

FEEDING ECOLOGY OF THREE SPECIES OF PLOVERS WINTERING ON THE BAY OF PANAMA, CENTRAL AMERICA

JOSEPH G. STRAUCH, JR.,¹ AND LAWRENCE G. ABELE²

ABSTRACT.—The feeding ecologies of three species of plovers, *Charadrius semipalmatus*, *C. collaris*, and *C. wilsonia*, were studied on two beaches on the Pacific side of the Panama Canal Zone, Central America. The three species fed in mixed flocks on intertidal flats during low tide. Whereas *semipalmatus* and *wilsonia* foraged only at low tide, *collaris* foraged independently of the tidal cycle. The diets of each species were determined to be different by analysis of stomach contents. The prey of *wilsonia* had a mean size of 7.8 mm and consisted of 96% crustaceans, that of *semipalmatus* had a mean size of 1.8 mm and consisted of 82% polychaete worms, while that of *collaris* had a mean size of 3.7 mm and consisted of 50% insects and 27% crustaceans. The relationships among prey size, bill size, and body weight (complex in these species) are discussed. Values of dietary overlap between pairs of species ranged from 2 to 30%. *Semipalmatus* and *wilsonia* were found to be considerably more specialized in diet than *collaris*. These findings, along with published reports of the food habits of these species in other areas, indicate that the dietary differences observed are probably not the result of local competitive interactions. The low diversity of shorebirds, especially sandpipers, on the study areas seems best explained by physical properties of the substrate which make it unsuitable for birds which feed by probing. Scarcity of roosting sites rather than availability of food probably limits the populations size of plovers in the study area.

Samples of shorebirds collected over a short period of time at a given location typically show a high degree of food specificity, indicating specialization in food preferences (Reeder 1951, Ehlert 1964, Recher 1966, Brooks 1967, Bengston and Svensson 1968, Anderson 1970, Davidson 1971, Thomas and Dartnall 1971, Prater 1972). These preferences are often cited as proof of competitive interactions among the species studied. This impression is reinforced by the diversity of bill morphologies found in shorebirds (Lack 1971), by reports that species that forage together during migration and winter often use different feeding techniques (Recher 1966, Goss-Custard 1970, Burton 1972), and by observations that closely related species wintering in the same area tend to feed in different habitats (Ashmole 1970, Thomas and Dartnall 1971). On the other hand, Holmes and Pitelka (1968) report that sandpipers (Scolopacidae) with diverse bill morphologies eat almost identical food on their breeding grounds, and Recher (1966) and Thomas and Dartnall (1971) found that shorebird species with different bill morphologies often eat the same food during migration.

Most species of shorebirds move from inland breeding habitats to marine habitats during migration and winter. Along with this change in habitat there must be a change in the types of prey available. Since marine habitats contain a wider diversity of prey taxa than freshwater habitats, shorebirds in marine habitats might have wider prey diversity than they have in freshwater habitats. A change in prey taxa, however, does not necessarily mean that shorebirds are not food specialists, since they may be specialized to take prey of a limited morphological type, may specialize in the type of habitat in which they feed, or sometimes may be forced by competitive interactions to take a particular prey. Unfortunately, little is known about the diets of most species throughout the year in the different habitats in which they forage.

¹ Science Applications, Inc., 2760 29th St., Boulder, Colo. 80301.

² Department of Biological Science, Florida State University, Tallahassee, Florida 32306.

Most studies of shorebird ecology have been based on sandpipers (Scolopaciidae). Most sandpipers breed in northern latitudes and migrate south for the winter. Plovers (Charadriidae), on the other hand, are more cosmopolitan; many species are resident in temperate and tropical regions. Thus, although sandpipers may winter with species which breed in other areas, all species in a given location are away from their breeding grounds. In contrast, northern plovers often winter in areas where congeneric species are resident. Whether there are fundamental differences in the interactions among shorebird species in these cases is unknown; indeed, the effect of northern migrants on resident species at more southerly localities is poorly understood (Willis 1966). But there is reason to expect that birds spending all of their lives in one habitat are likely to show different feeding adaptations from birds which face radically different competitive interactions and conditions of food availability each season.

Three species of plovers winter in the Canal Zone: Semipalmated Plover (*Charadrius semipalmatus*), Collared Plover (*C. collaris*), and Wilson's Plover (*C. wilsonia*). The three species feed together in the same habitat, use superficially similar feeding techniques, but differ in size and bill morphology. Two of the species (*collaris* and *wilsonia*) winter within their known breeding ranges, while *semipalmatus* migrates in winter far to the south of its breeding range. We examined the roles of food supply, behavior, and morphology in the feeding ecology of these species.

MATERIALS AND METHODS

Charadrius semipalmatus breeds on the Arctic coast of North America south to northern British Columbia, James Bay, and maritime Canada, and winters from central California, the Gulf Coast, and South Carolina south to Chile and Argentina (A.O.U. 1957). *C. collaris* is found in tropical America from Mexico (Michoacan, Oaxaca, and Veracruz) south to Chile, northern Argentina, and Uruguay (Peters 1934, Warner and Mengel 1951, Eisenmann 1955, Storer 1960). Breeding records north of South America have been confirmed only for Mexico (Amadon and Eckelberry 1955, Storer pers. comm.) and Honduras (Monroe 1968). *C. wilsonia* breeds coastally from Virginia and Baja California south to the Caribbean coast of South America and Perú (A.O.U. 1957). Breeding records in Panamá and the Canal Zone include Aguaduce and Fort Amador (Ridgely 1976).

We studied and collected plovers on two beaches on the Pacific side of the Isthmus of Panama: Venado Beach (8°54'N, 79°36'W) at the mouth of the Río Venado, just south of Howard Air Force Base, Canal Zone, and Skeet Beach, 7 km to the northeast behind the skeet range at Fort Amador. Our study was carried out mainly between August 1972 and May 1973, with three or four visits to one or the other of the study beaches each week.

In this region tidal differences have a maximum range of about 6 m; typically 1000 to 1500 m of intertidal flats are exposed during low tide at Venado Beach and about 500 m at Skeet Beach. Both beaches differ from nearby Naos Beach (Dexter 1972) in having considerably greater areas exposed during low tides and in that most of the exposed areas are shallow mud rather than pure sand. The study area at Venado Beach is about 800 m along the beach by about 1200 m wide, while that at Skeet Beach is about 200 m along the beach by 500 m wide. The Venado Beach area is bounded on the east by a rocky headland interspersed with several small sand beaches and on the west by a sand spit beyond which is an area covered by water at low tide. The Skeet Beach area is bounded on the north by a low, rocky headland and on the south by the Amador Causeway. As determined by aerial photographs and ground observations, the surface of the study area at Venado Beach during low tide consists of about 74% mud (containing much fine sand), 21% sand (about 50% quartz sand and 50% ground shell), and 5% exposed rocks. The area at Skeet Beach is about 90% mud, 9% sand, and 1% rocks. About 15% of the area of the flats at both beaches is covered by small, shallow pools at low tide.

A detailed study of the intertidal fauna was not made. Spot-sampling of the fauna at both beaches indicated that its composition was essentially the same as, but more dense than, that found by Dexter

(1972) at Naos Beach (which lies within 8 km of both study areas). Dexter's value of 1443 invertebrates/m² is a likely minimum value for the beaches we studied.

Feeding birds were observed with 7× binoculars or a 20× spotting scope. The type of substrate used, feeding movements, and interactions among individuals and species were recorded.

From October 1972 to March 1973, 58 plovers (13 *semipalmatus*, 16 *collaris*, and 29 *wilsonia*) were collected for analysis of stomach contents. All the birds were saved as specimens, which have been deposited in the collections of the Museum of Zoology, The University of Michigan. The majority of the birds (38) were collected during October and November 1972 after migration had stopped. Forty birds were collected while feeding during low tide at Venado Beach, while the remainder were collected during high tide at Skeet Beach.

Stomachs were removed and placed in 10% buffered formalin within an hour of collection. They typically contained hard and soft parts of prey animals as well as some sand and gravel. In all cases in which soft material could be identified, it proved to be part of an animal for which hard parts were also present in the stomach. If the birds had also been eating soft prey which digested rapidly, leaving no trace, however, analysis based on hard remains in the stomachs would give a biased estimate of diet. Since we were unable to determine that any such soft animals were taken by the species studied, we feel justified in using only hard parts in our analyses of stomach contents. In any case, most of the birds were collected while feeding, and crushed but undigested animals were often found in the stomachs.

Identification and size estimates of the prey were made by comparing hard parts found in the stomachs with a reference collection of whole animals collected in the study areas. Crustaceans were identified by LGA, the remainder of the prey by JGS. Dr. Henry Stockwell aided in identifying Coleoptera. Size measurements were based on the greatest exposed part of the prey animal, e.g., carapace width for crabs and total body length for Coleoptera. As only the head of polychaete worms was exposed to the feeding birds, head width was chosen as the measure of the actual target presented to a feeding plover. Though this choice of measurement was arbitrary, it was both expedient and reasonable, since plovers did appear to obtain only the anterior portion of a worm.

RESULTS

In both 1971–72 (when no feeding studies were made) and 1972–73, *collaris* began arriving on the beaches in groups of up to six birds early in September. The place of origin of these birds is unknown; evidence that the species breeds in Panama is circumstantial (Eisenmann in litt., Ridgely 1976). By the end of September the wintering populations had stabilized, with 10 to 25 birds regularly found feeding on the flats. *Semipalmatus* first arrived in late August in small numbers, and migrating flocks continued to pass through the area until November. The birds found after mid-November appeared to be wintering locally. Up to 100 birds could be found on the flats at this time. *Wilsonia* suddenly appeared in numbers in late September, and by mid-October flocks of up to 200 wintering birds were found.

In the spring *collaris* left the study area starting about mid-February, and by the end of the month no individuals remained. By the end of February migrating *semipalmatus* flocks began to appear. From then until the middle of April the numbers of *semipalmatus* fluctuated greatly as migrants passed through Panama. Exactly when the local wintering birds left is unknown. Migration of *semipalmatus* continued at least into early May. Individuals of this species sometimes summer in Panama (Eisenmann 1951). Most *wilsonia* left the area in the last half of March. During the first week of April a few individuals of *wilsonia* were found among the flocks of *semipalmatus*. In 1972 no plovers were seen in the study areas between mid-April and mid-August.

In January 1973 mixed flocks of plovers roosting on Skeet Beach at high tide averaged 193 birds (range 41–350), of which about 68% (66–73%) were *wilsonia*, 28% (17–35%) were *semipalmatus*, and 3% (0–10%) were *collaris*.

TABLE 1
MEASUREMENTS OF *Charadrius* PLOVERS FROM THE CANAL ZONE

Species	N ^a	Mean bill length (mm)	Mean wing length (mm)	Mean body weight (g)
<i>C. semipalmatus</i>	7	12.2	118.4	39.4
<i>C. collaris</i>	14	14.6	93.5	28.3
<i>C. wilsonia</i>	36	20.6	115.1	55.1

^a All specimens were collected in study area during 1971-73, but not all were used for stomach analyses. A few birds whose bills were damaged during collection are not included.

During low tide *semipalmatus* and *wilsonia* fed together in mixed flocks over the entire exposed area. *Collaris* was occasionally a member of these mixed flocks, but was usually found feeding on sandy areas nearer the high-tide line. The plovers fed in small groups of about 6 to 20 birds, spaced one to two meters apart. As the tide rose, these groups came together and occasionally moved on to dry beach to roost before being forced off the flats by the rising water. No obvious aggressive interactions were seen between the species or among conspecific individuals, although when one bird moved, the birds toward which it moved usually moved away from it.

During high tide *semipalmatus* and *wilsonia* roosted together on Skeet Beach. At that time they did not actively hunt for food, but did occasionally snap up prey which they encountered by chance. At high tide *collaris* sometimes roosted with the other two species but usually actively foraged on the beach and on nearby gravelly or short-grass areas. *Semipalmatus* and *wilsonia* foraged only at low tide, while *collaris* foraged independently of the tidal cycle.

The feeding behavior of the three species is typical of most plovers (Pearson and Parker 1973, Burton 1974): the birds run several steps, stop and stare, and then peck at prey. This sequence is performed repeatedly by a small group of birds moving along in parallel paths. The species studied here are strictly visual feeders. The actual method of prey capture is distinctive for each species. *Semipalmatus* catches prey by tipping forward at the ankle so that the tail is raised as the head goes down. *Collaris* usually jabs downward with little or no tipping of the entire body, although the ankle is also bent. This difference in feeding motion is correlated with the differences in body size and bill length of the two species; *semipalmatus* is a taller bird with a shorter bill compared to *collaris* (Table 1) and thus while feeding must bend over more in order for its bill to touch the ground. *Wilsonia* captures prey by lunging at it for up to one meter. Whereas the other two species usually take a few steps during prey capture, *wilsonia* actually runs during its forward lunge. At the moment of capture the bird is usually in a low crouch with neck extended.

Size measurements from birds collected in the study area are given in Table 1. No significant differences were found between the sexes. The size relationships among the species are complex. In body weight *wilsonia* is the largest bird and *collaris* the smallest. *Semipalmatus* has the longest wings, probably a reflection of its more migratory habits (Salomonsen 1955). *Wilsonia* has the largest bill, *semipalmatus* the shortest, while *collaris*, with lowest weight and wing length, has a bill intermediate in size. The ratio of bill lengths (in the order

TABLE 2
DIETS OF THREE SPECIES OF *Charadrius* PLOVERS WINTERING ON THE BAY OF PANAMA,
CENTRAL AMERICA, AS DETERMINED BY STOMACH CONTENTS ANALYSIS

Prey	<i>C. semipalmatus</i>			<i>C. collaris</i>			<i>C. wilsonia</i>		
	% prey individuals N = 408	Frequency (% stomachs) 13	Size range (mm)	% prey individuals 185	Frequency (% stomachs) 15	Size range (mm)	% prey individuals 188	Frequency (% stomachs) 26	Size range (mm)
Brachiopoda									
Inarticulata									
Atremata (<i>Lingula?</i>)	4.90	15.4	5.4-7.3	-	-	-	-	-	-
Mollusca									
Gastropoda									
Archaeogastropoda									
Neritidae	0.49	7.7	2.3	-	-	-	-	-	-
Mesogastropoda									
Naticidae	1.72	15.4	1-2	1.06	6.67	2	-	-	-
Neogastropoda									
Nassariidae	0.49	15.4	1-2	0.54	6.67	1-2	-	-	-
Marginellidae	0.49	15.4	2	-	-	-	-	-	-
Entomotaeniata									
Pyramidellidae	4.90	23.1	2-4	-	-	-	-	-	-
Annelida									
Polychaeta									
Nereidae	72.79	76.9	0.5-2.5	12.97	26.7	1-2	1.07	7.7	2
Glyceridae	6.86	38.5	1-2	0.54	6.7	1-2	-	-	-
Sp. 1	1.72	23.1	1-2	0.54	6.7	1-2	-	-	-
Sp. 2	0.98	7.7	1-2	-	-	-	-	-	-
Arthropoda									
Crustacea									
Isopoda									
Ancinus sp.	0.49	7.7	4	12.97	26.7	3-4	4.28	7.7	3-4
Sp. 1	-	-	-	1.62	13.3	4-6	-	-	-
Amphipoda									
Gammaridae	-	-	-	-	-	-	1.07	3.8	2
Decapoda									
Penaetidae (<i>Penaeus</i>									
<i>brevirostris</i>)	0.24	7.7	5	2.16	13.3	4-6	2.14	7.7	4-6
Caridae (<i>Palaemon</i>)	-	-	-	3.24	33.3	3-5	-	-	-
Paguridae (<i>Paguristes</i>)	-	-	-	-	-	-	0.54	3.8	1
Hippidae	-	-	-	0.54	6.7	6	-	-	-
Brachyryncha									
<i>Uca panamensis</i>	-	-	-	0.54	6.7	6	21.39	46.2	6-15
<i>Uca inaequalis</i>	-	-	-	4.86	13.3	3-9	11.22	23.1	3-9
<i>Uca beebei?</i>	-	-	-	-	-	-	0.54	3.8	10
<i>Eurypanopeus</i>									
<i>transversus</i>	0.24	7.7	1	-	-	-	19.79	38.5	6-10
<i>Speocarcinus</i>									
<i>ostreaticola</i>	-	-	-	-	-	-	10.70	11.5	7-11
Callinectes									
<i>arcatus</i> (juv.)	-	-	-	0.54	6.7	3	5.35	23.1	4-10
Goneplacid ? crab	-	-	-	-	-	-	4.81	7.7	7-11
Xanthid crab	0.24	7.7	4	0.54	6.7	10	10.16	30.8	7-11
<i>Panopeus chilensis</i>	-	-	-	-	-	-	2.67	7.7	6-9
<i>Eriphia squamata</i>	-	-	-	-	-	-	0.54	3.8	9
Crab megalopa	0.24	7.7	1	-	-	-	0.54	3.8	1
Insecta									
Orthoptera (non-roach)	0.49	15.4	6.5-10.3	10.27	53.3	2.5-14	-	-	-
Blattodea	-	-	-	1.08	13.3	5	-	-	-
Coleoptera									
Carabidae 1	0.24	7.7	5.5	-	-	-	-	-	-
Carabidae 2	-	-	-	0.54	6.7	3	-	-	-
Carabidae 3	-	-	-	0.54	6.7	5	-	-	-
Histeridae	-	-	-	0.54	6.7	2	-	-	-
Staphylinidae	-	-	-	0.54	6.7	3	-	-	-
Cucujidae	-	-	-	0.54	6.7	2.5	-	-	-
Tenebrionidae 1	-	-	-	0.54	6.7	3	0.54	3.8	0.5
Tenebrionidae 2	-	-	-	1.08	6.7	3.5	-	-	-
Tenebrionidae 3	-	-	-	0.54	6.7	3.5	-	-	-
Tenebrionidae 4	-	-	-	0.54	6.7	4	-	-	-

TABLE 2. (CONTINUED)

Prey	<i>C. semipalmatus</i>			<i>C. collaris</i>			<i>C. wilsonia</i>		
	% prey individuals	Frequency (% stomachs)	Size range (mm)	% prey individuals	Frequency (% stomachs)	Size range (mm)	% prey individuals	Frequency (% stomachs)	Size range (mm)
	N = 408	13		185	15		188	26	
Scarabaeidae 1	-	-	-	0.54	6.7	2.5	-	-	-
Scarabaeidae 2	-	-	-	0.54	6.7	2.5	-	-	-
Curculionidae 1	-	-	-	5.40	26.7	3.5	-	-	-
Curculionidae 2	-	-	-	1.08	6.7	4	-	-	-
Curculionidae 3	-	-	-	0.54	6.7	6.5	-	-	-
Curculionidae 4	-	-	-	1.08	6.7	4	-	-	-
Coleoptera 1	-	-	-	1.08	6.7	2.5	-	-	-
Coleoptera 2	-	-	-	1.08	6.7	3.5	-	-	-
Coleoptera 3	-	-	-	0.54	6.7	4	-	-	-
Coleoptera larvae	-	-	-	1.62	6.7	4	-	-	-
Hymenoptera									
Formicidae	1.22	30.8	2.5	16.76	73.3	1.4-6	2.67	11.5	3.5-5.5
Other Hymenoptera	0.73	15.4	4.5	2.16	20.0	5	0.54	3.8	5
Insect sp. ?	-	-	-	0.54	6.7	3	-	-	-
Animal sp. ?	-	-	-	0.54	6.7	?	-	-	-
Seed 1	-	-	-	0.54	6.7	1	-	-	-
Seed 2	0.49	7.7	3	2.70	6.7	3	-	-	-
Seed 3	-	-	-	2.70	6.7	1	-	-	-

collaris:semipalmatus:wilsonia) is 1.20:1.00:1.69; the ratio *collaris:wilsonia* is 1.00:1.41.

Except for four birds (one *collaris* and three *wilsonia*, all collected at Venado Beach), all the stomachs examined contained food items. Table 2 gives the results of the stomach contents analyses. Since we found no dietary differences between the sexes or between samples taken in different months or from different beaches, all samples of a species were lumped for final analyses. The diet of each species is distinct: *semipalmatus* takes about 82% polychaete worms, *collaris* takes 50% insects and 27% crustaceans, while *wilsonia* takes 96% crustaceans.

Figure 1 shows the percent of individuals of each general type of prey in all samples for each species, as well as the frequency of occurrence (percent of stomachs) for each type of prey.

Figure 2 is a plot on probability paper of prey size vs. cumulative percent of items in the diet. A straight line on such a plot would indicate a statistically normal distribution in the sizes of the prey taken. Clearly the diet of *semipalmatus* is skewed toward smaller food items (mean size 1.81 mm) while that of *wilsonia* is skewed toward larger items (mean size 7.82 mm). The size distribution of the prey of *collaris* shows a preference for prey near the mean size of 3.70 mm. The result for *semipalmatus* may be due to the method by which we measured the size of its major prey, polychaete worms.

Table 3 gives the percent overlap for the diet of each species pair calculated by the method of Horn (1966) for determining alpha and by the sum of shared frequencies, as used by Baker and Baker (1973) and Holmes and Pitelka (1968) for comparing shorebird diets. The same calculations were made for overlap

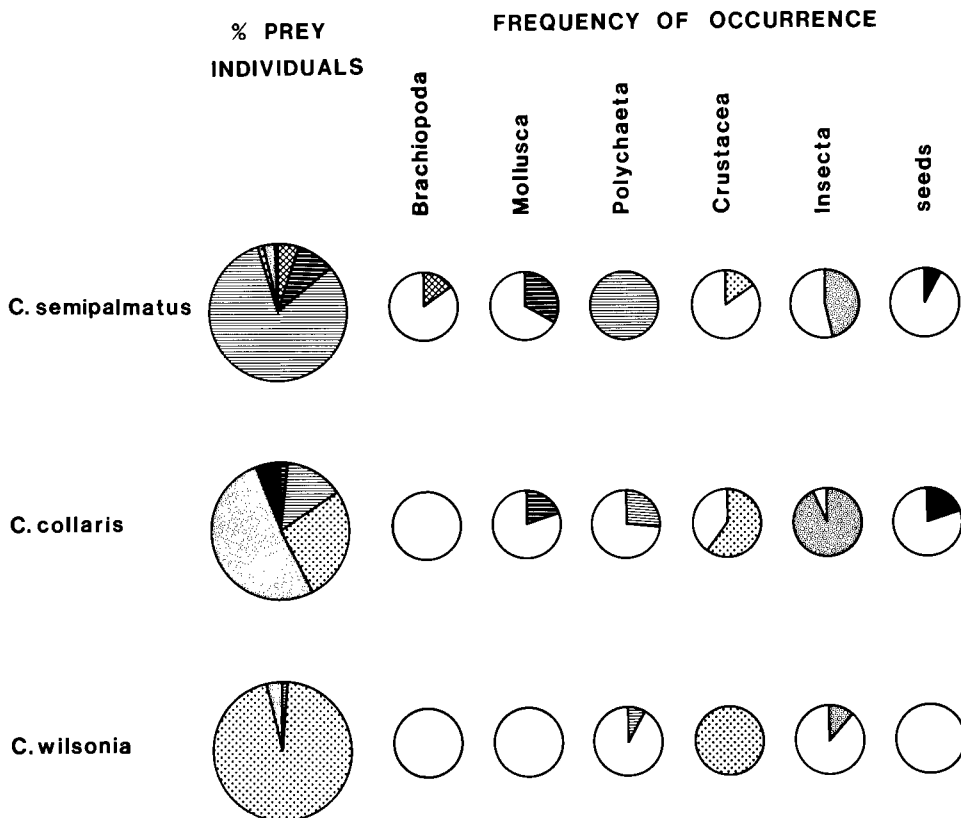


FIGURE 1. Percentage composition of stomach samples from three species of *Charadrius* plovers from the Canal Zone. Each complete circle represents 100%. Frequency of occurrence is the percentage of stomach containing the indicated prey.

based on taxon of prey items and on size of prey items. The resulting overlap measurements are similar whether based on taxon or size of prey.

The degree of specialization in feeding habits of the plovers may be examined by comparing the diversities of their diets. Table 4 gives the results of calculation of the informational-theoretical measure of diversity, H , based on natural logarithms (Lloyd et al. 1968) of the diets of the three species. The calculations were made, first, by using each prey species as a separate category of prey and, second, by lumping the prey into larger taxonomic units. The second calculation assumes

TABLE 3
DIETARY OVERLAP FOR SPECIES PAIRS OF PLOVERS FROM THE CANAL ZONE

Species pair	Percent overlap based on taxon of prey		Percent overlap based on size of prey	
	Alpha \times 100	Sum of shared frequencies	Alpha \times 100	Sum of shared frequencies
<i>C. semipalmatus</i> - <i>C. collaris</i>	30.7	18.7	21.1	29.9
<i>C. collaris</i> - <i>C. wilsonia</i>	19.7	17.1	6.2	15.1
<i>C. wilsonia</i> - <i>C. semipalmatus</i>	2.8	4.5	1.9	5.2

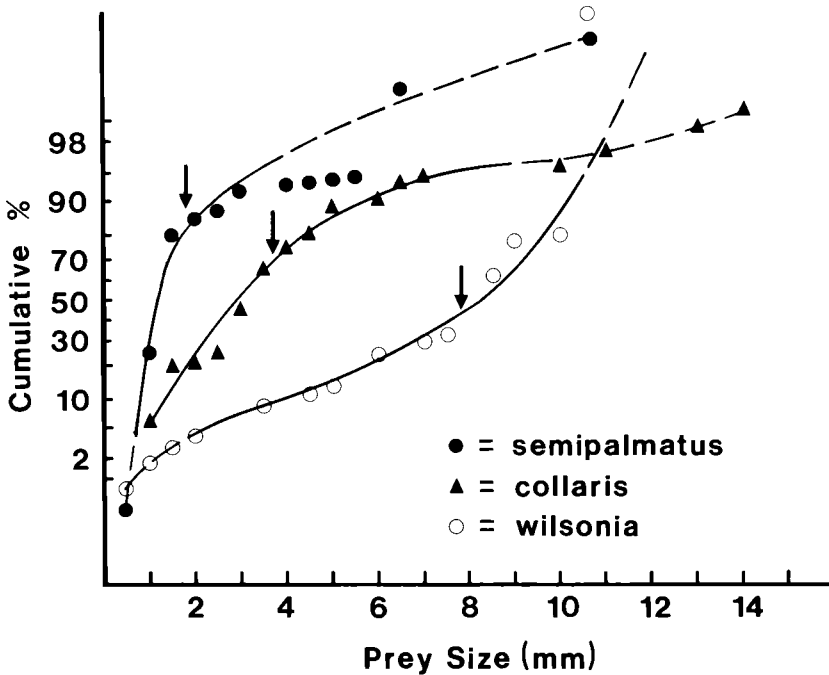


FIGURE 2. Distribution of prey size for three species of *Charadrius* plovers in the Canal Zone. The arrows indicate the mean prey size for each species.

that the plovers do not make use of fine taxonomic distinctions in what they eat, distinguishing crabs from worms but making no distinctions among different kinds of crabs or different kinds of worms.

We have evidence, however, that the plovers do distinguish between two different kinds of crabs. Some species of crab found on the flats use a cryptic posture or coloration as a defense mechanism, while others assume a lateral spread defense posture along with attack autotomy of the chelipeds if pursued (Robinson et al. 1970). Only crabs using cryptic postures or coloration were found in the plovers' stomachs. Only females of *Speocarcinus ostreaticola*, a species in which only the male uses the lateral spread posture, have been identified in the plovers' stomachs.

The diversity measures using each prey species as a separate category indicate that *semipalmatus* is more specialized (shows lower diversity) in its diet than the

TABLE 4
INDICES OF DIVERSITY OF DIET FOR THREE SPECIES OF *Charadrius* PLOVERS

Species	Single prey taxa		Lumped prey taxa	
	<i>H</i>	<i>e^H</i> ^a	<i>H</i>	<i>e^H</i> ^a
<i>C. semipalmatus</i>	1.145	3.1	0.801	2.1
<i>C. collaris</i>	2.636	14.0	1.942	7.0
<i>C. wilsonia</i>	2.184	8.9	0.517	1.7

^a *e^H* = number of equally common species in the diet.

other two species. When prey are lumped, however (the categories used were brachiopods, gastropods, polychaete worms, isopods, amphipods, shrimp, crabs, orthopterans, beetles, hymenopterans, and seeds), the diversity measures decrease unequally for the three species. The greatest drop in diversity occurs in *wilsonia*. The lumped diversities indicate that both *semipalmatus* and *wilsonia* are considerably more specialized in diet than is *collaris*.

DISCUSSION

Our results show a clear separation in the diets of the plovers studied. The mean prey sizes (1.8 mm for *semipalmatus*, 3.7 mm for *collaris*, and 7.8 mm for *wilsonia*) correlate well with the average bill lengths (12.2, 14.6, and 20.6 mm, respectively) of these species but not with their body weights (see Table 1). Holmes and Pitelka (1968) found a partial separation of modal size of prey to be correlated with bill size in sandpipers. Ashmole (1968), however, has shown that bill length alone is a poor indicator of prey size in some groups of sympatric terns. Hespeneide (1971) found body weight to be a better predictor of mean prey size than bill size for insectivorous birds. The discrepancy between our results and Hespeneide's is probably related to our choice of measurement used to estimate the size of the prey of *semipalmatus*. Had we used prey body weight as a measure of size instead of length (or width of head in the case of polychaetes), our results would probably agree with those of Hespeneide.

There is, however, a clear separation in the kinds of prey taken, regardless of size. *Semipalmatus* eats principally polychaete worms, *wilsonia* eats mainly crustaceans, while *collaris* eats a wide variety of prey.

The only other reported values of food diversity for shorebirds are those of Recher (1966). Since he did not report the details of his calculations, one must use caution when comparing his indices with ours. Of the species he studied, *semipalmatus* was the most specialized in diet. The dietary diversity that we find for *collaris* is almost twice that of the species with the most diverse diet in Recher's study.

Whether calculated according to taxon or prey size, overlap is about 25% in the diets of *semipalmatus* and *collaris*, about 10–20% in the diets of *collaris* and *wilsonia*, and about 4% in the diets of *wilsonia* and *semipalmatus* (Table 3). Holmes and Pitelka (1968) found about 15–88% food overlap for sandpipers on their Alaskan breeding grounds during a season when food was abundant. Except from late June to early July, when the variety of available prey was greatest, overlap in diet was greater than 30%. From the data of Recher (1966) and Anderson (1970) we calculated an average value of 52% (30–88%) overlap in diet for six congeneric pairs of shorebird species using about the same habitat for feeding during migration. Compared to other reports for shorebirds using the same or similar habitats, the overlap in food which we find is low. This is probably a reflection of an abundant and diverse food supply.

The similarity in overlap measurements, whether based on taxon or size of prey, may be fortuitous, considering how the size of the prey of *semipalmatus* was measured, or may be due to the relationship between size and taxon of prey (Hespeneide 1971). The specialization of prey type in *semipalmatus* and *wilsonia* indicates that attributes other than size are important in identifying potential prey.

The differences in morphology and diet which we found among these species

might be the result of local competitive interactions, or they might reflect selective forces operating during other times of the year or in different locations. Most important would be independent specialization on different food organisms. Overlap or its absence, considered alone, do not necessarily indicate competition or its absence (Vandermeer 1972, contra Levins 1968, Baker and Baker 1973).

Semipalmatus is found mainly on marine coasts during the winter; it breeds throughout a large inland area as well as in coastal habitats (Bent 1929, Todd 1963, Godfrey 1966, JGS pers. obs.). During migration it is found throughout North America wherever conditions are suitable for shorebirds (Bent 1929, Robbins et al. 1966, Parmelee et al. 1969). On inland areas the species takes mostly insects (Lönnerberg 1903, Bent 1929), especially larvae (JGS pers. obs.). Cottam and Hanson (1938) found the stomachs of a nesting pair of *semipalmatus* collected in Labrador to be gorged with insects, spiders, and a few seeds. In coastal California (Recher 1966) and South Carolina (JGS pers. obs.) *semipalmatus* eats mainly polychaete worms, as it does in Panama. In addition, it has been observed to eat unidentified marine worms in Peru (Ashmole 1970), New Jersey (Stone 1937), and Massachusetts (JGS pers. obs.). Other reports (Forbush 1916, Reeder 1951) indicate that it exploits other marine food when it is abundant.

Instead of being a food specialist *semipalmatus* appears to adapt its diet to locally abundant prey. The only other shorebird which has been shown to be similarly opportunistic is the Dunlin (*Calidris alpina*) (Vielliard 1973).

That *semipalmatus* is more likely to eat brachiopods and mollusks and less likely to eat crustaceans than are the other two species may be related to its short bill. *Collaris* and *wilsonia*, with their longer bills, are better adapted to catch fast-moving prey (Ashmole 1968). Since on our study area *semipalmatus* and *wilsonia* use exactly the same habitat for foraging, it seems unlikely that they encounter potential prey species on the beaches with different frequencies. *Wilsonia*, however, is better equipped for capturing and subduing fast prey; since food is abundant, it can ignore other kinds of potential prey (which also tend to be smaller). *Semipalmatus*, on the other hand, may be limited to eating slower-moving animals or those which can be taken by surprise while partially emerged from their burrows. Recher (1966) found that larger species of shorebirds feed selectively on larger prey but also take some smaller prey, while smaller species eat all food items that they encounter. The diets of *wilsonia* and *collaris* show this pattern of feeding behavior.

Of the three species we studied, *wilsonia* appears to be most specialized in habitat and food. Throughout its range it is confined to marine beaches and mudflats (Bent 1929), where it feeds mainly on crustaceans, especially crabs (Bent 1929, Tomkins 1944, Palmer 1967). We have no evidence that its diet and feeding behavior in Panama differ from those found elsewhere.

Collaris is known from both coastal and inland habitats (Warner and Mengel 1951, Amadon and Eckelberry 1955, Haverschmidt 1968) and may breed in a variety of situations. Although Haverschmidt reported insects as the only known food, we found that marine organisms are taken in coastal situations. Why *collaris* does not exploit the intertidal area for all its food needs like the other two species is unclear. This question is particularly interesting because *semipalmatus*, which is also a generalist, seems to be able to specialize in our study area while *collaris* does not. *Collaris* is a tropical species. Tropical areas are characterized by high

animal diversity but low abundance for any given taxon. Because of this perhaps there has been little selective pressure on *collaris* to specialize its diet. Conversely, *semipalmatus* occurs in subarctic and temperate regions where prey diversity is often low but where a given prey taxon may be superabundant. Selection has thus favored the ability to specialize in whatever prey happen to be locally abundant.

Since feeding habits of these plovers in Panama appear to be much the same as they are in areas where the three species do not occur together, we doubt that local competitive interactions are important in maintaining them. In our study areas the plovers have an abundant food supply. Dexter's (1972) estimate of 1443 invertebrates/m² for Naos Beach, Canal Zone, represents a lower limit for the abundance of prey animals on the beaches we studied. Recher (1966) found about 1300 animals/m² in the areas he studied in California. In addition, our observations of plovers leaving the flats to roost while up to 50% of the tidal areas were still available for feeding indicates that the birds were satiated before the incoming tide forced them off the flats. While this pattern held true for *semipalmatus* and *wilsonia*, *collaris* fed throughout the day independently of the tidal cycle. Bédard (1969) found a similar situation in his study of three species of auklets in Alaska during the breeding season. He reported that the species with the most diverse diet, *Cyclorhynchus psittacula*, spent more time on the feeding grounds, which it shared with two species of *Aethia*, even though all of the species seemed to have access to the same feeding depths.

In spite of the large diversity and abundance of food in our study area, few shorebirds other than plovers used the area. Plovers are limited to surface prey. Recher (1966) argued that the diversity of the habitat and not the diversity of food organisms appears to limit shorebird species diversity. He found, however, that tidal flats had relatively high habitat diversity due to the stratification of food organisms within the substrate. A possible explanation for the apparent lack of other shorebird species in our area is the density of the substrate. Although we classified most of the intertidal area as mud, almost all the mud areas are thin layers of soft material over a harder sand substrate on which we walked without difficulty. The only shorebirds observed to feed by "probing" in our study areas were occasional Western Sandpipers (*Calidris mauri*); the maximum depth to which this species can probe is about 28 mm, however. A greater diversity of shorebirds was found on the mudflats near Panamá Viejo at the mouth of the Río Matías Hernández. There the substrate is soft mud, and deep-probing species such as dowitchers (*Limnodromus* sp.) were commonly observed. It seems reasonable that the low diversity of shorebirds on Venado Beach is related to a preference of many species for a softer substrate, which can be found no more than 20 km away.

The populations of plovers on our study areas may be limited not by availability of food, but rather by a scarcity of roosting sites. During high tide the exposed beach is narrow at both Venado and Skeet beaches. Both beaches are often heavily used by people. Plovers were never observed to roost on Venado Beach, and those that roosted on Skeet Beach were frequently disturbed, sometimes leaving the beach entirely. Neither beach was used as a roost at night. The nocturnal roosting sites of the birds we studied remain unknown, but probably

are offshore rocks, where during the day we found dense aggregates of plovers, gulls, terns, and some herons. At Palo Alto, California, Recher (1966) found that available space appeared more important than food supply in limiting the size and density of migrant shorebird populations. Feare (1966) suggested that the numbers of wintering Purple Sandpipers (*Calidris maritima*) were limited by the availability of roosting sites on Robin Hood's Bay, North Yorkshire. These observations agree with the belief expressed by Miller (1967) that features of the habitat required for breeding or shelter may be more limiting than food for some species.

Since shorebirds are common, conspicuous birds which occur in relatively simple habitats, they are well suited for studies of feeding ecology and competition for food. Studies of sandpipers, however, are complicated by the large number of species which commonly occur together, making necessary consideration of many simultaneous species interactions, and by the ability of a species to use more than one feeding method, thus increasing the proportion of the habitat it can exploit. Studies of plovers, on the other hand, have fewer of these complications, since only a few species occur together at one time and since plovers are restricted to feeding on the surface of the substrate. Nevertheless, there is considerable opportunity for the comparative approach, since many different species mixes are available at different locations; *semipalmatus*, for instance, can be found with one or more of at least six different congeners at some time during the year.

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LITERATURE CITED

- AMADON, D., AND D. R. ECKELBERRY. 1955. Observation on Mexican birds. *Condor* 57:65-80.
- AMERICAN ORNITHOLOGISTS' UNION. 1957. Check-list of North American birds. 5th ed. Lord Baltimore Press, Baltimore.
- ANDERSON, W. 1970. A preliminary study of the relationship of saltponds and wildlife—south San Francisco Bay. *Calif. Fish and Game* 56:240-252.
- ASHMOLE, M. J. 1970. Feeding of Western and Semipalmated Sandpipers in Peruvian winter quarters. *Auk* 87:131-135.
- ASHMOLE, N. P. 1968. Body size, prey size, and ecological segregation in five sympatric tropical terns (Aves: Laridae). *Syst. Zool.* 17:292-304.
- BAKER, M. C., AND A. E. M. BAKER. 1973. Niche relationships among six species of shorebirds on their wintering and breeding ranges. *Ecol. Monogr.* 43:193-212.
- BÉDARD, J. 1969. Feeding of the Least, Crested, and Parakeet Auklets around St. Lawrence Island, Alaska. *Can. J. Zool.* 47:1025-1050.
- BENGTSON, S., AND B. SVENSSON. 1968. Feeding habits of *Calidris alpina* L. and *C. minuta* Leisl. (Aves) in relation to the distribution of marine shore invertebrates. *Oikos* 19:152-157.
- BENT, A. C. 1929. Life histories of North American shorebirds. Pt. 2. U. S. Natl. Mus. Bull. 146.
- BROOKS, W. S. 1967. Organisms consumed by various migrating shorebirds. *Auk* 84:128-130.
- BURTON, P. J. K. 1972. The feeding techniques of Stilt Sandpipers and dowitchers. *Trans. San Diego Soc. Nat. Hist.* 17:63-68.
- BURTON, P. J. K. 1974. Feeding and the feeding apparatus in waders: a study of anatomy and adaptations in the Charadrii. Trustees of the British Museum (Natural History), London.

- COTTAM, C., AND H. C. HANSON. 1938. Food habits of some Arctic birds and mammals. *Field Mus. Nat. Hist. Publ. Zool. Ser.* 20:405-426.
- DAVIDSON, P. E. 1971. Some foods taken by waders in Morecambe Bay, Lancashire. *Bird Study* 18:177-186.
- DEXTER, D. H. 1972. Comparison of the community structures in a Pacific and an Atlantic Panamanian sandy beach. *Bull. Mar. Sci.* 22:449-462.
- EHLERT, W. 1964. Zur Ökologie und Biologie der Ernährung einiger Limikolen-Arten. *J. Ornithol.* 105:1-53.
- EISENMANN, E. 1951. Northern birds summering in Panama. *Wilson Bull.* 63:181-185.
- EISENMANN, E. 1955. The species of Middle American birds. *Trans. Linnean Soc. New York.* 7.
- FEARE, C. J. 1966. The winter feeding of the Purple Sandpiper. *Brit. Birds* 59:165-172.
- FORBUSH, E. H. 1916. A history of the game birds, wildfowl and shore birds of Massachusetts and adjacent states. 2nd ed. Mass. St. Board of Agriculture, Boston.
- GODFREY, W. E. 1966. The birds of Canada. *Natl. Mus. Can. Bull.* 203.
- GOSS-CUSTARD, J. D. 1970. Feeding dispersion in some overwintering wading birds. Pp. 3-35 in J. H. Crook (ed.), *Social behaviour in birds and mammals*. Academic Press, London.
- HAVERSCHMIDT, F. 1968. The birds of Surinam. Oliver and Boyd, London.
- HESPENHEIDE, H. A. 1971. Food preference and the extent of overlap in some insectivorous birds, with special reference to the Tyrannidae. *Ibis* 113:59-72.
- HOLMES, R. T., AND F. A. PITELKA. 1968. Food overlap among coexisting sandpipers on northern Alaskan tundra. *Syst. Zool.* 17:305-318.
- HORN, H. S. 1966. Measurement of "overlap" in comparative ecological studies. *Amer. Nat.* 100:419-424.
- LACK, D. 1971. *Ecological isolation in birds*. Blackwell Scientific Publications, Oxford.
- LEVINS, R. 1968. *Evolution in changing environments*. Princeton Univ. Press, Princeton, New Jersey.
- LLOYD, M., J. H. ZAR, AND J. R. KARR. 1968. On the calculation of information-theoretical measures of diversity. *Amer. Midl. Nat.* 79:257-272.
- LÖNNBERG, E. 1903. On a collection of birds from Northwestern Argentina and the Bolivian Chaco. *Ibis* 1903:441-471.
- MILLER, R. S. 1967. Pattern and process in competition. *Adv. Ecol. Res.* 4:1-70.
- MONROE, B. L., JR. 1968. A distributional survey of the birds of Honduras. *Ornithol. Monogr.* 7.
- PALMER, R. S. 1967. Species accounts. Pp. 143-267 in G. D. Stout (ed.), *The shorebirds of North America*. Viking Press, New York.
- PARMELEE, D. F., M. D. SCHWILLING, AND H. A. STEPHENS. 1969. Charadriiform birds of Cheyenne Bottoms. Pt. 1. *Kans. Ornithol. Soc. Bull.* 20:9-13.
- PEARSON, R. G., AND G. A. PARKER. 1973. Sequential activities in the feeding behaviour of some Charadriiformes. *J. Nat. Hist.* 7:573-589.
- PETERS, J. L. 1934. Check-list of birds of the world. Vol. 2. Harvard Univ. Press, Cambridge.
- PRATER, A. J. 1972. The ecology of Morecambe Bay. III. The food and feeding habits of Knot (*Calidris canutus* L.) in Morecambe Bay. *J. Appl. Ecol.* 9:179-194.
- RECHER, H. F. 1966. Some aspects of the ecology of migrant shorebirds. *Ecology* 47:393-407.
- REEDER, W. G. 1951. Stomach analysis of a group of shorebirds. *Condor* 53:43-45.
- RIDGELY, R. S. 1976. *A guide to the birds of Panama*. Princeton Univ. Press, Princeton, New Jersey.
- ROBBINS, C. S., B. BRUUN, AND H. S. ZIM. 1966. *Birds of North America*. Golden Press, New York.
- ROBINSON, M. H., L. G. ABELE, AND B. ROBINSON. 1970. Attack autotomy: a defense against predators. *Science* 169:300-301.
- SALOMONSEN, F. 1955. The evolutionary significance of bird-migration. *Dan. Biol. Medd.* 22:1-62.
- STONE, W. 1937. *Bird studies at old Cape May*. Vol. I. Delaware Valley Ornithological Club, Philadelphia.
- STORER, R. W. 1960. A preliminary report on the summer bird life of southwestern Michoacán. Pp. 335-340 in D. D. Brand et al., *Coacomán and Motines del Oro*. Martinus Nijhoff, The Hague.
- THOMAS, D. G., AND A. J. DARTNALL. 1971. Ecological aspects of the feeding behaviour of two calidridid sandpipers wintering in south-east Tasmania. *Emu* 71:20-26.
- TODD, W. E. C. 1963. *Birds of the Labrador Peninsula and adjacent areas*. Univ. of Toronto Press, Toronto.

- TOMKINS, I. R. 1944. Wilson's Plover in its summer home. *Auk* 61:259-269.
- VANDERMEER, J. H. 1972. Niche theory. *Ann. Rev. Ecol. Syst.* 3:105-132.
- VIELLIARD, J. 1973. Autoécologie comparée due Bécasseau Variable *Calidris alpina* (L.). *Alauda* 41:1-33.
- WARNER, D. W., AND R. M. MENGEL. 1951. Notes on birds of the Veracruz coastal plains. *Wilson Bull.* 63:288-295.
- WILLIS, E. O. 1966. The role of migrant birds at swarms of army ants. *Living Bird* 5:187-231.