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Received 16 August 1994, accepted 27 January 1995.

The Auk 112(4):1073-1077, 1995

Sunning by Black Noddies (*Anous minutus*) May Kill Chewing Lice (*Quadraceps hopkinsi*)

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Birds are hosts for ectoparasites such as lice (Clayton et al. 1992), mites (Rothschild and Clay 1952, Møller 1993, Clayton and Tompkins 1994), bugs (Brown and Brown 1986, Møller et al. 1994), ticks (Duffy 1983), flies (Shields and Crook 1987, Whitworth and Bennett 1992), and fleas (Oppliger et al. 1994). The possible adverse effects of these ectoparasites are well documented. Infestation can cause a bird to attract fewer mates (Clayton 1990, Johnson and Boyce 1991), increases nest desertion (Moss and Camin 1970, Duffy 1983, Oppliger et al. 1994), lowers hatching success (Clayton and Tompkins 1994, Oppliger et al. 1994), and reduces clutch size (Møller 1993), as well as reduces the survival of nestlings (Møller 1987, Shields and Crook 1987, Richner et al. 1993), fledglings (Clayton and Tompkins 1994), and adults (Borgia and Collis 1989, Clayton 1989). Because ectoparasitic infestation may decrease fitness, avian behavior that minimizes infestation typically has a selective advantage (Møller et al. 1990, Hart in press).

Avian sunning may be a strategy for controlling ectoparasite populations (Dathe 1964, Fry 1972, Horsfall 1984, Simmons 1986, Blem and Blem 1992). De-

spite decades of interest in this behavior, however, no one has tested the hypothesis that sunning adversely affects ectoparasites (Blem and Blem 1993). We demonstrate experimentally that conditions experienced during normal sunning are lethal to chewing lice, which is consistent with the ectoparasite-control explanation of sunning.

Methods.—We studied the sunning behavior of Black Noddies (*Anous minutus*) at the Heron Island Research Station (HIRS; 23°26'S, 151°55'E) on the Great Barrier Reef of Australia. At this location, Black Noddies sun gregariously on bare sand and on the rooftops of HIRS buildings.

From 30 October through 2 November 1991, we investigated the relationship between sunning activity and temperatures at the sunning site. The typical sunning posture used by Black Noddies is a standing position with tail fanned and one wing extended (Fig. 1). To estimate the thermal environment experienced by a Black Noddy wing during sunning, we mounted thermometers about 6 cm above each of three sunning sites. The thermometers were exposed to the sun and mounted so they could be read from a distance with a spotting scope. The number of sunning noddies and the temperature at each site were noted periodically over two days. Any noddy that alighted on the exposed sunning sites was considered to be sunning. The longest time we observed any individual sunning

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Fig. 1. Sunning posture of an individual Black Noddy.

was 16 min, and observations were at least 30 min apart. Thus, observations were considered independent.

On 24 and 29 January 1994 we tested the hypothesis that wing temperatures achieved in sunning are lethal to feather lice. We constructed two identical model wings using Black Noddy primary feathers. Using thermal glue, we attached five 6- to 11-cm distal portions of separate primaries to white paper at their proximal end, resulting in a 5×11 cm model that approximated the size and shape of an extended wing tip, a region where we commonly found and collected lice on live birds.

At 2400 EST, the evening prior to the experimental trials, we collected *Quadriceps hopkinsi*, a louse of the suborder Ischnocera, from the wing feathers of hand-captured, live Black Noddies. These lice were stored in 3-ml plastic vials with a fragment of Black Noddy secondary feather.

We started each of 12 trials by placing one live louse on each model wing. A coin toss determined which of the two models would be placed in the sun and which in the shade. Trials were commonly conducted while live noddies basked at nearby sites. After a 10-min exposure, each louse was removed from the model and placed on a high-contrast medium. A louse that by unaided visual inspection was not moving and did not move in response to touch was considered

dead. We used each louse for one trial only. Trials were conducted between 1430 to 1800, which were sunny periods. We measured the temperature of the feathers of live birds and the model wings during sunning from a distance of 2.0 to 2.3 m with an infrared thermometer (model R2PHRSC Raynger, Raytek Inc., Santa Cruz, California), which can measure the temperature of a 2.5-cm diameter spot at 2.3 m.

Results.—The temperature at the sunning site and the number of birds sunning were positively associated (Spearman's rank correlation, $r_s = 0.483$, $df = 55$, $P < 0.001$). Black Noddies were not observed sunning when site temperatures were less than 29°C. The maximum number of noddies observed sunning occurred at a site temperature of 36°C (Fig. 2). Overall, temperatures at which birds sunned were greater than the temperatures at which no birds were observed sunning (Mann-Whitney, $U = 106$, $n = 56$, $P < 0.001$).

More lice died in the sun (6 of 12) than the shade (0 of 12; Fisher's exact test, $P = 0.015$). The sun trials that killed lice had higher temperatures ($68.7^\circ \pm SE$ of 2.1° , $n = 6$) than the sun trials that did not kill lice ($50.0^\circ \pm 5.8^\circ$, $n = 6$; Mann-Whitney, $U = 1.5$, $n = 12$, $P < 0.01$; Table 1). The maximum temperature of wings of live birds sunning at 1300 ($63.4^\circ \pm 0.83^\circ$, $n = 10$) did not differ from the maximum temperature of model wings exposed to the sun ($59.3^\circ \pm 4.1^\circ$, $n = 12$; Mann-Whitney, $U = 53.5$, $n = 22$, $P > 0.05$).

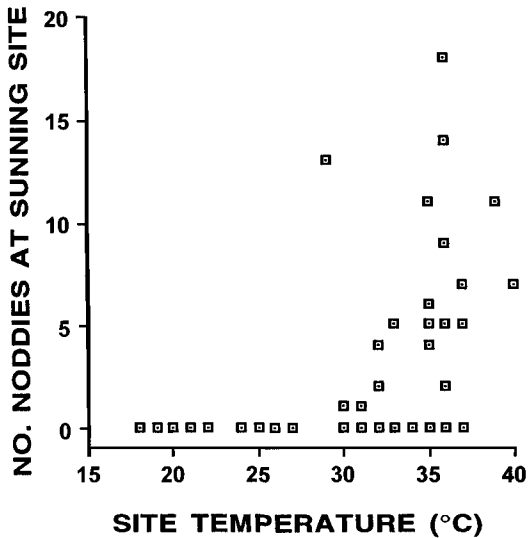


Fig. 2. Number of Black Noddies observed at different temperatures of the sunning sites.

Discussion.—This is the first study to show that sunning is sufficient to kill chewing lice, supporting the ectoparasite-control hypothesis of sunning behavior. Ischnoceran lice are sensitive to temperature and require between 30° and 40°C for maximum survival (Martin 1934, Matthyse 1944, Arora and Chopra 1957, Williams 1970, Nelson and Murray 1971). Temperatures only slightly above 40°C can be lethal to both eggs (Nelson and Murray 1971) and hatched lice (Williams 1970).

Elevated temperature probably is the lethal component of sunning. Lice died more often in the sun trials that reached higher temperatures (Table 1). Other factors, however, such as greater ultraviolet exposure, also may be correlated with elevated temperature. Further research is necessary to determine the exact cause of deaths.

In addition to killing adult lice directly, sunning may control louse populations indirectly by making lice more vulnerable to preening. Some feather lice, including *Q. hopkinsi*, are morphologically adapted to fit between the barbs of feathers, where they can avoid the bill of a preening bird (Rothschild and Clay 1952, Clayton 1991). Simmons (1986) suggested that the heat from sunning might cause these lice to leave their hiding places and become vulnerable to preening that frequently accompanies or follows sunning (Blem and Blem 1993). We observed both preening (in live noddies) and increased louse movement (on model wings) during the elevated temperatures characteristic of sunning. To what degree the slow-moving *Q. hopkinsi* or more motile ectoparasites of the Black Noddy are able to reduce thermal mortality by fleeing to cooler microclimates remains to be investigated.

Sunning may induce heat stress in Black Noddies

TABLE 1. Maximum feather temperature (°C) reached by wing model and resultant condition of associated louse in each of 12 sun-exposure treatments.

Maximum temperature	Louse condition
29°	Live
36°	Live
55°	Live
57°	Live
58°	Live
60°	Dead
65°	Live
65°	Dead
71°	Dead
72°	Dead
72°	Dead
72°	Dead

and other tropical birds (Cullen and Ashmole 1963, Simmons 1986). There may be fitness benefits accrued by controlling feather-lice populations, however, that more than compensate for this cost. Lice can impair the survival of their hosts (Clayton 1989) by increasing energetic costs (Booth et al. 1993) or transmitting endoparasites (Seegar et al. 1976, Marshall 1981). Furthermore, since louse-infested birds may be less attractive as mates (Borgia and Collis 1989, Clayton 1990, Johnson and Boyce 1991), infestation may reduce reproductive output. If sunning controls chewing-lice populations, it may confer fitness benefits.

Blem and Blem (1993) reduced both mite and louse populations on swallows with a pesticide treatment. Subsequently, treated birds sunned less often than controls. The results of their study, coupled with ours, offer considerable support for the ectoparasite-control explanation of sunning in some birds.

All birds for which the ectoparasite-control hypothesis is invoked—bee-eaters (Fry 1984), swallows (Blem and Blem 1993), and seabirds (Simmons 1986)—are colonial breeders or hole-nesting species. Ectoparasites are particularly troublesome in such species (Brown and Brown 1986, Shields and Crook 1987, Loye and Carroll 1991, Poulin 1991). Sunning also has been observed in colonial, hole-nesting mammals (Arnold and Lichtenstein 1993).

A variety of other hypotheses has been proposed to explain the widespread sunning of birds (Simmons 1986), including thermoregulation (Simmons 1986) and drying of wet feathers (Blem and Blem 1993). Many birds sun in cool temperatures to warm themselves and conserve energy by reducing metabolic expenditure (Morton 1967, Ohmart and Lasiewski 1971, Simmons 1986). This cannot explain the behavior of the Black Noddy and other tropical birds, since these birds sun in tropical heat to the point of possible hyperthermic stress even when shade is available (Cullen and Ashmole 1963, Simmons 1986). We ob-

served more noddies sunning at higher than lower temperatures, and some of these individuals showed signs of heat stress (e.g. panting). Furthermore, at no time did the feathers of sunning noddies appear wet, suggesting that feather drying was not a satisfactory explanation.

In summary, Black Noddy sunning is probably not thermoregulatory. Rather, it heats feathers to temperatures that kill chewing lice. Thus, sunning may help to control ectoparasite populations on live birds, providing yet another example of antiectoparasite behavior. Given the great costs of parasites and the numerous examples of limiting behaviors in the literature, future researchers would be wise to consider unexplained behavior and life-history traits in light of the selective pressures of parasites.

Acknowledgments.—We thank J. Greene for suggesting the infrared thermometer and B. Marcus for enthusiastically encouraging B.R.M. to pursue this investigation beyond a class project. The Heron Island Research Station and Rob Elvish of Field Biosearch Party Ltd. greatly aided fieldwork. C. Beittel, B. R. Chapman, D. Clayton, F. R. Gehlbach, J. E. Loye, M. McKone, R. S. Moyer, K. E. Moyer, T. W. Sherry, and A. M. Strong gave valuable comments on the manuscript. We also thank R. Price for louse identification. This project was partially funded by a grant from the Carleton College Dean's Discretionary Fund.

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Received 12 May 1995, accepted 14 July 1995.

The Auk 112(4):1077-1079, 1995

Within-pair Copulations: Are Female Tree Swallows Feathering Their Own Nests?

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A variety of hypotheses has been proposed to explain why socially monogamous birds copulate repeatedly with their mates when only a single copulation is necessary to fertilize an entire clutch (Birkhead and Møller 1992, Petrie 1992, Hunter et al. 1993). Petrie (1992) hypothesized that a female should copulate frequently with her mate so as to reduce her mate's involvement in extrapair copulations. By reducing her mate's involvement in extrapair copulations, a female may: (1) avoid the transmission of parasites and sexually transmitted diseases (Hamilton 1990); (2) may avoid sperm depletion by her mate; and (3) may monopolize her mate's paternal care (Petrie 1992).

Whittingham et al. (1994) tested Petrie's (1992) hypothesis on Tree Swallows (*Tachycineta bicolor*). Their results did not support part of Petrie's hypothesis. Whittingham et al. (1994:table I) found that within-pair copulation rates were higher in pairs where a female's mate gained extrapair copulations than in pairs where a female's mate was not involved in ex-

trapair copulations. They concluded that female Tree Swallows copulated frequently with their pair-bond mates so as to assure the fertilization of clutches by mates, especially if the mate was of high quality. In drawing this conclusion, they rejected the hypothesis that, by copulating frequently with their mates, females might gain material benefits such as mate feeding, assistance in nest building, or increased paternal care (Birkhead and Møller 1992, Petrie 1992, Hunter et al. 1993). However, Whittingham et al.'s rejection of the material-benefits hypothesis is premature because they failed to consider an important aspect of Tree Swallow natural history.

It is true that male Tree Swallows do not feed their mates (Robertson et al. 1992), and there appears to be no relationship between within-pair copulation rate and male parental care during the nestling period (Lifjeld et al. 1993, Whittingham et al. 1993). However, Whittingham et al.'s (1994) statement that male Tree Swallows do not assist their mates in nest building is incorrect. Tree Swallows build nests made of a