

The White-faced Whistling-Duck now has a disjunct distribution in the Neotropics (Blake 1977). In Panama it has not been reported since the 1940s, and the few records from before this date are from east of the Canal (Méndez 1979, Ridgely 1976:50, Wetmore 1965:140). The archaeological record from Sitio Sierra indicates that its range once included Coclé province. (*D. autumnalis* is still present in the area in small numbers; RGC saw recently-killed birds being offered for sale near Sitio Sierra in 1983.)

Pre-Columbian people are known to have affected the ranges of certain bird species. The Tufted Jay (*Cyanocorax dickeyi*) and the Great-tailed Grackle (*Quiscalus mexicanus*) were deliberately transported out of their original ranges (Haemig 1978, 1979), macaws were traded into the American Southwest (Hargrave 1970), and *Nesotrochis debooyi*, the extinct flightless rail of Puerto Rico, was probably both exterminated and carried to the Virgin Islands in prehistoric times (Olson 1983 and references cited therein).

The continuing analysis of bird bones from Panamanian archaeological middens (including the 7,000-year-old Cerro Mangote shellmound; McGimsey 1956; Cooke, Olson and Ranere, unpubl.) should provide more information on the pre-conquest distributions of other extant species whose present-day disjunct ranges are likely to have been affected by local hunting pressure.

LITERATURE CITED

- BLAKE, E. R. 1977. Manual of neotropical birds. Vol. 1. Univ. of Chicago Press, Chicago.
- CAMPBELL, K. 1979. The non-passerine avifauna of the Talara Tar Seeps, north-western Peru. Roy. Ont. Mus. Life Sci. Contrib. 118.
- COOKE, R. G. 1979. Los impactos de las comunidades agrícolas sobre los ambientes del Trópico estacional: datos del Panamá precolombino. Universidad de Panamá, Actas IV Simp. Inter. Ecol. Trop. 3:919-973.

- COOKE, R. G. 1981. Los hábitos alimentarios de los indígenas precolombinos de Panamá. Rev. Méd. Panamá 6 (1):65-89.
- COOKE, R. G. 1984a. Birds and men in prehistoric central Panama. In F. Lange [ed.], Recent developments in Isthmian archaeology. British Archaeological Reports, Oxford.
- COOKE, R. G. 1984b. Some current research problems in central and eastern Panama: a review. In F. Lange and D. Stone [eds.], The archaeology of lower Central America. Univ. of New Mexico Press.
- HAEMIG, P. D. 1978. Aztec Emperor Auitzotl and the Great-tailed Grackle. Biotropica 10:11-17.
- HAEMIG, P. D. 1979. Secret of the Painted Jay. Biotropica 11:81-87.
- HARGRAVE, L. L. 1970. Mexican macaws: comparative osteology and survey of remains from the southwest. Univ. Ariz. Anthropol. Pap. 20.
- MCGIMSEY, C. R., III. 1956. Cerro Mangote: a preceramic site in Panama. Am. Antiquity 22(2), Pt. 1:151-161.
- MÉNDEZ, E. 1979. Las aves de Caza de Panamá. Editora Renovación, Panama.
- OLSON, S. L. 1983. Biological archaeology in the West Indies. Fla. Anthropol. 35(4).
- RIDGELY, R. S. 1976. A guide to the birds of Panama. Princeton Univ. Press, Princeton, NJ.
- WETMORE, A. 1965. The birds of the Republic of Panama. Part 1: Tinamidae (Tinamous) to Rynchopidae (Skimmers). Smithson. Misc. Collect. Vol. 150.

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DEFENSE OF NEST BOXES BY WESTERN BLUEBIRDS DURING THE POST-BREEDING PERIOD

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Limited availability of usable cavities influences many aspects of the biology of secondary cavity-nesting birds. For example, density of cavities, i.e., nests and/or roosts, affects breeding (von Haartman 1971) and nonbreeding (Dhondt and Eyckerman 1980) population densities, residency status (Lundberg 1979), and mating system (Gowaty 1983). Here, I report on Western Bluebirds (*Sialia mexicana*) defending nest boxes during the post-breeding period, a behavior that may indicate a shortage of cavities.

STUDY PLOTS AND METHODS

As part of a study of the population biology of Western Bluebirds and other secondary cavity-nesters, I installed 60 nest boxes on each of three study plots, 40-60 km south of Flagstaff, Arizona, in ponderosa pine (*Pinus ponderosa*) forests. Western Bluebirds were common on the plots; during four breeding seasons, from 1980 through 1983, I inspected all boxes for nests (see Braun and Balda 1983). All nestlings ($n = 297$) and some adult bluebirds ($n = 11$) found in boxes were banded with USFWS aluminum and

colored plastic leg bands. Approximately 60% of the nestlings were sexed, based on plumage characteristics established for young Eastern Bluebirds (*Sialia sialis*) by Pinkowski (1974). Male Western Bluebird nestlings that are at least 12 days old typically are more strongly colored than females on the dorsal surface of the rectrices and remiges. Nestlings were not sexed during the 1980 and part of the 1981 breeding seasons. I visited each study plot at least once a week from mid-August until early October to investigate the activity of secondary cavity-nesters that fledged from boxes, and to assess use of boxes during the post-breeding periods. Approximately 120 hours of observation were made from 1980 through 1983.

RESULTS

I observed bluebirds defending boxes against conspecifics 57 times over the four post-breeding periods. Box defense typically consisted of a bird perching on or beside a box, interrupted by short "rushing" flights toward approaching or nearby bluebirds. Such flights usually caused the intruder to halt and/or move away, after which the defender returned to its perch.

All defenders ($n = 41$) were immature birds that had fledged from boxes during the previous breeding period. Twenty of these birds were known to be males (Table 1). Defenders of unknown sex either had not been sexed as nestlings or were not observed closely enough to confidently determine sex. Box defense was seen only within or adjacent to the defender's natal territory but the boxes from which the birds had fledged were not defended.

Defenders acted against both immature ($n = 37$) and

adult ($n = 20$) bluebirds. I did not see the bluebirds defend the boxes against siblings or parents. Thirty-two of the immature intruders were unbanded and therefore foreign to the study plots. I intensively searched for nests on all plots during each of the breeding seasons and did not find any bluebird nests in natural cavities. Of the four immature intruders that were reliably sexed, all were males.

All adult intruders were unbanded males that were probably either migrants travelling through the plots, birds that had moved onto the plots from surrounding areas, or non-parental adults that had bred on the plots.

DISCUSSION

The behavior described here is unusual because I did not find bluebirds roosting in boxes during late summer and fall. Therefore, the birds were defending boxes although they were not using them at the time. Box defense could serve to decrease future competition for nest sites by reducing the number of potential competitors that imprint (*sensu* Brown and Bitterbaum 1980) and return to the site. Reduction of future nest site competition has been suggested as the function of cavity defense against conspecific immature males by male Purple Martins (*Progne subis*) during the post-breeding period (Brown and Bitterbaum 1980).

Whether bluebird defense of boxes reduced competition is unclear, however, because bluebirds in my study have seldom returned to their natal area. To date, only seven individuals, all as second-year males, have bred on their natal areas. Three of seven returnees were among those immatures observed defending boxes.

Intraspecific competition for nest sites was probably occurring during this study. Prospective breeding birds consistently preferred boxes over natural cavities; and, importantly, bluebird breeding densities increased steadily from 1980 to 1983 (Brawn and Balda, unpubl.). Therefore, nest boxes were in increasingly short supply throughout this study. Installing more nest boxes on the plots might be a suitable test of the hypothesis concerning nest site competition.

Acquisition of a nest site and subsequent establishment of a breeding territory appear to be particularly difficult for first-year male Western Bluebirds because these are usually subordinate (as evidenced by supplanting) to older males in the spring (pers. obs.). I often saw banded first-year males ($n = 14$) defending boxes, in a manner similar to that seen in the fall, early in the breeding period (March to mid-April) but they were usually ($n = 13$) displaced by older males. Similar observations have been reported with first-year male Eastern Bluebirds (Pinkowski 1977).

Alternatively, box defense may be a manifestation of emerging aggressiveness in males. Pinkowski (1975) noted that intraspecific aggressive behavior and cavity inspection begin simultaneously in 40-day-old Eastern Bluebirds (sex was not distinguished). All immature Western Bluebirds described above were at least 40 days old when observed defending boxes. I never saw immatures from second broods, which are three to five weeks younger than first-brood birds, defending boxes. Male aggression in birds is usually infrequent during the post-breeding period because of photorefractivity, but the photoperiodic response system may develop slowly in first-year birds (Farner et al. 1983). Hormonal implants in adult male bluebirds during the fall, coupled with observation of behavior around nest boxes, would test this hypothesis.

The latter hypothesis is, circumstantially, opposed by observation that overt aggressive behavior did not occur away from boxes. In addition, the hypothesis could not account for the aforementioned behavior of Purple Martins since it was second-year males that defended against immature birds.

A third, albeit speculative, explanation for box defense is that it may represent a method by which males prepare

TABLE 1. Characteristics of bluebirds defending nest boxes in the post-breeding period.

Year	No. observations/ No. birds observed	Sex (%)			Age (%)	
		Male	Female	Unknown	Immature	Adult
1980	8/3	0	0	100	100	0
1981	14/12	33	0	67	100	0
1982	23/14	43	0	57	100	0
1983	12/12	92	0	08	100	0
Total	57/41	59	0	41	100	0

for or "attune" themselves to an ecological condition with which they must eventually contend (i.e., competition for nest sites).

In summary, immature male Western Bluebirds were seen defending nest boxes against male conspecifics during each of four post-breeding periods. A limited supply of nest sites seems to be an underlying factor that promotes box defense, but the exact function of this behavior is still unclear.

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LITERATURE CITED

- BRAWN, J. D., AND R. P. BALDA. 1983. Use of nest boxes in ponderosa pine forests, p. 159-164. *In* Snag habitat management: Proceedings of the symposium. USDA For. Serv. Gen. Tech. Rep. RM-99.
- BROWN, C. R., AND E. J. BITTERBAUM. 1980. Implications of juvenile harassment in Purple Martins. *Wilson Bull.* 92:452-457.
- DHONDT, A. A., AND R. EYCKERMANN. 1980. Competition between the Great Tit and the Blue Tit outside the breeding season in field experiments. *Ecology* 61:1291-1296.
- FARNER, D. S., R. S. DONHAM, K. S. MATT, P. W. MATTOCKS, JR., M. C. MOORE, AND J. C. WINGFIELD. 1983. The nature of photorefractoriness, p. 149-166. *In* S. Mikami, K. Homma, and M. Wasa [eds.], *Avian endocrinology: environmental and ecological perspectives*. Japan Scientific Society Press, Tokyo/Springer Verlag, Berlin.
- GOWATY, P. A. 1983. Male parental care and apparent monogamy among Eastern Bluebirds (*Sialia sialis*). *Am. Nat.* 121:149-157.
- LUNDBERG, A. 1979. Residency, migration and a compromise: adaptations to nest-site scarcity and food specialization in three Fennoscandian owl species. *Oecologia* 41:273-279.
- PINKOWSKI, B. C. 1974. Criteria for sexing Eastern Bluebirds in juvenal plumage. *Inl. Bird-Banding News* 46: 88-91.
- PINKOWSKI, B. C. 1975. Growth and development of Eastern Bluebirds. *Bird-Banding* 46:273-289.
- PINKOWSKI, B. C. 1977. Breeding adaptations in the Eastern Bluebird. *Condor* 79:289-302.
- VON HAARTMAN, L. 1971. Population dynamics, p. 391-459. *In* D. S. Farner and J. R. King [eds.], *Avian biology*. Vol. I. Academic Press, New York.

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