The Auk 117(4):1061–1065, 2000

Sexually Transmitted Diseases: A Possible Cost of Promiscuity in Birds?

ALDO POIANI[1,3] AND COLIN WILKS[2]
[1]*Department of Zoology, University of Melbourne, Parkville, Victoria 3052, Australia; and*
[2]*Victorian Institute of Animal Science, Attwood, Victoria 3049, Australia*

Avian mating systems range from monogamy to promiscuity. This variation has been explained by differences in the relative costs and benefits of deserting a partner during the period of parental care (Smith et al. 1982, Houston and Davies 1985, Wright and Cuthill 1989). However, recent studies suggest that the structure of mating systems and mate choice can be modulated by the probability of contracting sexually transmitted diseases (STD; Hamilton 1990, Sheldon 1993, Graves and Duvall 1995). In particular, promiscuity may be linked to an increased probability of obtaining a STD compared with monogamy because many pathogenic microorganisms can be transmitted during copulation in birds (Calnek et al. 1991).

To date, most studies that have investigated evolutionary relationships between mating systems, mate choice, and STD transmission have been from a theoretical point of view (e.g. May and Anderson 1990; Thrall and Antonovics 1997; Thrall et al. 1997, 1998; but see Lockhart et al. 1995, Lombardo et al. 1996). In general, these studies concluded that increased promiscuity in the host should favor the spread of pathogens in the host population and the evolution of virulence in sexually transmitted microparasites.

Birds are very good models to study effects of STD transmission on mating systems because they release semen and feces from the same route; i.e. the cloaca. Therefore, almost any pathogen present in the cloaca may become sexually transmitted (Reiber et al. 1995). Most studies on STD transmission in birds are confined to the orders Galliformes and Anseriformes (Lockhart et al. 1995), whereas little is known about the order Passeriformes, which is a very diverse group that contains many monogamous and promiscuous taxa.

The Australian avifauna contains some extremely promiscuous passerines (Brooker et al. 1990, Mulder et al. 1994), many of which are found in sympatry with monogamous species. For example, up to 76% of the young in the nests of Superb Fairy-Wrens (*Malurus cyaneus*) may result from extragroup fertilizations (Mulder et al. 1994), and White-browed Scrubwrens (*Sericornis frontalis*) are mainly cooperatively polyandrous, with up to two males siring all of the young in a brood (Whittingham et al. 1997). In contrast, Bell Miners (*Manorina melanophrys*) and Redbrowed Finches (*Neochmia temporalis*) are mostly socially monogamous (Immelmann 1967, Conrad et al. 1998). Although the mating system of *N. temporalis* has not been studied using molecular techniques, the closely related and also socially monogamous Zebra Finch (*Taeniopygia guttata*) has been found with only 2.4% of offspring resulting from extrapair fertilizations (Birkhead et al. 1990).

We compared the prevalence (percentage of hosts infected) of some cloacal microparasites in the above four host species. We tested for presence/absence of the bacteria *Chlamydia psittaci* and *Salmonella* sp., the yeasts *Candida albicans* and *Kloeckeria* sp., and the viruses *Orthomyxovirus* (OMV, avian influenza viruses) and *Paramyxovirus* (PMV, avian paramyxoviruses). *Chlamydia psittaci* can be transmitted sexually in birds and also can cause disease that results in variable levels of mortality (Grimes and Wyrick 1991). *Salmonella* also can be transmitted sexually as has been found in avian semen (Reiber et al. 1995); many diseases caused by *Salmonella* are identified under the common label of salmonelloses (e.g. Nagaraja et al. 1991, Pomeroy and Nagaraja 1991, Snoeyenbos 1991). *Candida albicans* can be transmitted sexually and is well known for causing disease of the digestive tract (Chute 1991). OMVs and PMVs are found in the avian cloaca (e.g. Austin and Hinshaw 1984, Mackenzie et al. 1984) and may cause disease in birds, especially the PMVs (e.g. Newcastle disease). Pathogenic effects of *Kloeckeria* are less well known.

If having multiple partners imposes costs via STDs, then we expected the promiscuous and polyandrous species (i.e. *Malurus cyaneus* and *Sericornis frontalis*) to exhibit higher levels of infection than the monogamous species (i.e. *Manorina melanophrys* and *Neochmia temporalis*).

Methods.—We captured birds in mist nets in Glen Waverley, Melbourne, Australia (38°55′S, 145°13′E), during the breeding season from November 1998 to January 1999. All four species are mainly confined to the understory of eucalypt forest except for *M. melanophrys*, which uses the understory and the canopy. Three cloacal swabs were obtained from each adult captured. The first swab was returned to its plastic sleeve after sampling to be used for chlamydial analyses, the second was cut and deposited in a tube containing a virus transport medium, and the third was cut and deposited in a vial containing Stuart's transport medium and used for *Salmonella* and yeast anal-

[3] E-mail: a.poiani@zoology.unimelb.edu.au

TABLE 1. Prevalence of cloacal microparasites found in four species of Australian passerines. No *Salmonella* nor viruses (*Orthomyxovirus* and *Paramyxovirus*) were found after analyzing the cloacal swabs.

Host species	Body mass (g)	Relative abundance[a]	*n*	Microparasite[b]		
				Chlamydia psittaci	*Candida albicans*	*Kloeckeria* sp.
Malurus cyaneus	9.5	36	32	2 (6.2)	2 (6.2)	0 (0.0)
Sericornis frontalis	12.9	16	25	6 (24.0)	0 (0.0)	2 (8.0)
Manorina melnophrys	30.9	50	30	2 (6.7)	5 (16.7)	0. (0.0)
Neochmia temporalis	10.5	8	16	0 (0.0)	0 (0.0)	0 (0.0)

[a] Relative abundance and sample size differ within species because we used captures from a section of the study site where all species were present and all captured birds were recorded for our estimate of relative abundance, whereas birds used for cloacal analyses were from all sectors of the study site. Most juveniles were recorded but no cloacal samples taken, whereas once we had large enough sample sizes for common species, we shifted our attention to the less-common species to have sample sizes large enough for analyses. Relative abundance values were recorded before we commenced targeted mist netting.

[b] Values are number of birds that had the given microparasite (percentage in parentheses).

yses. Swabs were maintained on ice until transported to the laboratory (2 to 5 h), where they were kept at 4°C until assayed.

Virus transport medium was centrifuged at 2,000 rpm for 10 min. The supernatant was filtered (0.45 μ) before inoculation into 10-day-old chicken eggs. Eggs were from a flock known to be negative for OMV and PMV. Allantoic fluid of any embryos that died over a five-day period was collected and tested for the presence of haemagglutinating (HA) agents. If HAs were present, we performed a haemagglutination inhibition (HI) test using a panel of known antisera against various OMVs and PMVs. After five days incubation (considered to be the first passage), allantoic fluid was collected and further eggs were inoculated for a second passage. Again, we performed HA tests on dead embryos, plus allantoic fluid from the eggs after five days.

Swabs used for bacterial analyses were placed in 10 mL of Mannitol-Selenite broth and incubated at 37°C for 18 to 24 h. After the incubation period, 0.5 mL of the broth was transferred to BG/XLD (selective media for *Salmonella* sp.) and incubated for 24 h. *Chlamydia psittaci* was detected by carrying out *Chlamydia* antigen detection using commercial kits (Clearview, Unipath Ltd.). To determine the presence of yeast in cloacae, swabs were streaked onto Sabouraud's dextrose agar and incubated for 14 days. Colonies were stained with lactophenol cotton blue for identification.

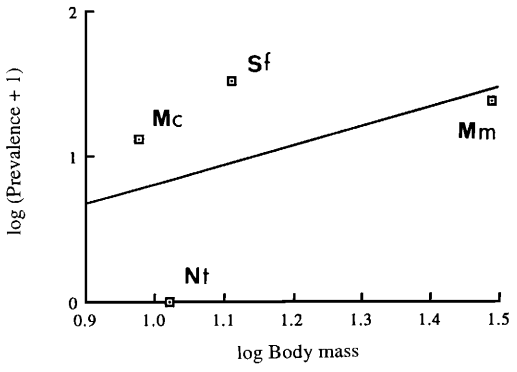

FIG. 1. Linear regression between $\log_{10}$ prevalence of all cloacal microparasites and $\log_{10}$ body mass (g). The regression line serves the purpose of subdividing the host species into those with positive or negative residuals ($r = 0.449$, $P > 0.25$). Mc = *Malurus cyaneus*, Mm = *Manorina melanophrys*, Sf = *Sericornis frontalis*, and Nt = *Neochmia temporalis*.

The four host species are from different families: Maluridae (*M. cyaneus*), Pardalotidae (*S. frontalis*), Meliphagidae (*M. melanophrys*), and Passeridae (*N. temporalis*). Therefore, we used a simplified version of Pagel and Harvey's (1988) nested ANOVA/allometry method and considered each species as an independent data point for statistical analyses. The small number of host species (four) makes it unwise to use alternative comparative methods such as independent contrasts (Harvey and Pagel 1991), which produce a sample size of $n - 1$ for statistical analyses.

Results and Discussion.—We sampled 103 individuals of the four passerine host species. We detected the presence of *Chlamydia psittaci* in three species, *Candida albicans* in two species, and *Kloeckeria* sp. in one species (Table 1). No *Salmonella* or viruses were found after analyzing the cloacal swabs. Figure 1 shows the relationship between prevalence of all microparasites and body mass for the four host species. Larger hosts usually harbor more parasites (see Poiani 1992) because a larger body provides more potential habitat for parasites to become established.

If multiple matings increase chances for STD transmission, we expected the promiscuous and polyandrous species to be infected more frequently (values lying above the regression line) than the monogamous species (values lying below the regression line), given their body mass. Our results supported this prediction, although positive residuals for the

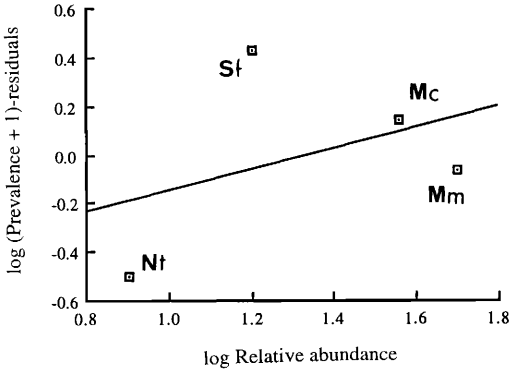

FIG. 2. Linear regression between $\log_{10}$ prevalence residuals of all cloacal microparasites with respect to the regression with body mass and $\log_{10}$ relative abundance of host species in the study site (r = 0.509, $P > 0.10$). Mc = *Malurus cyaneus*, Mm = *Manorina melanophrys*, Sf = *Sericornis frontalis*, and Nt = *Neochmia temporalis*.

promiscuous/polyandrous species and negative residuals for the monogamous species may have reflected the relative abundance of the host species in the study site. This is expected if the cloacal microparasites studied can be also transmitted through fecal contamination of the environment. To control for such an effect, we also regressed the residuals obtained from the prevalence versus body mass curve against estimated relative abundance of the host species in the study site (Fig. 2). This produced a second set of residuals that were independent from body size and relative abundance of the hosts. Again, the promiscuous/polyandrous species produced positive residuals, whereas the monogamous species produced negative residuals. Thus, the only result that unambiguously supported the STD hypothesis is the one we obtained. The probability of obtaining our result by chance is 0.0625 (i.e. $1/2^4$).

The probability of detecting a parasite in an assemblage of hosts may be affected by the number of hosts sampled (Gregory and Blackburn 1991, Poiani 1992). In our study, *N. temporalis* had no cloacal microparasites, but also the smallest sample size (Table 1). With 16 individuals sampled, the smallest nonzero prevalence value we could possibly detect was 1/16 (i.e. 6.2%). Therefore, we repeated the analysis using a prevalence value of 3.1 (i.e. the midpoint between 0 and 6.2) for *N. temporalis* to correct for the small sample size. This procedure did not alter our results.

Mean values for the set of "double residuals" (with respect to body mass and relative abundance) also can be directly compared with a Student's t-test. The difference between means approached significance (t = 2.29, df = 2, $P < 0.10$), with promiscuous/polyandrous species being more parasitized than monogamous species after accounting for effects of body mass and relative abundance in the study site.

We provide the first evidence for a bias in sexually transmitted parasites harbored by wild passerine hosts that have multiple sexual partners, as compared with monogamous passerines. Our findings suggest that to understand the evolution and maintenance of monogamy or polygamy and the fine structure of each mating system (presence/absence of extrapair copulations, number and quality of sexual partners, etc.), the potential costs of STD transmission should be considered and properly assessed. If a mating system involving multiple sexual partners is evolutionary stable (as it may be in *M. cyaneus* and perhaps *S. frontalis*), then fitness benefits of promiscuity or polyandry must offset STD transmission costs. However, even if costs of STD transmission are not high enough to override the polygamous mating system, they may still play a role in modulating the number and kind of sexual partners (mate choice) and the frequency distribution of copulations among partners. For example, preliminary results indicate that male *M. cyaneus* that display longer ear tufts (a secondary sexual trait used in courtship) harbor more cloacal microparasites than males with shorter ear tufts (Poiani and Wilks 2000).

Although *Chlamydia psittaci* and *Candida albicans* are well known to be sexually transmitted and to cause disease in birds, we cannot ascertain the current level of pathogenicity of the strains found in our study. Sexually transmitted microparasites are believed to evolve low levels of virulence rapidly (Anderson and May 1992, Knell 1999). The likelihood of such an evolutionary outcome will depend, however, on the level of parasite transmission, because high transmission rates are expected to favor the evolution of virulence (e.g. Mackinnon and Read 1999).

Acknowledgments.—We thank Parks Victoria and especially Mick Vandevreede for support during this project and M. Elgar and two anonymous referees for comments on the manuscript. The project was funded by a W. V. Scott Estate grant to AP and was carried out under permit 10000058 of the Department of Natural Resources and Environment of Victoria.

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Received 18 August 1999, accepted 28 April 2000.
Associate Editor: J. Ekman

The Auk 117(4):1065–1068, 2000

Seasonal Decline in Nestling Growth: Support for the Parental-Quality Hypothesis in Cassin's Auklets

YOLANDA E. MORBEY[1] AND RONALD C. YDENBERG
Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada

Growth rates of nestlings often decline over the breeding season (e.g. Birkhead and Nettleship 1982, Gaston et al. 1983, Morbey and Ydenberg 1997, Lepage et al. 1999). Although several mechanistic hypotheses have the potential to explain this phenomenon (see Nilsson 1999), we investigated the two that are considered most often. Under the date hypothesis, nestling growth depends indirectly on current environmental conditions through direct effects on parental provisioning. A seasonal decline in nestling growth is expected if feeding conditions deteriorate over the season. Under the parental-quality hypothesis, young or inexperienced parents, or those with lower provisioning ability, initiate breeding later, leading to a seasonal decline in nestling growth. We determined which hypothesis could best explain the observed seasonal decline in nestling growth rates of Cassin's Auklets (*Ptychoramphus aleuticus*) by comparing growth of nestlings whose hatching dates were normal versus experimentally delayed.

Study area and methods.—Breeding phenology and nestling growth of Cassin's Auklets were monitored in 1994 on Triangle Island (50°52'N, 129°05'W; Morbey and Ydenberg 1997). Cassin's Auklets lay one egg and incubate it for approximately 38 days, with parents switching incubation duties approximately every 24 h (Astheimer 1991). Prior to egg laying, we excavated 82 burrows to create access holes and began daily monitoring. If twigs that we placed in burrow entrances were knocked down the following day, we inferred that the burrow had been visited the previous night. Active burrows were checked every third day for eggs. Upon discovery of a newly laid egg, we alternately assigned the burrow to one of two experimental groups. In the delayed group (n = 27), the egg was replaced with a hard-boiled chicken egg for five days. In the interim, the auklet egg was left in a carton buried in the sand to keep it safe and cool. Enforcing egg neglect at the beginning of the incubation period was done to minimize any negative effects of interrupting embryonic growth. In the control group (n = 25), eggs were handled as in the delayed group but were not removed for more than a few seconds. Hatching dates of these experimental burrows were expected to span the natural range.

During the hatching period, we checked all burrows every three days and estimated hatchling ages using wing length (Morbey and Ydenberg 1997). Mass and wing length were measured at hatching, 5 days of age, 25 days of age, then every fifth day until chicks were fully feathered, and then every second day until chicks fledged (i.e. left their burrows). We measured nestling growth as the daily rate of mass increase during the linear growth phase, which occurs from 5 to 25 days of age (Vermeer 1981). We also measured nestling growth rates for an additional 70 chicks whose burrows were found after egg laying; these were considered controls for the experimental manipulation (low-disturbance group in Morbey and Ydenberg [1997]) and will be referred to as the natural group. These burrows likely represented the entire range of hatching dates (see Morbey and Ydenberg 1997: fig. 1).

We obtained growth rates for only 9 nestlings in the delayed group and 13 in the control group because of egg abandonment or predation (12 in the delayed group and 8 in the control group), nestling mortality (4 in the delayed group and 1 in the control group), extreme lateness (1 in the control group), and

[1] E-mail: ymorbey@sfu.ca