
Threats to Avifauna on Oceanic Islands

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Abstract: *Results of the study by Blackburn et al. (2004a) of avifauna on oceanic islands suggest that distance from the mainland and time since European colonization have major influences on species extinctions and that island area is a significant but secondary contributing factor. After augmenting the data of the study on geographical properties for some of the islands they examined, we used a causal analysis approach with structural equation modeling to reexamine their conclusions. In our model geographical properties of islands, such as island area and isolation, were considered constraints on biological factors, such as the number of introduced mammalian predators and existing number of avifauna, that can directly or indirectly influence extinction. Of the variables we tested, island area had the greatest total influence on the threat of extinction due to its direct and indirect effects on the size of island avifauna. Larger islands had both a greater number of threatened bird species and more avifauna, increasing the number of species that could become threatened with extinction. Island isolation also had a significant, positive, and direct effect on threats to island avifauna because islands farther from the mainland had fewer current extant avifauna. Time since European colonization had a significant negative, but relatively weaker, influence on threats compared with the traditional biogeographic factors of island area and distance to the mainland. We also tested the hypothesis that the amount of threat is proportionally lower on islands that have had more extinctions (i.e., there is a “filter effect”). Because the proportion of bird extinctions potentially explained only 2.3% of the variation in the proportion of threatened species on islands, our results did not support this hypothesis. Causal modeling provided a powerful tool for examining threat of extinction patterns of known and hypothesized pathways of influence.*

Keywords: biogeography, causal analysis, extinction threats, island geography, structural equation modeling

Amenazas a la Avifauna de Islas Oceánicas

Resumen: *Los resultados del estudio de Blackburn et al. (2004a) sobre la avifauna de islas oceánicas sugieren que la distancia al continente y el tiempo desde la colonización europea tienen influencia mayor sobre las extinciones de especies y que la superficie de la isla es un factor significativo pero secundario. Después de incrementar los datos de Blackburn et al. (2004a) de propiedades geográficas de algunas de las islas que examinaron, utilizamos un método de análisis causal con modelado de ecuación estructural para reexaminar sus conclusiones. En nuestro modelo, las propiedades geográficas de las islas, como la superficie y aislamiento de la isla, fueron considerados limitaciones sobre los factores biológicos, como el número de mamíferos depredadores introducidos y la avifauna existente, que pueden influir en la amenaza de extinción directa o indirectamente. De las variables que probamos, la superficie de la isla tuvo la mayor influencia total sobre la amenaza de extinción debido a sus efectos directos e indirectos sobre el tamaño de la avifauna de la isla. Las islas más grandes tuvieron un mayor número de especies de aves amenazadas y más avifauna, incrementando el número de especies que serían amenazadas con extinción. El aislamiento de la isla también tuvo un efecto directo, positivo y significativo sobre las amenazas a la avifauna insular porque las islas más alejadas del continente tuvieron menos avifauna actual. El tiempo desde la colonización europea tuvo una influencia negativa significativa, pero relativamente más débil, sobre las amenazas en comparación con los factores biogeográficos tradicionales de superficie de la isla y distancia al continente. También probamos la hipótesis de que la cantidad de amenazas es proporcionalmente menor en islas que tuvieron más extinciones*

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(i.e., hay un "efecto de filtro"). Debido a que la proporción de extinciones de aves potencialmente explicó 2.3% de la variación en a proporción de especies amenazadas en islas, nuestros resultados no sustentaron esta hipótesis. El modelado causal proporcionó una poderosa herramienta para examinar los patrones de amenaza de extinción de las trayectorias de influencias conocidas e hipotéticas.

Palabras Clave: amenazas de extinción, análisis causal, biogeografía, geografía de islas, modelo de ecuación estructural

Introduction

Oceanic islands are an important target for conservation efforts. For island avifauna the likelihood of being threatened with extinction is 40 times greater than that for continental populations. Consequently, oceanic islands contain 39% of all globally threatened bird species. Furthermore, 90% of threatened island avifauna is restricted to few islands (Johnson & Stattersfield 1990). Island avifauna may be more vulnerable to extinction due to their small population sizes, which are often a result of the constraint of island area (Pimm et al. 1988). Johnson and Stattersfield (1990) identify three main causes of extinction for island endemic bird species: habitat destruction, limited range, and introduction of exotic species. Island avifauna is a special concern in global conservation efforts because of their high rates of endemism and susceptibility to extinction.

To prioritize conservation efforts the biodiversity attributes of an area, such as species richness, uniqueness, degree of threat, and genetic contribution, must be known (Stattersfield et al. 1998). The degree of threat may be determined by several factors, such as island biogeography (e.g., area, elevation, isolation) and characteristics of introduced species (e.g., number of exotic species, time since introduction). Often, these factors are analyzed separately without consideration of the possibility that multiple causes are interacting to determine the biodiversity of an area (Sala et al. 2000).

Blackburn et al. (2004a) identify two main factors— isolation from the mainland and time since European colonization—that are positively and negatively associated, respectively, with the proportion of island avifauna that are threatened (ratio of number of threatened bird species to the number of extant avifauna found on an island; Fig. 1a). They contend that island area and elevation are also positively associated with the proportion of threatened avifauna, but to a lesser extent than island isolation and time since European colonization. In addition, evidence of a strong influence of introduced mammalian predators on past extinctions leads to the assertion that more of these introductions would cause additional extinctions. The influence of mammalian predators would be a concern for the majority of oceanic islands they considered in their study because 57% of the 220 islands had no known extinctions of the historical avifauna.

The model that Blackburn et al. (2004a) use to determine factors associated with threatened status assumes statistical independence as causal explanations for all independent variables (Fig. 1a). Didham et al. (2005) caution against analyses that do not account for likely intercorrelations among explanatory factors. Path analysis is causal modeling that tests interrelationships among numerous variables that are hypothesized to have an influence on a dependent variable of interest. Specifically, path analysis allows evaluation of direct effects of causal variables on the dependent variable and of indirect effects through links among independent variables (Li 1975). Path analysis also allows one to make statistical linkages among submodels and to test submodels that are organized hierarchically.

In a recent analysis we used an extensive data set to examine recent extinctions with a causal modeling approach (F.S.D. et al., unpublished data). Our path analysis (via structural equation modeling [SEM]; Shipley 2000) showed that the strongest predictors of avian extinctions were island area and isolation from the mainland. The number of introduced mammalian predators to islands was a significant, but secondary, influence. These results differ from the conclusion drawn by Blackburn et al. (2004a) that introduced mammalian predators have a greater influence on past avian extinctions than any biogeographical factor (i.e., island surface area and isolation from mainland).

Because factors that have been identified as associated with extinction of avifauna may not be the same as those associated with the threat of extinction, we reexamined the analysis of Blackburn et al. (2004a) of threats to species survival. We applied the same causal modeling used in our reanalysis of proportion of species that have become extinct to account for the interplay of environmental constraints and influences on threatened avifauna. Our working premise was that geographical properties of islands restrict island avifauna (i.e., that the number of avifauna and predators found on an island are determined by the size and location of that island). Biological phenomena, such as the number of extant avifauna and introductions of mammalian predators, influence threats to species survival but may be influenced themselves by the physical constraints of island geography (Ricklefs & Lovette 1999; Morand 2000; Nordström & Korpimäki 2004). We hypothesize that specific geographic

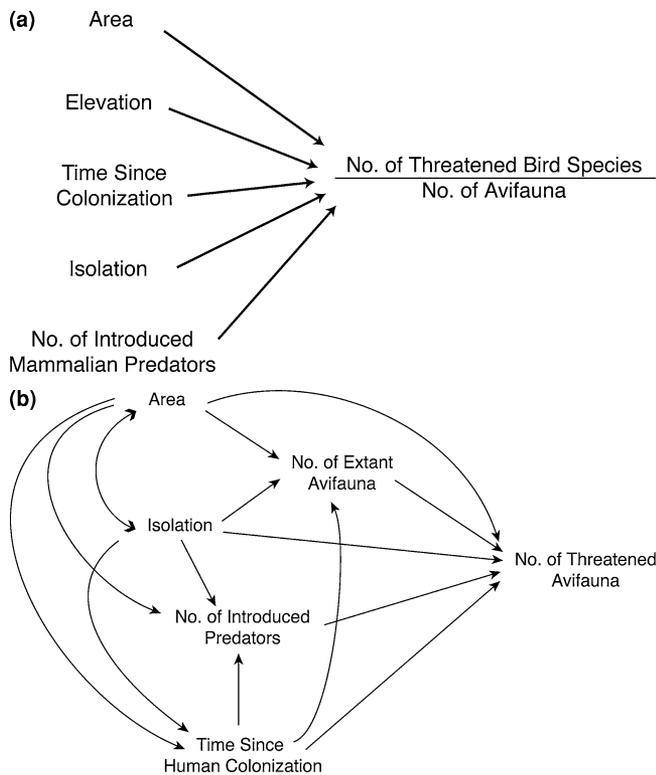


Figure 1. Schematic representation of regression models of threat of extinction used by Blackburn et al. (2004a) and in the present study, following the logic of Wright (1930) and Li (1975): (a) multiple regression model of Blackburn et al. (2004a) in the form of a path model and (b) path model in the current study. Single-headed arrows are direct causal effects on dependent variables. The double-headed arrow is an unanalyzed correlation, where the source for the covariance is unknown. All variables are log transformed (* $p < 0.05$, ** $p < 0.01$)

properties of islands will have an effect on the number of threatened bird species, often through intermediate biological processes. For example, island area may influence the number of extant avifauna, which will in turn affect the number of threatened bird species. We compared results of causal modeling with the results of the models of Blackburn et al. (2004a) to ascertain the robustness of both analyses of threats to avifauna and to reexamine previous conclusions about such threats.

Methods

Blackburn et al. (2004b) collated data on the number of threatened bird species and geographical and biological properties of oceanic islands. The islands that Blackburn et al. (2004a) included in their data set were oceanic islands (i.e., islands that were never connected to a conti-

mental land mass) and the geographic variables included island area and island isolation (Table 1). Island isolation was defined as the distance to the nearest continental land mass. The biological variables included time since first European colonization, number of introduced mammalian predators, and number of extant avifauna (Table 1). Introduced predators were exotic mammal species known to prey on birds or eggs and that were introduced after colonization by humans. They included elevation in their minimum adequate multivariate (MAM) model; however, we found that elevation was significantly associated with island area ($r = 0.566$). Such collinearity may artificially inflate path coefficients, which would then show an inflated influence of one of the variables on the dependent variable (Petratis et al. 1996). Because island area and elevation described a similar variation in the number of threatened bird species, we excluded elevation from our model.

Because some islands in the original data set were missing geographic information, we augmented the original data set of Blackburn et al. (2004b) with information on island area and isolation from the mainland for 18 additional islands (Environmental Systems Research Institute 2004; United Nations Environment Programme 2005). We included only islands that contained information on all variables in our analysis ($n = 218$).

Our hypothesis (Fig. 1b) integrates a series of cause-effect relationships among variables assembled into a single-path model (i.e., a testable hypothesis of threats to island avifauna). Our path analysis allowed us to take into account, through biological factors, both direct effects of factors on threat of extinction and indirect effects of physical attributes on the number of threatened species. A critical assumption of our hypothesis is that physical attributes of the islands can influence biological variables but that the reverse is unlikely to be true within the examined time frame.

Path analysis, originally devised by Sewall Wright (1934), is a specialized form of SEM that allows testing of the causal structure of a composite path model (Shipley 2000). Unlike standard statistical techniques such as multiple regression or canonical correlation in which variables are either dependent or independent, path analysis allows the specification of a variable as both a predictor of variables and dependent on other variables (Kline 2005). Specifically, in our path model (Fig. 1b), island area and isolation were specified as direct causes of threat of extinction, as were the number of bird species and the number of introduced mammalian predators. In addition, both number of bird species and number of mammalian predators may be influenced by those same physical causal factors that may also influence threat of extinction. Thus, these two biological factors are represented as mediators in path analysis and are responsible for indirect effects in which partial causal effects are conveyed from prior causal variables (Kline 2005). Time since colonization

Table 1. Means, ranges, and influences (from path analysis) of biological and geographical variables on number of threatened bird species on islands.^a

Causal variable	Mean	Range	Direct effects	Indirect effects	Total effect
No. extant avifauna	2.17	0–25	0.61 ^b	—	0.61
Island area (km ²)	5355.95	0.08–58,7713.3	0.33 ^b	0.27	0.60
Island isolation (km)	1999.64	80–5,800	0.53 ^b	–0.25	0.28
Time since first European colonization (years)	2360.30	100–10,000	–0.18 ^b	0.02	–0.16
No. introduced mammalian predators	1.94	0–10	–0.05	—	–0.05

^aDirect effects are equal to the path coefficients in Fig. 2. Indirect effects are equal to the path coefficients multiplied along the arrows through mediator variables. Total effect is the sum of the direct and indirect effects. There are no tests for significance for indirect and total effects. Means and ranges are untransformed. All variables were log transformed in the path analysis.

^bSignificance at 0.05 level.

may have direct and indirect influences on the number of threatened avifauna (Fig. 1b). Island geography may influence the time since colonization, which can then directly affect the number of threatened avifauna or indirectly affect threat by influencing the size of current avifauna or the number of introduced mammalian predators.

Path coefficients are standardized partial-regression coefficients derived from a multiple regression for each dependent variable in the path model (Wright 1934; Li 1975). Nevertheless, this approach is limited in its applicability to complex path models and violates the assumption of independence in ordinary least-squares methods because of the interdependence of structural equations (Tomer 2003). In SEM the entire causal structure of the path model is tested at once by estimation of parameters in the model via maximum likelihood estimation (MLE). The MLE minimizes the difference between the observed covariance matrix of variables included in the model and the predicted covariance matrix calculated from the model structure (Shipley 2000).

In our path model, all variables were log transformed because of nonnormality and to improve linearity among variables prior to use of SEM, as implemented by Program MX (Neale et al. 2003). Nevertheless, because the data set contained a large number of islands where the avifauna is facing little or no threat of extinction, normality could not be achieved by transformation of species threatened by extinction. This lack of normality increases the likelihood of rejecting the true model but does not influence parameter estimates (Kline 2005). We present all causal effects as standardized path coefficients with 95% confidence limits, which represent the rate of change in the dependent variable for every one standard deviation increase in the independent variable. Significance of a path coefficient was tested by constraining it to zero and determining the probability of the difference in chi-square values between the full and reduced model. Although there are no tests for significance, we examined indirect effects of biological variables with the products of the path coefficients of the biological factor and the biological factor's geographical mediator variable, where appropriate

(Schemske & Horvitz 1988). A log-likelihood ratio test was used to test the goodness of fit of the causal model to the data. To denote the difference between a path coefficient and a statistical probability value, the latter are represented by *p* and path coefficients are represented by *P*.

Results

The proportion of bird species that have become extinct since European colonization was not significantly correlated with the proportion of the current avifauna classified as threatened (Fig. 3; $r = 0.02$, $n = 220$, $p = 0.73$). This pattern, however, was strongly influenced by a single island, Fatu Huku in the Marquesan Archipelago, which had a single species classified as threatened and no historical extinctions. Without this outlier the association between proportion of extinct species and proportion of threatened species was positive and significant but had a low correlation value ($r = 0.15$, $n = 219$, $p = 0.02$). Because this weak association was positive, rather than, as expected, negative, we did not include measures of past extinctions in our path analysis.

The difference between the augmented data set and the original data of Blackburn et al. (2004a, 2004b) was trivial, so we present only the results of the analysis with the augmented data. There was no significant difference between the observed and predicted variance-covariance matrices in our path model (Figs. 1b & 2) ($\chi^2 = 0.08$, $df = 1$, $p = 0.77$), demonstrating that the data conformed to the predictions of the path model. The variables we examined explained 52% of the variation in the number of threatened avifauna, and this degree of prediction was highly significant. For the oceanic islands in the sample, 8.5% of avifauna were threatened with extinction (473 of 5560 island populations; some species occurred on more than one island).

The geographical and biological variables tested in this path analysis had direct effects on the number of threatened bird species. Island area ($P = 0.33$) and island

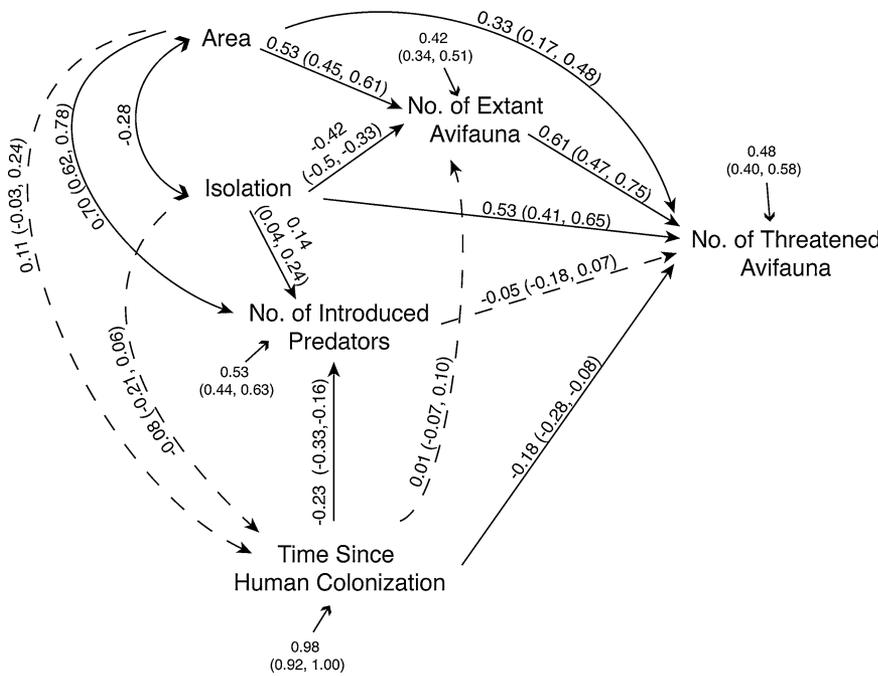


Figure 2. Path model for testing hypothetical influences of biological and geographical variables on the number of threatened bird species on islands. Solid arrows are significant paths ($p < 0.05$). Values with small unidirectional arrows directed at geographical factors are the proportion of unexplained variance remaining after accounting for all causal variables. Lower and upper 95% confidence limits on the path coefficients and on the proportion of unexplained variance of terms are in parentheses. Path coefficients are before or above respective confidence limits. Sample size for all variables is 218. All variables are log transformed.

isolation ($P = 0.53$), strongly and significantly affected the number of threatened bird species. The number of threatened species increased slightly as time since colonization by Europeans decreased ($P = -0.18$; Fig. 2). The number of species in the current avifauna had a significant, positive influence on the number of threatened bird species ($P = 0.61$; Fig. 2); the larger the avifauna on an island, the greater the number of bird species that can potentially become threatened with extinction. The number of introduced mammalian predators ($P = -0.05$) had no effect on the number of threatened species.

Of the variables we tested, only the geographical factors can have an indirect influence on the number of threatened bird species. Island area substantially affected the current avifauna ($P, 0.53 \times 0.61 = 0.32$): larger islands had larger avifauna and therefore more threatened bird species. Island isolation highly affected the number of threatened birds found on oceanic islands ($P, -0.42 \times 0.61 = -0.26$): more isolated islands had fewer threatened species because they had smaller avifauna. Even though island area ($P, 0.70 \times -0.05 = -0.04$), isolation ($P, 0.14 \times -0.05 = -0.01$), and time since colonization ($P, 0.23 \times -0.05 = 0.12$) had large effects on the number of introduced mammalian predators, none of these factors had any considerable indirect effects on the number of threatened avifauna because of the negligible impact of mammalian predators on the number of threatened bird species.

The sum of direct and indirect effects indicates total effect (Table 1). The number of extant avifauna had the greatest total influence on the number of bird species threatened on islands ($P = 0.61$), even without being able to affect other variables tested in this model. Islands that

contain larger avifauna will also have a greater number of bird species that can be threatened with extinction. Island area was also a primary factor ($P = 0.60$) due to its ability to affect the number of threatened bird species directly ($P = 0.33$) and indirectly ($P = 0.27$). Island isolation ($P = 0.28$) from the mainland secondarily affected the number of threatened avifauna and was influenced by direct ($P = 0.53$) and indirect effects ($P = -0.25$). The

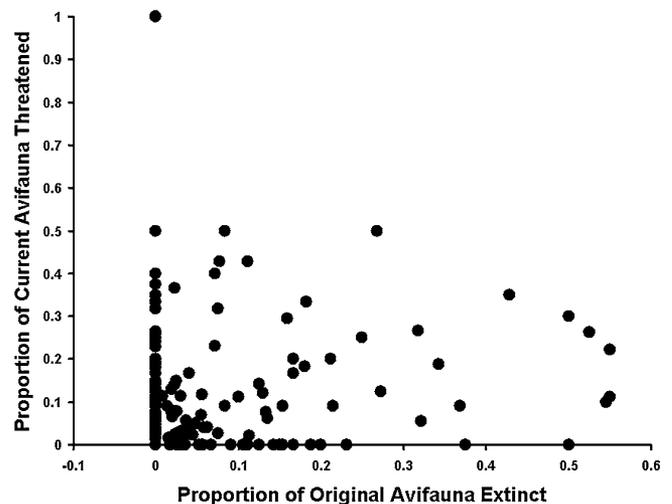


Figure 3. The relationship between the proportion of the current island avifauna that is threatened (number of threatened species divided by the extant avifauna) and the proportion of historical extinctions since European colonization of oceanic islands ($r = 0.023$, $n = 220$, $p = 0.73$) with the outlier removed ($r = 0.153$, $n = 219$, $p = 0.02$).

number of introduced mammalian predators had the least and almost minimal effect ($P = -0.05$) on the number of threatened bird species found on oceanic islands.

Discussion

In our reanalysis of the study of Blackburn et al. (2004b), we examined particular biological and geographical factors of islands and the causal structure of those factors to determine how they might explain the observed number of threatened avifauna on oceanic islands. Blackburn et al. (2004a) examined possible influences on the proportion of threat to oceanic avifauna. The proportion of current threat of extinction, in this case, confounds the causal variable, size of the avifauna, with the dependent variable of interest, number of threatened species on islands. Quantifying threat of extinction on islands as a per-island proportion can be misleading because it may put stronger emphasis on islands with smaller avifauna. For example, on the island of Fatu Huku, the only native bird, the Marquesan Ground Dove (*Gallicolumba rubescens*), is endangered, so the proportion of threat is 1.0 (BirdLife International 2000). In contrast, on the island of Madagascar, many more species are threatened, but the proportion of threat of extinction is low (0.13) because 25 of 192 native extant species are threatened with extinction (BirdLife International 2000, 2004). Although all threatened species deserve conservation awareness, a lack of attention on Madagascar would result in far more extinctions than on Fatu Huku.

Our model (Fig. 1b) represents proportions of avifauna threatened as paths from numbers of avifauna to numbers of threatened avifauna (the former is the denominator and the latter the numerator of the proportion). If the proportion of threatened species were a constant fraction of the avifauna, then the correlation of numbers of avifauna and numbers of threatened species would be 1.0. The actual path was strong and significant; thus, there was significant influence of a constant and common underlying probability of threat among islands on the number of threatened species. Other factors in the model, both direct and indirect, must influence both the number of threatened species in the avifauna and the proportion of species threatened on the islands.

Although the proportion of species threatened can be analyzed separately (e.g., Blackburn et al. 2004a), the path model has the advantage of allowing evaluation of influences on the number of threatened species and the proportion of threatened species in the same causal model. The size of the avifauna (the denominator of the proportion of species threatened) had a strong positive influence on the number of species threatened (the numerator of the proportion). In path analysis the direct influence of an independent variable, like island area or

isolation, is calculated with other effects held statistically invariant. So the size of the avifauna is accounted for when island area or isolation are evaluated. In addition, if the number of threatened species increases with some variable in the path analysis, then the proportion of species will increase as well because the number of species is the numerator of the proportion.

Blackburn et al. (2004a) found that introduced mammalian predators are not a significant influence on the proportion of species threatened. Rather, island isolation and time since colonization by Europeans have the strongest effect (Blackburn et al. 2004a, their Table 3). They also found that island area is significant in its effect on the proportion of threatened species but to a lesser degree.

In contrast with the conclusion of Blackburn et al. (2004a), we found that the influence of time since colonization, although significant, was of lesser importance in comparison with the geographical features of islands, such as size and isolation (Table 1). Islands colonized by humans for longer periods of time had fewer threatened bird species. Several studies, including ours, support the idea of a filter effect, in which human colonization acts as an extinction filter so that only resilient species remain, thereby reducing the proportion of species that may go extinct (Grueter 1995; Balmford 1996; Biber 2002). Pimm et al. (1995) found the same pattern: as time since colonization increases, the proportion of bird species that are endangered decreases. To test this idea more directly, we examined whether islands with proportionally more extinctions since European colonization had fewer threatened species as a proportion of the current avifauna.

In concordance with Blackburn et al. (2004a), our path analysis indicated no significant influence of mammalian predators on the number of threatened avifauna (Fig. 2). Although not investigated here or by Blackburn et al. (2004a, 2004b), nonmammalian predators may have an effect on the number of threatened bird species. The introduction of the brown tree snake (*Boiga irregularis*) to Guam has resulted in dramatic losses of the native bird species found on the island (Rodda et al. 1992). Because we only found a weak positive association between the proportion of avifauna threatened and the proportion of original avifauna gone extinct (Fig. 3), introduced mammalian predators appeared to provide a more pervasive (although partial) explanation for past extinctions than for presently threatened species. Therefore, we conclude that any filter effect must be influential during the periods of human occupation of islands that occurred before the more recent European colonization.

The theory of island biogeography states that more isolated islands have fewer species but a greater risk of extinction (MacArthur & Wilson 1967). This is supported by our finding that more-isolated islands had more threatened species and smaller numbers of extant avifauna (Fig. 2), likely owing to reduced probability of rescue

effects (Brown & Kodric-Brown 1977). Immigration of conspecifics decreases the likelihood of threat of extinction through demographic and genetic rescue of the population (Brown & Kodric-Brown 1977).

We found that island area, not isolation, as concluded by Blackburn et al. (2004a), was the most important geographical indicator of the threat of extinction due to both its indirect and direct effects on the number of threatened species (Fig. 2). Our conclusion is supported by Biber (2002), who also found that area is significantly related to the proportion of endangered bird species on islands. We found that island area indirectly determined the number of threatened avifauna, an obvious prediction, simply because there are a greater number of species on larger islands that can be threatened. Nevertheless, after controlling for this indirect effect, island area still had a positive direct effect on the number of threatened bird species. Therefore, larger islands had more threatened avifauna independent of the number of species on the islands, which is opposite to the theory of island biogeography. This may be because large islands are more likely to have permanent human populations engaging in agricultural and resource-based economies that result in habitat loss or degradation (Grayson 2001; Rolett & Diamond 2004; Didham et al. 2005). Although island area had less of a direct effect on the number of threatened species than island isolation, its positive influence on the number of extant avifauna resulted in area having a greater total influence (Table 1).

Traditional biogeographic variables, such as island area and isolation, are exceedingly important to understanding past extinctions, current threats of extinction, and what might be done to conserve avifauna on islands. Identifying the factors associated with threat of extinction only provides the pieces needed to assemble a strategy for conserving biodiversity. Nature is complicated and conservation biologists need to consider the causal structure among environmental factors in devising wise conservation plans. As a general principle we suggest starting with geographical elements and progressing to biological components of the environment while carefully factoring in the timing of ecological events. Conservation efforts directed at large isolated islands may have the most efficient positive impact on reducing the global loss of bird species on oceanic islands.

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