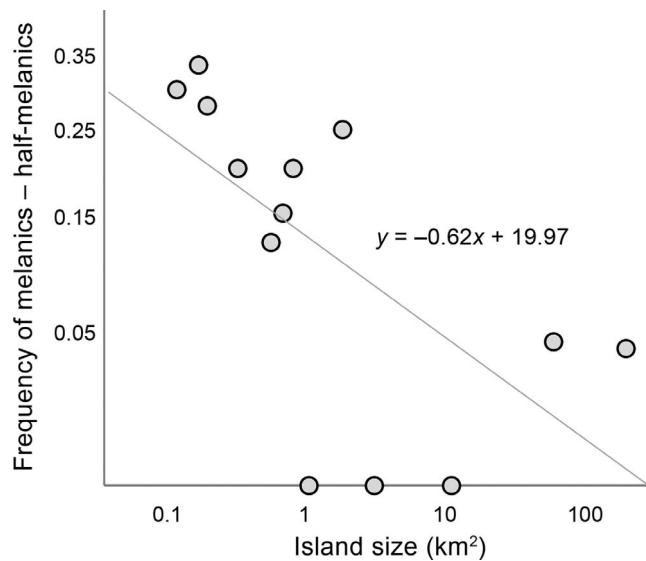


FIGURE 2. Ordinary least squares regression of frequency of melanistic birds (arcsine transformed scale) on island size (log transformed scale).

chestnut-bellied birds. That is, mostly melanistic birds were predominantly black, with a small patch of chestnut at the base of the belly near the cloaca (e.g., see Figure 1C). Frequency of melanistic birds was then calculated as the number of melanistic birds sighted divided by the total number of birds observed. After digitizing a 1:50,000 scale (1 inch = 1 km) map of the Russell Islands provided by the Ministry of Lands, Housing and Surveys, Solomon Islands, we used SigmaScan Pro version 5.0 (Systat, San Jose, California, USA) to quantify the nearest distance between islands and island area. Island area (km²) was log transformed, and the frequency of melanistic birds was arcsine transformed prior to analysis (as recommended by Sokal and Rohlf 1995).

Statistical Analyses

We tested whether island size predicted the frequency of melanism using an ordinary least squares (OLS) regression analysis with log-transformed island size as a predictor and the arcsine transformed frequency of melanistic birds as the dependent variable. Given that some islands are <1 km apart and birds are likely to disperse across these short barriers, the OLS regression model's assumption of independently distributed error could be violated by inherent spatial structuring (Lichstein et al. 2002; reviewed by Kissling and Carl 2008). As such, we tested for spatial autocorrelation by calculating global Moran's *I* (Moran 1950) using the residuals from our OLS regression analysis (as in Kissling and Carl 2008). For calculating Moran's *I*, we generated a matrix of inverse distance weights from the matrix of pairwise nearest distances between islands measured from the digitized map.

Given the possibility of spatial autocorrelation, we also implemented a simultaneous autoregressive model that accounts for spatial error (SAR_{err}) to concurrently consider spatial structuring and island size as predictors of frequency of melanism across islands (as in Kissling and Carl 2008). The SAR_{err} model assumes that the spatial structuring is in the error term, as in cases where the spatial autocorrelation is not fully explained by the explanatory variable (e.g., by island size alone) and is an inherent property of the response variable (e.g., dispersal ability of birds; for details of analysis and model assumptions, see Kissling and Carl 2008). For the SAR_{err} analysis, we used log transformed island area and the matrix of inverse inter-island distance as explanatory variables, and the arcsine transformed frequency of melanistic birds as the dependent variable. We assessed the utility of the OLS regression and the SAR_{err} methods by comparing the maximum model fit for each method (i.e. *R*²). The *R*² value for the SAR_{err} model was calculated using Nagelkerke's (1991) formula (as in Lichstein et al. 2002). Calculation of Moran's *I*, and the OLS regression and SAR_{err} analyses, were implemented in R (R Development Core Team 2005). Scripts for the SAR_{err} analysis were developed by Kissling and Carl (2008). All tests of hypotheses were 2-tailed.

RESULTS

There was considerable variation in the frequency of melanistic birds among the 13 islands sampled across the Russell Archipelago, with some islands having only chestnut-bellied birds while others had as many as one-third of birds with melanistic plumage (Appendix Table 2). An OLS regression analysis indicated that island size predicts the frequency of melanistic birds (*F*_{1, 11} = 7.10, *P* = 0.022; Figure 2). Exploration of the residuals from the OLS regression analysis indicate a nonsignificant effect of spatial structuring in explaining the frequency of melanism on islands (global Moran's *I* = 0.196, *P* = 0.073).

Because some islands are <1 km apart and the analysis of global Moran's *I* indicated a near significant trend for spatial autocorrelation, we also performed a SAR_{err} analysis to simultaneously account for spatial autocorrelation while testing for the effect of island size on the frequency of melanistic birds. The SAR_{err} model indicated that island size indeed predicts the frequency of melanism ($\beta = -0.469$, *z* value = -4.886, *P* << 0.001), while accounting for spatial structure. Further, the likelihood ratio (LR) test for the spatial autoregression coefficient (λ) was significant ($\lambda = 0.844$, LR = 9.210, *P* < 0.002), which suggests that the frequency of melanistic birds is indeed positively correlated among neighboring islands after accounting for variation explained by island size. As such, the SAR_{err} model, which included the effects of island size and spatial autocorrelation, explained more of the variation in the frequency of melanistic birds across islands than the OLS regression model that

considered only island size ($R^2 = 0.508$ for SAR_{err} model vs. 0.334 for the OLS regression model).

DISCUSSION

In the *Monarcha castanieiventris* flycatcher species complex, melanism has evolved independently at least twice, and exclusively on small islands (Uy et al. personal observation). In the Russell Islands, where *M. c. obscurior* has both melanic and chestnut-bellied forms, we found that island size was a significant predictor of the frequency of melanic birds, even after accounting for spatial autocorrelation. That is, smaller islands had higher frequencies of melanic birds than their larger counterparts, with melanic birds primarily found on small islets $\sim 1 \text{ km}^2$ or less in area (Figure 2). In fact, using a spatial autoregressive model that simultaneously considered island size and spatial autocorrelation explained more of the variation in frequency of melanism across islands than an OLS regression. In the Makira Island clade, another melanic subspecies, *M. c. ugiensis*, is found exclusively on small, satellite islands despite their short distance (approximately 8–10 km) from the large island of Makira, which harbors the chestnut-bellied subspecies *M. c. megarhunchus* (Mayr 1942, Mayr and Diamond 2001, Uy et al. 2009a, 2009b; see Figure 1A). In this island group, there is substantial gene flow between islands yet the color forms are essentially fixed within islands, indicating strong selection acting on plumage color (Uy et al. 2009b, Uy et al. personal observation). Given the pattern of island size predicting the frequency of melanic birds in the Russells and the observation that selection maintains melanism in the small islands of the Makira clade, deterministic processes are likely driving the convergent evolution and maintenance of melanism on small islands.

In a meta-analysis of birds, melanism was not consistently linked to advantages in reproduction or survival (Meunier et al. 2011), which suggests that selection on melanism is either taxon or trait specific. Given these patterns, what are the factors that dictate the frequency of melanism on the small islands of the Russell Archipelago? There are several hypotheses that could explain the variation in the frequency of melanic forms across islands.

First, melanic birds may simply be more vagile and thus can colonize islands farther away. Small islands tend to be farther from the larger islands of Pavuvu and Banika (Figure 1B), and perhaps melanic birds are better at colonizing these more distant islets. However, given the proximity of islands to each other—the entire archipelago is only $\sim 30 \text{ km}$ wide, and many islands are within 1 km of each other—it is unlikely that vagility can explain the higher frequency of melanic birds on smaller islands.

Second, directional selection may favor chestnut-bellied birds, but the efficacy of selection becomes weaker as

population size decreases. As such, genetic drift may allow for the persistence of the melanic forms on smaller islands, where selection is less effective. This is a distinct possibility, for drift can have significant effects on the evolution of small island populations (Clegg et al. 2002). However, given that melanism has evolved repeatedly on small islands across independent taxa (Table 1) and we have found that strong selection on plumage color counteracts gene flow in the Makira clade of *M. castanieiventris* (Uy et al. 2009b, Uy et al. personal observation), it is unlikely that drift alone can mediate the pattern of melanism occurring in higher frequencies on smaller islands in the Russell Archipelago.

Alternatively, selection could favor melanism, either through balancing selection that favors the maintenance of color polymorphism or through directional selection favoring melanism on small islands. In the case of balancing selection, islands may have different optima for the frequency of each morph, depending on their unique biotic and abiotic environment as mediated by island size. Examples of balancing selection favoring color polymorphism in the wild are numerous (reviewed by Gray and McKinnon 2007), and this remains a strong possibility in the Russells clade. In the case of directional selection favoring melanism on small islands, melanic birds should increase in frequency on small islands but perhaps are kept rare by substantial gene flow from neighboring larger islands that are dominated by chestnut-bellied birds (e.g., migration–selection balance). In essence, selection for melanism could be stronger on smaller islands, and the association between island size and frequency of melanism may reflect variation among islands in the balance between selection and gene flow (e.g., different points of equilibria at migration–selection balance). Similarly, the persistence of color polymorphism in island snakes has been attributed to a balance between directional selection for melanism on islands and gene flow from nonmelanic populations on the mainland (King 1993, Bittner and King 2003).

If balancing or directional selection is mediating the frequency of melanism on small islands, what could vary across islands that would generate a variable selective environment? Because islands of the Russell Archipelago are close to each other (Figure 1B), the plant and predator communities are very similar (Uy et al. personal observation). Therefore, it is unlikely that variation per se, in habitat or predators, is driving the association between island size and frequency of melanism. Likewise, because the entire archipelago is $\sim 30 \text{ km}$ in width and the islands have similar topography and climate, it is unlikely that selection for more efficient thermoregulation could favor melanism, as has been proposed in island populations of the Bananaquit (*Coereba flaveola*; Theron et al. 2001), snakes (Tanaka 2007), and spittlebugs (Berry and Willmer 1986). Instead, conditions on small islands may indirectly favor melanism. In several taxa,

melanism has been linked to increased aggression, which provides advantages in competitive interactions (Horth 2003, Ducrest et al. 2008, Loehr et al. 2008, McKinnon and Pierotti 2010). This link between melanism and aggression could be due to changes in the melanocortin-1 receptor complex, the major mediator of melanic coloration, which could have pleiotropic effects on other important life history traits (reviewed by Ducrest et al. 2008). Because breeding territories are fewer on small islands (Uy et al. personal observation), selection may favor more aggressive individuals. In support of this hypothesis, our taxidermy-mount and song-playback experiments in the Makira clade revealed that melanic *M. c. ugiensis* birds were more aggressive than their chestnut-bellied *M. c. megarhynchus* counterparts (Uy et al. 2009b). Therefore, it is possible that conditions on small islands favor aggression, thereby indirectly favoring melanism—a pattern similarly found in other color-polymorphic taxa (reviewed by McKinnon and Pierotti 2010).

In sum, melanism has evolved multiple times in small peripheral populations across a diverse set of taxa, including at least twice in the *M. castaneiventris* species complex of the Solomon Islands (Table 1). This recurrent evolution of melanism on small islands suggests that deterministic processes underlie the evolution of this trait. More detailed studies of the ecology of islands and the genetic basis of melanism are needed to more directly elucidate the mechanisms that may favor melanism in small populations.

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Appendix

TABLE 2. Populations in the Russell Islands sampled for the frequency of chestnut-bellied, melanic, and mostly melanic individuals of the subspecies *Monarcha castaneiventris obscurior* (see Figure 1B).

Island	Size (km ²)	Number of chestnut	Number of mostly melanic	Number of melanic
Pavuvu	122.84	24	0	1
Banika	39.33	21	0	1
Alokaun	7.82	16	0	0
Leru	2.30	10	0	0
Moie	1.37	15	4	1
Momolaun	0.82	14	0	0
Laumuan	0.63	8	1	1
Kakau	0.54	11	1	1
Koemurin	0.44	7	1	0
Tul	0.27	8	1	1
Kisan	0.16	5	1	1
Lolongan	0.14	4	1	1
Kiomie	0.10	9	1	3