LAND BIRD DENSITIES ON BAJA CALIFORNIA ISLANDS

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ABSTRACT.—Land bird populations were censused on four islands and three matching mainland sites in southern Baja California. Island densities (summed totals for all species) were more than twice as high as mainland densities in the dominant desert scrub habitat, and slightly higher in the secondary, riparian woodland habitat. Island-mainland ratios varied greatly in most species, ranging from 8.25:1 in the Black-throated Sparrow to 0.18:1 in the White-winged Dove. Contrary to the predictions of density compensation theory the consuming biomass of the various foraging guilds also differed greatly between island and mainland sites, island-mainland ratios ranging from 4.31:1 in the flower probers, to 0.15:1 in the large terrestrial granivores.

Environmental factors of food supply, predators, and climate apparently do not account for these differences in island vs. mainland densities. Instances of high island density are tentatively attributed to: a) higher mean adaptedness to local conditions due to isolation from the swamping and diluting effects of mainland interdeme gene flow, and/or b) overcrowding due to the blocking of normal, socially-induced dispersal movements by island coastline barriers (fence effect). Instances of low island density were encountered only in woodland species and are tentatively attributed to high extinction rates and tenuous population survival associated with the scarcity and small size of woodland habitat patches on islands. *Received 1 May 1978, accepted 28 October 1978.*

VARIATIONS in population density in ecologically similar but geographically separated land bird communities have received little attention because of the inadequacy of available census techniques, but several recent studies indicate that species densities, guild densities, and summed community densities may differ considerably between islands and closely matched mainland areas (Crowell 1962, Grant 1966, Diamond 1970, MacArthur et al. 1972, Emlen 1978).

In this paper I present data on island and mainland bird densities from the desert scrubland region of Baja California and then discuss possible explanations for the recorded differences in terms of a) extrinsic factors of climate, predation, and limited food resources, b) variations in mean adaptedness for local conditions as related to open vs. blocked gene flow patterns, and c) social spacing dynamics in open vs. blocked dispersal situations. A similar analysis has been made for lizard populations in the same area (Case 1975).

METHODS

The fieldwork, conducted between 5 and 28 April 1977, included bird censuses, vegetation measurements, and food resource (arthropod) sampling at four island and three mainland sites in southern Baja California (Table 1, Fig. 1). The sites were selected to provide island and mainland samples of each of the two dominant habitat types in the area (Fig. 2), a) the mixed desert scrubland that formed a rather uniform vegetational matrix over the lower slopes and bajadas, and b) the riparian, desert woodland that occurred in isolated strips and patches in arroyos and on sandy alluvial fans and coastal "bays." A third habitat type comprising the steep and relatively barren upper slopes of the hinterland was not sampled. Study sites were selected in island-mainland pairs along protected coasts where anchorage could be had for our boat within walking distance of good census areas. Island sites were selected first, and for each of these a mainland site was selected close by along a section of coast offering census areas with topography and vegetation as similar as possible to those on the island. For the most southerly island we found no good matching mainland situation.

Vegetation measurements were designed to detect and evaluate consistent differences in avian habitat

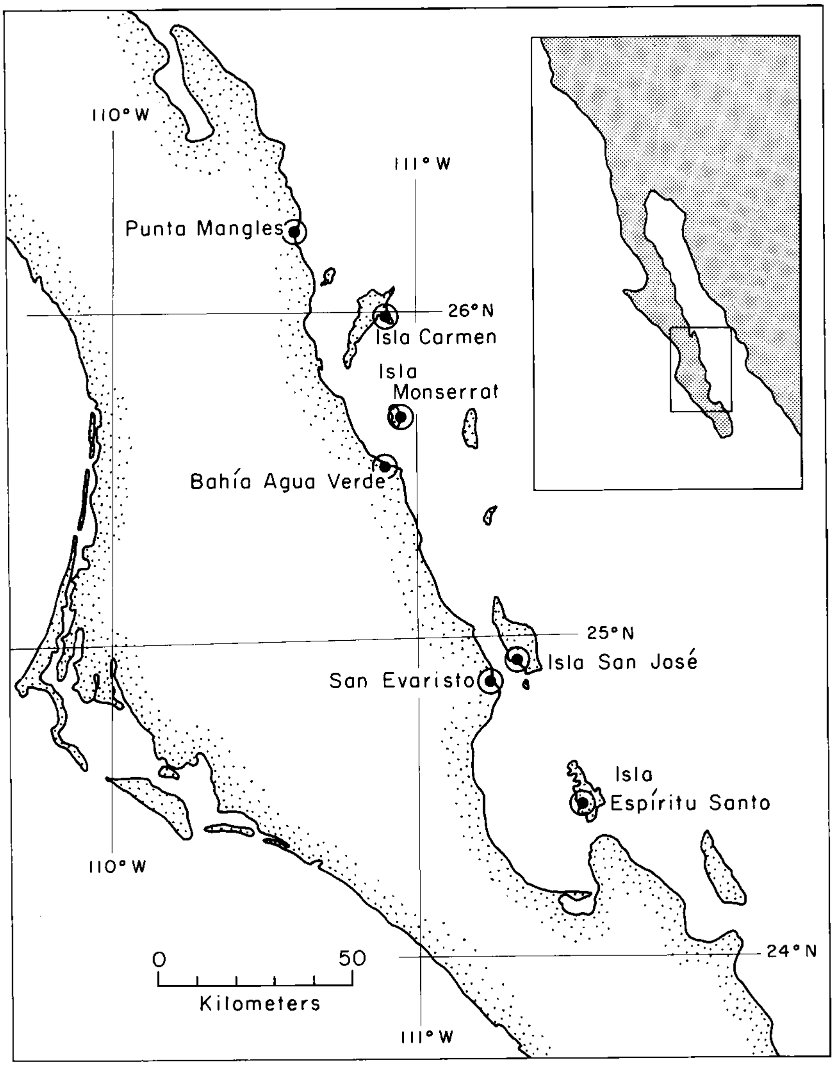

Fig. 1. Map of southern Baja California showing the locations of island and mainland study sites.

conditions between island and mainland sites (Table 2). At five or more representative stations of scrubland and woodland vegetation at each site I recorded: a) mean height and percent cover of trees (defined as woody plants 3–6 m high), high shrubs (1–3 m) and low shrubs (<1 m), b) height and percent cover of tall, medium, and low cactus types, and c) patchiness and mean density of the herbaceous ground cover. Procedures and conventions are described in the footnotes of Table 2. Common trees, shrubs, and cacti were identified to genus for ratings of relative dominance.

A rough index of arthropod abundance in tree foliage was obtained at each site by clipping and vigorously shaking representative branches of the dominant local tree species into a large plastic pail. Insects, spiders, etc. were counted as removed from the pail and the tally in each sample was related to the amount (weight) of foliage material sampled.

The bird censuses were early morning and late afternoon tallies of all detections in 60-m wide transect strips (30 m on each side of the advancing observer). Three experienced observers worked independently, totalling their counts for each locality after checking for interobserver variation. Procedures were similar

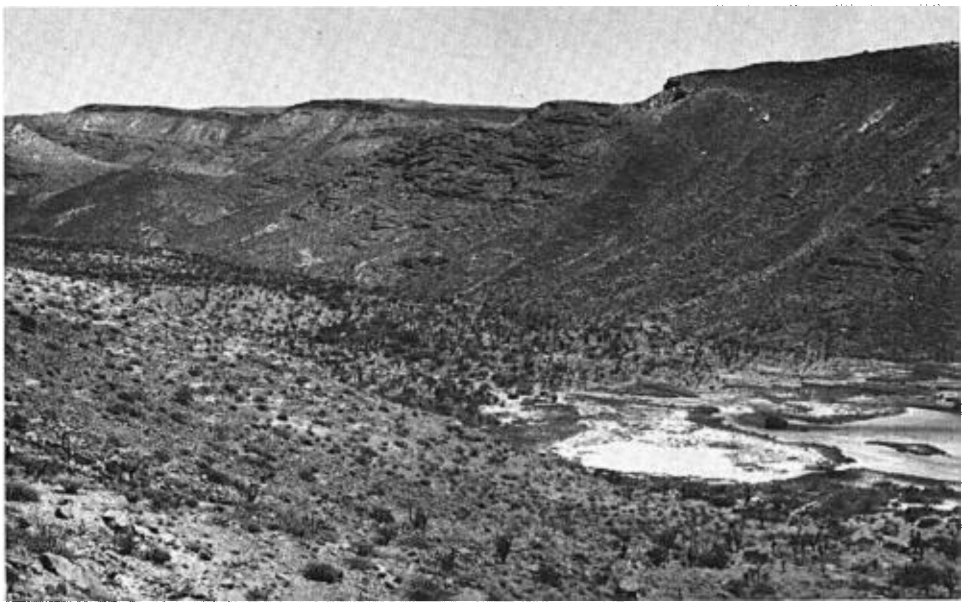

Fig. 2. Mixed desert scrub on the slopes and desert woodland (riparian scrub) in the bottomlands in a typical setting on Isla Espiritu Santo (photo J. J. Hickey).

to those developed for census work in Florida and the Bahamas (Emlen 1971), but as few species showed detectability attenuation inside the 30-m boundary in this open habitat, no density adjustments were made for low detectability species. From 8.4 to 16.0 km of transect line and 0.504 to 0.960 km^2 of transect strip were covered in two consecutive days at each site.

Population densities were calculated for each species in each of the two habitat types at each site and grouped for direct comparison of island and mainland conditions. Summed densities (total of all species) were calculated for each community and for each of eight foraging guilds in each community. For the

TABLE 1. Location and physiographic features of the seven study sites in Baja California, April 1977.

Site	Lat. N.	Long. W	Island distance offshore (km)	Island size (km^2)	Slope face	Alluvial[a] plains	Bajadas[a] & slopes
			Mainland sites				
Punta Mangles (2 km SW)	26°17′	111°26′	–	–	East	++ (fans)	++ (gentle)
Bahia Agua Verde (2 km S)	25°32′	111°03′	–	–	North	+ (fans)	+++ (steep)
San Evaristo (4 km S)	24°52′	110°41′	–	–	East	+++ (fans)	+ (steep)
			Island sites				
Isla Carmen (NE quarter)	25°59′	111°06′	6	151	SW	+ (fans)	+++ (gentle)
Isla Monserrat (E side)	25°41′	111°02′	13	7	SE	+ (arroyo)	+++ (steep)
Isla San José (W side)	24°55′	110°38′	5	194	West	+ (fans)	++++ (gentle)
Isla Espiritu Santo (W side)	24°29′	110°21′	8	99	SW	++ (fans)	++ (steep)

[a] +, ++, +++, ++++ indicate increasing amounts of the indicated feature.

latter I assigned each species to a single guild and calculated the guild biomass by summing the consuming biomass (density × body weight$^{0.633}$—Karr 1968) for all the member species. In the absence of local data on foraging behavior I was unable to make multiple assignments for single species as I have advocated for this type of study elsewhere (Emlen 1977).

RESULTS

COMPARISON OF ISLAND AND MAINLAND ENVIRONMENTS

Although the overall impression of a visitor to the Gulf of California is one of relatively uniform ruggedness, barrenness, and aridity, and although the study sites for this project were selected for similarity in topography and vegetation, the criteria used in the habitat measurements reveal considerable variation from site to site (Tables 1 and 2). For most of the vegetation parameters, however, variance was as great or greater in within-island and within-mainland series than between the two, and mean values showed no major or consistent island-mainland trends. In the scrublands woody vegetation averaged a little denser on the islands while cacti were slightly more numerous on the mainland. These ratios were reversed in the woodland habitats, where woody vegetation averaged denser on the mainland sites, presumably due to better ground water conditions associated with larger drainage basins, while cacti were denser on the islands. Annual grasses and herbs were slightly denser on the islands in the scrublands but denser on the mainland in the woodlands.

Food resources as sampled in the tree foliage invertebrates showed no major island-mainland difference (Table 2, last column). The widely variable values averaged higher in the mainland samples [86 ± 19 (SD) vs. 67 ± 30], but the second and third highest values were obtained on islands.

COMPARISON OF ISLAND AND MAINLAND BIRD COMMUNITIES

In terms of species richness, island and mainland resident communities were similar, with 20 species on the islands and 25 on the mainland (Table 3). Of the 25 species total, 8 were more abundant in the island communities, 10 were more abundant (5 found exclusively) on the mainland, and 7 were about equally common. Bird species diversity ($H' = p_i \ln p_i$) was higher on the mainland (2.54 vs. 1.97) due largely to a higher equitability ($J' = H'/H'$ max) of densities there ($J' = 0.85$ vs. 0.68). Migrants, a minor element in these desert communities at the time of our surveys in April, were more numerous on the mainland, where there were six species comprising about 7% of the total population. Only two migrant species were recorded in the island transects, where they comprised about 1% of the estimated population.

The summed density of resident birds was appreciably higher on the islands than on the mainland. The average for scrublands, the most extensive of the two surveyed habitats, was 303 birds per km^2 for the island communities and 136 for the mainland communities, a ratio of 2.23:1. In the more restricted woodland habitat, island communities had an average of 433 birds per km^2 and mainland communities 401, a ratio approximating equality.

Of the 25 resident species, 6 were widely distributed through both the scrubland matrix and the woodland patches at all sites, and 19 were specialists, restricted to or concentrated near special habitat features such as water sources, large trees, tree cacti, cactus thickets, or cliffs. The generalists as a group were numerically stronger on the islands in both scrubland and woodland with ratios of 2.47:1 in the former and 1.77:1 in the latter habitat type. The specialists, most of them woodland species,

TABLE 2. Vegetation characteristics of scrubland and desert woodland habitats at mainland and island survey sites.

	Scrublands on bajadas			Woodlands in arroyos and flats			Tree invertebrates
	Woody vegetation (percent cover)[a]	Cacti (percent cover)[a]	Herbs (density)[b]	Woody vegetation (percent cover)[a]	Cacti (percent cover)[a]	Herbs (density)[b]	Organisms per kg foliage[c]
Mainland sites							
Punta Mangles	26(4 + 18 + 4) F ≫ B = C = O J > B > S = F = L	8(tr + 8) Lam = P M = O	G > F 1	23(14 + 7 + 2)	0.2(0.2 + 0)	G > F 4	107
Bahia Agua Verde	8(3 + 4 + 1) L > O = F > C J ≫ A = R	tr(tr + O) P	G > F 18	—	—	—	81
San Evaristo	24(2 + 13 + 9) F > B = J = O J > F = B	3(tr + 3) P M > O	F > G 34	42(5 + 35 + 2)	9(1 + 8)	F > G 64	71
Mean	19(3 + 12 + 5)	4(tr + 4)	G > F 18	33(10 + 21 + 2)	5(1 + 4)	G > F 34	86
Island sites							
Isla Carmen	33(1 + 18 + 14) F > P > O J > F = B	1(tr + 1.2) P > Lop O > M	G > F 2	13(8 + 4 + 1)	14(tr + 13)	0	57
Isla Monserrat	19(4 + 13 + 2) F > O = C = L = B J > B = S	4(tr + 4) P O = Lam	G > F 30	—	—	—	97
Isla San José	60(11 + 40 + 9) F > O = C = J J > B = F = S	1(tr + tr) P ≫ Lam = Lop M > O	G > F 49	—	—	—	30
Isla Espiritu Santo	24(4 + 13 + 7)	1(tr + tr)	F > G 27	26(7 + 9 + 10)	1(tr + 1)	F > G 41	85
Mean	34(5 + 21 + 8)	2(tr + 1.5)	G > F 27	20(8 + 6 + 6)	7(tr + 7)	F > G 21	67
All sites	28(4 + 17 + 7)	2.6(0.3 + 2.3)	G > F 23	26(8 + 14 + 4)	6(0.5 + 5.5)	F > G 27	75

[a] Percent cover was determined at four or more representative points for trees (>3 m), high shrubs (1–3 m), low shrubs (<1 m), tree cacti (>3 m) and shrub cacti (<3 m) by summing the crown areas for all plants within a visually estimated 10-m (shrubs) or 30-m (trees) radius. Average crown areas were calculated for each plant type from rough measures of average crown diameters. Values for the woody vegetation cover at each site are recorded in this table as total cover, followed in parentheses by the values calculated for trees, high shrubs, and low shrubs. Values for cacti are the total cover, followed in parentheses by the values for tree and shrub cacti (tr = trace). Symbols under the percent cover values indicate the dominant (10% or more) plant species: woody plants—A = *Acacia* sp., B = *Bursera* sp., C = *Cercidium* sp., F = *Fouqueria* sp., L = *Lysiloma* sp., J = *Jatropha* sp., O = *Olneya* sp., P = *Prosopis* sp., R = *Ruellia* sp., S = *Simmondsia* sp.; cacti—Lam = *Lamaerocereus* sp., Lop = *Lophocereus* sp., M = *Machaerocereus* sp., O = *Opuntia* sp., P = *Pachycereus* sp.

[b] A rough index of herb abundance was calculated at each survey point by visually estimating the proportion (tenths) of the area within a 10-m radius of the observer that he subjectively classed, with the help of a reference chart, as dense, medium, sparse, or bare. The number of segments classed as dense were multiplied by 10; those classed as medium by 5; those as sparse by 2; and those as bare by 0. The sum of these products provided a density index potentially ranging from 0 to 100.

[c] Sum of all insects, spiders, larvae, etc. recovered from measured quantities of clipped tree twigs vigorously shaken into a large plastic container.

were slightly more numerous on the islands in scrubland situations (1.45:1) but less numerous in woodlands (0.38:1). The low woodland density on the islands is related to the absence of five and near absence of two mainland species. All 11 of the predominantly or exclusively mainland species were woodland rather than open scrubland birds.

Despite the similarity of habitat conditions most species showed marked differences in abundance between the islands and mainland (Table 3). Among the six generalist species two, the Black-throated Sparrow and the Costa's Hummingbird, were much denser on the islands (8.25:1 and 4.32:1, respectively); one, the Ladder-backed Woodpecker, was slightly denser (1.70:1); and three, the Ash-throated Flycatcher (0.87:1), the Verdin (1.16:1), and the Gnatcatchers (1.04:1), were roughly equal. None was clearly less common. Among the 14 regularly occurring specialist species (with more than 1.0 individual per km^2), 5 were found only on the mainland and 4 were definitely more common there, 3 species were more common on the islands, and 2 were about equally common.

A comparison of the summed densities for island and mainland foraging guilds suggests that the abundance or scarcity of other guild members in a community may not be important in determining a species' abundance. Thus the summed densities differed markedly between island and mainland communities in four of the eight recognized foraging guilds (Fig. 3). The island-mainland ratio (calculated as consuming biomass) for the flower probers, a one-species guild, was 4.31:1 (average for all sites in both habitat types). For the ground gleaning seed and small insect eaters, a four-species guild including the dominant Black-throated Sparrow, it was 3.33:1. Two guilds were less strongly represented on the islands, the large granivores with a ratio of 0.15:1, and the shrub-gleaning insectivores with 0.38:1. Four guilds had roughly equal representations, with island-mainland ratios ranging between 0.87 and 0.19 to 1.

DISCUSSION

It is possible, of course, that the spring of 1977 was atypical and that the observed island-mainland differences were transitory. Assuming that they were representative, however, the striking differences in density and consuming biomass between island and mainland populations observed in this study must have a basis in one or more features of the environment or in some aspect or aspects of insularity *per se*. As my density estimates and habitat evaluations are too imprecise to permit detailed analysis of all the data, I will focus on the species and guilds with wide island-mainland differences, considering first the environmental factors of resource abundance, predation, and climate, then the nature of population responses to insular protection from interdeme gene flow and the effects of physical blocking of density-regulating dispersal movements.

ENVIRONMENTAL FACTORS

Resource abundance.—Resources, particularly food supplies, are commonly regarded as the ultimate and often as the major proximate factor limiting population densities (Lack 1954), and many recent speculations on competition, displacement, ecological release, and density compensation are based on assumptions that resources are in limited supply.

TABLE 3. Land bird densities (birds per km^2)[a] on Baja California islands and opposing peninsular mainland sites.

	Scrubland habitat										Desert woodland habitat						
	Island sites					Mainland sites				Ratio	Island sites			Mainland sites			Ratio
Study sites[b]:	C	M	S.J.	E.S.	Total	P.M.	A.V.	Ev.	Total	I/M	C	E.S.	Total	P.M.	Ev.	Total	I/M
km of transect:	6.9	13.5	16.4	2.8	39.6	3.0	9.6	1.0	13.6		7.6	5.6	13.2	12.0	11.9	23.9	
Generalist residents [widely distributed species encountered at all study sites in the area (Matrix distribution)]																	
Costa's Hummingbird *Calypte costae*	4.8	7.3	24.2	17.8	14.6	5.5	1.7	+	2.5	5.84	11.0	83.0	41.5	11.1	9.8	10.5	3.97
Ladder-backed Woodpecker *Picoides scalaris*	+	2.5	7.1	11.8	4.6	+	1.7	16.6	2.5	1.84	4.3	26.7	13.8	5.5	11.1	8.3	1.67
Ash-throated Flycatcher *Myiarchus cinerascens*	12.0	9.8	40.5	+	22.2	16.6	12.1	66.4	17.1	1.30	30.5	38.5	34.0	51.1	43.3	47.3	0.72
Verdin *Auriparus flaviceps*	9.6	11.1	81.0	35.5	41.5	38.7	24.2	16.6	26.9	1.54	26.2	118.5	65.4	77.5	63.0	65.2	1.00
Gnatcatchers *Polioptila melanura* and/or *caerulea*[c]	9.6	13.4	42.5	47.5	27.2	27.7	31.0	+	28.1	0.97	52.5	94.8	70.4	67.7	64.2	65.9	1.07
Black-throated Sparrow *Amphispiza bilineata*	125.2	156.2	134.6	53.3	147.4	11.1	3.0	33.2	26.9	5.48	168.2	94.8	137.1	2.8	12.6	7.6	17.96
Total	161.2	200.4	330.0	165.8	256.5	99.6	101.8	132.8	103.9	2.47	292.7	456.3	362.2	215.8	194.1	204.8	1.77
Specialist residents [species concentrated in or restricted to special habitats or areas (Patchy distribution)]																	
California Quail *Lophortyx californicus*			11.1		4.6	+		49.8	3.7	1.27				48.5	20.9	34.7	0
White-winged Dove *Zenaida asiatica*	+		9.1	+	3.8	5.5	12.1	49.8	13.4	0.28	+	6.0	2.5	30.4	12.6	21.6	0.12
Mourning Dove *Zenaida macroura*			+		+				0	+			0	+		+	0
Roadrunner *Geococcyx californianus*					0	+		+	+	0			0	1.3	2.8	2.2	0
Gila Woodpecker *Melanerpes uropygialis*	+	1.2	28.4	+	12.1	+	1.7	16.6	2.5	4.87	4.3	26.7	20.1	15.3	30.7	22.9	0.88
Gilded Flicker *Colaptes auratus chrysoides*					0	+		+	+	0			0	1.3	11.1	6.3	0
Scrub Jay *Aphelocoma coerulescens*					0	11.1		+	2.5	0			0	+	18.1	9.0	0

TABLE 3. Continued.

	Scrubland habitat										Desert woodland habitat						
	Island sites					Mainland sites				Ratio	Island sites			Mainland sites			Ratio
Study sites[b]: km of transect:	C 6.9	M 13.5	S.J. 16.4	E.S. 2.8	Total 39.6	P.M. 3.0	A.V. 9.6	Ev. 1.0	Total 13.6	I/M	C 7.6	E.S. 5.6	Total 13.2	P.M. 12.0	Ev. 11.9	Total 23.9	I/M
Common Raven *Corvus corax*	2.5				0.5	+			+	+			0	+		+	0
Cactus Wren *Campylorhynchus brunneicapillum*					0	5.5		66.4	6.1	0			0	31.9	54.4	43.0	0
Canyon Wren *Catherpes mexicanus*				11.8	0.8	+			0	+		+	+	+		+	?
Gray Thrasher *Toxostoma cinereum*			1.0		0.5	+		+	+	+			0	7.0	1.3	4.2	0
Mockingbird *Mimus polyglottos*		1.2	16.3		7.1			+	+	+		59.3	25.2	1.3	23.7	12.5	2.03
Loggerhead Shrike *Lanius ludovicianus*	+		+		1.7			+	+	+	4.3		1.3		2.8	1.3	1.00
Yellow Warbler *Dendroica petechia*[d]					0				0			3.0	1.3			0	+
Hooded Oriole *Icterus cucullatus*			+		+	+	+		+				0	19.4		9.8	0
Cardinal *Cardinalis cardinalis*		2.5	20.3		8.8	+		+	+	+		+	+	23.6	4.2	13.9	0
Pyrrhuloxia *Cardinalis sinuatus*[d]		1.2			0.5				0	+			0			0	
House Finch *Carpodacus mexicanus*	2.5	13.4	2.0		5.8	5.5	3.5		3.7	1.59	21.9	17.8	20.1	4.2		2.2	9.31
Brown Towhee *Pipilo fuscus*					0	+		+	+	0			0	24.9	1.3	13.1	0
Total	5.0	19.4	88.1	11.8	46.3	27.7	17.3	182.6	31.9	1.45	30.5	112.7	70.6	209.0	184.1	196.5	0.36
Total residents	166.2	219.8	418.2	177.6	302.8	127.3	119.0	315.4	135.8	2.23	323.2	569.0	432.8	424.8	378.1	401.4	1.08

TABLE 3. Continued.

	Scrubland habitat										Desert woodland habitat						
	Island sites					Mainland sites				Ratio	Island sites			Mainland sites			Ratio
Study sites[b]: km of transect:	C 6.9	M 13.5	S.J. 16.4	E.S. 2.8	Total 39.6	P.M. 3.0	A.V. 9.6	Ev. 1.0	Total 13.6	I/M	C 7.6	E.S. 5.6	Total 13.2	P.M. 12.0	Ev. 11.9	Total 23.9	I/M
Migrants [Nonresident species present as winter or in-transit spring visitors]																	
Empidonax (sp.) *Empidonax* sp.			+			+		+						1.3	13.9	7.6	0
Phainopepla *Phainopepla nitens*						+		+						2.8	+	1.3	0
Orange-crowned Warbler *Vermivora celata*		+															
Black-headed Grosbeak *Pheucticus melanocephalus*			+	+		+		+				11.8	5.0	+	25.1	12.5	0.40
Green-tailed Towhee *Pipilo chlorurus*			6.1		2.5					+							
Lark Sparrow[e] *Chondestes grammacus*							70.9		50.0	0							
Brewer's Sparrow *Spizella breweri*								+							9.8	4.8	0
White-crowned Sparrow *Zonotrichia leucophrys*							+	+							1.7	0.7	0
Total	0	+	6.1	+	2.5	+	70.9	+	50.0	0.05	0	11.8	5.0	4.2	50.5	26.9	0.19

[a] A + in the data columns indicates the species was detected in the area but not recorded on the transect counts. A + in the ratio columns indicates presence on the islands and absence on the mainland.

[b] C = Isla Carmen, M = Isla Monserrat, S.J. = Isla San José, E.S. = Isla Espiritu Santo. P.M. = Punta Mangles, A.V. = Bahia Agua Verde, Ev. = San Evaristo.

[c] Two species of gnatcatcher not always distinguishable in the field are found in the area (Grinnell 1928, Banks 1963).

[d] Yellow Warblers and Pyrrhuloxias, although not recorded on the mainland in this study, are known to occur in the area.

[e] The Lark Sparrows at Bahia Agua Verde were in a single roving flock and the calculated density value is probably unrealistically high.

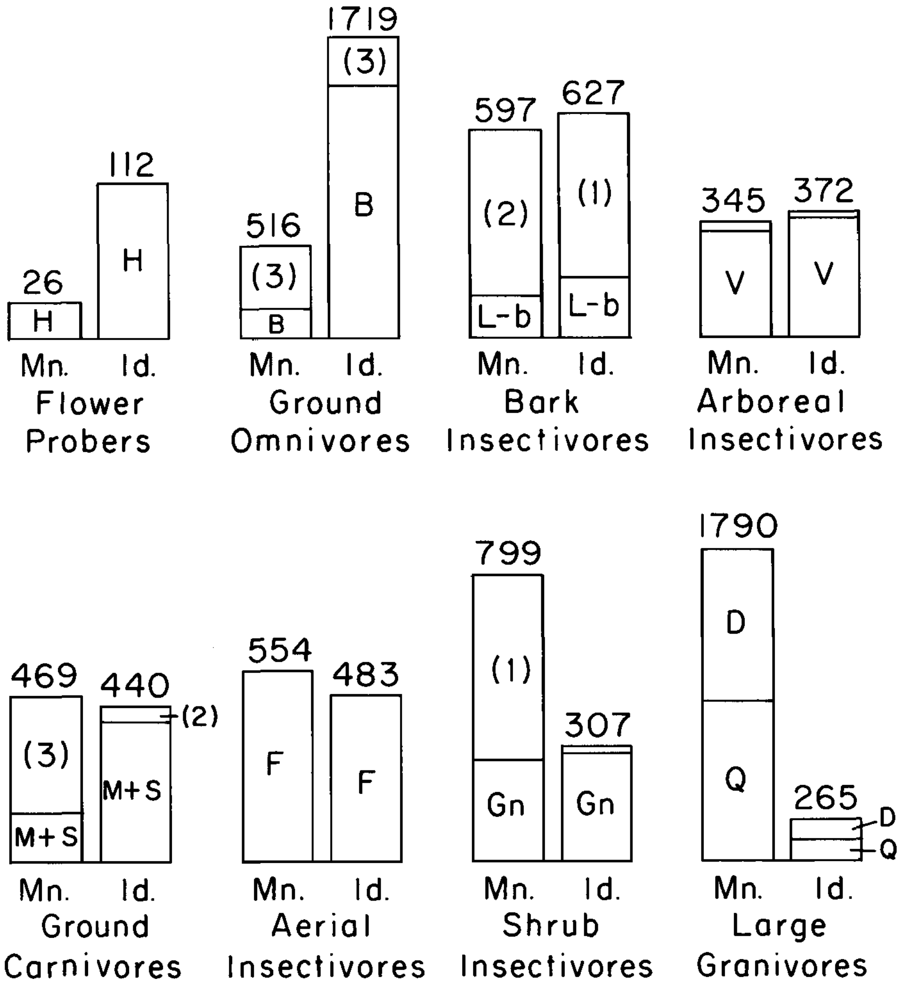

Fig. 3. Consuming biomass (see text) of the eight land bird foraging guilds on the Baja California mainland and islands. B = Black-throated Sparrow, Q = California Quail, D = White-winged Dove, M = Mockingbird, S = Loggerhead Shrike, V = Verdin, Gn = Gnatcatchers, Lb = Ladder-backed Woodpecker, H = Costa's Hummingbird, F = Ash-throated Flycatcher. Values in parentheses are the number of secondary species in the guild. Body weights for the consuming biomass values were taken from various sources including, notably, Miller and Stebbins (1964).

Resources were only roughly evaluated in this study, but no differences that could begin to account for the widely divergent island-mainland density ratios were detected. The sites were selected with specific attention to similarity in the vegetation and topography, presumed basic determinants of resource abundance and availability, and the subsequent measurements supported the correctness of these selections. The abundance of one resource base, that of the tree foliage gleaners, was measured and found to be roughly similar in the two situations. Seeds and small insects on the ground surface, the food base for the highly divergent ground omnivore guild, were not measured, but the abundance of annual grasses and forbs, the primary source of these food materials, was slightly less on the islands (Table 2), where the small ground-feeding omnivores were more abundant (Fig. 3). The correlation coefficient for grass-forb abundance vs. terrestrial omnivore biomass through the seven sites of the study was negative ($r = -.450$, $P = 0.31$).

The concept of density compensation and competitive release on islands with few species (Crowell 1962, MacArthur et al. 1972) is based on three assumptions: a) that the communities are resource regulated, b) that the niche space available is essentially filled to capacity in each case, and c) that the supply of resources is similar on the islands and mainland. A prediction of this model is that if and when these three qualifications are met, the total consuming biomass of birds in a foraging guild will be similar in the two situations, a reduced number of species in one situation permitting a compensatory increase of individuals in one or more of the persisting species. The third assumption of resource similarity appears to be reasonably supported for the Baja California island-mainland situation by my vegetation measurements. The large differences in consuming biomass seen in Fig. 3 therefore suggest that species in at least some of the foraging guilds are not resource regulated, and/or that some of the niche spaces are not filled to capacity. Errors arising from the crudeness of my guild categorizations and assignments and from the omission of non-avian consumer organisms are unfortunate but probably not great enough to invalidate these conclusions.

Looking at specific cases (Fig. 3), the Black-throated Sparrow with its 8.25:1 island-mainland ratio (mean for all sites in the two habitats—Table 3) faced nearly as much competing biomass on the islands (three additional species and 277 g of consuming biomass per km^2) as on the mainland (three species with 341 g per km^2). The Costa's Hummingbird with a 4.31:1 island-mainland ratio is the only regular flower prober on the islands or the mainland, and its only important part-time competitor, the Verdin, is also better represented on the islands (CB = 366 g and 316 g per km^2, respectively). The high number of Ladder-backed Woodpeckers on the island (1.70:1) could conceivably be attributed to density compensation, as there was only one other woodpecker species on the islands and two on the mainland; the biomass of the island competitor was slightly less (CB = 452 g per km^2) than the combined biomass of the two mainland competitors (494 g per km^2).

Among the specialist species with high island densities, the House Finch with a 4.39:1 ratio is a small ground seed and insect forager contributing to the already unbalanced ratio of this guild, as discussed above. The other two, the Mockingbrid and the Loggerhead Shrike, with ratios of 2.58:1 and 2.31:1, respectively, belong to the ground carnivore guild, which is otherwise better represented on the mainland (CB = 46 g and 315 g, respectively) and thus may reflect density compensation.

In addition to replacing reduced diversity with increased density of existing species on islands, resource-based compensation theory predicts that the niches of mainland species that are absent or rare on islands should be at least partially filled there by an ecological expansion of one or more of the island species. I found no evidence for such an expansion into the most obvious vacant or underexploited niches on the islands, the shrub-cactus niche of the mainland's Cactus Wren, or the large seed province of the mainland's California Quail and White-winged Dove populations. The quail was fairly common on the one island where it occurred, apparently a recent arrival; the dove was found at three of the four island sites but only in small numbers.

Predation.—Predators when abundant may operate as a limiting as well as a simple mortality factor on land bird populations. Avian predators were uncommon on both the islands and the mainland during the period of our study. Two hawks were seen on the mainland and three on the islands in 17 days of fieldwork. Shrikes were slightly more common on the islands; roadrunners and jays were absent on the islands (see Table 3). Ring-tailed cats (*Bassariscus astutus*), widely but sparsely distributed on the mainland, were present on at least one of the islands, San José. Small rodents were apparently widely distributed and comparably abundant at all sites. Lizards, at least potentially significant as nest predators, were appreciably more common on islands (Case 1975, personal observation). I have no way to appraise these pressures, but I see no evidence that the pressure was significantly lighter on the islands or that it was distributed in a way that could account for the assortment of density ratios recorded for the various species and guilds.

Climate.—Climatic differences between islands and neighboring coastal areas on the mainland cannot be discounted entirely as factors potentially affecting population density. However, I do not regard them as providing explanations for the large differences and irregular patterns of density distribution recorded in this study.

Water.—Fresh water is a rare commodity in this desert country, especially on the islands where catchment basins are small and arroyos steep and narrow. The low island densities of doves could be due to this factor, but House Finches, supposedly dependent on free water (Salt 1952) were substantially more abundant on the islands.

GENETIC FACTORS

Levels of adaptedness to local conditions.—The hypothesis of mean population underadaptedness proposed for the low densities of land birds in Florida *vis a vis* Bahama island pinelands (Emlen 1978) suggests that the southern Florida populations of widely distributed species were underadapted to their subtropical environment as a result of the swamping of incipient adaptations for local conditions by the annual influx (post-fledging dispersal) of birds carrying genes and gene combinations selected for other (more northern) conditions. Bahama populations were considered to have been shielded from this gene flow by the water barrier of the Florida Straits. Baja California should be and apparently is less susceptible to such peninsular swamping since it has more and higher barriers to gene flow. This is reflected in the large amount of subspeciation along the peninsula (19 of the 25 species considered in this study—American Ornithologists' Union 1957), and the high incidence of secondary centers of dispersal (Grinnell 1928).

In my Florida-Bahama comparison I also considered an interpatch gene flow hypothesis in explanation of the low population densities in northern Florida (Emlen 1978). In this hypothesis populations of a species in an environmentally patchy area were viewed as being prevented from evolving full adaptation for the environmental conditions of their patch by the continuing influx of genotypes from neighboring patches with slightly different characteristics. Populations in a relatively non-patchy area such as Grand Bahama, where more than 95% of the forested area is monotype pineland, would theoretically escape much of the constant dilution of adaptedness to which these Florida populations were subjected. This hypothesis could fit the Baja California setting, where the mainland has a wider assortment of accessible habitat and climatic patches in its highly dissected mountainous interior than do the islands.

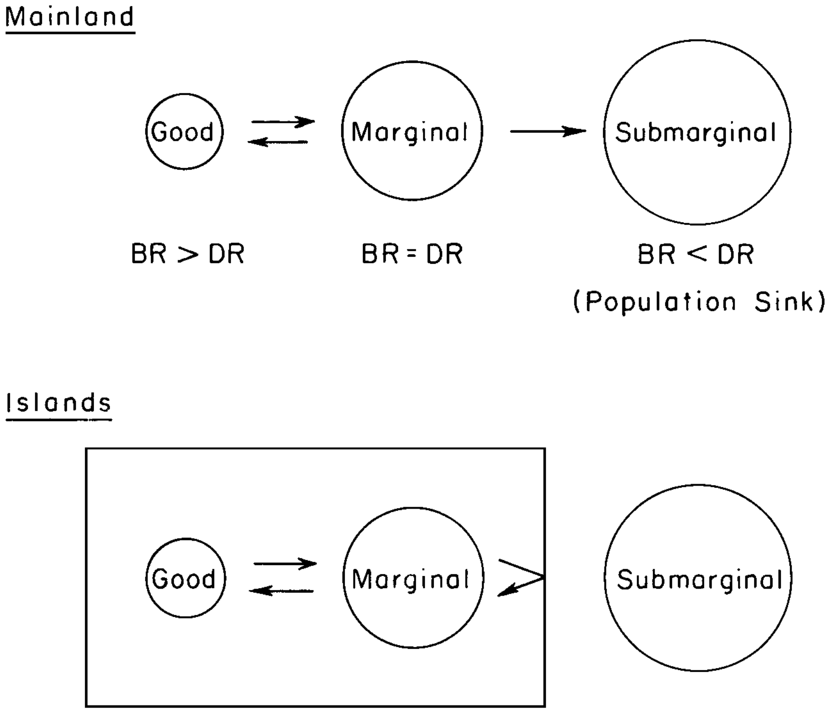

Fig. 4. Diagrammatic representation (hypothetical) of habitat availabilities (size of circles) and population movements (arrows) in mainland and island situations in the central portion of a species' range, where "good" situations are available for reproduction of population surpluses. BR = Birth rate, DR = Death rate.

SOCIAL FACTORS AND ISLAND BOUNDARIES

Physical constraints on normal dispersal movements.—A familiar but often neglected 'social saturation' model of population regulation (Howard 1920, Kluyver and Tinbergen 1953, Brown 1969, Emlen 1977, Verner 1977) assumes an adequate supply of resources and visualizes territorial behavior and other forms of local aggressiveness as initiating a dispersal of socially subordinate individuals out into inferior situations where survival is relatively poor and reproductive success curtailed. In this model densities in good areas are reduced below local, resource-determined carrying capacities by the socially induced emigration, while populations in marginal and submarginal areas are augmented, perhaps sustained entirely, by the influx of birds displaced from good areas. The pattern is depicted graphically in the upper part of Fig. 4.

Islands, with smaller residual areas of marginal and submarginal habitat than mainland areas, and with water barriers on all sides to block the escape of socially displaced birds, may under the same conditions experience a buildup of overall density as individual territories are squeezed or invaded under the pressure of expanding numbers. Territories have been recognized as resistingly compressible by most investigators since Huxley (1934), and a substantial 'silent minority' of nonterritorial floaters or of helpers may accumulate in and between territories at high densities (Stewart and Aldrich 1951, Smith 1978). This hypothetical island situation is depicted in the lower part of Fig. 4. The general pattern resembles that described by Krebs et al (1969) for populations of voles in large outdoor enclosures as the "fence effect" and discussed in a broader context by MacArthur (1972) as the "Krebs effect."

Conditions in Baja California provide the essential requirements of this model for the Black-throated Sparrow. The islands, despite their proximity to land, are effectively insulated against escape as indicated by the evolution of distinct breeding races on one or more of them (Banks 1963). They are mountainous, but the extent of low quality habitats for population overflow is far less than that available to mainland populations. Patterns of density distribution through the habitat types on the islands and mainland also support the fence-effect hypothesis: on the mainland where densities were low, sparrows spilled over into the woodlands from their preferred scrubland habitat only slightly (7.6 birds per km^2 in the woodlands, 26.9 in the scrublands) while on the islands under presumably high population pressures they were nearly as dense in the woodlands as in the scrub (137.1 and 147.4 birds per km^2, respectively). Unfortunately I have no data for the barren upland slopes. The same pattern of greater overflow into secondary habitats is indicated, though less strikingly, in the Costa's Hummingbird, a woodland species in which the secondary scrub habitat had 35% as many birds as the woodlands on the islands, 24% as many on the mainland.

The fence effect need not and probably does not apply to all of the 12 shared species with higher island densities; it obviously does not apply to the six with higher mainland densities. I will not attempt to analyze each case, but it is noteworthy that all but one of the six with high mainland densities are, like the five that do not reach the islands, woodland species (i.e. species that favor the smaller and more fragmented of the two available habitat types). Perhaps these woodland species, with larger available areas of secondary habitat for overflow, are more prone to disperse and thereby avoid some of the territory compression and density buildup conjectured for the scrubland species. Also, the position of the woodlands at the high productivity end of the habitat gradient should serve to enhance the buffering qualities of the alternate habitat (the scrublands) for the woodland species, and particularly the woodland specialists, against the rigid limits to dispersal presented by the island boundaries.

The fence effect hypothesis is essentially untested at this point. Intense field studies comparing social interactions, mating patterns, and breeding success in these island and mainland populations could presumably answer many questions posed by the concept.

LOW ISLAND DENSITIES

The genetic swamping and density dispersal mechanisms described above both relate to density regulation in mainland situations and are not applicable to species with low island densities. Low colonization rates in combination with relatively high extinction rates (MacArthur and Wilson 1967) may provide the best explanation for cases of low island densities.

All of the nine species absent from or with reduced population densities on the islands (island-mainland density ratios $<0.75:1$) were woodland species and thus closely restricted in the number and size of good habitat patches, especially on the islands. Demes restricted in this way are vulnerable to extinction by stochastic processes even under conditions of fairly frequent recolonization from nearby sources. I therefore tentatively attribute the apparent absence of the Roadrunner, Gilded Flicker, Scrub Jay, Cactus Wren, and Brown Towhee to the scarcity and small size of the wooded arroyos and alluvial fans on the islands. The California Quail is almost certainly a recent colonizer (natural or introduced) on the one island where it was found (San José). The White-winged Dove may owe its presence on three of the four surveyed islands to a recolonizing ability, associated with strong flight and wide-ranging habits. The two remaining species, the Hooded Oriole and Gray Thrasher, were each seen only once on the islands, individuals that may have been unestablished stragglers from the mainland.

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