Patterns of island occupancy in bats: influences of area and isolation on insular incidence of volant mammals

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ABSTRACT

Aim The influence of landscape structure on the distribution patterns of bats remains poorly understood for many species. This study investigates the relationship between area and isolation of islands and the probability of occurrence of six bat species to determine whether persistence and immigration abilities vary among bat species and foraging guilds.

Location Thirty-two islands in the Gulf of California near the Baja California peninsula in north-west Mexico.

Methods Using logistic regression and Akaike information criterion (AIC) model selection, we compared five a priori models for each of six bat species to explain patterns of island occupancy, including random patterns, minimum area effects, maximum isolation effects, additive area and isolation effects and compensatory area and isolation effects.

Results Five species of insectivorous bats (*Pipistrellus hesperus*, *Myotis californicus*, *Macrotus californicus*, *Antrozous pallidus* and *Mormoops megalophylla*) displayed minimum area thresholds on incidence. The probability of occurrence tended to decrease at moderate distances of isolation (*c.* 10–15 km) for these species (excepting *A. pallidus*). The distributions of two non-insectivorous species (*Leptonycteris curasoae* and *Myotis vivesi*) were not influenced by island size and isolation.

Main conclusions Minimum area thresholds on incidence suggest that island occupancy by insectivorous bats may be limited by resource requirements. Islands smaller than 100 ha typically did not support occupancy or use by insectivorous bats, except at minimal isolation distances. Insectivorous bat species may also be more sensitive to moderate levels of habitat isolation in some landscape contexts than previously expected. Our results suggest that differences in foraging habits may have important implications for understanding the distribution patterns of bats.

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INTRODUCTION

The equilibrium theory of island biogeography (MacArthur & Wilson, 1963, 1967) explains patterns of species richness in insular habitats in terms of recurring colonization and extinction events on ecological time-scales (Rosenzweig, 1995). The concepts of the equilibrium theory can be extended to species-level patterns to investigate interspecific differences in how distributions of species are influenced by immigration and persistence abilities (Lomolino, 1986, 2000; Peltonen & Hanski, 1991).

Investigation of the patterns of insular distributions may provide insights into how species may vary in persistence and immigration abilities by determining the influence of area and isolation of islands on the probability of occurrence of species (Diamond, 1975; Gilpin & Diamond, 1981; Adler & Wilson, 1985; Peltonen & Hanski, 1991; Taylor, 1991). Five potential patterns of insular distribution were proposed by Lomolino (1986), including random patterns, minimum area effects, maximum isolation effects, non-compensatory (or additive) area and isolation effects and compensatory (or interactive) area and
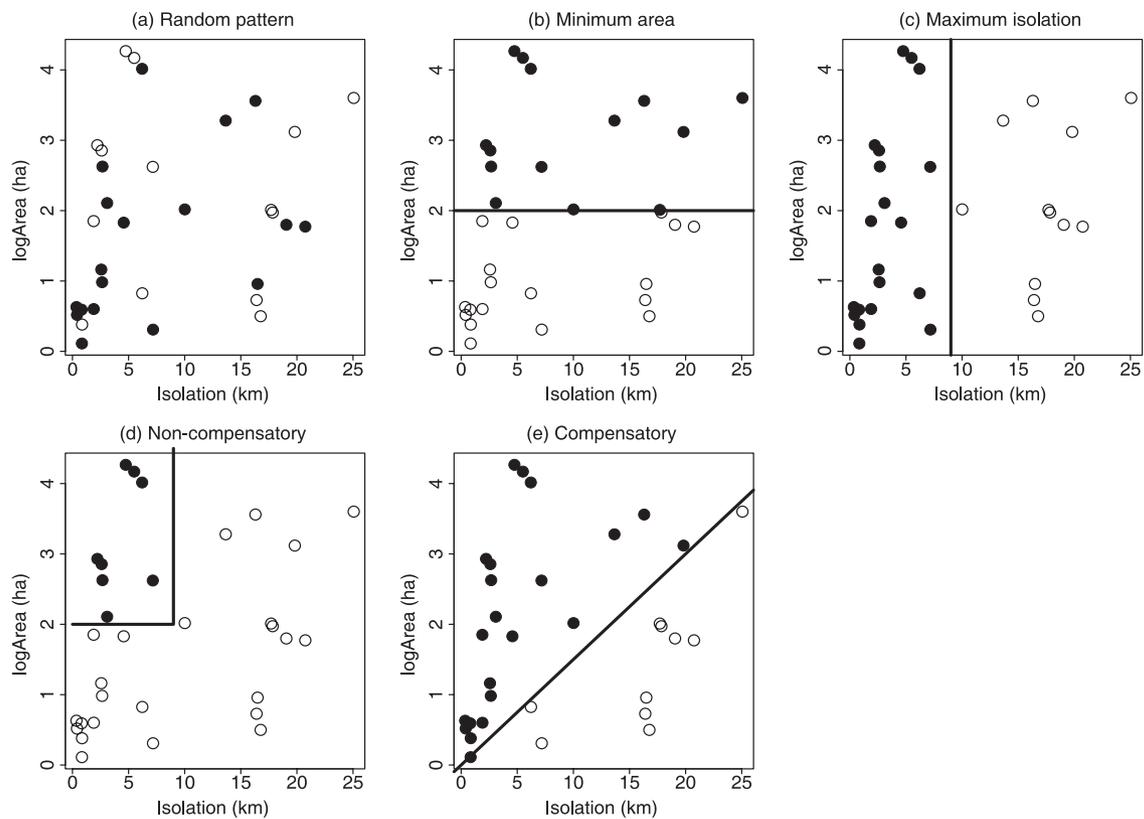
Figure 1 Hypothetical distributions of species corresponding to five biological hypotheses about patterns of species incidence (after Lomolino, 1986). Filled circles represent islands occupied by a species and open circles represent unoccupied islands. Values of area and isolation are from our data, but occupancy is hypothetical. (a) Random distribution pattern where the probability of occurrence is not affected by area or isolation. (b) Minimum area pattern where occurrence is only on islands greater than a minimum size threshold. (c) Maximum isolation pattern where occurrence is only on islands within some distance threshold. (d) Non-compensatory (or additive) patterns where incidence is affected by both area and isolation by only occurring on big, close islands. (e) Compensatory (or interactive) patterns where the relationship between probability of occurrence and area depends on the isolation value and the relationship between probability of occurrence and isolation depends on the size of an island.

isolation effects (Fig. 1). Each of these patterns corresponds to a biological hypothesis about the influence of vagility and persistence abilities of species on the probability of occurrence on islands (real or fragments). With the exception of random patterns, these hypothesized distributional patterns correspond to deterministic factors associated with characteristics of species that shape patterns of incidence in predictable ways (Lomolino, 2000).

Minimum area effects (Fig. 1b) occur when species incidence becomes negligible on islands below a threshold of island size (Robbins *et al.*, 1989; Peltonen & Hanski, 1991; Hinsley *et al.*, 1996; Watson *et al.*, 2005). Minimum area thresholds suggest that extinction dynamics are important determinants of species incidence, as populations cannot be sustained below a critical minimum area either due to demographic stochasticity or limited habitat availability (Lomolino, 1986; Hanski, 1991; Taylor, 1991; Gaggiotti & Hanski, 2004). Maximum isolation patterns (Fig. 1c) suggest that incidence of species is influenced by immigration rates via a threshold response such that, beyond some value of isolation, immigration (or arrival) rates become sufficiently

low so as to prevent colonization or rescue effects (Lomolino, 2000; Whittaker & Fernández-Palacios, 2007). Depending on the range of area and isolation values in the landscape and the capacities of the species, these two mechanisms (extinction or immigration) may independently explain incidence patterns.

If the range of area and isolation values in an archipelago encompass the extent of persistence and immigration abilities of species, then area and isolation may both influence the probability of occurrence on islands (Adler & Wilson, 1985; Lomolino, 1986). The additive (non-compensatory) hypothesis (Fig. 1d) incorporates the influences of area and isolation on incidence when immigration and extinction events are not interdependent (Lomolino, 1986). Compensatory effects (Fig. 1e) occur either when low immigration rates are compensated by low extinction rates or when high extinction rates are compensated by high immigration rates, such that presence on small islands is dependent on island isolation and presence on far islands is dependent on island size (Lomolino, 1986; Lomolino *et al.*, 1989). Compensatory patterns suggest species-level manifestations of the equilibrium model of island biogeography where probability of occurrence

results from recurrent immigration and extinction dynamics (Lomolino, 1986; Hanski & Gaggiotti, 2004).

Studies of non-volant mammals have demonstrated that vagility increases compensatory effects by increasing immigration rates relative to extinction rates (Adler & Wilson, 1985; Lomolino, 1986; Peltonen & Hanski, 1991). In this study, we extend Lomolino's (1986) hypotheses about insular distribution patterns to volant mammals (bats) to determine factors that may be important in shaping patterns of insular incidence of highly vagile mammals. Because of the high mobility of bats compared with other terrestrial mammals, we expected isolation to have a weak relationship with species incidence for bats in this near-shore archipelago. We hypothesized that differences in species traits that relate to persistence abilities, such as foraging habits, would be associated with area thresholds on insular incidence.

METHODS

Study region

Islands in the Gulf of California in north-west Mexico are characterized by Sonoran desert vegetation, dominated by columnar cacti (*Pachycereus pringlei* and *Stenocereus thurberi*) and desert trees (*Cercidium*, *Bursera* and *Jatropha*) (Shreve, 1951; Wiggins, 1980). The regional climate is hot and dry with un-predictable rainfall averaging between 100 and 150 mm year^{-1} (Cody *et al.*, 2002). Very few islands have permanent freshwater, but some larger islands with well-developed drainage courses support ephemeral freshwater (Cody & Velarde, 2002).

Data collection

We conducted presence–absence surveys for bats on 32 islands in the Gulf of California from 1 April to 1 June 2004–06. We sampled for the presence of bat species on each island for a 5-day period using passive Anabat acoustic stations (Titley Electronics, Ballina, Australia). On 10 islands, active acoustic monitoring and mist-net surveys were conducted to verify the species detected with passive acoustic stations. A species was considered present if it was detected at least once, without determination of breeding or residency status. Repeat sampling across years on 10 islands determined that patterns of species detection were consistent across years (Frick *et al.*, 2008), allowing islands sampled in different years to be pooled in a single analysis.

Acoustic sampling

We recorded bat echolocations using broadband ultrasonic bat detectors (Anabat II, Titley Electronics) to determine the presence of bat species (Hayes, 1997; O'Farrell *et al.*, 1999; Gehrt & Chelsvig, 2004). Passive monitoring stations included an Anabat II detector attached to a high-frequency microphone housed in a waterproof shroud with a 45° reflector mounted on a 1 m tall pole. The detector was connected to an Anabat Compact Flash Zero-Crossings Interface Module (Titley Electronics) recording device.

We sampled a total of 113 sites with passive acoustic stations across 32 islands. The number of passive acoustic stations on an island increased with island size (range 1–13 detectors per island). We placed detectors at randomly determined distances between 100 and 1000 m from safe boat landings. The number of landings ranged from 1 to 8 per island, and 18 islands (all < 105 ha) were sampled with only one detector.

On 10 islands, we conducted active monitoring of bat activity at mist-net survey locations using a spotlight, an Anabat II detector and a zero-crossings analysis recorder (Anapocket v.2.4) on a hand-held computer. Recordings of species identified with visual confirmation in the spotlight were used to verify the presence of species detected with passive acoustic detectors and to build a reference call library of echolocation signatures of free-flying bats.

Mist-net sampling

We conducted mist-net surveys to verify the identification of species detected with acoustic sampling, to build an echolocation call reference library from hand-release recordings and to train observers to recognize flight patterns and body shapes in the spotlight for identifying free-flying bats with active monitoring. Bats were released and recorded using Anapocket as long as they remained in constant view of the spotlight.

Mist-net sites were selected to maximize captures and were typically placed in dry arroyos (flyways) and desert scrub habitats, or over freshwater pools when available. Five locations were sampled on each island, except in two cases where access was limited. Mist-nets were opened at sunset and monitored at least every 15 min for 4 h. Captured bats were identified to sex, age and reproductive status (Anthony, 1988; Racey, 1988).

Echolocation analysis for species identification

We developed a graphical and descriptive key for identifying Anabat echolocation calls based on recordings from active monitoring of free-flying bats and recordings of hand-released individuals in Baja California, Mexico (Frick, 2007). Call sequences were identified to species if they had more than two diagnostic pulses that met defined criteria based on reference calls. Call parameters such as characteristic frequency, minimum and maximum frequencies, characteristic slope, call duration, interpulse interval and shape of the call body were measured from known reference calls and used to characterize call sequences of species (O'Farrell *et al.*, 1999; Gannon *et al.*, 2004). In general, the species in the assemblage were easily identifiable to the species level using the key (Frick *et al.*, 2008).

Data analysis

Species incidence

Species incidence was estimated using logistic regression with binomial errors (Taylor, 1991; Rita & Ranta, 1993; Crawley, 2005). Probability of occurrence (*P*) is the binomial response

Table 1 Model selection results for five a priori models on incidence for six bat species. Models are ranked by ΔAIC_c. log (L) is the maximized log likelihood for each model, K equals the number of parameters in each model, and R_N^2 is Nagelkerke's (1991) R^2 for generalized linear models.

Species	Model	ΔAIC_c	AIC weights	log (L)	K	R_N^2
Leptonycteris curasoae	Null	0.000	0.368	−16.81	1	−
	Isolation	0.585	0.275	−15.96	2	0.08
	Area + isolation	1.809	0.149	−15.35	3	0.13
	Area	1.813	0.149	−16.58	2	0.02
	Area*isolation	3.672	0.059	−14.97	4	0.17
Pipistrellus hesperus	Area	0.000	0.340	−17.30	2	0.35
	Area*isolation	0.027	0.335	−14.78	4	0.49
	Area + isolation	0.164	0.313	−16.16	3	0.42
	Null	7.363	0.009	−22.12	1	−
	Isolation	9.467	0.003	−22.03	2	0.01
Myotis californicus	Area + isolation	0.000	0.685	−11.90	3	0.55
	Area*isolation	2.093	0.241	−11.63	4	0.57
	Area	4.583	0.069	−15.41	2	0.34
	Null	11.231	0.002	−19.88	1	−
	Isolation	11.236	0.002	−18.74	2	0.10
Macrotus californicus	Area + isolation	0.000	0.724	−7.12	3	0.73
	Area*isolation	2.437	0.214	−7.03	4	0.73
	Area	4.931	0.062	−10.81	2	0.54
	Null	17.028	0.000	−17.99	1	−
	Isolation	17.810	0.000	−17.25	2	0.07
Antrozous pallidus	Area + isolation	0.000	0.507	−4.63	3	0.76
	Area	0.802	0.339	−6.25	2	0.65
	Area*isolation	2.406	0.152	−4.52	4	0.76
	Isolation	13.297	0.001	−12.40	2	0.15
	Null	13.759	0.001	−13.87	1	−
Mormoops megalophylla	Area + isolation	0.000	0.583	−3.88	3	0.68
	Area	1.820	0.235	−6.02	2	0.47
	Area*isolation	2.601	0.159	−3.87	4	0.68
	Null	7.422	0.014	−9.96	1	−
	Isolation	8.399	0.009	−9.30	2	0.09

AIC, Akaike information criterion; ΔAIC_c, values represent the relative support between the best approximating model (AIC_{min}) and each competing model (AIC_i).

(0 = unoccupied, 1 = occupied) and the logit link transformation is fit to the response variable in the form:

$$\text{logit}(P) = \beta_0 + \beta_1(X_1) + \beta_2(X_2) + ... \beta_k(X_k)$$

where βs represent parameter coefficients on the logit scale associated with $X_1 ... X_k$ explanatory variables. Parameter coefficients were estimated using maximum likelihood methods (Hosmer & Lemeshow, 1989).

Five models of incidence were fitted for each species to investigate factors associated with species-specific occurrence patterns, including null, area-only, isolation-only, additive area and isolation and interactive area and isolation (compensatory) models (Table 1).

Island characteristics were measured using a 'heads-up' digitized GIS layer created in ArcView 3.2 (ESRI Inc.) from Landsat 7 satellite images (Table 2). We measured the shortest over-water path (in km) to the Baja Peninsula as an index for isolation. This metric allowed for stepping-stone type movements by summing over-water legs if stepping-stone paths were

the shortest route to the peninsula. This approach accounts for the presence of neighbouring islands if they function as stepping-stones, but emphasizes the likely role of the Baja Peninsula as a predominant source pool. The range of island areas in the archipelago was skewed toward smaller islands (only nine islands were greater than 500 ha in area) (Table 2). The range of isolation values was more evenly distributed (Table 2).

Model selection and model averaging

To compare the five a priori models on species incidence (Table 1), we employed the Akaike information criterion (AIC, Burnham & Anderson, 2002), using the small sample-size correction form:

$$AIC_c = -2 \log[L \, (\hat{\beta}|\text{data}, \text{model}_i)] + 2K + 2K(K + 1)/n - K - 1$$

where K is the number of parameters in a model and n is sample size (Burnham & Anderson, 2002). All models had the same sample size ($n = 32$ islands). Models were ranked by AIC_c value

Table 2 Island characteristics of 32 islands in the Gulf of California, Mexico used for analysing patterns of species incidence.

Island	Area (ha)	Isolation (km)
Blanco	1.3	0.84
Bota	9.6	2.64
Cabezo Caballo	71.0	1.89
Carmen	14,801.4	5.50
Cayo	6.7	6.22
Coronados	715.8	2.60
Coronados Smith	852.1	2.22
Danzante	423.7	2.67
Espiritu Santo/Partida Sur	10,367.1	6.21
Galeras East	5.4	16.40
Galeras West	3.2	16.77
Gallina	2.0	7.18
Gemelitos East	3.9	0.82
Gemelitos West	2.4	0.86
Islitas	3.3	0.41
Las Animas Sur	9.1	16.49
Monserrat	1902.8	13.66
Pardo	4.3	0.36
Partida Norte	94.0	17.84
Pata	14.5	2.57
Piojo	67.6	4.57
Rasa	59.2	20.75
Salsipuedes	102.6	17.70
San Diego	62.9	19.06
San Francisco	419.0	7.16
San Ildefonso	104.2	10.01
San José	18,494.5	4.75
San Lorenzo	3632.3	16.31
Santa Catalina	3995.6	25.06
Santa Cruz	1315.1	19.81
Tijeras	4.0	1.90
Ventana	128.2	3.09

(the lowest AIC_c has the most support from the data) and were compared using ΔAIC_c and AIC_c model weights (w_i). The ΔAIC_c values represent the relative support between the best approximating model (AIC_{min}) and each competing model (AIC_i). We considered models with $\Delta AIC_c \leq 2$ to be strongly competing models (Burnham & Anderson, 2002). AIC_c model weights were used to assess the relative support of individual models, using the formula

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta AIC_{c_i}\right)}{\sum_{i=1}^{R}\exp\left(-\frac{1}{2}\Delta AIC_{c_i}\right)}$$

To account for model selection uncertainty, we model-averaged estimates of parameter coefficients (Burnham & Anderson, 2002) to determine a final model of species incidence. Model-averaged parameter estimates were computed as:

$$(\hat{\beta}_j) = \sum_{r=1}^{5} w_i(\hat{\beta}_j)$$

where w_i is the Akaike weight and $(\hat{\beta}_j)$ is the parameter coefficient estimate for explanatory variable *j* in model *i*. The unconditional sampling variance for the model-averaged parameter estimates was estimated as (Burnham & Anderson, 2002):

$$\text{var}(\hat{\beta}_j) = \left[\sum_{i=1}^{5}\hat{w}_i\sqrt{\text{var}(\hat{\beta}_j|Model_i) + (\hat{\beta}_j - \hat{\beta}_j)^2}\right]^2$$

When a given model did not include a given parameter, the coefficient value was assumed to be 0 (Burnham & Anderson, 2002). All statistical analyses were conducted in Program R v.2.4.1.

RESULTS

Logistic regression models were fitted for six species (Table 1) whose occurrences ranged from 3 to 25 islands in the archipelago. Estimation was not possible for *Myotis vivesi*, as this species occurred on all islands except one, nor for *Lasiurus xanthinus*, which occurred on only two islands (Fig. 2a,h). *Leptonycteris curasoae*; a nectar-feeding species, had a random pattern of distribution with no relationship to size and isolation (Fig. 2b). *Pipistrellus hesperus*, a small-bodied insectivore, displayed a compensatory pattern of distribution with the relationship between probability of occurrence and isolation dependent on island size (Fig. 2c). *Myotis californicus*, a small-bodied insectivore, and *Macrotus californicus*, a medium-bodied insectivore, displayed patterns intermediate between an additive and compensatory pattern, demonstrating that both area and isolation are associated with the probability of occurrence (Fig. 2d,e). *Antrozous pallidus*, a large-bodied insectivore, showed a minimum area effect on probability of occurrence (Fig. 2f). *Mormoops megalophylla*, a large-bodied insectivore, was only detected on three islands that were large and close to the peninsula (Fig. 2g).

Model selection results

Area, independently or in combination with isolation, was a variable in strongly competing models for each of five species of insectivorous bats (Table 1). The sum of the AIC_c weights for models which included area indicate strong support for the relative importance of area as an explanatory variable for incidence of these five species (Table 3). The model selection

Table 3 Relative variable importance for estimated parameter coefficients (area and isolation) based on the sum of Akaike information criterion using the small sample-size correction form (AIC_c) model weights that contain a given parameter.

Species	Area	Isolation
Leptonycteris curasoae	0.357	0.483
Pipistrellus hesperus	0.988	0.652
Myotis californicus	0.995	0.928
Macrotus californicus	0.999	0.938
Antrozous pallidus	0.999	0.660
Mormoops megalophylla	0.977	0.751
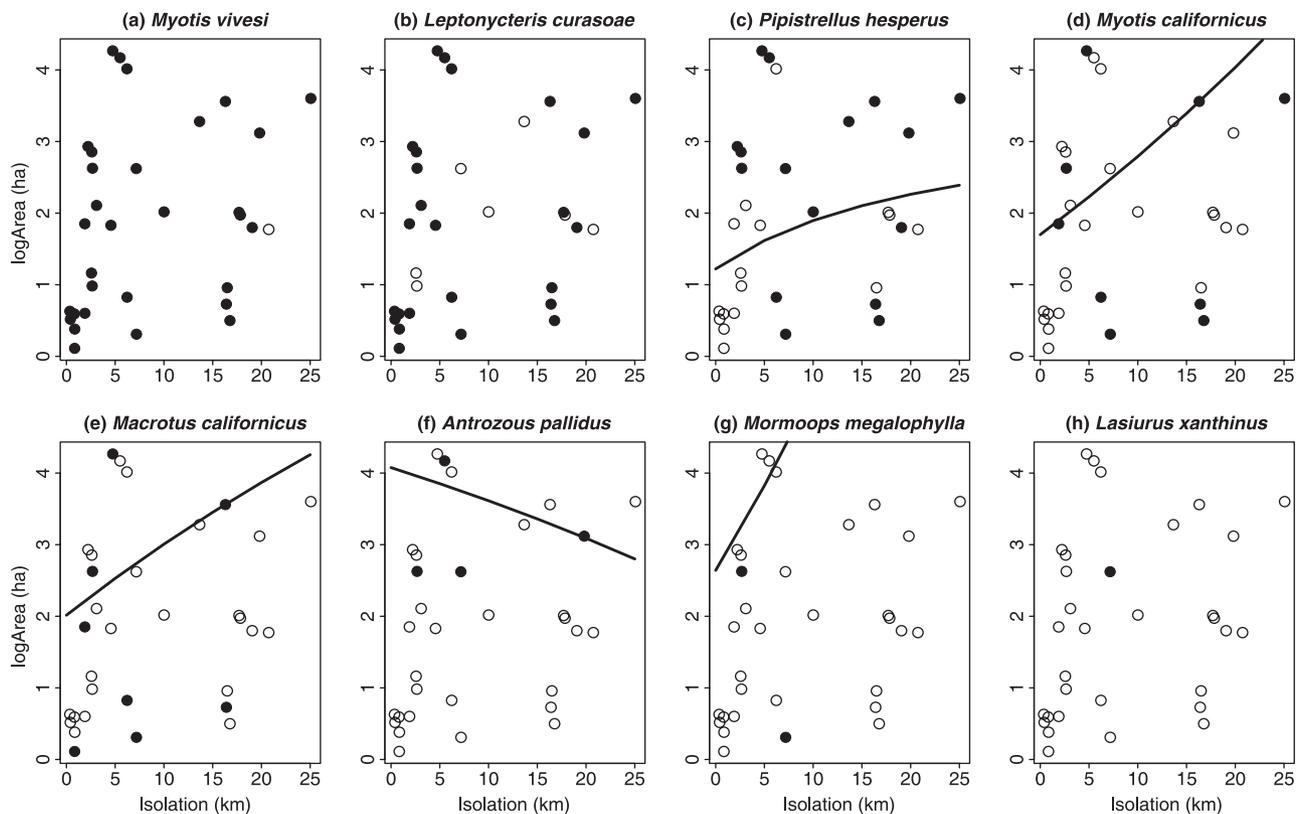
Figure 2 Insular distributions of eight species of bat on 32 islands in the Gulf of California, Baja California, Mexico. Filled circles represent occupied islands, open circles represent unoccupied islands. Lines represent the predicted threshold above which probability of occurrence is > 50% based on model-averaged parameter coefficients from logistic regression models: (a) *Myotis vivesi*, a fish-eating species; (b) *Leptonycteris curasoae*; a nectar-feeding species; (c) *Pipistrellus hesperus*, a small-bodied insectivore; (d) *Myotis californicus*, a small-bodied insectivore; (e) *Macrotus californicus*, a medium-bodied insectivore; (f) *Antrozous pallidus*, a large-bodied insectivore; (g) *Mormoops megalophylla*, a large-bodied insectivore; (h) *Lasiurus xanthinus*, a medium-bodied insectivore. Logistic regression models were not fitted for either *M. vivesi* or *L. xanthinus*.

results also suggest that isolation may be associated with probability of occurrence of these species. For the one nectarivorous bat, *Leptonycteris curasoae*, the null model had the lowest AIC_c value, but was not a strongly competing model for any other species.

The additive area and isolation model was the best-fit model for *Myotis californicus*, *Macrotus californicus*, *A. pallidus* and *M. megalophylla* (Table 1). The probability of occurrence of *Myotis californicus* and *Macrotus californicus* was strongly influenced by area and isolation and the relationship between incidence and area may depend on the level of isolation as the compensatory model (interactive area and isolation) was the second best model ranked by AIC_c weights for these species (Table 1). For *A. pallidus* and *M. megalophylla*, the area-only model had competing support from the data (i.e. $\Delta AIC_c < 2.0$) (Table 1). These species occurred on only a few islands (*A. pallidus*, $n = 5$; *M. megalophylla*, $n = 3$) (Fig. 2), affecting the precision of our estimates and limiting the strength of our inferences about their patterns of occupancy.

For *P. hesperus*, all three models that included area were strongly competing models ($\Delta AIC_c < 2.0$) with similar AIC_c weights for the three models (Table 1). Area appears to have the strongest influence on incidence for this species, but this may be dependent on the level of isolation (Fig. 3).

No species had overwhelming support ($w_i > 0.90$) for a single approximating model for incidence of species. Therefore, we present model results using model-averaged parameter estimates (Table 4), which account for the uncertainty in model selection (Burnham & Anderson, 2002). We recognize that further research on the effectiveness of model averaging is still necessary (Burnham & Anderson, 2002; Richards, 2005). Parameter estimates for each individual model for each species are provided in Appendix S1 in Supplementary Material.

Model-averaged parameter estimates

Model-averaged coefficient estimates were positive for area for all species and were negative for isolation for all species except *A. pallidus* (Table 4). This suggests that the probability of occurrence of most bat species tended to increase with island size (Fig. 3) and decrease with island isolation (Fig. 4). The positive relationship between isolation and incidence for *A. pallidus* (Fig. 4) may be due to a combination of a steep threshold of minimum area on occupancy for this species and statistical leverage caused by islands in the smallest size classes also being the least isolated. Confidence intervals on most model-averaged
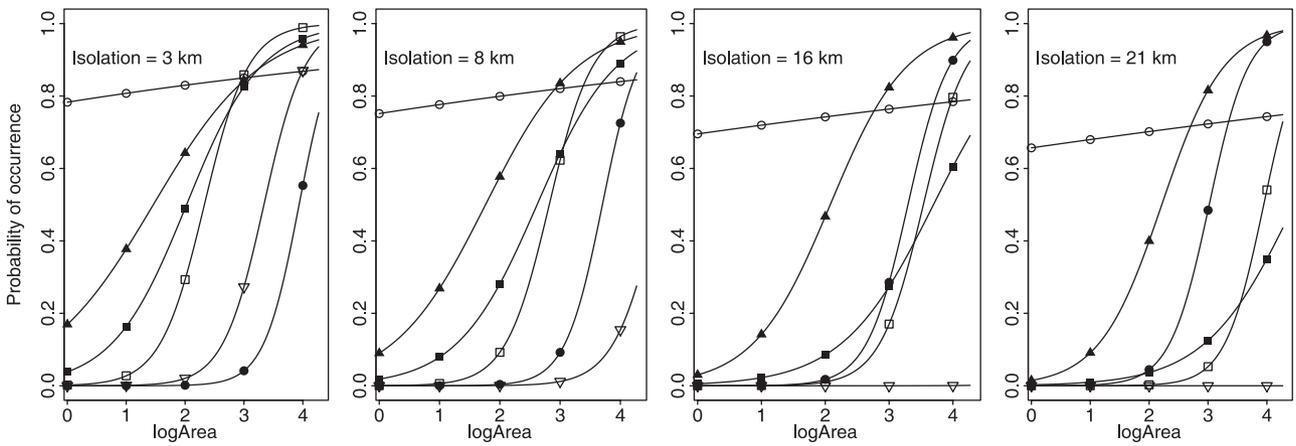
Figure 3 Incidence functions based on model-averaged parameter estimates showing the relationship between probability of occurrence on islands and island size at four values of isolation for six species: –○– , *Leptonycteris curasoae*; –▼– , *Pipistrellus hesperus*; –■– , *Myotis californicus*; –□– , *Macrotus californicus*; –●– , *Antrozous pallidus*; –▽– , *Mormoops megalophylla*. Points along lines are used to distinguish species and do not represent observed data values.
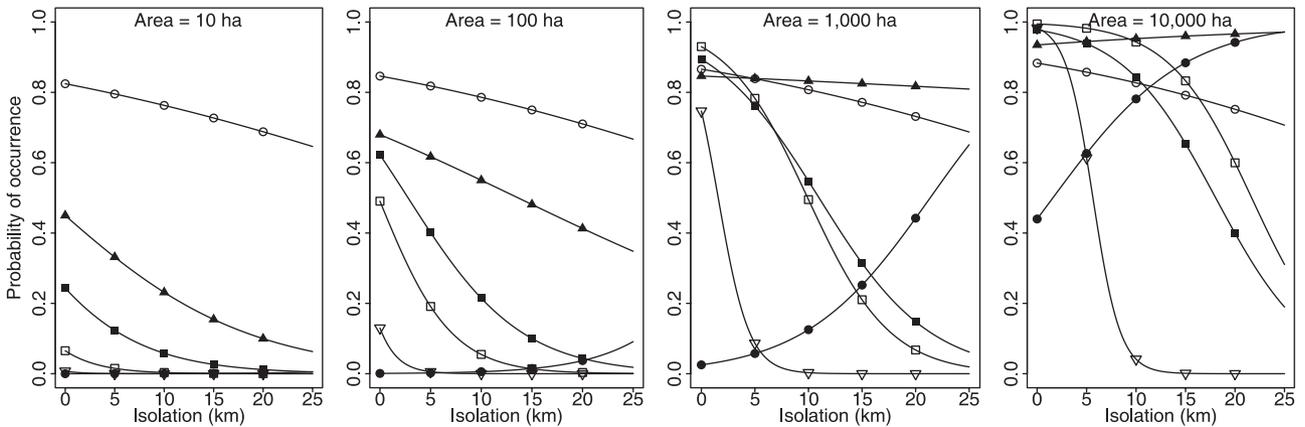
Figure 4 Incidence functions based on model-averaged parameter estimates showing the relationship between probability of occurrence and island isolation at four values of area for six species: –○– , *Leptonycteris curasoae*; –▼– , *Pipistrellus hesperus*; –■– , *Myotis californicus*; –□– , *Macrotus californicus*; –●– , *Antrozous pallidus*; and –▽– = *Mormoops megalophylla*. Points along lines are used to distinguish species and do not represent observed data values.

Table 4 Model-averaged parameter estimates and associated 95% confidence intervals in parentheses for the effects of area, isolation and an interaction term on incidence of bat species on islands in Baja California, Mexico. Parameter estimates are reported in logits.

Species	β_0 (intercept)	β_1 (log area)	β_2 (isolation)	β_3 (log area*isolation)
Leptonycteris curasoae	1.39 (−0.13, 2.91)	0.16 (−0.43, 0.75)	−0.04 (−0.15, 0.08)	0.00 (−0.02, 0.01)
Pipistrellus hesperus	−1.16 (−3.29, 0.98)	0.95 (−0.24, 2.14)	−0.14 (−0.49, 0.20)	0.04 (−0.11, 0.20)
Myotis californicus	−2.77 (−5.28, −0.26)	1.63 (0.32, 2.94)	−0.15 (−0.43, 0.13)	−0.01 (−0.08, 0.05)
Macrotus californicus	−5.28 (−10.34, −0.23)	2.62 (0.33, 4.92)	−0.32 (−0.93, 0.29)	0.02 (−0.12, 0.12)
Antrozous pallidus	−13.90 (−33.41, 5.61)	3.41 (−1.09, 7.92)	0.23 (−0.50, 0.96)	−0.02 (−0.15, 0.11)
Mormoops megalophylla	−7.87 (−21.16, 5.42)	2.98 (−2.46, 8.43)	−0.59 (−3.79, 2.62)	−0.03 (−0.54, 0.47)

parameter estimates were wide due to small sample sizes and from using the unconditional sampling variance to account for model selection uncertainty (Burnham & Anderson, 2002).

DISCUSSION

Our analysis extends Lomolino's (1986) hypotheses about insular distributions to a different group of mammals and

Table 5 Traits of bat species, including foraging and roosting guild classifications. Foraging guild classifications follow Schnitzler and Kalko (2001).

Species	No. islands occupied	Foraging guild	Roosting guild
Myotis vivesi	31	Piscivore	Crevice
Leptonycteris curasoae	25	Nectarivore	Cave obligate
Pipistrellus hesperus	17	Edge and gap insectivore	Crevice
Myotis californicus	10	Edge and gap insectivore	Crevice
Macrotus californicus	8	Narrow-space insectivore	Cave obligate
Antrozous pallidus	5	Narrow-space insectivore	Cave and crevice
Mormoops megalophylla	3	Edge and gap insectivore	Cave obligate
Lasiurus xanthinus	2	Edge and gap insectivore	Foliage

demonstrates that volant mammals display similar patterns of occupancy to non-volant mammals in island archipelagos. Insular distributions of insectivorous bats in this archipelago appear to be characterized by minimum area thresholds with some evidence that increasing isolation may also be associated with lower incidence (Figs 3 & 4). Patterns of island occupancy by insectivorous bats are consistent with the results from analyses of richness and composition of bat communities in the study region, which demonstrated that both area and isolation influence richness and composition, with area representing the strongest influence (Frick *et al.*, 2008).

The association of island size and incidence of the species we examined suggests that extinction dynamics may potentially be important in determining insular distributions of bats in this system. All five insectivorous species displayed minimum area thresholds on occupancy (Fig. 2), suggesting that these species do not use islands below a certain size or are unable to sustain populations due to lack of habitat or because of small population dynamics (Hanski, 1991). Area thresholds for insular occupancy of insectivorous bats at roughly 100 ha is similar to patterns of occupancy by breeding landbirds in the same archipelago (Cody & Velarde, 2002). Reduced plant and bird richness on islands below 200 ha in Baja California has been attributed to the lack of geological structure permitting formation of canyons and arroyos that increase both topographical and habitat diversity (Cody & Velarde, 2002; Cody *et al.*, 2002). Islands in our study varied in size by four orders of magnitude, with the smallest islands encompassing only a few hectares (Table 2). Many islands (*n* = 18) in our data set were less than 100 ha in size and were characterized by low topographical and habitat diversity. For insectivorous bats, both foraging and roosting habitat are likely to be related to topographical diversity in Sonoran desert ecosystems (Búrquez *et al.*, 1999; Frick *et al.*, 2008).

Multiple mechanistic processes could underlie the relationship with minimum area thresholds for species incidence. Lomolino's (1986) hypotheses were directed toward a species-specific extension of the equilibrium model of island biogeography and thus focus on population-level processes such as immigration and persistence as casual mechanisms behind relationships between island characteristics and species incidence. Minimum area thresholds on island occupancy generally suggest some limit to population persistence related to island area, although whether that limit is caused by demographic stochasticity, lack of habitat or species interactions may be difficult to ascertain.

Of the five insectivorous species that appear sensitive to area thresholds on occupancy (Fig. 3), two species (*Macrotus californicus* and *A. pallidus*) are medium- to large-bodied gleaners of large arthropods; two species (*Myotis californicus* and *P. hesperus*) are small-bodied aerial insectivores and one species (*M. megalophylla*) is a large-bodied aerial insectivore (Table 5). Although precision was poor for detecting significant parameter coefficients for *A. pallidus* and *M. megalophylla* due to small numbers of islands occupied (*n* = 5 and 3, respectively), distributions of these species appear to be limited by higher minimum area thresholds (*c.* 1000 ha) than those estimated for other species.

Use of islands smaller than 100 ha was largely limited to two non-insectivorous species: *Myotis vivesi*, a fish-eating bat, and *Leptonycteris curasoae*, a nectar-feeding species. A regional endemic, *M. vivesi* forages over the ocean for small bait fish (Blood & Clark, 1998). Small rocky islands provide habitat for roosting in close proximity to foraging areas (Blood & Clark, 1998), explaining the prevalence of this species across the range of island size and isolation values in the archipelago. Lack of a relationship between area and incidence for *L. curasoae* suggests that this species is capable of using small islands as foraging patches. Almost all small islands in the archipelago have at least a few cardon cacti (*Pachycereus pringlei*), a major source of nectar for this migratory species during the spring months when our sampling occurred. The stationary and temporally predictable nature of a floral food source, such as cactus nectar, may permit greater use of small, spatially isolated resource patches than other food resources, such as insects.

Isolation may also influence insular distributions for some insectivorous species, but it appears to have a weaker relationship with incidence than area (Table 3). Inference about the relationship of isolation and insular incidence is hampered by wide confidence intervals around model-averaged isolation coefficient estimates. Although the range of isolation values in this archipelago was moderate in comparison to the vagility of many bat species, there was a general trend toward a negative relationship between isolation and probability of occurrence of insectivorous bats (Fig. 4). These results suggest that some insectivorous bats may be sensitive to modest distances (10–15 km) between spatially separated habitat patches, especially if patch size is small. The two non-insectivorous bats are notable exceptions. For example, the migratory *L. curasoae* is highly vagile and capable of commuting long distances (*c.* 30 km) in a night (Horner *et al.*, 1998; Sahley *et al.*, 1993) and distances among islands in this
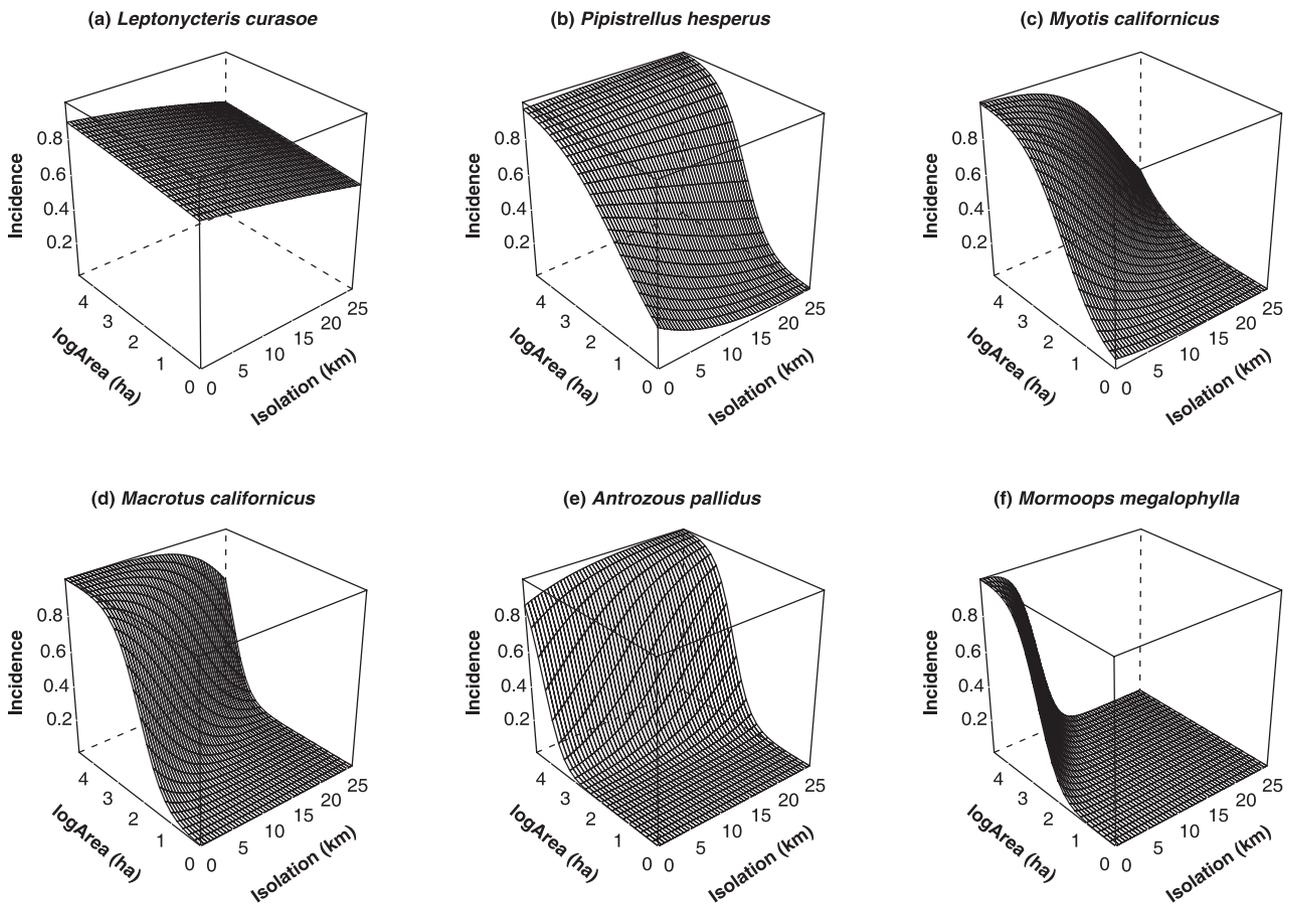
Figure 5 Incidence graphs for each species showing the relationship between probability of occurrence and area and isolation of islands. Model predictions are based on model-averaged parameter estimates.

archipelago do not appear to pose a significant immigration filter for this species.

Compensatory patterns in several insectivorous bat species are suggested by the change in the relationship between incidence and isolation at different levels of island size (Fig. 5). These patterns support the compensatory hypothesis that immigration (or arrival) rates can compensate for high extinction rates for close, small islands and that high persistence on large islands can compensate for low immigration rates at greater isolations (Lomolino, 1986). Compensatory patterns have been found in several studies of non-volant mammals (Adler & Wilson, 1985; Lomolino, 1986; Peltonen & Hanski, 1991) and are predicted to be most likely to occur when the range of area and isolation values is large relative to the resource requirements and mobility of the species in question (Lomolino, 1986; Whittaker & Fernández-Palacios, 2007). The tendency toward compensatory patterns in several insectivorous bats in an archipelago with moderately isolated islands relative to the presumed vagility of most bat species draws attention to the importance of the interaction between island size and isolation to support insular populations.

Our results demonstrate that Lomolino's (1986) hypothetical insular distribution patterns (Fig. 1) can be extended to explain insular distributions of volant mammals. Our research also suggests that foraging habits may influence distributional patterns among bats, as this probably influences both resource requirements and the potential mobility of species (Norberg & Rayner, 1987). Our results are consistent with other bat studies that determined that factors related to foraging habitats may be important predictors of ecological vulnerability to habitat fragmentation or extinction risk (Jones *et al.*, 2003; Safi & Kerth, 2004; Meyer *et al.*, 2008). Although incidence patterns may be context-specific (Watson *et al.*, 2005), our study provides one of the first perspectives on how landscape structure may influence insular distributional patterns of bats.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Parameter estimates and AIC$_c$ weights from five *a priori* models.

This material is available as part of the online article from:
http://www.blackwell-synergy.com/doi/abs/10.1111/j.1466-8238.2008.00401.x
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