

SHORT COMMUNICATIONS

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ADAPTIVE SIGNIFICANCE OF TRACHEAL ELONGATION IN MANUCODES (PARADISAEIDAE)¹

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The five species of manucode *Manucodia* (including *Phonygammus*) (Diamond 1972, Beehler and Finch 1985) are monogamous and sexually monomorphic, glossy blue-black, and are medium-to-large passerines of the family Paradisaeidae. They are confined to forests of New Guinea, certain satellite islands and tropical northeastern Australia (Cooper and Forshaw 1977, Beehler et al. 1986, Coates 1990). Of the 37 other, conspicuously sexually dimorphic, birds-of-paradise (two monomorphic *Paradigalla* spp. excepted), 35 are known or presumed to reproduce polygamously. In the latter 35 species, males are promiscuous, and females attend the nest, egg(s) and young alone and unaided (Gilliard 1969, Cooper and Forshaw 1977, Coates 1990, Frith 1992, Frith and Frith 1990, 1992, 1993a, 1993b and unpubl. data). The remaining two species constitute the little-known monotypic, sexually monomorphic and monogamous genera *Macgregoria* and *Lycocorax*.

Manucodes are of considerable interest within the Paradisaeidae because the two species that have been studied are monogamous and non-territorial, range widely, and are gregarious, fig-eating specialists (Beehler 1983, 1985, Beehler and Pruett-Jones 1983). In contrast, most monogamous passerines are territorial.

The rare avian phenomenon of an elongated and looped trachea has been long-known in *Manucodia* spp. (Lesson 1826 [cited in Forbes 1882a], Pavesi 1874 [cited in Forbes 1882a], Forbes 1882a, Beddard 1891). This adaptation in *Manucodia* is well-described (Clench 1978). Clench noted that young male *M. keraudrenii* have a simple, straight trachea that develops with increasing age into an elongate, coiled and looped trachea that lies subcutaneously upon the pectoral muscle(s). Trachea elongation is far greater in males than in females (which have a shorter looped trachea that bends laterally across the pectoral muscles but may not form

a coil), and males apparently develop it faster than females. Clench found that, in contrast to *M. keraudrenii*, in *M. atra*, *M. chalybata*, *M. jobiensis* and *M. comrii* this adaptation occurs only in males and is limited to elongation of a single loop. The degree of elongation varies, in these four, being shortest in *M. atra*, which has the highest-pitched call, and longest in *M. comrii*, the call of which has been described as mournful and low (Beehler et al. 1986).

Beehler (unpubl. data) noted sexual dimorphism in calls of *M. keraudrenii*, in which males give a low, tremulous, hollow note that is answered by the female with a harsh, coughing, higher-pitched note; and in *M. chalybata* which apparently duets by one sex giving a series of *hoo* notes while the other follows that with a higher-pitched *woo-oh woo-oh woo-oh woo-oh*.

Clench (1978) noted that while *Manucodia* is the only passerine genus in which looped tracheal elongation is known, it is found in a number of non-passerine genera. To assess the possible significance of this anatomical adaptation in *Manucodia*, it is helpful to review looped tracheal elongation in non-passerines.

CRACIDAE

An elongated trachea, located subcutaneously atop the pectoral muscle(s), is found in a number of Neotropical curassows and relatives. Delacour and Amadon (1973) note that this is assumed to be associated with amplification or modification of the voice, and that a long trachea lowers the pitch of a call. Marion (1977) found that the elongation of the trachea with age in male Plain Chachalacas *Ortalis vetula* lowered the pitch of their calls. In some species of Cracidae, the elongate trachea is exclusive to males, while in others it occurs in both sexes but is slightly shorter in females.

TETRAONIDAE

Male Rock Ptarmigan (*Lagopus mutus*), in which some males are monogamous while others are polygynous, have an elongate, looped trachea that gives their calls a markedly lower pitch than those of females (Macdonald 1970, Cramp and Simmons 1983).

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Male Capercaillie (*Tetrao urogallus*), large, polygynous grouse, have a trachea lengthened into a simple loop (Newton 1899, Johnsgard 1983a). Males call loudly from a traditional courtship area to attract multiple mates. Moss and Lockie (1979) demonstrated that male Capercaillie calls contain a high level of sound at low frequency that humans cannot hear and that the carrying power of this part of the call has been underestimated.

NUMIDIDAE

In monogamous African guineafowl of the genus *Guttera*, both sexes have an elongated trachea looped into the hollow of the furcula (Chapin 1932). This feature is better developed in the Crested Guineafowl (*G. pucherani*), which has a call lower in pitch than that of its only congener *G. plumifera* (Urban et al. 1986). Maclean (1985) described the call of *G. pucherani* as "deeper and more resonant than that of Helmeted Guineafowl" (*Numida meleagris*).

GRUIDAE

Both sexes of crane species exhibit various degrees of tracheal elongation and associated sternal modification. These correlate with loudness, penetration and far-carrying quality of call notes (Bollonius in Topsell 1972, Johnsgard 1983b). While there is apparently no definite relationship between tracheal length and the typical frequency of call notes by the various crane species, those with a longer trachea do show less fluctuation of frequencies (Johnsgard 1983a).

ROSTRATULIDAE

Females of the polyandrous Painted Snipe (*Rostratula benghalensis*) have a subcutaneous tracheal loop that lies partly on the pectoral muscles (Newton 1899, Niehammer 1966). This enables them to produce a deeper, more far-carrying call than males (Johnsgard 1981, Cramp and Simmons 1983). The elongated trachea probably assists mature females in attracting multiple mates from a greater area than would otherwise be possible.

ANSERANATIDAE

The male Magpie Goose (*Anseranus semipalmata*) has an elongated subcutaneous trachea that lies in a double coil on the pectoral muscle. The honking call of this nomadic flocking species is louder and lower-pitched in the male (Marchant and Higgins 1990, *contra* Schodde and Tidemann 1988).

ANATIDAE

Both sexes of the four *Cygnus* spp. have a convoluted trachea inside the sternum which increases "greatly the resonance of the call" (Johnsgard 1968) or "account(s) for the powerful calls, in the manner of a trombone" (Scott 1972).

DISCUSSION

From this brief review, it is clear that non-passerine birds with an elongated looped trachea produce calls that are louder, lower in pitch, or carry farther than the calls of close relatives that lack this anatomical modification. The modified trachea apparently allows communication over relatively greater distances.

While not elongated or looped, dissection of a single specimen indicates that the trachea of adult male Twelve-wired Birds of Paradise (*Seleucidis melanoleuca*) is modified by having eight rings (fourth to eleventh from the bottom) "slightly dilated and flattened antero-posteriorly" to be broader and ossified along their center. This contrasts to their broad cartilaginous borders. The ossified center of each ring is slightly concave and the interval between these peculiar rings is much deeper than those above and consists of a delicate membrane to make this modified length of the trachea highly elastic and "probably correlated with the very loud harsh note of these birds" (Forbes 1882b).

The trachea of the polygynous cotingas (Cotingidae), the Red-ruffed Fruit Crow (*Pyroderus scutatus*), the umbrellabirds (*Cephalopterus* spp.), and the Calfbird (*Perissocephalus tricolor*) is modified by being anteriorly expanded. This is greatest in males, to enhance "booming" or "bellowing" advertisement/display calls (Snow 1982).

Several observers have noted the deep, loud, or far-carrying quality of *Manucodia* spp. calls (Seth-Smith 1923, Rand 1938, Rand and Gilliard 1967, Gilliard 1969, Diamond 1972, Anon. 1972, Cooper and Forshaw 1977, Coates 1990, Beehler 1991, and pers. observ.). Coates (pers. comm.) considers the Paradise Crow (*Lycocorax pyrrhopterus*) most closely allied to *Manucodia*. It has a remarkable advertisement call which, on Obi and Bisa Islands, is a loud, deep, resonant disyllabic note of about 0.3 seconds duration (Coates *in litt.*) with the quality of a deep woodwind or brass instrument.

Clench (1978) suggested that *Manucodia* species can physiologically "afford a greatly elongated trachea because they are sedentary (non-migratory) and, being relatively large forest birds, their daily flight distances are probably short and predators can be avoided by short dodging flights around foliage." This scenario would, however, appear to fit numerous non-migratory and larger rainforest-dwelling passerines; yet no other passerine exhibits an elongated and looped trachea. It is now known that *M. keraudrenii* is a peculiar passerine in being monogamous, but non-territorial and specializing on feeding upon figs (Beehler 1985). These fruits may not be economically defensible due to their unpredictability in space and time within the forest (Beehler 1983, 1985, Beehler and Pruett-Jones 1983), thus making territoriality impractical. Thus, this bird is not sedentary to the usual extent of territorial and monogamous passerines. Rather, it ranges widely and may be semi-nomadic when not breeding. *Manucodia chalybata* also feeds predominantly upon figs (Beehler 1985), and probably over a large area.

The function of the "spectacular anatomical specialization" (Clench 1978) of tracheal elongation in *Manucodia* may be the same as in those non-passerines in which it is found: to produce amplified calls with a lower pitch (as speculated by Clench 1978) for communication over greater distances. Such calls would enable birds to attract mates to a courtship site in polygynous and polyandrous species or to maintain contact in monogamous or flocking species over distance. This common function of trachea elongation in taxonomically diverse non-passerines strongly suggests that the same function may underlie its origin in a bird-of-

paradise. Thus, an elongated trachea in adult *Manucodia* may have evolved as a means of males attracting a mate(s) or to allow these non-territorial birds to maintain contact among pairs or flock members while searching a large foraging area. What appear to be manucode contact notes are relatively simple and are higher-pitched than what are considered to be advertisement calls (Coates 1990). Studies are required to determine intra- and inter-sexual differences in advertisement calls relative to degree of trachea elongation and to determine social function of these and other notes.

Bock (1963) noted that the skull morphology of *Manucodia* and *Lycocorax* strongly indicates that these birds are not primitive within the family, but are as highly specialized as *Paradisaea*. He doubts that these genera diverged from the main line of evolution leading to the true birds-of-paradise (Paradisaeinae) "before the development of the specialized courtship [polygyny]." Clench (1978) agreed with Bock that the trachea modifications in *Manucodia* are also highly specialized.

Thus, the greater trachea elongation in male *Manucodia* may have evolved as a physiologically costly (Clench 1978) secondary sexual character as a result of sexual selection (i.e., "honest advertising" of Zahavi 1975). If elongate tracheas are a relic of discarded polygynous mating systems, the main function would presumably still be for courtship by males. In the case of *M. keraudrenii*, however, the trachea may also be modified for communication over an extensive, non-territorial, foraging home range.

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DETERMINATION OF NESTLING AGE AND LAYING DATE IN TENGMALM'S OWL: USE OF WING LENGTH AND BODY MASS¹

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Key words: Tengmalm's Owl; nestlings; aging; laying date; wing length; mass; food supply.

Laying date is a central parameter in many ecological studies on birds. The date of the first egg is commonly estimated by backdating during laying from number of eggs and laying interval. Alternatively, laying dates of first egg can be calculated by backdating from age of oldest nestlings and length of the incubation period. The latter method may be advantageous, for example, in birds which are sensitive to disturbances during the early phase of breeding. Wing length is a good indicator of age in nestlings of, for example, Willow Grouse (*Lagopus lagopus*) (Myrberget 1975), House Martin (*Delichon urbica*) (Bryant 1975), Ural Owl (*Strix uralensis*) (Eriksson et al. 1984), Red-tailed Hawk (*Buteo jamaicensis*) (Bechard et al. 1985), and Northern Harrier (*Circus cyaneus*) (Saunders and Hansen 1989). For

Tengmalm's Owl (*Aegolius funereus*) nestlings, Korpimäki (1981) presented data on wing length and mass for a few nestlings, suggesting that wing length is a good estimator of age in this species.

Tengmalm's Owl is a cavity breeder readily accepting nest boxes. In northern Sweden, voles are the most important prey, and the breeding success of the owls reflects vole abundance (Löfgren et al. 1986, Hörnfeldt et al. 1990). Voles fluctuate in a three- or four-year cycle (e.g., Hörnfeldt 1978, 1994; Hörnfeldt et al. 1986).

Here, we present age-wing length and age-mass curves for wild Tengmalm's Owl nestlings in northern Sweden. The results were obtained by measuring nestlings during two years, characterized by different food (vole) supply. We explore the consistency of these parameters in different years and thus the usefulness of wing length and mass for aging nestlings and determining laying dates.

MATERIALS AND METHODS

The study was carried out in the county of Västerbotten, northern Sweden (approximately 64°N, 20°E), as

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