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Generational habituation and current bald eagle populations

Jeremy E. Guinn,[1] Department of Biological Sciences, North Dakota State University, Fargo, ND 55801, USA *jguinn@ uttc.edu*

Abstract: Bald eagle (*Haliaeetus leucocephalus*) populations have expanded, even as increasing human presence and activity near nesting sites has increased. The generational habituation hypothesis may explain current bald eagle behaviors associated with human presence. Generational habituation begins when a juvenile imprints on a nest area near human activity, then selects a similar nest site when it is reproductively mature. Successive generations also may imprint on nest sites near human activity, expanding the population into areas that once were considered suboptimal nesting habitat. Generational habituation has implications in several areas important to basic and applied ecology in a wide range of taxa. Generational habituation may be responsible for relatively rapid changes in a population's general behaviors, particularly in human-dominated systems.

Key words: bald eagle, habituation, *Haliaeetus leucocephalus*, human–wildlife conflicts, natal habitat preference

Habituation is defined as a reduction in an animal's responsiveness upon repeated exposure to stimuli (Goodenough et al. 2001). In occurrences of habituation, an animal does not perform a characteristic behavior, because the stimulus has proved to be harmless and is not associated with any threat (Clark 1960, Hinde 1970, Goodenough et al. 2001). The adaptive benefit of habituation is conservation of the energy that would be used responding to frequently occurring stimuli that have no detrimental effect on the animal's welfare without diminishing reactions to significant stimuli (Goodenough et al. 2001). A habituated animal retains its instinctual ability to respond to threats without continually reacting to benign activities (Rose and Rankin 2001).

During the early years of eagle conservation efforts, the bald eagle (*Haliaeetus leucocephalus*) population had generally contracted to areas devoid of human persecution (Gerrard and Bortolotti 1988). Among the dangers of living in close proximity to humans was having a nest raided by egg collectors, being shot either for predator control purposes or for target practice, and having a tree cut out from beneath a nest (Redig et al. 1983, Stalmaster 1987). Fyfe and Olendorf (1976) and Stalmaster (1987) reported decreased reproductive success due to contact with human activities. In 1982, Andrew and Mosher (1982) stressed the importance of nest sites being located away from occupied human structures, but as early as 1990, Johnsgard (1990) identified that the requirement that nest locations be free from human presence was highly variable.

Bald eagles, which once were referred to as the wilderness monarchs (Gerrard and Bortolotti 1988), have shown an ability to successfully nest in areas closer to human activity than initially reported (Fraser et al. 1985, Guinn 2004, Millsap et al. 2004, Isaacs and Anthony 2011). In contrast to several decades ago, bald eagles are currently nesting in relatively high densities near human presence in many areas of the United States and Canada. Bald eagle populations have increased in the face of increasing human recreation and development along shorelines within prime eagle habitat, and they also have expanded into new areas close to human activities. Growth in both populations has resulted in more frequent interactions with humans (Johnsgard 1990).

Bald eagle populations in the contiguous United States present a useful research model for investigating habituation. Many studies have attempted to quantify the effects of human activities on nesting bald eagles, with varying results (Mathisen 1968, McEwan and Hirth 1979, Fraser et al. 1985, Anthony and Isaacs 1989). Many studies examined the distance at which eagles flushed in response to approaching human activity (Knight and Knight 1984, Fraser et al. 1985, Buehler et al. 1991, McGarigal et al. 1991). Steidl and Anthony

[1]Present Address: Department of Environmental Science, United Tribes Technical College, Bismarck, ND 58504, USA

(2000) reported changes in bald eagle behaviors related to human presence near nest sites and the diminishing responses by eagles throughout 24-hour treatments.

The purpose of this paper is to suggest a mechanism (i.e., the generational habituation hypothesis) that describes animal habituation to human presence over time and may explain recent changes in bald eagle distribution. Generational habituation concerns a specific circumstance by which habituation is carried over to subsequent generations. Consideration of the potential effects of generational habituation should be included in developing management strategies for wildlife species in human-dominated systems.

Previous habituation research

Buehler et al. (1991) suggested that eagles become more tolerant of human activity as the breeding season progresses. However, an alternative explanation is that individuals that appear more tolerant of human activities may actually be increasing their attentiveness to their young nestlings (i.e., staying near the nest rather than flushing) in contrast to when they were defending eggs during the incubation stage or defending an empty nest before egg laying. In other words, adult eagles have invested more energy in raising nestlings to the point of fledging and, therefore, may be less likely to abandon the nest in the presence of a similar activity. Steidl and Anthony (1996) did not detect habituation by bald eagles to repeated approaches throughout the breeding season, but they agreed with Russell (1980) and Knight and Knight (1984) that eagles in areas with high human activity levels either habituate to human presence or relocate to areas with lower levels of human presence.

Animal habituation to human presence, results in desensitization to disturbance over time and is well-studied under controlled conditions in both invertebrates (Clark 1960, Rushforth 1965, Maldenado 1972, Carew and Kandel 1973) and vertebrates (Gubernick and Wright 1979, Bonardi et al. 1991). It is important to recognize that habituation may occur only when human presence is not accompanied by any harmful activity (Grier 1984, Van Krunkelsven et al. 1999). Observations of the acceptance of human activities by some bald eagle pairs led to reports that those pairs became habituated to human presence during their lives, or perhaps, during a single breeding season (Stalmaster and Newman 1978, Russell 1980). Previous research has concentrated on quantifying an eagle's response to human activity through direct observations over a limited amount of time (Fraser et al. 1985, Smith 1988). Grubb and King (1991) studied bald eagle responses to a variety of human activities in northern Minnesota. Buehler et al. (1991) found that bald eagle flush-distances from boats and pedestrian traffic on the Chesapeake Bay were greater during winter than during summer.

Generational habituation

The question for long-term management is not whether a single individual (or breeding pair) becomes desensitized to human activity, but whether the bald eagle population is becoming habituated to human activities over several generations. Are bald eagles more tolerant of human presence today than they were in the 1970s? Although Bowerman et al. (2005) suggest that suitable remote habitats may limit nesting eagle populations, observations of current eagle populations suggest that many eagles are more accepting of human activities near nests and wintering sites (Watson et al. 1999, Anthony 2001, Millsap et al. 2004). Baker and Monstad (2005) reported an increase in active bald eagle nests within the metropolitan area of Minneapolis-St. Paul, Minnesota, from 35 nests in 2000 to 78 nests in 2005. It is likely that a nestling hatched and fledged in an area of high human activity will identify with that type of nesting area and choose a similar location when it becomes reproductively mature. Herlugson (1981) found that male and female mountain bluebirds (*Sialia currucoides*) chose the same style box as their natal nest box. Although genetics and experience may play some role in choosing a nest site, the nest-selection image is not likely to be either innate or obtained through a period of trial and error later in life. The nest-selection image is likely established during the nesting stage (Ratcliffe 1980) through nest-site imprinting. In New York, nestling eagles from as far away as Alaska were translocated in attempts to restore breeding bald eagle populations (Nye 1981, Engel and Isaacs 1982). These efforts relied heavily on

nest-site imprinting, as the plan predicted that the translocated eagles would eventually breed in the area. The first 2 eagles released during the program, successfully nested in 1980 and fledged young from a nest not far from the original hacking site.

The initial step in the generational habituation process is for a nestling to imprint on a nest site. The nestling experiences a certain level of human activity during surveys in the area around its nest before fledging. The nestling identifies human activity, but without any direct persecution by humans; it does not associate human presence with any negative effects. Over the next 4 to 5 years, the subadult eagle may continue to utilize areas with human activity levels similar to its natal site. Upon maturity, the eagle has no reason to avoid selecting a nest site with similar human activity levels. This process continues with the next generation of eagles born to that bird and raised in high human activity areas. Generational habituation provides a logical explanation for changes in nesting habitat selection in species that are experiencing human encroachment.

Changes in population behavior

Generational habituation not only provides a mechanism for understanding the transmission of the nest-selection image from parent to offspring, it also explains how the offspring develop a different nest-selection image from the parent. A major question in discussions of bald eagle management is the rapid recovery of the species and accounting for eagles nesting in close proximity to humans. Generational habituation provides a theoretical mechanism for explaining how bald eagles have developed from a wilderness species to a species that routinely nests near human presence in the matter of a few decades. The following example is a hypothetical case in which a nestling deviates from its parents' ideal nesting situation. A breeding pair returns to a traditionally secluded nest site and lays eggs. At the time of hatching (or, perhaps later in the season), some form of human activity begins (e.g., construction, recreational activity, a seasonal cabin becomes occupied). The adults, though possibly disturbed by the presence of this activity, continue to care for the nestlings until dispersal. When mature, the chicks from

Figure 1: Bald eagle nest on transmission tower in western Minnesota.

that nest choose a nest site without avoiding similar human activity. Habituation above the scale of the individual proceeds as successive generations choose not to avoid nest sites in close proximity to human activity.

Another change in behavior predicted by the generational habituation hypothesisis in the use of nesting substrate. Although osprey (*Pandion haliaetus*) readily nest on telephone poles, buoys, and other human constructions (Henny and Noltemeier 1975), eagle nests on man-made structures have been rare until recently. Hypothetically, eagles raised near human habitation would also begin to utilize man-made structures as nesting substrates. Millsap et al. (2004) described 9 bald eagle nests on human structures in Florida, while Isaacs and Anthony (2011) described the first record of bald eagles nesting on a man-made structure in Oregon in 2004. Bohm (1988) provided the first record of bald eagles nesting on transmission towers in Minnesota, and Guinn (2004) described several additional nests on similar structures in the state (Figure 1). This trend may continue if more eagles that fledged from these tower nests survive to maturity, select similar nest sites, and reproduce (Millsap et al. 2004).

The generational habituation hypothesis potentially is testable in an experimental field

project with bald eagles. Groups of nests within different disturbance regimes would be selected and evaluated for human activity and eagle productivity, and fledglings would be marked for individual identification. Generational habituation would be detected by following the fledglings until they are of reproductive age and by evaluating their nest sites. If nest sites are similar to natal sites, generational habituation would be supported. However, this study would be challenging to complete. To limit the biases associated with unknown effects of inheritance, nestlings would need to be transferred from nests in high human activity areas to nests in low activity areas. Low survival of eagles entering the breeding population would be a concern, reducing sample size, and, therefore, requiring banding of a large number of nestlings that are within each disturbance regime. Bald eagles become reproductively mature at 4 to 5 years of age, requiring resilient tracking equipment, as well as good fortune throughout the study.

In addition, the mechanism controlling a pair's nest-site choice is not well-understood and would confound the study further. For example, if 1 gender is responsible for choosing the nest site, then the other gender simply complies. Similarly, complexities may arise due to a collective selection if both genders contribute to choosing the nest site. Is there a compromise between a male from a high human activity natal site and a female from a low activity site? Perhaps, even the essence of pair formation is driven by the nest site image of each individual. This is an area that requires much more research for bald eagles and other species.

Bald eagle populations may be undergoing generational habituation in many areas, including Minnesota and Florida, where they increasingly are nesting close to human presence with no observed effects on their productivity (Guinn 2004, Millsap et al. 2004; Figure 2). As habituation focuses the animal's attention and energy on the important aspects of the environment, such as prey and territory defense (Leibrecht and Askew 1980), it is likely that humans no longer pose a strong threat-association for many bald eagles. However, the need for certain protective measures near nest sites is still necessary, as there is likely a threshold distance within which human activity will disturb the majority of eagles (McGarigal et al. 1991). Currently, protective measures, such as buffer zones, continue to be useful management strategies in many areas.

Figure 2: Typical view during aerial survey of bald eagle nest (circle) in western Minnesota prairie and croplands. Note freshly plowed agricultural field within 80 m of nest.

Natal habitat preference induction

Recently, researchers have identified an important area of animal behavior that is closely related to generational habituation (Davis and Stamps 2004, Stamps and Swaisgood 2007). Natal Habitat Preference Induction (NHPI) describes a state in which experience with stimuli in an individual's natal habitat increases the probability that the individual will, following dispersal, select a habitat that contains comparable stimuli (Davis and Stamps 2004). Davis and Stamps (2004) provide a thorough review of research related to this phenomenon and describe necessary measures for future research projects. Little vertebrate research has been conducted in this area, although NHPI has applications in translocations, captive-release programs, and colonization of empty or restored habitats (Stamps and Swaisgood 2007).

Davis and Stamps (2004) provide 3 essential factors for conducting future research in this area, including: (1) assigning individuals to alternative habitats; (2) moving animals to alternative habitats just before normal dispersal from the natal area; and (3) examining habitat preferences when the animals would normally

begin dispersal. However, habitat imprinting research on avian species must begin before the crucial learning period during the nesting stage (i. e., much sooner than at the time of dispersal). Eagles likely become acquainted with their natal habitat and human presence in an area while still on the nest, not at dispersal.

If habitat preferences are formed independently of natal experience, offspring would be likely to return to the types of habitat used by the rest of the population. However, if natal experience is a key determinant of a habitat search image, offspring are more likely to recruit to a novel type of habitat. Biased dispersal may affect the rates of colonization of empty patches, which is apparent in the range expansion of bald eagles into the prairies of western Minnesota in the past 10 years (Baker and Monstad 2005) and into arid south-central Oregon in the past 15 years (Isaacs and Anthony 2011). If habitat preferences are formed independently of natal experience, their offspring would be likely to return to the types of habitat used by the rest of the population. If eagles respond in accordance with NHPI, offspring would be more likely to recruit to a novel type of habitat. Natal philopatry has been observed in breeding bald eagles (Nye 1981, Buehler 2000, Wood 2009, Isaacs and Anthony 2011); however, the distance from the natal area often allows for different habitat types and degrees of human presence.

The generational habituation hypothesis extends NHPI to include nest site selection and behavioral changes of populations over time. Bald eagle nestlings that are surrounded by human presence before and immediately after fledging likely will not avoid sites with similar human presence levels after dispersal and for nesting. Generational habituation suggests that next-generation chicks also will not avoid nesting in areas of similar human presence. Populations of bald eagles in areas with increasing human development will respond through generational habituation; however, there will be an interval of time before populations begin to recover, and there is likely a threshold amount of human development beyond which eagles will no longer find the environmental features necessary for successful nesting (Steidl and Anthony 2000, Guinn 2004). This threshold has proven to be much higher than predicted, as there are now eagles nesting in many suburban areas and in close proximity to houses (Watson et al. 1999, Millsap et al. 2004, Baker and Monstad 2005).

Management implications

Generational habituation, which is an important type of learning often overlooked by researchers, is not limited to bald eagles or to other bird species, but it can be observed in many species that thrive in urban areas with constant human activity. The tolerance of a species to human presence may be associated with innate knowledge or learned experience.

Identifying this type of developmental learning at the population level is more critical than quantifying habituation within a single pair or single generation. A population that is undergoing generational habituation is more important, from an evolutionary and management perspective than a single individual that has become habituated to a disturbance. In individual habituation, each individual during every successive generation must become habituated to human presence gradually over their lifetime. In generational habituation, however, each successive generation builds upon the behavioral changes made by immediately prior generations. Generational habituation may be responsible for faster changes in behavioral responses to human activities. Therefore, generational habituation may be a primary mechanism by which some species respond relatively quickly to the rapid human encroachment and habitat fragmentation that has occurred since the early twentieth century.

Future management of species, including bald eagle populations, near areas of human activity would benefit from incorporating the generational habituation hypothesis. For example, areas that traditionally have been described as suboptimal habitat for nesting bald eagles are now being used regularly and successfully (Baker and Monstad 2005, Johnson 2011). Isaacs and Anthony (2011) found low productivity of eagles during any new breeding area's first year, but a higher than usual productivity after 3 to 5 years of use. Many nests in these and other nontraditional areas are very productive (Guinn, unpublished data), while nesting eagles in traditional wilderness areas may suffer from high conspecific competition

(Grim and Kallemeyn 1995, Anthony 2001), which may occur when nests are closer than 3.2 km of shoreline distance apart (Isaacs and Anthony 2011). But nesting is also highly dependent on the productivity of the fishery (Gerrard and Bortolotti 1988). Therefore, there is a trend in some areas that a higher number of offspring per nest are being produced from nests in nontraditional areas. If the generational habituation hypothesis holds true and wilderness habitat is limited, then, the number of young eagles that will choose a nest site with little regard to human presence may increase faster than those that require a wilderness setting for the nest. Baker and Monstad (2005) indicated that the greatest increases in nesting bald eagles in Minnesota were at the edge of their range in the state, expanding into the prairies and cropland of southwestern Minnesota. Similar trends were observed in North Dakota, as bald eagles are now nesting in shelterbelts or single trees surrounded by cropland (Johnson 2011).

It is important to recognize that generational habituation is a dynamic and continuing process. It is unlikely that bald eagle populations currently are fully habituated to human presence. Although relatively recent research in Minnesota (Guinn 2004) and Florida (Millsap et al. 2004) suggested that eagles do not avoid areas of human activity, there is likely a threshold of human activity that will cause many eagles to abandon their nests. Tinkler (2000) suggested that refugia are still actively sought out by eagles nesting in suburban areas. Generational habituation provides a method for explaining previous trends in eagle biogeography associated with human presence and predicts future changes in the behavior of individuals of the population. If protections are enforced and public support continues, it is likely that bald eagles will become increasingly habituated to human presence near their nests. This bodes well for bald eagles and other species that may be more resilient than initially suspected.

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Jeremy E. Guinn is a faculty member and grant director at United Tribes Technical College in Bismarck, North Dakota. He holds a B.S. degree in biology from Bridgewater College (Virginia), an M.S. degree in biological sciences from Western Illinois University, and a Ph.D. degree in zoology from North Dakota State University. He is an educator, focusing on the integration of research in undergraduate science curricula, a falconer, and a predator specialist.