On the insularity of islands

Michael D. Rose (†) and Gary A. Polis (†)

Rose, M. D. and Polis, G. A. 2000. On the insularity of islands. – Ecography 23: 693–701.

We propose that islands are "less insular" than is generally perceived. This belief results, in part, from the paucity of studies on vagrant species that exploit islands but are not permanent residents with continual breeding populations. We show, via anecdotal evidence extracted from the literature and data acquired on Gulf of California islands, that visitors to insular systems are fairly common. We delineate three types of events beyond the bounds of current biogeographical analysis that make islands less insular: 1) migrants and "accidental" visitors, 2) individuals of a species whose foraging areas encompass many islands or the mainland and islands, and 3) species who "colonize" islands during opportune periods or years but become extinct during difficult times (source-sink situations). Such events potentially significantly affect the ecology and evolution of island inhabitants by such means as increased predation and/or competition, transport of parasites and pathogens, dispersal of seeds and eggs, and genetic introgression and hybridization. Discussion of other "insular" habitats such as freshwater lakes and wildlife refuges illustrate that vagrancy events may be nearly ubiquitous. Studies addressing the frequency and ecological and evolutionary significance of vagrants are required, especially in light of recent and rapid extinctions on islands and the increasing fragmentation of habitats.

M. D. Rose and G. A. Polis, Dept of Environmental Science and Policy, Univ. of California, Davis, CA USA.

Are islands as insular and isolated as generally perceived? With the exception of species turnover, we tend to view islands as rather self-contained units with segregated evolutionary and ecological trajectories, rarely influenced by introgression, disperal, or visitors from other locations. One understudied aspect of insularity is the effect of visitors and unsuccessful colonizers, i.e. "vagrants," on islands. The presence of vagrants makes islands "less insular" and can significantly alter the ecology and evolution of resident insular biota. Consequently, we assert that one cannot fully understand island ecology and evolution without including non-resident interactions and influences. In this paper, we focus on cases where individuals of non-resident species periodically exploit islands during forays from other areas. These vagrants do not play by the rules of classic island theory, as they do not colonize or go extinct. This situation is probably quite common on islands close to mainlands, but also occurs on more isolated

Copyright © ECOGRAPHY 2000 ISSN 0906-7590 Printed in Ireland – all rights reserved

ECOGRAPHY 23:6 (2000)

islands when highly vagile species visit (e.g. birds, insects, and some mammals).

We discuss two other situations that are outliers of classic island biogeography, but nonetheless significantly affect the insularity of islands: 1) individual fauna whose foraging range consists of several islands or island-mainland regions and 2) species whose populations are characterized by mainland-island or islandisland source-sinks. These species may significantly influence island ecology and evolution via several pathways akin to vagrancy effects. Moreover, in source-sink situations, species turnover likely does not reach a dynamic equilibrium as factors other than isolation and island area determine the colonization rates and sustainability of these island residents.

We first establish that many species move across water barriers. We then describe types of vagrants that visit islands and discuss consequences and implications of island non-residents. Finally, we address the impor-

693

Accepted 1 February 2000

tance of understanding the possible effects vagrants may have on other isolated ("island") habitats and urge studies of vagrants in the contexts of island biogeography, ecology, evolution, and under other applicable circumstances.

On the vagility of island inhabitants

We know that movements across oceans to islands and subsequent colonizations are common across many time scales. For example, dispersal events over thousands to millions of years have populated all isolated archipelagoes, e.g. the Hawaiian and Galápagos Islands (Gulick 1932, Darlington 1957, Carlquist 1965, Paulay 1994, Peck 1994a, b). We also know that colonization events can happen swiftly. Colonizations of newly created or sterilized islands (e.g. Krakatau; Motmot, New Guinea; San Benedicto, Mexico; Surtsey, Iceland; Long and Ritter Islands, New Guinea) occurred soon after volcanic explosions or surfacing events (Dammerman 1948, Carlquist 1965, Diamond 1974, 1975, Fridriksson 1975, Williamson 1981, Thornton 1996).

Experimental manipulations support this view. Upon removing all bird fauna on a small island 3 km from New Guinea, Diamond (1975) found that recolonization occurred extremely rapidly, initially at 1 avian species per hour, until "equilibrium" was reached < 2d later. Moreover, Simberloff and Wilson (1969) found that it took < 36 weeks to re-establish previous levels of species richness of arthropods on 5 of 6 experimental mangrove islands, with immigration and extinction rates ranging from 0.05-0.50 species d⁻¹. These colonizations indicate that dispersal is continuous and can occur at a grand scale. In addition, these data are very conservative and do not indicate two potentially frequent types of colonization/dispersal events. First, the "rescue effect" (Brown and Kodric-Brown 1977) is a dispersal event that generally goes unrecognized because colonists merge into extant populations. Second, not all arrivals ultimately establish populations, either because of improper sex ratios, small colonizing groups eventually become extinct, or they arrive at a premature period during the species assembly of island food webs (e.g. Allee 1931, Terborgh and Winter 1980, Pimm et al. 1988, Holt et al. 1999).

It is commonly accepted that colonization takes place with regularity on islands. In fact, much research has been conducted on the turnover and colonizations of plant (e.g. Herwitz et al. 1996), avian (e.g. Diamond 1969, Thornton 1996), mammalian (e.g. Heaney 1984, Laurance 1991), and invertebrate (e.g. Simberloff and Wilson 1969, Thornton 1996) species. It should not be much of an extension, then, to appreciate that vagrants and other "non-residents" also reach far and near islands routinely.

Types of non-resident visitors to islands

Vagrants and migrants

Some taxa consistently visit islands for short periods, but depart and do not establish viable populations (Saunders and De Rebeira 1985). It is highly probable that many varieties of animals access islands and then return to the mainland (either by swimming, flight, or wind and sea-surface transport), especially on nearshore islands. Johnson (1980) noted several historic records of elephants Loxodonta africana and Elephas maximus from coastal regions swimming to exploit island resources and potentially escape from mainland predators when giving birth. He also recorded an incident of lions Panthera leo swimming to islands as well, presumably to hunt or scavenge insular prey. In Baja California, Mexico, a coyote Canis latrans was observed swimming ~ 2 km from the mainland to Gemelitos West, a tiny island (0.02 km²) in Bahía de los Angeles containing double-crested cormorant Phalacrocorax auritus and yellow-legged gull Larus livens colonies (~ 70 and 15 breeding pairs, respectively; Vazquez pers. comm.).

Terrestrial avian species are also common vagrants, using small islands as roosting and feeding sites and migratory stopover points. Numerous instances of avian vagrancy have been recorded on nearshore and distant islands (e.g. Simberloff and Wilson 1969, Diamond 1975, DeSante 1983, McNab 1994, Scott 1994). McNab (1994) reported that pigeons (Ducula pacifica) on Anuta Island (0.4 km²), an outlier of the Solomon chain, relocated from 137 to > 300 km in their search for fruit. Black-shouldered kites Elanus caeruleus utilized periods of favorable wind direction to inhabit San Clemente Island > 80 km from the California coast, whereupon their relatively large population (16-26 individuals for two months) fed on mice *Mus musculus* and Peromyscus maniculatus but did not breed (Scott 1994). Likewise, several raptors (Falco peregrinus, F. sparverius, Circus cyaneus, Accipiter cooperi, and A. striatus) visited Socorro Island 460 km from Cabo San Lucas, Baja California Sur, Mexico (Walter 1990). De-Sante (1983) gives an account of > 215 species of migrant birds that visited Southeast Farallon Island off Point Reyes, California; he credits long-range, large scale weather factors as determinants of atypical peaks in vagrant abundance.

Such records indicate that avian vagrants locate islands and then make their way back to the mainland. Nevertheless, these visitors may alter the islands that they visit. For example, the first vertebrate visitors on Motmot, a volcanic island created within a large freshwater lake on Long Island, New Guinea, were seabirds and vagrants (avian predators and black ducks *Anas superciliosa*). These species facilitated the ecological development of this island through seed dispersal and allochthonous nutrient deposition (Ball and Glucksman 1975).

There are undoubtedly numerous other examples of vagrant species either swimming or flying roundtrip to small islands from the mainland (or from larger islands). However, witnessed or documented events are infrequent because interested observers are in place so rarely, the dispersal may occur at night or be of short duration, and visitors are often inconspicuous. Thus, the frequency of such behavior is largely unreported and unknown. To remedy this shortage, we recorded resident and vagrant bird species on 21 islands over 700 estimated visits for 10 yr (1990-1999) in the Midriff area of the Gulf of California. Our data suggest that short-term island visits are likely very common. For example, in the Midriff area of the Gulf of California alone, we recorded 32 species within 16 families of migrants and visitors that rested and foraged on islands for short periods but did not establish multi-year residency (Appendix). Utilization of these arid islands by avian vagrants and migrants is significantly linked to wet years associated with El Niño events ($R^2 = 0.45$, DF = 1, 7, F = 7.59, p = 0.03). Case and Cody (1983); Appendix 8.8) report 35 additional migrant and vagrant species on Gulf of California islands.

Our data also show that other vagrant and migratory groups visit islands. In March 1998, we recorded ~ 100 monarch butterflies *Danaus plexippus* resting on two *Pachycormis discolor* elephant trees on Isla Ventana. Moreover, in the wet El Niño years of 1992/1993, 1995, and 1998, we commonly observed butterflies from several families (e.g. Danaidae, Lycaenidae, Nymphalidae, Pieridae, Papilionidae) flying over the ocean between the mainland and islands and among islands (see also Askew 1988, Ferguson et al. 1991).



Fig. 1. Winter precipitation and mean % difference in the number of breeding songbird species (S + 1) between years. Data was collected on 7 small (< 1.5 km²) Gulf of California islands from 1990 to 1999. Significantly more species inhabited islands during wet (El Niño) years (1992–1995) than dry (non-El Niño) periods (1990–1991, 1996–1997, 1999).

ECOGRAPHY 23:6 (2000)

Individuals with multi-island and mainland-island foraging ranges

There are some vagile species whose foraging ranges extend across water boundaries and encompass one to many islands. Approximately 10% of insect species sighted on Simberloff and Wilson's (1969) experimental islands, including cicadas, odonates, bees, wasps, butterflies, and moths (and birds as well), were this type of vagrant. Simberloff and Wilson (1969) did not analyze how the presence of these predators and competitors altered colonization and extinction rates; a study that could have proved interesting. Whitakker (1998) reported island-mainland and island-island range overlap for fruit bats Pteropus vampyrus and fruit pigeons Ducula bicolor, respectively, that inhabited Krakatau. These species were prime contributors to the plant assembly and successional dynamics of this island through seed dispersal (Whitakker 1998). In Baja California, individual turkey vultures Cathartes aura, Anna's and Costa's hummingbirds Calypte anna and C. costae, red-tailed hawks Buteo jamaicensis, and ravens Corvus corax have foraging areas that apparently regularly encompass mainland and island locations. We have likewise observed large spider wasps (tarantula hawks, *Pepsis* spp.: Pompilidae) and dragonflies (Order: Odonata) flying over open ocean in direct lines to, and foraging among, islands.

Source-sink inhabitants

Although not vagrants per se, a source-sink configuration with rapid species turnover likens these individuals to non-resident visitors. Habitat quality in local patches varies temporally and may control the dynamics of "sink" populations (Pulliam 1988, Moilanen and Hanski 1998). Thomas and Hanski (1997) note that some species breed and/or persist over larger areas during optimal seasons or years and then withdraw to more suitable habitats during bad periods.

This is the case in our study system. Over the last 10 yr, we have observed seven instances of colonization (from the mainland and larger islands), persisting for months to two years, with reproduction and extinction events by two spider species (Peucetia viridens and Argiope argentata) on islands in the Midriff region of the Gulf of California. On these same islands, we also recorded multiple episodes of colonization and breeding by Costa's hummingbirds, black-throated sparrows Amphispiza bilineata, virdens Auriparus flaviceps, cactus wrens Campylorhynchus brunneicapillus, and rock wrens Salpinctes obsoletus (Appendix). These birds colonize (from the mainland and larger islands) in wet El Niño years, breed, sometimes repeatedly, and then "become extinct" (i.e. die or return to the mainland) in subsequent dry years (Fig. 1). For example, on Isla Piojo in 1995 (a wet year), black-throated sparrows colonized and produced three clutches that persisted into early 1996, a very dry year. By late 1996, no individuals remained and we actually found carcasses on the island. Overall, we have observed 13 events on 7 islands of songbird colonization and breeding followed by extinction. Lastly, one *Scleroporus* lizard species colonized Isla Cerraja during a good year (1995), but has subsequently disappeared. Clearly these are examples of source-sink driven populations where extinction rates exceed colonization rates during bad (dry) seasons/ years.

Many other species colonize and become extinct with regularity during opportune and inopportune periods (MacArthur 1972, Schoener and Spiller 1987, Thomas and Hanski 1997). Diamond's "supertramps" (1974, 1975) follow this scheme. Even individuals within an island population can be vagrants; Pimm et al. (1988) pointed out that roughly half of the insular pairs of Hawaiian crows *Corvus hawaiiensis*, hawks, and owls died or dispersed to other islands before breeding. Hence, range contractions and expansions within source-sink and metapopulation systems potentially create vagrancy-like situations for some species.

Consequences and implications of reduced island insularity

Our data illustrate that islands may be relatively more open to non-resident species than previously thought. The potential frequency of (successful and unsuccessful) colonizations and short term visits by vagrant and migratory species does not conform smoothly with the notion that islands are immune to the influences of non-insular species. We argue that many islands are actually quite open to individuals of species that can move from other islands and the mainland. This view carries several consequences:

Island isolation

Islands are not as species-poor as species-area curves would implicate. The arrival of vagrants and utilization of islands by biota during opportune periods means that apparently depauperate islands may experience many more species than expected by species lists of long term residents made at a particular time. This decreased isolation carries ecological and evolutionary implications.

Island biogeography

Classic island biogeography models equilibrium turnover, i.e., no net gain or loss in species number over

time. However, source-sink populations in our system counter this principle. Significantly more songbird species colonize small islands ($< 1.5 \text{ km}^2$) during wet (El Niño) periods than dry (non-El Niño) years ($R^2 = 0.55$, DF = 1, 7, F = 10.61, p = 0.01; Fig. 1). Extinctions occur relatively quickly (within < 1-2 yr) as dry years soon follow El Niño. Colonization rates are dependent on precipitation; high rates correspond with opportune wet years, low rates with inopportune periods. Thus, source-sink occurrences on Gulf of California islands represent non-equilibrium turnover, with net losses (extinctions) of species during dry years. This is likely true for many other mainland-island source sink situations, due in part because other factors besides island area and distance from the mainland determine colonization and extinction rates.

Vagrants may influence bigeography measures in other ways. For example, failure to distinguish vagrants from residents may erroneously alter classic equilibrium analyses of immigration and extinction rates. Over-estimated extinction rates for plants and butterflies on Krakatau and Rakata were the result of inclusion of several migratory and non-residents in initial species surveys (Whitakker 1998).

Island ecology

Vagrants, even when uncommon and few in number, may significantly affect the flow of energy, nutrients, and resources, and population spatial, temporal, and behavioral organization on islands. Transient species can exert a variety of effects on island resources and the food webs which they exploit temporarily (e.g. Spiller and Schoener 1994, Polis et al. 1998). We delineate five types of interactions. 1) Predation: brief but intensive predation may be central to resident dynamics (see Polis 1994). For example, during their annual migration from Africa to Europe, thousands of white storks Ciconia alba remove up to 95% of adult tenebrionid beetles in certain regions of the Negev desert, Israel (Ayal and Merkl 1994). 2) Parasites and pathogens: vagrants potentially significantly affect insular populations and island dynamics in their role as vectors for the transport of parasites or disease. For example, it is well known that migrant birds can spread avian diseases and transport Ixodes ticks which carry Lyme disease to island residents (Smith et al. 1996). 3) Competition: vagrants may compete with residents for resources. Patten and Burger (1998) found that spruce budworm Choristoneura fumiferana outbreaks attracted vagrant warbler species who subsequently decreased resident magnolia warblers Dendroica magnolia. 4) Zoogeomorphology: vagrants can also affect island ecology directly through habitat alteration: i.e. geophagy, trampling, wallowing, digging, burrowing, and transport/accumulation of material for nest-building (Butler 1995). 5) Cascading events: lastly, infrequent visitors on islands may initiate cascading events that can affect most elements in an island food web. For example, transport of seeds (via mud on feet, stuck in feathers, excreta, or on prey carried to islands) and eggs (of aquatic invertebrates) can influence island assembly structure and succession of species with effects from the base of the food web upward (Fridriksson 1975, Ball and Glucksman 1975, Porter 1983). Additionally, top-down effects, e.g. by vagrants, may influence species compositions, nutrient dynamics, NAPP, and the distribution of biomass via several pathways (Polis 1999) on islands.

Evolution of island biota

Island vagrants may influence the direction of evolution on islands in many ways. First, occasional genetic introgression via visitors could undoubtedly impede the evolution of all traits particular to island life (see Slatkin 1987). Most notably, traits associated with absence of predators (flightlessness, changes in body size, tameness) and competitors (niche expansion, adaptive radiation) would evolve at a slower rate, or cease altogether. Coincidentally, such "non-insular" traits could be advantageous for island species that are now facing increased predation and competition by invasives (Stone et al. 1994). Second, hybridization of island species with vagrants will alter their genetic (and evolutionary) existence via introgression, hybrid sterility, or outbreeding depression (Rhymer and Simberloff 1996). These phenomena may occur rather rapidly and with few interbreeding (vagrant) individuals (Huxel 1999). In fact, Rhymer and Simberloff (1996) suggest that hybridization may be more common on islands (especially small ones) where breeding populations are isolated and diminished, and the "other" hybridizing population (here vagrants) is concurrently small. Conversely, hybridization with vagrants has the potential to promote prompt evolutionary change (Lewontin and Birch 1966, Barton and Hewitt 1989) and increase fitness through hybrid vigor, augmented genetic variation, and adjustment to novel environments (Grant and Grant 1992, Arnold and Hodges 1995, Rhymer and Simberloff 1996, Huxel 1999).

On the insularity of habitat and other "islands"

Non-oceanic islands

We have restricted our examples to marine islands. But, vagrancy occurs within other types of insular systems. For example, islands in lakes experience visitors with some frequency, from migratory birds (e.g. Ball and Glucksman 1975) to small mammals (e.g. Hanski 1986)

ECOGRAPHY 23:6 (2000)

to large herbivores and predators. Moose *Alces alces* and (especially) caribou *Rangifer tarandus* inhabit islands in Lake Nipigon, Canada for the summer months to escape timber wolf predation (Bergerud et al. 1990). Vagrant *Sorex* shrews on islands in Lake Sysmä, Finland, exist for the summer months but disperse to larger islands to breed or, more likely, annually "go extinct" (Peltonen and Hanski 1991). Indeed, Brown and Kodric-Brown's (1977) "rescue effect" is empirically derived from populations of arthropods that "visited" thistle plants (habitat islands) but did not colonize or maintain breeding populations.

Insularity of refuges and reserves

Habitat refuges/reserves and oceanic islands are similar in that ecologically influential yet distinctly different environments surround each. Vagrants from non-reserve habitats undoubtedly visit refuges and reserves, probably regularly. A common, yet presently controversial, example of this involves avian predation (e.g. by blue jays Cyanocitta cristata, weasels Mustela erminea, and raccoons Procyon lotor) and brood-parasitism by cowbirds Molothrus ater along the edges of woodland habitats and/or in forest fragments (e.g. Wilcove et al. 1986, Donovan et al. 1995, Evans and Gates 1997). Similar to situations on marine islands, genetic "homogenization" of locally adapted traits with characteristics of rife agricultural vagrants from juxtaposed croplands may decrease resident fitness (Janzen 1986). As continental "island" refuges become smaller, vagrants will have greater access to insular resources (Crooks and Soulé 1999), and thus a mounting role in determining refuge structure, species composition within reserves, and evolutionary pathways of residents.

In contrast, it is important to note that refuge/reserve residents also act as vagrants, moving between refuges and/or exploiting urban areas, fields, and domestic taxa (e.g. most canid species, raccoons, waterfowl, insects, vampire bats; Janzen 1983, 1986). This exploitation carries positive and negative consequences. For instance, coyotes indirectly increased bird diversity by killing domestic cats within urban habitat islands (Crooks and Soulé 1999), a positive consequence. However, high predation by domestic predators and pesticide-induced mortality of visitors utilizing urban areas and croplands negatively impacted insular populations (Churcher and Lawton 1987, Boutin et al. 1999). Janzen (1986) describes further how utilization of adjacent habitats by refuge populations can alter insular systems. Resource subsidy (e.g. for peccary Tayassu spp.) from foraging outside of a Costa Rican reserve influenced the park in three distinct ways. Subsidized peccaries, with higher densities than enabled by reserve resources alone, foraged within the refuge and greatly decreased insular resources, trampled soils and vegetation, and dispersed invasive species of seeds fed upon during forays to juxtaposed areas (Janzen 1986). Such direct and indirect impacts can significantly influence refuges and reserves.

Studies on the ecological and evolutionary effects of vagrants

"One of the features imposed by the equilibrium paradigm has been the restriction of focus to species that are residents on islands" (Whitakker 1998, p. 187).

Little has been done, empirically and otherwise, to understand the effects of vagrants on "island" systems. Yet understanding vagrancy events is important for island conservation, ecology, and evolution. Although difficult in practice, we nevertheless urge empirical examination of the frequency and importance of island visitation by vagrants. Are vagrants more common in some geographical regions or on islands with certain features? If so, what geographical and ecological factors predict vagrant visitation to islands – distance to mainland, archipelago geometry, high food availability, low competition and/or predation, a combination of these factors, or other causes? We advocate studies that examine how vagrants influence island residents via competition, predation, parasitism, or transport of seeds and nutrients. In conjunction, we stress the importance of identifying what species are likely to be highly influenced by vagrants; this could carry significant conservation implications for endemics. Lastly, there is a need to analyze the effect of vagrants on species turnover, i.e. are island colonization and extinction events influenced by visits from non-residents?

To address impacts of vagrants on insular evolution, we encourage studies looking at the frequency of hybridization of residents and vagrants on islands. What are the potential positive and negative effects of hybridization and how does this alter the survival/evolution of insular species? To what extent do vagrants impose "non-insular" qualities on island residents? There are many other facets of vagrancy to study, as this area remains relatively untouched. We recognize that vagrant interactions within mainland habitat "islands" need further empirical assessment and could provide novel insights into important conservation issues such as the SLOSS debate (i.e. benefits of isolation, edge effects for small reserves and corridors, and minimum viable area and populations).

Conclusions

"Vagrancy" is an unrecognized yet potentially important factor in the evolution and ecology of island biotas. Movement and dispersal of animals and plants are ubiquitous, and likely affect islands worldwide, especially nearshore ones. We propose that vagrancy events are much more prevalent than past documentation suggests. Moreover, if our view of islands is expanded to encompass lake island refuges, habitat preserves and parks, caves, mountaintops, and isolated bodies of waters (ponds, lakes and streams), then vagrancy is arguably a near ubiquitous and potentially significant phenomenon. Janzen (1983, p. 403) noted a self-induced naiveté of researchers, in part, about vagrancy and its effects: "Every field biologist...is aware to some degree of this problem, but none of us wish to fully acknowledge its potential impact on biotic interactions and our ecological/evolutionary interpretations of them." Consequently, models and studies of such topics as species turnover, community assembly, island ecology, species evolution, extinctions, effects of competition and predation, and other facets of island systems underrate or neglect entirely the importance of vagrants (Laurance 1991). In fact, many accounts of island vagrancy in this paper were gleaned from statements of exclusion from analyses by other authors (e.g. Simberloff and Wilson 1969, Diamond 1975, Walter 1990, Peltonen and Hanski 1991). In light of recent and rapid extinctions on islands and the extent of habitat fragmentation on mainlands, the role vagrants play in population, community and food web dynamics for all "islands" cannot remain an ignored phenomenon.

Acknowledgements – We extend our gratitude to those who contributed discussion, reviews, and advice that greatly improved this paper: Susan Harrison, Caitlyn Harvey, Gary Huxel, Antonio Resendiz, Susan Rose, Francisco Sanchez-Piñero, Anna Sears, David Spiller, Paul Stapp, Candy Supnet, and Abraham Vazquez. This project was supported by the National Science Foundation (grants DEB-9207855 and DEB-9527888 to GAP) and the Earthwatch Foundation. The Mexican government provided research permits 603-1412 and DAN-02201.

References

- Allee, W. C. 1931. Animal aggregations, a study in general sociology. – Univ. Chicago Press.
- Arnold, M. L. and Hodges, S. A. 1995. Are natural hybrids fit or unfit relative to their parents? – Trends Ecol. Evol. 10: 67–71.
- Askew, R. R. 1988. Butterflies of Grand Cayman [British West Indies], a dynamic island fauna. – J. Nat. Hist. 22: 875– 882.
- Ayal, Y. and Merkl, O. 1994. Spatial and temporal distribution of tenebrionid species (Coleoptera) in the Negev Highlands, Israel. – J. Arid. Environ. 27: 347–361.
- Ball, E. and Glucksman, J. 1975. Biological colonization of Motmot, a recently-created tropical island. – Proc. R. Soc. Lond. B 190: 421–442.
- Barton, N. H. and Hewitt, G. M. 1989. Adaptation, speciation and hybrid zones. Nature 341: 497-503.
- Bergerud, A. T., Ferguson, R. and Butler, H. E. 1990. Spring migration and dispersion of woodland caribou at calving.
 Anim. Behav. 39: 360–368.
- Boutin, C., Freemark, K. E. and Kirk, D. A. 1999. Farmland birds in southern Ontario: field use, activity patterns and

vulnerability to pesticide use. – Agricult. Ecosyst. Environ. 72: 239–254.

- Brown, J. H. and Kodric-Brown, A. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. – Ecology 58: 445–449.
- Butler, D. R. 1995. Zoogeomorphology: animals as geomorphic agents. Cambridge Univ. Press.
- Carlquist, S. 1965. Island life: a natural history of the islands of the world. – Nat. Hist. Press, Garden City, NY.
- Case, T. J. and Cody, M. L. (eds) 1983. Island biogeography in the Sea of Cortez. – Univ. of California Press.
- Churcher, P. B. and Lawton, J. H. 1987. Predation by domestic cats in an English [UK] village. – J. Zool. 212: 439– 456.
- Crooks, K. R. and Soulé, M. E. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. – Nature 400: 563–566.
- Dammerman, K. W. 1948. The fauna of Krakatau 1883–1933. – Verhandel. Koninkl. Ned. Akad. Wetenschap. Afdel. Natuurk. 44: 1–594.
- Darlington, P. J. 1957. Zoogeography: the geographical distribution of animals. John Wiley.
- DeSante, D. F. 1983. Annual variability in the abundance of migrant landbirds on southeast Farallon Island, California. – Auk 100: 826–852.
- Diamond, J. M. 1969. Avifaunal equilibria and species turnover rates on the Channel Islands of California. – Proc. Natl. Acad. Sci. USA 64: 57–63.
- Diamond, J. M. 1974. Colonization of exploded volcanic islands by birds: the supertramp strategy. – Science 184: 803–806.
- Diamond, J. M. 1975. Assembly of species communities. In: Cody, M. L. and Diamond, J. M. (eds), Ecology and evolution of communities. Harvard Univ. Press, pp. 342– 444.
- Donovan, T. M. et al. 1995. Reproductive success of migratory birds in habitat sources and sinks. – Conserv. Biol. 9: 1380–1395.
- Evans, D. R. and Gates, J. E. 1997. Cowbird selection of breeding areas: the role of habitat and bird species abundance. – Wilson Bull. 109: 470–480.
- Ferguson, D. C., Hilburn, D. J. and Wright, B. 1991. The Lepidoptera of Bermuda: their food plants, biogeography, and means of dispersal. – Memoirs Entomol. Soc. Can. 158: 3–105.
- Fridriksson, S. 1975. Surtsey: evolution of life on a volcanic island. John Wiley.
- Grant, P. R. and Grant, B. R. 1992. Hybridization of bird species. Science 256: 193–197.
- Gulick, A. 1932. Biological peculiarities of oceanic islands. Quart. Rev. Biol. 7: 405–427.
- Hanski, I. 1986. Population dynamics of shrews on small islands accord with the equilibrium model. – Biol. J. Linn. Soc. 28: 23–36.
- Heaney, L. R. 1984. Mammalian species richness on islands on the Sundra Shelf, southeast Asia. – Oecologia 61: 11–17.
- Herwitz, S. R., Wunderlin, R. P. and Hansen, B. P. 1996. Species turnover on a protected subtropical barrier island: a long-term study. – J. Biogeogr. 23: 705–715.
- Holt, R. D. et al. 1999. Trophic rank and the species-area relationship. Ecology 80: 1495-1504.
- Huxel, G. R. 1999. Rapid displacement of native species by invasive species: effects of hybridization. – Biol. Conserv. 89: 143–152.
- Janzen, D. H. 1983. No park is an island: increase in interference from outside as park size decreases. – Oikos 41: 402–410.
- Janzen, D. H. 1986. The eternal external threat. In: Soulé, M. E. (ed.), Conservation biology: the science of scarcity and diversity. Sinauer, pp. 286–303.
- Johnson, D. L. 1980. Problems in the land vertebrate zoogeography of certain islands and the swimming powers of elephants. – J. Biogeogr. 7: 383–398.

ECOGRAPHY 23:6 (2000)

- Laurance, W. F. 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. – Conserv. Biol. 5: 79–89.
- Lewontin, R. C. and Birch, L. C. 1966. Hybridization as a source of variation for adaptation to new environments. – Evolution 20: 315–336.
- MacArthur, R. H. 1972. Geographical ecology: patterns in the distribution of species. Harper and Row.
- McNab, B. K. 1994. Resource use and the survival of land and freshwater vertebrates on oceanic islands. Am. Nat. 144: 643–660.
- Moilanen, A. and Hanski, I. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. – Ecology 79: 2503–2515.
- Patten, M. A. and Burger, J. C. 1998. Spruce budworm outbreaks and the incidence of vagrancy in eastern North American wood-warblers. – Can. J. Zool. 76: 433–439.
- Paulay, G. 1994. Biodiversity on oceanic islands: its origin and extinction. – Am. Zool. 34: 134–144.
- Peck, S. B. 1994a. Aerial dispersal of insects between and to the islands in the Galápagos Archipelago, Ecuador. – Ann. Entomol. Soc. Am. 87: 218–224.
- Peck, S. B. 1994b. Sea-surface (pleuston) transport of insects between islands in the Galápagos Archipelagos, Ecuador.
 Ann. Entomol. Soc. Am. 87: 576–582.
- Peltonen, A. and Hanski, I. 1991. Patterns of island occupancy explained by colonization and extinction rates in shrews. – Ecology 72: 1698–1708.
- Pimm, S. L., Jones, H. L. and Diamond, J. 1988. On the risk of extinction. – Am. Nat. 132: 757–785.
- Polis, G. A. 1994. Food webs, trophic cascades and community structure. – Aust. J. Ecol. 19: 121–136.
- Polis, G. A. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. – Oikos 86: 3–15.
- Polis, G. A. et al. 1998. Multifactorial population limitation: variable spatial and temporal control of spiders on Gulf of California islands. – Ecology 79: 490–502.
- Porter, D. M. 1983. Vascular plants of the Galápagos: origins and dispersal. – In: Bowman, R. I. and Leviton, A. E. (eds), Patterns of evolution in Galápagos organisms. Am. Ass. Advanc. Sci., Pacific Div., San Francisco, pp. 33–96.
- Pulliam, H. R. 1988. Source, sinks, and population regulation. - Am. Nat. 132: 652–661.
- Rhymer, J. M. and Simberloff, D. 1996. Extinction by hybridization and introgression. – Ann. Rev. Ecol. Syst. 27: 83–109.
- Saunders, D. A. and De Rebeira, C. P. 1985. Turnover in breeding bird populations on Rottnest Island, Western Australia. – Aust. Wildl. Res. 12: 467–478.
- Schoener, T. W. and Spiller, D. A. 1987. High population persistence in a system with high turnover. – Nature 330: 474–477.
- Scott, T. A. 1994. Irruptive dispersal of black-shouldered kites to a coastal island. – Condor 96: 197–200.
- Simberloff, D. S. and Wilson, E. O. 1969. Experimental zoogeography of islands: the colonization of empty islands. – Ecology 50: 278–289.
- Slatkin, M. 1987. Gene flow and the geographic structure of natural populations. – Science 236: 787–792.
- Smith Jr, R. P. et al. 1996. Role of bird migration in the long-distance dispersal of *Ixodes dammini*, the vector of Lyme disease. – J. Infect. Diseases 174: 221–224.
- Spiller, D. A. and Schoener, T. W. 1994. Effects of top and intermediate predators in a terrestrial food web. – Ecology 75: 182–196.
- Stone, P. A., Snell, H. L. and Snell, H. M. 1994. Behavioral diversity as biological diversity: introduced cats and lava lizard wariness. – Conserv. Biol. 8: 569–573.
- Terborgh, J. and Winter, B. 1980. Some causes of extinction. – In: Soulé, M. E. and Wilcox, B. (eds), Conservation biology: an evolutionary-ecological perspective. Sinauer, pp. 119–133.

- Thomas, C. D. and Hanski, I. 1997. Butterfly metapopulations. - In: Hanski, I. and Gilpin, M. (eds), Metapopulation biology: ecology, genetics and evolution. Academic Press, pp. 359-386.
- Thornton, I. 1996. Krakatau: the destruction and reassembly of an island ecosystem. – Harvard Univ. Press. Walter, H. S. 1990. Small viable populations: the red tailed
- hawk of Socorro Island. Conserv. Biol. 4: 441-443.
- Whitakker, R. J. 1998. Island biogeography: ecology, evolution, and conservation. – Oxford Univ. Press. Wilcove, D. S., McLellan, C. H. and Dobson, A. P. 1986.
- Habitat fragmentation in the temperate zone. In: Soulé, M. E. (ed.), Conservation biology: the science of scarcity and diversity. Sinauer, pp. 237–256. Williamson, M. 1981. Island populations. – Oxford Univ.
- Press.

Appendix. A list of migrant and visiting avifauna present on Midriff Islands in the Gulf of California from 1990 to 1999. Islands of occupancy are listed by number. Bold numbers indicate sited nesting events.

Apodiformes	
1 rocnillade A nu s's house in shinds(8, 15, 20, 21)	(C_{1})
Anna s nummingbirds ^{(α, α, α, α, α, α, α, α,}	(Calypie anna)
	(Calypie coside)
Apoalaae $(3, 4, 7, 10, 11, 13)$	
white-throated swifts ⁽³⁾ , <i>i</i>	(Aeronautes saxatalis)
Columbiformes	
Columbidae	
mourning doves ⁽⁹⁾	(Zenaida macroura)
Coracitormes	
Alcedinidae	
belted kingfishers ^(3, 21)	(Ceryle alcyon)
Falconiformes	
Accipitridae	
red-tailed hawks ⁽²¹⁾	(Buteo jamaicensis)
Cathartidae	
turkey vultures ^(6, 20, 21)	(Cathartes aura)
Passeriformes	
Corvidae	
ravens ^(19, 20, 21)	(Corvus corax)
Emberizidae	
magnolia warblers ^(13, 17)	(Dendroica magnolia)
brown-headed cowbirds ⁽¹³⁾	(Molothrus ater)
American tree sparrows $^{(13,20)}$	(Spizella arborea)
black-throated sparrows ^(3, 6, 9, 10, 13, 17, 20, 21)	(Amphispiza bilineata)
Brewer's sparrows ^(13, 20)	(Snizella breweri)
savannah sparrows ⁽²⁰⁾	(Passerculus sandwichensis)
white-throated sparrows ⁽²¹⁾	(Aeronautes saxatalis)
Hirundinidae	(Heronautes sustaines)
violet-green swallows ⁽²¹⁾	(Tachycineta thalassina)
barn swallows	(Hirundo rustica)
Laniidae	(IIII ando Fastica)
loggerhead shrikes ^(9, 20, 21)	(Lanius Indovicianus)
Mimidae	(Lunius indobiciunus)
northern modelinghirds ⁽²⁰⁾	(Minus nabialattas)
Mussiagnidas	(Mimus polygiotios)
Muscicupique	(\mathbf{p}_{1})
Diack-tailed gnatcatchers ⁽¹⁾	(Ponopina melanura)
Pariaae	
verdins ^(0, 14)	(Auriparus flaviceps)
Troglodytidae	
Bewick's wrens $(3, 17)$	(Thryomanes bewickii)
cactus wrens $(0, 14, 20, 21)$	(Campylorhynchus brunneicapillus)
canyon wrens ^(3, 4)	(Catherpes mexicanus)

ECOGRAPHY 23:6 (2000)

rock wrens ^(2, 3, 5, 6, 7, 9, 10, 11, 12, 13, 15, 17, 18, 20, 21)	(Salpinctes obsoletus)
wrentits ⁽¹⁴⁾	(Chamaea fasciata)
Tyrannidae	
ash-throated flycatchers ^(1, 5, 20, 21)	(Myiarchus cinerascens)
Cassin's kingbirds ⁽²⁰⁾	(Tyrannus vociferans)
thick-billed kingbirds ⁽²¹⁾	(Tyrannus crassirostris)
tropical kingbirds ⁽¹³⁾	(Tyrannus melancholicus)
Say's phoebes ^(20, 21)	(Sayornis saya)
Strigiformes	
Tytonidae	
elf owls ⁽²¹⁾	(Micrathene whitneyi)
1. Almagres Chico 2. Bota 3. Cabeza de Caballo 4. Cala	avera 5. Cardonosa 6. Cerraja 7. Cor

 Almagres Chico 2. Bota 3. Cabeza de Caballo 4. Calavera 5. Cardonosa 6. Cerraja 7. Coronadito 8. Danzante 9. Flecha 10. Gemelos West 11. Jorobado 12. Mejia 13. Mitlan 14. Pajaros 15. Partida Norte 16. Pata 17. Piojo 18. San Luis 19. San Pedro Martír 20. Smith 21. Ventana