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Source: The Wilson Bulletin, 114(1):106-113.

Published By: The Wilson Ornithological Society

DOI: [http://dx.doi.org/10.1676/0043-5643\(2002\)114\[0106:OPITLW\]2.0.CO;2](http://dx.doi.org/10.1676/0043-5643(2002)114[0106:OPITLW]2.0.CO;2)

URL: <http://www.bioone.org/doi/full/10.1676/0043-5643%282002%29114%5B0106%3AOPITLW%5D2.0.CO%3B2>

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OPPORTUNISTIC POLYGyny IN THE LOUISIANA WATERTHRUSH

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ABSTRACT.—We monitored the nesting biology of color-banded populations of the Louisiana Waterthrush (*Seiurus motacilla*) at up to 25 sites across Pennsylvania from 1996–2001. Opportunistic polygyny in this species was documented for the first time during our study. Four out of 283 paired males were polygynous; one male and female were involved in a polygynous trio during two successive years. Opportunistic polygyny may have occurred primarily as a result of female territory fidelity and a locally skewed sex ratio in two cases, but appeared to be actively pursued as a mating strategy in the case of the male who was bigamous during two successive years. His aggressive territorial behavior was consistent with that reported for polygynous birds having naturally and experimentally elevated plasma levels of testosterone. The rate of nestling provisioning by this male at a failed secondary nest was substantially lower compared to his successful primary nest and compared to mean provisioning rates for monogamous males. In addition to reduced male parental care, protraction of the re-nesting interval following nest failure was another possible component cost of polygyny observed for one of the mates of this male. In this instance, both costs were borne by the first mated female, who was relegated to secondary status after her initial nest was depredated. Received 9 April 2001, accepted 31 January 2002.

Polygyny has been reported to occur opportunistically or facultatively in more than 15% of North American passerines generally characterized as having a monogamous mating system (Ford 1983). Since Ford's (1983) review, which listed differing levels of polygyny in 13 parulines, polygyny has been documented in several more wood warblers, typically during the course of long term population studies involving large numbers of uniquely color-marked individuals followed over several nesting seasons: Black-throated Blue Warbler (*Dendroica caerulescens*; Petit et al. 1988), American Redstart (*Setophaga ruticilla*; Secunda and Sherry 1991), Hooded Warbler (*Wilsonia citrina*; Evans-Ogden and Stutchbury 1994), Worm-eating Warbler (*Helminthos vermivorus*; Hanners and Patton 1998), and Kentucky Warbler (*Oporornis formosus*; McDonald 1998). Within the genus

Seiurus, early studies of nesting Ovenbirds (*Seiurus aurocapillus*) and Northern Waterthrushes (*S. noveboracensis*) found circumstantial evidence that polygyny may occur rarely (Hann 1937, Eaton 1949), but similar studies of Louisiana Waterthrushes (*S. motacilla*) did not (Eaton 1958).

Here, we document the first known cases of polygyny in the Louisiana Waterthrush based on observations made during ongoing studies of the breeding biology of the species in Pennsylvania. We studied nestling provisioning rates at two nests of one of the bigamous males and compared these to provisioning at nests of monogamous males at the same study site.

STUDY AREA AND METHODS

We confirmed polygyny during a study investigating the Louisiana Waterthrush as a bioindicator of the ecological integrity of forested headwater streams across Pennsylvania. Our study sites were 2–3 km reaches of 25 forested headwater streams in the three major river drainages in western (12 sites), central (seven sites), and eastern (six sites) regions of the state. Depending on the site, waterthrush populations were studied for 3–6 consecutive years between 1996 and 2001. We observed polygyny at three sites: Laurel Run (Huntingdon Co.; 40° 41' N, 77° 51' W; elevation 300 m) and Garner Run (Huntingdon Co.; 40° 40' N, 77° 57' W, elevation 400 m) in central Pennsylvania; and Powdermill Run (40° 09' N, 79° 16' W, elevation 500 m) in western Pennsylvania. In the following case histories, observations are referenced spatially according to numbered flags that were set at 50-m intervals from

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the lower end of each study stream, Flag 0, to the upper end, Flag 40–60, depending on overall stream reach length.

Each year we uniquely color banded most of the adult and nestling birds on our study sites. We attempted to locate and observe the nesting attempts of all nesting pairs. Nests were checked at least every 3–4 days, and selected nests were under almost daily observation from blinds placed 10–20 m away as part of detailed studies of incubation and nestling provisioning behavior in the species (RSM unpubl. data). Clutch initiation date (first egg laid), if not directly observed, was back calculated from known or estimated hatching and/or fledging dates, assuming 14-day incubation (beginning with the last egg laid) and 10-day nestling periods. The former, based on our own observations, is 1–2 days longer than indicated in most literature (e.g., Eaton 1958, Robinson 1995).

We conducted a total of 18 0.5- to 4.0-h nest watches in order to compare nestling provisioning rates of one bigamous male (total of 12.5 h of observation at his primary nest, 17.5 h at his secondary nest) and compared this with data collected during 253 h of observation at 20 nests of monogamous pairs on the same stream.

RESULTS AND DISCUSSION

Polygyny occurred very rarely during our study, in about 1% (4/283) of paired males. In western Pennsylvania one male was polygynous during two successive years. In each of the four confirmed cases, we observed a color-banded male during the same season in association with the nesting attempts of two different females, either both uniquely color-banded, or one banded and the other not.

The first case occurred on Laurel Run during 1999. During 1998, female BG (blue over green) nested successfully with male WR (white over red) on a territory that extended from Flags 0–7. She had nested with a different male in this territory the year before. In 1999, WR returned to the same 350-m long territory. We observed him with an unbanded female on 26 April, and their nest containing four nestlings was found on 24 May at Flag 5; their four young fledged on 28 May. By back calculation, the first egg was laid in this nest on 2 May (Fig. 1). Then, on 16 June, WR was seen associating with female BG, his mate from 1998, whom we had not observed previously on Laurel Run during 1999. We found a nest containing five young near fledging on 25 June near Flag 0, or about 250 m downstream of WR's first nest. We estimate that WR and BG initiated their clutch within

a day or two of when young fledged from WR's primary nest with the unbanded female (Fig. 1). Presumably, WR and BG associated with one another (e.g., pairing, nest searching, nest building) for at least several days prior, during the nestling stage of WR's nest with the unbanded female.

Female Louisiana Waterthrushes show high levels of territory fidelity, with up to 50% of returning females reoccupying their territory from the previous year, not infrequently reuniting with the same mate (RSM unpubl. data), and this may have contributed to this case of polygyny. In Blackpoll Warblers (*Dendroica striata*), females returning to formerly held territories already occupied by a mated male were hypothesized to have the costs of sharing a mate offset by advantages associated with early nest initiation and familiarity with the territory (Eliason 1986; see also Wheelwright et al. 1992). Female BG and the unbanded female nested within the same territory used by WR and BG during the previous year, and by BG and a different male the year before that. It is possible that BG's arrival in 1999 on the territory she used during at least two previous years may have occurred after WR had already paired with an earlier-arriving female. BG may have accepted secondary status rather than incur possible costs related to delaying her breeding further by dispersing in search of a territory with an unmated male (Slagsvold et al. 1988). Alternatively, BG may in fact have been the primary female in terms of settling date, with loss of an earlier nesting attempt effectively relegating her to secondary status in terms of nesting (see Powdermill Run case histories below).

On Garner Run we discovered the nest of an unbanded waterthrush pair containing half-grown nestlings about 450 m below Flag 0 on 22 May 2000. We banded the male (blue over blue; BB) and female (blue over red; BR) associated with this nest on 26 May. We estimated that the pair initiated nesting on 30 April (Fig. 1). On 23 June, we observed BB with an unbanded female at Flag 11, or >1,000 m upstream of his earlier nest. Shortly thereafter, we found the pair's nest, which contained four nestlings estimated 4–5 days old, and we observed BB and the unbanded female feeding these nestlings. When we returned on 26 June to band the nestlings and

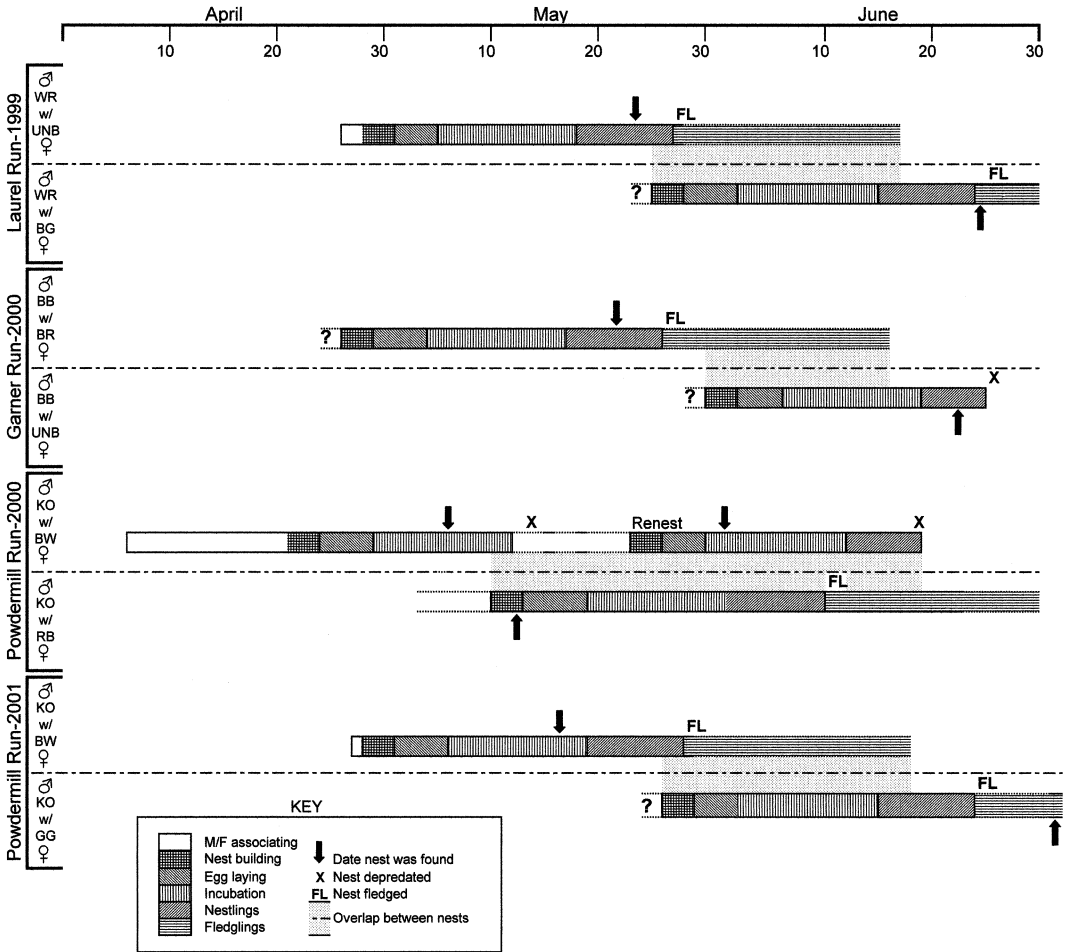


FIG. 1. Nesting chronologies of polygynous Louisiana Waterthrushes in Pennsylvania, 1999–2001. Transition dates for nesting stages prior to when nests were found were estimated based on back calculation from observed hatching or fledging dates (see Methods). Observed associations between members of a pair prior to the nest-building stage are bounded by solid lines, and inferred periods of associations have dashed lines. Question marks indicate cases where there was no observation of a pair prior to discovery of their nest. Similarly, solid lines indicate dates when fledging care was directly observed; dashed lines when it was inferred. For nesting overlaps we assumed a 3-day nest-building period and maximum 3-week postfledging period.

the female, we found that the nest had been depredated. Based on the estimated age of the nestlings when the nest was found, the nest was initiated on 3 June, or about a week after the BB's first brood had fledged. As with the previous case, BB and the unbanded female must have been paired at least several days prior to clutch initiation, but perhaps not during the nestling stage of BB's first nest (Fig. 1).

Larger than average territories are typical for polygynous males of ordinarily monoga-

mous species (e.g., Nolan 1978, Yosef et al. 1991, Breitwisch et al. 1999). The comparatively long territory (1,100 m) used by the polygynous male on Garner Run, however, likely reflected degraded water quality and not BB's polygynous status, *per se*. Garner Run is impacted by acid deposition, and such streams ordinarily have a lower density of nesting Louisiana Waterthrushes due to reduced aquatic macroinvertebrate prey density and diversity (Mulvihill 1999). It is likely, therefore, that the two females present on Garner Run

had the choice of just one territorial male. Consequently, a locally skewed sex ratio may have been the proximate cause for this instance of polygyny (Powell and Jones 1978, Smith et al. 1982, Wheelwright et al. 1992). It is possible, however, that the secondary female was associated earlier with another male who subsequently disappeared, a scenario that frequently accounts for opportunistic polygyny in monogamous birds (Smith et al. 1982, Ford 1983).

At Powdermill Run, a male waterthrush (black over orange; KO) banded as a nestling in 1999 returned on the very early date of 26 March 2000. On 28 March, he was recaptured during a territorial dispute with an unbanded male at Flag 32. From 7–20 April, KO was seen and heard singing frequently between Flags 25 and 32, often in the company of an unbanded female. The territory immediately downstream was occupied by another nesting waterthrush pair. On 21 April, we observed KO and his unbanded mate copulating near Flag 31, during which time another male waterthrush (paired status unknown) was heard singing from upstream.

We found a nest containing five eggs near Flag 26 on 6 May. During morning and afternoon nest watches on 11 May, we observed KO bringing food to Nest 26. Because the unbanded female was still incubating eggs during the early morning on 12 May, the last day that Nest 26 was known to be active, KO's food delivery probably represented a case of anticipatory feeding, commonly observed in Louisiana Waterthrushes when eggs are within a day or two of hatching (Eaton 1958, RSM unpubl. data). Nest 26 was found depredated on 16 May, but assuming the eggs had begun hatching on 12 May, the clutch was initiated no later than 25 April (Fig. 1).

On 2 May, KO was flushed up from the stream at Flag 33, a little beyond his usual territory. He flew upstream where he had a loud territorial interaction, including intense chipping and countersinging, with another male upstream of Flag 34. Over the next week, we repeatedly encountered one or two waterthrushes between Flags 33 and 37, but each time just one bird was seen well, and it was unbanded. We assumed, therefore, that the unbanded male in the territory above KO's had attracted an unbanded mate. We believe a

partially completed nest found at Flag 37 on 4 May was this new pair's first attempt, but it never contained eggs. A completed nest found at Flag 33 on 13 May contained one egg the following day and a complete clutch of six eggs on 19 May (Fig. 1).

On 24 May we caught an unbanded male in a net set just upstream of Nest 33. We assumed that this male, which we banded black over yellow (KY), was the one associated with Nest 33. A short time later we caught KO and an unbanded female in a net set just downstream of Nest 33. We banded the female red over blue (RB), but at this time we were uncertain whether she was the female from Nest 33, caught while being chased out of KO's territory, or if KO and his mate from Nest 26 had simply strayed upstream out of their territory. Later that day, however, KO and an unbanded female, presumably his mate from the depredated Nest 26, were seen nest searching between Flags 29 and 32 and again copulating near Flag 31. We observed female RB entering and leaving Nest 33 during a nest watch on 25 May, and we observed KO foraging unchallenged upstream past Nest 33 on the same day. We never again saw male KY near Nest 33. However, an apparently unmated male, never clearly observed despite our continual efforts, but presumably KY, sang frequently during the succeeding weeks between Flags 37 and 42. By this time KO had extended his territory 250 m upstream, giving him an overall territory nearly twice as long as that typically held by monogamous males on Powdermill Run (Mulvihill 1999). In retrospect, we think that KO may have directly interfered with the initial nesting attempt of KY and RB (the partial nest found on 4 May at Flag 37), in the process usurping much of KY's territory and his mate.

We discovered KO and the unbanded female's renest on 1 June (Fig. 1) near Flag 29. Nest 29 contained four eggs and was found following an observation of KO and the female vigorously defending the nest site against an eastern chipmunk (*Tamias striatus*). On 1 June, the eggs in Nest 33 began hatching, and we observed KO in front of the nest carrying a small amount of food. Based on nest watches conducted over the course of the following week, KO provisioned nestlings at Nest 33 at a rate comparable to monoga-

TABLE 1. Comparison of nestling provisioning by monogamously paired Louisiana Waterthrushes on Powdermill Run (western Pennsylvania), 1997–2000, with provisioning at two nests of a polygynous male in 2000.

Variable	Nestling stage ^a	Monogamous pairs (<i>n</i> = 20) ^b	Polygynous male	
			Primary Nest 33	Secondary Nest 29 ^c
Percent feeds by male	early	68.4	72.7	22.0
	mid	56.1	46.5	26.3
	late	51.0	64.5	—
Number of feeds by male/h	early	3.6	3.6	0.9
	mid	5.7	6.7	1.7
	late	6.1	9.8	—
Total number of feeds/h	early	5.4	4.9	4.1
	mid	10.5	14.3	6.3
	late	12.3	15.2	—

^a Early (0–3 days), mid (4–7 days), late (8–10 days).

^b Unweighted means based on a total of 253 h of observation.

^c Nestlings depredated before late stage.

mous males (Table 1), nonetheless regularly appearing near Nest 29, where his unbanded mate was incubating. On at least two occasions we observed him gathering food directly in front of Nest 29 and he did so at least once while in the company of the unbanded female during one of her incubation absences. KO was not seen near Nest 29, however, during the last few days of provisioning at Nest 33, when his feeding rates were at their highest levels (Table 1).

All six nestlings from Nest 33 fledged on 11 June (Fig. 1). The eggs in Nest 29 hatched the next day. KO was not observed at Nest 29 during 3.5 h of nest watching at Nest 29 on 13 June, but he was seen feeding Nest 33 fledglings that day. On 14 June, we observed KO throughout the day providing care to fledglings from Nest 33, and he fed nestlings just three times during 4.5 h of observation at Nest 29. During three separate 1- to 2-h nest watches on 15 June, KO fed at Nest 29 a total of 10 times. However, he did not appear there for as long as 1.5 h at a time, when he was providing care to fledglings from Nest 33. On 15 June the unbanded female from Nest 29 was caught and banded blue over white (BW).

KO's rate of nestling provisioning at Nest 29 was considerably less than at his primary Nest 33 and, importantly, his level of provisioning did not increase as expected with nestling age, nor did BW compensate by increasing her feeding rate (Table 1). Overall feeding rates at Nest 29 changed little after nestling day four, when feeding rates typically increase

substantially (Table 1). Although BW initially would have had to be considered the primary female in this polygynous trio, timing of the loss of her first nest clearly relegated her to secondary status in terms of KO's parental contribution. Nest 29 was last observed active on the morning of 18 June, at which time the nestlings appeared noticeably underdeveloped for their age (six days); the nest was found depredated on the following morning. We did not observe BW again after the loss of Nest 29. We observed KO and RB feeding their fledglings in separate brood units until at least 23 June.

Benefits associated with biparental care for the reproductive success of both sexes is believed to be the principal factor promoting monogamy in territorial altricial birds (Wittenberger and Tilson 1980). Monogamous male waterthrushes typically contribute the larger share of nestling provisioning, especially during the early nestling stage (Table 1). Females ordinarily spend the majority of time at this stage brooding their young (Robinson 1995), which presumably do not develop homeothermy for several days after hatching (Hann 1937). KO's contribution at Nest 29 was minimal during the critical early nestling period (Table 1). We did not observe KO feed newly hatched nestlings at his secondary nest until two days posthatching, and then at only comparatively very low rates (Table 1). In contrast, at all nestling stages KO provisioned his primary nest at rates nearly equal to monogamous males (Table 1), and he subse-

quently also provided substantial postfledging care to that brood. If, as preliminary observations of several broods indicate, Louisiana Waterthrushes completely divide their brood immediately upon fledging (AC and LQ unpubl. data), then this further increases the importance of biparental care to nesting success in this species.

Secondary nesting female wood warblers sometimes increase their overall feeding rate to compensate for reduced male contribution (e.g., Blackpoll Warbler, Eliason 1986; Yellow Warbler, *Dendroica petechia*, Hobson and Sealy 1989), however, BW did not (Table 1), and the development of her nestlings appeared to be affected negatively. A similar observation was made at the second nest of a bigamous Black-throated Blue Warbler (Petit et al. 1988). In that case, retarded development of the nestlings was believed to have contributed to their inability to escape squirrel predation when they were within a day of fledging. Given that we found Nest 29 as a result of the vigorous and successful joint nest defense by KO and BW against a chipmunk just one day before KO's primary nest hatched (Fig. 1), KO's preoccupation with recent fledglings from Nest 33 may have contributed to the depredation of nestlings in his later hatched Nest 29. Thus, one of the principal "costs of sharing" (Bensch 1997) associated with polygyny, reduced male parental care at secondary nests, actually was borne by BW, KO's primary (or first-mated) female due to her earlier nest loss.

In the Powdermill Run case, costs of sharing may not have been limited to reduced male assistance with parental care; they also may have included a substantial protraction of the renesting interval for the first mated female (Czapka and Johnson 2000). Waterthrushes are persistent renesters following nesting failure at any stage, not infrequently making as many as three attempts during a season (RSM unpubl. data), and the interval between these attempts typically is just 5–6 days, approximately the physiological minimum for oocyte maturation (Scott et al. 1987). We estimated that the interval between nesting attempts for female BW was 12–16 days (Fig. 1). Because of both reduced parental care and delayed renesting, the possibility of losing status following nest loss represents a clear po-

tential cost of sharing for primary females who might, therefore, be selected to interfere with a male's ability to form additional pair bonds (Temrin 1991, Bensch 1997). On the other hand, the possibility of attaining primary status in the current nesting season, or perhaps in future nesting seasons (Clemmons 1994), may at least partially compensate female waterthrushes that choose to mate with already mated males.

In the Powdermill Run case, polygyny seemed to be a direct result of the sustained aggressive take over by one male of the territory (and possibly also the mate) of another. KO's behavior in acquiring a comparatively very large territory and an additional mate in the presence of competition was very similar to that observed for males having naturally or experimentally elevated plasma levels of testosterone (Wingfield 1984, Wingfield et al. 1987). This suggested that KO's behavior itself was the proximate cause of polygyny in this case. The possibility that KO had an innate tendency to pursue this mating strategy was strengthened when he was confirmed polygynous again in 2001.

We observed fewer details of KO's breeding activity during 2001, but he was once again the first waterthrush to return to territory on Powdermill Run. Female BW, although not seen after their second nest failure the year before, was again KO's primary female, but this time their initial nesting attempt near Flag 34 was successful; we observed KO feeding a newly fledged young from Nest 34 on 29 May (Fig. 1). Although we never found the nest, a successful nesting attempt with a second color-banded female (green over green; GG) was confirmed when we observed KO and GG feeding recently fledged young near Flag 29 on 2 July. Estimated dates of nesting indicate that there was much less overlap between KO's two nests during 2001, the chronologies of which were similar to the observed nests of polygynous males on Laurel Run and Garner Run (Fig. 1). We do not know, however, if there had been an earlier nesting attempt by KO and GG, which would have resulted in considerably more overlap between broods, perhaps similar to his nestings in 2000.

Regardless of the specific circumstances leading to it, the nestling phase of the later-

hatched nests in three of the four observed polygynous pairings at most overlapped only during the late stages of fledgling care of the primary nests (Fig. 1). Although we did not observe nest provisioning behavior in these cases, it is likely that the costs of sharing for females at the secondary nests were much less compared to the first observed case on Powdermill Run (Table 1). Importantly, any mitigation of sharing costs from a reduction of nesting overlap is contingent upon comparatively very late initiation of any secondary nests. The initiation dates for the secondary nests at Laurel Run (29 May), Garner Run (3 June), and Powdermill Run in 2001 (30 May) were among the latest that we have observed during our study. In addition, because of protraction of the renesting interval, the second nest of the primary female on Powdermill Run in 2000 also was initiated on the comparatively late date of 27 May. During our study, just over 12% of all waterthrush nesting attempts were initiated after 26 May. Several possible costs of late breeding, also considered in the context of constraints on double brooding in the species (RSM unpubl. data), might similarly negate any advantages of staggered nesting for polygynous waterthrushes; these include reliance on off-peak food resources, delayed molt, molt-breeding overlap, and delayed migration.

In summary, because our observations spanned several nesting seasons and numerous study sites, we are confident in concluding that polygyny is very rare in Pennsylvania populations of the Louisiana Waterthrush. We believe that this likely stems from greater selective advantages for both sexes related to biparental nest defense and care of young, as well as short renesting intervals following nest loss. Given the degree to which monogamy appears to be enforced in this species, some theories predict that male waterthrushes should be selected to pursue a mixed mating strategy involving extrapair copulations (EPCs; Trivers 1972, Ford 1983). Extraterritorial intrusions, a behavioral correlate of the EPC strategy (Ford 1983, Pitcher and Stutchbury 2000), have been observed in waterthrushes many times during our study, but the occurrence and/or extent of extrapair fertilizations in the species remains to be determined.

ACKNOWLEDGMENTS

We thank the dozens of excellent field assistants who have assisted us over the course of our study, but would like to name the following who contributed directly to the observations of polygyny presented in this paper: M. Demarines, J. Hampton, B. Jones, K. Keto, S. Laubscher, A. Leppold, A. Lindsay, P. Marchand, J. Merchant, J. Paul, J. Puschock, and M. Retamosa. R. P. Brooks at Penn State's Coop. Wetlands Center, and J. F. Merritt and R. C. Leberman at Powdermill Nature Reserve greatly facilitated our efforts. We appreciate the cooperation given to us by the bureaus of Forestry and State Parks of Pennsylvania's Dept. of Conservation and Natural Resources, as well as the Delaware Water Gap National Recreation Area. Dr. and Mrs. H. Croft, Mr. and Mrs. S. Miller, Mr. and Mrs. A. Picadio, Mr. and Mrs. W. Rea, Mr. L. Ream, Dr. and Mrs. C. Thatcher, and Mr. M. Walsh kindly allowed us access to study sites on their properties. This study was supported in part by a grant from the U.S. Environmental Protection Agency to R. P. Brooks, with subcontracts from The Pennsylvania State Univ. to RSM and TLM. Additional funding came from Pennsylvania's Wild Resource Conservation Fund; the Netting; O'Neil and Rea field research funds of Carnegie Museum of Natural History; the Rea Internship in Applied Ecology, T. H. Nimick, Jr., and the Loyalhanna Watershed Association; and the M. Graham and Jane S. Netting Environmental Fund of The Pittsburgh Foundation. S. W. Eaton, R. C. Leberman, and A. Leppold provided helpful comments on an earlier draft of this manuscript.

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