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ARTICLE

Recent switch by the Great Blue Heron *Ardea herodias fannini* in the Pacific northwest to associative nesting with Bald Eagles (*Haliaeetus leucocephalus*) to gain predator protection

I.M. Jones, R.W. Butler, and R.C. Ydenberg

Abstract: The Great Blue Heron *Ardea herodias fannini* Chapman, 1901 in the Pacific northwest appears to have modified nesting behaviour in response to the strong recent recovery of the Bald Eagle (*Haliaeetus leucocephalus* (L., 1766)) population. Previously undescribed, herons now often nest in close association with some breeding eagles, even though eagles depredate heron nestlings, are implicated in the recent reproductive decline of herons, and may induce abandonment of heron breeding colonies. We tested the hypothesis that breeding herons gain protection from the territorial behaviour of eagles. Natural observations and simulated incursions showed that nesting eagles actively repel other eagles within at least 250 m around the nest site, thereby establishing a relatively safe place for herons to nest. Surveys showed that 70% of heron nests and 19% of heron colonies were located within 200 m of eagle nests with high reproductive success. These herons had greater reproductive success than those nesting far from eagle nests.

Key words: Bald Eagle, *Haliaeetus leucocephalus*, Great Blue Heron, *Ardea herodias fannini*, predation, predator protection hypothesis.

Résumé : Le Grand Héron *Ardea herodias fannini* Chapman, 1901 du Pacific Northwest semble avoir modifié leur comportement de nidification en réponse au récent rétablissement marqué de la population de pygargues à tête blanche (*Haliaeetus leucocephalus* (L., 1766)). Adoptant un comportement qui n'avait pas été décrit auparavant, les hérons nidifient maintenant en étroite association avec certains pygargues nicheurs et ce, même si les pygargues s'attaquent aux héronneaux, sont impliqués dans la baisse récente de la reproduction des hérons et pourraient provoquer l'abandon de colonies de nidification de hérons. Nous avons testé l'hypothèse selon laquelle les hérons nicheurs tirent une protection accrue du comportement territorial des pygargues. Des observations en milieu naturel et des incursions simulées ont démontré que les pygargues nicheurs éloignent activement les autres pygargues d'un rayon d'au moins 250 m de leur site de nidification, établissant ainsi une aire relativement sûre où les hérons peuvent nidifier. Des levés ont démontré que 70 % des nids de hérons et 19 % des colonies de hérons étaient situés à 200 m ou moins de nids de pygargues présentant un succès de reproduction élevé. Ces hérons avaient un succès de reproduction plus élevé que celui de hérons nichant loin de nids de pygargues. [Traduit par la Rédaction]

Mots-clés : Pygargue à Tête Blanche, *Haliaeetus leucocephalus*, Grand Héron, *Ardea herodias fannini*, prédation, hypothèse de protection associée aux prédateurs.

Introduction

Some avian species are known to nest in the vicinity of a potential predator, thereby obtaining benefits from its nest defence behaviour (e.g., Blanco and Tella 1997; Tremblay et al. 1997; Bogliani et al. 1999; Richardson and Bolen 1999; Ueta 2001; Quinn and Kokorev 2002; Quinn et al. 2003); a situation referred to as "predator protection" (Richardson and Bolen 1999). For example, Red-breasted Geese (*Branta ruficollis* (Pallas, 1769)) may nest in close association with Snowy Owls (*Bubo scandiacus* (L., 1758)) or Peregrine Falcons (*Falco peregrinus* Tunstall, 1771) that aggressively defend the area around their nests from arctic foxes (*Alopex lagopus* (L., 1758) = *Vulpes lagopus* (L., 1758)), which are effective predators of ground-nesting birds. Geese thereby gain safety, but occasionally lose nestlings to these raptors, or may even fall prey themselves (Tremblay et al. 1997; Quinn et al. 2003). Similarly, in central Italy, Woodpigeons (*Columba palumbus* L., 1758) nest with territorial Hobby Falcons (*Falco subbuteo* L., 1758). Both natural and artificial Woodpigeon nests located far from hobby nests experience greater predation and reproductive failure than those located near (Bogliani et al. 1999). Woodpigeons used this strategy despite making up 15% of the diet of hobbys (Bogliani et al. 1999). In this study, we consider predator protection of Great Blue Heron (*Ardea herodias* L., 1758) colonies by Bald Eagles (*Haliaeetus leucocephalus* (L., 1766)) in British Columbia.

The Great Blue Heron *Ardea herodias fannini* Chapman, 1901 is nonmigratory and endemic to the Pacific northwest region (Butler 1997). The highest concentration of Great Blue Herons in British Columbia occurs in Georgia Strait and the Fraser River Valley (Butler 1997; Vennesland and Butler 2004). Population size and reproductive success of *A. h. fannini* have shown an apparent decline over the last 30 years (Vennesland 2000; Vennesland and Butler 2004), and it has been designated a species of special concern by the Committee On The Status of Endangered Wildlife in Canada (COSEWIC). *Ardea herodias fannini* may nest alone or in colonies containing several hundred pairs (Butler 1992; Vennesland 2000; Kenyon et al. 2007). The largest colonies historically have been located adjacent to large intertidal foraging sites. The availability of nesting trees and the absence of human disturbance

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have also been cited as influences on colony size and location (Gibbs and Kinkel 1997; Vennesland and Butler 2004; Kenyon et al. 2007).

Predators of heron nestlings or eggs include Bald Eagles, Red-tailed Hawks (*Buteo jamaicensis* (Gmelin, 1788)), Turkey Vultures (*Cathartes aura* (L., 1758)), and raccoons (*Procyon lotor* (L., 1758)). Bald Eagles are the primary predator of adult herons (Norman et al. 1989; Vennesland and Butler 2004). In contrast to herons, Bald Eagles have shown a strong increase in the Pacific northwest over the last 40 years, having largely been released from poisoning due to pesticides (Gerrard and Bortolotti 1988; Buehler 2000) and from persecution. They are known to attack Great Blue Heron nesting colonies to seize nestlings, and persistent raiding by eagles often leads to abandonment (Norman et al 1989; Vennesland and Butler 2004). The continuing population increase of Bald Eagles has led some to question the sustainability of *A. h. fannini* (Vennesland and Butler 2004).

Kenyon (2005) and Kenyon et al. (2007) suggested that predator protection may be a viable nesting strategy for *A. h. fannini*, noting they sometimes nest near active Bald Eagle nests (Vennesland 2000). For example, the largest heronry in the region, located at Point Roberts, was abandoned following frequent eagle incursions (R.W. Butler, personal communication, 2004) and relocated near a large tree a few kilometres away containing an active Bald Eagle nest. Bald Eagles are known to defend their nest sites during the breeding season (Newton 1979; Stalmaster 1987; Gerrard and Bortolotti 1988), especially from other raptors. Studies suggest that there are local and regional differences in the size of the defended area (Hancock 1970; Sherrod et al. 1976; Mahaffy and Frenzel 1987; Gerrard and Bortolotti 1988). As food for Bald Eagles is thought to be plentiful, some authors have speculated that territories are small or perhaps even nonexistent in the Pacific northwest (Gerrard and Bortolotti 1988). The lack of territorial defense suggests that Bald Eagles could not provide predator protection for Great Blue Herons.

Here we test whether the predator protection hypothesis applies to nesting Great Blue Herons in the Pacific northwest by (*i*) quantifying the degree to which Great Blue Herons associate with nesting Bald Eagles, (*ii*) documenting whether eagles defend an area around their nests and so keep potential predators of Great Blue Heron away, and (*iii*) measuring reproductive success in Great Blue Heron colonies in relation to Bald Eagle nest proximity.

Materials and methods

We studied 16 Great Blue Heron colonies and 13 Bald Eagle nests located in the Fraser River Valley and Georgia Strait regions of British Columbia, Canada, between 6 May and 29 June 2005 and between 18 April and 24 June 2006. General information on the study area and the biology of the Great Blue Heron and Bald Eagle can be found in Jones (2009).

Bald Eagle nest defense – natural observations

We observed 12 nesting pairs for a total of 200.5 h to measure their behavioural responses to other Bald Eagles and raptors. We selected for observation those nests that had been consistently used over many years, with relatively good access from the ground, good sight lines, and where landowners permitted access. We noted the time and species identity of each raptor that approached the nest, estimated the minimum approach distance using a laser range finder (Bushnell Yardage Pro), and recorded the behaviour of the intruder during the incursion. Intruding Bald Eagles were classed as either adult or juvenile, based on plumage (McCollough 1989). We recorded defensive responses by the resident pair, including vocalizations, "hop-hovers" (an eagle in the nest or perched nearby hops or lifts off and hovers above the nest), flight (circling the nest or flying toward or over the intruder), talon displays (an eagle flies and drops its feet to display the talons), and stoops. We assume this sequence of behaviours reflects increasing aggressiveness by the nesting pair.

Bald Eagle nest defense – experiment

We presented a decoy of an adult Bald Eagle in combination with eagle call playbacks to measure the extent and intensity of Bald Eagle nest defence at the 12 Bald Eagle nests described above (see Mahaffy and Frenzel 1987). We used a decoy made from high-density polyurethane foam, based on measurements of an adult female Bald Eagle specimen in the Simon Fraser University Museum, painted to resemble adult Bald Eagle plumage.

Trials were carried out during the incubation period. Prior to each trial, the decoy was affixed in a perched position atop a 3 m pole. A tubular drop curtain placed over the decoy could be tripped remotely to reveal the decoy and commence a trial. A repeating loop of Bald Eagle calls was created using calls from a commercially published CD (Peterson 2005). Once the curtain was dropped, we broadcast calls for 20 s at 5 min intervals, using a 40 W speaker powered by a 20 W amplifier. A trial ran for 1.5 h.

There were three treatments, with decoy presentations at 50, 100, and 200 m, and a control presentation at 50 m. Control treatments consisted of a black block of the same size and displayed in the same manner as the decoy treatments, and with call playback apparatus set out but not activated. The order of treatments was randomized for each nest and no nest received a duplicate treatment. A minimum of 5 d were allowed between successive treatments to the same nest, and to minimize exposure of the eggs, trials were not carried out when raining. We were able to complete nine control trials, eight trials at 50 m, seven trials at 100 m, and seven trials at 200 m. We recorded the number of eagles present, and the time and type of each defensive behaviour, categorized as above. We report the responses of the resident that responded with the greatest frequency and intensity.

Great Blue Heron nesting success surveys

Surveys of known heron colonies were conducted using standardized protocols developed by the Heron Working Group (see Vennesland 2000; Vennesland and Butler 2004). Heron colonies ($n = 15$) were visited up to three times during the nesting season to count the number of nests, to determine which were active, to count the number of associated adults and young, and to determine the age of young. A colony was defined as two or more nests within 10 m of one another. Steps specified in the protocol to minimize disturbance at nesting colonies were followed closely. A nesting attempt was considered to have been initiated if an incubating heron was present in a nest. Nestlings were considered to have fledged when they perched on branches near the nest or when they reached about 8 weeks old (Moul et al. 2001). Nesting productivity was estimated by observing samples of initiated nests that were mapped and followed through the nesting season. Sample sizes varied at each colony site depending on the size of colonies and the ease of viewing nests. All nests were sampled at small colonies (<50 nests), and at least 30% of the total number of nests was observed at larger colonies (50–400 nests). Nesting success is defined as the number of fledglings per active nest. The location of Bald Eagle nests in proximity to heron colonies was determined during surveys in 2005 and 2006 (full details in Jones 2009) and from information provided by Ministry of Environment and Canadian Wildlife Service biologists.

Tsawwassen Heronry case study

We studied interactions between Bald Eagles and Great Blue Herons at English Bluff in Tsawwassen, adjacent to the BC Ferry Causeway (49°1′34″N, 123°06′04″W), between 27 March and 29 June 2006. Here an eagle pair and many herons nested together. Resident eagle defensive behaviour toward other Bald Eagles and to raptors in proximity to their nest, incursions by eagles into the heronry causing disturbance of nesting herons, and the depreda-

tion of heron nests were recorded from a vantage point 100 m from the colony. Observation periods (2–8 h in duration; 130 h in total) were rotated through available daylight hours spread throughout the survey period. A disturbance of the colony was defined as any behavioural response from more than one heron when an antagonist was present (after Vennesland 2000, Vennesland and Butler 2004). A predatory disturbance was recorded if an avian or terrestrial predator was noted entering the colony and attempting to depredate an adult or nestling heron or heron eggs. Typically, herons responded to predation attempts by alarm calling, challenging the intruder through posture, kicking and jabbing at predators, or flushing from the nest (as described in Vennesland 2000). Depredation was recorded when a predator removed a chick from a heron nest. We were able to discern the resident pair of nesting Bald Eagles from other intruding eagles in the territory through distinctive features in their plumage and their high degree of fidelity to the nest site.

Statistical procedures

We used contingency analysis to compare the response frequency of resident Bald Eagles to different classes of intruders. We compared the responses of nesting Bald Eagles to control and model presentations at different distances using Student's *t* tests. The nesting success of Great Blue Herons in colonies close to and far from breeding eagles was compared using Student's *t* tests within each of the study years. All statistical analyses were completed using the statistical software JMP version 7 (SAS Institute Inc., Cary, North Carolina, USA).

Results

Natural nest defense observations

A total of 298 intrusion events were recorded in 200.5 h of observation, yielding a rate of 1.49 incurisons/h. Residents responded to 57.4% of approaches by all raptors to within 250 m horizontal distance from the nest. Contingency analysis revealed significant differences among the response to the different classes of intruder (df = 2; likelihood-ratio $\chi^2 = 74.94$, $P < 0.0001$; Pearson $\chi^2 = 69.81$, $P < 0.0001$), with more frequent responses to adult Bald Eagles (75.9%) than to immature Bald Eagles (50.7%) and less often to other species (Red-tail Hawks, Northern Harriers (*Circus cyaneus* (L., 1758)), and Turkey Vultures; 17.1%). We detected a significantly (df = 1, whole-model $\chi^2 = 4.10$, $P = 0.0405$) diminishing probability of response by resident eagles with distance from their nests (Fig. 1). There were few responses beyond 300 m.

Nest defense experiment

Behaviours noted by resident pairs during decoy presentations were similar to those displayed during natural incursions by other eagles. During experimental trials, a total of 167 individual behavioural events were recorded, at mean rate of 3.6 responses/h. Of these, 55.7% were vocalizations, 32.3% were flight responses (fly toward and return to the nest or fly over the decoy), 6.5% were talon displays, 3.6% were stoops, and 1.7% were hop-hovers (Fig. 2). Eagles never struck either the decoy or the control block. Eagles exhibited all six behavioural responses at 50 m, five of the responses at 100 m (no stooping), and four of the responses at 200 m (no stooping or hop-hovering).

During the nine control presentations, resident eagles gave only a single call and did not perform any other of the defensive responses noted in experimental trials. Call response frequency was significantly greater during treatment than control when compared using one-way analysis ($t = 2.05$; control crossed with 50 m, 100 m, and 200 m treatments yields $P = 0.0016$, 0.0277, and 0.0409, respectively).

Heron reproductive success surveys

In total, 1165 nests were counted within the 15 colonies surveyed. Colonies ranged in size from 3 to 400 nests. Most nests (825, or 70.8%) were in the three largest colonies, each of which was associated with a Bald Eagle nest within 200 m (Fig. 3). These colonies are 2–4 times larger than the largest colony without an active eagle nest within 200 m. In pairwise comparisons, nesting success is significantly greater in nests close to than far from eagles in both 2005 (Student's *t* test, $t = 3.34$, $P < 0.001$) and 2006 ($t = 8.44$, $P < 0.001$). Mean nesting success close to active eagle nests was 1.75 (95% confidence limit = ±0.15) and 1.81 (±0.15) in 2005 and 2006, respectively. Comparatively, mean nesting success was 1.04 (±0.25) and 0.93 (±0.14) in 2005 and 2006, respectively, at heron nests located far from an active eagle nest (see Fig. 4). The comparison indicates that predator protection is worth 0.5–0.7 fledglings per active nest.

A natural comparison is provided by events at the heronry at the Canadian Forces Base (CFB) Chilliwack, which in 2005 had an active Bald Eagle nest within 200 m of the colony throughout the duration of the heron breeding period. In 2006, the eagle nest was blown down by strong winds just after the herons had laid eggs. The Bald Eagles intermittently worked on rebuilding the nest, and though they sometimes defended their territory, they were often absent for long periods. This event provided a natural removal experiment, enabling comparison of Great Blue Heron nesting success in successive years at the same site, with and without actively nesting Bald Eagles. Mean nesting success at the Chilliwack colony was 1.62 (95% confidence interval = ±0.33) fledglings per active nest in 2005 when eagles were present and 1.11 (±0.23) in 2006 when eagles were absent (Fig. 4). Heron nesting success was higher in the Chilliwack colony than in other colonies far from eagle nests (Student's *t* test, $t = 2.10$, $P < 0.05$) in 2005, but lower

Fig. 1. Logistic fit of response (dependant variable) toward all Bald Eagle (*Haliaeetus leucocephalus*) intruders with distance from the resident eagle's nest. A yes (Y) response was determined if resident nesting Bald Eagles displayed any of the territorial behaviour responses recorded (see text) to an intruding Bald Eagle. A no (N) response was determined if resident nesting eagles did not display territorial behaviour during intrusion by nonresident eagles. The *x* axis represents the nearest horizontal distance that an intruder approached, while the *y* axis represents the frequency of defensive responses, and is read by measuring the distance from the trend line to the appropriate axis. The expected frequency of a yes response is read by measuring the distance between the trend line and 1.00. Individual data points are jittered for each distance showing the total number of data points represented. The probability of response declines significantly with distance (df = 1, whole-model $\chi^2 = 4.198$, $P = 0.0405$).

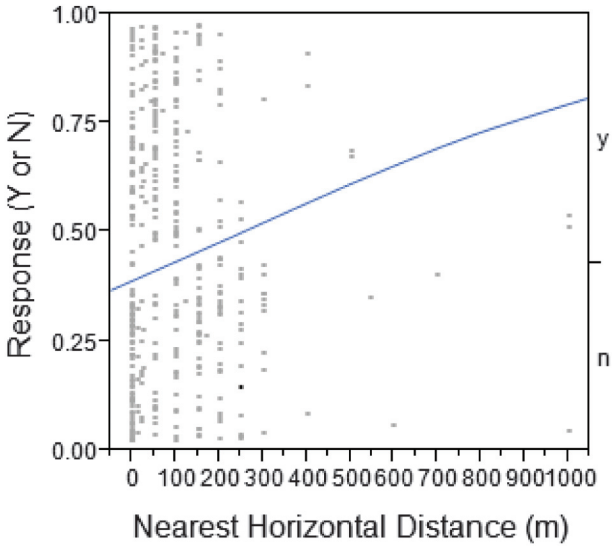
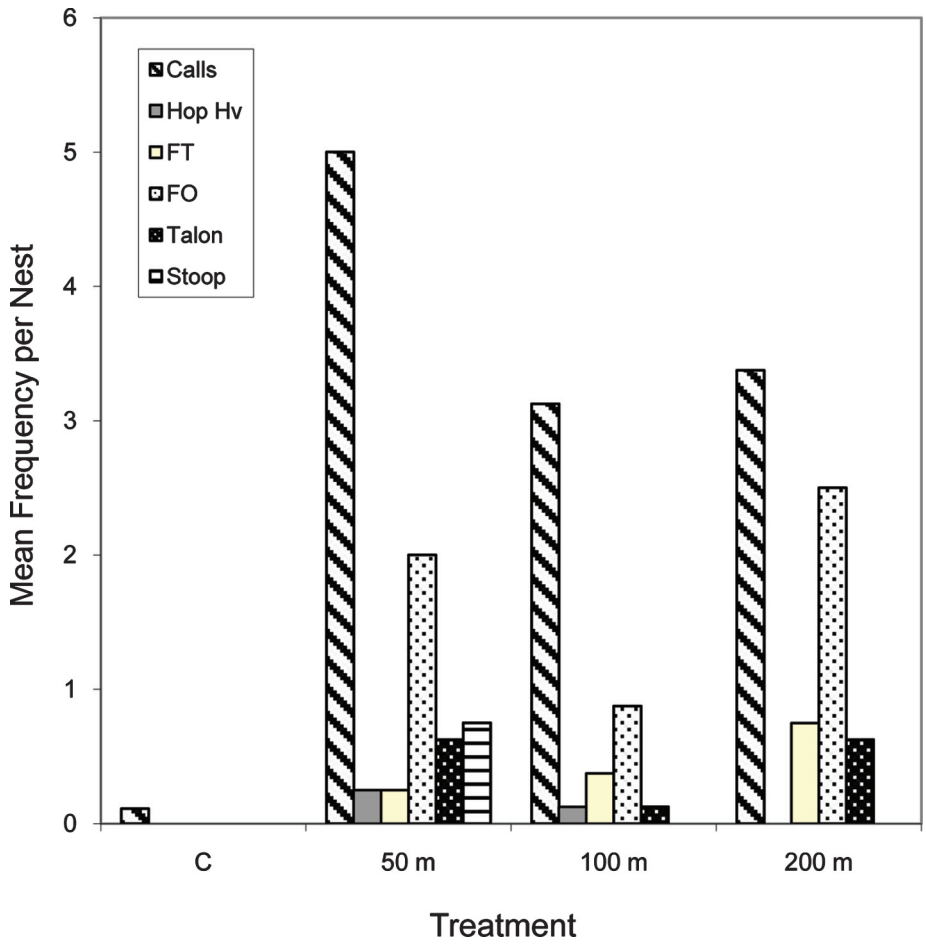


Fig. 2. Comparisons of the mean frequency of behaviours that resident Bald Eagles (*Haliaeetus leucocephalus*) performed during control (C), 50, 100, and 200 m experimental treatments. Behaviour displayed by resident eagles is coded as follows: Calls, calling; Hop Hv, hop and hover in flight above the nest; FT, fly toward and return to the nest; FO, fly over the decoy; Talon, drop talons as fly over decoy; Stoop, folding wings and stooping at the decoy. Controls elicited almost no response. Resident Bald Eagles exhibited all six behavioural responses at 50 m, five of the responses at 100 m (no stooping), and four of the responses at 200 m (no stooping or hop-hovering).



than in other colonies close to eagle nests in 2006 (t = 4.03, $P < 0.001$). These results are based on nesting success measures in 324 (2005) and 471 (2006) heron nests with the same 15 colonies measured in each year.

Observational case study at the Tsawwassen Heronry

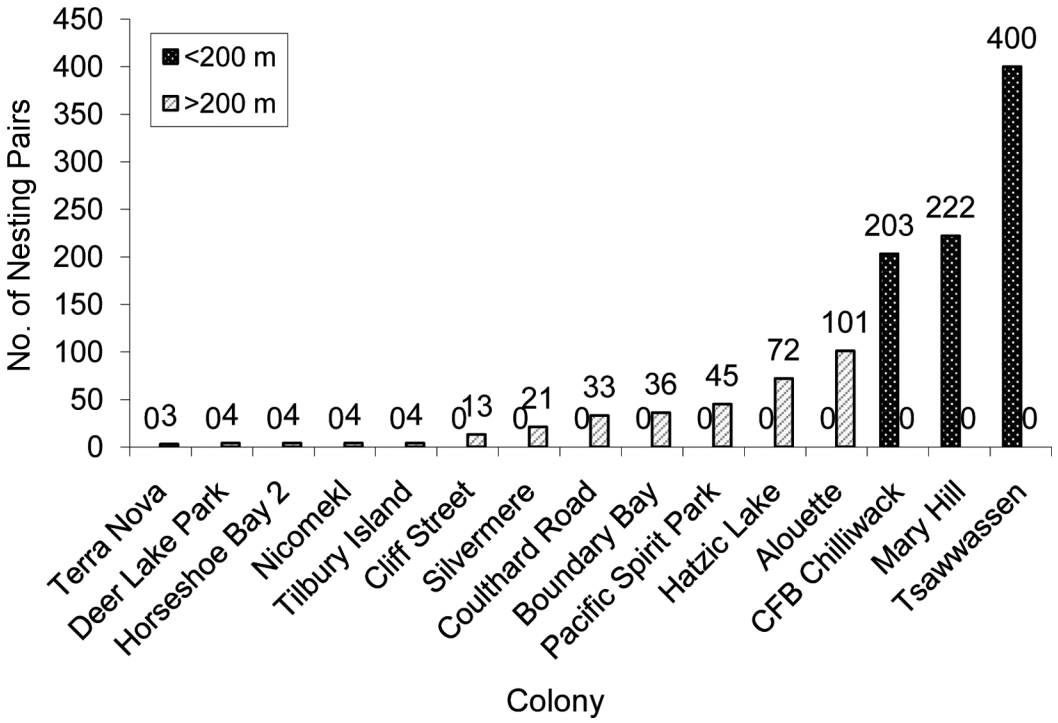
A pair of Bald Eagles nested in the colony throughout the heron breeding season and raised two eaglets. Heron nests ranged from approximately 0 to 100 m (horizontal) from the nest, with some nests in the same tree. All herons nested at a lower elevation than the eagles. A total of 192 incursions occurred during the 130 h of observation (1.47 incursions/h, almost identical to that recorded during natural nest defense observations, above), ranging in intensity from overflights to attacks on adult herons and landing on heron nests. The resident pair of eagles responded to 75% of all incursions by other Bald Eagles and responded to all attempts to attack herons or depredate nests in the colony by chasing and striking eagles that did not leave immediately following calls or flight displays. These behaviours were similar to those witnessed during our observations and experiment on the territorial defence. Low-level overflights by resident Bald Eagles, circling over the colony in proximity to their nest, transiting to and from their nest site, or perching in trees above the colony rarely induced a response among nesting herons.

No herons or nestlings were depredated by nonresident eagles, but the resident Bald Eagles made eight attempts, succeeding on four occasions. In seven of the eight attempts, adult herons defended their chicks by kicking and pecking at the eagle, successfully defending their nest on four occasions. On two of these four occasions, the nesting herons pecked the intruding eagle vigorously enough to knock the eagle off the nest and onto the ground. In total, resident eagle incursions occurred 0.06 times/h of observation. Depredation of chicks by resident eagles occurred 0.03 times/h of observation.

Discussion

Our findings support the predictions of the hypothesis that breeding *A. h. fannini* associated with breeding Bald Eagles gain protection from nest predators. Our survey showed that the majority of *A. h. fannini* (70.8% of 1165 nests) nested in three large colonies, each of which was closely (<200 m) associated with an active and long-standing Bald Eagle nest. Our observations showed that eagles defended an area around their nest that extended to a least 200 m, aggressively responding to other eagles and raptors that might possibly depredate heron nestlings. Furthermore, our experiment showed that the response is specific to raptors, as our control decoy elicited no responses, and other birds such as crows and gulls were also ignored by eagles. Our survey showed that heron colonies in close proximity to eagle nests enjoyed higher nesting success than those far from eagle nests. Finally, our observations at the Tsawwassen colony showed

Fig. 3. The distribution of colony size (number of nests) in the 15 colonies of the Great Blue Heron *Ardea herodias fannini* surveyed. Nests are classed as close to (<200 m; shaded cross-hatched bars) or far from (>200 m; open hatched bars) the nearest active Bald Eagle (*Haliaeetus leucocephalus*) nest. In total, 1165 nests were counted within the 15 colonies surveyed. Colonies ranged in size from 3 to 400 nests. Of those nests, 70.8% (n = 825) were in the three largest colonies, each of which was close to a Bald Eagle nest.



that the resident eagle pair successfully drove off intruding Bald Eagles attempting to depredate heron nestlings, but did themselves on occasion take heron nestlings.

A majority of the herons in the 15 colonies surveyed were located in just three colonies, each within 200 m of an active Bald Eagle nest. These colonies were at least twice as large as the largest colony located far (>200 m) from an active eagle nest. Birds nesting colonially often benefit from predation dilution, collective nest defence, and increased vigilance (Fuchs 1977; Burger 1984; Blanco and Tella 1997). Hence, it is possible that the higher success of nests in colonies close to a Bald Eagle nest is attributable to their large size, rather than to the proximity of the eagle pair. The measurements made at the CFB Chilliwack colony, at which nesting success fell to the level of other non-eagle associated colonies in the year that the eagle nest blew down (see Fig. 4), suggest that the proximity of the eagle plays an important role.

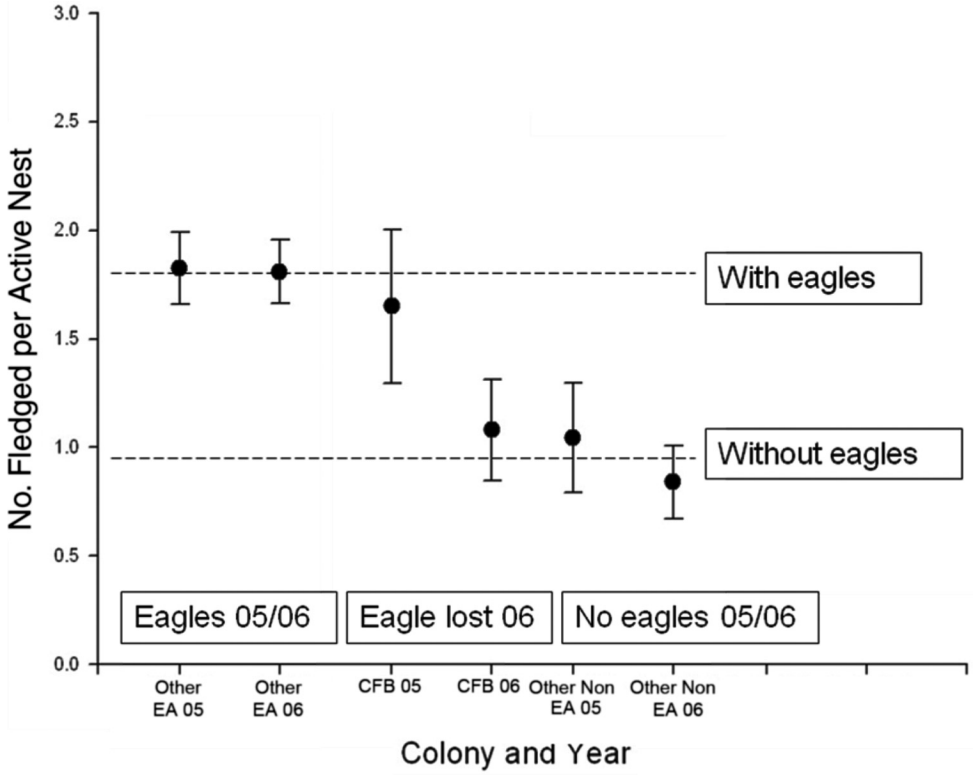
The benefits gained from colonial nesting and predator protection need not be mutually exclusive and may reinforce each other. Herons do not collectively defend nest sites, but do use a distinctive alarm call when predators approach the colony and may therefore incur a benefit from collective vigilance (Vennesland 2000). We observed that alarm calling by nesting Great Blue Herons often alerted the resident Bald Eagles to the presence of other eagles. This potentially benefits both species by allowing for more efficient defence of the territory from other eagles due to an increase in vigilance by the group (Campobello et al. 2011).

Another possibility is that Bald Eagles preferentially nested near some heron colonies, because the open mudflats that support successful heronries also provide eagles with good hunting opportunities. Although the river and estuarine mudflats in the study area likely represent good hunting opportunities for aquatic and avian prey for Bald Eagles, it does not seem likely that Bald Eagles would be successful in initiating this association. Great Blue Heron nests are small, quickly built, and colonies readily relocate when disturbance becomes too great (Vennesland 2000). Bald Eagle nests, in contrast, are large structures, take weeks or months to construct, and last for years. Significantly, we have recorded a number of cases in which herons established colonies in trees with existing eagle nests, which suggests that herons seek predator protection, at least under some circumstances. Indeed, we observed herons at the Tsawwassen colony appeared to discern between intruding and resident eagles, and largely ignored overflights by the resident Bald Eagle.

The association of Great Blue Heron colonies with nesting Bald Eagles in the Pacific northwest was first noticed in about the year 2000. Prior to that, heron reproductive success had fallen and colony abandonments had been documented, but were attributed to disturbance from the expanding urban and suburban areas in the Georgia Basin, or to pollution. Vennesland (2000) and Vennesland and Butler (2004) first showed that colony abandonment is strongly associated with persistent raiding by Bald Eagles. We surmise that in the course of the 1990s, good-quality eagle breeding sites became occupied as the Bald Eagle population in the Fraser Valley and Georgia Strait regions rose steadily after the 1970s (Elliott et al. 2011). Eagles without a breeding territory (or with a poor one) were increasingly forced to adopt foraging tactics like raiding heron nests, which led to the spate of abandonments and reduced reproductive success noted above. Eventually, even the very large colonies that had persisted for decades at sites near the large intertidal mudflats of the Fraser River estuary were forced to be abandoned and herons sought other nesting options.

Kenyon et al. (2007) analyzed possible heron nesting strategies and showed theoretically that depending on the intensity of eagle raiding, heron reproduction could benefit by nesting in small scattered colonies, as they apparently did in our study areas for several years before the association with Bald Eagles became prevalent after 2000. They even suggested that predator protection might be a viable strategy (Kenyon et al. 2007). By the time of this study (2005, 2006), most herons in our study areas nested in association with a breeding Bald Eagle pair.

Fig. 4. Comparisons of nesting success (number of fledglings per active nest of the Great Blue Heron *Ardea herodias fannini*) close to and far from active Bald Eagle (*Haliaeetus leucocephalus*) nests. Error bars are 95% confidence intervals and the broken horizontal lines are the overall mean values. The comparison indicates that predator protection is worth 0.5–0.7 fledglings per active nest. Abbreviations along the *x* axis are as follows: Other EA 05 and Other EA 06, other herons located within 200 m of an active eagle within 2005 or 2006, respectively; CFB 05 and CFB 06, the Chilliwack Canadian Forces Base heron colony in 2005 or 2006, respectively; Other Non EA 05 and Other EA 06, other nesting herons without an eagle nests within 200 m of the colony in 2005 or 2006, respectively. Points grouped and labelled as "Eagles 05/06" are based on nests in colonies with eagles. Points grouped and labelled as "No eagles 05/06" indicate nests in colonies without eagles. The points labelled "Eagle lost 06" is the colony at CFB Chilliwack, in which the eagle nest occupied in 2005 blew down at the start of the 2006 heron breeding season (see text). In pairwise comparisons, nesting success is significantly greater in nests close to than far from eagles in both 2005 (Student's *t* test, $t = 3.34$, $P < 0.001$) and 2006 ($t = 8.44$, $P < 0.001$). Heron nesting success was higher in the CFB Chilliwack colony than in other colonies far from eagle nests ($t = 2.10$, $P < 0.05$) in 2005, but lower than in other colonies close to eagle nests in 2006 ($t = 4.03$, $P < 0.001$). Analysis based on nesting success measures in 324 (2005) and 471 (2006) heron nests measured within the same 15 colonies in each year.



Predator protection would be favoured by natural selection as a nesting strategy when the benefits (higher nesting success) outweigh the costs (nestlings lost to the guardian eagles). Our measures show that the gain from predator protection is about 0.5–0.75 nestlings per active nest (see Fig. 4). Depredation of heron nestlings by resident eagles at the Tsawwassen colony occurred at a rate of 0.03 chicks/h. Assuming that nestlings are vulnerable throughout the 60 d rearing period, this suggests that these guardian eagles took 29 nestlings (60 d × 16 h/d × 0.03 chicks/h), meaning that the colony has to contain at least 39–58 active nests for the gain in nest success to outweigh losses to the guardian eagle. The three eagle-associated colonies had 202, 222, and 400 nests, while the three largest non-eagle associated colonies had 101, 72, and 46 nests (see Fig. 3).

The advantage of predator protection thus depends on the size of the colony (larger colonies further dilute the cost), the level of protection afforded by eagles, and also by the number of heron nestlings taken by the resident eagle pair. Presumably, eagle pairs with access to good feeding opportunities do not need to resort to raiding heron nests, which may be somewhat dangerous because herons may defend vigorously. Therefore, we expect herons using predator protection to associate with the most successful eagle nests over time.

In summary, the data reported here support the hypothesis that *A. h. fannini* in the Pacific northwest changed their nesting habits during the 1990s in response to the continued growth of the Bald Eagle population. Breeding colonies, even large long-established colonies and even in the midst of chick-rearing, began to be abandoned in the face of persistent predatory behavior by Bald Eagles. Initially, it appeared that Great Blue Herons took up nesting individually or in small groups, but by the time of this study (2005, 2006), most pairs in the study area nested in just a few large colonies, each of which was co-located (<200 m) with a resident pair of Bald Eagles. Our data show that Bald Eagles in the study area strongly defend an area around their nests of at least 200 m from other Bald Eagles, and to a lesser extent, from other raptors. Great Blue Herons in colonies close to an eagle nest experienced higher reproductive success than those far from eagle nests. Breeding colonies close to eagle nests were large enough that the occasional losses of chicks to the resident pair were outweighed by the higher reproductive success. All these observations support the predator protection hypothesis.

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