

ADAPTIVE SIGNIFICANCE OF
EAR TUFTS IN OWLS

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About 50 of the world's 132 species of owls have on their heads tufts of feathers commonly called "ears" or "horns." The adaptive value of ear tufts has been construed in two ways. First, the presence or absence of tufts may help distinguish species at short range (Sparks and Soper 1970, Burton 1973). That is, tufts provide a silhouette which, when combined with voice, facilitates species recognition; owls can see well enough at night to distinguish head shapes, and tufted and untufted species are often sympatric.

Myserud and Dunker (1979) proposed that ear tufts mimic the ears of mammals, and make an owl's face resemble that of a mammal during threat displays. They suggested that owl nest sites often are visited by mammalian predators such as lynx, fox and pine marten, and that in a confrontation, a defense-displaying owl that mimics the mammal's face, complete with ears, would make the predator withdraw.

Sparks and Soper (1970) offered the germ of a third idea in describing the response of the Long-eared Owl (*Asio otus*) when danger approaches: "The owl stretches upward, ear tufts erect . . . and then looks more like a broken-off stub." Catling (1972) showed that two untufted species, the Boreal Owl (*Aegolius funereus*) and Saw-whet Owl (*A. acadicus*), assume tufted poses when alarmed during diurnal roosting. He stated that the change in body shape "from rounded to narrowly oblong with outer crown feathers erected (as ear tufts) certainly makes the owl less conspicuous . . . It seems reasonable . . . that this pose is designed to conceal." I propose that ear tufts are the key feature in a camouflage in which the head simulates the end

of a broken vertical branch. This effect is possible because owls sit upright and most are colored in gray-browns and grays.

The camouflage effect can occur only if owls with ear tufts roost on branches in daylight. Diurnal owls often would lose the camouflage effect because of their activity. Furthermore, they roost chiefly at night when darkness itself hides them from visually directed animals and makes ear tufts superfluous as camouflage. Thus the camouflage hypothesis predicts the presence of conspicuous ear tufts only on nocturnal owls that roost in trees or shrubs and predicts their absence on all diurnal species.

The species recognition hypothesis likewise predicts the absence of ear tufts on diurnal owls, since such species presumably need not rely on silhouettes for identification. Thus, if diurnal species have conspicuous ear tufts, both the camouflage and species recognition hypotheses are weakened. The correlation of tufts with activity period does not test the predator mimicry hypothesis, which requires only the co-occurrence of owls and their potential mammalian predators. Thus, it predicts the absence of ear tufts on species in regions without such predators, e.g., on small remote islands.

In sum, to test the three hypotheses we must know the incidence of tufted species among nocturnal, forest-dwelling owls, among diurnal owls, and among owls in regions without mammalian predators. I have collected these data (Table 1) from Grossman and Hamlet (1964), Greenway (1967), Sparks and Soper (1970), and Burton (1973) and corroborated them with information from regional field guides.

The diurnal or chiefly diurnal owls include 21 species. None has well-developed ear tufts, as predicted by the species recognition and camouflage hypotheses. Of the nocturnal, forest-dwelling owls, 49 species have conspicuous ear tufts and 60 species do not. All the tufted species are in this group, as predicted by the camouflage and species recognition hy-

TABLE 1. Incidence of ear tufts among owls in three ecological categories.

Diurnal or chiefly diurnal species	Nocturnal, forest-dwelling species with ear tufts
Pygmy owls <i>Glaucidium</i> (13 spp.)	Scops- and Screech-owls <i>Otus</i> (25 spp.)
Great Gray Owl <i>Strix nebulosa</i>	Eagle-owls <i>Bubo</i> (12 spp.)
Hawk Owl <i>Surnia ulula</i>	Asian fish owls <i>Ketupa</i> (4 spp.)
Snowy Owl <i>Nyctea scandiaca</i>	Eared-owls <i>Asio</i> (4 spp.)
Short-eared Owl <i>Asio flammeus</i>	Crested and Maned owls <i>Lophotrix</i> (2 spp.)
African Marsh Owl <i>A. capensis</i>	Striped Owl <i>Rhinoptynx clamator</i>
Burrowing Owl <i>Athene cucularia</i>	Jamaican Owl <i>Pseudoscops grammicus</i>
Little Owl <i>A. noctua</i>	
Laughing Owl <i>Sceloglaux albifacies</i>	
Species in regions without mammalian predators	
Without tufts	With tufts
Palau Scops-Owl <i>Otus podarginus</i>	Flores Scops-Owl <i>Otus alfredi</i>
Lesser Sunda Scops-Owl <i>O. silvicolus</i>	Mentaur Scops-Owl <i>O. umbra</i>
Cuban Screech-Owl <i>O. lawrencii</i>	Bare-legged Scops-Owl <i>O. insularis</i>
Puerto Rican Screech-Owl <i>O. nudipes</i>	Giant Scops-Owl <i>O. gurneyi</i>
Fearful Owl <i>Nesasio solomonensis</i>	Andaman Scops-Owl <i>O. balli</i>
Laughing Owl <i>Sceloglaux albifacies</i>	São Thomé Scops-Owl <i>O. hartlaubi</i>
New Ireland Hawk-Owl <i>Ninox solomonis</i>	Jamaican Owl <i>Pseudoscops grammicus</i>
Solomon Islands Hawk-Owl <i>N. jacquinoti</i>	
Admiralty Islands Hawk-Owl <i>N. meeki</i>	
New Britain Hawk-Owl <i>N. odiosa</i>	
Andaman Islands Hawk-Owl <i>N. affinis</i>	
New Britain Barn-Owl <i>Tyto aurantia</i>	

potheses. The group of owls in regions without mammalian predators includes those restricted to smaller and more remote islands, since larger islands and continents have or recently had mammalian predators. Full species on islands include 7 tufted forms and 12 forms with tufts that are inconspicuous or lacking. These data weaken the hypothesis of predator mimicry, which predicts that owls of small and remote islands should lack ear tufts. Of the island species, 7 of 19 (37%) are tufted, while on continents 41 of 113 (36%) species are tufted. Thus, islands and continents have similar proportions of tufted owl species.

These results support the camouflage and species recognition theories but not the predator mimicry hypothesis. The evidence also points to a problem with the species recognition hypothesis, i.e., its assumed mechanism may fail to operate. All species with ear tufts are nocturnal and inhabit forest or brushland. For two such owls to approach each other close enough to see silhouettes, they first must communicate in the dark, usually amidst vegetation. This prerequisite long-distance link surely must occur by voice and not by sight. It seems likely that species identification is established during the vocal encounter. If so, the only proposal concerning the function of ear tufts that finds support from my tests is that of camouflage. However, the camouflage hypothesis does not fully explain the occurrence of tufts either, since more than half of the nocturnal, forest-dwelling owls lack tufts, despite the advantage these structures presumably confer. A firmer conclusion awaits field observations of perching and

roosting behavior of owls, including site preferences and postures. Such studies should be carried out in part at the vegetation heights at which owls sit, since it is at these heights that owls are seen by most other animals, including other owls.

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LITERATURE CITED

- BURTON, J. A. [ed.]. 1973. *Owls of the world: their evolution, structure and ecology*. Dutton, New York.
- CATLING, P. M. 1972. A behavioral attitude of Saw-whet and Boreal owls. *Auk* 89:194-196.
- GREENWAY, J. C. 1967. *Extinct and vanishing birds of the world*. Dover, New York.
- GROSSMAN, M. L., AND J. HAMLET. 1964. *Birds of prey of the world*. Potter, New York.
- MYSTERUD, I., AND H. DUNKER. 1979. Mammal ear mimicry: a hypothesis on the behavioural function of owl "horns." *Anim. Behav.* 27:315.
- SPARKS, J., AND T. SOPER. 1970. *Owls: their natural and unnatural history*. Taplinger, New York.

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WHAT IS THE SONG OF THE BLACK-CAPPED CHICKADEE?

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For most species of songbird, song and call notes are readily distinguishable in structure, usage and function (i.e., Thorpe 1961). Songs are usually complex, species-specific vocalizations given during the reproductive period, often showing individual differences, and sometimes dialect patterns. They usually function in pair formation and territorial advertisement. Call notes are usually simple vocalizations given throughout the year.

The whistled "Fee Bee" vocalization of the Black-capped Chickadee (*Parus atricapillus*) is generally considered to be the bird's song, but this vocalization differs in several respects from songs of other oscines (Dixon and Stefanski 1970, Ficken et al. 1978). Another vocalization, the "Gargle" (Ficken et al. 1978) shows some song-like characteristics. Thus, what vocalization or vocalizations in this species correspond to song in other oscines? Here I compare Gargle and Fee Bee vocalizations and explore their relationships to song. Since Dixon and Stefanski (1970) and Ficken et al. (1978) discussed the Fee Bee vocalization in detail, I will refer to Fee Bees mainly in comparison to Gargles.

METHODS

I recorded chickadee vocalizations at the University of Wisconsin-Milwaukee Field Station, Saukville, Ozaukee Co., Wisconsin from 1969 to 1980. Most chickadees

were individually color-banded by C. M. Weise. For several years I recorded vocalizations throughout the year, but since 1975 have concentrated on recordings near feeders in winter. Most recordings were made with a Nagra 4.2 tape recorder using a Sennheiser 104 microphone. They were analyzed with a Kay 6061 B Sona-graph using an intermediate band setting (150 kHz). I recorded several hundred Fee Bees from at least 11 different males and over 4,000 Gargles from at least 100 individuals.

RESULTS

Structure of the vocalizations. The Fee Bee is a pure tone whistle (Fig. 1A), showing little frequency modulation, with the first note higher than the second. A Gargle (Fig. 1B) consists of a series of syllables composed of transients and often with terminal trills. Both vocalizations exhibit specific distinctiveness as compared to similar vocalizations of other members of the genus and are clearly homologous with the vocalizations of the closely related Carolina Chickadee (*P. carolinensis*; Smith 1972, Ficken et al. 1978).

Occasionally a male gave a Fee Bee consisting of only the first note and even more rarely included a third note. However, over 95% of the Fee Bees (N = 111) consisted of only two notes in my study population. Measurements of sonograms are given in Ficken et al. (1978) and different males have similar vocalizations. Thus, in this study area at least, the song was quite stereotyped among individuals.

The Gargle, on the other hand, is very complex, usually consisting of 2 to 12 different syllables that can be variously combined. Each unique combination of syllables is referred to as a type. Any individual may utter several types of Gargles. For example, in 1978