ALLOPREENING IN OWLS: WHAT ARE ITS FUNCTIONS?

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ABSTRACT.—Allopreening occurs in at least 10 owl species, but its functions are poorly understood. Observations on the Spotted Owl (*Strix occidentalis*) in western Oregon between 1970 and 1978 indicated that allopreening was common between paired individuals during spring and summer (the breeding season) but was uncommon between sibling owlets or between adults and their young. A captive Spotted Owl that was imprinted on the senior author frequently solicited or initiated allopreening during spring and summer, directing such activity toward the senior author. Although Harrison (1965) proposed that the principal function of allopreening was to reduce or redirect agonistic tendencies, the relationship between aggression and allopreening in owls is not clear; outwardly, it looks like a peaceful interaction without aggressive overtones. A possible explanation for the lack of aggressive overtones associated with allopreening in owls is that selection has resulted in a display that is so ritualized that it no longer resembles the aggressive behavior from which it evolved. We do not believe allopreening is important as a means of sexual or individual recognition in owls, as was suggested by Fitzpatrick (1975) and Harrison (1965). *Received 12 October 1977, accepted 2 March 1979.*

ALLOPREENING has been reported in at least 43 avian families (Harrison 1965, 1969, Sparks 1965). Its functions are poorly understood, but prevailing hypotheses are that it (1) functions in plumage maintenance, (2) functions in individual or sexual recognition in monomorphic species, or (3) reduces or redirects aggressive tendencies that might otherwise cause one bird to attack another (Kunkel 1959, Harrison 1965, Sparks 1965, Rothstein 1977). As applied to solitary, non-parasitic species, hypotheses 2 and 3 above should probably be viewed as proximate explanations for the evolution of allopreening, the ultimate selective factor being maintainence of the pair bond to facilitate reproduction (Harrison 1965, Fitzpatrick 1975). In this paper we summarize the literature on allopreening in owls and present data on allopreening in the Spotted Owl (*Strix occidentalis*), a species we studied in western Oregon between 1970 and 1978. Possible functions and evolutionary origins of allopreening are also discussed.

PUBLISHED RECORDS OF ALLOPREENING IN OWLS

Interspecific.—Harrison (1965) described an instance in which a Tawny Owl (*Strix aluco*) and a Little Owl (*Athene noctua*) allopreened while confined together in a cage. In this instance, the Tawny Owl preened the head of the Little Owl. To our knowledge, this is the only record of interspecific allopreening in owls, and it is unlikely that it would have occurred outside captivity.

Intraspecific.—Haverschmidt (1946: 219) reported that, on two occasions before and after a pair of Little Owls copulated, they "nibbled each other in the feathers of the head." McQueen (1972: 101) reported a similar instance in which, before copulating, a pair of Screech Owls (*Otus asio*) sat in one place for over 10 min, "calling frequently, and nibbling one another around the area of their bills." Harrison (1969) described a single instance of allopreening between four juvenile Barn

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Owls (*Tyto alba*) in captivity, in which allopreening was concentrated around the edges of the facial discs and around the base of the bill.

Walker (1974: 48) reported that a displaying pair of Great Horned Owls (*Bubo virginianus*) walked toward each other, posturing and calling softly, and then the female "nibbled at the male's beak," closing her nictitating membranes as she did so. The female then lowered her head, and "the male ran his beak through her feathers in a touching caress, the epitome of gentleness."

Ligon (1968: 21) reported that, after a male Elf Owl (*Micrathene whitneyi*) fed its mate, the female followed the male closely, "fluttering her wings rapidly as the two birds moved through the foliage." Then, the male "approached his mate and they 'billed' for 30 or more seconds."

Thomsen (1971: 185) observed occasional instances in which pairs of Burrowing Owls (*Athene cunicularia*) engaged in "head scratching" between 1 February and 24 May, which is the period of pair formation and nest site selection. She stated, "usually, one bird nibbled the other's head and face feathers with its bill, and the bird being scratched usually lowered its head. Head scratching was sometimes solicited by one bird standing in front of the other with lowered head." According to Thomsen, male Burrowing Owls preened females more frequently and for longer periods than females preened males. Among adults, allopreening apparently occurred only between pair members; some instances of allopreening were observed between juveniles.

Fitzpatrick (1975) described an instance of reciprocal allopreening between a pair of wild adult Barred Owls (*Strix varia*). Allopreening was concentrated around the edges of the facial discs and the feathers around the bill, and each bird appeared to stretch its neck in efforts to offer parts of its head to the other for preening. The bird initiating allopreening appeared to be the smaller of the two, and was probably, therefore, the male. This observation occurred on 17 July, when this species would normally be feeding fledged young; the breeding status of the pair was unknown.

Oeming (1955: 47) described allopreening in a pair of captive Great Gray Owls (*Strix nebulosa*). "The male would fly to the female's stump and face her. Standing face to face with breasts touching, he would commence rubbing his beak over hers, at the same time uttering a faint droning or humming sound. Often he would circle her face with his beak in a similar manner. This was observed regularly for eight days and would occur at anytime during the day or night."

Fleay (1944: 101) reported that whenever a pair of Powerful Owls (*Ninox strenua*) roosted together during the summer, the male would usually "affectionately nibble the feathers at the base of the crown of his mate's head," before flying off to hunt. Fleay did not mention whether the female reciprocated. This species and the Burrowing Owl differ from most owls in that the male is as large or larger than the female.

ALLOPREENING IN THE SPOTTED OWL

Peyton (1910: 122) reported that after he forced a female Spotted Owl to leave her nest, she perched beside her mate in a tree near the nest and they "stuck their bills into the feathers of each other's necks and talkt [sic] in soft cooing tones." More recently, Miller (1974: 131) observed a mated pair of Spotted Owls perched side by side in a tree, "running their bills through each other's neck feathers." She also

Fig. 1. Allopreening: male Spotted Owl preening female.

mentioned, but did not describe, allopreening between a female Spotted Owl and its young.

Our observations of 127 Spotted Owl pairs between 1970 and 1978 revealed that most, if not all, paired individuals allopreened regularly with their mates during the spring and summer period. All observed instances of allopreening occurred during daylight or early twilight, when paired adults were roosting near each other. We were unable to make observations at night. Usually, the bird that initiated allopreening indicated its intent by staring at the other bird and uttering low cooing or whistling calls. If the other bird was receptive, it usually stared back, sometimes giving low cooing calls. After this brief solicitation exchange, one bird would fly or walk to a position beside the other (if it was not already in this position), where it would lean over and begin to preen the other's head. Typically, allopreening birds perched side by side, facing in the same direction (Fig. 1). Both birds partially or entirely closed their eyelids and nictitating membranes while allopreening, a behavior also described for the Oilbird (*Steatornis caripensis*) (Harrison 1965). Preening was concentrated around the facial area, the top of the head, and the side of the head facing the preener. The recipient usually moved its head, as if to facilitate preening in whatever area was being preened. Most frequently, this consisted of lowering the head to expose the nape and top of the head or turning the head slightly toward the preener to expose the facial area. Although most bouts began with one bird preening the other, preening usually became reciprocal or simultaneous as bouts proceeded. One bird would preen the other for a period, then roles would be reversed, often several times in a single bout. Simultaneous allopreening (both birds

allopreening at the same time) occurred most frequently during periods of a few seconds when birds were changing roles as reciprocal allopreeners. While allopreening, owls frequently made vocal cooing or whistling sounds that were just barely audible. Infrequently, a short staccato series of chittering notes was also given. Both sexes initiated allopreening bouts, but we did not record which sex initiated them most frequently. Bouts lasted from only a few seconds (infrequently) to several minutes and usually ended when one or both birds seemed to lose interest in allopreening and went to sleep or began to autopreen. When one bird wished to terminate allopreening but the other bird persisted, the former usually sidled (or flew) away.

The mechanics of allopreening were similar to autopreening; the preener would mandibulate or nibble the feathers of the other bird, occasionally sliding one or more feathers between its mandibles with a gentle vibrating motion. The principal differences between allopreening and autopreening were that allopreening motions were more rapid, and no attempt was made to preen a particular area or feather thoroughly. The rapidity of allopreening motions left the impression that owls were "running their bills through each others' . . . feathers," as described by Miller (1974). We never observed any instance in which owls jabbed or tugged at each other in an aggressive manner while allopreening.

SEASONAL TRENDS IN THE INCIDENCE OF ALLOPREENING

During winter (October–February), paired Spotted Owls did not forage or roost together, and there was little opportunity for allopreening to occur (Forsman unpubl. obs.). The earliest date we observed allopreening was 21 February, shortly after most pairs had rejoined near their nest sites, prepatory to nesting. Interestingly, however, allopreening occurred infrequently during pair formation, nest site selection, incubation, and brooding, and became common only after the young fledged. Furthermore, allopreening did not appear to play an important role in pre- or postcopulatory behavior; we witnessed 19 copulations, but allopreening took place on only one of those occasions, shortly after a pair had copulated.

After the young fledged in late May or early June, breeding adults began to roost together again, and we observed allopreening regularly. In July and August, allopreening seemed to be an almost daily activity for pairs that roosted together (some pairs roosted together less frequently than others). By late September or early October, pair members had begun to roost separately again, and we observed allopreening infrequently.

Although allopreening between a female Spotted Owl and her young was observed by Miller (1974), we did not observe such behavior. We did, however, see a fledged 3-month-old owlet preen its sibling momentarily.

ALLOPREENING BY A CAPTIVE SPOTTED OWL

The allopreening behavior of a female Spotted Owl that we held in captivity between 1970 and 1978 appeared identical with that of wild birds except that, because the bird was imprinted on Forsman, she directed her allopreening behavior toward him. She would not allopreen with strangers; she attacked them. This bird responded to being scratched on the head, neck, or face by reciprocally or simultaneously allopreening the hand that was scratching (preening) her. There was a

distinct seasonal pattern regarding her receptiveness to allopreening. If allopreening was initiated during winter, she was only moderately receptive and would often fly or hop away. With the onset of the breeding season in late February, she began to solicit or initiate allopreening with increasing regularity, and by midsummer (July–August) she did so nearly every time Forsman entered her cage. During the latter period, she would usually fly to a perch near him and solicit by giving low calls and leaning towards him with her eyes partially closed. If he then scratched her head, she would lower her head so that the top of her head and neck was exposed. If the preener paused momentarily, she would usually preen his hand reciprocally. In July and August, when she was most receptive to allopreening, this owl would usually continue reciprocal or simultaneous allopreening as long as Forsman had the patience to endure it. By late October or early November she again became less receptive to allopreening, soliciting infrequently.

Discussion

The individual or sexual recognition hypothesis.—We do not agree with Harrison (1965) and Fitzpatrick (1975) that allopreening is important as a means of sexual or individual recognition, at least in owls. Most owls can probably recognize the sex of other individuals by sexual differences in pitch and repertoire of vocalizations (Miller 1934, Fleay 1944, Ligon 1968, Forsman 1976). Also, the fact that allopreening often occurred repeatedly while a pair of owls roosted together during the day indicated that it served some function(s) other than individual recognition, because these birds could hardly have been uncertain about individual identities.

The plumage maintenance hypothesis.—We also doubt that allopreening is particularly important in plumage maintenance in owls because (1) owls that we kept in captivity maintained their plumage in excellent condition without allopreening, and (2) the perfunctory nature in which allopreening was performed did not appear to contribute greatly to plumage maintenance.

The ritualized aggression hypothesis.—In most instances described by Harrison (1965) and Sparks (1965), allopreening occurred in situations of obvious aggression. For instance, when a Red Avadavat (*Amandava amandava*) attempted to perch beside a potentially aggressive bird in a flock of avadavats, it assumed a solicitation posture and allowed the more aggressive individual to allopreen it, sometimes quite roughly (Sparks 1965). Harrison and Sparks (op. cit.) suggested that the submissive posture assumed by a subordinate bird informs a more aggressive individual that the subordinate is not aggressive; the agonistic tendencies of the aggressive individual are thereby thwarted and redirected into a ritualized form of aggressive behavior, allopreening. This interpretation suggests that allopreening has evolved as a ritualized form of aggressive pecking or biting behavior (Harrison 1965). By sublimating aggressive tendencies, it facilitates coexistence and thus ultimately serves to maintain the pair bond in birds, such as owls, that live much of the year in pairs. Cowbirds (*Molothrus ater*) deviate from this general pattern in that it is usually the dominant individual that solicits allopreening, and solicitation is most commonly directed toward other species rather than conspecifics (Rothstein 1971, 1977).

At first glance, our data seem to contradict Harrison's theory, because there is no indication from our observations or from the literature that allopreening in owls ever occurs in overtly aggressive situations, nor does the behavior itself resemble aggressive behavior. It generally appears to be a peaceful interaction between paired

individuals, or, infrequently, between siblings or between adults and their young. The staccato chittering call that was sometimes given during allopreening bouts was the only indication that aggression may have been involved in the display. The only other situation in which we heard this call was when we handled owls. In the latter context, the call appeared to connote irritation at being handled. The fact that Spotted Owls partially or entirely closed their eyes while allopreening (Fig. 1) could also be construed as a sign that agonism was involved. Harrison (1965) suggested that closing the eyes may act as a "cutoff" mechanism by simply removing the threatening individual from view, thereby reducing the stimulus to flee. In the case of owls, however, a more probable explanation is that the eyes are closed to prevent accidental injury while two birds are in close contact. We noticed that Spotted Owls closed their eyelids whenever there was any chance of injury (e.g. when they preened their own feathers, scratched themselves around the face, or tore prey apart).

Harrison (1965: 185) accounted for the lack of aggression (associated with allopreening) in some species by postulating that, through constant repetition of allopreening behavior, birds refine or "facilitate" their performance to the extent that, at a later stage, any agonistic tendencies are expressed as allopreening. If this were true, one should expect overt aggression to be associated with allopreening during the period of facilitation (pair formation); as already stated, we did not see evidence of overt aggression associated with allopreening at any stage in the annual cycle.

An alternative explanation for the lack of overt aggression associated with allopreening in some birds is that allopreening has become so ritualized that it is difficult to detect the origins of the behavior or the selective pressures responsible for its evolution. In owls, for instance, the gentle "nibbling" associated with allopreening could be ritualized biting behavior that has become so modified that all appearances of aggression have been eliminated. In raptors such a high degree of ritualization is to be expected, because the weapons of aggression are so well developed that even the slightest amount of overt aggression in this type of display could lead to injury.

ACKNOWLEDGMENTS

Frank McKinney, Charles Meslow, Richard Reynolds, and Dan Thompson reviewed drafts of the manuscript. We especially thank Stephen Rothstein, who refereed the paper and made numerous constructive suggestions. Any errors in interpretation are our own. The study was conducted under the auspices of the Oregon Cooperative Wildlife Research Unit: Oregon Department of Fish and Wildlife, Oregon State University, U.S. Fish and Wildlife Service, and the Wildlife Management Institute, cooperating. The USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, La Grande, Oregon funded the study (Range and Wildlife Habitat Research Project USDA-FS-PNW-1701). This is Oregon State University Agricultural Experiment Station Technical Paper No. 4571.

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