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A COMPARISON OF AVIAN HEMATOZOAN EPIZOOTIOLOGY IN TWO CALIFORNIA COASTAL SCRUB COMMUNITIES

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ABSTRACT: Passerine birds within two California (USA) coastal scrub ecosystems, an island and a mainland site, were examined for hematozoa from 1984 to 1990. Island birds had a significantly lower hematozoan prevalence than mainland birds. This prevalence difference can be related to a lack of appropriate hematozoan vectors on the island. *Haemoproteus* spp. and *Leucocytozoon* spp. were the most commonly encountered hematozoa; four new species of *Leucocytozoon* spp. and one new *Haemoproteus* sp. were found in five host families. No transmission of hematozoan parasites was detected at the island site during the study. At the mainland coastal scrub site, *Leucocytozoon* spp. was transmitted each year while *Plasmodium* spp. and *Haemoproteus* spp. transmission varied between years. There was evidence that some species of birds acquired infections outside of their breeding season. Results of this study lend further support to the prediction of decreased disease on remote island ecosystems.

Key words: Avian hematozoans, passerine birds, epizootiology, California coastal scrub, *Haemoproteus* spp., *Leucocytozoon* spp., vectors, island biogeography.

INTRODUCTION

Since the publication of Hamilton and Zuk (1982), where avian hematozoa were used to test evolutionary hypotheses, the study of avian blood parasites has continued to spark scientific interest (Kirkpatrick and Suthers, 1988; Atkinson and van Riper, 1991; Forrester, 1991; Zuk, 1991). Yet as the behavioral correlates between these parasites and their hosts are being studied, much remains unknown regarding the epizootiology of hematozoa in many regions.

The only previous epizootiological study of avian hematozoa in a California (USA) bird community was conducted in the San Joaquin Valley (Herman et al., 1954), and focused almost exclusively on *Plasmodium* spp. Most other studies of avian hematozoa in the state have been the development of presence and absence species lists (Wood and Herman, 1943; Clark and Swinehart, 1966). In this study we compare the epizootiology of avian hematozoa in a coastal scrub community of mainland northern California with that of an insular coastal scrub community on San Miguel Island off the coast of southern California.

Many of the avian species that we examined are year-round residents of their respective coastal scrub communities. San Miguel is an isolated California Channel Island with several avian species completing their entire life cycle on that island (Diamond and Jones, 1980). Other breeding species migrate from the island to mainland California during the nonbreeding period (Grinnell and Miller, 1944). This mix of avian post-breeding dispersal strategies, concomitant with an influx of migratory species, made California coastal scrub communities on islands and the mainland ideal for exploring biogeographic questions about where, when, and how blood parasite transmission occurs.

We examined the role that isolation plays in hematozoan prevalence levels among avian host populations. We also examined the seasonal timing of when birds received new infections, and if this occurred outside of the breeding season. Two null hypotheses (H_0) were tested: there is no significant difference of hematozoan prevalences between passerine birds found in island versus continental California coastal scrub communities; and there is no significant difference in hematozoan prevalences between resident breeding versus migratory

non-breeding birds in California coastal scrub communities.

MATERIALS AND METHODS

Our northern California study area was at the Palomarin Field Station of the Point Reyes Bird Observatory (PRBO), located just inside the southern edge of Point Reyes National Seashore in western Marin County, California (37°56'N, 122°45'W). Most of our effort was expended within a 36-ha study plot, as described by DeSante (1981), a location that has been used since 1980 by PRBO for a study of the breeding ecology of coastal scrub birds. A second study area was on the north side of San Miguel Island (34°02'N, 120°21'W), the western-most island of Channel Islands National Park, 69 km across the Pacific Ocean from Santa Barbara, California. Most birds were sampled from a 9.2-ha plot of tableland approximately 400 m northwest of the Nidever Canyon Ranger Station, as described by Kern et al. (1990).

We captured passerine birds on San Miguel Island between 1984 and 1986 and at both study sites in 1989 and 1990, using mist nets (specially located at PRBO and part of an on-going constant-effort program) and baited Potter-type traps (Roy Vail Sparrow Trap Co., Antwerp, Ohio, USA). The age and sex of each bird was determined by external characteristics. Each captured bird then was marked with a U.S. Fish and Wildlife Service leg band and, for some species, with a unique randomized combination of color bands.

Bird taxonomy follows the standards of the American Ornithologists' Union Checklist (American Ornithologists' Union, 1983) and their 37th supplement in 1989. We classified a bird species as a resident breeder if it was observed during all months of the year. Based on observations of color-banded breeding adults, they did not wander more than a few kilometers from the study area. We classified the remaining captured bird species as non-resident breeders if individuals were observed only during the spring and summer months and did not make use of the study areas outside of the breeding season; they were classified as non-breeders if they did not breed in the study areas, but were present only during either the spring or the fall migrations, during the winter, or as post-breeding visitors.

We obtained blood from each bird for thin smears by clipping a toe nail. Smears were air-dried and fixed in absolute methanol for 30 to 60 sec in the field. After being transported to the laboratory, smears were immersed for 30 min in commercially prepared Giemsa stain concentrate (azure B type, Harleco, EM Diagnostic Systems, Gibbstown, New Jersey, USA) diluted in 50 volumes of buffered pH neutral water.

We examined stained smears for 10 min under 630X magnification. Smears then were scanned a second time at 315X magnification until all cells on the slide had been observed to detect very low infections of *Leucocytozoon* spp. and *Trypanosoma* spp.

Trypanosoma spp. were not identified to species as this genus was not included in any analyses. Representative slides of the *Haemoproteus* spp., *Leucocytozoon* spp., and *Trypanosoma* spp. were deposited with the International Reference Centre for Avian Haematozoa, Memorial University of Newfoundland, St. John's Newfoundland, Canada (accession numbers 11639 to 11671, 114019, and 114368). Parasitological terminology follows Margolis et al. (1982).

We operated Center for Disease Control light traps (Hausherr's Machine Works, Tom's River, New Jersey) most nights during the main study years 1989 and 1990 preceding blood sampling, to provide a relative activity estimate for culicine, simuliid, and ceratopogonid flies. Traps were baited with either dry ice or a CO_2 cylinder set at a low flow-rate, following the protocol of Service (1976). Trap openings averaged 1 m above the ground. We also conducted visual surveys to locate potential vector larval forms in pools, seepages, streams, and other open water at both study sites.

All birds caught at the banding stations were searched for ectoparasites, particularly hippoboscid flies, when in the nets and during the banding process to provide a relative estimate of the flies per bird per week. Fly identification was based on Wirth (1952), Maa (1969), and Bohart and Washino (1978). Fly specimens were donated to the Bohart Museum at the University of California, Davis, California.

Graphs were constructed with the SYGRAPH module of the SYSTAT PC package (SYSTAT, 1992). All curves were smoothed with a LOWESS (SYSTAT, 1992) weighted running mean function, with a tension of 0.2. Hematozoan prevalence within each residency class and within a cohort between years were compared by the chi-square (χ^2) test of homogeneity (Daniel, 1990). Statistical significance was accepted when $P \leq 0.05$.

RESULTS

At least 10 *Haemoproteus* species, seven *Leucocytozoon* species and one *Plasmodium* species were identified (Table 1). At the mainland site of Palomarin, we collected 691 blood smears from 667 individ-

ual birds (Table 2). *Leucocytozoon* spp. was detected in 22% of the birds sampled (142 of 667 individuals; 22 of the 40 species) and was the most commonly encountered genus of hematozoa; *Leucocytozoon* spp. was detected in four avian host families (Troglodytidae and Vireonidae) or subfamilies (Sylviinae and Cardinalinae) for which the taxonomy of this genus has not been described. *Haemoproteus* spp. was the only other hematozoan genus represented with a substantial prevalence, detected in 15% of the examined birds (102 of 667 individuals; 22 of 40 species); *Haemoproteus* sp. was detected for the first time in the avian host family Aegithalidae and would represent a new and undescribed species under the current system of hematozoan taxonomy. The hematozoa of *Chamaea fasciata*, formerly of the mono-typic family Chamaeidae and now a isolated representative of the sub-family Timaliinae in the family Musicapidae are listed in Table 1 based on species from an African representative of the Timaliinae, though this also is subject to review. Of the other hematozoan genera, only a single white-crowned sparrow at Palomarin was positive over a 2-yr period for *Plasmodium circumflexum*. We examined 667 birds for *Trypanosoma* spp. and found 27 infected individuals among 11 species.

At Palomarin, large sample sizes of birds infected with *Haemoproteus* spp. and *Leucocytozoon* spp. permitted a detailed analysis of annual prevalences. Resident breeding birds had prevalences of both parasites that were over two times as high as either non-resident breeders and non-breeders ($\chi^2 = 18.07$ for *Haemoproteus* spp., df = 2, and 54.20 for *Leucocytozoon* spp., df = 2, test of homogeneity among all three classes; $P < 0.05$; Table 3). *Haemoproteus* spp. and *Leucocytozoon* spp. were detectable year-round in the community of birds present in any given season (Figs. 1D, 2D), with their pattern of seasonal prevalence similar when only resident breeding bird species were considered (Figs. 1C, 2C).

Resident bird species at Palomarin had a bi-modal peak for *Haemoproteus* spp. prevalence in 1990, but only a single peak in 1989; the single 1989 peak occurred at the same time of year as the first peak of 1990 (May through June; Fig. 1C). Adult birds constituted all of the first peak in 1990 and virtually all of the 1989 peak (Fig. 1B); only a single immature bird proved positive for *Haemoproteus* spp. in 1989 (Fig. 1A). The second 1990 peak, from September through October, consisted of both adults and hatch-year birds (Fig. 1A, B).

Leucocytozoon spp. prevalence had a much wider single peak that began in February and continued to the end of July (Fig. 2D). Adult resident birds had a drop in *Leucocytozoon* spp. prevalence during the winter months (Fig. 2B), but *Leucocytozoon* spp. could be detected during the winter months in non-resident birds over-wintering at the field site and in birds that could not be accurately aged but probably were less than 1-yr-old (Fig. 2C, D). Juvenile birds were infected each year and detectable parasitemias were seen as early as when the first young of the year were being caught in the nets (Fig. 2A).

We detected no *Haemoproteus* spp. in hatch-year wrentits or white-crowned sparrows in 1989 and no *Haemoproteus* spp. was detected in any adult white-crowned sparrows that year (Table 4). *Haemoproteus* spp. was detected in all age groups of both species in 1990 except for hatch-year white-crowned sparrows. In both species, the second-year and after-second-year classes in 1990 had an increased prevalence over the hatch-year and second-year classes, respectively, in 1989, though neither increase was significant.

No *Culicoides* spp. (Diptera: Ceratopogonidae) were collected in light traps during 1989 at Palomarin, but we collected *C. cockerelii, C. unicolor, C. utahensis* and *C. variipennis* from 2 May until 4 August 1990. *Culicoides cockerelii* was the most frequently collected ceratopogonid when flies were most numerous in the traps

TABLE 1. Hematozoan species encountered in birds collected between 1989 and 1990 at Palomarin, Point Reyes National Seashore, Marin County, California (USA), and in birds collected between 1984 and 1990 on San Miguel Island, Channel Islands National Park, Santa Barbara County, California, including the genera *Haemoproteus* (*H*), *Leucocytozoon* (*L*), and *Plasmodium* (*P*); taxonomic sources for identification are referenced in superscripts.

Bird species (family: subfamily)	Hematozoan species
Contopus borealis (Tyrannidae)	*H. tyranni*[a]
Empidonax difficilis (Tyrannidae)	*H. tyranni*[a]
Cyanocitta stelleri (Corvidae)	*H. picae*[b] and *L. sakharoffi*[c]
Aphelocoma coerulescens (Corvidae)	*L. sakharoffi*[c]
Parus rufescens (Paridae)	*L. majoris*[c]
Psaltriparus minimus (Aegithalidae)	*Haemoproteus* sp. (un-named)
Thryomanes bewickii (Troglodytidae)	*Leucocytozoon* sp. (un-named)
Regulus calendula (Muscicapidae: Sylviinae)	*Leucocytozoon* sp. (un-named)
Catharus ustulatus (Muscicapidae: Turdinae)	*H. fallisi*[d] and *L. dubreuili*[e]
Catharus guttatus (Muscicapidae: Turdinae)	*L. dubreuili*[e]
Turdus migratorius (Muscicapidae: Turdinae)	*H. fallisi*[d] and *L. dubreuili*[e]
Chamaea fasciata (Muscicapidae: Timaliinae)	*H. timali*[f] and *L. liothricis*[f]
Vireo solitarius (Vireonidae)	*H. vireonis*[g]
Vireo huttoni (Vireonidae)	*H. vireonis*[g]
Vireo gilvus (Vireonidae)	*H. vireonis*[g] and *Leucocytozoon* sp. (un-named)
Vermivora celata (Emberizidae: Parulinae)	*H. paruli*[h] and *L. parulis*[i]
Dendroica coronata (Emberizidae: Parulinae)	*L. parulis*[i]
Dendroica townsendi (Emberizidae: Parulinae)	*H. paruli*[h]
Piranga ludoviciana (Emberizidae: Thraupinae)	*H. thraupi*[h]
Pheucticus melanocephalus (Emberizidae: Cardinalinae)	*H. mazzai*[h] and *Leucocytozoon* sp. (un-named)
Pipilo erythrophthalmus (Emberizidae: Emberizinae)	*H. coatneyi*[h] and *L. cambournaci*[i]
Pipilo crissalis (Emberizidae: Emberizinae)	*H. coatneyi*[h] and *L. cambournaci*[i]
Aimophila ruficeps (Emberizidae: Emberizinae)	*H. coatneyi*[h]
Passerella iliaca (Emberizidae: Emberizinae)	*H. coatneyi*[h] and *L. cambournaci*[i]
Melospiza melodia (Emberizidae: Emberizinae)	*L. cambournaci*[i]

TABLE 1. Continued.

Bird species (family: subfamily)	Hematozoan species
Melospiza lincolnii (Emberizidae: Emberizinae)	*L. cambournaci*[i]
Zonotrichia atricapilla (Emberizidae: Emberizinae)	*H. coatneyi*[h] and *L. cambournaci*[i]
Zonotrichia leucophrys (Emberizidae: Emberizinae)	*H. coatneyi*,[h] *L. cambournaci*,[i] and *P. circumflexum*[j]
Junco hyemalis (Emberizidae: Emberizinae)	*H. coatneyi*[h] and *L. cambournaci*[i]
Carpodacus purpureus (Fringillidae: Carduelinae)	*H. chloris*[h] and *L. dutoitti*[e]
Carpodacus mexicanus (Fringillidae: Carduelinae)	*H. chloris*[h]
Carduelis pinus (*Fringillidae: Carduelinae*)	*H. chloris*[h] and *L. dutoitti*[e]
Carduelis tristis (Fringillidae: Carduelinae)	*H. chloris*[h] and *L. dutoitti*[e]

[a] Bennett et al. (1986).
[b] Bishop and Bennett (1990).
[c] Bennett and Peirce (1992).
[d] Bennett et al. (1991).
[e] G. F. Bennett (pers. comm.).
[f] Earle et al. (1991).
[g] Bennett et al. (1987).
[h] Burry-Caines and Bennett (1992).
[i] Bennett and Squires-Parsons (1992).
[j] van Riper et al. (1994).

the second week in June. *Culicoides* spp. appeared in the traps contemporaneously with the peak of infection in resident adult birds, but before any parasites were detected in immature birds in 1990. Black files (Diptera: Simuliidae) were not attracted to our light traps at Palomarin. We also failed to find any simuliids in the stream bordering the study area, but did collect larvae during a visit in March 1991 outside the study area. Presumably this colony existed during the years of our study.

We collected two species of louseflies (Diptera: Hippoboscidae) from birds, with *Ornithomya anchineuria* (Speiser; syn. *O. fringillina*, after Maa, 1969) appearing to be more common than *Ornithoica vicina* (Walker). We found both hippoboscid species active during the same period of the annual cycle, predominantly during the summer and fall. However, in 1990 these flies did not appear on the birds caught in mist nets until 27 July, and continued to be present into the first week in December. Hippoboscid presence did not coincide with hematozoan presence, as this group of ectoparasite was notably absent from all birds when the first hematozoan infections were detected in immature birds (Fig. 1A). Hippoboscid flies were not noted during nest checks or during nestling banding.

Culex tarsalis (Diptera: Culicidae) occurred during a very short time interval, being found in traps 2 to 12 July 1989, 23 to 24 February 1990, and 2 to 26 July 1990. We collected *Culiseta* spp. mosquitoes (*C. inornata* or *C. incidens*) every month except March and April 1990.

On San Miguel Island, 361 birds were examined for hematozoa; 281 of these belonged to five species that breed on the island (Table 2). Prevalence was 1% in breeding birds (m = 281 individuals) and

TABLE 2. Prevalence of hematozoa in birds collected 1989 and 1990 at Palomarin, Point Reyes National Seashore, Marin County, California, and of birds collected between 1984 and 1990 on San Miguel Island, Channel Islands National Park, Santa Barbara County, California, USA.

	Palomarin									San Miguel Island					
	Sample size	Plas[a]	Haem	Leuc	Tryp	Mult	Total	Prev	Res[b]	Sample size	Haem	Leuc	Tryp	Total	Res
Contopus borealis (Olive-sided flycatcher)	2	0	1	0	0	0	1	50%	B	—[c]	—	—	—	—	—
Contopus sordidulus (Western wood-pewee)	1	0	0	0	1	0	1	100%	N	—	—	—	—	—	—
Empidonax hammondii (Hammond's flycatcher)	—	—	—	—	—	—	—	—	—	1	0	0	0	0	N
Empidonax difficilis (Western flycatcher)	41	0	1	0	1	0	2	5%	B	5	1	0	0	1	N
Sayornis nigricans (Black phoebe)	1	0	0	0	0	0	0	0%	B	1	0	0	0	0	R
Sayornis saya (Say's phoebe)	—	—	—	—	—	—	—	—	—	1	0	0	0	0	N
Hirundo rustica (Barn swallow)	—	—	—	—	—	—	—	—	—	2	0	0	0	0	N
Cyanocitta stelleri (Steller's jay)	4	0	2	3	0	1	4	100%	R	—	—	—	—	—	—
Aphelocoma coerulescens (Scrub jay)	4	0	0	2	1	0	3	75%	R	—	—	—	—	—	—
Parus rufescens (Chestnut-backed chickadee)	11	0	0	4	0	0	4	36%	R	—	—	—	—	—	—
Psaltriparus minimus (Bushtit)	13	0	11	0	2	2	11	85%	R	—	—	—	—	—	—
Thryomanes bewickii (Bewick's wren)	20	0	0	4	0	0	4	20%	R	—	—	—	—	—	—
Troglodytes aedon (House wren)	—	—	—	—	—	—	—	—	—	3	0	0	0	0	H
Troglodytes troglodytes (Winter wren)	2	0	0	0	0	0	0	0%	R	—	—	—	—	—	—
Regulus satrapa (Golden-crowned kinglet)	13	0	0	0	—	0	0	0%	N	—	—	—	—	—	—
Regulus calendula (Ruby-crowned kinglet)	39	0	0	1	9	0	10	26%	N	10	0	0	0	0	N

TABLE 2. Continued.

	Palomarin									San Miguel Island					
	Sample size	Plas[a]	Haem	Leuc	Tryp	Mult	Total	Prev	Res[b]	Sample size	Haem	Leuc	Tryp	Total	Res
Catharus ustulatus (Swainson's thrush)	25	0	1	1	0	0	2	8%	B	—	—	—	—	—	—
Catharus guttatus (Hermit thrush)	27	0	0	4	0	0	4	15%	N	3	0	0	0	0	N
Turdus migratorius (American robin)	3	0	2	1	0	1	2	67%	B	—	—	—	—	—	—
Chamaea fasciata (Wrentit)	66	0	27	21	5	13	39	59%	R	—	—	—	—	—	—
Sturnus vulgaris (European starling)	2	0	0	0	0	0	0	0%	B	—	—	—	—	—	—
Vireo solitarius (Solitary vireo)	—	—	—	—	—	—	—	—	—	2	1	0	0	1	N
Vireo huttoni (Hutton's vireo)	4	0	1	0	0	0	1	25%	R	—	—	—	—	—	—
Vireo gilvus (Warbling vireo)	14	0	5	3	2	2	7	50%	B	4	2	2	1	2	N
Vermivora celata (Orange-crowned warbler)	25	0	0	4	0	0	4	16%	B	81	1	0	1	2	R
Dendroica petechia (Yellow warbler)	11	0	0	0	0	0	0	0%	N	—	—	—	—	—	—
Dendroica coronata (Yellow-rumped warbler)	—	—	—	—	—	—	—	—	—	8	0	1	0	1	N
Dendroica nigrescens (Black-throated gray warbler)	1	0	0	0	0	0	0	0%	N	—	—	—	—	—	—
Dendroica townsendi (Townsend's warbler)	15	0	1	0	0	0	1	7%	N	3	0	0	0	0	N
Dendroica occidentalis (Hermit warbler)	1	0	0	0	0	0	0	0%	N	—	—	—	—	—	—
Oporornis tolmiei (MacGillivray's warbler)	—	—	—	—	—	—	—	—	—	1	0	0	0	0	N
Geothlypis trichas (Common yellowthroat)	—	—	—	—	—	—	—	—	—	3	0	0	0	0	N

TABLE 2. Continued.

	Palomarin									San Miguel Island					
	Sample size	Plas[a]	Haem	Leuc	Tryp	Mult	Total	Prev	Res[b]	Sample size	Haem	Leuc	Tryp	Total	Res
Wilsonia pusilla (Wilson's warbler)	37	0	0	0	1	0	1	3%	B	2	0	0	0	0	N
Piranga ludoviciana (Western tanager)	1	0	1	0	0	0	1	100%	N	—	—	—	—	—	—
Pheucticus melanocephalus (Black-headed grossbeak)	1	0	1	1	0	1	1	100%	B	—	—	—	—	—	—
Pipilo erythrophthalmus (Rufous-sided towhee)	15	0	3	11	1	3	12	80%	R	1	0	0	0	0	N
Pipilo crissalis (California towhee)	3	0	1	3	0	1	3	100%	R	—	—	—	—	—	—
Aimophila ruficeps (Rufous-crowned sparrow)	2	0	1	0	0	0	1	50%	B	—	—	—	—	—	—
Passerculus sandwichensis (Savannah sparrow)	1	0	0	0	0	0	0	0%	N	—	—	—	—	—	—
Passerella iliaca (Fox sparrow)	12	0	4	4	0	2	6	50%	N	2	1	0	0	1	N
Melospiza melodia (Song sparrow)	129	0	0	22	1	0	23	18%	R	192	0	0	0	0	R
Melospiza lincolnii (Lincoln's sparrow)	3	0	0	0	0	0	0	0%	N	2	0	1	0	1	N
Zonotrichia atricapilla (Golden-crowned sparrow)	16	0	3	5	0	1	7	44%	N	15	2	0	0	2	N
Zonotrichia leucophrys nuttalli (Nuttall's white-crowned sparrow)	44	1	2	23	0	2	24	55%	R	—	—	—	—	—	—
Zonotrichia leucophrys ssp. (other White-crowned sparrows)	2	0	0	1	0	0	1	50%	N	12	4	0	0	4	N
Junco hyemalis (Dark-eyed junco)	11	0	6	2	0	1	7	64%	N	—	—	—	—	—	—
Carpodacus purpureus (Purple finch)	32	0	23	19	3	16	27	84%	R	—	—	—	—	—	—
Carpodacus mexicanus (House finch)	—	—	—	—	—	—	—	—	—	6	2	0	0	2	R

TABLE 2. Continued.

	Palomarin										San Miguel Island					
	Sample size	Plas[a]	Haem	Leuc	Tryp	Mult	Total	Prev	Res[b]	Sample size	Haem	Leuc	Tryp	Total	Res
Carduelis pinus															
(Pine siskin)	5	0	1	1	0	1	1	20%	N	—	—	—	—	—	—
Carduelis psaltria															
(Lesser goldfinch)	—	—	—	—	—	—	—	—	—	1	0	0	0	0	R
Carduelis tristis															
(American goldfinch)	8	0	4	2	1	2	4	50%	R	—	—	—	—	—	—
Totals	667	1	102	142	28	49	219	33%		361	14	4	2	17	

[a] Plas = *Plasmodium* spp., Haem = *Haemoproteus* spp., Leuc = *Leucocytozoon* spp., Tryp = *Trypanosoma* spp., Mult = multiple infections (different genera), Total = total number of individuals with infections, Prev = detected prevalence (%) within each host species.

[b] Res = residency status: (R = year round resident; B = migrant breeder; N = transient or non-breeding winter resident).

[c] dash = species not captured at that location.

16% in non-breeders (m = 80 individuals). *Plasmodium* spp. was not detected in any bird and *Leucocytozoon* spp. not found in any birds that might have bred on the island. Thus, the prevalence of hematozoa in island breeding birds was dramatically lower than in the mainland birds at Palomarin; 1% were infected with all genera of hematozoans on San Miguel as compared to 35% at Palomarin.

Due to the very low prevalence of hematozoa on San Miguel Island, it was not appropriate to statistically analyze annual prevalence changes. However, in each year of this study migrants had higher prevalences than did breeding birds by at least a factor of seven.

The hematophagous dipteran fauna on San Miguel Island was depauperate, when compared to Palomarin. We collected only five *Culiseta incidens* during our trips to the island; none of the five had detectable oocysts or sporozoites. Five male *Anopheles freeborni* were collected, two in 1984, one in 1989 and two in 1990. We collected no other hematophagous insects in the light traps, nor did we detect simuliid larvae in the small, seep-fed stream near the study site during any of our collecting trips. Hippoboscid flies were found primarily in the fall, and all were the same species, *Ornithoica vicina*. We detected only one *O. vicina* on 200 birds between January 1984 and June 1986; it was noted on three birds in October 1989 and on 12 birds during the fall of 1990 (range = one to five flies per bird).

DISCUSSION

We found a significant difference in total hematozoan prevalence between the continental site at Palomarin and the San Miguel Island site for all birds sampled (χ^2 = 104.8, df = 1, $P < 0.005$). Therefore, we must reject H_0 1, that avian hematozoan prevalence was the same in island and mainland coastal scrub bird communities. This finding was even more pronounced when only the resident breeding species were compared between sites (χ^2 = 154.8,

TABLE 3. A comparison of avian hematozoan prevalences from passerine birds captured in California coastal scrub habitats at the Palomarin and San Miguel Island study areas in California between 1984 and 1990. Note that because of multiple infections the total birds examined is less than total birds in which parasites occur.

Study area	Residency status	Hematozoan*					Total birds examined
		P	H	L	T	PNF	
San Miguel Island	Resident breeders	0	3	0	1	277	281
	Non-breeders	0	11	4	1	67	80
Palomarin	Resident breeders	1	74	114	14	196	355
	Non-resident breeders	0	12	10	4	132	153
	Non-breeders	0	16	18	10	120	159
Total		1	116	146	30	792	1,028

* P = *Plasmodium* spp.; H = *Haemoproteus* spp.; L = *Leucocytozoon* spp.; T = *Trypanosoma* spp.; PNF = no parasites found in these birds.

df = 1, $P < 0.005$). Only four (1.4%) of 281 breeding birds were positive on San Miguel Island, whereas 159 (45%) of 355 resident breeders were positive for at least one hematozoan species at the mainland Palomarin study site.

One probable cause for the extremely low prevalence on San Miguel Island was lack of appropriate vectors. This was a consequence of distance from the mainland, coupled with the fact that the island had only a few brackish or freshwater seeps that might harbor breeding populations of *Culicoides* spp. or simuliid flies. In addition, the nearly constant westerly diurnal winds would have inhibited dispersal of day-flying vectors from the mainland (Lillie et al., 1988). The only ornithophilic biting fly that we found on the island was the hippoboscid *Ornithoica vicina*. There is as yet no reason to incriminate this genus of hippoboscid as a major vector of avian hematozoa (Bennett, 1961). Work et al. (1990) found that the mosquitoes present on the island (*Anopheles freeborni* and *Culiseta incidens*), are not suitable vectors of avian hematozoa in California. Moreover, *Cu-*

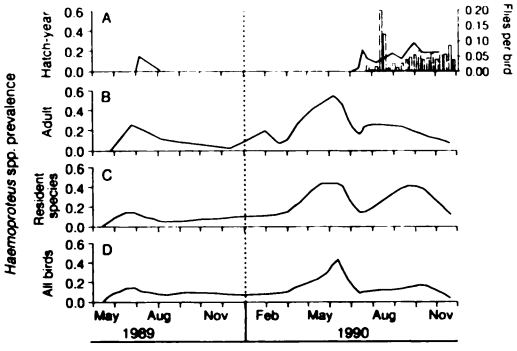

FIGURE 1. Weekly prevalences of *Haemoproteus* spp. in: (A) hatch-year birds: (B) adult birds: (C) resident birds: and (D) all birds, sampled at Palomarin, California (USA), study area. All lines were smoothed by a LOWESS weighted running mean, tension = 0.2. Superimposed on Fig. 1A is a histogram of the weekly occurrence of hippoboscid flies on all birds throughout 1990. At the right of Fig. 1A is a vertical scale of the number of hippoboscid flies per bird. Ages of birds could not be determined after 31 October.

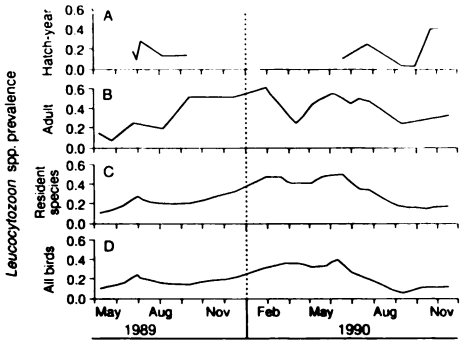

FIGURE 2. Weekly prevalences of *Leucocytozoon* spp. in: A hatch-year birds: B adult birds; C resident birds; and D all birds, sampled at Palomarin, California (USA), study area. All lines were smoothed by a LOWESS weighted running mean, tension = 0.2. Ages of birds could not be determined after 31 October.

liseta incidens feeds primarily on large ungulates (Tempelis and Washino, 1967). *Culex tarsalis* was the only mosquito we collected that previously has been identified as a vector of avian hematozoa (Work et al., 1990), and that has been strongly associated with birds as a blood meal source (Bohart and Washino, 1978). Bennett et al. (1974) and Bennett and Coombs (1975) found a similarly low prevalence of hematozoa in birds from a wind-blown coastal site on Newfoundland (Canada) and speculated that this was the result of insufficient vector activity.

The prevalence of hematozoa in breeding birds on San Miguel Island was much lower than reported for any other region of North America except the high Arctic (Greiner et al., 1975). There was, however, no significant difference in prevalence between Palomarin and San Miguel Island for the migratory non-breeding species ($\chi^2 = 2.14$, df = 1, $P > 0.1$), nor was there a significant difference in prevalence of the two major parasite genera between the two study areas for the migratory non-breeding species (*Haemoproteus* spp. $\chi^2 = 0.71$, df = 1, $P > 0.1$; *Leucocytozoon* spp. $\chi^2 = 2.54$, df = 1, $P > 0.1$). Overall, our study data are consistent with island biogeographic theory (MacArthur and Wilson, 1967) and support other empirical studies (van Riper et al., 1986; van Riper 1991a, b; Savidge et al., 1992) that low avian hematozoan prevalences within resident host populations occur on remote islands.

When we examined hematozoan prevalence in breeding versus non-breeding avian hosts at our two study sites, we found opposite situations. At the island site, non-breeding birds had significantly higher prevalences than breeding birds ($\chi^2 = 30.48$, df = 1, $P < 0.005$); but at Palomarin, breeding birds had significantly higher prevalences than non-breeders ($\chi^2 = 49.17$, df = 1, $P < 0.005$). Thus we reject H_0 2, that migrant and resident host species had the same prevalences, but for opposite reasons at each study location.

Although both *Haemoproteus* spp. and *Leucocytozoon* spp. could be detected year round in the bird community present at Palomarin, the late spring and summer peaks in hematozoan prevalence among the resident breeders is evidence that transmission was limited mostly to the avian hosts' breeding season, which would be typical for an annual recrudescence (Applegate, 1971). Based on the increase in *Haemoproteus* spp. prevalence within a cohort between years, transmission did not occur exclusively during the first summer of the host's life. Thus the prevalence of hematozoa in hatch-year birds can be used to determine variation in transmission between years.

Transmission occurred every year at Palomarin for *Leucocytozoon* spp., based on the appearance of this genus in hatch-year birds (Fig. 2A). Simuliid flies generally are recognized as the only vector of *Leucocytozoon* spp. (Greiner, 1991). At Palomarin the perennial streams outside the study site probably provided a relatively stable habitat for simuliid production. The broad uni-modal or slightly bi-modal peak observed in *Leucocytozoon* spp. prevalence in resident birds (Fig. 2C) is evidence either for a multiple vector system, with the dominant vector species changing over time, or for a single vector with a long time interval of activity (Allan and Mahrt, 1989). *Leucocytozoon* spp. can pass through its life-cycle in the invertebrate host and become infective in less than

TABLE 4. The prevalence (%) of *Haemoproteus* spp. in Nuttall's white-crowned sparrows (WCSP) and wrentits (WREN) at Palomarin, California, by age class. Note that hatchling year birds in 1989 become second year birds in 1990 and second year birds in 1989 become after second year birds in 1990.

	Year	Hatchling year	Second year	After second year
WCSP	1989	0(8)*	0(8)	0(4)
	1990	0(8)	14(7)	13(16)
WREN	1989	9(4)	50(4)	17(6)
	1990	33(27)	53(17)	100(4)

* Prevalence (sample size).

one gonotrophic cycle (Cupp, 1987), thereby allowing transmission during the fly's next blood meal and enhancing transmission even if conditions limit simuliid longevity. Therefore, transmission of *Leucocytozoon* spp. should have less annual variation than other hematozoa; such was the case in this study.

The most likely vector for *Haemoproteus* spp. was one or more *Culicoides* spp. *Culicoides* spp. went undetected by light traps in 1989 while *Haemoproteus* spp. transmission was rare (Fig. 1), but this vector was active during the entire period of *Haemoproteus* spp. transmission in 1990. *Haemoproteus* spp. prevalence in resident birds followed a pattern of sharp, bimodal peaks that may be evidence for transmission by a single vector species (Allan and Mahrt, 1989). This pattern was the same activity period as *Culicoides cockerelii*, the primary ceratopogonid species that we collected. But perhaps another, less abundant, ornithophilic species was involved in *Haemoproteus* spp. transmission during this study, because Centers for Disease Control light traps do not always attract flies specific to avian hosts.

Haemoproteus spp. was much less prevalent at Palomarin than has been reported for the western third of the United States, but *Leucocytozoon* spp. prevalence was roughly the same (Greiner et al., 1975). The prevalence of *Plasmodium* spp. at Palomarin also was lower than the reported regional prevalence (Greiner et al., 1975). Perhaps the 1986 to 1993 drought in California reduced the number of new infections of one or more hematozoan species through a reduction in vector populations. Unfortunately, comparable long-term monitoring records for hematophagous species along the northern California coastal area were not available for determining if vector populations were significantly lower during the drought. The prevalence of *Trypanosoma* spp. likely was underestimated due to the blood collection technique that we employed (Kirkpatrick and Suthers, 1988) and, therefore, we could not draw conclusions about the transmission of this blood parasite genus.

The few breeding bird species at the San Miguel study site that were infected did not necessarily remain on the island throughout the year. The island race of orange-crowned warbler, which has been regularly encountered on the mainland of California following the breeding season (Sogge et al., 1994), harbored *Haemoproteus* sp. and *Trypanosoma* sp. (Table 2). House finches also may move back and forth, at least as far as the larger and more topographically diverse Santa Rosa Island, less than 6 km to the east (Grinnell and Miller, 1944). These avian species are in contrast to the endemic race of song sparrow (*Melospiza melodia micronyx*) that has never been recorded off San Miguel Island and for which we were unable to detect any hematozoan infections in 192 individuals.

Under certain conditions in southern latitudes, some species of *Haemoproteus* spp. and *Leucocytozoon* spp. have been transmitted year round (Atkinson et al., 1988). Such conditions may apply to coastal southern California, making it possible for San Miguel Island house finch and orange-crowned warblers to become infected during their post-breeding or winter wanderings. Therefore, the few cases of hematozoan infection in breeding birds on San Miguel Island may be evidence for transmission to these individuals while they were on the mainland during the non-breeding period.

Laird (1960) speculated that migratory birds may be capable of introducing avian hematozoa to island populations. At least three genera of avian hematozoa were present in migrant birds captured on San Miguel Island. Infected migrant birds still were on the island well after the resident birds started breeding and after the temperature and rainfall conditions would seem propitious for vector activity. Only the lack of appropriate vectors seemed to prevent the transmission of hematozoa to San Miguel Island resident birds.

Bennett et al. (1976) were unable to detect any increase of annual hematozoan prevalence in Neotropical migrants between years, thus failing to show acquisition of infection away from the breeding grounds. Although the breeding birds on San Miguel were not Neotropical migrants, wintering-ground transmission was shown to be a real phenomenon. Therefore, although hematozoan transmission may occur for most avian species primarily on their breeding grounds, as we demonstrated at Palomarin, transmission away from the breeding grounds can occur. This form of transmission probably is less common, but could be important for increasing hematozoan distributions throughout the ranges of appropriate hosts and vectors.

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