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RELATIONSHIPS BETWEEN TIDAL OSCILLATIONS AND RUDDY TURNSTONE FLOCKING, FORAGING, AND VIGILANCE BEHAVIOR

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ABSTRACT.—Ruddy Turnstone (*Arenaria interpres*) flocking behavior, aggression, vigilance, prey choice, foraging rate, and foraging success were examined in relation to tidal fluctuations and food distribution on a Pacific beach in Costa Rica. Turnstones foraged only when the tidal flat was exposed; they rested in flocks during high tide. Flock size, peck rate, and success rate decreased during the ebb and increased with the flood. Foraging velocity increased until low tide and then decreased. Vigilance was related only to flock size and flock size did not affect foraging rates or success. Vigilance apparently did not directly reduce foraging efficiency or deter flock breakup. Increased aggression, however, decreased foraging efficiency, and may have partly caused reduction in flock size. Turnstones fed on invertebrates close inshore and on crabs farther out on the flat, where the latter were more abundant. Rates of predation on crabs were correlated with crab density, decreased foraging rate, and success. The switch in the birds' diet and the substrate zonation appeared to be largely responsible for the tidally and spatially correlated patterns in foraging rate. Possibly the nature and distribution of the prey influenced the turnstones' levels of aggression and hence, determined the optimal sizes of their flocks.

Many shorebirds forage in intertidal habitats where tides cause predictable changes in the foraging substrate. Exposed areas fluctuate and the timing of tides varies regularly. Food items may be clumped in tidal pools and their availability may vary according to when (Green and Hobson 1970) or how long different areas have been exposed to sun and air (Vader 1964, Recher 1966).

The effects of tidal fluctuations on shorebird activities have had little study. Several researchers have documented changes in shorebird abundance, habitat choice, or dispersion in relation to the tides (Recher 1966, Thomas and Dartnall 1971, Burger et al. 1977, Hartwick 1978, Harris 1979, Kelly and Cogswell 1979, Connors et al. 1981). Others have attempted to relate levels of feeding or foraging activity to tidal changes (Ehlert 1964, Harris 1979, Hartwick and Blaylock 1979, Morrell et al. 1979). In order to avoid such tide-related variations, Baker (1974) recorded data only during the low tide.

As the ebb tide exposes the foraging area, shorebirds may occupy the space, flocks may disperse and different prey may be taken. As individuals spread out and new prey types are sought, foraging success or techniques may change. In addition, the breakup of flocks could significantly alter relations among the birds and the susceptibility to predation. Increasing flock size often heightens aggression and competition (Recher and Recher 1969, Silliman et al. 1977, Burger et al. 1979), and lowers individual vigilance (Abramson 1979, Barnard 1979, Caraco 1979, etc.) and the likelihood of predation (Page and Whitacre 1975). Increasing flock size also usually improves foraging success (Krebs 1974, Abramson 1979, Barnard 1979, Caraco 1979; but see Smith 1977), but if this is balanced against the costs of competition and vigilance, flocking may yield no foraging benefits (Krebs and Barnard 1980).

I studied the foraging activities of Ruddy Turnstones (*Arenaria interpres*) on the Pacific coast of Costa Rica, and attempted to determine some of the relationships among tidal oscillations, food distributions, and various aspects of turnstone behavior.

STUDY AREA AND FLOCKS

I made my observations on a clay tidal flat at Playa Sirena, Corcovado National Park, Puntarenas Province, Costa Rica, from 6 to 16 August 1979, and from 9 to 23 April 1980. Playa Sirena frames a crescent-shaped bay and stretches about 2 km between the mouths of the Rio Sirena and the Rio Claro. A sandy beach slopes downward about 20 m from a second-growth woodland to the edge of the extensive clay flat (hereafter called the "beach's edge"). Regardless of the tide, turnstones were never seen feeding on the sandy beach. The clay flat itself was fairly level and at low tide extended 150–250 m from the beach's edge. Extent of total exposure depended on location within the bay, temporal fluctuation in amount of tide drop (i.e., phase of the moon) and wind. At high tide, which occurred twice daily, the water generally flooded a few meters into the woodland zone, and at these times the turnstones rested in flocks at the river mouths. Unlike Harris (1979) who found turnstones commonly feeding on beaches during high tide in Wales, I only rarely observed such activity at the river mouths. Shortly after the tide exposed the edge of the flat, groups from these flocks moved to the flat to commence feeding.

METHODS

PHYSICAL FEATURES

The substrate of the tidal flat is a hard, unabsorptive clay. I defined four zones: 0–10 m (from the beach's edge), smooth surface, with algal mat; 10–25 m, smooth surface, no algae; 25–100 m, rough, jagged surface; 100–250 m, jagged surface, mostly covered with tidal pools. In order to quantify these zones I made five transects perpendicular to the beach's edge, extending outward to 100 m. Every 10 m from the beach's edge I counted the number of invertebrate-excavated holes in a 20 × 20-cm quadrat. I measured the diameters of the first 10 holes on the beachward edge with dial calipers (to 0.1 mm). In each quadrat I measured the difference between the highest and lowest points to gauge the roughness of the surface. For 10 transects I also estimated the percent of a 2 × 2-m quadrat that was covered by tidal pool.

FOOD DISTRIBUTION

To estimate the numbers of fish and crabs available, I made 10 transects perpendicular to the beach's edge, ranging from 80 to 100 m in length. At 10-m intervals on each transect, I set a 2 × 2-m quadrat marker in place. I stood motionless for 60 s, then counted the number of crabs (mostly *Pachygrapsus transversus,* some *Uca* spp. and *Eriphia* spp.), the number of crabs greater than 1 cm across the carapace (generally *Leptodius taboganus*), and the total number of small fish that had resumed activity during a 2-min observation period. I made nine 35-m transects in order to census small, burrowing clams. In each 10 × 10-cm quadrat at 3- or 5-m intervals I counted the number of surface holes and then dug 3–5 cm into the clay with a knife to find the clams.

FORAGING BEHAVIOR

I studied the foraging behavior of Ruddy Turnstones throughout the low phase of the tide. As I walked the beach and encountered a flock, I unsystematically chose an individual for observation. This bird's activities were followed for as long as possible while I timed the period with a stopwatch. My 305 observations had an average duration of 92.5 s. I defined "flock size" as the number of turnstones all within 10 m of each other, and all moving in a similar direction. Lone birds were the objects of 33% of my observations.

The time when the beach's edge was exposed to air became the reference point for the "time (number of minutes) after exposure." Because I found curvilinear and symmetrical relationships between time after exposure and several other variables, I transformed time after exposure by subtracting it from the number of minutes between flat exposure and low tide (165 min) and squaring: i.e., $(165 - \text{time after exposure})^2$. Thus, high values of the transformed variable occur at high tide levels, either on the incoming or outgoing tide, while low values occur around the low tide.

For three days, as the tide ebbed, I laid out a grid on the flat at 40-m intervals from the beach's edge. From these references I estimated a bird's distance from the water's edge and from the beach's edge. During the April study period I estimated distances between birds and myself at the onset of a foraging sequence ("observer distance").

For most observations I determined the rate of pecking (peck/s). During the August period I also measured the forward speed of foraging birds (m/s), and during the April period I also measured the success rate (prey captures/s; captures often deduced by swallowing motions), and efficiency (prey captures/peck). Identifiable prey items were noted. The birds' efficiency and success rate did not appear to be biased by my proximity; the correlation between observer distance and success rate was −0.087 (n.s.), and the correlation between observer distance and efficiency was −0.097 (n.s.). In order to measure an individual's vigilance, I timed the "stop-look rate" (the rate at which an individual stopped, for about 1 s or more, and looked around; stop-looks/s). I also recorded intra- and interspecific supplanting behavior.

Data were analyzed using the SPSS (Nie et al. 1975) and Minitab (Ryan et al. 1978) statistical programs. Because of the correlations among flock size, stop-look rate, supplant rate, and transformed time after exposure, it was difficult to tell which of these variables best predicted the variation in foraging. I therefore used path analysis (Wright 1921, Nie et al. 1975), a technique that uses multiple regression to statistically control the interactions of two or more variables, and then quantifies the relationships of these to others. Reasonable, anticipated, causal pathways are modeled, and

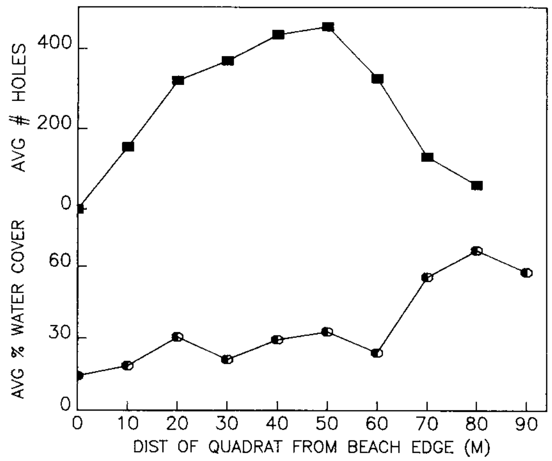

FIGURE 1. Upper line is the average number of holes per quadrat plotted against the distance of the quadrat from the beach's edge. Below is the relationship between the percent of a quadrat that is pool-covered and the quadrat's distance from the beach's edge.

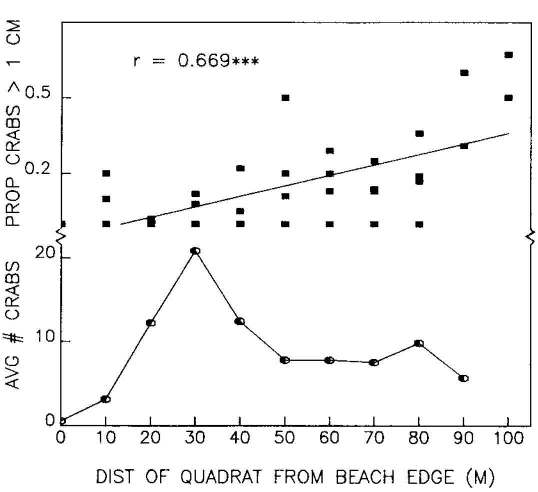

FIGURE 2. Average number of crabs per quadrat (below) and the proportion in a quadrat of crabs with a carapace greater than 1 cm across, plotted against distance from the beach's edge. ***$P < 0.001$.

multiple regressions are performed to reflect these pathways. Pathways with partial, standardized regression coefficients (betas or partial correlations) that are not significantly different from zero, are excluded from the model. In my case, I regressed each foraging variable on transformed time after exposure, flock size, stop-look rate and the number of supplants. Correlations of flock size with transformed time after exposure, stop-look rate, and number of supplants were also included. The correlation between transformed time after exposure and stop-look rate is partial while controlling for the effects of flock size.

RESULTS

PHYSICAL FEATURES AND DISTRIBUTION OF FOOD

The surface of the tidal flat was progressively more pitted and water-covered the farther out from the beach's edge (Fig. 1); both the mean and standard deviation of hole size were positively correlated with distance from the beach's edge (mean: $r = 0.484$, $P < 0.01$; SD: $r = 0.639$, $P < 0.001$).

I found consistent trends in the distribution of algae, clams, crabs and fish. Crabs were most abundant 30 m from the beach's edge, and they tended to be larger with distance from the beach's edge (Fig. 2). Densities of fish were relatively constant across the flat. Clams were most plentiful about 15 m from the beach's edge, but the proportion of holes with clams diminished with the distance from the beach's edge ($r = -0.578$, $P < 0.001$). Algae were found only within the first 10 m from the beach's edge.

In the algal mat I found small polychaete worms and minute crustaceans. Within and around this zone (especially early in the ebb tide and late in the flood tide) I observed turnstones pecking at and swallowing tiny objects that I could not identify, probably the invertebrates, and bits of carrion left by the tide. I also saw turnstones feeding on crabs (with carapaces up to 2 cm across), clams (occasionally dug from the clay with difficulty), small live fish from drying pools, and dead fish and other carrion.

FORAGING BEHAVIOR

Flock size varied in a symmetrical, curvilinear manner according to the time after exposure of the flat (Fig. 3). The correlation between flock size and the transformed time after exposure ($r = 0.458$, $P < 0.001$) indicated that flocks diminished on the ebb and increased on the flood. The birds followed the water's edge on the ebb and spread over the flat during low tide and part of the flood tide. I noted a significantly larger proportion of birds foraging within 10 m of the water's edge ($G = 12.83$, $P < 0.005$) during the ebb than during the flood. The latter proportion was in turn greater (but not significantly so) than that of the low tide hiatus.

Statistics for five measures of foraging are given in Table 1. Peck rate, success rate, and efficiency varied in a similar, symmetric, curvilinear manner according to time after exposure (Fig. 3, Table 2), indicating that peck and success rates, and efficiency fell and rose with the tide. I correlated all foraging variables individually with time after exposure, time after exposure transformed, and flock size (Table 2). Correlations with the transformed time

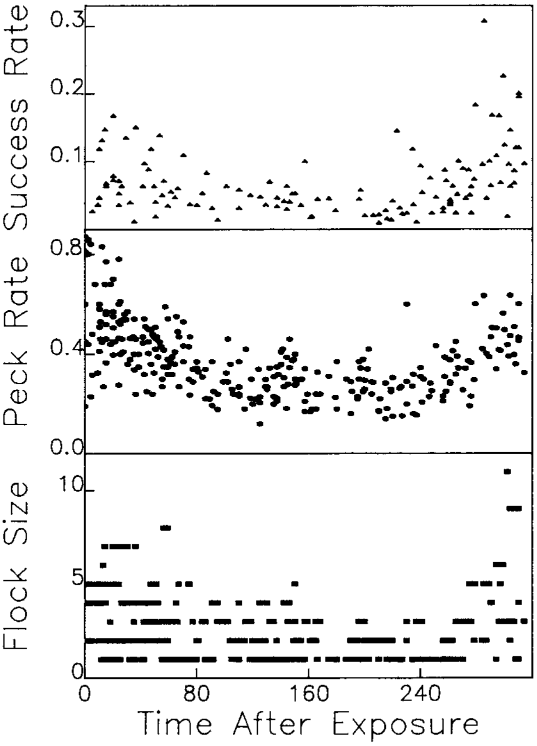

FIGURE 3. Plots of flock size, peck rate, and success rate versus time after exposure of tidal flat. Low tide occurred at about 165 min after exposure.

variable were greater than those for time after exposure in all cases except efficiency (where both correlations were very small). The transformed time after exposure was inversely correlated with speed of foraging, meaning that the birds moved more rapidly during low tide. This opposes the patterns of peck and success rates and efficiency.

Foraging variables were also regressed on stop-look and supplant rates. Stop-look rate was significantly correlated with flock size (Table 2) and, of the four foraging variables, only with peck rate ($r = -0.13$, $P < 0.05$, $n = 284$). The rate of supplanting was correlated with flock size (Table 2) and, of the foraging variables, only with efficiency ($r = -0.20$, $P < 0.05$). Supplant rate was not significantly correlated with stop-look rate ($r = 0.12$, $P < 0.10$).

TABLE 2. Correlation coefficients (Pearson r) among time after exposure, transformed time after exposure, flock size and each of the foraging variables.

Variable	Flock size	Time after exposure	Time after exposure (transformed)
Peck rate	0.340***	−0.361***	0.685***
Stop-look rate	−0.304***	0.124*	−0.156**
Success rate	0.241**	0.165	0.455***
Efficiency	0.023	0.241**	0.213*
Speed	0.261**	0.392***	−0.508***
Supplant rate	0.350**	−0.003	0.153

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Path analysis indicated that transformed time after exposure (a) was a good predictor of flock size, peck rate, success rate, efficiency, and speed (Fig. 4, Table 3). Only stop-look rate and supplant rate were predicted by flock size (d). The relatively low correlation between stop-look rate and flock size may have related to either large error in either variable or the variability induced by other factors. Including the number of individuals of other species near to the turnstone flocks improved the correlation slightly ($r = 0.41$, $P < 0.001$). Observer distance had no apparent effect on this variable ($r = 0.01$, $P > 0.5$). When the effects of transformed time after exposure and flock size were controlled, stop-look rate (b) had no significant relationship with any of the foraging variables. Supplant rate (c), however, was still negatively related to both success rate and efficiency.

Correlations between a bird's location on the flat and each of the foraging variables (Table 4) were consistently lower (with lower significance levels) than those involving transformed time after exposure. Reduced significance may largely be a result of the substantial error induced by my method of estimating a bird's distance from the shore or water. Flock size was not correlated with distance from the beach's edge. Turnstones did peck faster near the water's edge.

RELATIONSHIPS AMONG RESOURCE DISTRIBUTIONS AND FORAGING BEHAVIOR

Crabs, clams and fish were the kinds of prey that I was able to identify most easily, and crabs were probably the most abundant and

TABLE 1. Means, standard deviations and sample sizes for five foraging variables.

Variable	Units	Mean	SD	n	Period*
Peck rate	pecks/s	0.375	0.146	284	A, B
Stop-look rate	stoplooks/s	0.014	0.016	284	A, B
Success rate	captures/s	0.069	0.050	125	A
Efficiency	captures/peck	0.184	0.098	125	A
Speed	m/s	0.166	0.126	168	B

* A—April study period; B—August study period (for dates see text).

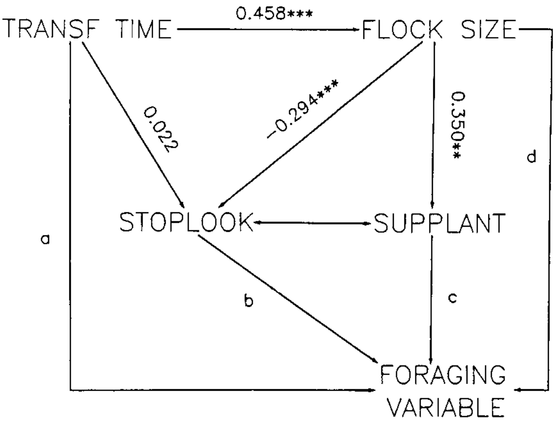

FIGURE 4. Generalized path analysis. This represents the anticipated relationships (i.e., pathways) among the behavioral variables. Arrows indicate potential directions of causality. Numbers are standardized partial regression coefficients (betas). If a beta is not significantly different from zero ($P < 0.05$), the pathway is excluded from the model. Betas for pathways a–d, for each of the four foraging variables, are presented in Table 3. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

important item in the turnstone diet. Turnstones fed on crabs more than on clams or fish (46% of the observations included predation on crabs, 13.6% on clams, and only 5.6% on fish; $G = 50.9$, $P < 0.001$). They took crabs mostly between 25 and 75 m from the beach's edge (Fig. 5), and during the low tide period (73% of observations during the low tide included crabs vs. 42% during the ebb, and 41% during the flood; $G = 8.1$, $P < 0.025$). Relative rates of predation on crabs within successive 10-m zones from the beach's edge were positively correlated with the average crab densities within those zones ($r = 0.84$, $P < 0.025$).

The turnstones' foraging behavior also appeared to be related to predation on crabs. The proportion of observations including predation on crabs (during eight 40-min periods from the time of initial flat exposure) was inversely related to the mean peck rate for the periods ($r = -0.75$, $P < 0.05$; Fig. 6). No trends were apparent for either fish or clams, but this may have been due to the small number of observations of predation on these foods. Average peck rate, success rate, and efficiency were significantly lower in observations involving crabs (Table 5), perhaps indicating the difficulties turnstones have in finding, catching, and handling such prey. The birds supplanted each other more often when crabs were involved than when they were not (14.6% of observations vs. 4.8%), but the difference was not significant ($G = 3.21$, $P < 0.10$).

Although turnstones often probed into holes in the clay, the number of holes within a 20-m zone from the beach's edge was not significantly correlated with the mean peck rate for that zone ($r = -0.24$, $P > 0.5$). However, percent tide pool coverage was significantly negatively correlated with mean peck rate ($r = -0.97$, $P < 0.05$).

TABLE 3. Path analysis results (betas or standardized partial regression coefficients) for the effects of (a) transformed time after exposure, (b) stop-look rate, (c) supplant rate, and (d) flock size on each of four foraging variables. See text and Figure 4 for explanation of path analysis.

Variable	(a)	(b)	(c)	(d)
Peck rate	0.670***	0.027	−0.094	0.034
Success rate	0.431***	0.036	−0.242**	0.057
Efficiency	0.249**	0.123	−0.220*	0.084
Speed	0.463***	0.005	—	0.023

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

DISCUSSION

TIDES, FOODS, AND FORAGING BEHAVIOR

The tidally correlated patterns in peck rate, success rate, foraging speed, and efficiency in this situation can be largely explained by the relationships of these variables to prey behavior during the tidal cycle, resource zonation, and substrate variation with distance from the beach's edge. Turnstones are opportunistic feeders (Nettleship 1973; pers. observ.), and appear to shift prey types and foraging modes as distribution of food changes (Harris 1979, this study). They tend to follow the water's edge while it is dropping quickly, presumably to take advantage of the small invertebrates and bits of carrion that are being deposited. This habit, along with the presence of easily caught invertebrates in the algal zone, probably accounts for the high peck and success rates and efficiency noted at the start and finish of flat exposure. Harris (1979) found that turnstones in Wales stayed near the water's edge, feeding on amphipods through the low tide period, and that only after the tide had turned did they gradually disperse over the flat to feed in seaweed beds.

TABLE 4. Correlation coefficients (r) between the distance of a bird to the beach's edge, the water's edge, and five variables.

Variable	Distance to beach's edge	Distance to water's edge
Flock size	−0.185	0.169
Peck rate	−0.393**	−0.476**
Stop-look rate	0.121	0.105
Efficiency	−0.310*	−0.169
Success rate	−0.434**	−0.176

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

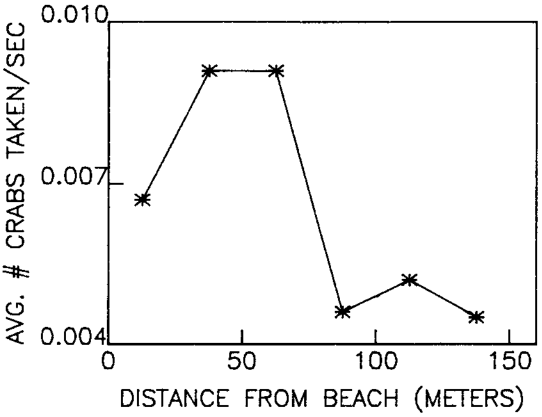

FIGURE 5. The average number of crabs taken per second by turnstones as a function of the bird's distance from the beach's edge.

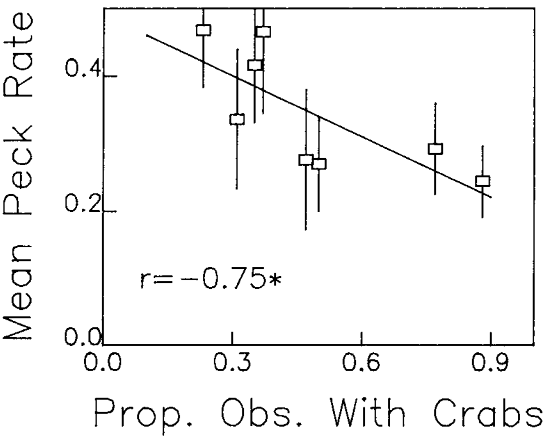

FIGURE 6. The mean peck rate of all observations during a 40-min interval versus the proportions of observations involving predation on crabs during the same period. *$P < 0.05$.

Turnstones travelled more slowly nearer the beach, and pecked at a faster rate, suggesting that prey were more plentiful. Therefore, hunger can perhaps be eliminated as a major cause of the faster peck rates. Alternatively, a hungry turnstone may be less discriminating, and by choosing prey items that might later be ignored, it could also increase its peck rate without travelling more rapidly.

Turnstones begin taking crabs as the flat becomes exposed, either because they prefer such food or because prey have become hard to find in the algal zone. Crabs, however, are relatively mobile, defensive, and highly dispersed. They probably are less frequently pecked at and caught than prey items in the algal zone. My findings (Table 5, Fig. 6) suggest that this switch to crabs is the factor most responsible for the lowering of peck and success rates associated with time after exposure and the distance from the beach's edge. Harris (1979) also found that turnstones adjusted their diet to take advantage of prey availability. In his study, the birds generally switched from amphipods (evidently the preferred prey) to littorinid snails after the tide began to return.

The changes in the substrate with distance from the beach's edge also may have influenced the foraging rates. Of the physical features examined here, only the amount of tidepool coverage correlated strongly with foraging rates. Because turnstones rarely fed in tide pools, decreasing the area available for foraging may have caused them to travel farther between pecks.

Groves (1978) found significant differences among turnstones foraging in different habitats in coastal Massachusetts. Different prey types occurred in each environment: barnacles in the rocky intertidal zone and crustaceans on the "sand and weed littered flats." The average peck rate for turnstones in the latter habitat did not differ significantly from those reported in this study ($t = 0.95$, $P > 0.40$). Success rate and efficiency, however, were both significantly lower in my study ($t = 2.61$, $P < 0.01$; $t = 6.67$, $P < 0.001$, respectively). Prey items were similar, but local differences in abundance and distribution make comparisons difficult.

FLOCKING, VIGILANCE AND AGGRESSION

The larger the flock, the less often a bird stopped and looked about (Table 2, Fig. 4). Assuming that the stop-look rate indicates the level of individual vigilance (as was used in other studies, e.g., Powell 1974, Abramson 1979, Barnard 1979, Caraco 1979, Jennings and Evans 1980, but see Krebs 1974), then lone birds were more vigilant than flocking ones. This higher level of vigilance did not affect foraging or success rates (Table 3), contrary to most of the above-mentioned studies. In support of previous work, however, I also found that flock size correlated positively with aggression (Recher and Recher 1969, Silliman et al. 1977, Burger et al. 1979, Caraco 1979). Level of aggression also correlated negatively with success rate and efficiency, even when the effects

TABLE 5. Mean peck rate, success rate and efficiency for observations with and without an incident of predation on crabs. Standard deviations in parentheses; t assesses the differences between means.

Variable	With crabs ($n = 57$)	Without crabs ($n = 68$)	t
Peck rate	0.332 (±0.116)	0.380 (±0.114)	2.29*
Success rate	0.054 (±0.033)	0.081 (±0.056)	3.07**
Efficiency	0.150 (±0.070)	0.207 (±0.109)	3.24**

* $P < 0.05$, ** $P < 0.01$.

of other variables were controlled. Hence, the benefit of foraging alone may come from the reduced chance of conflict. Many factors can affect aggression levels, and flock size could be largely a response to aggression. The two variables are interrelated yet the increased wariness required of single foragers or individuals in small groups may not counteract the advantage of avoiding aggression or deter flock breakup. Similar trade-offs have been hypothesized to exist in flocking species (Stinson 1980, Krebs and Barnard 1980), but little evidence has been provided (however, see Caraco 1979). I examined neither levels of exploitative competition nor facilitation of finding food, both of which may be additional density-dependent factors that importantly affect foraging rates.

What initiates flocking in turnstones and why do flocks later disband? Resting turnstones at the river mouth may flock for self-protection and perhaps for social facilitation. Parts of these flocks may then move together to the flat to feed, or perhaps individuals merely assemble at the earliest feeding sites to be exposed. Flocks did not disperse in relation to the widening span of the tidal flat, i.e., the distance between the water's edge and the beach's edge ($r = -0.18$, $P > 0.10$, $n = 70$), but in relation to the (transformed) time after exposure. Hence, flocks may not disband chiefly to occupy more area. Since turnstone densities on the flat appeared low (perhaps 25 individuals along 1 km of beach), spatial limitations seem unlikely.

Alternatively, a dietary switch may affect aggression levels, which in turn affect prey capture rates and flocking tendencies. Aggression in shorebirds has been related to patchy distribution of food (Recher and Recher 1969, Mallory and Schneider 1979) and increased handling time of prey (Vines 1980). Turnstones shift from small invertebrates (which are abundant, small, and easy to handle) during the ebb to crabs (which are patchily distributed, large and difficult to handle) during the low, then back to small invertebrates during the flood. Aggression rate does not appear to be related to time after exposure (Table 2). Nevertheless, flocks may persist during the ebb because aggression is low, disbanding when prey availability changes and aggression increases. On the flood, small invertebrates are again abundant, aggression lessens, and flocks re-form. I did not examine temporal variation in the probability of predation, another factor that may affect flocking behavior (as in Myers 1980).

CONCLUSIONS

My study indicates that the foraging habits of turnstones can be ultimately and strongly affected by tidal fluctuations. Tides alter food distribution and the area suitable for foraging, which in turn affect food taken, vigilance, and social behavior. The complex interrelationships discussed here suggest that tidal conditions should be noted carefully in studies of shorebird ecology or behavior.

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RECENT PUBLICATIONS

Avian Biology. Volume VI.—Edited by Donald S. Farner, James R. King, and Kenneth C. Parkes. 1982. Academic Press, New York. 490 p. This volume appears seven years after its predecessor (noticed in Condor 77:521), in a move to treat some of the important subjects not previously covered and to update material that has significantly advanced since earlier volumes. It contains chapters on avian mating systems (Lewis W. Oring), avian migration systems (Sidney A. Gauthreaux, Jr.) social organization in the nonreproductive season (H. Ronald Pulliam and George C. Millikan), the uropygial gland (Jürgen Jacob and Vincent Ziswiler), stomach oils [of procellariiforms] (Jürgen Jacob), the glycogen body (Louis D. De Gennaro), domestication in birds (Roland Sossinka) and respiration and the control of breathing (Peter Scheid). In preparing these reviews, the authors have not merely compiled and organized, but have also synthesized their information so as to develop new insights. Authoritative and detailed, these articles will be benchmarks for their fields. Illustrated; lists of references at the end of each chapter; indexes.

Avian incubation: egg temperature, nest humidity, and behavioral thermoregulation in a hot environment.—Gilbert S. Grant. 1982. Ornithological Monographs No. 30, American Ornithologists' Union, Washington, DC. Paper cover. 75 p. $9.00 prepaid ($7.00 to AOU members). Source: Assistant to the Treasurer of the AOU, Glen E. Woolfenden, Department of Biology, University of South Florida, Tampa, FL. 33620. Lesser Nighthawks and several charadriiform species nest in the area of the Salton Sea in southeastern California. The nesting environment of this artificial saline lake, below sea level, is extremely arid, hot, and subjected to intense sunlight. In order to learn how birds cope with these harsh conditions while protecting their eggs and young, Grant observed and experimented with eight species. Comparing Salton Sea birds with those on the coast, he examined the timing of breeding and the humidity and thermal microenvironment of the nest-egg complex. In addition, he investigated the birds' thermoregulatory behavior, paying particular attention to belly-soaking and its consequences. This monograph is an excellent continuation of the long series of studies at UCLA of the ways by which nesting birds adapt to desert environments. Graphs, photographs, and references.