

Incidences of Polygyny and Extrapair Copulation in the Northern Oriole

NANCY J. FLOOD

Department of Zoology, University of Toronto, 25 Harbord Street, Toronto, Ontario M5S 1A1, Canada

Trivers (1972) proposed that monogamously mated males are actually selected to pursue a mixed reproductive strategy: they are selected to capitalize on, or even actively seek out, opportunities to fertilize females other than their own mates. Recently, this hypothesis has become the focus of considerable interest (e.g. Fitch and Shugart 1984). Gladstone (1979) provides data on the existence of promiscuity among males in 18 species of monogamous colonial birds. McKinney et al. (1983) list 104 monogamous species in 26 families for which they have found published evidence of extrapair copulation (EPC) or attempted EPC. A review by Ford (1983) presents reliable reports of observed EPC in a total of 115 species from 30 families.

In the absence of direct observation of copulation, other types of data may provide circumstantial evidence of EPC. For example, mate guarding by males during what is presumed to be the female's fertile period has been interpreted by many workers as an anti-EPC strategy, thus implying that EPC does occur (Birkhead 1979, Power and Donner 1980, Power et al. 1981, Buitron 1983, Ford 1983). Additionally, in many species mated, territorial males have been observed intruding into the territories of other, also-mated males. The fact that these intrusions most frequently occur during nest building or egg-laying, when resident females probably are fertile, suggests that they may constitute attempts at EPC (Buitron 1983, Ford 1983). Finally, the occurrence of low rates of polygyny among normally monogamous species suggests that males may be selected to mate with more than one female if possible. Ford (1983) listed 61 species of North American passerines, many of them regarded as monogamous, for which he had found reliable records of polygynous matings. Only 14 of these he considered regularly polygynous (rates of polygyny exceeded 20%), while the remaining 47 he characterized as either facultatively polygynous (multiple matings occur regularly, at least in some populations, but at rates lower than 20%) or opportunistically polygynous (polygyny occurs rarely and only in unusual circumstances, such as when a male disappears and his mate is taken over by a neighbor).

The Northern Oriole (*Icterus galbula*), which consists of two well-known races, the western "Bullock's Oriole" (*I. g. bullockii*) and the eastern "Baltimore Oriole" (*I. g. galbula*), has either been described as, or assumed to be, monogamous (e.g. Bent 1958, Orians 1972). However, Williams (1982) discovered 2 bigamous males among the total of 96 males she followed during a 4-yr study of Bullock's Oriole in California. Here, I provide the first published evidence of polygyny in the Baltimore Oriole. In addition, I furnish

other data that show, or indirectly suggest, that Baltimore Oriole males, like those of many passerine species, are selected to pursue a mixed reproductive strategy.

From 1 May to 1 July in 1978 and 1979, with the help of 2 assistants, I studied a population of Baltimore Orioles near Protection, Comanche Co., Kansas. We monitored 132 nests (in most cases from initiation to failure or fledging) and banded 269 after-hatch-year orioles. Most of the birds in the study population were individually recognizable on the basis of colored leg bands or unusual plumage characteristics. All females and ASY (= after second year, i.e. one or more years old) males bred, as did approximately one-third of the SY males (= second year; SY males hatched the previous summer and are female-like in appearance; Flood 1984). We spent 626 h observing these birds, timing and recording a variety of behaviors and/or events.

Removal experiments.—I removed 10 mated, territorial males from the study population, 3 after their mates had initiated a clutch. In all 3 cases, the widowed females incubated and then fed the young alone; all 3 nests eventually fledged at least 1 young. Three other newly created widows deserted their nests before it could be determined whether they had laid. In the remaining 4 cases, the males were removed before their mates had initiated laying. Three of the 4 were replaced by previously unmated SY males. The fourth was replaced by his nearest territorial neighbor, an already-mated ASY male (hereafter called M1), whose female (F1) had a nest 63 m away from that of the new widow (F2).

F2's original mate was removed on 26 May, while she was still building a nest. On 28 May, and on several occasions thereafter, I saw M1 apparently courting F2, singing in her vicinity and accompanying her in the nest tree. On 3 June, F2 performed a precopulatory display in the presence of M1, and on approximately 4 June she began laying eggs in her now complete nest. F1 incubated from approximately 26 May on, and began feeding her own newly hatched young on about 9 June. Her mate, M1, assisted her, making 18.0% of the feeding trips recorded during 6 h spent observing feeding at this nest. The average proportion of parental care performed by adult males in 1978 was 43.1% (SD = 14.2%). F1's young fledged on 21 June. On approximately 19 June, F2's young hatched, and with the assistance of M1 she fed the nestlings until they fledged on 30 June. M1 made approximately 22.6% of the total number of feeding trips observed at this nest (during 6 h of feeding observations).

A second observed EPC involved a female that

abandoned her first nest, nest 30, approximately 1 week after her mate was removed on 22 May. An unidentified adult male attempted to copulate with this female near her nest on 23 May. On 24 May the adult male from nest 31 (112 m away from nest 30) was observed twice near nest 30, and on one of these occasions copulated with the widow. On 7 June the widow was discovered at a new nest, 70, built approximately 100 m away from nest 30 and 190 m away from nest 31. There she successfully raised a brood of 5 young with no apparent assistance from any male (the nest was observed for 7 h during feeding). The eggs in nest 31 hatched on approximately 5 June and fledged on 17 June, while the corresponding dates for nest 70 were approximately 19 June and 1 July. A similarly unassisted female was not observed at any other nest (other than those at which the male had been removed) in either year of study. Although it is possible that this second clutch was fertilized by stored sperm from the female's original mate (Hatch 1983), the length of time involved and the fact that this female copulated with another male after the death of her first mate make EPC seem the more likely method of fertilization; the male from nest 31 apparently did not form a pair bond with the female since he did not help her feed her nestlings even though they hatched 2 days after those in nest 31 had fledged.

The third EPC we observed involved a female whose original ASY mate had been removed 4 days earlier and another ASY male who had a mate and a nest elsewhere (>500 m away) in the study area. A SY male had begun accompanying this female, however, soon after she became a widow, and he was observed chasing the intruding ASY male several times on the day this EPC occurred. The SY male continued to escort and defend this female throughout the incubation period (she initiated a clutch on 28 May, 2 days after the above-mentioned EPC) and helped to feed the nestlings until they fledged on 24 June.

Observed copulations.—During 1979, all copulations and copulation attempts seen were recorded. Ten such events were observed, 3 of which (as described above) were EPCs. The significance of these figures is uncertain. The fact that only 10 copulations were witnessed during many hours of observation suggests that copulation in this species is somewhat cryptic and thus rarely seen; EPCs may be expected to be even more cryptic, and thus proportionately less likely to be observed. This relatively high observed frequency of EPC may therefore indicate that it is actually a fairly common occurrence.

All observed EPCs involved widows. This may lend support to the contention that widows are more willing to engage in copulation with nonmates than are paired females (Fitch and Shugart 1984). Alternatively, it may be that EPCs with females whose mates are still alive are simply less likely to be witnessed; some

TABLE 1. Intrusions into territories of Baltimore Orioles.

Stage of the nesting cycle	No. of hours of observation	Adult males	First-year males	Females
Nest building				
and incubation	81.25	35 (0.43) ^a	3 (0.04)	0
Feeding	179.75	16 (0.09)	19 (0.11)	3
After feeding	13.50	0	0	0
Unknown	35.25	1	0	0

^a Numbers in parentheses are number of intrusions per hour.

aspect of the behavior of a widow may signal to intruding males that the usual amount of discretion needed for stolen copulation is not necessary in her case. This latter interpretation is supported by my observations of intruding male orioles trespassing near nests belonging to conspecific males that were still living. Death of the territory holder obviously is not a prerequisite for intruding into a territory, and there may in fact be many opportunities for EPC involving females whose mates are still alive. The attendant risks for the trespassers are not as great, however, when a widow is involved, and copulation may thus be conducted in a less cryptic and/or more leisurely fashion. EPCs involving females whose mates are alive have been observed in a number of other bird species (Birkhead 1979, Gladstone 1979, Fitch and Shugart 1984).

Intrusion events.—In 1979 we recorded all observed intrusion events. Intruders were defined as birds other than the members of the pair associated with the nest under observation that approached to within 3 m (and usually within 0.5 m) of the nest. The sex and identity (from color bands) of the intruder were recorded if possible, as was the stage of the breeding cycle during which the intrusion event occurred (Table 1). Intruding birds usually stayed in the area of the nest less than 10 s and if seen, most were chased out of the area by the male or female associated with the nest.

The majority of observed intruders were male. We saw only 3 birds identified as females trespassing. Although a large number of dull-plumaged birds of unknown sex intruded, most of these probably were SY males (Flood 1980). We were able to determine the full color-band combination of only 23 of the intruders: 7 ASY males, 3 females, and 13 SY males. Of these, all of the ASY males and females were mated and nesting elsewhere in the study area, as were 6 of the young males. The remaining 7 SY males were unpaired. Only 3 of the 16 intruders known to be mated trespassed into the area of the nest belonging to their nearest neighbor; most trespassed in the vi-

cinity of nests greater than 500 m from their own. Of the total 117 intrusion events, 46 occurred during 38.0 h of observation (1.2/h) at nests where the male had been removed (i.e. the female was a widow), while 71 took place during 275.75 h of observation (0.3/h) at nests where both members of the pair were still alive (although not necessarily in attendance at the moment of intrusion). Thus, intrusions were much more likely to occur in the absence of a defending male (G test, $G = 55.76$, $P < 0.001$). We observed ASY males intruding much more often during the nest-building and/or incubation periods—which encompass the fertile period of females—than while nestlings were being fed ($G = 30.16$, $P < 0.005$). SY males, as well as the birds of unknown sex (again, most of which probably were SY males), appeared to trespass more often during feeding than during the earlier stages of the breeding cycle, although the difference was not significant in either case. The two male age groups may have different reasons for intruding; ASYs may be seeking EPC, whereas younger males may also, or more often (since most are unmated), be simply familiarizing themselves with high-quality territory (i.e. that possessed by breeding pairs) in preparation for the next breeding season (Flood 1980).

As the reproductive behavior of more monogamous birds is studied, the list of species in which males pursue a mixed reproductive strategy grows (Ford 1983). Since Verner and Willson's (1969) compilation, the number of typically monogamous species in which polygynous matings have been recorded has increased from 25 to 47. Of the 291 species for which Verner and Willson (1969) sought such information, no data were found for 38, and 204 were considered to be only poorly known. The situation has improved, but continues to be such that 14 years later, Ford (1983) remarked on the need for still more study, particularly using techniques such as color-banding that enable observers to detect EPC and/or polygyny.

Although the Baltimore Oriole is commonly considered monogamous (e.g. Bent 1958, Orians 1972, Sealy 1980), Verner and Willson (1969) noted that there was a dearth of precise data on the breeding system of the species and Ford (1983) did not include it on his list of species breeding in North America for which polygyny has been reported. My data suggest that the Baltimore Oriole is regularly monogamous, but that opportunistically polygynous matings are possible. Direct observation of EPC as well as additional circumstantial evidence (timing of intrusions, etc.) further indicates that males, while generally monogamous, may pursue what Trivers (1972) called a mixed reproductive strategy.

I am grateful to G. Honeyman and D. Kerrigan for assistance in the field and to G. Bortolotti, P. Fetterolf, N. Ford, E. Nol, J. Rising, and B. Woodward for comments on the manuscript. This research was sup-

ported by the Frank M. Chapman Fund of the American Museum of Natural History and by the Natural Sciences and Engineering Research Council of Canada through a grant (No. A5999) to J. Rising and scholarships to the author.

LITERATURE CITED

- BENT, A. C. 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. Washington, D.C., Bull. Smithsonian Inst. 211.
- BIRKHEAD, T. R. 1979. Mate guarding in the Magpie *Pica pica*. Anim. Behav. 27: 866-874.
- BUITRON, D. 1983. Extra-pair courtship in Black-billed Magpies. Anim. Behav. 31: 211-220.
- FITCH, M. A., & G. W. SHUGART. 1984. Requirements for a mixed reproductive strategy in avian species. Amer. Natur. 124: 116-126.
- FLOOD, N. J. 1980. The adaptive significance of delayed plumage maturation in *Icterus galbula*. Unpublished M.Sc. thesis, Toronto, Ontario, Univ. Toronto.
- . 1984. The adaptive significance of delayed plumage maturation in *Icterus galbula*. Evolution 38: 267-279.
- FORD, N. L. 1983. Variation in mate fidelity in monogamous birds. Pp. 329-351 in Current Ornithology (R. F. Johnston, Ed.). New York, Plenum Press.
- GLADSTONE, D. E. 1979. Promiscuity in monogamous colonial birds. Amer. Natur. 114: 545-557.
- HATCH, S. A. 1983. Mechanism and ecological significance of sperm storage in the Northern Fulmar with reference to its occurrence in other birds. Auk 100: 593-601.
- MCKINNEY, F., K. M. CHENG, & D. J. BRUGGERS. 1983. Sperm competition in apparently monogamous birds. In Sperm competition and the evolution of animal mating systems (R. L. Smith, Ed.). New York, Academic Press.
- ORIAN, G. H. 1972. The adaptive significance of mating systems in the Icteridae. Proc. 15th Intern. Ornithol. Congr.: 389-398.
- POWER, H. W., & C. G. P. DONNER. 1980. Experiments on cuckoldry in the Mountain Bluebird. Amer. Natur. 116: 689-704.
- , E. LITOVICH, & M. P. LOMBARDO. 1981. Male starlings delay incubation to avoid being cuckolded. Auk 98: 386-389.
- SEALY, S. G. 1980. Reproductive responses of Northern Orioles to a changing food supply. Canad. J. Zool. 58: 221-227.
- TRIVERS, R. L. 1972. Parental investment and sexual selection. Pp. 136-179 in Sexual selection and the descent of man. 1871-1971 (B. Campbell, Ed.). Chicago, Aldine.
- VERNER, J., & M. F. WILLSON. 1969. Mating systems, sexual dimorphism, and the role of male North

American passerine birds in the nesting cycle. *Ornithol. Monogr.* 9: 1-76.

WILLIAMS, P. L. 1982. A comparison of colonial and non-colonial nesting by Northern Orioles in

central coastal California. Unpublished M.S. thesis, Berkeley, California, Univ. California.

Received 27 April 1984, accepted 16 November 1984.

The First Recorded Cory's Bittern (*Ixobrychus "neoxenus"*) from South America

DANTE MARTINS TEIXEIRA¹ AND HERCULANO M. F. ALVARENGA²

¹Museu Nacional, Rio de Janeiro (RJ), CEP 20942, Brazil, and

²Rua Colômbia 99, Taubaté (SP), CEP 12100, Brazil

Described by Cory (1886), *Ixobrychus "neoxenus"* is considered a variant morph of the Least Bittern (*Ixobrychus e. exilis*), characterized by contrasting dark chestnut underparts and blackish upperparts. About 30 specimens are known, mostly from southern Florida and Ontario, but there are also records from Massachusetts, New York, Ohio, Illinois, Michigan, and Wisconsin (Bent 1926, Hancock and Elliot 1978). Thus, it was quite a surprise for us to obtain a specimen of the South American *Ixobrychus exilis erythromelas* in this rather uncommon plumage. Apparently, this is the first time this morph has been reported outside North America.

The bird was collected on 13 May 1967 in the rice fields of the Paraíba do Sul drainage, county of Taubaté, São Paulo (approx. 23°01'S, 45°33'W), southeastern Brazil. In this area, "normal" colored *I. exilis erythromelas* are common, as are other herons such as *I. involucris*, *Botaurus pinnatus*, *Butorides striatus*, *Casmerodius albus*, and *Egretta thula*. Another species, *Bubulcus ibis*, has been recorded as a recent invader of the surrounding dry pastures. The specimen collected was a young male, with nonossified skull and very small gonads. Its stomach contained a small, 50-mm long characid (Tetragonopterinae) and unidentified seeds of a monocotyledon.

Like normal-colored *I. exilis erythromelas*, this specimen in the *neoxenus* plumage showed a light yellow iris and yellowish bare lores, but its bill was blackish brown and the tarsus brownish, without yellow tinges. The plumage agreed more or less with the description of Sharpe (1898), but some conspicuous differences were observed: the specimen did not show any greenish or bronze gloss in the blackish parts of the plumage, and its secondaries were plain black without rufous. The ashy black feathers of nape, hindneck, back, and rump were fringed with ochraceous to light gray, giving the bird a discrete scaled appearance. The sides of upper breast, thigh, center of abdomen, and crissum were ashy black, rather washed out, and marked with deep, dark chestnut rather than dusky rufous. These differences (at least the scaled upperparts) probably are related to age, as the young of normal-colored *I. exilis erythromelas* also show the upperparts inconspicuously barred with

ochraceous, and all previously described *I. "neoxenus"* have been adults.

Bent (1926) considered *I. "neoxenus"* to be an example of melanism and erythrism, and a comparison of our specimen with typically colored *I. exilis erythromelas* seems to point to hyperpigmentation. Indeed, a superproduction of eumelanins and pheomelanins perhaps could explain the deep blackish tinges of the upperparts and the rufous chestnut color of the foreneck, breast, etc. observed in this unusual plumage (Vevers 1964).

As mentioned above, *I. "neoxenus"* is considered a rare morph, and our observations in southeastern Brazil seem to reinforce this supposition. Although *I. exilis erythromelas* is common in the rice fields of Taubaté, only one specimen in the "*neoxenus*" plumage has been recorded after almost 20 yr of observation. In addition, our field research in coastal Rio de Janeiro and in Alagoas has never revealed any other specimen in this peculiar coloration. Thus, it is impossible to evaluate if the "*neoxenus*" morph has, in Brazil, a local occurrence or not, as was observed in the North American Least Bittern.

We would like to thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), which partially supported our studies on Brazilian birds.

LITERATURE CITED

- BENT, A. C. 1926. Life history of North American marsh birds. *Smithsonian Inst., Bull. U.S. Natl. Mus.* 135: 84-91.
- CORY, C. B. 1886. Description of a new North American species of *Ardetta*. *Auk* 3: 262, 408.
- HANCOCK, J., & H. ELLIOT. 1978. *Hérons of the world*. London, London Editions Ltd.
- SHARPE, R. B., & W. R. OLGIVIE-GRANT. 1898. *Catalogue of birds in the British Museum*, vol. 26. London, Brit. Mus. of Nat. Hist.
- VEVERS, G. 1964. Colour. Pp. 142-144 in *The new dictionary of birds* (L. Thomson, Ed.). London, Nelsons and Sons.

Received 20 August 1984, accepted 16 November 1984.