

up to 3 h (Fig. 1d). The simplicity and flexibility of this technique, combined with the high quality of its results, are singular advantages, and much needed in developing avian cytogenetic studies.

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LITERATURE CITED

- DE BOER, L. E. M. 1980. Do the chromosomes of the kiwi provide evidence for a monophyletic origin of the ratites? *Science* 287: 84-85.
- , & R. H. BELTERMAN. 1980. The somatic chromosomes of three parrots: the Kea (*Nestor notabilis*), the Yellow-headed Parrot (*Amazona ochrocephala*) and the Grey Parrot (*Psittacus erithacus*). *Acta Zool. Pathol. Antverpiensia* 75: 9-18.
- JENSEN, R. A. C. 1975. Application of a simple chromosome technique in field studies. *Emu* 74 (Suppl.): 321.
- LU, M. R. 1969. A widely applicable technique for direct processing of bone marrow for chromosomes of vertebrates. *Stain Tech.* 44: 155-158.
- SHIELDS, G. F. 1983. Bird chromosomes. Pp.189-209 in *Current ornithology*, vol. 1 (R. F. Johnston, Ed.). New York, Plenum Publ. Corp.
- SHOFFNER, R. N., A. KRISHAN, G. J. HAIDEN, R. K. BAMMI, & J. S. OTIS. 1967. Avian chromosome methodology. *Poultry Sci.* 46: 333-344.
- STOCK, A. D., & T. O. BUNCH. 1982. The evolutionary implications of chromosome banding pattern homologies in the bird order Galliformes. *Cytogenet. Cell Genet.* 34: 136-148.

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The Effect of Allopreening on Tick Burdens of Molting Eudyptid Penguins

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Formerly, there was a tendency to neglect the effect of ectoparasites on social birds. It now is being realized that such parasites may precipitate colony desertion and so have powerful short-term effects on colonial seabirds (Feare 1976; King et al. 1977a, b; Duffy 1983), may influence nesting behavior (Houston 1979), and may maintain variability in populations subject to sexual selection (Hamilton and Zuk 1982).

Allopreening, the behavior whereby one bird preens another, is one means by which ectoparasite burdens could be reduced. Goodwin (1983) considered the function of allopreening to be the removal of ectoparasites but provided no substantiation. Other authors either implicitly (Welty 1982) or explicitly (Harrison 1965) doubted that allopreening was of value for plumage maintenance, and considered the behavior primarily served sexual or social purposes (Simmons 1967, Gaston 1977). Similar uncertainty surrounds the role of allogrooming by mammals (Bell and Clifford 1964, Sparks 1967, Jolly 1972, Broom 1981).

The degree of uncertainty surrounding the function of avian allopreening is due, in large part, to the lack of any demonstration that allopreening actually reduces the ectoparasite load of wild birds. Ticks are conspicuous ectoparasites of penguins. I compared parasite loads of paired penguins that are allopreened and unpaired penguins that are not, to show that allopreening does reduce the parasite load.

I studied two colonial penguin species, the Maca-

roni (*Eudyptes chrysolophus*) and the Rockhopper (*E. chrysocome*), that breed on Marion Island (46°53'S, 37°52'E). The Macaroni Penguin colony studied was at Kildalkey, a large expanse of stony ground holding about 195,000 pairs (FitzPatrick Inst. unpubl. data). Rockhopper Penguins were studied in the vicinity of the island's meteorological station, where the birds nest in small colonies (ca. 100 pairs) among boulders a few meters above high tide. Both areas have numerous moist cracks and rocky crevices to which the ticks (*Ixodes uriae* White) can return after feeding on their penguin hosts.

Penguins were first caught in mid-February 1984 when the colonies contained adults in seagoing plumage, well-grown chicks, and molting birds. Some molting birds were immature, as judged by their short, drab head plumes. All birds were caught by hand and examined thoroughly, and any ticks discovered were counted. The ticks were mostly adult females and nymphs.

Further counting was done at the end of March (Macaroni Penguin) or in mid-April (Rockhopper Penguin) at a time when all birds were molting and when it was easy to see which birds were single and which were paired. Paired birds stood very close, if not in actual contact, allopreened each other, and acted in concert to display aggressively to intruding penguins. It was possible, therefore, to sample both single and paired birds. The selection ensured that the birds in the two groups were at the same stage of molt, because this influences the tick load (Murray and Vestjens 1967, pers. obs.). Control for location was achieved by catching paired and single birds within a few meters of each other. The ticks on the head and neck of the penguins caught then were

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counted. Ticks could be found only on the head and neck of the adults.

On 16 April 1984 a Rockhopper colony was watched for 4 1-h sessions starting at 0655, 0856, 1215, and 1447 GMT. In each session 4 or 5 pairs and 5 single Rockhopper Penguins were watched. Because the birds were unmarked, I could not be certain exactly how many birds were watched in the course of the day; judging by the birds' locations, the total was probably 25–30. Each preening or allopreening bout was timed. Allopreening was directed exclusively at the head and neck. This concentration on areas that are difficult or impossible for a bird to reach by itself is normal (Harrison 1965, Hudson 1979). No allopreening was directed toward neighbors (cf. Birkhead 1978). Each instance of head scratching (using a foot) during a preening bout was recorded.

In mid-February all of 5 molting Rockhopper Penguins bore ticks, whereas 0 of 5 adults in seagoing plumage did so (Fisher exact test, $P < 0.01$). Three of 5 chicks had ticks, although these ticks appeared less fully engorged than those on molting penguins. The parent penguins, when allopreening their chicks, might have removed ticks before the ticks became fully engorged.

A similar pattern was observed in Macaroni Penguins. Ten of 14 molting birds bore ticks, whereas 0 of 12 adults in seagoing plumage did so ($\chi^2_1 = 13.93$, $P < 0.001$). Six of 17 chicks carried ticks. I conclude that ticks particularly infest molting penguins.

In late March ticks were found on 19 of 20 unpaired molting Macaroni Penguins but on only 8 of 20 paired penguins ($\chi^2_1 = 13.79$, $P < 0.001$). The median number of ticks counted on unpaired birds was 5 (range 0–51) and on paired birds 0 (range 0–20; median test, $P < 0.01$). A mean is not an appropriate measure of infestation level because the number of ticks on different host penguins followed an aggregated distribution typical of such parasitic infestations (Hassell and May 1974).

In mid-April ticks were found on 17 of 20 unpaired molting Rockhopper Penguins but on only 6 of 20 paired birds ($\chi^2_1 = 12.38$, $P < 0.001$). The median number of ticks counted on unpaired birds was 3 (range 0–33) and on paired birds 0 (range 0–5; median test, $P < 0.01$).

There was no significant diurnal variation in the amount of autopreening. The mean time in each hour spent preening (excluding allopreening) was 8.03 ± 6.80 (SD) min ($n = 38$) by paired Rockhopper Penguins and 12.70 ± 9.56 min ($n = 20$) by unpaired penguins. This difference was not quite significant ($t = 1.94$, $P = 0.06$). If allopreening, which occupied 2.03 ± 2.20 min/h ($n = 38$), is added to the preening time of paired birds, then the difference is much reduced. Ninety-eight percent of the allopreening was mutual, with both members of the pair preening each other at the same time.

Every instance ($n = 41$) of head scratching by

Rockhopper Penguins was noted during 34 bird-hours of observation of paired birds and 17.5 bird-hours of observation of unpaired birds. If the two classes of penguin scratched equally often, 27.1 head scratches by paired birds and 13.9 by unpaired would have been observed. In fact, 17 head scratches by paired birds and 24 by unpaired birds were seen, which was significantly different from expectation ($\chi^2_1 = 11.03$, $P < 0.001$).

Paired Macaroni and Rockhopper penguins were more frequently free of ticks than were their unpaired neighbors within the colony. This difference was not due to differences of season, of location within the colony, or of stage of molt. The present data do not rigorously exclude the possibility that penguins prefer to pair with lightly infested partners and that the heavily infested birds remain unpaired because of their heavier tick infestation. This possibility is improbable, however, because birds come ashore to molt in seagoing plumage (i.e. uninfested; pers. obs.). They then remain single or join a partner. The two birds of a pair are commonly at about the same stage of molt and remain together for the duration of the molting period (Richdale 1951). Thus, the division of the penguins into paired and unpaired categories occurs before the period of heaviest tick infestation, in the middle of the molt.

Accordingly, the difference in the tick load of paired and unpaired penguins can be attributed to allopreening. Paired Rockhopper Penguins spend about 3% of their time allopreening. This activity is directed exclusively to the head and neck, the parts of the body where ticks are found. Presumably to compensate for the lack of allopreening, unpaired Rockhopper Penguins use their feet more often to scratch their tick-infested heads.

In reviewing allopreening, Cullen and Ashmole (1963) and Harrison (1965) recognized that the behavior is particularly developed in bird species where individuals are forced into close proximity. Such conditions facilitate transfer of ectoparasites from one individual to another. Assuming that such parasites are harmful rather than beneficial (none of the penguins studied appeared unhealthy), there will be selection for the individual whose individual distance (Conder 1949) is breached to allow allopreening rather than to act aggressively. Reciprocation of allopreening is made feasible by the very nature of the behavior and by the fact that the birds most likely to be forced into close proximity, namely mates, probably recognize each other as individuals. Thus, I suggest that allopreening initially evolved because it uniquely combined cleansing and social functions. The cleansing role persists in the penguins investigated in this study, but other roles may have developed greater importance in the course of other species' behavioral evolution (Selander and La Rue 1961).

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LITERATURE CITED

- BELL, J. F., & C. CLIFFORD. 1964. Effects of limb disability on lousiness in mice. II. Intersex grooming relationships. *Exp. Parasitol.* 15: 340-349.
- BIRKHEAD, T. R. 1978. Behavioural adaptations to high density nesting in the Common Guillemot *Uria aalge*. *Anim. Behav.* 26: 321-331.
- BROOM, D. M. 1981. *Biology of behaviour*. Cambridge, England, Cambridge Univ. Press.
- CONDER, P. J. 1949. Individual distance. *Ibis* 91: 649-655.
- CULLEN, J. M., & N. P. ASHMOLE. 1963. The Black Noddy *Anous tenuirostris* on Ascension Island. Part 2, *Behaviour*. *Ibis* 103b: 423-446.
- DUFFY, D. C. 1983. The ecology of tick parasitism on densely nesting Peruvian seabirds. *Ecology* 64: 110-119.
- FEARE, C. J. 1976. Desertion and abnormal development in a colony of Sooty Terns *Sterna fuscata* infested by virus-infested ticks. *Ibis* 118: 112-115.
- GASTON, A. J. 1977. Social behaviour within groups of Jungle Babblers (*Turdoides striatus*). *Anim. Behav.* 25: 828-848.
- GOODWIN, D. 1983. *Pigeons and doves of the world*, 3rd ed. London, Brit. Mus. (Nat. Hist.).
- HAMILTON, W. D., & M. ZUK. 1982. Heritable true fitness and bright birds: a role for parasites. *Science* 218: 384-387.
- HARRISON, C. J. O. 1965. Allopreening as agonistic behaviour. *Behaviour* 24: 161-209.
- HASELL, M. P., & R. M. MAY. 1974. Aggregation of predators and insect parasites and its effects on stability. *J. Anim. Ecol.* 43: 567-594.
- HOUSTON, D. C. 1979. Why do Fairy Terns *Gygis alba* not build nests? *Ibis* 121: 102-104.
- HUDSON, P. J. 1979. *Survival rates and behaviour of British auks*. Unpublished Ph.D. dissertation, Oxford, Univ. Oxford.
- JOLLY, A. 1972. *The evolution of primate behaviour*. London, Macmillan.
- KING, K. A., D. R. BLANKINSHIP, R. T. PAUL, & R. C. A. RICE. 1977a. Ticks as a factor in the 1975 nesting failure of Texas Brown Pelicans. *Wilson Bull.* 89: 157-158.
- , J. O. KEITH, C. A. MITCHELL, & J. A. KEIRANS. 1977b. Ticks as a factor in nest desertion of California Brown Pelicans. *Condor* 79: 507-509.
- MURRAY, M. D., & W. J. M. VESTJENS. 1967. Studies on the ectoparasites of seals and penguins. III. The distribution of the tick *Ixodes uriae* White and the flea *Parapsyllus magellanicus heardi* de Meillon on Macquarie Island. *Australian J. Zool.* 15: 715-725.
- RICHDALE, L. E. 1951. *Sexual behavior in penguins*. Lawrence, Univ. Kansas Press.
- SELANDER, R. K., & C. J. LA RUE. 1961. Interspecific preening invitation display of parasitic cowbirds. *Auk* 78: 473-504.
- SIMMONS, K. E. L. 1967. Ecological adaptations in the life history of the Brown Booby at Ascension Island. *Living Bird* 6: 187-212.
- SPARKS, J. 1967. Allogrooming in primates—a review. Pp. 148-175 in *Primate ethology* (D. Morris, Ed.). London, Weidenfeld & Nicolson.
- WELTY, J. C. 1982. *The life of birds*, 3rd ed. Philadelphia, Saunders College Publ.

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