MAINTENANCE AND ANTI-INSECT BEHAVIOR OF SIX SPECIES OF CICONIIFORM BIRDS IN SOUTH FLORIDA

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Host behavior is important in determining the success with which mosquitoes obtain blood meals from ciconiiform birds (Edman and Kale 1971). Detailed observations of anti-mosquito behavior of captive birds (Webber and Edman 1972), as well as the effects of mosquito density on this anti-insect behavior (Edman et al. 1972) have been made. The effects of age and individual variation in behavior on the feeding success of mosquitoes also have been investigated (Kale et al. 1972). These studies indicate that the frequency and type of defense correspond to the ability of the host individual to reject annoying insects. The present study examines species-specific variation in frequency and persistence of maintenance behavior and frequency of anti-insect behavior among both captive and wild populations of birds. It also estimates the percentage of time captive birds spend resting, feeding, and in body maintenance. An activity index, calculated for each species, serves as a comparative guide for estimating the energy expended in body maintenance and anti-insect behavior.

METHODS

Wild birds were observed from a blind located on Riomar Island, a 2.8–ha mangrove spoil island in the Indian River, Vero Beach, Florida. Maxwell and Kale (1974) described the study site and investigated the breeding biology of the herons on this Island. Captive adult birds used in the observations were obtained initially as fully-fledged young, and all were maintained in 3.0 × 3.7 m outdoor aviaries constructed of chicken wire (2.5 × 7.5 cm mesh) and located on the grounds of the Florida Medical Entomology Laboratory near Vero Beach. The birds in the aviaries were exposed to natural populations of biting insects; all had a previous but similar history of experimental exposure to such insects. The insect populations at the laboratory were sampled nightly with a New Jersey light trap.

The activity of each species of heron on Riomar Island was recorded for 10 h between 08:00 and 12:00 over a two week period during April and May, 1973. No afternoon and evening observations were made due to time limitations and the difficulty of viewing birds at dusk. Birds were chosen at random and data recorded until the subject disappeared from view. The activity of captive individuals (N = 2 species, except Black-crowned Night Heron, *Nycticorax nycticorax*, N = 1) was recorded at one-h intervals for a total of 28 h for each species during January, February and April, 1973 between 08:00–12:00, 16:00–18:00 and 18:30–19:30 (¼ h pre-sunset to ¾ h post-sunset). The frequency (no. activities/h) of each observed maintenance and anti-insect activity was then established for all birds studied. The persistence (min/h) of all maintenance activities was also determined.

Heron maintenance and anti-insect behaviors were identified from descriptions in Simmons (1957), Meyerriecks (1960), Maxwell and Putnam (1968), McAllister and Maxwell (1971), and Webber and Edman (1972).

RESULTS AND DISCUSSION

ANTI-INSECT BEHAVIOR

The captive Little Blue Heron (*Florida caerulea*), Louisiana Heron (*Hydranassa tricolor*), White Ibis (*Eudocimus albus*), and Cattle Egret (*Bubulcus ibis*) with, respectively, an average of 40.7, 39.8, 31.7, and 29.0 anti-insect (15 different) movements/h repelled insects aggressively. The Snowy Egret (*Egretta thula* and Black-crowned Night Heron, exhibiting 18.4 and 16.9 anti-insect movements/h, respectively, were less aggressive.

The local populations of biting insects consisted of low numbers of 25 species (9 genera) of mosquitoes and 9 species (1 genus) of sandflies (*Culicoides* spp.) according to samples captured in a light trap on the days the anti-insect behaviors were recorded. Most mosquitoes are crepuscular or nocturnal (see Bidlingmayer 1967 for references) and spend the day resting on the ground or in vegetation close to the ground. Usually, mosquitoes that take a blood meal during the day are those nocturnal or crespuscular species that have been disturbed from their resting places by a host animal (Kale 1968). Mosquitoes seldom fly above the tree canopy (for discussion of mosquito behavior see Bates 1949, Horsfall 1955, Laarman 1959, Kalmus and Hocking 1960, Clements 1963). Thus mosquitoes would be present in the heron nesting area on Riomar Island as well as in the aviaries during the period just after sunset. Moderate mosquito activity (continuous biting attempts all the time on the authors by 1–5 mosquitoes in vegetated areas) was noted on Riomar Island during the morning.

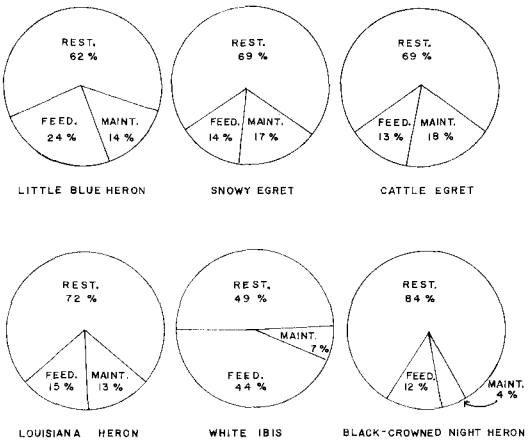

FIGURE 1. Percentage of time spent resting, feeding, and preening by individuals of six species of captive herons.

Biting insects must discriminate between potential hosts and other nearby objects after they have been stimulated to fly. Wright (1975) has shown that mosquitoes are attracted to warm blooded hosts by convection currents which emanate from the potential hosts' skin. Mosquitoes fly at random until exposed to these currents, which guide them to the host. In a mixed heron colony, several hosts may be available simultaneously. The response of a host to the insect may be the factor determining the insects' choice of hosts. An active host may receive significantly fewer bites than an inactive host and thus be more likely to avoid infected vectors.

Webber and Edman (1972) worked with the same captive individuals used in this study but kept them in smaller cages (2.4 m) with a higher mosquito density (300/night) and studied them up to 90 min post-sunset. They reported a frequency of anti-insect movements eight times greater than those in this study. The difference was due to the difference in mosquito density and to a greater tolerance of the birds to insect pests when exposed to low numbers, as in this study. Except for the Snowy Egret, the ranking of the frequency of defensive movements displayed by the 5 species observed was nearly the same between the two studies. The Snowy Egret was almost as inactive as the Black-crowned Night Heron in this study, but was third most active in the earlier study. The difference noted could be due to many factors. Snowy Egrets may be more tolerant of low numbers of biting insects than other species. Also, if pest insect populations increase past 45 min after sunset, when our observations terminated, we would not have recorded the increased anti-insect activity noted in the earlier study.

The results obtained in the two studies support our original hypothesis that birds exposed to artificially high levels of mosquitoes and to natural populations of biting insects will react similarly. This confirmation makes it possible to investigate with greater confidence the heron-mosquito relationship under less time-consuming laboratory conditions.

MAINTENANCE BEHAVIOR

The captive Snowy Egrets, Louisiana Herons, and Little Blue Herons all averaged approximately 54 maintenance behavior movements/h, while 36/h were recorded for the Cattle Egret and White Ibis. The Black-crowned Night Heron was even less active with 24/h. These results represent the mean from 28 h of observation.

During the same observation periods, the Cattle Egret, Snowy Egret, Little Blue Heron, and Louisiana Heron spent an average of 14.3 to 19.7 min/h in maintenance activities. The White Ibis and the Black-crowned Night Heron devoted 8.5 and 5.3 min/h, respectively.

The percentage of time spent resting (sitting, sleeping), feeding (foraging on ground), and preening was similar for the captive Little Blue Heron, Snowy Egret, Cattle Egret, and Louisiana Heron (fig. 1). The captive White Ibis spent 25% more time than any other species foraging and 20% less time resting. The Black-crowned Night Heron spent the greatest proportion of time resting and the least of all species preening. The percentage of time devoted to preening the major body areas of the six species of captive ciconiiforms during 28 h of observation is summarized in table 1.

COMPARISON OF MAINTENANCE AND ANTI-INSECT BEHAVIOR

A comparison of the captive herons' frequency of maintenance with frequency of anti-insect behavior ($\bar{x}$ no. movements/h) showed that 5 of the 6 species were similarly ranked. Although maintenance activity occurred at greater frequency than anti-insect activity, the herons did maintain their approximate relative positions in ranking. The Snowy Egret was the exception; it was the most active species in maintenance behavior but next to the least active in anti-insect behavior.

A comparison of the maintenance and anti-insect behavior of captive herons with similar behavior in wild herons (table 2) indicates that these behaviors did not differ signifi-

TABLE 1. Percentage of time devoted to preening in each major body area by six species of ciconiiforms[a].

Region	Little Blue Heron		Louisiana Heron		Snowy Egret		Cattle Egret		White Ibis		Black-crowned Night Heron			
	Time[b] (min)	%	Time (min)	%	Time (min)	%	Time (min)	%	Time (min)	%	Time (min)	%	Total (min)	Mean %
Under wing-sides	62	26	66	30	121	43	139	47	16	13	14	21	418	30
Breast-belly	48	21	33	15	42	15	30	10	33	27	17	25	203	19
Upper wing	29	12	30	13	32	13	34	11	30	25	5	8	166	14
Neck	31	13	40	18	18	6	32	11	10	8	11	16	142	12
Head	40	17	11	5	25	9	211	8	6	5	8	12	114	9
Back	18	8	32	14	27	9	15	5	14	12	6	9	112	9
Primaries	5	2	10	4	11	4	21	7	6	5	4	6	57	5
Tail	2	1	2	1	3	1	2	1	6	5	2	3	17	2
Total Min	235		224		285		484		121		67			

[a] Two individuals of each species except one Black-crowned Night Heron.
[b] Min recorded during 28 h of observation/species.

cantly between the two groups in each of the ciconiiform species. The birds' behavior also did not vary according to nest height, distance from shore, or location of the nesting colony, all of which could affect the juxtaposition of biting insects and their avian hosts. Exceptions were that maintenance behavior persists significantly longer in captive Cattle Egrets and White Ibis than in the wild ones; also, wild Black-crowned Night Herons exhibit maintenance behavior significantly more frequently than captive birds.

ACTIVITY INDEX

Earlier studies have tried to link specific behavior patterns with a bird's defense against biting insects. Observations of King Eiders (*Somateria spectabilis*; Corbet and Downe 1966) and heron nestlings (Stamm 1958) provided the first evidence that a host's response played an important role in the success of blood-feeding by mosquitoes and provided defense against insects. Studies cited in the introduction of this paper confirmed these observations. In order to quantify this concept, we calculated an activity index (r) that gives a comparative measure of both maintenance and anti-insect activities (table 3). In the following equation (R. Wernick, pers. comm.), r denotes the activity index of the i^{th} species and is given by:

$$r_i = \sum_{j=1}^{\infty} M_{ij}/N_j$$

TABLE 2. Comparison of maintenance and anti-insect behavior in captive and wild birds at Vero Beach, Florida.[1]

	Little Blue Heron		Louisiana Heron		Snowy Egret		Cattle Egret		White Ibis		Black-crowned Night Heron	
	a[2]	b[2]	a	b	a	b	a	b	a	b	a	b
Maintenance (no. activities/h)												
Captive[3]	53.8	29.7	54.0	39.2	55.7	38.3	36.9	19.8	36.5	10.4	24.5	2.3*
Wild[4]		38.5		46.8		37.1		26.5		9.3		7.5*
Anti-insect (no. activities/h)												
Captive	40.7	8.4	39.8	11.8	18.4	10.2	29.0	5.5	31.7	3.2	16.9	2.2
Wild		7.3		7.2		4.5		6.2		4.2		5.9
Total frequency of both		83.9		105.0		90.1		58.0		27.1		15.9
Maintenance (min/h)												
Captive	16.0	11.0	14.3	12.5	18.7	15.7	19.7	15.5*	8.5	4.7*	5.3	1.0
Wild		8.3		5.5		5.9		3.2*		1.2*		1.3
Total		19.3		18.0		21.6		18.7		5.9		2.3

[1] * Indicates that means are significantly different, $P \leq 0.05$, by "t" test.
[2] a = birds observed between 08:00–12:00, 16:00–18:00, 18:30–19:30; b = birds observed between 08:00–12:00 only.
[3] Two birds of each species (only one Black-crowned Night Heron) were observed for 28 h (a) or 16 h (b).
[4] Fifty Snowy Egrets observed for 11.7 h; 58 Louisiana Herons for 10.9 h; 35 Cattle Egrets for 10.6 h; 35 Little Blue Herons for 10.9 h; 26 White Ibis for 10.7 h and 18 Black-crowned Night Herons for 10.1 h.

TABLE 3. Activity Index for six species of captive herons.

Species	i	Activity - j: Maint. freq. (no./h)	Anti-insect freq. (no./h)	Maint. persistence (min/h)	Activity Index
Little Blue Heron	1	54	41	16	0.63[a]
Louisiana Heron	2	54	40	14	0.61
Snowy Egret	3	56	18	19	0.54
Cattle Egret	4	37	29	20	0.54
White Ibis	5	37	32	9	0.43
Black-crowned Night Heron	6	25	17	5	0.26
	N_j	263	177	83	

[a] Example: 54/263 + 41/177 + 16/83 = 0.63, etc.

where M_{ij} denotes the j^{th} activity of the i^{th} species ($j = 1, 2, 3$);

the first activity is maintenance frequency (no./h);

the second activity is anti-insect frequency (no./h);

the third activity is maintenance persistence (min/h);

and $N_j = \sum_{i=1}^{6} M_{ij}$ = sum of all species of the j^{th} activity.

The Little Blue Heron and Louisiana Heron ranked highest and also displayed the most frequent anti-insect activity (table 3). The Snowy Egret and Cattle Egret ranked next, then the White Ibis. The Black-crowned Night Heron ranked lowest of the six species and also had the lowest frequency of anti-insect behavior.

The species specific differences in activity are difficult to explain. Those species with similar activity indices are grouped together taxonomically in the A.O.U. Checklist (1957). Closely related species exposed to the same conditions would be expected to behave similarly. This appears to be verified by the activity index and by the percentage of time spent in maintenance activities (fig. 1). The greater maintenance activity for four species corresponds to the same four more active species as determined by the activity index. The same correlation is true for the least active species.

The population of the more active species was larger than that of the least active species in the heronry studied. Active species may be more successful at food gathering, nest building, predator and territorial defense as well as insect pest defense, as compared with a less active species. Perhaps a species activity is related to its ability to be successful in its habitat and niche.

Ranking of the activity index and the bird's anti-insect or maintenance frequency will not always be similar. However, recognizing the difficulty in obtaining data from wild or outside caged birds during periods of low light when biting insects are most active, it seems appropriate to include maintenance behavior data as a measure of a bird's activity. We propose the activity index because it is based upon a wider range of the birds' daily activity. A ranking of avian species according to their activity level is a measure of effort expended toward feather care and rejection of annoying or potentially harmful insects. Feathers in preened areas of the body maintain their integrity and thus reduce the ability of biting insects to reach through them to skin areas. Also, active birds may be a more attractive though less acceptable target for biting insects due to the bird's continual motion. Clearly, the birds' behavior can be used to determine which species are active, and the activity index may allow investigators to rank ciconiiforms according to their probability of being bitten by an insect vector.

SUMMARY

The frequency and persistence of maintenance and frequency of anti-insect movements of the Little Blue Heron, Cattle Egret, Snowy Egret, Louisiana Heron, Black-crowned Night Heron and White Ibis were recorded in 1973 near Vero Beach, Florida. Captive individuals of each species were studied for 28 h and wild ones for 10 h. The six species differed considerably in activity and an index (r) was calculated to provide an indication of the relative ability of each species to maintain feather integrity and reject annoying insects. The Little Blue Heron and Louisiana Heron ranked highest with activity indices of 0.63 and 0.61, respectively. These two species also displayed the most frequent anti-insect activity. The White Ibis (0.43) and the Black-crowned Night Heron (0.26) ranked lowest of the six species.

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LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1957. Checklist of North American birds. Fifth ed. Am. Ornithol. Union, Baltimore.

BATES, M. 1949. The natural history of mosquitoes. Macmillan Co., New York.

BIDLINGMAYER, W. L. 1967. A comparison of trapping methods for adult mosquitoes: species response and environmental influence. J. Med. Entomol. 4:200–220.

CLEMENTS, A. N. 1963. The physiology of mosquitoes. Macmillan Co., New York.

CORBET, P. S., AND A. E. R. DOWNE. 1966. Natural hosts of mosquitoes in northern Ellesmere Island. Arctic. 19:153–61.

EDMAN, J. D., AND H. W. KALE, II. 1971. Host behavior: Its influence on the feeding success of mosquitoes. Ann. Entomol. Soc. Am. 64:513–516.

EDMAN, J. D., WEBBER, L. A., AND H. W. KALE, II. 1972. Effect of mosquito density on the interrelationship of host behavior and mosquito feeding success. Am. J. Trop. Med. Hyg. 21: 487–91.

HORSFALL, W. R. 1955. Mosquitoes: Their bionomics and relation to disease. Ronald Press, New York.

KALE, H. W., II. 1968. The relationship of purple martins to mosquito control. Auk 85:654–661.

KALE, H. W., II, EDMAN, J. D., AND L. A. WEBBER. 1972. Effect of behavior and age of individual ciconiiform birds on mosquito feeding success. Mosq. News 32:343–50.

KALMUS, H., AND B. HOCKING. 1960. Behavior of *Aedes* mosquitoes in relation to blood-feeding and repellents. Entomol. Exp. Appl. 3:1–26.

LAARMAN, J. J. 1959. Host seeking behavior of malaria mosquitoes. Proc. 15th Int. Cong. Zool. (1958):648–649.

MAXWELL, G. R., II AND L. S. PUTNAM. 1968. The maintenance behavior of the Black-crowned Night Heron. Wilson Bull. 80:467–78.

MAXWELL, G. R., II, AND H. W. KALE, II. 1974. Population estimate of breeding birds on a spoil island in the Indian River, Indian River County, Florida. Fla. Field Nat. 2:32–39.

MCALLISTER, J. R., AND G. R. MAXWELL, II. 1971. Locomotion, maintenance and feeding behavior of the Great Blue Heron in northern New York. Kingbird 21:183–203.

MEYERRIECKS, A. J. 1960. Comparative breeding behavior of four species of North American herons. Nuttall Ornithol. Club Publ. No. 2.

SIMMONS, K. E. L. 1957. The taxonomic significance of the head scratching methods in birds. Ibis 99:178–81.

STAMM, D. D. 1958. Studies on the ecology of equine encephalomyelitis. Am. J. Public Health 48:328–35.

WEBBER, L. A., AND J. D. EDMAN. 1972. Anti-mosquito behavior of ciconiiform birds. Anim. Behav. 20:228–32.

WRIGHT, R. H. 1975. Why mosquito repellents repel. Sci. Am. 233:104–111.

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