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# BURROWING FLY LARVAE (*PHILORNIS PORTERI*) ASSOCIATED WITH MORTALITY OF EASTERN BLUEBIRDS IN FLORIDA

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ABSTRACT: We investigated mortality among nestling eastern bluebirds (*Sialia sialis*) in Polk and Highlands counties, Florida (USA) in 1999–2001. At least six species of maggots from three families of muscoid flies, Calliphoridae, Sarcophagidae, and Muscidae were found associated with the nestlings. *Philornis porteri*, the only species of obligate bird parasite collected, was found in the contents of two nests, in the ear canal and the musculature of the jaw of one nestling, and in the abdominal subcutis of another. This is the first record of bluebird parasitism by *P. porteri*. Although some nestlings were infested by tissue-invading fly larvae antemortem, the role of these maggots in the overall mortality was not clear.

Key words: Eastern bluebird, fly larvae, maggots, mortality, myiasis, *Philornis porteri, Sialia sialis.* 

### INTRODUCTION

Nestling birds are hosts to a wide range of ectoparasites that capitalize on the brief period of rapid host development and resource availability (Loye and Carroll, 1995). Among the parasites of such birds are haematophagous larvae from three dipteran families Calliphoridae, Muscidae, and Piophilidae (Uhazy and Arendt, 1986; Ferrar, 1987). Within the Muscidae, many species of the genus Philornis parasitize nestlings and sometimes adults of cavityor open-nesting birds throughout the New World subtropics and tropics (Arendt, 1985a, b). Fifty species of Philornis are known, and in the United States, six species have been collected from Texas, Puerto Rico, Louisiana, and Florida, with others reported from Mexico, Central America, other parts of the West Indies, and northern South America (Couri, 1989, 1999).

Avon Park Air Force Range (APAFR) is a 42,958 ha bombing and gunnery range located in Polk and Highlands Counties, Florida (USA; 27°38′39″N, 81°17′39″W) (US Air Force, 2001). Basic vegetation communities include scrub, oak hammock, flatwoods/prairies, swamps and marshes, pine plantations, and cutthroat grass seeps. Parts of the range include improved pasture areas used by cattle.

Nesting of eastern bluebirds (Sialia sialis) has been monitored annually since 1992 at APAFR. Weekly checks of nests in 62 to 105 artificial nest boxes were made each year during the period mid-March through mid-August. The mean annual production at Avon Park from 1992-2001 was 574 bluebird hatchlings (n=10, range=384-715). Observers noted presence/absence of adults, total number of eggs, number of young, week fledged, number of infertile eggs, number of dead nestlings, and cause(s) of mortality for each nest. Over the 10-yr period, most mortality (64%, or 653 of 1,014 deaths) in the nest boxes was attributed to predation. Raccoons (Procyon lotor) were the assumed predator when the outside of the nest box bore recent scratch marks and the nest material was pulled out. Snakes (usually corn snakes [Elaphe guttata]) were implicated when the snake itself was found in the nest box or when the box and nest seemed undisturbed, but all young were gone. Imported red fire ants, Solenopsis invicta, were the assumed mortality agent



FIGURE 1. Cross sections of fly larvae from eastern bluebirds illustrating A) skin with feather follicle (f), fly larvae (l) with cuticular spines (arrowhead), and associated inflammation (i) in the subcutis, and B) larvae with the felt chamber of a spiracle or breathing tube and cuticular spines. HE stain.

when they were present in the nest box with dead young.

From 1992–1998 and in 2000 the number of nestlings that died annually from unknown causes ranged between 0–15. In 1999 and 2001, however, an unusually high number of dead and dying nestlings was observed, and 59 and 55 nestlings respectively were known to have died from unidentified causes. This stimulated us to look more closely at a sample of the dead birds and their nests. In this paper we report the finding of maggots of *Philornis porteri* and other species associated with mortality of nestling eastern bluebirds in central Florida in 1999 and 2001.

## MATERIALS AND METHODS

Carcasses of dead nestlings were collected and preserved in 10% formaldehyde solution, frozen, or maintained on wet ice until examined. Seventeen nestlings from 11 nests were collected and examined externally, seven were examined by necropsy, and six were examined histologically. Tissues collected at necropsy were fixed in 10% neutral buffered formalin, embedded in paraffin, sectioned at 5 µm, and stained with hematoxylin and eosin. In addition, maggots were collected from six nests, and some were observed in plastic bags with the dead nestlings. These were fixed in 70% ethanol. The maggots were identified following the characteristics given in Hall (1948), Teskey (1981), Skidmore (1985), and Foote (1991). One nest associated with nestling mortality contained two second instar *P. porteri* maggots, identified first as muscids using general keys (Teskey, 1981; Foote, 1991) and then as *Philornis* using published keys and figures (Skidmore, 1985; Ferrar, 1987) supplemented by comparison with reference specimens in the National Veterinary Services Laboratories (NVSL, USDA, Ames, Iowa, USA) parasite collection. Voucher specimens were deposited in the NVSL Parasitology Reference Collection (Accession Nos. 99-30735, 99-36758 to 99-36764, 99-37282 to 99-37283, and 117373).

# RESULTS

Examined nestlings weighed 5.8–15.2 g. Externally, all 17 nestlings looked normal and only one had a small area of hemorrhage in the inguinal area. No gross abnormalities were observed at necropsy. All necropsied nestlings had fat and/or yolk sacs, and insect parts were present in their stomachs.

Cross sections of maggots (Fig. 1) were observed in three of the nestlings and a brain lesion (Fig. 2) was seen in one of the six nestlings examined histologically. The maggots were located in either the head (near or within the ears) or subcutis of the abdomen (one case). In all but one case, they were surrounded by tissue infiltrated with mixed inflammatory cells and debris. In the one case without signs of inflammation, the maggot was within neck musculature and probably migrated there after



FIGURE 2. Photomicrograph of an eastern bluebird cerebrum with presumed migration tract showing areas of necrosis and inflammation. HE stain.

the bird died. A section through a maggot tracheal trunk is illustrated in Fig. 1b. The brain lesion was present in the largest nestling examined (body weight 15.2 g) and consisted of a linear tract of neuronal necrosis and inflammation characterized by an infiltrate of multinucleate giant cells, heterophils, and macrophages containing brown pigment (Fig. 2). No larvae were observed in this nestling grossly or histologically.

The maggots were identified as members of three different families of muscoid flies: Calliphoridae, Sarcophagidae, and Muscidae. Fourteen small larvae of a calliphorid blowfly, *Phaenicia coeruleiviridis*, were identified from one large decomposing nestling. One hundred twenty-two specimens of at least three different species of sarcophagid (flesh fly) maggots, varying from small to large size, were found in six different dead nestlings or their nests. Two species of muscid fly maggots (*Sythesiomyia nudiseta* and *Philornis porteri*) were identified from nestlings and nests. One maggot of the former species was found on each of two nestling carcasses in separate nests.

#### DISCUSSION

The green-bottle blow fly, *P. coeruleiviridis*, is common in the southeastern United States and usually breeds in decaying animal carcasses. Occasionally, maggots of this species infest wounds on living mammalian wildlife or domestic animals, especially cats and dogs, but birds are rarely infested except post-mortem. Only a few species of North American flesh flies are obligate parasites of vertebrates (Baumgartner, 1988), but no species known from Florida is associated as such with birds. Perhaps a dozen species of American sarcophagids facultatively infest wounds of living vertebrates, primarily mammals (James, 1947; Baumgartner, 1988), but it is very difficult to specifically identify most of their maggots without rearing them to adults. The sarcophagid maggots we found all seemed to be saprophages. These might belong to one or more of a large number of other, non-parasitic species, which presents an even more difficult problem for definitive identification. One of the muscid flies (S. nudiseta) is a circumtropical fly with maggots that typically feed in decaying organic materials, including both invertebrate and vertebrate carcasses, particularly mammalian. Facultative myiasis may occur occasionally in living mammals (Siddons and Roy, 1942) and possibly in birds (Skidmore, 1985).

While the presence of inflammation associated with larvae in some nestlings may be an indication of antemortem infestation, it is not clear whether this contributed to mortality. In the case of the nesting with the brain lesion it is possible that the nestling survived long enough for the maggot to mature and leave before its host died, or perhaps it exited the carcass postmortem. All examined nestlings seemed to be in good nutritional condition and many contained insect parts in their stomachs. The possibility of parental nest abandonment cannot be ruled out as a primary or contributing mortality factor inasmuch as nestlings could have died from hypothermia before showing evidence of starvation.

*Philornis porteri* was the only species of obligate bird parasite collected and is the only species of *Philornis* known from Florida. These specimens compared favorably with the only known published illustration of this species (Skidmore, 1985) and with known specimens from Florida in the reference collection. Although the larvae of *P. porteri* have never been formally described, the structure of the posterior spiracular plates, the ampulliform cuticular spines, and their arrangement on the somatic segments seem to present distinctive features. Two more maggots, one in an ear canal invading bone and the other in jaw musculature, were seen in histological sections of the head of a dead bluebird nestling from this same nest. The ampullaceous shape of the cuticular spines on the sectioned maggots (Fig. 1) matched that of the spines on both the intact maggots from the nest and those in the reference collection, and it provided strong support for the identification of these maggots as P. porteri, as well. Histological sections of the abdominal musculature of a dead nestling from one other nest also contained an embedded maggot. The few visible cuticular spines of the maggot in these sections were not so distinctively shaped as those in the preceding case, but they did resemble some of the less prevalent spines on the body surfaces of reference specimens, and it is circumstantially likely that this maggot also is P. porteri.

Little is known about the life history and biology of *P. porteri*, although a few other *Philornis* spp. have been studied (Arendt, 1985a, b; Uhazy and Arndt, 1986; Teixeira et al., 1990; Couri, 1991; Delannoy and Cruz, 1991; Young, 1993; Nores, 1995), and bionomics of the genus has been reviewed generally (Skidmore, 1985; Couri, 1985). Most references to *P. porteri* deal with description and taxonomy of the adult flies (Dodge, 1955; Couri, 1989), and only one report briefly discusses its life history (Kinsella and Winegarner, 1974).

Based upon the specific observations of Kinsella and Winegarner (1974), and general knowledge from cited works on other *Philornis* spp., the life history of *P. porteri* may be summarized. Adult Philornis flies are active, loud-buzzing, and conspicuous (Smith, 1968). Gravid female flies frequent active songbird nests where they deposit several eggs in the nest or directly on nestlings, often within a few hours to 2 days following hatching of the bird's eggs. One or more subsequent waves of infestation may develop from subsequent ovipositions on each host brood. The fly egg incubation period is very brief, and within hours, using their sclerotized mouthparts, the neonate maggots burrow through the skin of

Year of collection	County	Life stage	Collected from	Reference
1947	Orange	Adult	Light trap	Dodge (1955)
1949	Dade	Adults	Fly trap	Dodge (1955)
1953	Dade	Adult	Fly trap	Dodge (1955)
1973	Highlands	Maggots reared to adults	Great crested flycatcher	Kinsella and Winegarner (1974)
1979-89	Orange	Maggots	Great crested flycatcher	Taylor and Kershner (1991)
1988	Dade	Maggots	Northern mockingbird	NVSL <sup>a</sup> reference collection
1989	Dade	Maggot	"Treepie" (captive exotic)	NVSL reference collection
1997	Clay	Maggots	Great crested flycatcher	NVSL reference collection
1999	Highlands and Polk	Maggots	Eastern bluebirds	Present study

TABLE 1. Collection records for Philornis porteri in Florida, USA.

<sup>a</sup> NVSL=National Veterinary Services Laboratory, USDA, Ames, Iowa.

a host bird. Within the host larvae feed on blood and body fluids in a cyst that forms within the subcutaneous space between the dermis and the underlying skeletal muscles. Larvae breathe through a respiratory pore in the bird's skin. Cysts are most frequent on the bird's head or in the remigial areas of the wings, but they also occur on the neck, back, and tail. Feeding and development last for 4-6 days, during which the larvae pass through three stadia and reach a maximal length of about 1.6 cm. Mature maggots exit their cysts through the respiratory pores, and occasionally may feed briefly on a nestling before moving into the nest substrate. There, each secretes a frothy cocoon in which it pupariates, emerging as an adult 11-12 days later.

In Table 1 the known/surmised collecting records for P. porteri are listed. Specimens are known from at least eight localities in four or five counties in Florida. Great crested flycatchers (Myiarchus crinitus) seem to be preferred hosts, comprising three of the six instances where maggots were collected. The NVSL Parasite Reference Collection rearing records (Accession Nos. 88-34510 and 89-41309, respectively) from an unspecified captive exotic treepie (Dendrocitta/Crypsirina/Temnurus sp.) and a northern mockingbird (Mimus polyglottos) are new host records for P. porteri. Taylor and Kershner (1991) record and nominally cite heavy infestations of Protocalliphora larvae in four Orange County flycatcher nests. However, in their monographic treatment of the Protocalliphora of North America Sabrosky et al. (1989) noted that occasional authors improperly interchange the names of the two quite different bird-parasitic fly genera Protocalliphora and Philornis. Protocalliphora spp. are relatively uncommon (though some occur in high altitudes) in warmer climates and no species is known in the southeastern United States south of central Georgia (USA). In light of the host association and the earlier (Dodge, 1955) Orange County collecting record for P. porteri, we suggest that the Taylor and Kershner (1991) Protocalliphora record properly refers to P. porteri.

Parasitism by *Philornis* spp. may be an important cause of nestling mortality in cavity- and open-nesting species of birds. Arendt (1985b) reported that 97% of nestling pearly-eyed thrasher (*Margarops fuscatus*) mortality in Puerto Rico was attributable to philornid parasitism. Reported mortality of nestlings of various species resulting from *Philornis* spp. infestations have ranged from 31–50% (Fraga, 1984; Arendt, 1985a; Nores, 1995). Parasite intensity may be related directly to nestling mortality (Delannoy and Cruz, 1991).

Although few, if any, reports of nestling mortality caused by *Philornis* spp. are the result of controlled or experimental studies, parasite removal may decrease nestling mortality. Fraga (1984) demonstrated increased nestling survival following removal of Philornis larvae by adult bay-winged cowbirds (Molothrus badius) from their own nestlings as well as from those of their screaming cowbird (*M. rufoaxillaris*) brood parasite. Smith (1968) found that preening by giant cowbird brood parasites (Scaphidura oryzivora) or nest location near stingless bee or wasp nests resulted in decreased *Philornis* parasitism and greater fledging success of nestlings of Montezuma oropendola (Gymnostinops montezuma), crested oropendola (Psarocolius decumanus), chestnut-headed oropendola (Psarocolius wagleri), and yellowrumped cicique (*Cacicus cela*).

On the other hand, infestation of various nestling bird species by *Philornis* spp. may produce only sub-lethal consequences such as decreased body mass, retarded growth, or delayed fledging (Arendt, 1985a; Young, 1993). Thomas and Shutter (2001) studied the effects of a variety of other nestling ectoparasites and found little or no adverse effect on the brood, even when infestations were of high intensity. Most of the bluebird nestlings we examined were very small and may not have survived long enough for maggots to mature. Perhaps bluebirds exemplify the opposite extreme in response to parasitism and are especially sensitive to infestation by larvae of *P. porteri*, and die sooner than other more suitable species such as the great crested flycatcher. Kinsella and Winegarner (1974) observed sometimes heavy infestations of P. porteri on nestling great crested flycatchers, but expressed doubt that the maggots had any serious effect on the host population. Taylor and Kershner (1991) alluded to P. porteri in a paragraph on mortality of great crested flycatcher nestlings, but expressed no judgment about a relationship between the two.

The largest *Philornis* larva we found in the 1999 nest collection was about 1 cm long and we never observed the larval cysts described by others, perhaps because the nestlings died shortly after infestation and before the maggots attained their normal mature size. This could account also for our failure to find puparia in the nests of infested birds. On the other hand, Kinsella and Winegarner (1974) did find P. porteri maggots encysted on nestling great crested flycatchers, and they saw some evidence that even small, less-than-fully-fed maggots could successfully metamorphose to smaller-than-normal flies. The maggots in our 2001 nest collection were 1.4-1.6 cm long and evidently fully mature; they probably would have pupariated within 24 hr. This collection indicates that, at least occasionally, P. porteri can successfully parasitize bluebird nestlings.

This is the first published report of *Phi*lornis infestation in bluebird nestlings, although several previous studies dealt with Protocalliphora spp. infestations of various North American bluebirds in areas where those bird blow flies occur (Krug, 1941; Zeleny, 1970; Pinkowski, 1977; Demas, 1989; Loye and Carroll, 1998). The effects of protocalliphorid maggots on their bluebird hosts range from negligible to fatal, but a general statement on the seriousness of bird blow fly infestations for the survival of host individuals, broods, or populations seems difficult because of the complexities of a multitude of interacting factors and circumstances (Sabrosky et al., 1989; Loye and Carroll, 1995; Heeb et al., 2000; O'Brien et al., 2001; Thomas and Shutter, 2001). Protocalliphora larvae typically do not kill their nestling hosts, but under some conditions they may do so outright, or in combination with a variety of other stresses; the same might be said of *Philor*nis larvae.

Rapid autolysis and scavenging frequently preclude a determination of the cause of mortality in passeriforms. Without both gross and histologic examination, the *Philornis* maggots would not have been recognized as a possible factor in the 1999 die-off. We suspect that *P. porteri* maggots might leave the carcass soon after host mortality in some cases and might not be found if carcasses are not examined immediately. Therefore, in any case of unexplained nestling mortality, but especially in Florida bluebirds, we recommend that nestlings be collected and stored in a variety of fashions including, fresh, frozen, and fixed immediately in formalin, pending later examination.

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#### LITERATURE CITED

ARENDT, W. J. 1985a. *Philornis* ectoparasitism of pearly-eyed thrashers. I. Impact on growth and development of nestlings. The Auk 102: 270– 280.

——. 1985b. *Philornis* ectoparasitism of pearlyeyed thrashers. II. Effects on adults and reproduction. The Auk 102: 281–292.

- BAUMGARTNER, D. L. 1988. Review of myiasis (Insecta: Diptera: Calliphoridae, Sarcophagidae) of Nearctic wildlife. Wildlife Rehabilitation 7: 3–46.
- COURI, M. S. 1985. Considerações sobre as relações ecológicas das larvas de *Philornis* Neinert, 1890 (Diptera, Muscidae) com aves. Revista Brasileira de Entomologia 29: 17–20.

—. 1989. *Philornis* Meinert, 1890—Key to adults (Diptera, Muscidae, Reinwardtinae). Revista Brasileira de Zoologia 6: 569–576.

—. 1991. *Philornis carinatus* Dodge, 1968 (Diptera, Muscidae) data on morphology, biology and taxonomy. Revista Brasileira de Entomologia 35: 109–112.

—. 1999. Myiasis caused by obligatory parasites. Ia. *Philornis* Meinert (Muscidae). *In* J. H. Guimaraes and N. Papavero (eds.). Myiasis in man and animals in the Neotropical region. A Bibliographic database. Pleidae/FAPESP, Sao Paulo, Brazil.

- DELANNOY, C. A., AND A. CRUZ. 1991. *Philornis* parasitism and nestling survival of the Puerto Rican sharp-shinned hawk. Oxford Ornithology Series 2: 93–103.
- DEMAS, V. P. 1989. Effects of parasitism by blowfly larvae *Protocalliphora sialia* (Diptera: Calliphoridae) on western bluebird (*Sialia mexicana*) nestlings. M.S. Thesis, University of Florida, Gainesville, 35 pp.
- DODGE, H. R. 1955. New muscid flies from Florida

and the West Indies (Diptera: Muscidae). Florida Entomologist 38: 147–151.

- FERRAR, P. 1987. A guide to the breeding habits and immature stages of Diptera Cyclorrhapha. Scandinavian Science Press Ltd., Copenhagen, Denmark, 907 pp.
- FOOTE, B. A. 1991. Order Diptera. *In* Immature insects, Vol. 2, F. W. Stehr, (ed.). Kendall/Hunt Publishing Co., Dubuque, Iowa, pp. 690–915.
- FRAGA, R. M. 1984. Bay-winged cowbirds (*Moloth-rus badius*) remove excess ectoparasites from their brood parasites, the screaming cowbirds (*M. rufoaxillaris*). Biotropica 16: 223–226.
- HALL, D. G. 1948. The blowflies of North America. Thomas Say Foundation (Entomological Society of America), Lafayette, Indiana, 477 pp.
- HEEB, P., M. KOLLIKER, AND H. RICHNER. 2000. Bird-ectoparasite interactions, nest humidity, and ectoparasite community structure. Ecology 81: 958–968.
- JAMES, M. T. 1947. The flies that cause myiasis in man. US Department of Agriculture Miscellaneous Publication 631: 1–175.
- KINSELLA, J. M. AND C. E. WINEGARNER. 1974. Notes on the life history of *Neomusca porteri* (Dodge), parasitic on nestlings of the great crested flycatcher in Florida. Journal of Medical Entomology 11: 633.
- KRUG, H. H. 1941. Bluebird banding in Chesley, Ontario. Bird Banding 12: 23–26.
- LOYE, J., AND S. CARROLL. 1995. Birds, bugs and blood: Avian parasitism and conservation. Trends in Ecology and Evolution 10: 232–235.
- , AND \_\_\_\_\_, 1998. Ectoparasite behavior and its effects on avian nest site selection. Annals of the Entomological Society of America 91: 159–163.
- NORES, A. I. 1995. Botfly ectoparasitism of the brown cacholote and the firewood-gatherer. Wilson Bulletin 107: 734–738.
- O'BRIEN, E. L., B. L. MORRISON, AND L. S. JOHNSON. 2001. Assessing the effects of haematophagous ectoparasites on the health of nestling birds: Haematocrit vs haemoglobin levels in house wrens parasitized by blow fly larvae. Journal of Avian Biology 32: 73–76.
- PINKOWSKI, B. C. 1977. Blowfly parasitism of eastern bluebirds in natural and artificial nest sites. Journal of Wildlife Management 41: 272–276.
- SABROSKY, C. W., G. F. BENNETT, AND T. L. WHIT-WORTH. 1989. Bird blow flies (*Protocalliphora*) in North America (Diptera: Calliphoridae) with notes on the Palearctic species. Smithsonian Institution, Washington, D.C., 312 pp.
- SIDDONS, L. B., AND D. M. ROY. 1942. On the biology of *Synthessiomyia nudiseta* v. d. Wulp. Parasitology 34: 239–245.
- SKIDMORE, P. 1985. The biology of the Muscidae of the world. Series Entomologica, Vol. 29. Dr. W.

Junk Publishers/Kluwer Academic Publishers Group, Dordrecht, The Netherlands, 550 pp.

- SMITH, N. G. 1968. The advantage of being parasitized. Nature 219: 690–694.
- TAYLOR, W. K., AND M. A. KERSHNER. 1991. Breeding biology of the great crested flycatcher in central Florida. Journal of Field Ornithology 62: 28– 39.
- TEIXEIRA, D. M., M. S. COURI, AND G. LUIGI. 1990. Notes on the biology of *Philornis rufoscutellaris* Couri, 1983 (Diptera, Muscidae) and its association with bird nests. Revista Brasileira de Entomologia 34: 271–276.
- TESKEY, H. J. 1981. Key to families—larvae. *In* Manual of Neactic Diptera, Vol. 1. J. F McAlpine, B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth and D. M. Wood (eds.). Agriculture Canada, Research Branch Monograph Number 27, pp. 125–147.
- THOMAS, K., AND D. SHUTTER. 2001. Ectoparasites, nestling growth, parental feeding rates, and beg-

ging intensity of tree swallows. Canadian Journal of Zoology 79: 346–353.

- UHAZY, L. S., AND W. J. ARENDT. 1986. Pathogenesis associated with philornid myiasis (Diptera: Muscidae) on nestling pearly-eyed thrashers (Aves: Mimidae) in the Luquillo rain forest, Puerto Rico. Journal of Wildlife Diseases 22: 224–237.
- US AIR FORCE. 2001. Plan for management of the Florida grasshopper sparrow, Florida scrub-jay and red-cockaded woodpecker at Avon Park Air Force Range, Florida. Miscellaneous Publications, Avon Park Air Force Range, Avon Park, Florida, 136 pp.
- YOUNG, B. E. 1993. Effects of the parasitic botfly *Philornis carinatus* on nestling house wrens, *Troglocytes aedon*, in Costa Rica. Oecologia 93: 256–262.
- ZELENY, L. 1970. Most serious bluebird parasite is the blowfly. Purple Martin Capital News, July 29, 1970: p. 12.

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